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Bird Occupancy and Nesting Success in Relation to Habitat Structure in the Cross Timbers Oak Savanna of Kansas

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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. My objective was to quantify avian habitat associations and nest success across a gradient from open-canopy oak savanna to closed-canopy, afforested conditions in the Cross Timbers region of southeastern Kansas during the typical songbird breeding season. Species-specific site occupancy probabilities and daily nest survival rates were modeled against vegetative variables along the habitat gradient. Occupancy for 14 species was strongly associated with vegetative variables, such as landscape-level canopy cover and point-count-scale tree density, tree canopy cover, and shrub density. Savanna-associated species included Northern Bobwhite (*Colinus virginianus*), Bewick’s Wren (*Thryomanes bewickii*), Northern Mockingbird (*Mimus polyglottos*), Field Sparrow (*Spizella pusilla*), Dickcissel (*Spiza americana*), and Orchard Oriole (*Icterus spurius*). Arboreal habitat structure had less of an effect on daily nest survival rate. Daily nest survival showed positive trends with increasing shrub density for Brown Thrasher

(*Toxostoma rufum*) and Northern Mockingbird. Daily nest survival of Mourning Dove (*Zenaida macroura*) was negatively, but weakly, associated with increasing canopy cover. Daily nest survival of Yellow-billed Cuckoos (*Coccyzus americanus*) was unrelated to any habitat variable. Several of the species I found to be associated with savanna are of conservation concern in Midwestern states. Local occurrences of these species might benefit from reductions in tree density within otherwise closed-canopy forest.

Keywords: bird occupancy, canopy cover, Cross Timbers, nest survival, oak savanna, tree density.

BIRD OCCUPANCY AND NESTING SUCCESS IN RELATION TO HABITAT STRUCTURE IN THE CROSS TIMBERS OAK SAVANNA OF KANSAS

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PREFACE

This manuscript consists of one chapter. I will begin by discussing the loss of oak savanna habitat, once widespread across central North America, and its probable impacts on avian species. I will describe my study procedures and findings on how the bird community changes across a gradient of open oak savanna to closed canopy oak forest in the Cross Timbers of Kansas. Additionally, I assess possible differences in reproductive success (via nest survival) across this same gradient. I follow the format of the peer-reviewed *Journal of Wildlife Management*.

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INTRODUCTION

The extent of native oak-prairie savanna across mid-continental North America has been severely reduced by land conversion or degraded due to fire suppression (Apfelbaum and Haney 1987, Abrams 1992). Historically, periodic fires maintained a landscape composed predominantly of low density stands of oaks with a largely herbaceous understory of tallgrass prairie species, likely containing small stands of more densely wooded woodlands and forests (Penfound 1962, Abrams 1992, Henderson 1995, Brawn et al. 2001, Stotts et al. 2007). Oak-prairie savanna is also one of the most degraded ecosystems in North America, with an estimated 99.98% of oak savanna lost across the Midwest since pre-industrialized settlement (Nuzzo 1986, Henderson 1995, Noss et al. 1995). Fire was, historically, a major component of the disturbance regime that maintained this system and, along-side mechanical tree thinning, is currently used to restore and maintain oak savanna and prairie (Penfound 1962, Stotts et al. 2007). Reintroduction of fire in oak savannas at an appropriate frequency maximizes floristic diversity (Tester 1989), allows oak persistence (Abrams 1992, Peterson and Reich 2001), and promotes native herbaceous plants over exotics (Apfelbaum and Haney 1987). 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*a*) in addition to livestock production (Bernardo et al. 1992).

Migratory birds are a major conservation concern in North America, and have experienced significant population losses in recent decades (Sauer et al. 2011). These declines are likely related to habitat loss or fragmentation (Herkert 1994, Donovan et al.

1995). The loss of savanna habitat across North America has very likely impacted bird populations, especially of those that are dependent on—or commonly found in—disturbance maintained habitats (Brawn et al. 2001). For example the Red-headed Woodpecker (*Melanerpes erythrocephalus*), Red-cockaded Woodpecker (*Picoides borealis*), and Loggerhead Shrike (*Lanius ludovicianus*) have all experienced population declines and are known to make extensive use of savanna habitat (Hunter et al. 2001, Brawn et al. 2001, Brawn 2006). Bird population declines may be directly linked to long term fire suppression and resulting habitat changes in some California oak woodlands (Huff et al. 2005). Although many species that are generally thought to prefer savanna habitats have survived in edge habitat (Henderson 1995), these areas are often sub-optimal (Hunter et al. 2001). Avian reproductive success in edge habitat may be limited by nest predation (Suarez et al. 1997) and Brown-headed Cowbird (*Molothrus ater*) parasitism (Strausberger and Ashley 1997).

Few studies have evaluated avian use of oak savanna in North America. However, several studies have indicated oak savannas may be valuable as bird habitat. In oak-dominated savanna of the southwestern U.S., restoring fire disturbance at an appropriate frequency is important for structuring avian habitat and increases abundances of some birds (Bock and Block 2005). In Indiana, Grundel and Pavlovic (2007*a*) found the highest densities of threatened bird species in savanna and woodland communities compared to open areas, scrublands, or forests. In Illinois, oak savanna or woodlands are potentially valuable foraging habitats for a variety of insectivorous songbirds (Hartung and Brawn 2005). Savanna restoration changes avian community composition and has been shown to increase abundance of several species of declining eastern and central

North American birds (Davis et al. 2000). In surveys in Illinois, Brawn (2006) found some species to be unique to the savanna habitat, including Northern Bobwhite (*Colinus virginianus*) and Red-headed Woodpecker. Even though most of the same species were present in both habitat types, avian community structures between oak savannas and closed canopy forests in Illinois were distinct (Brawn 2006).

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). Nesting studies in oak savannas are also limited in number, but evidence exists for comparatively high nesting success in savannas. Brawn (2006) found greater nesting success in savannas for many species breeding in both restored savanna and forest. At a larger scale, Kendrick et al. (2013) found Eastern Wood-Pewee (*Contopus virens*) daily nest survival in Missouri increased with decreasing forest cover within 10 km of the nest. Presumably the above patterns in nest success were due to variation in nest predator communities or habitat-mediated behavior of nest predators.

The Cross Timbers is a savanna ecoregion dominated by blackjack oak (*Quercus merilandica*) and post oak (*Q. stellata*) that has remained largely intact compared to other savanna ecoregions in North America, although it has remained relatively unstudied ecologically (Stotts et al. 2007). The Cross Timbers covers a large geographic area, stretching from southeastern Kansas and southward through Oklahoma to central Texas. The Cross Timbers has suffered from problems common to savannas across the eastern U.S., predominently fire suppression and encroachment of woody species that have resulted in conversion to closed canopy forest (Stotts et al. 2007). Despite need for restoration to savanna from areas of closed canopy forest in the region, the Cross Timbers remains one of the least degraded oak savanna and woodland ecoregions in North America (Stotts et al. 2007). Unlike savanna remnants in the forested and cropland landscapes of the Midwest, the landscape of the Cross Timbers is largely dominated by native tallgrass prairie, which is used as rangeland due to the soil's unsuitability for row crops (EPA 2013). Prescribed burns are often used to manage woody vegetation and increase cattle forage. Herbicide application, another common management tool, was found to change the avian community composition in the Cross timbers, but not overall species richness or diversity (Shultz et al. 1992). Aside from Shultz et al. (1992), no other study has determined the importance of savanna habitat structure to avian habitat use and nesting success within the Cross Timbers ecoregion.

I investigated avian responses to variable habitat structure along an oak savanna-forest gradient in the Cross Timbers ecoregion in Kansas. The aim of my project was to use the unique Cross Timbers setting to predict avian responses to oak savanna restoration. I compared species occupancy and nest survival to variation in tree density and other habitat variables across a habitat gradient from oak savanna (naturally occurring and restored), to woodland and forest. I classified the habitats in the same manner as Faber-Langendoen (1995), considering forest as >60% canopy cover, woodland as 25-60%, and savanna as 1-25% canopy cover.

STUDY AREA

I accessed portions of two, adjacent cattle ranches (approximately 2,507 and 130 ha) in Elk County, Kansas in the summers of 2012 and 2013 for data collection (Fig. 1). The ranches were dominated by native tallgrass prairie, while my study sites within these properties were upland oak savanna, woodland, and forest. The oak species present were primarily blackjack and post oak. Both ranches use prescribed fire and herbicide to control woody vegetation. My study areas contained forest, woodland, and both remnant savanna and restored savanna (latter ranging in size from 4.6 to 7.9 ha). The majority of savanna restoration occurred between 2009 and 2010 and included mechanical tree removal, reintroduction of fire, and herbicide application to control oak re-sprouts. My study area, as well as a large portion of the Midwest, was under drought conditions in 2012. The historical average precipitation (March to July, most relevant to the growing season during my study) for Southeast Kansas (Climate Division: Kansas 09) is 521.0 mm (1901 to 2013), however during that same time period in 2012 only 447.0 mm was received (73.9 mm below average) (NOAA 2014). In 2013 mean precipitation during the same time period was 659.9 mm, surpassing normal levels (NOAA 2014). 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 23.0° C (1901 to 2013) (NOAA 2014). Thus, the two years of my study represented hot, dry (2012) and cooler, wetter (2013) conditions.

METHODS

Point Counts

I used point counts (Fig. 1) to assess avian site occupancy (i.e., probability of species occurrence) across the savanna-woodland-forest habitat gradient (Fig. 2A). I chose to estimate occupancy instead of density because my study site required small radius point count circles (50 m), which are not well suited to abundance estimation. I predominantly surveyed species which, because of territory size, would likely only have 1 or 2 territories included within each circle. Additionally, many detections in dense vegetation were auditory and cryptic individuals could have been counted multiple times, artificially inflating density estimations. This detectability issue also made accurate distance estimation problematic for distance sampling approaches.

Before visiting the study area during the avian breeding season, I systematically established 60 points using Esri ArcMap 10.0 Advanced (ESRI. Redlands, CA) and 2011 National Agriculture Inventory Program (NAIP) imagery to select sites across a gradient of tree densities. Points were placed to comprehensively cover the upland oak savanna, woodlands, and forests on the site. I visited each point four times per year in 2012 and 2013, rotating the order that points were visited for each round of surveys. A minimum distance of 200 m separated point centers. I surveyed points every other week between mid-May and early July. Point counts consisted of a five minute visit between sunrise and 09:15 local time, where all birds detected within a 50 m radius were recorded, as well as the sex (if known) and method of detection (i.e., song, call, visual). I estimated approximate wind speed at the beginning of each survey using the Beaufort scale. I did not conduct surveys during rain.

Nest Searching

Nest searching occurred across a gradient of tree and shrub densities from mid-May through July 2012 and mid-May to early August 2013 (Fig. 2B). I divided the search effort equally between thirds of a portion of study area (a 279 ha area with a representative habitat gradient; Fig. 3), rotating so every area was visited twice weekly on a regular schedule. Nests were found using both systematic and haphazard searches, including direct observation of nests as well as following parent bird behavioral clues. Once a nest was located, species was identified and nest location recorded using a hand-held Garmin GPS (Model: eTrex Legend H. Olathe, KS) and a blue marker flag placed a minimum of 5 m away with bearing (measured with a compass) and approximate distance from flag to the nest. Nests were monitored twice weekly (every 3 or 4 days) until young either fledged or the nest failed. During visits the number of host eggs and young, number of Brown-headed Cowbird eggs and young, approximate developmental stage of young, parental behavior, and nest disturbance (if evident) was recorded. I took care to limit the impact of observations on nest success by limiting time near the nest, minimizing disturbance to vegetation, using different routes to approach a nest (when possible) and placing flagging a reasonable distance from the nest (≥5m). I estimated nest fate by observations made at the final nest check and expected fledging date.

Habitat Surveys

I completed vegetation surveys at each point count and nest site, generally following the BBird Field Protocol (Martin et al. 1997). I collected vegetation measurements on nests in both years, but on point counts in 2012 only. The measurements made in 2012 were during an extreme drought; however, I assumed the major variables of interest (woody vegetation structure) were unlikely to change dramatically since no large disturbance (i.e. stand replacing fire, severe wind-throw, etc.) occurred between years. I did one survey at the center point (location of count center or nest), and three others at satellite points located 30-m away at 0°, 120°, and 240°. The location of each vegetation survey point was recorded using the same GPS unit described above. Vegetation data included % canopy cover, estimated in each cardinal direction using a spherical densiometer (Model – A, Robert E Lemmon Forest Densiometers. Bartlesville, OK), and visual estimates of % grass, % forb, and % low shrub (woody plants <50cm high) within a 5 m radius of the vegetation point center, species and number of trees within a 11.5 m radius, species and number of shrubs (≥50 cm height) within a 2.5 m radius (or 1 m radius in extremely dense areas), and number of snags (dead trees) within a 11.5 m radius. I considered tree stems forking below breast height to be separate stems. Trees were categorized according to diameter at breast height (DBH) as follows: small ≤ 8 cm, medium >8 to 23 cm, large >23 to 38 cm, and extra large >38 cm. I combined small sized trees with shrubs for analysis in the shrub category. Trees/ha calculations therefore do not include small trees, only medium sized and larger trees. Snags were categorized as small if less than 12 cm DBH and large if ≥ 12 cm DBH.

I estimated canopy cover at a 100-m radius (canopy/100-m) around count points and nests in order to investigate habitat relationships at a larger spatial scale. The 100-m radius was the maximum radius that allowed non-overlapping sampling units among point count points. I imported NAIP imagery from 2012 (visible light bands only) to ESRI ArcMap 10.2 Advanced. Imagery prior to 2010 was unrepresentative because of significant tree clearing on the study sites, so infrared band data, available in those years, was not usable. I chose 2012 over other years because severe drought conditions on the study site enhanced the contrast between tree cover and herbaceous prairie. I used the green band (band 2) to classify pixels as either tree (pixel value <100) or non-tree (pixel value ≥100). Water bodies were classified as “tree” pixels, but these were essentially absent from my dry upland study areas and did not significantly influence the dataset. The proportion of tree pixels was calculated within 100-m buffer around each count point and nest center. I assessed accuracy of the canopy/100-m estimates by using the same process to obtain canopy cover estimates within a 50 m radius buffer and comparing them with canopy cover data collected on the ground (i.e., via densitometer) that was intended to sample a 50 m radius buffer. The correlation analysis of 50 m radius estimated values and ground measurements yielded a Pearson correlation coefficient of 0.724 ($p<0.0001$) ($n=328$). I did not use GIS estimated canopy cover at the 50-m radius for any other analyses, all other canopy/50-m analyses used densiometer data.

I standardized all habitat variables (Z scores; i.e., mean = 0) for occupancy analyses in order to comply with the requirements of the analysis software. I did not standardize variables for nest survival analyses as these data were analyzed using a different statistical package. I ran a principal component analysis using SAS 9.2 (SAS Institute, Inc. Cary, North Carolina) to combine tree density and canopy cover into a principal component variable for analyses (PC1). I also ran a correlation analysis among all habitat variables using SAS ($\alpha=0.10$).

Occupancy Analyses

I summarized point count data according to detection (1) or non-detection (0) per species for each visit to each point. Vegetation data was averaged across all four points surveyed within each point count circle or nest point. Three model structures were used for occupancy analyses (Table 1): linear, quadratic, and pseudothreshold (Franklin et al. 2000, Dugger et al. 2005) in order to investigate varying habitat relationships including a preference for intermediate values (quadratic) or a minimum/maximum ψ that is not 0 or 1 (pseudothreshold). Each habitat attribute (e.g. trees/ha, % canopy cover, etc.) at each point was squared for quadratic models. Pseudothreshold model structure consisted of taking the natural logarithm of habitat measurements plus 0.5 to ensure non-zero numbers (i.e., *ln*(trees/ha + 0.5)).

Species detected at a minimum of five point count points each year were included in occupancy models. The program PRESENCE Version 5.9 (www.mbr-pwrc.usgs.gov/software/presence.shtml, accessed 30 July 2013) was used for analyzing occupancy while accounting for imperfect detection. For each species, detection was modeled first with occupancy held constant. Detection predictors considered were: tree density, shrub density, % grass cover, wind speed, Julian date, year, and survey specificity. I modeled detection using combinations of uncorrelated variables using all four available parameterizations offered by PRESENCE for the multi-season modeling option (Mackenzie et al. 2003). I only used a linear model structure to determine detection predictors. The top model (lowest Akaike's Information Criterion [AIC] value) among variables and parameterization options was selected for all occupancy modeling for a particular species.

After the top detection predictors and parameterizations were found per species, occupancy was modeled for each species. I created 10 sets of candidate models (Table 1) containing uncorrelated variables that appeared in global models and models with additive subsets of covariates (e.g., canopy cover and shrub density were combined in a global model for that "set"; however, tree density was correlated with both canopy cover and shrub density and was run in a separate "set"). Such structuring of model sets prevented correlated variables from appearing within the same model or among competing models in a candidate set (the latter prevented redundant variables being included among plausible models across which particular covariates could be averaged). Seasonal (inter-annual) and habitat effects were modeled in a hierarchical fashion. I first ran constant models and seasonal models per species to assess possible inter-annual differences in ψ. I then used the top ranked model (lowest AIC) between these to analyze all habitat relationships. I modeled all possible variable combinations within each set. Models from all candidate model sets with a ΔAIC ≤2 of the overall top model were considered plausible. Within each plausible model set, all model runs within ΔAIC of 2 of the top model (for that set) were model averaged using Akaike weights (w_i). No model averaging occurred between models sets or between model structures (i.e., linear, quadratic, or pseudothreshold were kept separate). I considered models uninformative if ΔAIC ≤2 but they contained one or more additional covariates (e.g., the model: trees/ha + shrubs/m^2 is uninformative if model: trees/ha is higher ranked) (Arnold 2010). I used model averaging (Mazerolle 2006, Burnham and Anderson 2002) to obtain average β values and unconditional standard errors for each covariate determined to be a plausible predictor by AIC values. I considered β values to indicate strong effects for a given variable if the 85% confidence interval of the β did not include 0 (Arnold 2010).

Nest Survival Analyses

I analyzed daily nest survival (DSR) of four species with the most nests found over two years among the species available: Mourning Dove (*Zenaida macroura*), Yellow-billed Cuckoo (*Coccyzus americanus*), Brown Thrasher (*Toxostoma rufum*) and Northern

Mockingbird (*Mimus polyglottos*). Vegetation data were summarized for each nest as above. Vegetation sampling units (including 100-m GIS canopy cover estimates) overlapped among different nests within species, with few instances of nests being re-used within the same year. I used the logistic-exposure method (Shaffer 2004) in SAS to model DSR in relation to habitat variables. Candidate model sets and model structures were partitioned as above (Table 1). I used the same vegetative variables for nest success as for occupancy modeling, with the addition of Julian date and nest stage (incubation or nestling). I performed model selection for DSR as done for occupancy. I determined average nest period survival by calculating the average values of the nest habitat variables for each species, multiplying them by the appropriate β values and adding together values that were in the same model. I estimated the total number of exposure days needed for a nest to fledge (from the start of incubation) from the median values for each species in Baicich and Harrison (2005). I then raised the DSR to the power of the number of exposure days needed for a nest to fledge for each species. I 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

Habitat Surveys

Habitat variables included a wide range of values at all levels (arboreal, shrub, and ground cover) across the savanna-forest gradient at all spatial scales measured (Table 2, Fig. 2). The most open habitat surveys measured no canopy cover or trees within individual 11.5-m radius circles. The two most common tree species recorded were blackjack oak and post oak. The most common shrub species were *Rubus* spp., *Symphoricarpos orbiculatus*, and *Rhus copallina*. Snags (dead standing trees) were present in all areas surveyed, but were especially dense in areas that had experienced recent canopy fires. The variables used for the principle component analysis were strongly correlated (canopy/50-m and trees/ha, Pearson correlation coefficient=0.79) and produced a PC1 variable with an eigenvalue of 1.795 with 0.897 of proportional variation explained.

Occupancy (ψ)

I completed 480 point counts between 2012 and 2013. Sixty-seven species were detected total (Table 3), 63 species were detected in 2012 and 49 in 2013. Twenty-seven species were detected at $\geq$5 points each year and were used for analyses of occupancy (Table 3). I discarded models that did not converge, which was indicated in several ways: by a non-convergence warning in the output from PRESENCE, parameter estimates with significant digits <2.0, an invalid SE (i.e., SE=−1.#INF00 or SE=1.#QNAN0), or an extremely high (>1,000) or an extremely low (<0.000001) SE. At least one valid occupancy model was obtained for each species modeled.

Top detection (*p*, i.e., the probability of detecting a species were it there) models varied by species (Table 4). The most common predictors of *p* were tree density, wind speed, and Julian date of survey. The survey specific model (having a unique detection constant for each individual survey) was not found to best predict detection for any species. Relationships with wind speed and Julian date were generally negative, but relationships of *p* with trees/ha, shrubs/m^2, and % grass varied among species.

Occupancy (ψ, e.g., probability a species occurs) predictors and the strength of these predictors varied greatly among species (Table 5). Summer Tanager (*Piranga rubra*) was the only species in which a seasonal model out-ranked a constant model. All models run for this species contained unique constants for 2012 and 2013. Season was not included as an effect in models for any other species. Occupancy models containing no habitat parameters (constant models) were top ranked (lowest AIC) for Mourning Dove, Red-bellied Woodpecker, Great-crested Flycatcher, Blue Jay, and Northern Cardinal, rendering all lower ranked models uninformative (Arnold 2010). Plausible models for all other species contained at least one habitat variable. Downy Woodpecker, Eastern Kingbird, Carolina Chickadee, Blue-gray Gnatcatcher, Eastern Bluebird, Brown Thrasher, Summer Tanager and Brown-headed Cowbird had plausible models (ΔAIC≤2) that contained habitat variables, but the relationships were weak (85% confidence interval for β included 0).

Strong ψ predictors.– Canopy/100-m was an important (85% confidence interval for β ≠ 0) predictor of ψ in plausible models (ΔAIC≤2) for many species (Table 5) (Fig. 4A). Occupancy of Eastern Wood-Pewee and White-breasted Nuthatch both increased as canopy/100-m increased. Occupancy of Northern Bobwhite, Bewick's Wren, Northern Mockingbird, and Orchard Oriole all decreased as canopy cover at the 100-m radius increased.

Canopy/50-m was an important predictor in plausible ψ models of Northern Bobwhite, Eastern Wood-Pewee, Tufted Titmouse, Northern Mockingbird, and Field Sparrow (Table 5) (Fig. 4B). The only species for which ψ increased as canopy/50-m increased were Eastern Wood-Pewee (with a quadratic relationship) and Tufted Titmouse; the other species had negative relationships with canopy/50-m.

Tree density predicted ψ in plausible models for Northern Bobwhite, Carolina Wren, Blue Grosbeak, Indigo Bunting, and Dickcissel (Table 5) (Fig. 4C). Indigo Bunting was the only species to have a positive relationship with tree density. Occupancy of Carolina Wren and Blue Grosbeak both had a quadratic relationship, peaking at intermediate tree densities. Northern Bobwhite and Dickcissel were negatively associated with tree density.

I found PC1 (composite of canopy/50-m and tree density) to be important for predicting ψ of Yellow-billed Cuckoo and Blue Grosbeak (Table 5) (Fig. 4D). Both of these species had strong positive relationships with PC1.

Shrub density was important for predicting ψ for Eastern Wood-Pewee, Tufted Titmouse, Lark Sparrow, and Indigo Bunting (Table 5) (Fig. 4E). Eastern Wood-Pewee and Indigo Bunting increased in expected ψ as shrub density increased. Lark Sparrow decreased in expected ψ as shrubs/m^2 increased. Tufted Titmouse had a quadratic relationship, with their highest ψ at high and low shrub densities and lowest ψ at intermediate values.

Nest Survival

I monitored 268 nests of the target nest species over 2 years. 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). Few habitat variables were included in plausible

DSR models (Table 6) and only one habitat variable (shrubs/m^2) strongly influenced DSR for any species (85% confidence interval of β did not include 0).

DSR predictors.– Mourning Dove DSR was strongly influenced by nest stage and Julian date, and negatively, but weakly (85% confidence interval of β included 0), influenced by *ln*(canopy/50-m) (Table 6). Daily survival rate increased with both nestling stage and Julian date (Table 6).

Daily survival rate for Yellow-billed Cuckoos was only strongly influenced by nest stage (Table 6). Daily survival rate was higher during the nestling stage than during incubation (Table 6).

Brown Thrasher DSR was strongly influenced by shrub density (Fig. 5) and nest stage (Table 6). Daily survival rate peaked at intermediate shrub densities, and increased once nestling stage was reached.

Northern Mockingbird DSR was also influenced by shrub density (Fig. 5) and nest stage and weakly (85% confidence interval included 0) influenced by Julian date (Table 6). Daily survival rate increased with increasing shrub density. As with all other species, DSR was higher during the nestling stage than during incubation (Table 6). Daily survival rate weakly increased with Julian date.

DISCUSSION

Occupancy (ψ)

Using ψ models I am able to understand largely how the bird community composition changes as savanna becomes afforested or savanna is restored from forest in the Cross Timbers ecoregion. The species I found associated with forests generally had high expected ψ over a wide range of habitats and are not necessarily unique to the forest environments. Woodland species spanned savanna and forests and were also generally common species. The species with the most constrained habitat preferences appeared to be the savanna species. Savanna habitats also contained most of the species that are of conservation concern in Midwestern states (Table 3), and was the habitat most likely to be occupied by Northern Bobwhite, a prominent game species of conservation concern.

Forest species.–While I had many areas of high tree density and canopy cover that could be considered forest habitat (>60% canopy cover), blocks of contiguous forest were absent from my study site. The forest habitat that was present was highly fragmented by more open woodland habitat. This being said, I considered species to be forest-associated if they had a positive relationship between ψ and canopy cover (at any scale), tree density, or the principle component of these metrics (Fig. 4A, B, C, D). This included Yellow-billed Cuckoo, Eastern Wood-pewee, Tufted Titmouse, White-breasted Nuthatch, Blue Grosbeak, and Indigo Bunting. Many of these forest species were generally ubiquitous, with an expected ψ >50% at a wide range of sites. Yellow-billed Cuckoo and Tufted Titmouse are especially notable in this way. Tufted Titmouse is generally considered a forest species (Grubb and Pravasudov 1994) and occupied much more open habitat in my study than expected. White-breasted Nuthatch is also considered a forest species (Grubb and Pravasudov 2008), and exhibited ψ trends in accordance with what I would expect. Eastern Wood-Pewee has been found to use both woodland and forest habitats (McCarty 1996). I found increasing ψ of this species as canopy cover increased, similar to results of recent research (Kendrick et al. 2013). Yellow-billed Cuckoos and Blue Grosbeaks are generally considered open woodland, edge and clearing-associated species (Hughes 1999, Lowther and Ingold 2011). The interspersion of forest and woodland habitat on my study site might have afforded these two species widespread acceptable habitat. High expected ψ in all but the most open savannas suggest these species are habitat generalists in the Cross Timbers. Indigo Bunting increased in ψ as tree density increased, an opposite trend to what was described by Brawn (2006). I expect this is partially a reflection of the habitat heterogeneity of my study area since this species often inhabits diverse successional growth and is usually absent from large blocks of closed canopy forest (Payne 2006). The apparent preference for higher tree density might be of lesser importance (lower β) compared to the species' preference for higher shrub density (see below).

Woodland species.—I considered species that had a quadratic relationship between ψ and tree variables (with ψ peaking at intermediate levels of tree density, canopy cover, etc.) to be woodland species (Fig. 4B, C). This includes Eastern Wood-Pewee, Carolina Wren, and Blue Grosbeak. Occupancy of Eastern Wood-pewee showed different habitat relationships at different spatial scales. Recall that their ψ increased with increasing canopy cover at the 100-m scale, but at the 50-m scale they had highest ψ at an intermediate canopy cover. I expect this reflects a preference for higher canopy coverages at a larger spatial scale and selection of forest clearings or edge-like habitat at a smaller spatial scale. Other studies have found Eastern Wood-Pewees to be more common in areas of intermediate forest cover (McCarty 1996, Grundel and Pavlovic 2007*b*). Blue Grosbeak had a quadratic ψ relationship with tree density, indicating woodland preferences over a wide range of tree densities. This, taken in conjunction with the other plausible models for this species, supports that Blue Grosbeaks are a generalist in the heterogeneous forests and woodlands of the Cross Timbers. Carolina Wren, commonly considered a forest generalist species (Haggerty and Morton 1995), occurred in a wide range of intermediate tree densities, only having below 50% ψ at the highest tree densities (Fig. 4C). This relationship leads me to consider this species to be a generalist in the Cross Timbers as well, even occupying relatively open savanna sites.

Savanna species.—Northern Bobwhite, Bewick's Wren, Northern Mockingbird, Field Sparrow, Dickcissel, and Orchard Oriole all decreased in expected ψ as tree cover and density increased and could thus be considered savanna species (Fig. 4A, B, C). Northern Bobwhite had by far the highest expected ψ (for this species) in open savanna habitat, and exhibited this relationship in all 5 of its most plausible ψ models. Northern Bobwhite prefer a wide range of early successional habitats across the Midwest and southern U.S. and frequently used hedgerows and agricultural fields prior to modern agricultural intensification and mechanization (Brennan 1999). I expect Northern Bobwhite made extensive use of former oak savanna habitat and simply moved to alternative habitats as westward settlement and land conversion advanced. In Illinois, Brawn (2006) found Northern Bobwhites only in restored savanna, not closed canopy forest. Both Northern Mockingbird and Field Sparrow had high ψ in savanna habitats but declined sharply with increase in canopy cover. This relationship is expected for Northern Mockingbird, a bird of open and edge habitats (Farnsworth et al. 2011). Field Sparrow has also been found by others to have highest densities in restored savanna (Davis et al. 2000, Au et al. 2008) or areas of low tree density (Grundel and Pavlovic 2007*b*). Dickcissel, a grassland obligate species (Temple 2002), made extensive use of the open savanna habitat, but quickly decreased in ψ as tree density increased. Oak savanna restoration should benefit grassland birds, such as the Dickcissel, that are intolerant of even moderate tree densities and are of conservation concern (Vickery and Herkert 2001). Several other grassland species were detected within savanna point count circles (albeit in numbers too low for occupancy modeling), including Grasshopper Sparrow, Henslow's Sparrow, and Eastern Meadowlark. Their presence within savanna habitat suggests they might at least tolerate close proximity of open savanna habitat and possibly use it to some limited extent, although I was not able to assess this with my data. Conversely, it is possible that the addition of a savanna edge within a grassland system could have negative edge effects on breeding grassland birds (Johnson and Temple 1990, Winter et al. 2000, Jensen and Fink 2004). Orchard Oriole had high ψ in savanna habitat, but was essentially absent from areas of higher tree density. Orchard Orioles have been generally described as preferring open park-like woodlands (Scharf and Kren 2010), resembling oak savanna. Bewick's Wren declined in ψ with increasing canopy cover. This is generally a species of open and riparian areas with mixed thick vegetation (Kennedy and White 2013). The savanna-forest habitat mosaic in the Cross Timbers appears to align with their need for habitat hetergeneity, reflected in a relatively high ψ (>50%) across a wide range of what could be considered savanna and open woodland habitat.

Shrub relationships.—Eastern Wood-Pewee and Indigo Bunting both had a positive relationship with shrub density (Fig. 4E). For Indigo Bunting shrub density is likely the dominant variable in determining ψ, which is supported by other research (Payne 2006). Eastern Wood-Pewee increased in ψ as shrub density increased, contrary to previous observations (McCarty 1996). This may be due to the composition of the shrub layer, composed primarily of low growing (<1.5m high) species (i.e., *Rubus* spp. and *Symphoricarpos orbiculatus*), which are unlikely to interfere with aerial foraging. Lark Sparrow was the only species to have a negative relationship with shrub density, decreasing in ψ rapidly as shrubs/m^2 increased. Au et al. (2008) found Lark Sparrows most common in savannas and associated with high percent of bare ground. I expect the negative relationship between Lark Sparrow ψ and shrubs/m^2 is driven by a preference for open ground habitat in the Cross Timbers. Tufted Titmouse had a quadratic relationship with shrub density, with peak occupancy at low and high shrub levels but reaching a low value at intermediate levels. The basis for this relationship is unclear.

Generalist species.— Mourning Dove, Red-bellied Woodpecker, Downy Woodpecker, Great Crested Flycatcher, Eastern Kingbird, Blue Jay, Carolina Chickadee, Blue-gray Gnatcatcher, Eastern Bluebird, Brown Thrasher, Summer Tanager, Northern Cardinal, and Brown-headed Cowbird all had either constant occupancy or weak relationships with habitat variables. These species were expected to be present relatively uniformly across my study site. Three other species that had positive or quadratic relationships with forest variables are also considered generalists: Yellow-billed Cuckoo, Tufted Titmouse, and Carolina Wren. All of these species, while having strong occupancy predictors, had generally high (near 100%) expected occupancies at nearly every site within my study (Fig. 4B, C, D). Brawn (2006) also found several of these species to be generalists in Illinois forest-savanna systems. Davis et al. (2000) also found Blue Jays to be generalists in Minnesota. Contrary to my results, several other species I found to be generalists were more associated with restored savanna habitat in Illinois (Brawn 2006), including Mourning Dove, Great Crested Flycatcher, Brown Thrasher, and

Summer Tanager. However, Davis et al. (2000) also found Brown Thrasher, Brown-headed Cowbird, and Eastern Bluebird to increase as savanna restoration advanced and Great Crested Flycatcher decreased with savanna restoration. Such conflicting results imply that habitat associations may be geographically variable or that such species are habitat generalists but with relatively weak or mutable habitat associations.

Of special note is the consistent presence of Brown-headed Cowbird on my site. I found no distinct habitat associations for this nest parasite and would expect relatively homogeneous nest parasitism rates across the habitat gradient, although I was not able to evaluate this from my nest data. I found no cases of parasitism on the species I used for modeling DSR. Most of the species I monitored are rejecters or otherwise rarely parasitized by Brown-headed Cowbirds (Rothstein 1975, Otis et al 2008, Farnsworth et al. 2011). Yellow-billed Cuckoos are apparently an acceptor species and are occasionally parasitized by cowbirds (Hughes 1999), but it is unlikely nest parasitism by cowbirds would be successful due to the Yellow-billed Cuckoo’s short nestling period (Hughes 1999). Similar to my expectations, Brawn (2006) found Brown-headed Cowbird abundance and parasitism to be uniform between restored savannas and forest habitats.

Nest Survival

Among all vegetative variables I only found shrub density to be a strong predictor of DSR, this being the case for Brown Thrasher and Northern Mockingbird. Nest stage and date of the nesting season were important predictors as well, the former being a strong predictor of DSR for all species monitored. Mourning Dove was the only species whose DSR was negatively related to tree canopy cover, but the relationship was weak.

The lack of strong effects of arboreal habitat structure found in my study contrasts with observations of other nesting studies in savanna-forest systems which have found higher nest success in savanna habitat (Brawn 2006) or in landscapes (10-km radius) with lower tree cover (Kendrick et al. 2013). Brawn (2006) found higher nest success for 6 of 13 species studied in restored savanna compared to closed-canopy forest. My study system differs greatly from Brawn's in that the landscape matrix in my study consisted of native tallgrass prairie versus the fragmented agriculture and forest landscapes in Illinois. Landscape context has been shown to affect nest predator communities and nest predation rates (Donovan et al. 1997).

Higher nest survival at higher shrub densities for Brown Thrasher and Northern Mockingbird is not unexpected as both of these species commonly nest in shrubs. This pattern might be partially attributed to increased cover immediately surrounding the nest (Martin and Roper 1988, Martin 1993, Frey et al. 2008), although I did not measure nest concealment. 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 with shrub density could indicate that Brown Thrasher and Northern Mockingbird nest site selection and nesting behaviors are adapted to a "scrub savanna" versus an "open savanna" (Nuzzo 1986).

Reaching the nestling stage increased DSR for all species. Others have found the opposite trend, lower DSR during the nestling stage (Mitchell et al. 1996, Liebezeit and George 2002, Conner et al. 2010), possibly as a result of increasing parental activity (Skutch 1949). However, Martin et al. (2000) demonstrated that nest predation rates can be higher during the incubation stage due to nest failure at nest sites with high predation threat, while sites with lower nest predation allow nest persistence to fledging. I found many nests failed quickly in the incubation stage, presumably discovered by predators soon after incubation was initiated. For Brown Thrasher and Northern Mockingbird increased nest survival in the nestling stage might also be attributed to noticeably increased parental aggression once the young hatched (Cavitt and Haas 2000, Farnsworth et al. 2011, N. S. Holoubek, Emporia State University, personal observation). Peak et al. (2004) also found higher nest success during nestling stage for another mimid, the Gray Catbird. Higher DSR in the nestling stage has been observed for Mourning Dove (Otis et al. 2008). This species also feigns injury if flushed from the nest, which appears to increase in frequency when nestlings are present (Otis et al. 2008, N. S. Holoubek, personal observation).

Daily nest survival for Mourning Dove and Northern Mockingbird increased with date of the nesting season. This trend has been found by others (Best 1978) and could be due to changes in nest predator behavior, which I did not evaluate. Mourning Dove nest period survival was notably low, around 11-13%. Other studies report nest period survival greater than 35% (Otis et al. 2008), but my 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. I was 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 but with punctured (not consumed) eggs. This was the only species in which I found this to occur. Yellow-billed Cuckoos also had the highest period survival of all my species monitored (57%), which may be partially due to an extremely short nesting period (17.5 days from start of incubation to fledging) compared to other species. Yellow-billed Cuckoo period survival was greater than other studies, which ranged from 18% (Twedt et al. 2001) to 22% (Twedt et al. 2010).

My study site was under drought conditions during the first year of my study. While I only found little seasonal effect on occupancy (only for one species, Summer Tanager), it might have influenced my nest monitoring data to some unknown extent. Nest predation by snakes and birds has been shown to increase with maximum daily temperature (Cox et al. 2013) and the mean temperature on my site was higher in 2012 (25.3° C) than in 2013 (22.2° C).

MANAGEMENT IMPLICATIONS

I found more bird species to be associated with oak savanna, classified as <25% canopy cover (Faber-Langendoen 1995) than with woodland or forest habitats, contain the most species of conservation concern in Midwestern states (Table 3), and be composed of species with comparatively narrow habitat preferences. My occupancy models also provide specific habitat measurements that can be used to guide management objectives for species of concern, as well as predict changes in the avian community with savanna restoration. Since I found no strong relationships between nest survival and tree variables (canopy cover, tree density, etc.), I expect savanna and forest habitats are equally valuable nesting habitats for the species I monitored in the Cross Timbers region. Lack of observable habitat patterns in nest survival, in contrast to other savanna research in the Midwest, might be attributable to the Cross Timbers unique landscape (largely a tallgrass prairie matrix) or the particular species investigated for the nesting study. Positive relationships between nest survival and shrub density for 2 species highlights the importance to some species of maintaining a habitat mosaic of open and shrub savanna on the landscape by carefully managing fire and other forms of brush control.

Because of the conservation concern for many disturbance associated birds (Brawn et al. 2001), it is imperative to identify factors that may benefit habitat use and nesting success by these species. The loss of tens of millions of hectares of oak savanna across the Midwest (Nuzzo 1986) undoubtedly reduced breeding habitat for birds, forcing some species into alternative habitats. Information such as mine on habitat associations and nesting success of birds across the oak savanna-woodland-forest gradient is vital for effective restoration of oak savanna to benefit conservation.

LITERATURE CITED

Abrams, M. D. 1992. Fire and the development of oak forests. Bioscience. 42:346-353.

Apfelbaum, S. I., and A. Haney. 1987. Management of degraded oak savanna remnants in the upper Midwest. Applied Ecological Services, Brodhead, WI.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management. 74:1175-1178.

Au, L., D. E. Anderson, 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. Natural Areas Journal. 28:330-341.

Baicich, P. J., and C. J. O. Harrison. 2005. Nests, eggs, and nestlings of North American birds. Second edition. Princeton University Press, Princeton, New Jersey, USA.

Bernardo, D. J., D. M. Engle, R. L. Lochmiller, and F. T. McCollum. 1992. Optimal vegetation management under multiple-use objectives in the Cross Timbers. Journal of Range Management. 45:462-469.

Best, L. B. 1978. Field sparrow reproductive success and nesting ecology. Auk. 95:9-22.

Bock, C. E., and W. M. Block. 2005. Fire and birds in the southwestern United States. Studies in Avian Biology. 30:14-32.

Brawn, J. D., S. K. Robinson, and F. R. Thompson III. 2001. The role of disturbance in the ecology and conservation of birds. Annual Review of Ecology and Systematics. 32:251-276.

Brawn, J. D. 2006. Effects of restoring oak savannahs on bird communities and populations. Conservation Biology. 20:460-469.

Brennan, L. A. 1999. Northern Bobwhite (*Colinus virginianus*). *In* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://0-bna.birds.cornell.edu.www.whitelib.emporia.edu/bna/>. Accessed 22 November 2013.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multinomial Inference: A Practical Information-Theoretic Approach. Second Edition. Springer, New York, New York, USA.

Cavitt, John F. and Carola A. Haas. 2000. Brown Thrasher (*Toxostoma rufum*), The Birds of North America Online. *In* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://0-bna.birds.cornell.edu.www.whitelib.emporia.edu/bna/>. Accessed 22 November 2013.

Conner, L. M., J. C. Rutledge, and L. L. Smith. 2010. Effects of mesopredators on nest survival of shrub-nesting songbirds. Journal of Wildlife Management. 74:73-80.

Cox, A. W., F. R. Thompson III, and J. L. Reidy. 2013. The effects of temperature on nest predation by mammals, birds, and snakes. Auk 130:784-790.

Davis, M. A., D. W. Peterson, P. B. Reich, M. Crozier, T. Querty, E. Mitchell, J. Huntington, and P. Bazakas. 2000. Restoring savanna using fire: Impact on the breeding bird community. Restoration Ecology. 8:30-40.

Donovan, T. M., F. R. Thompson, J. Faaborg, J. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology. 9:1380-1395.

Donovan, T. M., P. W. Jones, E. M. Annand, F.R. Thompson, III .1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology 78:2064-2075.

Dugger, K. M., F. Wagner, R. G. Anthony, and G. S. Olson. 2005. The relationship between habitat characteristics and demographic performance of northern spotted owls in southern Oregon. The Condor. 107:863-878.

Environmental Protection Agency [EPA]. 2013. Western Ecology Division. Primary distinguishing characteristics of level III ecoregions of the continental United States. <http://www.epa.gov/wed/pages/ecoregions/level_iii_iv.htm>. Accessed 14 Nov 2013.

Faber-Langendoen, D. 1995. Appendix A: The Nature Conservancy's natural community classification and its application to Midwest oak savannas and woodlands. *In* M. K. Leach, and L. Ross, editors. Midwest Oak Ecosystems Recovery Plan: A Call to Action. <http://www.epa.gov/glnpo/ecopage/upland/oak/oak95/call.htm> . Accessed 03 Dec 2013.

Farnsworth, G., G. A. Londono, J. U. Martin, K. C. Derrickson, and R. Breitwisch. 2011. Northern Mockingbird (*Mimus polyglottos*). *In* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://0-bna.birds.cornell.edu.www.whitelib.emporia.edu/bna/>. Accessed 22 November 2013.

Franklin, A. B., D. R. Anderson, R. J. Gutierrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs. 70:539-590.

Frey, C. M., W. E. Jensen, and K. A. With. 2008. Topographic patterns of nest placement and habitat quality for grassland birds in the Flint Hills. American Midland Naturalist 160:220-234.

Grubb, T. C. Jr., and V. V. Pravasudov. 1994. Tufted Titmouse (*Baeolophus bicolor*). *In* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://0-bna.birds.cornell.edu.www.whitelib.emporia.edu/bna/>. Accessed 22 November 2013.

Grubb, T. C. Jr., and V. V. Pravasudov. 2008. White-breasted Nuthatch (*Sitta carolinensis*). *In* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://0-bna.birds.cornell.edu.www.whitelib.emporia.edu/bna/>. Accessed 22 November 2013.

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

Grundel, R., and N. B. Pavlovic. 2007*b*. Response of bird species densities to habitat structure and fire history along a Midwestern open-forest gradient. Condor. 109:734-749.

Haggerty, T. M. and E. S. Morton. 1995. Carolina Wren (*Thryothorus ludovicianus*). *In* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://0-bna.birds.cornell.edu.www.whitelib.emporia.edu/bna/>. Accessed 22 November 2013.

Hartung, S. C., and J. D. Brawn. 2005. Effects of savanna restoration on the foraging ecology of insectivorous songbirds. Condor. 107:879-888.

Henderson, R. 1995. Oak savanna communities. Wisconsin's Biodiversity as a Management Issue. Wisconsin Department of Natural Resources. p. 88-96.

Herkert, J. R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. Ecological Applications. 4:461-471.

Huff, M. H., N. E. Seavy, J. D. Alexander, and C. J. Ralph. 2005. Fire and birds in maritime Pacific Northwest. Studies in Avian Biology. 30:46-62.

Hughes, J. M. 1999. Yellow-billed Cuckoo (*Coccyzus americanus*). *In* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://0-bna.birds.cornell.edu.www.whitelib.emporia.edu/bna/>. Accessed 22 November 2013.

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. Wildlife Society Bulletin. 29:440-455.

Jensen, W. E. and E. J. Fink. 2004. Variation in edge effects on nesting Dickcissel (*Spiza americana*) in relation to edge type of remnant tallgrass prairie in Kansas. American Midland Naturalist. 151:192-199.

Johnson, R. G. and S. A. Temple. 1990. Nest predation and brood parasitism of tallgrass prairie birds. Journal of Wildlife Management 54:106–111.

Jones, B., S. F. Fox, D. M. Leslie, Jr., D. M. Engle, and R. L. Lochmiller. 2000. Herpetofaunal responses to brush management with herbicide and fire. Journal of Range Management. 53:154-158.

Kendrick, S. W., F. R. Thompson III, and J. L. Reidy. 2013. Eastern Wood-Pewee (*Contopus virens*) breeding demography across a gradient of savanna, woodland, and forest in the Missouri Ozarks. Auk. 130:355-363.

Kennedy, E. D. and D. W. White. 2013. Bewick's Wren (*Thryomanes bewickii*). *In* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://0-bna.birds.cornell.edu.www.whitelib.emporia.edu/bna/>. Accessed 22 November 2013.

Komdeur, J., and R. K. H. Kats. 1999. Predation risk affects trade-off between nest guarding and foraging in Seychelles warblers. Behavioral Ecology 10:648-658.

Liebezeit, J. R., and T. L. George. 2002. Nest predators, nest-site selection, and nesting success of the dusky flycatcher in a managed ponderosa pine forest. Condor. 104:507-517.

Lochmiller, R. L., J. F. Boggs, S. T. McMurry, D. M. Leslie, Jr., and D. M. Engle. 1991. Response of cottontail rabbit populations to herbicide and fire applications on cross timbers rangeland. Journal of Range Management. 44:150-155.

Long, A. M., W. E. Jensen, and R. S. Matlock. 2012. Effects of prescribed burning on avian nest survival in the southern great plains. Journal of Wildlife Management. 76:899-906.

Lowther, P. E. and J. L. Ingold. 2011. Blue Grosbeak (*Passerina caerulea*). *In* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://0-

bna.birds.cornell.edu.www.whitelib.emporia.edu/bna/>. Accessed 22 November 2013.

Mackenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology. 84:2200-2207.

Martin, T. E. 1993. Nest predation and nest sites. BioScience 43:523-532.

Martin, T. E., and J. R. Roper. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90:51-57.

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, Montana.

Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. Proceedings of the Royal Society of London B 267:2287-2293.

Mazerolle, M. J. 2006. Improving data analysis in herpetology: Using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. Amphibia-Reptilia. 27:169-180.

McCarty, J. P. 1996. Eastern Wood-Pewee (*Contopus virens*). *In* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://0-bna.birds.cornell.edu.www.whitelib.emporia.edu/bna/>. Accessed 22 November 2013.

Mitchell, M. C., L. B. Best, and J. P. Gionfriddo. 1996. Avian nest site selection and nesting success in two Florida citrus groves. Wilson Bulletin. 108:573-583.

National Oceanic and Atmospheric Administration [NOAA]. 2014. National Climatic Data Center. < http://www.ncdc.noaa.gov/>. Accessed 12 Feb. 2014.

Noss, R. F., E. T. Laroe III, and J. M. Scott. 1995. Endangered ecosystems of the United States. United States Geological Survey [USGS] Publishing Utilities for the Biological Sciences. http://biology.usgs.gov/pubs/ecosys.htm. Accessed 27 September 2011.

Nuzzo, V.A. 1986. Extent and status of Midwest oak savanna: Presettlement and 1985. Natural Areas Journal. 6:6-36.

Otis, D. L, J. H. Schulz, D. Miller, R. E. Mirarchi, and T. S. Baskett. 2008. Mourning dove (*Zenaida macroura*). *In* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://0-bna.birds.cornell.edu.www.whitelib.emporia.edu/bna/>. Accessed 22 November 2013.

Payne, R. B. 2006. Indigo Bunting (*Passerina cyanea*). *In* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://0-bna.birds.cornell.edu.www.whitelib.emporia.edu/bna/>. Accessed 22 November 2013.

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.

Penfound, W. T. 1962. The savanna concept in Oklahoma. Ecology. 43:774-775.

Peterson, D. W., and P. B. Reich. 2001. Prescribed fire in oak savanna: Fire frequency effects on stand structure and dynamics. Ecological Applications. 11:914-927.

Powell, L. A. 2007. Approximating variance of demographic parameters using the delta method: A reference for avian biologists. The Condor. 109:949-954.

Rothstein, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor. 77:250-271.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2011. North American breeding bird survey, results and analysis 1966 - 2009. USGS Patuxent Wildlife Research Center, Laurel, MD.

Scharf, W. C., and J. Kren. 2010. Orchard Oriole (*Icterus spurius*). *In* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://0-bna.birds.cornell.edu.www.whitelib.emporia.edu/bna/>. Accessed 22 November 2013.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk. 12:526-540.

Shultz, C. A., D. M. Leslie, Jr., R. L. Lochmiller, and D. M. Engle. 1992. Herbicide effects on CrossTimbers breeding birds. Journal of Range Management. 45:407-411.

Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430-455.

Stotts, C., M. W. Palmer, and K. Kindscher. 2007. The need for savannah restoration in the cross timbers. Oklahoma Native Plant Record. 7:78-90.

Strausberger, B. M., and M. V. Ashley. 1997. Community-wide patterns of parasitism of a host "generalist" brood-parasitic cowbird. Oecologia. 112:254-262.

Suarez, A. V., K. S. Pfennig, and S. K. Robinson. 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. Conservation Biology. 11:928-935.

Temple, S. A. 2002. Dickcissel (*Spiza americana*). *In* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://0-bna.birds.cornell.edu.www.whitelib.emporia.edu/bna/>. Accessed 22 November 2013.

Tester, J. R. 1989. Effects of fire frequency on oak savanna in east-central Minnesota. Bulletin of the Torrey Botanical Club. 116:134-144.

Twedt, D. J., R. R. Wilson, J. L. Henne-Kerr, and R. B. Hamilton. 2001. Nest survival of forest birds in the Mississippi alluvial valley. Journal of Wildlife Management. 65:450-460.

Twedt, D. J., S. G. Somershoe, K. R. Hazler, and R. J. Cooper. 2010. Landscape and vegetation effects on avian reproduction on bottomland forest restorations. Journal of Wildlife Management. 74:423-436.

Vickery, P. D., and J. R. Herkert. 2001. Recent advances in grassland bird research: Where do we go from here? Auk 118:11-15.

Winter, M., D. H. Johnson, J. Faaborg. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. Condor. 102:256-266.

Table 1. Candidate sets of global models for bird species occupancy and nest survival using three covariate structures (linear, quadratic, and pseudothreshold). Each set contains only non-correlated variables. Model averaging could occur only within, not between model sets. Constant (i.e., intercept-only) models were included in every set. All covariates data were from Elk County, Kansas, 2012-2013.

Occupancy models
Linear structure
Canopy/100-m[a]
Canopy/50-m[b] + shrubs/m^2[c]
Trees/ha[d]
PC1[e]
Quadratic structure
Canopy/100-m[a] + (canopy/100-m[a])^2

Canopy/50-m^{b} + (canopy/50-m^{b})^{2} + shrubs/m$^{2\ c}$ + (shrubs/m$^{2\ c}$)^{2}

Trees/ha^{d} +(trees/ha^{d})^{2}

Pseudothreshold structure

ln(canopy/100-m^{a})

ln(canopy/50-m^{b}) + *ln*(shrubs/m$^{2\ c}$)

ln(trees/ha^{d}) + *ln*(shrubs/m$^{2\ c}$)

Nest survival models

Linear

Canopy/100-m^{a}

Canopy/50-m^{b} + shrubs/m$^{2\ c}$ + nest stage^{g}

Trees/ha^{d} + shrubs/m$^{2\ c}$ + nest stage^{g}

PC1[e] + shrubs/m^2[c] + nest stage[g]

Shrubs/m^2[c] + Julian date[h]

% forb[f]

Quadratic

Canopy/100-m[a] + (canopy/100-m[a])^2

Canopy/50-m[b] + (canopy/50-m[b])^2 + shrubs/m^2[c] + (shrubs/m^2[c])^2

Trees/ha[d] + (trees/ha[d])^2 + shrubs/m^2[c] + (shrubs/m^2[c])^2 + nest stage[g]

Shrubs/m^2[c] + (shrubs/m^2[c])^2 + Julian date[h]

% forb[f] + (% forb[f])^2

Pseudothreshold

ln(canopy/100-m[a])

ln(canopy/50-m[b]) + nest stage[g]

ln(canopy/50-m[b]) + Julian date[h]

ln(trees/ha[d]) + nest stage[g]

ln(shrubs/m^2 [c]) + Julian date[h]

ln(% forb[f])

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[a] GIS estimated canopy cover within a 100-m radius.

[b] Densiometer estimated canopy cover within a 50-m radius.

[c] Number of shrub and small size class tree stems /m^2. See text for size classes.

[d] Number of medium or greater size class trees/ha. See text for size classes.

[e] Principal component of canopy/50-m and trees/ha.

[f] Percent of ground cover composed of herbaceous broadleaf species.

[g] Categorical variable indicating incubation stage (0) or nestling stage (1).

[h] Date, using the Julian calendar, of each nest check.

Table 2. Mean (± SE) and range of habitat measurements taken at 50-m radius point count circles, and proximate to nests (averaged across 4 points per point count or nest), by species, in Elk County, Kansas, 2012-2013. See Table 1 for covariate definitions.

Parameter	Point count circles	Mourning Dove	Yellow-billed Cuckoo	Brown Thrasher	Northern Mockingbird
Canopy/100-m					
Mean (±SE)	44.2 (27.4)	26.4 (18.7)	32.6 (19.5)	20.1 (15.4)	13.2 (10.7)
min., max.	2.6, 90.4	1.3, 78.8	2.3, 7.4	0.4, 64.5	1.7, 38.2
Canopy/50-m					
Mean (±SE)	37.0 (28.5)	35.7 (19.7)	40.0 (22.7)	31.8 (16.8)	20.6 (8.9)
min., max.	0.0, 96.8	0.0, 91.8	1.6, 89.5	0.0, 74.5	7.3, 39.0
Trees/ha					
Mean (±SE)	261.8 (190.3)	149.3 (143.8)	201.2 (137.1)	118.6 (105.1)	48.8 (35.2)
min., max.	0.0, 716.1	6.0, 661.9	6.0, 529.5	0.0, 505.5	6.0, 174.5
Snags/ha					
Mean (±SE)	15.2 (16.8)	7.5 (9.6)	8.0 (14.5)	4.1 (9.0)	2.1 (5.3)

min., max.	0.0, 84.3	0.0, 54.2	0, 90.3	0.0, 36.1	0.0, 30.1
Shrubs/m^2					
Mean (±SE)	2.0 (2.0)	1.8 (8.4)	1.6 (1.7)	1.3 (2.1)	0.7 (0.9)
min., max.	0.0, 8.0	0.1, 85.5	0.1, 7.4	0.1, 14.2	0.03, 6.1
% Forb					
Mean (±SE)	26.0 (12.7)	25.0 (11.5)	26.3 (10.7)	24.9 (10.8)	27.4 (10.3)
min., max.	2.5, 53.1	7.8, 53.1	3.4, 50.0	6.25, 49.4	5.9, 58.1
% Grass					
Mean (±SE)	42.9 (18.7)	39.0 (17.7)	32.9 (16.5)	41.0 (17.3)	45.8 (15.6)
min., max.	7.8, 89.4	2.5, 85.6	0.3, 65.0	9.4, 86.9	15.9, 70.0
% Low shrub					
Mean (±SE)	18.6 (12.7)	13.2 (6.5)	15.1 (8.8)	11.5 (6.8)	7.9 (3.7)
min., max.	1.3, 63.8	2.5, 33.1	2.5, 36.9	0.9, 39.4	0.0, 16.6

Table 3. All bird species detected during point counts in Elk County, Kansas, 2012- 2013.

Species (scientific name)	Alpha code	SC[a]
Northern Bobwhite (*Colinus viriginianus*) [b]	NOBO	WI, TX
Ring-necked Pheasant (*Phasianus colchicus*)	RNEP	
Wild Turkey (*Meleagris gallopavo*)	WITU	
Great Blue Heron (*Ardea herodias*)	GBHE	
Great Egret (*Ardea alba*)	GREG	
Turkey Vulture (*Cathartes aura*)	TUVU	
Cooper's Hawk (*Accipiter cooperii*)	COHA	
Red-tailed Hawk (*Buteo jamaicensis*)	RTHA	
Mourning Dove (*Zenaida macroura*) [b]	MODO	
Yellow-billed Cuckoo (*Coccyzus americanus*) [b]	YBCU	
Common Nighthawk (*Chordeiles minor*)	CONI	
Chimney Swift (*Chaetura pelagica*)	CHSW	
Ruby-throated Hummingbird (*Archilochus colubris*)	RTHU	
Red-bellied Woodpecker (*Melanerpes carolinus*) [b]	RBWO	
Downy Woodpecker (*Picoides pubescens*) [b]	DOWO	

Hairy Woodpecker (*Picoides villosus*)	HAWO	
Northern Flicker (*Colaptes auratus*)	NOFL	
Pileated Woodpecker (*Dryocopus pileatus*)	PIWO	
Eastern Wood-Pewee (*Contopus virens*) [b]	EAWP	
Acadian Flycatcher (*Empidonax virescens*)	ACFL	
Least Flycatcher (*Empidonax minimus*)	LEFL	
Great Crested Flycatcher (*Myiarchis crinitus*) [b]	GCFL	
Eastern Kingbird (*Tyrannus tyrannus*) [b]	EAKI	
Scissor-tailed Flycatcher (*Tyrannus forficatus*)	STFL	
Bell’s Vireo (*Vireo bellii*)	BEVI	
Red-eyed Vireo (*Vireo olivaceus*)	REVI	
Blue Jay (*Cyanocitta cristata*) [b]	BLJA	
American Crow (*Corvus brachyrhynchos*)	AMCR	
Barn Swallow (*Hirundo rustica*)	BARS	
Carolina Chickadee (*Poecile carolinensis*) [b]	CACH	TX
Tufted Titmouse (*Baeolophus bicolor*) [b]	TUTI	
White-breasted Nuthatch (*Sitta carolinensis*) [b]	WBNU	

Carolina Wren (*Thryothorus ludovicianus*)[b]	CARW	
Bewick's Wren (*Thryomanes bewickii*)[b]	BEWR	IL[c], TX
Blue-gray Gnatcatcher (*Polioptila caerulea*)[b]	BGGN	
Eastern Bluebird (*Sialia sialis*)[b]	EABL	
Wood Thrush (*Hylocichla mustelina*)	WOTH	
Gray Catbird (*Dumetella carolinensis*)	GRCA	
Brown Thrasher (*Toxostoma rufum*)[b]	BRTH	
Northern Mockingbird (*Mimus polyglottos*)[b]	NOMO	
Cedar Waxwing (*Bombycilla cedrorum*)	CEDW	
Worm-eating Warbler (*Helmitheros vermivorum*)	WEWA	
Louisiana Waterthrush (*Parkesia motacilla*)	LOWA	
Black-and-white Warbler (*Mnilotilta varia*)	BAWW	
Common Yellowthroat (*Geothlypis trichas*)	COYE	
Northern Parula (*Setophaga americana*)	NOPA	
Yellow Warbler (*Setophaga petechia*)	YEWA	
Yellow-throated Warbler (*Setophaga dominica*)	YTWA	
Yellow-breasted Chat (*Icteria virens*)	YBCH	

Eastern Towhee (*Pipilo erythrophthalmus*)	EATO	
Field Sparrow (*Spizella pusilla*) [b]	FISP	TX
Lark Sparrow (*Chondestes grammacus*) [b]	LASP	WI, MN, MI, TX
Grasshopper Sparrow (*Ammodramus savannarum*)	GRSP	
Henslow’s Sparrow (*Ammodramus henslowii*)	HESP	
Summer Tanager (*Piranga rubra*) [b]	SUTA	TX
Northern Cardinal (*Cardinalis cardinalis*) [b]	NOCA	
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	RBGR	
Blue Grosbeak (*Passerina caerulea*) [b]	BLGR	
Indigo Bunting (*Passerina cyanea*) [b]	INBU	
Painted Bunting (*Passerina ciris*)	PABU	
Dickcissel (*Spiza americana*) [b]	DICK	MI, TX
Red-winged Blackbird (*Agelaius phoeniceus*)	RWBL	
Eastern Meadowlark (*Sturnella magna*)	EAME	
Brown-headed Cowbird (*Molothrus ater*) [b]	BHCO	
Orchard Oriole (*Icterus spurius*) [b]	OROR	TX
Baltimore Oriole (*Icterus glabula*)	BAOR	

American Goldfinch (*Spinus tristis*)	AMGO

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[a] Midwestern states that rank species as of special conservation concern, but not threatened or endangered (or similar designation, only assessed for species for which occupancy was modeled).

[b] Species detected at ≥5 of 60 points in both 2012 and 2013, for which occupancy was modeled.

[c] Listed as endangered by the indicated state.

Table 4. Top detection predictor models (lowest Akaike's Information Criterion (AIC) value, from 16 competing models) obtained using data from Elk County, Kansas, 2012 and 2013. AIC values and model weights (w_i) by species (indicated by 4-letter alpha code; see Table 3) are included. See Table 1 for covariate definitions.

Species	Top model	AIC	w_i
NOBO	Trees/ha	163.08	0.30
MODO	Constant	519.49	0.16
YBCU	Constant	317.80	0.14
RBWO	Wind	243.70	0.21
DOWO	Julian date	200.46	0.16
EAWP	Year	467.65	0.41
GCFL	Julian date	263.19	0.40
EAKI	Trees/ha + Julian date	165.06	0.47
BLJA	Trees/ha + Julian date	175.70	0.48
CACH	Shrubs/m^2	494.47	0.28
TUTI	Trees/ha + wind + Julian date	507.08	0.56
WBNU	Wind + Julian date	181.60	0.31
CARW	Shrubs/m^2 + wind	163.30	0.20
BEWR	% grass + wind + Julian date	241.82	0.63
BGGN	Trees/ha + wind + Julian date	461.06	0.69
EABL	Constant	299.06	0.19
BRTH	Trees/ha + Julian date	176.87	0.57

NOMO	Trees/ha + wind	194.67	0.50
FISP	Julian date	388.56	0.22
LASP	Trees/ha + wind	145.92	0.15
SUTA	Trees/ha + wind + Julian date	413.30	0.68
NOCA	% grass	457.03	0.35
BLGR	Trees/ha + wind + Julian date	232.05	0.14
INBU	Shrubs/m^2	427.80	0.58
DICK	Trees/ha	252.78	0.47
BHCO	Julian date	610.19	0.37
OROR	Year	256.65	0.22

Table 5. Most plausible (ΔAIC≤2) occupancy (ψ) models for bird species (indicated by 4-letter alpha code; see Table 3) in Elk County, Kansas, 2012 and 2013. See Table 1 for covariate definitions. Plausible models from different model sets (Table 1) for the same species are shaded in alternating white and gray.

Species	AIC[a]	w_i[b]	Covariate	Covariate structure	β (±SE)[c]
Northern Bobwhite	159.01	0.89	Canopy/100-m[d]	Pseudothreshold	-1.23 (0.52)
	159.02	0.88	Canopy/100-m[d]	Linear	-1.33 (0.57)
	159.78	0.84	Trees/ha[d]	Linear	-1.06 (0.44)
	160.76	0.70	Canopy/50-m[d]	Pseudothreshold	-0.92 (0.42)
	160.81	0.64	Canopy/50-m[d]	Linear	-1.15 (0.54)
Mourning Dove	519.41	N/A[f]	Constant	N/A[e]	2.06 (1.20)
Yellow-billed Cuckoo	312.49	0.94	PC[d]	Linear	26.43 (3.11)

Red-bellied Woodpecker	243.70	N/A[f]	Constant	N/A[e]	-0.11 (0.58)
Downy Woodpecker	199.93	0.48	Shrubs/m^2	Pseudothreshold	0.34 (0.51)
Eastern Wood-Pewee	447.08	0.99	Canopy/100-m[d]	Pseudothreshold	1.80 (0.57)
	448.30	0.77	Canopy/50-m[d]	Quadratic	4.35 (1.38)
		0.77	(Canopy/50-m)^2[d]	Quadratic	-3.16 (1.23)
		0.77	Shrubs/m^2[d]	Quadratic	0.93 (0.39)
Great-crested Flycatcher	263.19	N/A[f]	Constant	N/A[e]	0.37 (0.73)
Eastern Kingbird	164.77	0.51	Shrubs/m^2	Quadratic	3.40 (7.24)
		0.51	(Shrubs/m^2)^2	Quadratic	-3.63 (7.59)
Blue Jay	275.70	N/A[f]	Constant	N/A[e]	2.66 (>0.01)
Carolina Chickadee	493.34	0.65	Canopy/50-m	Pseudothreshold	0.92 (0.68)

		0.39	Shrubs/m^2	Pseudothreshold	0.28 (0.61)
	493.38	0.63	Canopy/100-m	Linear	4.01 (3.38)
	493.48	0.62	Canopy/100-m	Pseudothreshold	2.44 (2.45)
	493.80	0.50	Canopy/50-m	Linear	0.93 (0.72)
Tufted Titmouse	498.70	0.72	Canopy/50-m^d	Quadratic	2.10 (0.90)
		0.72	Shrubs/m^{2d}	Quadratic	-16.22 (9.59)
		0.72	(Shrubs/m^2)^{2d}	Quadratic	28.41 (16.50)
White-breasted Nuthatch	173.96	0.98	Canopy/100-m^d	Pseudothreshold	1.55 (0.70)
	174.43	0.97	Canopy/100-m^d	Linear	1.44 (0.68)
Carolina Wren	160.40	0.81	Trees/ha	Linear	5.28 (3.81)
	160.66	0.62	Canopy/50-m	Pseudothreshold	2.57 (2.64)

	160.80	0.78	Trees/ha	Pseudothreshold	2.24 (1.62)
	160.92	0.77	Trees/ha[d]	Quadratic	6.93 (<0.01)
		0.77	(Trees/ha)^{2}[d]	Quadratic	-6.26 (<0.01)
	161.21	0.66	Canopy/50-m	Linear	7.82 (7.99)
Bewick's Wren	237.09	0.89	Canopy/50-m	Linear	-8.17 (5.68)
	237.09	0.88	Canopy/50-m	Pseudothreshold	-28.09 (23.31)
	237.64	0.89	Canopy/100-m[d]	Linear	-2.35 (1.57)
	237.75	0.89	Canopy/100-m[d]	Pseudothreshold	-2.85 (1.83)
	239.04	0.80	Canopy/100-m	Quadratic	2.66 (6.12)
		0.80	(Canopy/100-m)^{2}	Quadratic	-4.11 (6.65)
Blue-gray Gnatcatcher	445.44	0.99	Canopy/100-m	Quadratic	1.58 (1.36)

		0.99	(Canopy/100-m)^2	Quadratic	-0.42 (1.33)
Eastern Bluebird	297.25	0.71	Shrubs/m^2	Pseudothreshold	-1.04 (1.04)
	297.81	0.65	Canopy/100-m	Quadratic	-40.77 (28.99)
		0.65	(Canopy/100-m)^2	Quadratic	55.24 (39.05)
Brown Thrasher	172.21	0.62	Shrubs/m^2	Quadratic	8.58 (6.61)
		0.62	(Shrubs/m^2)^2	Quadratic	-8.66 (7.41)
Northern Mockingbird	187.25	0.98	Canopy/100-m[d]	Linear	-2.68 (1.04)
	187.84	0.97	Canopy/100-m[d]	Pseudothreshold	-2.13 (0.89)
	188.42	0.96	Canopy/50-m[d]	Pseudothreshold	-1.98 (1.18)
Field Sparrow	373.14	0.99	Canopy/50-m[d]	Linear	-3.28 (1.45)
	373.53	0.99	Canopy/50-m[d]	Pseudothreshold	-9.42 (3.78)

Lark Sparrow	137.53	0.51	Canopy/50-m	Pseudothreshold	-0.43 (0.56)
		0.98	Shrubs/m^2[d]	Pseudothreshold	-1.36 (0.58)
	137.57	0.51	Trees/ha	Pseudothreshold	-0.49 (0.64)
		0.98	Shrubs/m^2	Pseudothreshold	-1.40 (0.57)
Summer Tanager	408.53	0.78	Canopy/50-m	Linear	1.31 (3.00)
Northern Cardinal	457.03	N/A[f]	Constant	N/A[e]	3.60 (4.03)
Blue Grosbeak	227.94	0.89	Trees/ha[d]	Quadratic	14.31 (6.06)
		0.89	(Trees/ha)^2[d]	Quadratic	-17.85 (7.62)
	228.77	0.84	Trees/ha[d]	Linear	11.58 (5.75)
	229.50	0.78	PC[d]	Linear	10.13 (4.77)
	229.85	0.75	Trees/ha	Pseudothreshold	1.92 (1.35)

Indigo Bunting	413.13	0.99	Trees/ha[d]	Pseudothreshold	0.84 (0.35)
		0.99	Shrubs/m^2[d]	Pseudothreshold	1.43 (0.46)
Dickcissel	239.25	0.99	Trees/ha	Quadratic	-2.04 (3.56)
		0.99	$(\text{Trees/ha})^2$	Quadratic	-3.10 (7.46)
	239.56	0.99	Trees/ha[d]	Pseudothreshold	-2.49 (0.61)
Brown-headed Cowbird	607.18	0.53	Shrubs/m^2	Quadratic	-51.76 (48.27)
		0.53	$(\text{Shrubs/m}^2)^2$	Quadratic	72.59 (67.74)
		0.36	Canopy/50-m	Quadratic	-78.93 (85.81)
		0.36	$(\text{Canopy/50-m})^2$	Quadratic	38.64 (42.03)
Orchard Oriole	228.00	0.99	Canopy/100-m	Quadratic	3.96 (3.78)
		0.99	$(\text{Canopy/100-m})^2$[d]	Quadratic	-13.59 (7.86)

	229.08	0.99	Canopy/100-m	Linear	-3.38 (1.27)

[a] Akaike’s Information Criterion (AIC) value for top model (lowest AIC) within set.

[b] Combined weight from top models containing covariate within model set.

[c] Model averaged covariate β and unconditional SE for given model set.

[d] Covariate strongly predicts occupancy (85% CI of β does not include 0).

[e] Top model in every set. All lower ranked models considered uninformative (Arnold 2010).

Table 6. Daily survival rate (DSR) models per species (indicated by 4-letter alpha code; see Table 3) monitored in Elk County, Kansas, 2012 and 2013. Average DSR (± SE), and average nest period survival (± SE) are given. Average DSR and period survival were calculated using mean levels of covariates. See Table 1 for covariate definitions.

Species	AIC[a]	w_i[b]	Covariate	Covariate Structure	β (±SE)[c]	DSR	Period Survival
Mourning Dove	311.82	0.69	Canopy/50-m	Pseudothreshold	-0.20 (0.22)	0.93 (0.05)	0.13 (0.22)
		0.69	Nestling stage[d]	Pseudothreshold	0.96 (0.30)		
	313.67	0.53	Canopy/50-m	Pseudothreshold	-0.14 (0.18)	0.93 (0.10)	0.11 (0.33)
		0.53	Julian date[d]	Pseudothreshold	0.02 (0.01)		
Yellow-billed Cuckoo	116.82	0.99	Nestling stage[d]	Linear	2.68 (0.74)	0.97 (0.02)	0.57 (0.24)
Brown Thrasher	177.65	0.75	Shrubs/m^2[d]	Quadratic	0.77 (0.34)	0.94 (0.03)	0.22 (0.20)
		0.75	(Shrubs/m^2)^2[d]	Quadratic	-0.05 (0.02)		
		0.75	Nestling stage[d]	Quadratic	0.93 (0.40)		
Northern Mockingbird	180.49	0.52	Shrubs/m^2	Linear	0.28 (0.36)	0.96 (0.03)	0.31 (0.22)
		0.52	Nestling stage[d]	Linear	0.92 (0.39)		

182.05	0.59	Shrubs/m^{2}[d]	Linear	0.72 (0.41)	0.95 (.10)	0.30 (0.81)
	0.59	Julian date	Linear	0.01 (0.01)		
182.45	0.55	Shrubs/m^{2}[d]	Pseudothreshold	0.89 (0.43)	0.95 (0.10)	0.28 (0.78)
	0.55	Julian date	Pseudothreshold	0.01 (0.01)		

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[a] Akaike's Information Criterion (AIC) value for top model within set.

[b] Combined weight of top models containing covariate within model set.

[c] Model averaged covariate β and unconditional SE for given model set.

[d] Covariate strongly predicts daily survival rate (85% CI of β does not include 0).

Figure 1. Study area and point-count centers (red) in the Cross Timbers of Elk County, Kansas. Imagery is 2012 National Agriculture Inventory Program photography.

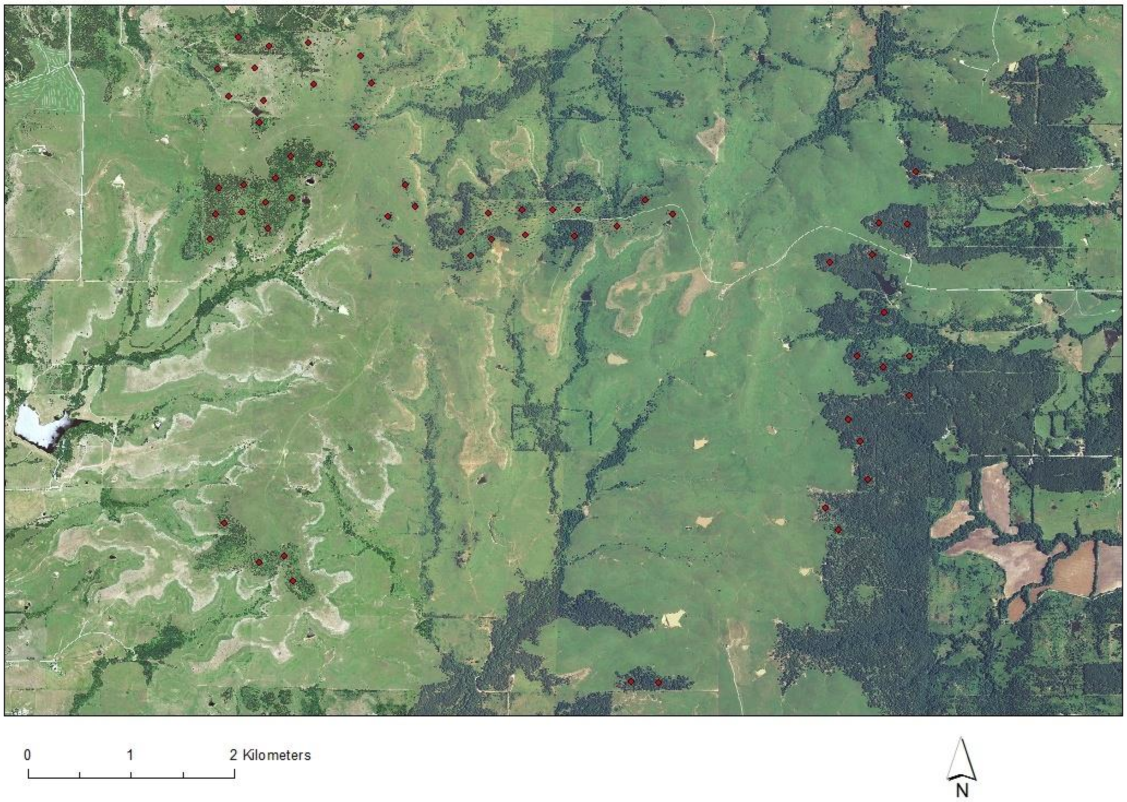

0
1
2 Kilometers
N

Figure 2. Distribution of point-count points (A) and nests per bird species (B) across a gradient of canopy cover values in the Cross Timbers of Elk County, Kansas, 2012 and 2013.

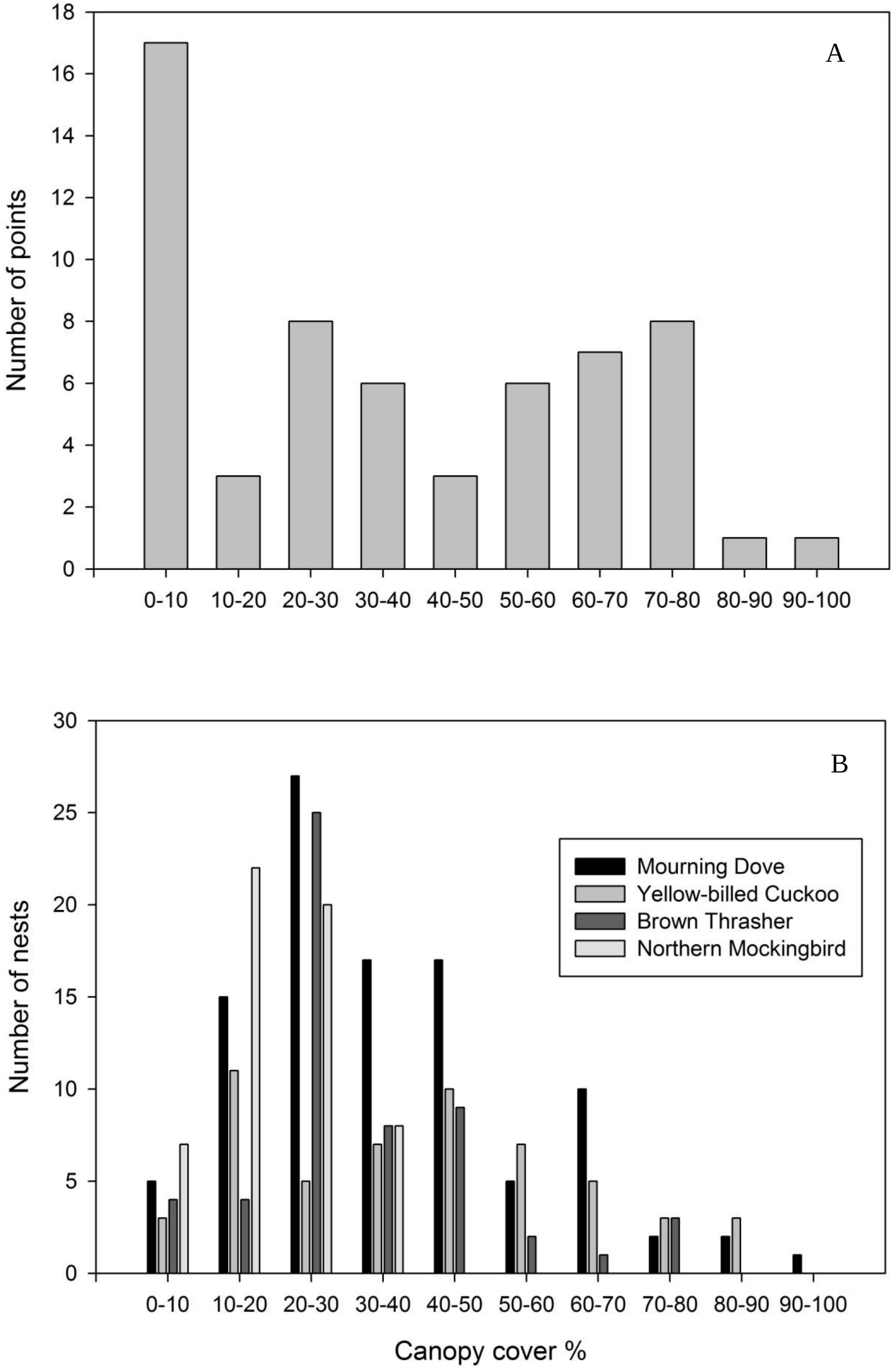

A
Number of points
0
2
4
6
8
10
12
14
16
18
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
90-100
B
Number of nests
0
5
10
15
20
25
30
Mourning Dove
Yellow-billed Cuckoo
Brown Thrasher
Northern Mockingbird
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
90-100
Canopy cover %

Figure 3. Portion of study area used for nest searching and all nests monitored in 2012 and 2013 in Elk County, Kansas. Dots indicate nests monitored, colored coded by species as follows: red = Mourning Dove, yellow = Yellow-billed Cuckoo, blue = Brown Thrasher, and green = Northern Mockingbird.

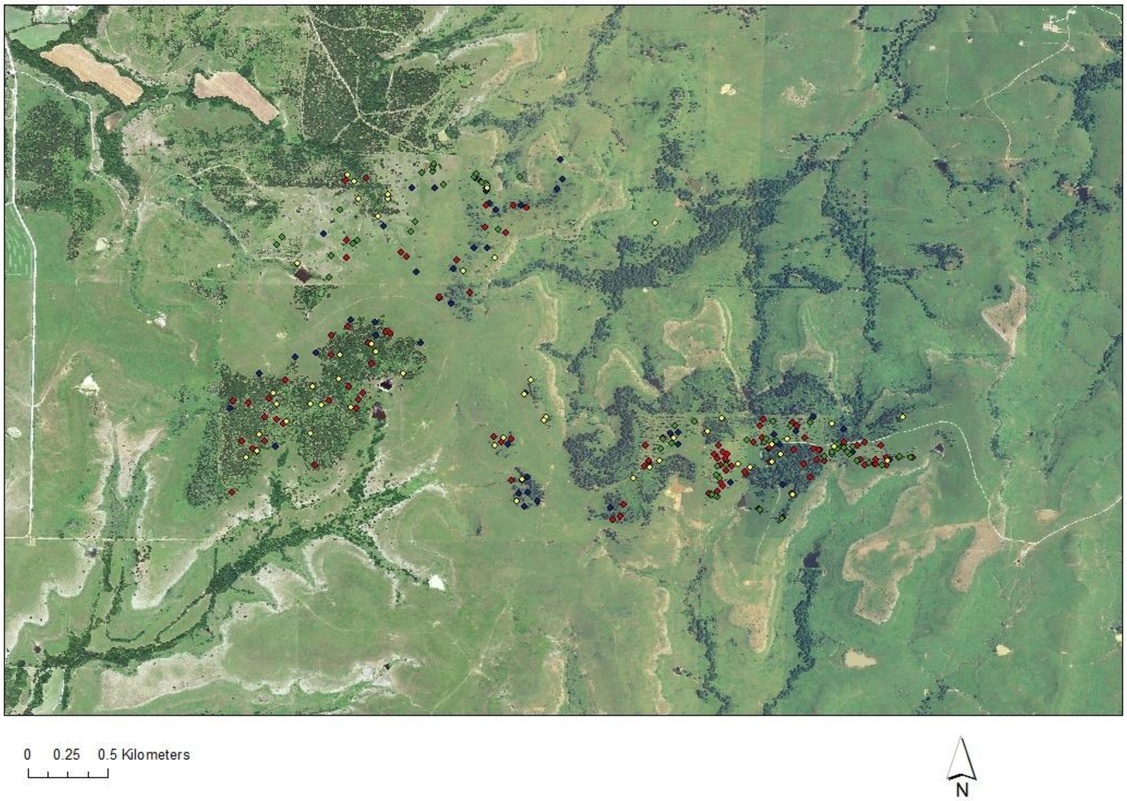

0 0.25 0.5 Kilometers
N

Figure 4 (A-E). Strong predictors (85% CI of β does not include 0) of occupancy by species (indicated by 4-letter alpha code; see Table 3). If multiple model structures (linear, quadratic, or pseudothreshold) with the same variable were strong indicators, only the top ranked model is shown. Data from Elk County, Kansas, 2012-2013.

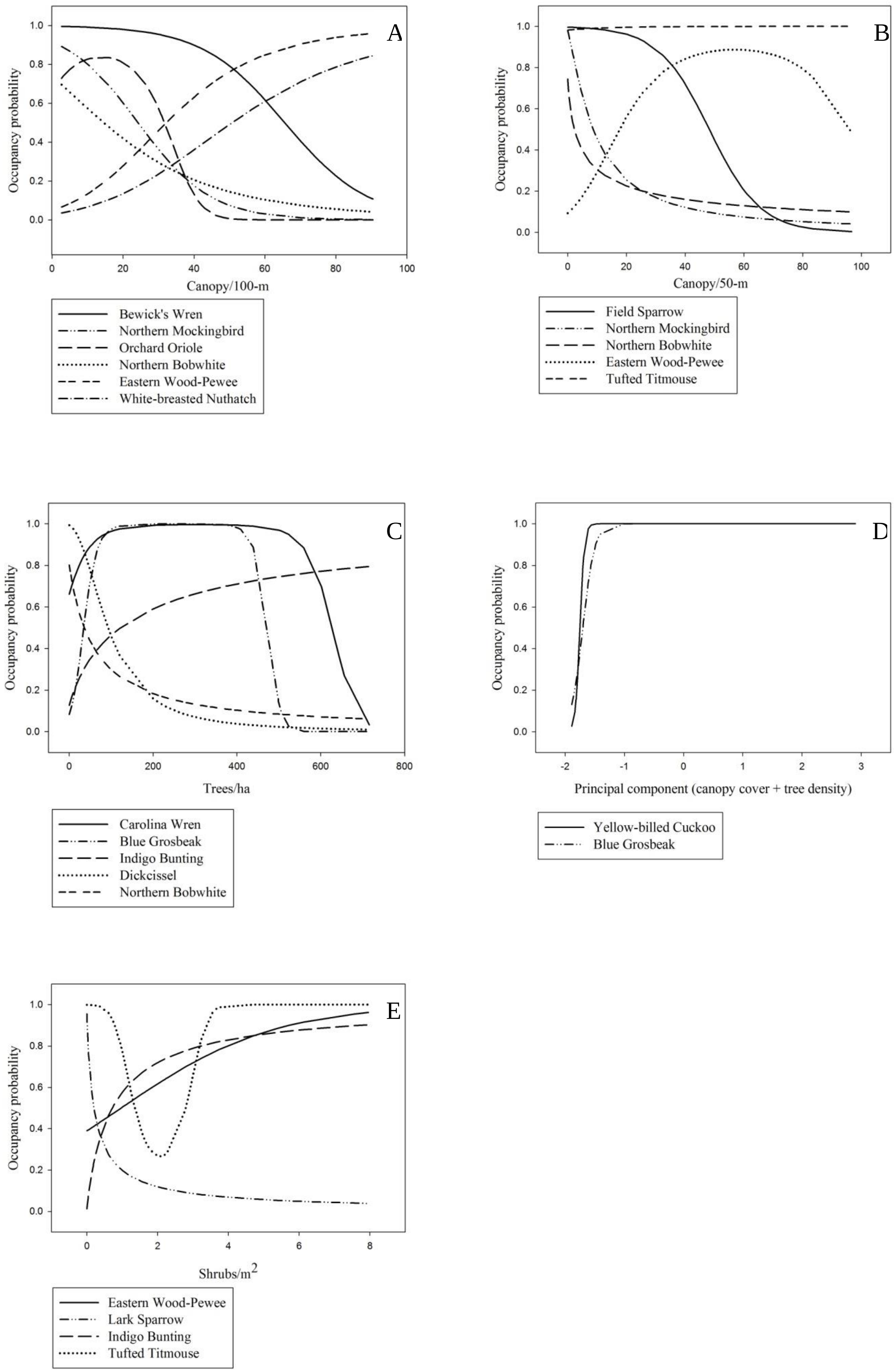
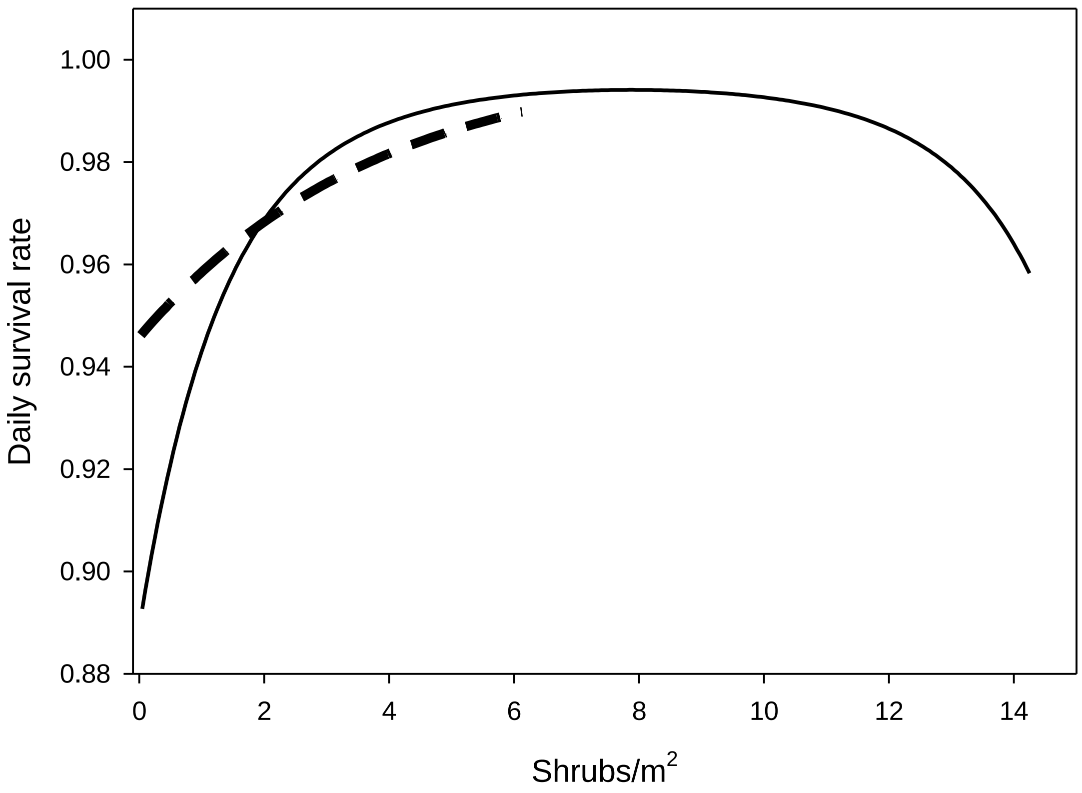

A
Occupancy probability
Canopy/100-m
Bewick's Wren
Northern Mockingbird
Orchard Oriole
Northern Bobwhite
Eastern Wood-Pewee
White-breasted Nuthatch
B
Occupancy probability
Canopy/50-m
Field Sparrow
Northern Mockingbird
Northern Bobwhite
Eastern Wood-Pewee
Tufted Titmouse
C
Occupancy probability
Trees/ha
Carolina Wren
Blue Grosbeak
Indigo Bunting
Dickcissel
Northern Bobwhite
D
Occupancy probability
Principal component (canopy cover + tree density)
Yellow-billed Cuckoo
Blue Grosbeak
E
Occupancy probability
Shrubs/m2
Eastern Wood-Pewee
Lark Sparrow
Indigo Bunting
Tufted Titmouse

Figure 5. Top ranked daily survival rate models showing strong (85% CI of β does not include 0) habitat influences for Brown Thrasher (BRTH, solid line) and Northern Mockingbird (NOMO, dashed line) in Elk County, Kansas, 2012-2013. Lines extend only to minimum/maximum habitat values in which nests for each species were found.



Daily survival rate
1.00
0.98
0.96
0.94
0.92
0.90
0.88
0
2
4
6
8
10
12
14
Shrubs/m^2

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BIRD OCCUPANCY AND
NESTING SUCCESS IN RELATION TO
HABITAT STRUCTURE IN THE CROSS
TIMBERS OAK SAVANNA OF KANSAS

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