Am. Midl. Nat. (2018) 180:189–206

Songbird Nest Survival in Managed Oak Savannas and Woodlands in the Missouri Ozarks

JENNIFER L. REIDY[1]
302 Anheuser-Busch Natural Resources Building, University of Missouri, Columbia 65211

AND

FRANK R. THOMPSON III
U.S.D.A. Forest Service, 202 Anheuser-Busch Natural Resources Building, University of Missouri, Columbia 65211

ABSTRACT.—Midwestern savannas and woodlands were once dominant transitional communities but are now considered endangered. Savanna and woodland habitat is being restored and managed throughout the central and east-central portions of the United States, but few studies have investigated the effects of management on songbird nest survival. We monitored songbird nests in managed savanna and woodland sites in southern Missouri from 2009 to 2011 to estimate nest survival and to predict the relationships between nest survival and temporal, vegetation structure, and nest site variables. Daily nest survival was generally higher for the four canopy-nesting species, Acadian flycatcher (*Empidonax virescens*), blue-gray gnatcatcher (*Polioptila caerulea*), Eastern wood-pewee (*Contopus virens*), and summer tanager (*Piranga rubra*) (0.96-0.98), than the four shrub-nesting species, field sparrow (*Spizella pusilla*), indigo bunting (*Passerina cyanea*), prairie warbler (*Setophaga discolor*), and yellow-breasted chat (*Icteria virens*) (0.92-0.95), for which we estimated survival rates. In general vegetation structure around the nest had little influence on nest survival, except for canopy cover, which occurred in the top model set for four species. Nest survival of yellow-breasted chats was much higher in areas of lower canopy cover, whereas nest survival of Eastern wood-pewees was moderately lower and indigo buntings and summer tanagers peaked at low and intermediate levels of canopy cover, respectively. Therefore, savanna and woodland management, which tends to open the tree canopy, may benefit some bird species in this forested landscape, particularly those associated with low to intermediate canopy cover.

INTRODUCTION

Oak savannas and woodlands were dominant natural communities in the Midwestern United States prior to European settlement but are now considered endangered (Nuzzo, 1986; Noss *et al.*, 1995). These transitional communities are typically characterized by generally low canopy cover (10-30% in savannas and 30-80% in woodlands), with a predominately herbaceous ground cover and little to no understory, and are maintained by disturbance such as fire and grazing (McCarty, 1998; Nelson, 2002; Dey and Kabrick, 2015). Most savanna and woodland habitat has been converted to other land uses since European settlement or succeeded to closed-canopy forest in the absence of disturbance (Anderson, 1998; Nelson, 2005; Dey and Kabrick, 2015). Restoration and management of savannas and woodlands is currently occurring on public lands in Missouri in an effort to restore floristic diversity, increase ecosystem function, and reduce the risk of catastrophic fire by reducing fuel loads (Nelson, 2002; MTNF, 2005; Hanberry *et al.*, 2014; Dey and Kabrick, 2015).

Restoration of Midwestern savannas and woodlands may also benefit wildlife (Grundel and Pavlovic, 2007: Thompson *et al.*, 2012; Starbuck *et al.*, 2015). Many songbirds adapted to

[1] Corresponding author: e-mail: jennifer.reidy@gmail.com

open-canopy communities, such as glades, barrens, scrublands, savannas, and woodlands are declining in the eastern and central United States, likely due to the loss of open-canopy habitat (Askins, 1993; Thompson and Dessecker, 1997; Brawn *et al.*, 2001; Hunter *et al.*, 2001). Restoration and management of savannas and woodlands may provide additional habitat for early-successional species without sacrificing habitat for species dependent on more heavily wooded habitats. Savannas and woodlands support a diverse array of bird species including early successional species, woodland generalists, and forest interior species (Thompson *et al.*, 2012; Reidy *et al.*, 2014; Holoubek and Jensen, 2015; Roach, 2017), often supporting higher bird diversity than grasslands or forests (Davis *et al.*, 2000; Brawn, 2006; Au *et al.*, 2008). However, many species in these transitional communities may be at the periphery of their breeding range. As such, they may experience lower productivity than in the core of their range, which is typically either central grasslands or eastern forests (Temple, 1998), highlighting the importance of monitoring breeding birds to document reproductive success.

Nest survival is commonly used as an indicator of reproductive success, because it is easier to measure than seasonal productivity and can be related to vegetation structure or management. Predation is often the leading cause of nest failure for songbirds (Barber *et al.*, 2001; Thompson, 2007; Shake *et al.*, 2011). We are not aware of any studies specifically identifying nest predators in Midwestern oak savannas and woodlands; however, other Midwestern habitats, such as old fields, shrublands, and forests have identified diverse predator communities including snakes, raptors, corvids, Brown-headed Cowbirds (*Molothrus ater*, hereafter cowbird; Robinson *et al.*, 1999), small mammals, and mesopredators such as raccoons (*Procyon lotor*) (Thompson and Burhans, 2003; Cox *et al.*, 2012; Thompson and Ribic, 2012; Degregorio *et al.*, 2016). While few studies have documented nest survival of songbirds breeding in Midwestern oak savannas or woodlands, most report either beneficial or neutral effects of management activities on nest survival. For example 11 of 13 bird species had higher nest survival in savannas and woodlands than in fragmented forests in Illinois (Brawn, 2006) and nest survival was invariant or positively affected by management or vegetation structure altered by management (such as changes to canopy cover) in pine-oak woodland sites in southern Missouri (Roach *et al.*, 2018) and savannas and woodlands in Kansas (Holoubek and Jensen, 2016).

In order to obtain additional information in this understudied ecosystem, our objective was to estimate nest survival rates of songbirds breeding in savanna and woodland management sites in central and southern Missouri as they relate to vegetation structure. We focused on vegetation structures that were likely impacted by management practices and which likely affected nest survival through changes in nest concealment, nest site availability, and predator behavior and abundance (Thompson 2007).

METHODS

STUDY AREA

We monitored nests at nine sites being managed for savanna and woodland habitat in the Ozark Highlands of Missouri (Fig. 1). These sites occurred within a forested landscape that was once interspersed with oak (*Quercus* spp.) and oak-pine (*Pinus* sp.) savannas in the uplands and woodlands throughout (Nelson, 2005; Hanberry *et al.*, 2014). All nine sites were within 200 miles of a centrally located site with Global Positioning System (GPS) coordinates of 37.97 N. 92.76 W. Historically, surface fires occurred every 2-24 y and averaged every 6 y in landscapes dominated by savannas and woodlands in the Ozarks of Missouri (Nelson, 2005).

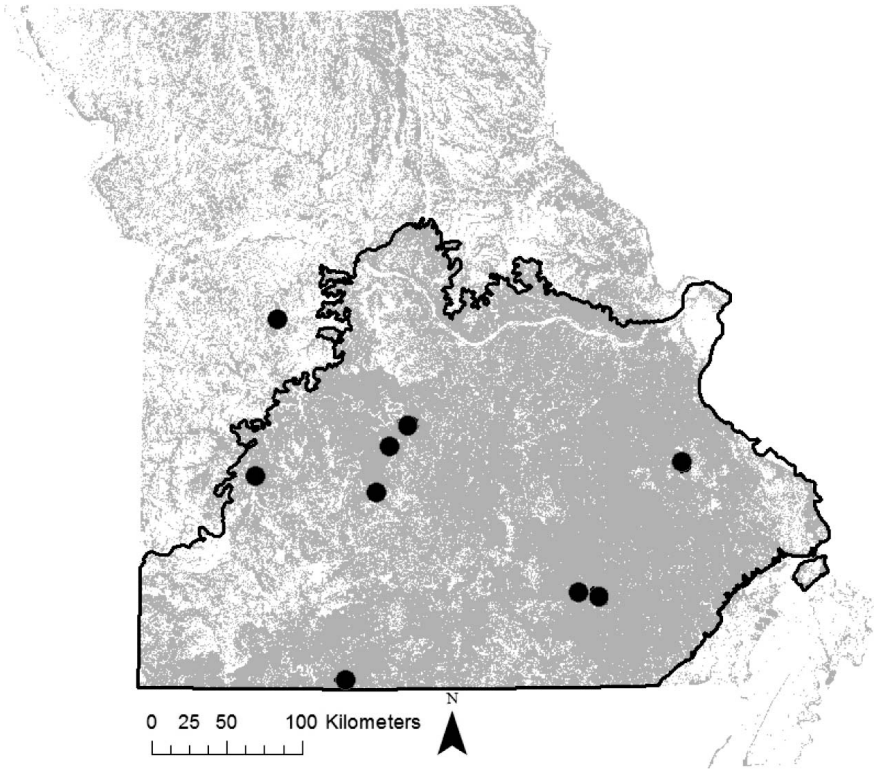

FIG. 1.—Savanna and woodland management sites within or near the Ozark Highlands (black outline) of Missouri (forested area shaded in gray) where we monitored songbird nests in 2009-2011

The current landscape is predominantly forested in the eastern half and a mixture of forest and grassland or agriculture in the western half (Karstensen, 2010). Study sites were owned and managed by the Missouri Department of Natural Resources, Missouri Department of Conservation, The Nature Conservancy, and the U.S. Department of Agriculture Forest Service and were managed with prescribed fire, mechanical thinning, or both to reduce tree density and canopy cover and increase herbaceous ground cover. The vegetation structure and species composition of our nest-monitoring plots was highly heterogeneous within and between sites because of differences in disturbance history, management prescriptions, and terrain, thus allowing us to investigate nest survival across a range of habitats spanning the vegetation gradient from open-canopy savanna, to woodland, to forest. Dominant canopy species included post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*), white oak (*Q. alba*), Northern red oak (*Q. rubra*), bitternut hickory (*C. cordiformis*), shortleaf pine (*P. echinata*), and flowering dogwood (*Cornus florida*) (Nelson, 2005). Dominant woody understory species included oak, hickory, and pine seedlings and saplings, as well as red maple (*Acer rubrum*), sumac (*Rhus* spp.), buckbrush (*Symphoriocarpus orbiculatus*), blackberry (*Rubus* sp.), and grapevine (*Vitis* sp.) (Nelson, 2005).

DATA COLLECTION

Nest searching and monitoring.—We searched for nests of open-cup nesting songbirds from early May through mid-August 2009–2011 using a combination of parental behavior and systematic searching. Study sites were only sampled during a single year, except one site sampled in both 2009 and 2011. We monitored active nests every 2 to 4 d and more frequently near expected hatching and fledging dates (determined from our monitoring data and incubation and chick-rearing lengths for each species reported in the literature and from our own data). We recorded parental activity and the number of host and cowbird eggs and nestlings (when possible) at each nest check. We directly observed nest contents for nests $\leq$ 2 m high and tried to verify nest contents for nests $>$ 2 m high with a mirror pole that extended to nests $\sim$8 m high (2009–2011) or a telescoping pole with video camera that reached nests $\sim$16.5 m high (2010–2011). If we were unable to observe nest contents directly, we used parental behavior (*e.g.*, parent sitting on nest or feeding nestlings), observing the nest for up to 30 min to confirm nest status. For nests monitored through parental behavior, we continued to observe nests with no parental activity for up to two additional nest checks before declaring it failed but used the first date we did not observe activity as the final nest date. To minimize the probability of attracting predators to nests, we did not approach nests if we detected potential predators in the area, we approached and left nests from different directions when possible, and we delayed checking nests until vegetation around the nest was dry to avoid trampling the area.

In 2011 we also monitored a subset of nests at one site using miniature infrared video cameras (Fuhrman Diversified, Inc., Seabrook, Texas) to identify potential nest predators. We focused our efforts on shrub-nesting species because we had limited resources and they were the most accessible. We positioned cameras 1-2 m from nests when parent birds were away from the nest and removed cameras if parents did not resume normal activity at the nest within 2 hrs. Video footage was saved to an SD memory card that was changed every 48-72 h, along with the battery. If the nest contents changed between monitoring intervals, we scanned the video footage to identify potential causes of the change (*e.g.*, predation event).

We classified nest fate as successful or failed during each nest monitoring interval. A nest was classified as successful if it contained $\geq$ 1 egg or nestling and was attended by an adult or if at least one young fledged, which we confirmed by observing adults feeding fledglings, hearing begging calls of fledglings near adults or alarm calls of adults, seeing the adults carrying food after documenting the nest was empty, or confirming it with video footage. A nest was considered as failed if nest activity ceased before fledging was possible (nestlings were too young to have successfully fledged). The fate of a nest was marked as unknown, if we confirmed nestlings close to fledge at the last nest check, but were subsequently unable to verify fledglings using the above criteria. We considered a nest as failed due to cowbird parasitism if the adults abandoned the nest after it was parasitized by a cowbird (whether this included a predation event or not). Nests were considered depredated if all nest contents were removed and there was no sign or possibility of fledge or if we documented predation with video footage or eye-witnessing it. We right-truncated the final monitoring interval for those nests with unknown nest fates.

Vegetation sampling.—We measured vegetation around nests within 1 wk of cessation of nest activity using a modified BBIRD approach (Martin *et al.*, 1997). We recorded the nest substrate type (ground, shrub, tree) and nest height. Trees were defined as woody stems that reached 1.4 m in height and were $\geq$ 3 cm at this height as measured with a Biltmore stick; woody stems smaller and/or shorter than this were classified as shrubs. We measured nest height with a measuring tape to the nearest tenth of a meter or with a clinometer if $>$ 2 m.

For nests placed in trees, we measured diameter-at-breast-height (1.4 m above ground; hereafter "DBH") with a Biltmore stick and estimated the distance from the main trunk to the nest along the supporting trunk or branch. For nests placed in shrubs, we recorded the distance from the nest to the edge of the shrub (distance to foliage edge). We estimated the percent of nest cover 1 m over, under (if applicable), and to the side in each cardinal direction, and averaged these to arrive at a single estimate of nest cover. We measured percent canopy cover of leaf cover $>$ 5 m tall by averaging readings from a spherical densiometer taken standing at the nest and facing each cardinal direction. We estimated the percent cover of shrub, grass, leaf litter, and bare ground in the 5 m radius around the nest. The DBH of all live trees $\geq$ 2.5 cm and snags $>$ 12.5 cm wide within an 11.3 m radius were measured. Snag density and tree density were calculated for three DBH classes: sapling (2.5-12.5 cm), pole timber (12.5-27.5 cm for hardwoods and 12.5-23 cm for evergreens), and saw timber ($>$ 27.5 cm for hardwoods and $>$23 for evergreens).

DATA ANALYSIS

Species-specific nest survival was estimated for species for which $>$ 45 active nests were monitored. Daily survival rates were estimated using the logistic exposure method (Shaffer, 2004). Only nests with confirmed activity (eggs or nestlings confirmed visually or through monitoring parental behavior; *see* above) were included in analyses. We fit models with PROC GENMOD (SAS Version 9.1, SAS Institute, Cary, North Carolina) using a binomial response distribution for each monitoring interval (nest success = 1; nest failure = 0), and the logit link function defined by Shaffer (2004).

We compared support for models composed of temporal, vegetation structure, and nest site covariates using an information-theoretic approach (Burnham and Anderson, 2002). We first examined support for singular and additive combinations of the temporal variables year, nest stage (egg or nestling), and day of year (linear = day, quadratic = day + day^2, cubic = day + day^2 + day^3). We evaluated multiple forms of day of year because several studies have shown nonlinear trends of nest survival (Burhans *et al.*, 2002; Roach *et al.*, 2018). We then included the most supported (defined below) temporal variables in all models evaluating vegetation structure and nest site effects because we considered them to be nuisance parameters that we wanted to control for while evaluating support for vegetation or nest site effects. Our nest site model included the variables nest height, nest cover, and distance to main trunk (for nests in trees) or distance to foliage edge (for nests in shrubs). We chose to group these nest site variables to reduce the number of competing models and because they represented an alternative effect related to nest positioning rather than a more direct effect of management on vegetation structure. The remaining models were composed of the vegetation structure variables tree density (grouped as sapling, pole timber, saw timber, snag), canopy cover, herbaceous ground (grass) cover, and shrub cover. Preliminary analyses were conducted comparing support for linear and quadratic forms of canopy cover and shrub cover given these effects may depend on predator habitat use (Roach *et al.*, 2018); the more supported form of each variable were included in final models. Because of the likelihood of species-specific preferences to localized vegetation structure within our plots and species-specific nest defense tactics, nests were not grouped into guilds or functional groups, such as early successional or forest interior, and conduct guild-level analyses.

We calculated tolerance values for covariates in the global model to detect multicollinearity and eliminated highly correlated variables (tolerances $<$ 0.4) before proceeding with model fitting (Allison, 1999). We evaluated goodness of fit of the global model with a Hosmer and Lemeshow (2000) test and examined the overdispersion parameter for

evidence of lack of fit (Burnham and Anderson, 2002). Candidate models were ranked by Akaike's information criterion for small sample sizes (AICc), which is calculated using the effective sample size (n_{eff}) (Burnham and Anderson, 2002; Rotella *et al.*, 2004). We report the AIC_c, ΔAIC_c, and model weight (w_i) for models with $\Delta AIC_c \leq 2$ and model-averaged parameter estimates, standard errors (SE), and 95% confidence intervals, as well as predictions from the subset of these that were composed of informative parameters (Burnham and Anderson, 2002; Arnold, 2010).

We predicted model-averaged daily survival rates as a function of explanatory variables of interest (Shaffer and Thompson, 2007). For continuous variables, we varied the value of the factor of interest at incremental levels spanning the range of observed values while holding the other variables at their median value to control for their effects. We held categorical variables constant at levels representing the proportions of the observations in each category level.

RESULTS

We monitored a total of 1197 active nests (283, 302, and 612 in 2009, 2010, and 2011, respectively) representing 32 species (Appendix I) and > 10 nests for 14 species (n = 1137 nests). Predation was the leading cause of nest failure for these 14 species; other causes of nest failure were abandonment (unknown reason), abandonment attributed to cowbird parasitism, and weather (Table 1). Parasitism was confirmed for 142 of 488 (29%) active nests for which we documented parasitism status, but few parasitized nests fledged only cowbird young (<2%, Table 1). We monitored 23 nests with video cameras and recorded one mouse (unknown species), one flying squirrel (*Glaucomys volans)*, one wasp, and four snake (*Elaphe* spp.) predation events; five unknown predation events due to equipment failure; five abandonments after eggs failed to hatch; and one nest fledging only a cowbird. We also witnessed a cowbird depredating a nest with young.

We monitored 997 active nests of eight species with sufficient sample sizes to fit nest survival models including 73 Acadian flycatcher (*Empidonax virescens,* $n_{eff} = 1276$), 172 blue-gray gnatcatcher (*Polioptila caerulea,* $n_{eff} = 1980$), 256 Eastern wood-pewee (*Contopus virens,* $n_{eff} = 5344$), 72 field sparrow (*Spizella pusilla,* $n_{eff} = 608$), 207 indigo bunting (*Passerina cyanea,* $n_{eff} = 2206$), 47 prairie warbler (*Setophaga discolor,* $n_{eff} = 504$), 66 summer tanager (*Piranga rubra,* $n_{eff} = 893$), and 102 yellow-breasted chat (*Icteria virens,* $n_{eff} = 1021$) nests. Vegetation structure around nests varied by species and covered a range of conditions (Table 2). For example nests of forest interior (*i.e.,* Acadian flycatcher) and woodland generalist species (*i.e.,* blue-gray gnatcatcher, Eastern wood-pewee, summer tanager) were typically found in areas with greater canopy cover, whereas early successional species (*i.e.*, field sparrow, indigo bunting, prairie warbler, and yellow-breasted chat) were in areas with lower canopy cover and greater shrub cover.

None of our explanatory covariates in the global model had tolerances < 0.4; therefore, we proceeded with the full suite of 32 candidate models (Appendix II) for each species. Our goodness-of-fit test indicated that the global model fit the data well for all species ($P > 0.05$). Mean daily survival was generally lower for the four early successional, shrub-nesting species (0.919-0.952), than the four woodland generalist and forest interior species that nested in trees (0.955 to 0.981; Table 3). Temporal effects on daily survival differed by species (Table 3). Daily survival was higher in the egg stage than the nestling stage for Acadian flycatcher, blue-gray gnatcatcher, and Eastern wood-pewee but lower in the egg stage for prairie warbler (Fig. 2). Day (linear effect) or day^3 (cubic effect) was supported in the top temporal model for Acadian flycatcher, indigo bunting, prairie warbler, and summer tanager, with survival

TABLE 1.—Fate of nests monitored in savannas and woodlands in the Ozark Highlands, Missouri, 2009-2011. We only show species for which we monitored ≥10 active nests

Common name	Position[c]	Nest fate[a]					Cowbird effects[b]		
		F	D	A	W	U	CP	FC	AC
Acadian flycatcher	Tree	24	41	2	1	5	6/29	3	0
Blue-gray gnatcatcher	Tree	94	72	0	1	5		0	
Chipping sparrow	Tree	11	13	1	0	3		0	1
Eastern wood-pewee	Tree	120	119	2	1	14[d]		2	
Field sparrow	Shrub	20	34	13	0	7	17/72	1	10
Indigo bunting	Shrub	75	92	31	0	9	80/200	9	21
Kentucky warbler	Ground	9	2	0	0	2		0	
Northern cardinal	Tree	11	16	0	0	1		0	
Prairie warbler	Shrub	24	19	0	1	3	5/34	2	
Red-eyed vireo	Tree	4	10	1	0	1	7/8	1	1
Summer tanager	Tree	28	29	0	0	9	6/8	2	
White-eyed vireo	Shrub	9	4	1	0	0		0	1
Yellow-billed cuckoo	Tree	12	17	1	1	10		0	0
Yellow-breasted chat	Shrub	46	41	7	0	8	14/88	0	3
Total shrub nests		151	182	50	1	23		11	35
Total tree nests		303	319	9	4	51		9	2

[a] Nest fate: F = number of nests that fledged, includes nests that fledged only brown-headed cowbirds; P = number of nests that were depredated; A = number of nests that were abandoned including those attributed to brown-headed cowbird parasitism; W = number of nests that failed due to weather events (heavy rain or high winds); U = number of nests with an unknown fate, fledglings not confirmed but possible

[b] Cowbird effects: CP = number of nests confirmed with cowbird eggs or nestlings/total number of nests with confirmed nest contents; FC = fledged only cowbirds, included in total number of fledged nests; AC = number of nests abandoned likely due to presence of cowbird eggs or nestlings, included in total abandoned

[c] Position describes nest position typically found by this species at our study sites and referencing Rodewald (2015)

[d] One nest was still active at the end of the season

being highest early in the season for all four species (Fig. 3). Predicted nest survival varied annually for indigo bunting and prairie warbler (Table 4). No temporal effects were supported for field sparrow and yellow-breasted chat.

Vegetation structure or nest site variables were included in top model sets for all eight species (Table 3); however, only two effects had 95% confidence intervals that did not overlap zero. Yellow-breasted chat daily nest survival decreased from 0.965 (95% CI: 0.946, 0.978) to 0.914 (95% CI: 0.866, 0.946) as canopy cover increased from 0% to 100% in the 100 m radius around the nest. Indigo bunting daily nest survival increased from 0.909 (95% CI: 0.877, 0.932) to 0.983 (95% CI: 0.942, 0.995) as nest height increased from 0.2 m to 5.1 m. Canopy cover was also included in supported model sets for three other species, but confidence intervals included zero. Eastern wood-pewee nest survival showed a weak positive relationship with canopy cover in the 100 m radius around the nest, whereas indigo bunting and summer tanager nest survival had a weak negative and positive quadratic relationship with canopy cover, peaking at 0% and ~60% canopy cover, respectively (Table 4). Nest site variables (*i.e.*, distance from main trunk, nest cover, and nest height) were also included in

TABLE 2.—Mean values (± SD) of temporal, nest site, and vegetation structure measured around nests for eight songbirds monitored in the Missouri Ozarks, 2009-2011

Variable	Acadian flycatcher	Blue-gray gnatcatcher	Eastern wood-pewee	Field Sparrow	Indigo bunting	Prairie warbler	Summer tanager	Yellow-breasted chat
Number of nests	73	172	256	74	207	47	66	102
Nest stage[a]	0.56	0.45	0.47	0.52	0.46	0.47	0.46	0.42
Day of year	169.5 ± 18.7	162.9 ± 20.1	175.1 ± 18.8	176.2 ± 21.3	176.1 ± 20.7	153.3 ± 13.7	172.8 ± 20.2	167.0 ± 17.5
Nest height (m)	5.1 ± 2.6	10.5 ± 4.5	11.8 ± 4.3	0.6 ± 0.4	1.1 ± 1.0	2.3 ± 1.7	8.2 ± 4.3	1.0 ± 0.4
Nest cover (%)	28.9 ± 20.9	47.5 ± 23.2	32.9 ± 20.0	76.2 ± 18.2	52.1 ± 22.4	64.5 ± 24.2	54.2 ± 22.0	57.9 ± 23.8
Distance to main trunk or shrub edge (cm)	260 ± 145.9	226.2 ± 175.9	383.1 ± 158.3	15.6 ± 6.6	25.2 ±19.4	30.2 ± 19.3	295.0 ± 163.2	48.9 ± 58.1
Grass cover (%)	29.7 ± 26.0	39.8 ± 22.6	30.5 ± 24.2	45.2 ± 23.6	40.4 ± 24.4	30.7 ± 20.0	34.4 ± 26.5	32.9 ± 19.3
Shrub cover (%)	14.1 ± 14.9	25.9 ± 22.6	20.9 ± 17.3	32.6 ± 18.3	33.2 ± 21.2	39.0 ± 23.5	22.7 ± 16.9	54.7 ± 23.3
Canopy cover (%)	93.9 ± 9.7	74.4 ± 22.5	79.5 ± 18.0	39.3 ± 27.9	65.8 ± 29.1	50.5 ± 34.8	72.7 ± 22.6	43.1 ± 36.1
Canopy height (m)	19.8 ± 5.4	15.2 ± 5.3	18.5 ± 4.9	12.3 ± 5.1	14.6 ± 6.2	9.7 ± 7.4	16.1 ± 5.2	8.7 ± 7.7
Sapling density	561.3 ± 329.8	212.7 ± 296.6	188.0 ± 250.0	59.0 ± 158.8	228.9 ± 301.5	220.7 ± 275.0	245.5 ± 302.7	200.3 ± 355.3
Pole timber density	227.1 ± 151.0	117.9 ± 104.6	125.7 ± 112.9	64.6 ± 111.5	122.2 ± 139.9	73.4 ± 97.4	132.2 ± 132.1	55.6 ± 80.5
Saw timber density	129.5 ± 79.8	94.9 ± 70.8	138.9 ± 71.6	68.4 ± 57.2	86.2 ± 66.3	59.6 ± 84.1	115.9 ± 80.1	30.9 ± 53.6
Snag density	4.0 ± 5.5	3.8 ± 7.2	4.9 ± 6.5	1.5 ± 4.4	3.8 ± 6.8	2.0 ± 4.2	6.5 ± 8.7	2.9 ± 5.8

[a] Frequency represents egg stag

TABLE 3.—Number of parameters (K), Akaike's information criterion (AIC_c), the difference between AIC_c of the current model and top model (ΔAIC_c), and model support (w_i) for models with $\Delta AIC_c < 2.00$ that predicted nest survival of eight songbirds in savanna and woodland sites in the Ozark Highlands of Missouri, 2009-2011. We model-averaged daily survival rate (DSR) and coefficients from the subset of models that only contained informative parameters, which are shown in bold

Species	Model[a]	K	AIC_c	ΔAIC_c	w_i	DSR
Acadian flycatcher	**Stage[a] + date^3** [b]	5	289.89	0.00	0.29	0.955 (0.933, 0.970)
	Stage + date^3 + grass	6	291.25	1.36	0.15	
	Stage + date^3 + shrub	6	291.71	1.82	0.12	
	Stage + date^3 + canopy	6	291.80	1.91	0.11	
Blue-gray gnatcatcher	**Stage + nest site**[c]	5	507.60	0.00	0.24	0.963 (0.953, 0.971)
	Stage + grass + nest site	6	509.28	1.69	0.11	
	Stage	2	509.42	1.83	0.10	
	Stage + canopy + nest site	6	509.54	1.94	0.09	
	Stage + shrub + nest site	6	509.59	1.99	0.09	
Eastern wood-pewee	**Stage + canopy**	3	926.84	0.00	0.12	0.981 (0.976, 0.986)
	Stage + canopy + shrub	4	927.16	0.32	0.10	
	Stage + canopy + nest site	6	927.55	0.71	0.09	
	Stage + nest site	5	927.61	0.77	0.08	
	Stage + canopy + shrub + nest site	7	927.72	0.88	0.08	
	Stage	2	927.78	0.94	0.08	
	Stage + canopy + grass	4	928.82	1.98	0.05	
Field sparrow	**Null**	1	257.20	0.00	0.28	0.919 (0.895, 0.938)
	Shrub	2	258.75	1.54	0.13	
	Canopy	2	258.94	1.74	0.12	
	Grass	2	259.08	1.88	0.11	
Indigo bunting	**Year + date^3 + nest site**	9	820.16	0.00	0.19	0.927 (0.905, 0.944)
	Year + date^3 + grass + nest site	10	820.56	0.40	0.15	
	Year + date^3 + shrub + nest site	10	821.67	1.51	0.09	
	Year + date^3 + canopy^2 + grass + nest site	12	821.74	1.56	0.08	
	Year + date^3 + canopy^2 + nest site	11	821.78	1.61	0.08	
Prairie warbler	**Year + stage + date^3**	7	136.80	0.00	0.29	0.950 (0.910, 0.973)
	Year + stage + date^3 + canopy	8	138.37	1.58	0.13	
	Year + stage + date^3 + shrub	8	138.43	1.63	0.13	
	Year + stage + date^3 + grass	8	138.45	1.65	0.13	
Summer tanager	**Date**	2	229.61	0.00	0.29	0.968 (0.950, 0.979)
	Date + canopy^2	4	230.77	1.16	0.16	
	Date + shrub	3	231.46	1.85	0.11	
	Date + grass	3	231.56	1.95	0.11	
Yellow-breasted chat	**Canopy + grass**	3	309.11	0.00	0.25	0.952 (0.937, 0.964)
	Canopy + shrub	3	309.71	0.60	0.19	
	Canopy + shrub + grass	4	311.00	1.89	0.10	

[a] Stage = nest stage (egg or nestling)

[b] Date^3 refers to the cubic form of date

[c] Nest site includes nest cover, nest height, and either distance to foliage edge (shrub nest) or distance to main trunk (tree nest)

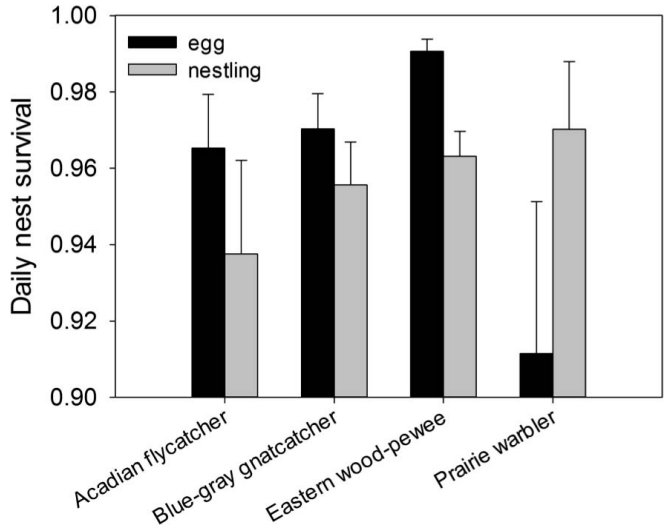

FIG. 2.—Daily survival and 95% confidence intervals as a function of nesting stage for nests of four songbirds monitored in savanna and woodland sites in the Missouri Ozarks in 2009-2011

the top model set for blue-gray gnatcatcher and Eastern wood-pewee, although confidence intervals included zero. Blue-gray gnatcatcher nest survival was positively related to distance from the main trunk and nest cover, and negatively related to nest height, whereas Eastern wood-pewee showed the opposite response to each of these variables (Table 4).

DISCUSSION

In general we found limited support that vegetation structure around the nest influenced nest survival of either shrub- or canopy-nesting species at our sites. Canopy cover was the most influential factor; it occurred in the top model set for four species (two shrub- and two canopy-nesters), with the strongest effect occurring for the yellow-breasted chat. Yellow-breasted chat nest survival was negatively related to canopy cover, consistent with other studies on yellow-breasted chat that reported nest survival being positively affected by tree thinning (Roach *et al.*, 2018), but negatively affected by canopy cover around the nest (Ricketts and Ritchison, 2000). We also found weak and differing relationships between canopy cover and nest survival for Eastern wood-pewee (positive), indigo bunting (negative quadratic), and summer tanager (positive quadratic). The latter two relationships resulted in nest survival peaking at low (indigo bunting) or intermediate (summer tanager) levels of canopy cover. These results are similar to a previous study that showed a similar positive quadratic response to canopy cover in the summer tanager (Roach *et al.*, 2018). Eastern wood-pewees, however, had the opposite relationship, with nest survival increasing with increasing canopy cover. This was in contrast to a previous study that showed a negative effect of canopy cover within a 150 m radius in pine-oak woodlands in southern Missouri on nest survival of Eastern wood-pewees (Roach *et al.*, 2018). The lack of support for vegetation structure variables on the other species may be due to the small sample of nests we monitored for some individual species or because survival was invariant to vegetation at the spatial scale we measured.

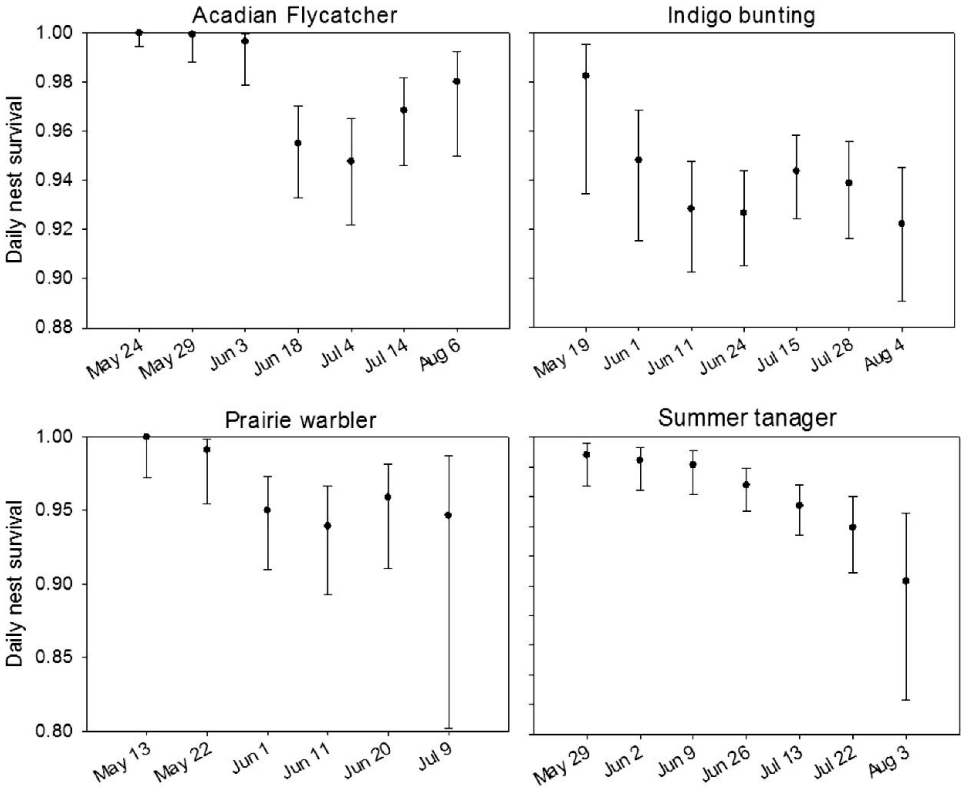

FIG. 3.—Daily survival and 95% confidence intervals as a function of day of season for nests of four songbirds monitored in savanna and woodland sites in the Missouri Ozarks in 2009-2011

We also found limited support for effects of nest site variables (nest height, nest cover, distance to main trunk, or shrub edge) on nest survival. The strongest effect was a positive relationship between nest survival of indigo bunting and nest height, similar to the effect found in old fields in Missouri (Burhans *et al.*, 2002) and shrub-nesting species in forests in Iowa, Minnesota, and Wisconsin (Knutson *et al.*, 2007). Nest site variables, were not supported for any other shrub-nester. Of the four canopy-nesting species, nest site variables were supported for two species, blue-gray gnatcatcher and Eastern wood-pewee and in opposite ways for each variables, suggesting that patterns of nest predation as they pertain to nest site attributes are species-specific. These two species showed different preferences for nest site attributes, with Eastern wood-pewees generally farther out on limbs and away from the main trunk, with lower nest cover, and positioned higher in trees than blue-gray gnatcatchers. Our overall lack of strong effects of nest site variables on nest survival corresponds to results from other studies conducted in Midwestern habitats (Burhans and Thompson, 1998, Ricketts and Ritchison, 2000; Peak *et al.*, 2004; Knutson *et al.*, 2007). These collective results suggest nest predation risk is fairly ubiquitous across Midwestern habitats and that songbird species are likely unable to assess predation risk and position their nests in "safer" nest sites.

TABLE 4.—Model-averaged coefficients, standard errors (SE), and 95% lower (LCL) and upper (UCL) confidence limits for supported variables from nest survival models with significant support ($\Delta AIC_c \leq 2$) for eight songbird species

Species	Covariate	Coefficient	SE	LCL	UCL
Acadian flycatcher	Day	-7.604	2.613	-12.830	-2.379
	Day^2	0.040	0.014	0.012	0.067
	Day^3	0.000	0.000	0.000	0.000
	Stage (egg)	0.617	0.320	-0.023	1.256
Blue-gray gnatcatcher	Stage (egg)	0.420	0.240	-0.060	0.900
	Distance to main trunk	0.001	0.001	-0.001	0.003
	Nest height	-0.037	0.032	-0.100	0.026
	Nest cover	0.002	0.005	-0.008	0.011
Eastern wood-pewee	Stage (egg)	1.403	0.224	0.955	1.851
	Canopy	0.006	0.006	-0.006	0.018
	Shrub	0.001	0.003	-0.004	0.007
	Distance to main trunk	-0.001	0.001	-0.002	0.001
	Nest height	0.001	0.013	-0.025	0.026
	Nest cover	-0.003	0.004	-0.011	0.005
Field sparrow	Intercept	2.428	0.142	2.143	2.713
Indigo bunting	Day	-2.194	0.839	-3.873	-0.515
	Day^2	0.012	0.005	0.003	0.021
	Day^3	0.000	0.000	0.000	0.000
	Year (2009)	0.603	0.227	0.148	1.057
	Year (2010)	0.403	0.226	-0.050	0.855
	Canopy	-0.007	0.011	-0.028	0.015
	$Canopy^2$	0.000	0.000	0.000	0.000
	Grass	-0.002	0.003	-0.008	0.004
	Distance to foliage edge	0.004	0.005	-0.006	0.013
	Nest height	0.359	0.141	0.078	0.640
	Nest cover	0.002	0.004	-0.007	0.011
Prairie warbler	Day	-12.483	6.236	-24.954	-0.010
	Day^2	0.075	0.038	-0.001	0.150
	Day^3	-0.000	0.000	-0.000	0.000
	Stage (egg)	-1.152	0.501	-2.155	-0.150
	Year (2009)	-0.145	0.576	-1.297	1.010
	Year (2010)	-1.579	0.569	-2.718	-0.440
Summer tanager	Day	-0.027	0.009	-0.045	-0.008
	Canopy	0.025	0.037	-0.049	0.098
	$Canopy^2$	-0.000	0.000	-0.000	0.000
Yellow-breasted chat	Canopy	-0.010	0.004	-0.017	-0.002
	Grass	0.010	0.011	-0.012	0.031
	Shrub	-0.005	0.007	-0.20	0.010

Temporal variables influenced nest survival for six of the eight species. Patterns related to nesting stage and day of year and annual variation are well documented sources of variation in nest survival (Burhans *et al.*, 2002; Grant *et al.*, 2005; Knutson *et al.*, 2007; Cox *et al.*, 2012; Roach *et al.*, 2018) and likely reflect changes in nest predator habitat use or abundance (Cox *et al.*, 2012; DeGregorio *et al.*, 2014). Survival was higher in the egg stage than the nestling stage for three canopy-nesting species, Acadian flycatcher, blue-gray gnatcatcher, and Eastern wood-pewee, whereas egg survival was substantially lower than nestling survival for

one early-successional species, the prairie warbler. Increased adult visitation and increased olfactory, auditory, and visual cues from nestlings may explain higher predation on nestlings than on eggs for the canopy-nesting species (Fontaine and Martin, 2006; Cox, 2011). Nest predators in the shrub layer likely differ somewhat from nests in the canopy (Cox *et al.*, 2012), and the cues these predators use to locate nests are likely different, including that predators are more likely to randomly locate nests in shrubs while moving through the area than nests in trees. Roach *et al.* (2018) reported similar temporal effects for Eastern wood-pewee, prairie warbler, and summer tanager in Missouri pine-oak woodlands. Seasonal patterns of nest survival for Acadian flycatchers and indigo buntings were similar to those reported for these species in forests in Missouri and Illinois (Cox *et al.*, 2012).

Nest survival on our sites varied by species and was generally higher for the four canopy-nesting species than for the four shrub-nesting species. Higher nest survival for canopy-nesting than shrub-nesting species has also been observed in other studies across the Midwest (Brawn, 2006; Cox *et al.*, 2012; Roach *et al.,* 2018). Nests in shrubs may be accessible to a greater number or diversity of predators than nests in trees and are also parasitized and depredated more often by cowbirds (Cox *et al.*, 2012; Morris *et al.,* 2013). Although we confirmed parasitism for 15-40% of nests of early-successional species, few nests fledged only cowbirds. However, the total effects of parasitism on productivity of birds nesting in these sites is unknown and may warrant further investigation. Actual parasitism was higher than what we reported here, given nests with already cracked or abandoned cowbird eggs were excluded from analysis and our focus was on nest survival, rather than individual host egg or nestling survival, which would be lower because host nestling survival was often lower in parasitized nests. In addition we were unable to confirm nest contents for the majority of nests $>$ 2 m high; therefore, it is likely we underreported parasitism for canopy-nesting species. Cowbird parasitism was higher than that reported from several studies in the region ($<$5%, Morris *et al.*, 2013; 5%, Roach *et al.*, 2018), but lower than savannas and forests in Illinois (11-100%, Brawn, 2006) and old fields and forests in Missouri (11-64%, Burhans, 1997), in line with evidence that parasitism is higher in habitats that are more fragmented at a landscape scale.

Management Implications

Prescribed fire and tree thinning are being used to restore or maintain savanna and woodland habitat structure within a forested landscape on public lands in southern Missouri. Despite our sites spanning the spectrum of vegetation structure and composition from open-canopy savanna to forest, nest survival of most species was not strongly related to vegetation structure, suggesting habitat management may have little effect on nest survival of these species. Our strongest effect was a negative relationship between canopy cover and yellow-breasted chat nest survival. Yellow-breasted chats are a species of regional concern in the Central Hardwoods Bird Conservation Region (Central Hardwoods Joint Venture, 2015; Sauer *et al.*, 2017). Restoration and management may benefit this species by allowing sunlight to penetrate the canopy to provide substantial ground and shrub cover. Indigo bunting and summer tanager also had negative relationships between canopy cover and nest survival, though not as strongly supported, suggesting they also benefit from savanna and woodland restoration. These relationships between canopy cover and nest survival also parallel relationships with abundance (Reidy *et al.*, 2014; Roach, 2017), providing evidence restoration benefits multiple aspects of these species' demography. We consider the diverse suite of songbirds breeding on our study sites to be an indicator savanna and woodland management is providing additional open-canopy habitat to early-successional or

disturbance dependent birds, including several species of regional management concern (Central Hardwoods Joint Venture, 2015), while still supporting species that may require more canopy cover.

Acknowledgments.—We are grateful to K. Bader, S. Bialecki, S. Caird, R. Evans, S. W. Kendrick, J. Kester, W. Lewis, S. Miller, M. Roach, D. Westrich, and M. Wickens for assistance with data collection. We thank the Missouri Department of Conservation, Missouri Department of Natural Resources, and The Nature Conservancy for assistance with site selection and access. Funding or other support was provided by U.S. Department of Agriculture Forest Service Northern Research Station and Mark Twain National Forest, the Missouri Department of Natural Resources, the Missouri Department of Conservation, and The Nature Conservancy.

LITERATURE CITED

ALLISON, P. D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute. Cary, North Carolina, U.S.A. 308 p.

ANDERSON, R. C. 1998. Overview of Midwestern oak savanna. *T. Wisc. Acad. Sci., Arts Lett.,* **86**:1–18.

ARNOLD, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *J. Wild. Manage.*, **74**:1175–1178.

ASKINS, R.A. 1993. Population trends in grassland, shrubland, and forest birds in eastern North America. *Current Ornithol.*, **11**:1–54.

AU, L., D. E. ANDERSEN, AND M. DAVIS. 2008. Patterns in bird community structure related to restoration of Minnesota dry oak savannas and across a prairie to oak woodland ecological gradient. *Nat. J. Areas*, **28**:330–341.

BARBER, D. R., T. E. MARTIN, M. A. MELCHIORS, R. E. THILL, AND T. B. WIGLEY. 2001. Nesting success of birds in different silvicultural treatments in southeastern U.S. pine forests. *Conserv. Biol.*, **15**:196–207.

BLOUIN-DEMERS, G. AND P. J. WEATHERHEAD. 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology*, **82**:2882–2896.

BRAWN, J. D. 2006. Effects of restoring oak savannas on bird communities and populations. *Conserv. Biol.*, **20**:460–469.

———, S. K. ROBINSON, AND F. R. THOMPSON, III. 2001. The role of disturbance in the ecology and conservation of birds. *Ann. Rev. Ecol. Systematics*, **52**:251–176.

BURHANS, D. E. 1997. Habitat and microhabitat features associated with cowbird parasitism in two forest edge cowbird hosts. *Condor*, **99**:866–872.

——— AND F. R. THOMPSON, III. 1998. Effects of time and nest-site characteristics on concealment of songbird nests. *Condor*, **100**:663–672.

———, D. D. DEARBORN, F. R. THOMPSON, III, AND J. FAABORG. 2002. Factors affecting predation at songbird nests in old fields. *J. Wildl. Manage.*, **66**:240–249.

BURNHAM, K. P. AND D. R. ANDERSON. 2002. Model selection and multinomial inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, U.S.A.

CENTRAL HARDWOODS JOINT VENTURE. 2015. Open-oak woodland and savanna birds. <https://fw.ky.gov/Wildlife/Documents/SavannaWoodlandManagement.pdf> Accessed 1 June 2018.

COX, W. A. 2011. Cause specific mortality and anti-predator behavior in Midwestern songbirds. Ph.D. Dissertation, University of Missouri, Columbia. 178 p.

———, F. R. THOMPSON, III, AND J. FAABORG. 2012. Landscape forest cover and edge effects on songbird nest predation vary by nest predator. *Landsc. Ecol.*, **27**:659–669.

DAVIS, M. A., D. W. PETERSON, P. B. REICH, M. CROZIER, T. QUERY, E. MITCHELL, J. HUNTINGTON, AND P. BAZAKAS. 2000. Restoring savanna using fire: impact on the breeding bird community. *Restor. Ecol.*, **8**:30–40.

DEGREGORIO, B. A., S. J. CHIAVACCI, P. J. WEATHERHEAD, J. D. WILLSON, T. J. BENSON, AND J. H. SPERRY. 2014. Snake predation on North American bird nests: culprits, patterns and future directions. *J. Avian Biol.*, **45**:325–333.

———, S. J. Chiavacci, T. J. Benson, J. H. Sperry, and P. J. Weatherhead. 2016. Nest predators of North American birds: continental patterns and implications. *BioScience*, **66**:655–665.

Dey, D. C. and J. M. Kabrick. 2015. Restoration of Midwestern oak woodlands and savannas p. 401–428. *In*: J. A. Stanturf (ed.). Restoration of boreal and temperate forests. Second edition. CRC Press, Boca Raton, Florida, U.S.A.

Fontaine, J. J. and T. E. Martin. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecol. Letters*, **9**:428–434.

Grant, T. A., T. L. Shaffer, E. M. Madden, and P. J. Pietz. 2005. Time-specific variation in passerine nest survival: new insights into old questions. *Auk*, **122**:661–672.

Grundel, R. and N. B. Pavlovic. 2007. Distinctiveness, use, and value of Midwestern oak savannas and woodlands as avian habitats. *Auk*, **124**:969–985.

Hanberry, B. B., D. T. Jones-Farrand, and J. M. Kabrick. 2014. Historical open forest ecosystems in the Missouri Ozarks: reconstruction and restoration targets. *Ecol. Restor.*, **32**:4.

Harper, C. A., W. M. Ford, M. A. Lashley, C. E. Moorman, and M. C. Stambaugh. 2016. Fire effects on wildlife in the Central Hardwoods and Appalachian regions, USA. *Fire Ecol.*, **12**:127–159.

Holoubek, N. S. and W. E. Jensen. 2015. Avian occupancy varies with habitat structure in oak savanna of the south-central United States. *J. Wildl. Manage.*, **79**:458–468.

——— and W. E. Jensen. 2016. Avian nest success along a habitat gradient in the Cross Timbers oak savanna. *Am. Midl. Nat.*, **176**:234–246.

Hosmer, D. W. and S. Lemeshow. 2000. Applied logistic regression. John Wiley and Sons, Inc., New York, New York, USA.

Hunter, W. C., D. A. Buehler, R. A. Canterbury, J. L. Confer, and P. B. Hamel. 2001. Conservation of disturbance-dependent birds in eastern North America. *Wildl. Soc. Bull.*, **29**:440–455.

Karstensen, K. A. 2010. Land-cover change in the Ozark Highlands, 1973-2000. USGS, Open-file report 2010-1198, 13 p. <https://pubs.usgs.gov/of/2010/1198/pdf/OFR2010-1198.pdf> Accessed 13 September 2017.

Knutson, M. G., B. R. Gray, and M. S. Meier. 2007. Comparing the effects of local, landscape, and temporal factors on forest bird nest survival using logistic-exposure models. *Studies in Avian Biol.*, **34**:105–116.

Mark Twain National Forest (MTNF). 2005. Mark Twain National Forest Land and Resource Management Plan. USDA Forest Service, Mark Twain National Forest, Rolla, Missouri, USA. <https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsm8_045308.pdf> Accessed 12 September 2017.

Martin, T. E., C. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD Field Protocol. Breeding Biology Research and Monitoring database. Montana cooperative wildlife research unit. University of Montana, Missoula.

McCarty, K. 1998. Landscape-scale restoration in Missouri savannas and woodlands. *Restoration Manage. Notes*, 1622–32.

Morris, D. L., P. A. Porneluzi, J. Haslerig, R. L. Clawson, and J. Faaborg. 2013. Results of 20 years of experimental forest management on breeding birds in Ozark forests of Missouri, USA. *For. Ecol. Manage.,* **310**:747–760.

Nelson, P. W. 2002. Classification and characterization of savannas and woodlands in Missouri, p. 9–25. *In*: G. Hartman, S. Holst, and B. Palmer (eds.). Proceedings of SRM 2002: Savanna/Woodland Symposium. Conservation Commission of the State of Missouri, Jefferson City, MO, USA.

———. 2005. The terrestrial natural communities of Missouri. Missouri Natural Areas Committee, Jefferson City, USA.

Noss, R. F., E. T. LaRoe, III, and J. M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Vol. 28. USDI, National Biological Service, Washington, D.C., U.S.A.

Nuzzo, V. A. 1986. Extent and status of Midwest oak savanna: presettlement and 1985. *Nat. Areas J.*, **6**:6–36.

Peak, R. G., F. R. Thompson, III, and T. L. Shaffer. 2004. Factors affecting songbird nest survival in riparian forests in a Midwestern agricultural landscape. *Auk,* **121**:726–737.

REIDY, J. L., F. R. THOMPSON, III, AND S. W. KENDRICK. 2014. Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks. *For. Ecol. Manage.*, **313**:34–46.

RICKETTS, M. S. AND G. RITCHISON. 2000. Nesting success of yellow-breasted chats: effects of nest site and territory vegetation structure. *Wilson Bull.*, **112**:510–516.

ROACH, M. C. 2017. Breeding bird response to pine-savanna and woodland restoration in the Ozark-Ouachita interior highlands. M.Sc. Thesis, University of Missouri, Columbia. 140 p.

———, F. R. THOMPSON, III, AND T. JONES-FARRAND. 2018. Songbird nest success is positively related to restoration of pine-oak savanna and woodland in the Ozark Highlands, Missouri, USA. *Condor*, **120**:543–556.

ROBINSON, S. K, J. D. BRAWN, S. E. MORSE, AND J. R. HERKERT. 1999. Use of different habitats by breeding brown-headed cowbirds in fragmented Midwestern landscapes. *Studies in Avian Biology*, **18**:52–61.

RODEWALD, P. (ed.). 2015. The Birds of North America. Cornell Laboratory of Ornithology, Ithaca, NY. <https://birdsna-org.proxy.mul.missouri.edu> Accessed 18 May 2018.

ROTELLA, J. J., S. J. DINSMORE, AND T. L. SHAFFER. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Cons.*, **27**:187–205.

SAUER, J. R., D. K. NIVEN, J. E. HINES, D. J. ZIOLKOWSKI, JR., K. L. PARDIECK, J. E. FALLON, AND W. A. LINK. 2017. The North American Breeding Bird Survey, results and analysis 1966-2015. Version 2.07.2017. USGS Patuxent Wildlife Research Center, Laurel, MD. <https://www.mbr-pwrc.usgs.gov/bbs/> Accessed 1 November 2017.

SCHILL, K. L. AND R. H. YAHNER. 2009. Nest-site selection and nest survival of early successional birds in central Pennsylvania. *Wilson. J. Ornithol.*, **121**:476–484.

SHAFFER, T. L. 2004. A unified approach to analyzing nest success. *Auk*, **121**:526–540.

——— AND F. R. THOMPSON, III. 2007. Making meaningful estimates of nest survival with model-based methods. *Studies in Avian Biol.*, **34**:84–95.

SHAKE, C. S., C. E. MOORMAN, AND M. R. BURCHELL, II. 2011. Cropland edge, forest succession, and landscape affect shrubland bird nest predation. *J. Wildl. Manage.*, **75**:825–835.

STARBUCK, C. A., S. K. AMELON, AND F. R. THOMPSON, III. 2015. Relationships between bat occupancy and habitat and landscape structure along a savanna, woodland, forest gradient in the Missouri Ozarks. *Wildl. Soc. Bull.*, **39**:20–30.

TEMPLE, S. A. 1998. Surviving where ecosystems meet: ecotonal animal communities of Midwestern oak savannas and woodlands. *T. Wisc. Acad. Sci., Arts Lett.*, **86**:207–222.

THOMPSON, F. R., III. 2007. Factors affecting nest predation on forest songbirds in North America. *Ibis*, **149**:98–109.

——— AND D. E. BURHANS. 2003. Predation of songbird nests differs by predator and between field and forest habitats. *J. Wildl. Manage.*, **67**:408–416.

——— AND D. R. DESSECKER. 1997. Management of early-successional communities in central hardwood forests: with special emphasis on the ecology and management of oaks, ruffed grouse, and forest songbirds. USDA, Forest Service, Gen. Tech. Rep. NC-195.

———, W. DIJAK, AND D. E. BURHANS. 1999. Video identification of predators at songbirds nests in old fields. *Auk*, **116**:259–264.

———, T. M. DONOVAN, R. M. DEGRAAF, J. FAABORG, AND S. K. ROBINSON. 2002. A multi-scale perspective of the effects of forest fragmentation on birds in eastern forests. *Stud. Avian Biol.*, **25**:8–19.

———, J. L. REIDY, S. W. KENDRICK, AND J. A. FITZGERALD. 2012. Songbirds in managed and non-managed savannas and woodlands in the central hardwoods region. USDA, Forest Service, Gen. Tech. Rep. NRS-P-102.

——— AND C. A. RIBIC. 2012. Conservation implications when the nest predators are known. *Stud. Avian Biol.*, **43**:23–34.

SUBMITTED 14 DECEMBER 2017 ACCEPTED 12 JULY 2018

APPENDIX I.—Dominant habitat association (DHA) and number of active nests for 32 species monitored on savanna-woodland plots in the Missouri Ozarks, 2009-2011

Common name	Scientific name	DHA[a]	N
Acadian flycatcher	*Empidonax virescens*	FI	73
American goldfinch	*Spinus tristis*	ES, WG	1
American robin	*Turdus migratorius*	WG	1
Black-and-white warbler	*Mniotilta varia*	FI	3
Blue grosbeak	*Passerina caerulea*	ES, WG	7
Blue jay	*Cyanocitta cristata*	WG	5
Blue-gray gnatcatcher	*Polioptila caerulea*	WG	172
Blue-winged warbler	*Vermivora cyanoptera*	ES	2
Chipping sparrow	*Spizella passerina*	ES, WG	28
Common yellowthroat	*Geothlypis trichas*	ES	5
Eastern towhee	*Pipilo erythrophthalmus*	ES	6
Eastern wood-pewee	*Contopus virens*	WG	256
Field sparrow	*Spizella pusilla*	ES	74
Indigo bunting	*Passerina cyanea*	ES	207
Kentucky warbler	*Geothlypis formosa*	FI	13
Louisiana waterthrush	*Parkesia motacilla*	FI	4
Northern cardinal	*Cardinalis cardinalis*	ES, WG	28
Northern parula	*Setophaga americana*	FI	1
Orchard oriole	*Icterus spurius*	WG	2
Ovenbird	*Seiurus aurocapilla*	FI	1
Pine warbler	*Setophaga pinus*	FI	1
Prairie warbler	*Setophaga discolor*	ES	47
Red-eyed vireo	*Vireo olivaceus*	WG	16
Ruby-throated hummingbird	*Archilochus colubris*	WG	7
Scarlet tanager	*Piranga olivacea*	FI	8
Summer tanager	*Piranga rubra*	WG	66
White-eyed vireo	*Vireo griseus*	ES, WG	14
Wood thrush	*Hylocichla mustelina*	FI	1
Worm-eating warbler	*Helmitheros vermivorum*	FI	2
Yellow-billed cuckoo	*Coccyzus americanus*	WG	41
Yellow-breasted chat	*Icteria virens*	ES	102
Yellow-throated vireo	*Vireo flavifrons*	WG	3

[a] General habitat associations: ES = early successional (prefer areas of heavy shrub cover with varying amounts of tree cover), FI = forest interior (prefer areas of mature forest), WG = woodland generalist (found in variety of wooded habitats across a range of canopy covers) (Rodewald 2015)

APPENDIX II.—List of 32 candidate models evaluating the effects of vegetation structure on nest survival of eight songbird species monitored in savanna and woodland sites in the Ozark Highlands of Missouri, 2009-2011. Supported species-specific temporal variables (nest stage, day of year, year) were included in all models

Model name	Covariates
Null	Intercept or supported temporal variables
Canopy[a]	Canopy cover
Shrub[b]	Shrub cover
Grass	Grass cover
Nest site	Nest height, nest cover, distance to main trunk[c]
Canopy + shrub	Canopy cover, shrub cover
Canopy + grass	Canopy cover, grass cover
Canopy + nest site	Canopy cover, nest height, nest cover, distance to main trunk
Canopy + shrub + grass	Canopy cover, shrub cover, grass cover
Canopy + shrub + nest site	Canopy cover, shrub cover, nest height, nest cover, distance to main trunk
Canopy + grass + nest site	Canopy cover, grass cover, nest height, nest cover, distance to main trunk
Canopy + shrub + grass + nest site	Canopy cover, shrub cover, grass cover, nest height, nest cover, distance to main trunk
Shrub + grass	Shrub cover, grass cover
Shrub + nest site	Shrub cover, nest height, nest cover, distance to main trunk
Shrub + grass + nest site	Shrub cover, grass cover, nest height, nest cover, distance to main trunk
Grass + nest site	Grass, nest height, nest cover, distance to main trunk
Tree density	Sapling, pole timber, saw timber, snag
Tree density + canopy	Sapling, pole timber, saw timber, snag, canopy cover
Tree density + shrub	Sapling, pole timber, saw timber, snag, shrub cover
Tree density + grass	Sapling, pole timber, saw timber, snag, grass cover
Tree density + nest site	Sapling, pole timber, saw timber, snag, nest height, nest cover, distance to main trunk
Tree density + canopy + shrub	Sapling, pole timber, saw timber, snag, canopy cover, shrub cover
Tree density + canopy + grass	Sapling, pole timber, saw timber, snag, canopy cover, grass cover
Tree density + canopy + nest site	Sapling, pole timber, saw timber, snag, canopy cover, nest height, nest cover, distance to main trunk
Tree density + canopy + shrub + grass	Sapling, pole timber, saw timber, snag, canopy cover, shrub cover, grass cover
Tree density + canopy + shrub + nest site	Sapling, pole timber, saw timber, snag, canopy cover, shrub cover, nest height, nest cover, distance to main trunk
Tree density + canopy + grass + nest site	Sapling, pole timber, saw timber, snag, canopy cover, grass cover, nest height, nest cover, distance to main trunk
Tree density + canopy + shrub + grass + nest site	Sapling, pole timber, saw timber, snag, canopy cover, shrub cover, grass cover, nest height, nest cover, distance to main trunk
Tree density + shrub + grass	Sapling, pole timber, saw timber, snag, shrub cover, grass cover
Tree density + shrub + nest site	Sapling, pole timber, saw timber, snag, shrub cover, nest height, nest cover, distance to main trunk
Tree density + shrub + grass + nest site	Sapling, pole timber, saw timber, snag, shrub cover, grass cover, nest height, nest cover, distance to main trunk
Tree density + grass + nest site	Sapling, pole timber, saw timber, snag, grass cover, nest height, nest cover, distance to main trunk

[a] Included the quadratic form of canopy cover if supported in preliminary analyses
[b] Included the quadratic form of shrub cover if supported in preliminary analyses
[c] Distance to main trunk for nests in trees and distance to foliage edge for nests in shrubs