

Avian Nest Success along a Habitat Gradient in the Cross Timbers Oak Savanna

NATHAN S. HOLOUBEK AND WILLIAM E. JENSEN¹

Dept. Biol. Sciences, Emporia State University, 1 Kellogg Circle, Emporia, Kansas 66801

ABSTRACT.—Oak savanna, once widespread across central North America, has functionally vanished from most of its range due to land conversion or fire suppression and subsequent afforestation. Savanna-associated bird species have exhibited population declines as a result. One of the few areas containing remnant oak savanna is the vast Cross Timbers ecoregion of the south-central United States. Previous research in the Midwest showed some bird species exhibited higher rates of nest success (*i.e.*, lower predation of eggs and nestlings) in restored savannas than in closed-canopy forests. Our objective was to quantify patterns of avian nest success across a gradient from open-canopy oak savanna to closed-canopy forest in the Cross Timbers ecoregion of southeastern Kansas. Daily nest survival rates for four common bird species—mourning dove (*Zenaidura macroura*), yellow-billed cuckoo (*Coccyzus americanus*), brown thrasher (*Toxostoma rufum*), and northern mockingbird (*Mimus polyglottos*)—were modeled against covariates of woodland structure along the habitat gradient. Tree density and canopy cover had no significant effects on daily nest survival rate, but daily survival rates of brown thrasher and northern mockingbird nests showed positive trends with increasing shrub density. We expect restoration of oak savanna habitat would have little effect on nest survival of some common bird species in the naturally heterogeneous Cross Timbers ecoregion.

INTRODUCTION

Oak-prairie savanna habitat in the Midwestern United States has largely disappeared (Nuzzo, 1986; Henderson, 1995; Noss *et al.*, 1995). Land conversion and degradation due to fire suppression have been primary causes of this loss (Apfelbaum and Haney, 1987; Abrams, 1992; Brawn *et al.*, 2001). Prescribed fire, mechanical tree thinning, and grazing are currently used to restore and maintain oak savanna and prairie (Penfound, 1962; Stotts *et al.*, 2007). Restoration of woodland, savanna, and prairie mosaics is predicted to benefit wildlife populations and communities (Lochmiller *et al.*, 1991; Shultz *et al.*, 1992; Jones *et al.*, 2000; Grundel and Pavlovic, 2007) in addition to livestock production (Bernardo *et al.*, 1992).

Many migratory birds have experienced significant population declines in recent decades (Sauer *et al.*, 2011) and the loss of savanna habitat has likely contributed to population declines of bird species dependent on disturbance-maintained habitats (Brawn *et al.*, 2001). Formerly large areas of oak savanna may have served as a prime breeding habitat for bird species that are currently of conservation concern (Brawn, 2006). Although many species that are generally thought to prefer savanna habitats also occur in edge habitat (Henderson, 1995), reproductive success in edge habitat may be limited by nest predation (Suarez *et al.*, 1997) and nest parasitism by brown-headed cowbirds (*Molothrus ater*) (Strausberger and Ashley, 1997; Jensen and Finck, 2004). Studies of avian nest success in oak savannas are limited in number, but evidence exists for comparatively high nesting success (*i.e.*, lower rates of depredation on eggs and nestlings) in oak savannas relative to birds nesting in closed-canopy forest. In Illinois, Brawn (2006) found greater nesting success of several bird species in restored oak savannas as compared to nest success of the same species in closed-canopy forest. At a landscape scale in Missouri, Kendrick *et al.* (2013) found eastern wood-

¹ Corresponding author: wjensen1@emporia.edu

pewee (*Contopus virens*) daily nest survival increased with decreasing forest cover within 10 km of nests.

We investigated avian daily nest survival in relation to variable habitat structure along a gradient from oak savanna to closed-canopy oak forest in the Cross Timbers ecoregion in southeastern Kansas. The Cross Timbers covers a large geographic area, ranging from southeastern Kansas, through Oklahoma, to central Texas. As with much of the Midwest, the Cross Timbers has experienced afforestation of its characteristic oak savanna (Stotts *et al.*, 2007). Concomitant declines in nest success of birds due to afforestation of savanna (Brawn 2006) could have major demographic consequences for avian populations of the Cross Timbers region. However, we know of no other study that explicitly investigated the effects of variation in tree and shrub density on avian nest survival in the Cross Timbers region. We compared nest survival rates of four regionally-common bird species to variation in tree density, canopy cover, and shrub density across a habitat gradient from oak savanna (1–25% tree canopy cover) to woodland (25–60% canopy cover) and forest (>60% canopy cover) (cover classifications following Faber-Langendoen, 1995) in the Cross Timbers ecoregion.

STUDY AREA

The Cross Timbers is a savanna ecoregion with blackjack oak (*Quercus merilandica*) and post oak (*Q. stellata*) as dominant tree species. This savanna has remained largely intact compared to other savanna ecoregions in North America, although it has received less ecological attention (Stotts *et al.*, 2007). The Cross Timbers has experienced problems common to savannas across the eastern U.S.; predominantly encroachment of woody species due to fire suppression, which has resulted in conversion to closed canopy forest (Stotts *et al.*, 2007). However, unlike savanna remnants in the forest-cropland landscape matrix of much of the Midwest, the landscape of the Cross Timbers is commonly dominated by native tallgrass prairie, which is used as rangeland due to the soil's unsuitability for row crops (EPA, 2013).

We accessed portions of two, adjacent cattle ranches (approximately 2507 ha and 130 ha) in Elk County, Kansas, in the summers of 2012 and 2013 for data collection. The ranches were dominated by native tallgrass prairie (including the grasses *Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, and *Schizachyrium scoparium*), while our study sites within these properties were upland oak savanna, woodland, and forest. The oak species present were primarily blackjack and post oak. The most common shrub species were *Rubus* spp., *Symphoricarpos orbiculatus*, and *Rhus copallina*. Both ranches use prescribed fire and herbicide to control woody vegetation. Our study sites included 5 somewhat distinct patches of savanna (1–25% tree canopy cover, Faber-Langendoen, 1995) which developed via natural succession; however, these patches were amorphous (Fig. 1) and occurred within a larger matrix containing higher density stands of trees. Additionally, we studied four stands of oaks (4.6–7.9 ha) where tree density was mechanically thinned to resemble savanna (5-m nearest-neighbor canopy spacing between trees) in the winter-spring of 2009. Our study area was under drought conditions in 2012. The historical average precipitation (March to July, most relevant to the growing season during our study) for Southeast Kansas is 521 mm. During 2012, only 447 mm was received; while 2013 surpassed normal levels with 659.9 mm of precipitation (NOAA, 2014; Climate Division: Kansas, 09). Temperature was also higher during data collection (from May to July) in 2012 (May to July mean = 25.3 C) and lower in 2013 (mean = 22.2 C) compared to the historical mean of 23 C (NOAA, 2014). Therefore,

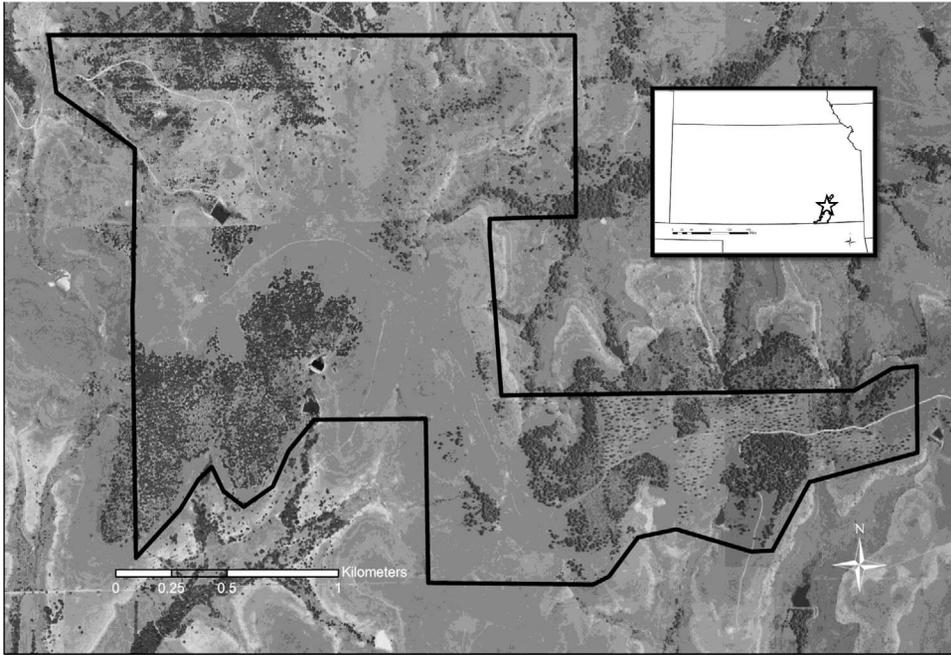


FIG. 1.—Aerial photograph of the study site (star in inset) located in the Cross Timbers ecoregion within Kansas (outline in inset) in Elk County, Kansas, 2012 and 2013. Darker objects are trees within the lighter landscape matrix of tallgrass prairie

the 2 y of our study represented hot, dry (2012) and cooler, wetter (2013) conditions, respectively.

METHODS

NEST SEARCHING

We searched for nests of all bird species occurring on the site from mid-May through July 2012 and mid-May to early August 2013. We divided search effort equally between thirds of our approximately 279-ha study area, with each third visited twice weekly. Nests were either found by seeing them outright or by following parent birds to nests. Once a nest was found, we recorded species and nest location using a hand-held Garmin GPS (Model: eTrex Legend H, Olathe, Kansas) and a blue marker flag was placed a minimum of 5 m away. Bearing (measured with a compass) and approximate distance between the nest and flag were recorded. We monitored nests every 3 or 4 d until young fledged or the nest failed (due to predation or weather-related losses). During visits, we recorded the number of host eggs and young, number of brown-headed cowbird eggs and young, approximate developmental stage of young, parental behavior, and described any nest disturbance. During monitoring visits, we took care to limit time near the nest, minimized disturbance to vegetation, used different routes to approach a nest (when possible) among successive visits, and placed flagging a reasonable distance from the nest (≥ 5 m). We estimated nest fate by observations made at the final nest check and expected fledging date.

HABITAT SURVEYS

We completed vegetation surveys at each nest site, generally following the BBird Field Protocol (Martin *et al.*, 1997). We sampled one survey point at the nest and three others at satellite points located 30 m away at 0°, 120°, and 240°. Vegetation data included: % canopy cover of trees estimated in each cardinal direction using a spherical densiometer (Model – A, Robert E. Lemmon Forest Densimeters, Bartlesville, Oklahoma) (“canopy/50-m” hereafter); visual estimates of % grass, % forb, and % low shrub (woody plants < 50 cm high) within a 5-m radius of the vegetation point center; species and number of tree stems within a 11.5-m radius; and species and number of shrub (≥ 50 cm height) and small tree (≤ 8 cm diameter at breast height (dbh) stems within a 2.5-m radius (or 1-m radius in extremely dense areas). We considered tree stems forking below breast height to be separate stems. Trees were categorized according to dbh as follows: medium >8 to 23 cm, large >23 to 38 cm, and extra-large >38 cm. We combined small trees with shrubs for the calculation of shrub density (shrubs/m²). The tree density metric (trees/ha) included medium size and larger trees.

We estimated canopy cover within a 100-m radius (“canopy/100-m” hereafter) by importing National Agriculture Imagery Program (NAIP) data from 2012 to ESRI ArcMap Version 10.2 Advanced (ESRI, Redlands, California). Drought conditions in 2012 enhanced the contrast between tree cover and herbaceous prairie and there were no large disturbances between years (*e.g.*, stand replacing fire, severe wind-throw, *etc.*) that substantially changed arboreal habitat structure. We used the green band (band 2) to classify pixels as either tree (pixel value < 100) or non-tree (pixel value ≥ 100). We calculated the proportion of tree pixels within a 100-m buffer around each nest. We assessed the accuracy of the canopy/100 m estimates by using the same process to obtain canopy cover estimates within a 50-m radius of nests and comparing them with canopy cover estimates collected via densiometer within the 50-m radius. The parameters were correlated, with a Pearson correlation coefficient of 0.724 ($P < 0.0001$) ($n = 328$, including nests and point count survey data; latter from Holoubek and Jensen, 2015). Canopy cover estimates at the 50-m radius derived from densiometer estimates were later used in nest survival analyses. The 50-m estimates from NAIP imagery were not used again because they were only created for validating GIS estimated canopy cover within the 100-m radii and were redundant with densiometer measurements.

We averaged vegetation data across all four points surveyed for each nest (center plus three satellite points). Vegetation sampling units at times overlapped among different nests within species. There were three instances of nest vegetation data being identical (*e.g.*, nesting in the same tree) among nests within the same year for the same species. These occurred because of nest re-use or a new nest placed <0.5 m from a nest used earlier that year. Identical satellite points for vegetation surveys among nests were used for multiple nests when satellite survey centers were within 15 m of each other, which occurred for 11 other nest pairs (six mourning dove, four northern mockingbird, and one brown thrasher nest pairs). We ran a Pearson correlation analysis among all habitat variables using SAS ($\alpha = 0.10$, $r = 0.05\text{--}0.81$) to determine uncorrelated covariates that could be included together in models.

STATISTICAL ANALYSES

We analyzed daily nest survival (DSR) of four species with the largest sample sizes of nests over our 2 y study period: mourning dove, yellow-billed cuckoo, brown thrasher, and

northern mockingbird (nests of other species were far less common and were determined to be unusable for inferential statistical analysis). We used the logistic-exposure method (Shaffer, 2004) in SAS to model DSR in relation to habitat covariates and used an information theoretic approach (Burnham and Anderson, 2002) to select plausible models of DSR using habitat covariates. The habitat covariates included in our model selection process were: trees/ha, canopy/50 m, canopy/100 m, and shrubs/m². All herbaceous habitat metrics we recorded were strongly correlated with many of the aforementioned woody habitat measures, are of less focus in savanna/woodland management, and were therefore omitted from model selection. All habitat covariates were modeled as linear effects, but also as quadratic and “pseudothreshold” (*ln*-transformed; Franklin *et al.*, 2000) effects to account for non-linear relationships. Pseudothreshold models were created by adding 0.5 to the variable to ensure nonzero numbers and taking the natural logarithm of that value [*e.g.*, *ln*(trees/ha + 0.5)]. We also included nesting stage (incubation or nestling) as a temporal covariate. Nesting stage was correlated with day of the year for all species ($P < 0.001$, $r = 0.21\text{--}0.39$) and was consistently ranked as a more important variable than day of the year in preliminary modeling exercises. All additive combinations of habitat covariates and nestling stage were included in the selection process in addition to intercept-only (constant DSR) models. However, as the tree-related habitat variables were correlated ($P < 0.0001$, $r = 0.73\text{--}0.79$), this prevented not only their inclusion in the same models but averaging of their redundant β estimates within plausible ($\Delta\text{AIC}_c \leq 2$) model sets. In such cases, results from separate plausible models are presented. The covariate shrubs/m² was not correlated with any tree variable and therefore was able to be included in models with tree covariates. Only informative parameters were included in plausible models sets (*i.e.*, we excluded models with one additional covariate than occurred in better fit models within plausible sets) (Arnold, 2010). Where possible (among models with uncorrelated covariates), we accounted for model uncertainty within plausible model sets by using model averaging (Mazerolle, 2006; Burnham and Anderson, 2002). We considered model-averaged ($\Delta\text{AIC}_c \leq 2$) habitat covariates to be biologically important if the 85% confidence interval of β did not include zero (Arnold, 2010). We calculated mean DSR from averaged models or independent models (if covariates among models plausible models were correlated) within plausible model sets per species using mean covariate values. We then raised the DSR to the power of the number of exposure days needed for development to fledging for each species (using median values for days per stage from Baicich and Harrison, 2005). We calculated standard errors for daily and period survival rates using the delta method (Powell, 2007) in R Version 3.0.2 (www.r-project.org, accessed 6 October 2013).

RESULTS

We monitored 427 nests in 2012 and 2013 (Fig. 2). These included 101 mourning dove nests (1024 exposure days), 54 yellow-billed cuckoo nests (575 exposure days), 56 brown thrasher nests (666 exposure days), and 57 northern mockingbird nests (731 exposure days). The remaining nests belonged to species with sample sizes that we determined to be insufficient for analysis. Other nests found included those of chuck-will's-widow (*Caprimulgus carolinensis*, four nests), red-bellied woodpecker (*Melanerpes carolinus*, one nest), downy woodpecker (*Picoides pubescens*, one nest), eastern wood-pewee (two nests), great-crested flycatcher (*Myiarchus crinitus*, five nests), eastern kingbird (*Tyrannus tyrannus*, 29 nests), scissor-tailed flycatcher (*Tyrannus forficatus*, four nests), blue jay (*Cyanocitta cristata*, six nests), Bewick's wren (*Thryomanes bewickii*, one nest), blue-gray gnatcatcher (*Poliophtila caerulea*, two nests), eastern bluebird (*Sialia sialis*, seven nests), gray catbird (*Dumetella carolinensis*, one

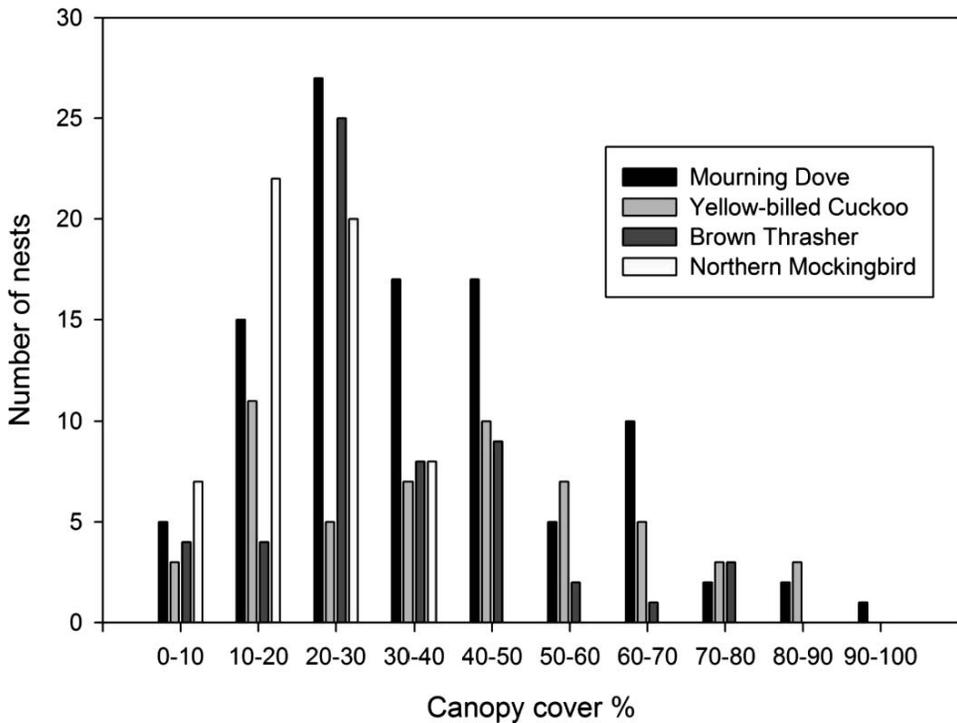


FIG. 2.—Distribution of nests of four common bird species across a gradient of tree canopy cover values (measured using a densitometer within 50 m of nests) in the Cross Timbers of Elk County, Kansas, 2012 and 2013

nest), eastern towhee (*Pipilo erythrophthalmus*, one nest), field sparrow (*Spizella pusilla*, 22 nests), lark sparrow (*Chondestes grammacus*, 15 nests), summer tanager (*Piranga rubra*, seven nests), northern cardinal (*Cardinalis cardinalis*, 24 nests), blue grosbeak (*Passerina caerulea*, one nest), indigo bunting (*Passerina cyanea*, one nest), dickcissel (*Spiza americana*, 20 nests), eastern meadowlark (*Sturnella magna*, one nest), and orchard oriole (*Icterus spurius*, 22 nests).

Plausible informative models ($\Delta AIC_c \leq 2$) were not symptomatic of over- or under-dispersion (range of deviance/*df*: 0.84, 1.1). Intercept-only models did not appear as plausible candidate models of DSR for any species. Nesting stage appeared in all plausible models for all species and in each case DSR was higher in nestling stage vs. incubation (Table 1, Figs. 3 and 4). Although habitat variables were included in plausible DSR models (Table 1), only one habitat variable (shrubs/m²) strongly influenced DSR for any species (85% confidence interval of β did not include 0). Brown thrasher DSR was positively influenced by $\ln(\text{shrubs/m}^2)$ (Table 1, Fig. 3A), though one plausible model showed a quadratic relationship with shrub density, with highest DSR during the incubation stage at intermediate shrub densities (Table 1, Fig. 3B). Northern mockingbird DSR also increased positively with $\ln(\text{shrubs/m}^2)$ (Table 1, Fig. 4). Period nest survival estimates, based on best fit models, ranged from 0.12 (0.19 SE) in the mourning dove to 0.28 (0.21 SE) in the northern mockingbird (Table 1).

TABLE 1.—Plausible ($\Delta AIC_c \leq 2$) models of daily nest survival (DSR) models for four bird species in Elk County, Kansas, 2012 and 2013. Model averaged covariates (β) \pm unconditional SE are shown in addition to DSR (\pm SE) and nest period survival estimates (\pm SE) calculated using covariate means. Multiple models are listed for some species where correlated covariates occurred among competing, plausible ($\Delta AIC_c \leq 2$) models, thus preventing model averaging

Species	AIC _c ^a	Covariate	w _i ^b	β (\pm SE)	DSR	Period survival
Mourning dove	311.5	Canopy/50-m	0.21	-0.05 (0.04)	0.93 (0.05)	0.12 (0.19)
		Canopy/50-m ²	0.21	0.0005 (0.0004)		
		Nest stage	0.37	0.92 (0.29) ^c		
Yellow-billed cuckoo	116.8	Nest Stage	0.47	0.94 (0.29) ^c	0.93 (0.02)	0.27 (0.11)
Brown thrasher	177.3	\ln (Shrubs/m ²)	0.37	0.74 (0.34) ^c	0.94 (0.03)	0.20 (0.17)
		Nest stage	0.49	0.98 (0.39) ^c		
	177.7	Shrubs/m ²	0.12	0.77 (0.34) ^c	0.94 (0.03)	0.21 (0.19)
		(Shrubs/m ²) ²	0.12	-0.05 (0.02) ^c		
Northern mockingbird	180.5	Nest stage	0.49	0.93 (0.40) ^c	0.95 (0.03)	0.28 (0.21)
		Shrubs/m ²	0.29	0.47 (0.37)		
	180.9	Nest stage	0.55	0.87 (0.39) ^c	0.95 (0.03)	0.28 (0.22)
		\ln (Shrubs/m ²)	0.17	0.64 (0.43) ^c		
		Nest stage	0.55	0.86 (0.39) ^c		
181.3	Nest stage	0.55	0.98 (0.38) ^c	0.95 (0.02)	0.28 (0.15)	

^a Akaike's Information Criterion corrected for small sample size (AIC_c) per model

^b Summed model weight across plausible models ($\Delta AIC_c \leq 2$) containing the covariate

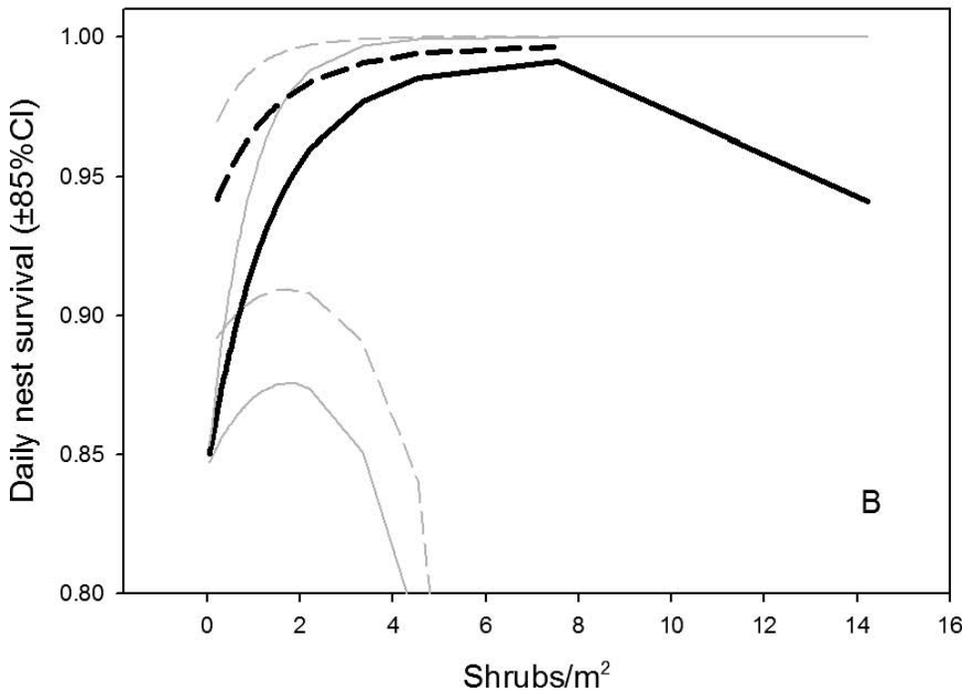
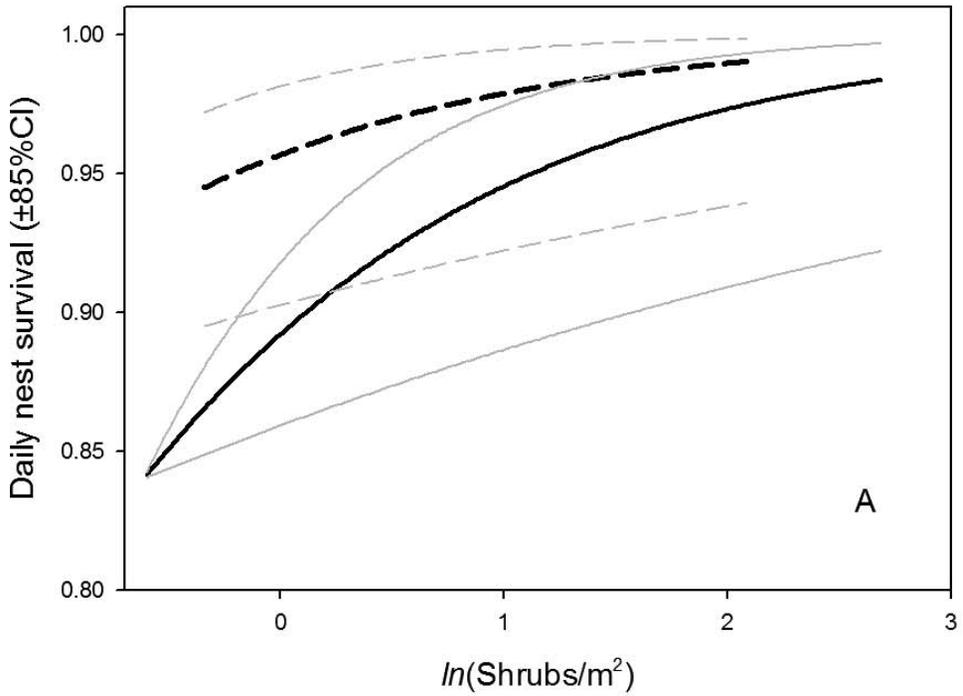
^c Covariate strongly predicts daily survival rate (85% CI of β does not include 0)

DISCUSSION

Among all habitat covariates we only found shrub density to be a strong predictor of DSR, but only for brown thrasher and northern mockingbird. The lack of strong relationships between DSR and tree density or canopy cover could be due to insufficient sample sizes of nests, natural history aspects of the species we included in our analyses, or the unique landscape context and predator community of the Kansas portion of the Cross Timbers ecoregion. The species we chose for analyses were the most commonly found and widespread across the landscape, which might mean they are also the least likely to exhibit variation in nest success among habitats.

Other research on avian nest success in Midwestern savanna-forest systems found higher nest success in savanna habitat (Brawn, 2006) or in wooded landscapes (10-km radius) with lower tree cover (Kendrick *et al.*, 2013). Brawn (2006) found higher nest success in savanna vs. closed-canopy forest for 6 of 13 species that nested in both habitat types. However, of the species included in our analyses, only the brown thrasher was included in Brawn's (2006) study and he similarly found no significant difference in nest success of that species between restored savannas and closed-canopy forest. Our study system differed greatly from Brawn's

FIG. 3.—Predicted daily nest survival of brown thrasher during incubation (solid line) and nestling stage (dashed line) in relation to (A) the natural log (\ln) of shrub density (stems/m²) and (B) as a quadratic relationship with shrub density in Elk County, Kansas, 2012–2013. Gray lines indicate \pm 85% confidence intervals (these include a slope >0 and thus are considered to depict a biologically significant relationship)



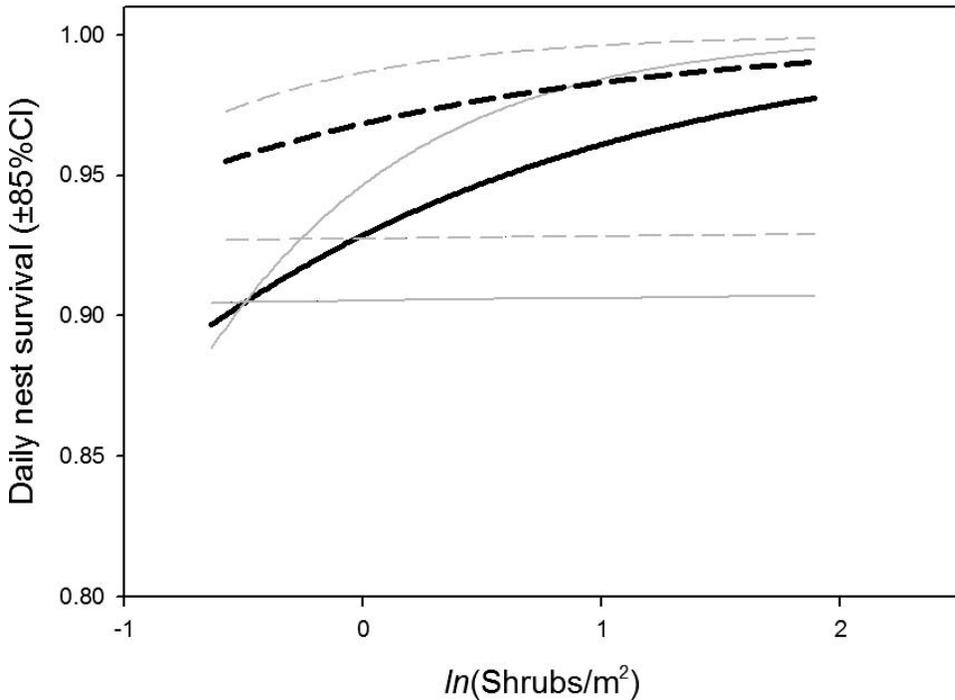


FIG. 4.—Predicted daily nest survival of northern mockingbird during incubation (solid line) and nesting stage (dashed line) in relation to the natural log (\ln) of shrub density (stems/m²) in Elk County, Kansas, 2012–2013. Gray lines indicate $\pm 85\%$ confidence intervals (these include a slope > 0 and thus are considered to depict a biologically significant relationship)

in that the landscape matrix of our Cross Timbers study consisted of native tallgrass prairie, vs. the dominant cropland and forested landscape matrix in Brawn's (2006) Illinois landscapes. Landscape context has been shown elsewhere to affect nest predator communities and nest predation rates (Donovan *et al.*, 1997), and might be related to the extent of agriculture (Dijak and Thompson, 2000). It is also noteworthy that—despite equal nest search effort in forests and savannas—the nest distributions of the species we analyzed were biased toward the savanna end of the savanna-forest gradient (Fig. 1); therefore, our data set might not represent the full range of nest predation experienced by other bird species along this habitat gradient.

Higher nest survival at higher shrub densities, as we found for both the brown thrasher and northern mockingbird, is not unexpected as both of these species commonly nest in shrubs (though we observed these species to commonly nest in the lower boughs of trees > 8 cm dbh; N. S. Holoubek, W. E. Jensen, Emporia State University, pers. obs.) and occur more frequently in open, shrubby habitats (Holoubek and Jensen, 2015). This pattern might be partially attributed to increased cover immediately surrounding the nest (Martin and Roper, 1988; Martin, 1993; Frey *et al.*, 2008). It is also possible that foraging is easier for these species in high shrub density habitats, allowing adults to spend more time guarding nests (Komdeur and Kats, 1999). Strong relationships between DSR and shrub density could indicate that

brown thrasher and northern mockingbird nest site selection and nesting behaviors are adapted to a “scrub savanna” vs. an “open savanna” (Nuzzo, 1986).

Daily nest survival was higher during the nestling (vs. incubation) stage for all species. Often DSR is lower during nestling stage, presumably as a result of increasing parental activity (Skutch, 1949; Eicholz and Koeining, 1992; Davis, 2003). However, Martin *et al.* (2000) demonstrated that nest predation rates can be higher during the incubation stage due to nest failure at sites with high predation threat, while sites with lower nest predation allow nest persistence to fledging. We found many nests failed quickly in the incubation stage, presumably discovered by predators soon after incubation was initiated. Increased DSR in the nestling stage has been found in other mimids (Peak *et al.*, 2004) and in brown thrasher and northern mockingbird may be partially attributed to increased parental aggression once the young hatch (Cavitt and Haas, 2000; Farnsworth *et al.*, 2011; N. S. Holoubek, Emporia State University, pers. obs.). Similarly, mourning dove parents often increase the frequency of injury feigning displays once the nestling stage of their offspring is reached (Otis *et al.*, 2008; N. S. Holoubek, pers. obs.), which might result in increased DSR during the nestling stage (Otis *et al.*, 2008). Mourning Dove nest period survival was also notably low, around 12%. Other studies report nest period survival greater than 35% (Otis *et al.*, 2008), but our results are similar to at least one other study which estimated 9% nest period survival in the southern Great Plains (Long *et al.*, 2012).

Daily nest survival of yellow-billed cuckoos was not related to any vegetative variable, being only positively related to advancement of nesting stage. We were not reliably able to assess the cause of failure for nests; however, many yellow-billed cuckoo nests were found with the entire clutch present in the nest with punctured eggs and egg contents unconsumed. This was the only species in which we found this to occur. Because these observations were limited to one species we suspect that such losses could be conspecific egg destruction in this facultative, intraspecific brood parasite (Hughes, 2015); although we had no direct observations of this behavior. Yellow-billed Cuckoo period survival (0.27) was slightly greater than reported in other studies, which ranged from 18% (Twedt *et al.*, 2001) to 22% (Twedt *et al.*, 2010).

The 17 other bird species for which we found nests included species commonly found in savanna and forest in the region (Holoubek and Jensen, 2015). Their omission from our analyses due to insufficient sample sizes of nests probably had as much to do with detection bias among species as lower relative abundances of those species. Our nest searching was focused on arboreal and shrub-nesting species, but some proved secretive and many of their nests likely evaded detection (*e.g.*, summer tanager). Some (*e.g.*, dickcissel, eastern meadowlark) were grassland birds that occur in savanna, but generally avoid wooded areas (Jensen and Finck, 2004). Longer term or more spatially expansive data sets of bird nests from the Cross Timbers might provide sufficient sample sizes of nests for future analyses. We expect species, such as indigo bunting, might exhibit higher nest survival in savanna vs. forest, as had been found by Brawn (2006).

We expect that savanna restoration in the Cross Timbers eco-region will have little effect on nest success of some common bird species (particularly our four focal species) that nest across the savanna-woodland-forest habitat gradient. It should be noted that while nest success was generally uniform in relation to tree density and canopy cover, occupancy by bird species was not (Holoubek and Jensen, 2015). For instance, northern mockingbird nest success was not influenced by canopy cover; however, their occupancy was much higher in savanna than closed-canopy forest (Holoubek and Jensen, 2015), which might explain why canopy cover was not a strong predictor of nest survival for this species. Strong occupancy-

habitat patterns did not exist for the other species for which we analyzed patterns of nest survival (Holoubek and Jensen, 2015). However, we also note that there might be habitat patterns in nest success of many of the other species for which we surveyed occupancy (Holoubek and Jensen, 2015), but for which we lacked sufficient sample sizes of nests for analysis of DSR, including many of the species included in Brawn's (2006) analysis of nest success. Species that are less common and more constrained to savanna habitats are more likely to be of conservation concern and therefore more likely to benefit from savanna restoration. It is also worth reminding that the landscape context in our study might have played a role in our finding no patterns of DSR with tree density or canopy cover. Our system is unique in that it consists of a heterogeneous mix of savanna, woodland, and forest embedded in a tallgrass prairie landscape. While we might expect no widespread change in avian nest success from savanna restoration in the Cross Timbers, restoration of savannas from closed-canopy forest in cropland landscapes has been found to increase nest success (Brawn, 2006). Finding higher nest success in areas with denser shrubs indicates that habitat heterogeneity within savanna should be considered as it may be important to nest success for certain species. This may be especially true for those that historically utilized scrub savanna habitats vs. open savanna. In addition to published patterns in nest success, landscape context and patterns of habitat use of bird species should be carefully considered when planning savanna restoration from closed-canopy forests.

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