WINTER BIRD DENSITIES AND EASTERN WOOD-PEWEE BREEDING DEMOGRAPHY ACROSS A SAVANNA-WOODLAND-FOREST GRADIENT IN THE MISSOURI OZARKS

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WINTER BIRD DENSITIES AND EASTERN WOOD-PEWEE BREEDING DEMOGRAPHY ACROSS A SAVANNA-WOODLAND-FOREST GRADIENT IN THE MISSOURI OZARKS

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ABSTRACT

Savanna and woodland habitats were historically prevalent in the midwestern United States and efforts to restore these communities are growing. Better knowledge of the responses of breeding and non-breeding birds to restoration of savanna and woodland is needed to inform management. Our objective was to determine densities of common winter migrants and resident birds in savannas, woodlands, and non-managed forests in the Missouri Ozark Highlands. We estimated detection probabilities and densities using distance and time-removal models to obtain robust density estimates. We surveyed 561 points along 42 transects, with 10-minute unlimited-radius point counts at 10 sites across the Missouri Ozarks, December-February, 2009-2011. We fit distance models for 14 species and time-removal models for 6 species. Detection probabilities varied between distance and time-removal models and were affected by covariates such as observer, temperature, wind, vegetation type (savanna, woodland, and forest), and distance. Estimates from both model types followed similar patterns amongst vegetation types. Generally, restoration did not have a substantial impact on most winter birds, because density did not vary greatly for species across savanna, woodland, or non-managed forest. Dark-eyed Junco and Eastern Bluebird were the only species with considerably higher densities in restored savanna or woodland.

We also studied the breeding demography of the Eastern Wood-Pewee (*Contopus virens*; hereafter Pewee), because it breeds across a gradient of wooded habitats ranging from open-canopy savanna, to woodland, to closed-canopy forest. Our objectives were to determine relationships between temporal factors and habitat structure and breeding demography and densities of the Pewee across the savanna-woodland-forest vegetation gradient during the breeding season. We determined nest success, clutch size, fledge rate, and breeding densities of the Pewee across the vegetation types and tested for effects of year, stage, ordinal date, nest height, percent stocking, and percent forest in a 10-km radius. We conducted point counts at 906 points at 15 sites and estimated detection probability and density of Pewees using distance models to examine the effects of observer, type of detection, minutes since sunrise, habitat type, day of year, and distance on detection probability. We found and monitored 310 nests at 13 study sites across the Missouri Ozark Highlands from 2009-2011. Year, ordinal date, nest height, and stocking had very weak or no effect on nest survival. Nest stage had a strong effect on daily survival rate. Contrary to previous studies examining the effects of forest fragmentation in the landscape, period survival increased with decreasing forest cover in a 10-km radius. Daily survival rate was 0.977 (95% CI: 0.972, 0.981) overall. Average clutch size was 2.568 (95% CI: 2.456, 2.679; n=111) and average fledge rate was 2.2 (95% CI: 2.034, 2.366; n=65) young per nest. Only 4 (1.25%) nests were parasitized by Brown-headed Cowbirds (*Molothrus ater*). Average feeding rate was 7.89 visits per hour (n=56), and frequency of parent visits to the nest was positively correlated with nestling age (p=0.049). We recorded 20 cases of double brooding in the Pewee, and some successful nests were reused for a second brood. Pewee densities were greater in woodland and forest vegetation types compared to savanna. In general, restoration did not have a substantial impact on Pewee nest survival, because survival did not vary greatly across savanna, woodland, or non-managed forest. Given the negative effect of stocking on clutch size, weak negative effect on nest survival, and lower densities in savanna, we suggest Pewees are well-adapted to intermediate stocking levels found in woodland.

THESIS FORMAT

Thesis chapters were formatted as two separate manuscripts for peer-reviewed journal submission. Therefore, sections of the introduction are repeated within each chapter, and a list of citations follows each chapter.

CHAPTER 1

WINTER BIRD DENSITIES ACROSS A SAVANNA-WOODLAND-FOREST GRADIENT IN THE MISSOURI OZARKS

ABSTRACT

Savanna and woodland habitats were historically prevalent in the midwestern United States and efforts to restore these communities are growing. Better knowledge of the responses of breeding and non-breeding birds to restoration of savanna and woodland is needed to inform management. Our objective was to determine densities of common winter migrants and resident birds in savannas, woodlands, and non-managed forests in the Missouri Ozark Highlands. We surveyed 561 points along 42 transects, with 10-minute unlimited-radius point counts at 10 sites across the Missouri Ozarks, December-February, 2009-2011. We estimated detection probabilities and densities using distance and time-removal models to obtain robust density estimates. We fit distance models for 14 species: American Robin (*Turdus migratorius*), Black-capped and Carolina Chickadee (*Poecile atricapillus, P. carolinensis*) pooled, Brown Creeper (*Certhia americana*), Carolina Wren (*Thryothorus ludovicianus*), Dark-eyed Junco (*Junco hyemalis*), Downy Woodpecker(*Picoides pubescens*), Eastern Bluebird (*Sialia sialis*), Golden-crowned Kinglet (*Regulus satrapa*), Hairy Woodpecker (*Picoides villosus*), Northern Flicker (*Colaptes auratus*), Pileated Woodpecker (*Dryocopus pileatus*), Red-bellied Woodpecker (*Melanerpes carolinus*), Tufted Titmouse (*Baeolophus bicolor*), and White-breasted Nuthatch (*Sitta carolinensis*). We fit time-removal models for 6 species: Brown Creeper, Downy Woodpecker, Golden-crowned Kinglet, Hairy Woodpecker, Tufted Titmouse, and White-breasted Nuthatch. Detection probabilities varied between distance and time-removal models and were affected by covariates such as observer, temperature, wind, vegetation type (savanna, woodland, and forest), and distance. Distance model density estimates were almost always higher than those from time-removal models. However, estimates from both model types generally followed similar patterns amongst vegetation types. Generally, restoration did not have a substantial impact on most winter birds, because density did not vary greatly across savanna, woodland, or non-managed forest. Dark-eyed Junco and Eastern Bluebird were the only species with considerably higher densities in restored savanna or woodland in winter.

INTRODUCTION

Savanna and woodland are natural communities that were historically prevalent in Missouri and across the Midwestern United States. Oak savanna covered 11-13 million hectares prior to European settlement, but only 2607 hectares remained in the Midwest by 1985(Nuzzo 1986). An estimated 971,000 hectares of degraded oak woodland exists in Missouri and is primarily found in the Ozark Highlands (Spencer et al. 1992). Approximately 22 000 hectares of oak woodland are currently being restored in the state by the Missouri Department of Conservation (MDC), the Missouri Department of Natural Resources (DNR), and The Nature Conservancy (TNC; K. Borisenko, pers. comm.; K. McCarty, pers. comm.; D. Ladd, pers. comm.). Various land-use changes with the arrival of settlers and prolonged fire suppression led to forest succession that degraded most oak savanna within 20-40 years (Nuzzo 1986; Peterson and Reich 2001). An estimated 24 700-49 400 hectares of restorable oak savanna maintain floristic diversity to justify preservation in the state of Missouri (Currier 1993), or 0.1-0.2% of the state’s total area. Common management tools for savanna and woodland restoration include mechanical thinning and prescribed fire. Mechanical thinning is used to open the canopy, allowing sunlight to reach ground vegetation. Prescribed fire kills small diameter woody species and encourages growth of grasses and forbs. The effects of different fire frequencies were observed over a 32-year period across a gradient of burned savanna in Minnesota (Peterson and Reich 2001). Tree density and basal area decreased with increased fire frequency, and these declines were correlated with fire frequency (Peterson and Reich 2001). Thus, vegetation structure is affected by fire frequency in woodland and savanna restoration. Restoring savanna and woodland can promote biodiversity and may provide additional habitat for species best-adapted to open wooded habitats or adjacent, larger patches of forest or grassland (Davis et al. 2000).

Savanna and woodland restoration has varied effects on bird communities. Species richness was higher on burned savanna sites, with an average of 31 species, compared to unburned savanna sites, with an average of 20 species in central Minnesota (Davis et al. 2000). Densities of all bird species were also higher on burned units with 6.95 ± 1.26 birds/ha, compared to unburned units with 3.82 ± 0.065 birds/ha (Davis et al. 2000). In Indiana, fire frequency in savannas and woodlands was positively correlated with species diversity and density of the most threatened species (Grundel and Pavlovic 2007a). Most studies of avian response to restoration occurred during the breeding season, though a few examined temperate areas in the winter months (Zeller and Collazo 1995; Kreisel and Stein 1999). Winter studies, however, usually take place in non-temperate overwintering habitat (Gutzwiller 1991; Cox and Jones 2009) or use a focal species to illustrate the effects of fire (Kreisel and Stein 1999; Covert-Bratland et al. 2006; Cox and Jones 2009). However, Grundel and Pavlovic (2007a, 2007b) determined bird abundance during winter, spring and fall migrations, and breeding season across a gradient of wooded habitats ranging from open savanna to forest in northwestern Indiana. Otherwise, there is little information on non-breeding bird densities in savanna and woodland restoration areas in the Midwest.

We estimated densities of winter resident bird species across savanna, woodland, and forest habitats throughout the Missouri Ozarks using distance and time-removal models. We hypothesized that winter bird densities differed among savanna, woodland, and forest habitats. We predicted densities of bark-gleaning birds would increase across a gradient of increasing tree stocking, because an increase in the number of trees may provide increased foraging substrate. For example, bark-gleaning insectivores preferred selectively logged plots in burned areas and unlogged plots in unburned areas compared to heavily logged sites in winter in Arizona; this included common species such as Hairy Woodpecker (*Picoides villosus*) and White-breasted Nuthatch (*Sitta carolinensis*; Blake 1982). Finally, we predicted that birds associated with open or early successional habitats would decrease across a gradient from savanna to woodland to forest because of an increase in tree stocking. Winter species associated with open habitats like Western Bluebird (*Sialia mexicana*) and Dark-eyed Junco (*Junco hyemalis*) preferred areas with the most logging in both burned and unburned plots in Arizona (Blake 1982).

METHODS

Study Areas

We selected 10 study areas across the Missouri Ozark Highlands owned by MDC (conservation areas), DNR (state parks), and TNC by contacting managers and asking for examples of managed savannas or woodland that had largely achieved desired conditions and had adjacent areas of non-managed mature forest on similar landforms (Table 1). The total managed and unmanaged area of study sites ranged from 162 – 15 378 hectares. The Ozark Highlands Region is equally divided between steep and rolling hills, and gently rolling plains, ranging in elevation from 100-600 m (McNab and Avers 1994). The region includes mosaics of oak-hickory and oak-hickory-pine forest, bluestem (*Andropogon gerardii, Schizachyrium* *scoparium*) prairie, and Eastern red cedar (*Juniperus virginiana*) glades (McNab and Avers 1994). Upland and mesic slopes include post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*), shortleaf pine (*Pinus echinata*), white oak (*Q. alba*), northern red-oak (*Q. rubra*), bitternut hickory (*Carya cordiformis*) and flowering dogwood (*Cornus florida*;(McNab and Avers 1994).

Point Counts

We surveyed bird abundance by point counts. We located points by randomly placing a 250-m grid over a site so that 9-14 points fell within the boundaries, and points were > 50 m from the edge of the site. We conducted 10-minute unlimited-radius point counts in all temperatures and weather with the exception of rain and winds above roughly 13 kph. We measured the distance to each bird detection with a Bushnell Yardage Pro laser range-finder (Bushnell, Overland Park, KS, USA), or distance was estimated when obstructions existed between the observer and detection. We recorded the time of each detection, and the temperature, wind speed, cloud cover, and precipitation at the beginning of each count. Wind speed was measured as 0-3 on the Beaufort scale. All counts took place between sunrise and noon, except for 2 transects conducted later in the day due to time and travel constraints. Two observers conducted all surveys with nearly equal survey effort between observers. Each point was surveyed once so we could maximize the number of points and study areas.

Vegetation Measurements

We recorded diameter at breast height (DBH) and species of all trees in an 11.3-m radius around each surveyed point and calculated percent tree stocking based on trees > 4 cm DBH. Tree stocking is a measure of the amount of growing space occupied by trees based on basal area, tree diameters, and stems/ha (Johnson et al. 2009). We classified points as savanna, woodland, or forest if stocking was < 50%, 50%-80%, or > 80%, respectively. These categories are similar to those based on canopy closure used to classify these vegetation types (Nelson 1985; Forest Service 2005), however, we believed percent stocking was a better measure of dominance of trees on a site.

Data Analyses

We estimated detection probabilities and bird densities in savanna, woodland, and forest using distance and time-removal models in Program Distance and Program MARK, respectively. We ran analyses for species with nearly 50 detections because models performed poorly or failed to converge for species with < 50 detections. We truncated the plot radius at the 90th percentile of distances to detections for each species (Buckland et al. 2001). We considered candidate models with the effects of observer, temperature, wind, vegetation type, and distance, singly and in all additive combinations. We evaluated model support using Akaike's information criterion adjusted for small sample sizes (AIC_c). Modeled species were chosen based on sample size and how well raw data fit the assumptions of each modeling approach. We report detection probabilities and densities from the best distance and time-removal model as well as the mean density from both models to provide robust results. We also provide uncorrected count data of all species detected as the mean number of detections/point for each species in each vegetation type.

Distance Models

Distance sampling estimates density based on distance to detected individuals, assuming detectability decreases with increasing distance between the detection and the observer (Buckland et al. 2001). This method assumes 1) objects at a distance of zero are always detected, 2) objects are detected at their initial location (no movement in response to the observer or other influences), and 3) distances are measured accurately (Buckland et al. 2001).

We first fit null models in Program Distance 6.0 (Thomas et al. 2010) with hazard-rate and half-normal key functions with manual selection of zero model parameters to determine which key function best fit the data. We then proceeded using the most-supported function and fit a conventional distance sampling model (CDS) with a global detection function and a CDS model with detection functions stratified by vegetation type (models labeled CDS HABITAT). CDS models were used for null models, and multiple covariate distance sampling for all others. We also considered multiple covariate distance models for single and additive combinations of observer, temperature, wind, and vegetation type. If species were often found in flocks (defined here as 4 or more individuals of the same species equidistant from the observer), observations were coded as clustered instead of single and each detection was assigned a cluster (or flock) size. Wind was coded binomially as low (levels 0 or 1 on the Beaufort scale) or high (levels 2 or 3 on the Beaufort scale). We manually selected starting points for parameter adjustment, based on the parameter point estimates of the null model. We assessed model fit using Kolmogorov-Smirnov goodness-of-fit and ranked model support using AIC_c.

Time-removal Models

We also estimated detection probability and density using a removal-model framework (Farnsworth et al. 2002) based on Huggins closed-capture and Huggins full heterogeneity models (Huggins 1989) in Program MARK (White and Burnham 1999). Huggins models are based on conditional likelihood theory, where individuals not detected are not included in analysis and allow for the incorporation of covariates affecting detection. Time-removal models base density estimates on the time interval in which an individual is first detected, and detection probability is modeled as a decline in the number of individuals detected through subsequent time intervals (Farnsworth et al. 2002). We considered time-removal models that allow for heterogeneity by estimating detection probabilities for an easy-to-detect group (group 1) and a hard-to-detect group (group 2). The assumptions for time-removal models are 1) the population of interest is closed, 2) there is no double-counting, 3) all members of group 1 are detected in the first interval, 4) all members of group 2 not detected in the first interval have a constant detection probability, and 5) for limited-radius counts, observers accurately assign birds to appropriate radii (Farnsworth et al. 2002). Time-removal models address both components of detection probability: availability (probability that a bird sings during a count) and detectability (probability that the bird is detected, given that it sings). We created encounter histories by dividing a 10-minute count into 5, 2-minute intervals (i.e. encounter history of '10000' if detected in the first 2-minute interval of the count, '01000' if detected in the second interval, and so on). We first evaluated support for null models with and without heterogeneity and used the most-supported model to construct models incorporating singular and additive combinations of observer, temperature, wind, distance, and vegetation type. We ranked models using AIC_c and report the detection probability and density estimate for each species from the top-ranked model. Density estimates were based on the area sampled by all points surveyed to account for points where species were not detected, since Huggins models are based on a conditional likelihood theory.

RESULTS

Two observers surveyed 292 and 269 points in the winter of 2009-10 and 2010-11, respectively, from 12 December to 22 February and detected 37 species. We classified 165 points as savanna, 179 as woodland, and 217 as forest based on tree stocking levels. We detected 1-224 individuals of 37 species (Appendix 1).

We fitted 14 species with distance models and 6 species with time-removal models (Tables 2 and 3). Due to the sensitivity of Programs MARK and Distance to small sample size, many species lacked adequate number of detections and resulted in models with poor goodness-of-fit or models that failed to converge. Buckland suggests a sample size of 60-80 detections as a general minimum (Buckland 2001), and nearly all species modeled with distance sampling met this suggestion and most exceeded it with detections ranging from 49 to 202 detections. Only 2 of 14 species had < 60 detections (Brown Creeper (*Certhia americana*): 49; Eastern Bluebird (*Sialia sialis*): 57), but exploratory histograms of the raw data for these species showed adequate fit according to model assumptions. We detected covariate effects in both analysis approaches, and these effects varied by species and approach.

We report detection probabilities and density estimates derived using distance models and report density by vegetation type for 14 species (Table 2). Most models were best fit using a hazard-rate key function, except for Black-capped and Carolina Chickadees (*Poecile atricapillus, P. carolinensis*; hereafter Chickadees), Brown Creeper, and Downy Woodpecker (*Picoides pubescens*), which were best fit using a half-normal key function. American Robin and Dark-eyed Junco were sometimes detected in large flocks, so detections of these species were analyzed as clustered observations. The null model was the top-ranked model for Downy Woodpecker and Golden-crowned Kinglet (*Regulus satrapa*). Observer was included in the top-ranked models for American Robin (*Turdus migratorius*), Brown Creeper, Hairy Woodpecker, Pileated Woodpecker (*Dryocopus pileatus*), Tufted Titmouse (*Baeolophus bicolor*), and White-breasted Nuthatch. Temperature had a positive effect on detection probability for American Robin, Chickadees, Carolina Wren (*Thryothorus ludovicianus*), and Tufted Titmouse, and a negative effect on 2 species: Northern Flicker (*Colaptes auratus*) and Red-bellied Woodpecker (*Melanerpes carolinus*). Wind had a negative effect on the detection probabilities of American Robin, Dark-eyed Junco, Northern Flicker, and Tufted Titmouse, and a positive effect on Eastern Bluebird and White-breasted Nuthatch. Savanna had a positive effect on detection probability for Brown Creeper, Chickadees, Pileated Woodpecker, Red-bellied Woodpecker, Tufted Titmouse, and White-breasted Nuthatch and a negative effect on American Robin. Forest had a positive effect on detection probability for Brown Creeper and Red-bellied Woodpecker, and a negative effect on American Robin, Chickadees, Pileated Woodpecker, Tufted Titmouse, and White-breasted Nuthatch. Four species had highest density estimates in forest, and 8 species had highest densities in savanna or woodland (Table 2).

We fit time-removal models for 6 species (Table 3). For many species, the number of detections was too small to fit time-removal models, resulting in poor goodness-of-fit or models failed to converge. Models with heterogeneity were not supported over models without heterogeneity for any species. Covariate effects on detection probability varied widely, but observer was included in the top-ranked model for 3 species: Downy Woodpecker, Golden-crowned Kinglet, and Hairy Woodpecker. Temperature had a positive effect on detection probability for Tufted Titmouse. Distance had a negative effect on the detection probability of Golden-crowned Kinglet and White-breasted Nuthatch. Wind was not included in any of the top-ranked time-removal models. Five of 6 species had their greatest densities in forest and Tufted Titmouse was at greatest density in woodland. Density estimates for 6 species that were fit with both distance and time-removal models were averaged to provide more robust results (Fig. 1).

Detection probabilities derived using distance models were higher than those of time-removal models for species that fit both model approaches, with the exception of Brown Creeper, which had equal detection probability for both modeling approaches. All time-removal model detection probabilities were less than 0.5 (Table 3).

Raw count data suggested habitat preferences for a few species that could not be fit with distance or time-removal models. American Crow had substantially more detections/point in forest than savanna or woodland, Northern Cardinal and White-throated Sparrow had higher detections/point in savanna, and Yellow-rumped Warbler detections suggested a preference for woodland and forest over savanna (Appendix 1).

DISCUSSION

We were able to fit models for 14 species: 6 with time-removal models and 14 with distance models. Detection probabilities and densities varied widely by species and vegetation type, respectively. Prior studies that used distance and/or time-removal models to analyze count data were conducted during the breeding season (Selmi and Boulinier 2003; Heltzel and Leberg 2006; Thompson III and LaSorte 2008; Reidy et al. 2011) when birds are more vocal because of territory and mate defense. Detection probabilities in our study were generally low, potentially because of decreased audible territorial singing or calling compared to the breeding season. Detection probabilities of breeding songbirds estimated with time-removal models are generally > 0.6 and much greater than those we observed (Farnsworth et al. 2002; Thompson III and LaSorte 2008; Reidy et al. 2011). However, breeding season distance models generally produce lesser detection probabilities in the range of 0.1-0.7 (Thompson III and LaSorte 2008; Reidy et al. 2011). Distance models may have produced higher detection probabilities for winter birds compared to breeding birds because a lack of foliage may make birds more visible or audible at longer distances. Birds may also be more detectable in winter because fewer species and cues are present to compete for the observer’s attention.

Covariate effects on detectability varied widely by species and modeling approach. Temperature almost always had a positive effect. Winter birds may be more active and vocal in warmer temperatures, especially compared to some of the very cold temperatures we observed (< -20° C). Wind had an equal number of positive and negative effects on 4 species' detectability. Negative effects of high wind were likely because wind made birds harder to hear. Eastern Bluebird and White-breasted Nuthatch were not negatively affected by high wind in distance models, possibly because White-breasted Nuthatch has a loud call. Effects of vegetation type on detection probability showed that, with the exception of American Robin, open habitats had a positive effect on detectability. Forest habitat had a negative effect on detectability based on distance models for 5 of 7 species, potentially due to increased tree density and vegetation that may have decreased detectability at farther distances. Detectability was greater in savanna for 6 of 7 species, likely because of low tree density and increased visibility.

Most birds in our study acted as habitat generalists. Most bird densities did not vary greatly across vegetation types and all modeled species were detected in all three vegetation types. However, Dark-eyed Junco and Eastern Bluebird were considerably more abundant in savanna and woodland, respectively. So with the exception noted above, we did not find strong effects of restoration on winter bird densities. Densities of some bark-gleaning birds increased with percent stocking but varied by analysis approach. Densities estimated by time-removal models increased with percent stocking for most bark-gleaning birds modeled (Brown Creeper, Hairy Woodpecker, and White-breasted Nuthatch) except Downy Woodpecker, mostly supporting our prediction. Densities estimated by distance models increased with percent stocking for some bark gleaning birds (Hairy Woodpecker, Pileated Woodpecker, Red-bellied Woodpecker, and White-breasted Nuthatch), but not for Brown Creeper and Downy Woodpecker, providing less support for our prediction. Densities of most species associated with open habitats (Carolina Wren, Eastern Bluebird, and Northern Flicker) had greatest densities in intermediate percent stocking (woodland), failing to support our prediction.

However, Dark-eyed Junco is a species associated with open habitats and had greater densities in areas with lesser percent stocking, supporting our prediction. Grundel and Pavlovic (2007b) used univariate nonparametric multiplicative regression to derive density estimates for White-breasted Nuthatch and found density decreased from approximately 0.34 birds/ha in unburned areas to a density of zero in areas with a fire frequency of 6 burns in 15 years, similar to our results of greater White-breasted Nuthatch densities in unburned forest (0.31 birds/ha).

Some species' patterns of habitat use during the breeding season are similar to those we observed in winter. Grundel and Pavlovic (2007a) found Dark-eyed Junco and Golden-crowned Kinglet at greatest abundance in restored savanna or woodland habitats when compared to forest, and Tufted Titmouse were most abundance in forest, similar to our results. Patterns in abundance of Northern Flicker, White-breasted Nuthatch, Tufted Titmouse, and Chickadees between savanna and non-managed forest were also similar to what we found for savanna and woodland versus forest (Brawn 2006). These similarities in habitat use give us further confidence that winter resident birds may be using these vegetation types similarly across seasons.

Winter bird densities derived with distance models (Table 2) were generally similar to mean densities reported by Grundel and Pavlovic (2007a) in the breeding season: Dark-eyed Junco (0.08 ± 0.03 to 1.19 ± 0.70 birds/ha), Golden-crowned Kinglet (0.12 ± 0.06 to 0.74 ± 0.21 birds/ha), and Tufted Titmouse (0.12 ± 0.03 to 0.76 ± 0.08 birds/ha). Winter densities generally overlapped those reviewed in Birds of North American Online (Poole 2005) species accounts. Downy Woodpecker breeding densities range from 0.14-0.34 birds/ha (Jackson and Ouellet 2002), which overlapped our averaged densities (Tables 2 and 3). Golden-crowned Kinglet winter densities range from 0.1-0.23 birds/ha (Ingold and Galati 1997), which was less than our averaged densities (Tables 2 and 3). Hairy Woodpecker breeding season densities range from 0.003-0.075 birds/ha (Jackson et al. 2002), which overlapped our averaged densities (Table 2 and 3). White-breasted Nuthatch winter densities range from 0.12-0.19 birds/ha (Grubb and Pravosudov 2008) and were similar to our averaged densities (Tables 2 and 3). Carolina Wren breeding densities range from 0.45-1.08 males/ha (Haggerty and Morton 1995), which is greater than our distance-model results (Table 2). Breeding season densities of Dark-eyed Junco range from 0.38-2.6 males/ha (Nolan et al. 2002) and were greater than our distance-model densities (Table 2). Pileated Woodpecker breeding densities range from 0.003-0.16 (Bull and Jackson 2011) and this range includes our distance-model estimate (Table 2).

Examining raw count data to make assumptions about species' habitat use or differences amongst vegetation types assumes equal and constant probability of detection regardless of species, habitat, and other factors that could affect detectability, such as wind or temperature. Most of the 14 species fit with distance and time-removal models showed effects of multiple covariates on detectability, and those effects are altogether ignored when raw counts are reported. Indices also may not be ideal when comparing abundance across habitat or species, because detectability may vary by habitat and species (Johnson 2008). However, raw count data provide a way to examine abundances of species when the number of detections is too small for other analytical approaches, like distance or time-removal models (Johnson 2008).

Five of 6 species had similar patterns of abundance across vegetation types based on distance and time-removal models (Tables 2 and 3). Since these methods use different approaches to estimate detectability, similar results from both models give greater confidence in our results. Future studies estimating bird detection probability and density using point counts should choose a modeling approach that best fits their study system and examine how well data meet model assumptions. If uncertain, we suggest averaging density estimates from multiple analysis approaches to obtain robust results. While species' densities varied by vegetation type, differences were not great for most species and differed by species and sometimes the modeling approach. Dark-eyed Junco and Eastern Bluebird had substantially greater densities in managed savanna or woodlands, and this is important when managing for these species. However, most winter residents occurred across these habitats and therefore most do not appear to be greatly affected by management of savanna and woodlands. In addition, we found support for factors affecting detection probabilities of birds in winter, so winter bird surveys should consider factors affecting detection probability through model- or design-based methods.

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Figure 1. Mean density and 95% confidence intervals based on the most-supported distance and time-removal model of birds in savanna, woodland, and forest, in Missouri, winter 2009-10 and 2010-11.

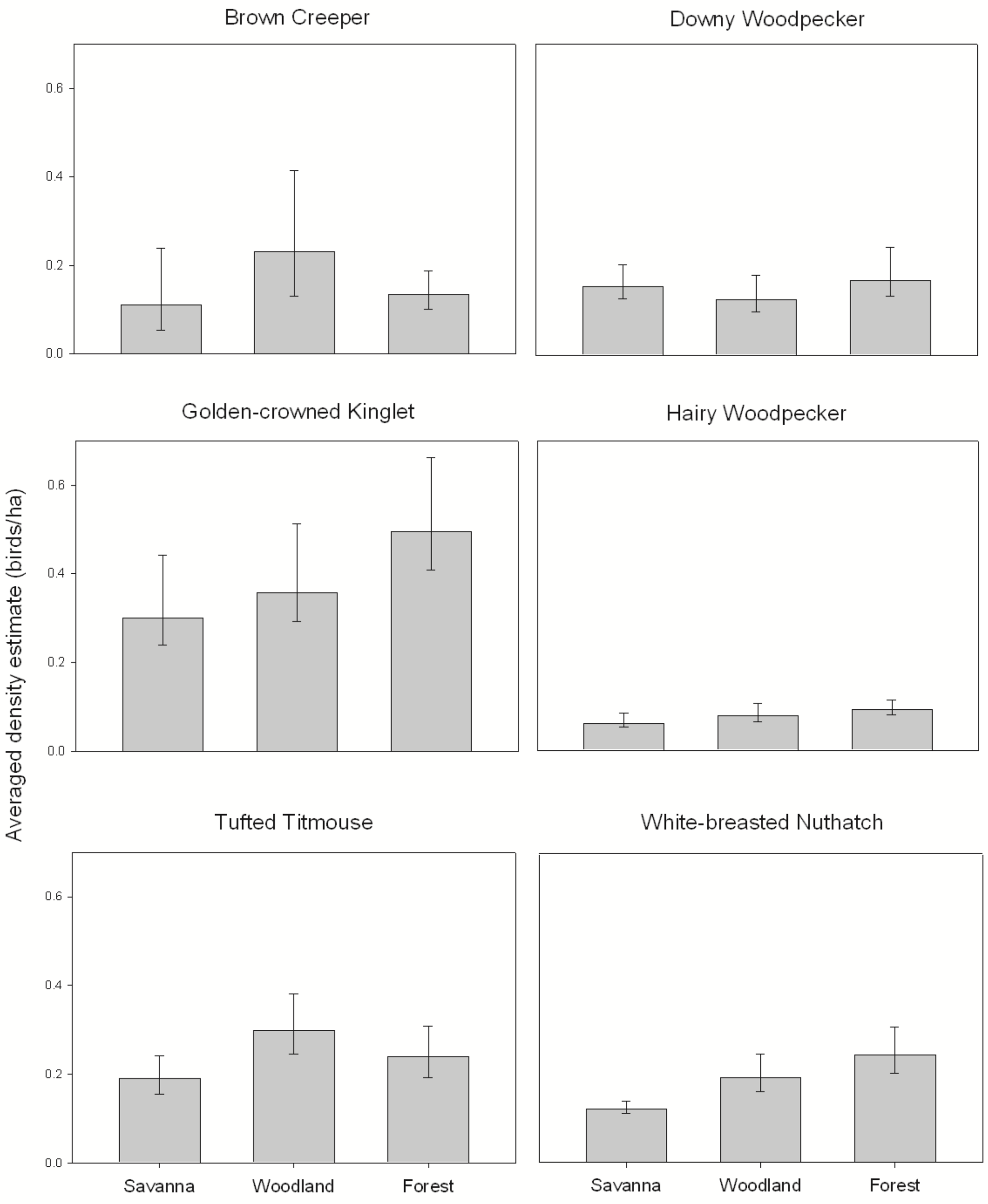

Table 1. Study areas on which we determined winter bird densities by point counts in savanna, woodland, and forest, in Missouri, winter 2009-10 and 2010-11.

Site name	County	Total area (ha)	No. points
Bennett Spring State Park	Dallas	1301	24
TNC Bennett Spring Savanna	Dallas	372	14
Ha Ha Tonka State Park	Camden	384	40
Knob Noster State Park	Johnson	1550	33
Lake of the Ozarks State Park	Miller	7133	71
Lead Mine Conservation Area	Dallas	255	45
Little Black Conservation Area	Ripley	162	26
Peck Ranch Conservation Area	Carter	9328	220
Rocky Creek Conservation Area	Shannon	15378	37
Sunklands Conservation Area	Shannon	2327	51

Table 2. Estimates of detection probability and density of birds in savanna, woodland, and forest based on the most-supported distance sampling model, in Missouri, winter 2009-10 and 2010-11.

Species	Model [a]	Detection probability (SE)	K-S GOF[b]	Vegetation type	Density esimate (birds/ha)	Density SE	Farthest distance[c] (m)
American Robin	OBS TEMP WIND HAB	0.39 (0.05)	0.27	Savanna	0.26	0.06	86
				Woodland	0.16	0.03	
				Forest	0.20	0.03	
Black-capped and Carolina Chickadees	TEMP HAB	0.29 (0.03)	0.49	Savanna	0.18	0.03	85
				Woodland	0.23	0.05	
				Forest	0.31	0.06	
Brown Creeper	OBS HAB	0.28 (0.05)	0.98	Savanna	0.20	0.07	56
				Woodland	0.42	0.12	
				Forest	0.21	0.03	
Carolina Wren	TEMP	0.69 (0.03)	0.39	Savanna	0.10	0.009	120
				Woodland	0.12	0.009	
				Forest	0.08	0.006	
Dark-eyed Junco	WIND	0.58 (0.12)	0.6	Savanna	0.50	0.18	72
				Woodland	0.11	0.05	
				Forest	0.09	0.04	

Species	Model [a]	Detection probability (SE)	K-S GOF[b]	Vegetation type	Density esimate (birds/ha)	Density SE	Farthest distance[c] (m)
Downy Woodpecker	NULL	0.47 (0.05)	0.52	Savanna	0.20	0.02	97
				Woodland	0.15	0.02	
				Forest	0.19	0.02	
Eastern Bluebird	WIND	0.85 (0.05)	0.41	Savanna	0.03	0.003	102
				Woodland	0.05	0.004	
				Forest	0.02	0.002	
Golden-crowned Kinglet	NULL	0.45 (0.04)	0.3	Savanna	0.47	0.05	65
				Woodland	0.55	0.05	
				Forest	0.75	0.07	
Hairy Woodpecker	OBS	0.64 (0.04)	0.6	Savanna	0.07	0.01	100
				Woodland	0.09	0.01	
				Forest	0.10	0.01	
Northern Flicker	TEMP WIND	0.85 (0.04)	0.7	Savanna	0.04	0.004	106
				Woodland	0.05	0.004	
				Forest	0.03	0.003	
Pileated Woodpecker	OBS HAB	0.63 (0.03)	0	Savanna	0.03	0.001	200
				Woodland	0.05	0.004	
				Forest	0.05	0.005	
Red-bellied Woodpecker	TEMP HAB	0.75 (0.04)	0.77	Savanna	0.04	0.006	97
				Woodland	0.09	0.01	

Species	Model [a]	Detection probability (SE)	K-S GOF[b]	Vegetation type	Density esimate (birds/ha)	Density SE	Farthest distance[c] (m)
				Forest	0.09	0.006	
Tufted Titmouse	OBS TEMP WIND HAB	0.43 (0.03)	0.97	Savanna	0.24	0.02	86
				Woodland	0.42	0.04	
				Forest	0.32	0.04	
White-breasted Nuthatch	OBS WIND HAB	0.54 (0.04)	0.6	Savanna	0.12	0.005	96
				Woodland	0.23	0.03	
				Forest	0.31	0.04	

[a] OBS is observer, TEMP is temperature, WIND is wind speed, HAB is habitat type.

[b] Kolmogorov-Smirnov goodness of fit.

[c] Plot radius truncated at the 90th percentile of distances.

Table 3. Estimates of detection probability and density of birds in savanna, woodland, and forest based on the most-supported time-removal model, in Missouri, winter 2009-10 and 2010-11.

Species	Model [a]	Vegetation type	Detection probability	Density estimate (birds/ha)	Density SE	c-hat[b]
Brown Creeper	NULL	Savanna	0.28 (0.07)	0.02	0.00	3.08
		Woodland		0.04	0.01	
		Forest		0.06	0.01	
Downy Woodpecker	OBS	Savanna	0.25 (0.05)	0.11	0.01	3.06
		Woodland		0.10	0.02	
		Forest		0.15	0.03	
Golden-crowned Kinglet	OBS DIST	Savanna	0.28 (0.06)	0.13	0.04	2.98
		Woodland		0.16	0.05	
		Forest		0.24	0.05	
Hairy Woodpecker	OBS	Savanna	0.41 (0.05)	0.05	0.00	2.74
		Woodland		0.07	0.01	

Species	Model [a]	Vegetation type	Detection probability	Density estimate (birds/ha)	Density SE	c-hat[b]
		Forest		0.09	0.01	
Tufted Titmouse	TEMP	Savanna	0.26 (0.04)	0.14	0.02	3.04
		Woodland		0.18	0.02	
		Forest		0.16	0.02	
White-breasted Nuthatch	DIST	Savanna	0.34 (0.04)	0.12	0.01	2.91
		Woodland		0.16	0.01	
		Forest		0.18	0.01	

[a] OBS is observer, TEMP is temperature, and DIST is distance.

[b] c-hat is a measure of overdispersion (deviance/degrees of freedom).

Appendix 1. Mean detections/point of birds from unlimited radius point counts at 165 savanna, 179 woodland, and 217 forest points, in Missouri, winter 2009-10 and 2010-11.

Species	Vegetation type	Mean	SE	Maximum detections/point	Total detections
American Crow	Savanna	0.152	0.029	2	25
	Woodland	0.168	0.038	3	30
	Forest	0.415	0.192	41	90
American Goldfinch	Savanna	0.055	0.032	5	9
	Woodland	0.011	0.011	2	2
	Forest	0.000	0.000	0	0
American Robin	Savanna	0.133	0.035	3	22
	Woodland	0.279	0.096	16	50
	Forest	0.267	0.096	20	58
American Tree Sparrow	Savanna	0.024	0.019	3	4
	Woodland	0.000	0.000	0	0
	Forest	0.000	0.000	0	0
Black-capped and Carolina Chickadees	Savanna	0.182	0.039	3	30
	Woodland	0.184	0.038	3	33
	Forest	0.175	0.033	3	38
Blue Jay	Savanna	0.109	0.030	3	18
	Woodland	0.151	0.038	3	27

Species	Vegetation type	Mean	SE	Maximum detections/point	Total detections
Brown Creeper	Forest	0.111	0.026	2	24
	Savanna	0.067	0.023	2	11
	Woodland	0.089	0.025	2	16
Carolina Wren	Forest	0.124	0.028	3	27
	Savanna	0.358	0.053	4	59
	Woodland	0.380	0.057	4	68
Dark-eyed Junco	Forest	0.276	0.037	3	60
	Savanna	0.521	0.229	32	86
	Woodland	0.067	0.027	4	12
Downy Woodpecker	Forest	0.051	0.023	4	11
	Savanna	0.309	0.047	3	51
	Woodland	0.229	0.037	2	41
Eastern Bluebird	Forest	0.290	0.037	2	63
	Savanna	0.103	0.027	2	17
	Woodland	0.162	0.040	4	29
Eastern Towhee	Forest	0.078	0.022	2	17
	Savanna	0.024	0.012	1	4
	Woodland	0.006	0.006	1	1
Field Sparrow	Forest	0.005	0.005	1	1
	Savanna	0.018	0.018	3	3
	Woodland	0.000	0.000	0	0
	Forest	0.000	0.000	0	0

Species	Vegetation type	Mean	SE	Maximum detections/point	Total detections
Fox Sparrow	Savanna	0.000	0.000	0	0
	Woodland	0.006	0.006	1	1
	Forest	0.000	0.000	0	0
Golden-crowned Kinglet	Savanna	0.315	0.056	4	52
	Woodland	0.369	0.053	3	66
	Forest	0.488	0.061	5	106
Hairy Woodpecker	Savanna	0.170	0.034	2	28
	Woodland	0.201	0.036	3	36
	Forest	0.212	0.038	3	46
Hermit Thrush	Savanna	0.006	0.006	1	1
	Woodland	0.000	0.000	0	0
	Forest	0.005	0.005	1	1
Lincoln's Sparrow	Savanna	0.012	0.012	2	2
	Woodland	0.000	0.000	0	0
	Forest	0.000	0.000	0	0
Northern Cardinal	Savanna	0.109	0.031	2	18
	Woodland	0.039	0.020	3	7
	Forest	0.023	0.010	1	5
Northern Flicker	Savanna	0.158	0.032	2	26
	Woodland	0.173	0.032	2	31
	Forest	0.115	0.024	2	25
Pileated Woodpecker	Savanna	0.382	0.050	3	63

Species	Vegetation type	Mean	SE	Maximum detections/point	Total detections
	Woodland	0.385	0.048	3	69
	Forest	0.359	0.042	3	78
Purple Finch	Savanna	0.006	0.006	1	1
	Woodland	0.000	0.000	0	0
	Forest	0.005	0.005	1	1
Red-breasted Nuthatch	Savanna	0.012	0.009	1	2
	Woodland	0.017	0.012	2	3
	Forest	0.032	0.012	1	7
Red-bellied Woodpecker	Savanna	0.121	0.028	2	20
	Woodland	0.207	0.034	2	37
	Forest	0.249	0.032	2	54
Ruby-crowned Kinglet	Savanna	0.000	0.000	0	0
	Woodland	0.006	0.006	1	1
	Forest	0.000	0.000	0	0
Red-headed Woodpecker	Savanna	0.006	0.006	1	1
	Woodland	0.000	0.000	0	0
	Forest	0.005	0.005	1	1
Red-tailed Hawk	Savanna	0.000	0.000	0	0
	Woodland	0.006	0.006	1	1
	Forest	0.009	0.009	2	2
Red-winged Blackbird	Savanna	0.024	0.024	4	4
	Woodland	0.000	0.000	0	0

Species	Vegetation type	Mean	SE	Maximum detections/point	Total detections
Savannah Sparrow	Forest	0.000	0.000	0	0
	Savanna	0.000	0.000	0	0
	Woodland	0.011	0.011	2	2
Song Sparrow	Forest	0.000	0.000	0	0
	Savanna	0.006	0.006	1	1
	Woodland	0.000	0.000	0	0
Tufted Titmouse	Forest	0.028	0.028	6	6
	Savanna	0.382	0.055	3	63
	Woodland	0.441	0.062	4	79
White-breasted Nuthatch	Forest	0.318	0.039	3	69
	Savanna	0.358	0.047	3	59
	Woodland	0.425	0.054	3	76
Wild Turkey	Forest	0.406	0.047	3	88
	Savanna	0.000	0.000	0	0
	Woodland	0.000	0.000	0	0
Winter Wren	Forest	0.134	0.099	19	29
	Savanna	0.000	0.000	0	0
	Woodland	0.000	0.000	0	0
White-throated Sparrow	Forest	0.005	0.005	1	1
	Savanna	0.133	0.041	3	22
	Woodland	0.039	0.020	2	7
	Forest	0.014	0.010	2	3

Species	Vegetation type	Mean	SE	Maximum detections/point	Total detections
Yellow-bellied Sapsucker	Savanna	0.012	0.009	1	2
	Woodland	0.011	0.008	1	2
	Forest	0.023	0.012	2	5
Yellow-rumped Warbler	Savanna	0.038	0.016	2	7
	Woodland	0.067	0.025	3	12
	Forest	0.063	0.022	3	14

CHAPTER 2

EASTERN WOOD-PEWEE BREEDING DEMOGRAPHY ACROSS A SAVANNA-WOODLAND-FOREST GRADIENT IN THE MISSOURI OZARKS

ABSTRACT

Better knowledge of the responses of birds to restoration or management of savanna and woodland is needed to inform management of these communities. We studied the breeding demography of the Eastern Wood-Pewee (*Contopus virens*; hereafter Pewee), because Pewees breed across a gradient of wooded habitats including open-canopy savanna, woodland, and closed-canopy forest. Our objective was to determine temporal and habitat effects on the breeding demography and densities of the Pewee across savanna, woodland, and forest to better understand the effects of restoration efforts on wildlife in the Missouri Ozarks. We determined nest success, clutch size, fledge rate, and breeding densities of the Pewee across the vegetation gradient and evaluated support for effects of year, stage, ordinal date, nest height, percent stocking, and percent forest in a 10-km radius. We also conducted point counts at 906 points using 10-minute unlimited radius point counts. We estimated detection probability and density of Pewees using distance models to examine the effects of observer, type of detection, minutes since sunrise, habitat type, day of year, and distance on detection probability. We monitored 310 nests at 13 study sites and conducted 10-minute unlimited-radius point counts at 15 sites across the Missouri Ozark Highlands from 2009-2011. Year, ordinal date, nest height, and stocking had weak or no effects on nest survival. Nest stage (incubation or nestling) had a strong effect on daily survival rate. Contrary to previous studies examining the effects of forest fragmentation in the landscape, period survival increased with decreasing forest cover in a 10-

km radius. Daily survival rate was 0.977 (95% CI: 0.972, 0.981) overall. Average clutch size was 2.568 (95% CI: 2.456, 2.679; n=111) and average fledge rate was 2.2 (95% CI: 2.034, 2.366; n=65) young per nest. Only 4 (1.25%) nest attempts were parasitized by Brown-headed Cowbirds (*Molothrus ater*). Average feeding rate was 7.89 visits per hour (n=56), and frequency of parental visits to the nest was positively correlated with nestling age (p=0.049). We recorded 20 cases of double brooding in the Pewee, and some successful nests were reused for a second brood. Pewee densities were greater in woodland and forest than savanna. Increasing nest success with decreasing forest in a 10-km radius may indicate that Pewees are less susceptible to fragmentation effects in the Missouri Ozarks, as evidenced by very low brood parasitism in this study. Therefore, passerine nest survival may not always decrease with fragmentation or less forest cover and this relationship likely depends on the dominant predators. Given the negative effects of stocking on clutch size, weak negative effect on nest survival, and lower densities in savanna, we suggest Pewees are well-adapted to the intermediate stocking levels found in woodlands. Further research is needed to understand the trade-offs of Pewee abundance and nest survival at different spatial scales.

INTRODUCTION

Savanna and woodland are natural communities that were historically prevalent in Missouri and across the Midwest. Oak savanna once covered 11-13 million hectares prior to European settlement, and only 2607 hectares remained in the Midwest by 1985 (Nuzzo 1986). An estimated 971 000 hectares of degraded oak woodland exist in Missouri and is primarily found in the Ozark Highlands (Spencer et al. 1992). Various land-use changes with the arrival of settlers and prolonged fire suppression led to forest succession that eventually depleted most oak savanna within 20-40 years (Nuzzo 1986; Peterson and Reich 2001). An estimated 24 700-49

400 hectares of restorable oak savanna maintain sufficient floristic diversity to justify preservation in the state of Missouri. Approximately 24 000 hectares of oak woodland are currently being restored in the state by the Missouri Department of Conservation (MDC), the Missouri Department of Natural Resources (DNR), and The Nature Conservancy (TNC; K. Borisenko, pers. comm.; K. McCarty, pers. comm.; D. Ladd, pers. comm.). Common management tools for savanna or woodland restoration include mechanical thinning and prescribed fire. Mechanical thinning is used to reduce tree density and open the canopy to allow more sunlight to reach the ground. Prescribed fire is used to maintain an open understory by reducing sapling density. Different fire frequencies were observed over a 32-year period across a gradient of burned areas in Minnesota and tree density and basal area were found to decrease with increased fire frequency, and these declines were correlated with fire frequency (Peterson and Reich 2001). Savanna and woodland restoration can promote biodiversity and may provide additional habitat for species best-adapted for open wooded habitats or adjacent, larger patches of forest or grassland (Davis et al. 2000).

Restoration efforts have increased substantially in the past two decades, and better knowledge of the responses of birds to restoration of savanna and woodland is needed to inform management of these communities. The few studies that have examined the effects of savanna or woodland restoration on nest survival in the Midwest show varied responses by species. Brawn (2006) found higher daily survival rate in restored savanna compared to closed-canopy forest for 10 of 13 species monitored, including the Pewee. A study in southeast Ohio comparing shelterwood harvest sites to unharvested forest sites showed marginally higher daily survival rate for Pewees in unharvested forest (0.969 ± 0.005; n=127) compared to shelterwood sites (0.963 ± 0.004; n=109; (Newell and Rodewald 2011a).

In the Midwest, species richness and densities tend to be greater in savanna managed with prescribed fire compared to unburned, non-managed areas. Davis et al. (2000) found species richness to be nearly 65% higher and densities of all birds 80% higher on burned savanna restoration sites across a fire frequency gradient in central Minnesota, when compared to unburned sites. In Indiana, frequent fires in restored savanna and woodland areas were positively correlated with species diversity and density of the most threatened species (Grundel and Pavlovic 2007b).

The Eastern Wood-Pewee (*Contopus virens*; hereafter Pewee) is a medium-sized flycatcher of the family Tyrannidae and a Neotropical migrant whose range generally covers the Eastern half of the United States up into the southern regions of Canada (McCarty 1996). The Pewee is a species of regional conservation concern in the Central Hardwood Region because of the reduction of oak and pine woodland due to logging and fire suppression (Fitzgerald and Nigh 2005), though the flycatcher is abundant in Missouri and uses a variety of forested habitats (Peck and James 1987). Understanding the breeding demography of Neotropical migrants that use managed and unmanaged habitats allows us quantify the effects of management on bird populations. Studying species that occur across a large habitat gradient is a good way to elucidate factors affecting demography; however, few species occur across a wooded habitat gradient. The Pewee breeds in savanna, woodland, and forest habitats, and is therefore a candidate species for understanding the effects of savanna and woodland restoration on demography.

Our objectives were to evaluate Pewee nest success, clutch size, fledge rate, brood parasitism rate, and breeding density in savanna, woodland, and forest to determine relationships between demographic parameters and temporal and habitat factors across this gradient. This information is needed to better understand the effects of restoration management in the Missouri Ozark Highlands on wildlife and to fill in gaps in knowledge of the breeding biology of the Pewee, since no published study has focused solely on the species. We hypothesized that restoration has an effect on Pewee nest survival and predicted nest survival increases with percent stocking and increases with percent forest in the landscape, is greater in incubation stage than nestling stage, and increases with nest height. Nest survival has been found to be greater in incubation stage compared to nestling stage, potentially due to decreased activity at the nest and fewer parental visits (Martin et al. 2000). Increased nest height can decrease the probability of predation (Burhans et al. 2002), and Pewee nests high in the canopy may be more difficult for a predator to detect or access. We predicted that nest survival increases with stocking because nests in areas with higher stocking (forest) may be more difficult to detect, given the number of trees for predators to search compared to savanna. However, species that nest across a range of wooded habitats are few, and no published data exist to compare nest survival between forest and non-forest. Nest survival has also been positively correlated with percent forest in the landscape due to fragmentation effects like increased nest predation and nest parasitism (Donovan et al. 1995; Robinson et al. 1995). We also predicted that Pewee density is highest at intermediate levels of percent tree stocking. Pewee densities were greatest at intermediate tree density (Grundel and Pavlovic 2007b) and also in forest when a gradient of wooded habitats were sampled in the Midwest (Grundel and Pavlovic 2007a).

METHODS

Study Areas

We selected 13 nest searching sites and 19 point count survey sites across the Missouri Ozark Highlands owned by MDC, DNR, TNC, and the U.S. Forest Service (Table 1). We selected sites by contacting managers and asking for examples of managed savanna or woodland that had largely achieved desired conditions and that had adjacent areas of non-managed forest on similar landforms. The total managed and unmanaged area of study sites ranged from 162 – 15 378 hectares. The Ozark Highlands Region is equally divided between steep and rolling hills, and gently rolling plains, ranging in elevation from 100-600 m (McNab and Avers 1994). The region includes oak-hickory and oak-hickory-pine forest, bluestem (*Andropogon gerardii, Schizachyrium scoparium*) prairie, and Eastern red cedar (*Juniperus virginiana*) glades (McNab and Avers 1994). Upland and mesic slopes include post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*), shortleaf pine (*Pinus echinata*), white oak (*Q. alba*), northern red-oak (*Q. rubra*), bitternut hickory (*Carya cordiformis*) and flowering dogwood (*Cornus florida*; (McNab and Avers 1994). Savanna and woodland restoration varied widely by burn frequency, ranging from 2 to 15 burns in 20 years preceding the study.

Nest-searching and Monitoring

We searched for Pewee nests between early May and mid-August 2009-2011 using parental behavior and systematic searches within a territory. Nests were monitored every 3-4 days, or daily near fledge date, to determine if nests were active, the stage of the nest, and nest contents.

Pewees nest across a wide range of heights, from 1.8-21 m high (Peck and James 1987). We constructed a telescoping video pole using a Spiderbeam antenna (WiMo, Herxheim, Germany) and a Defender Phoenix surveillance system (Defender, Niagara Falls, Ontario) to monitor nest contents. The video pole included a wireless camera attached to the top of the pole and a wireless monitor to view the live feed. A two-person team used the video pole to acquire nest contents once per nest stage (incubation and nestling stages). We did not use the video pole if Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), or Brown-headed Cowbirds (hereafter Cowbirds) were present to minimize time at the nest, attention drawn to the nest, or other potential impacts on predation or nest parasitism. We also observed feeding rates for nests of varying ages for one hour between sunrise and 1100, recording the frequency and duration of visits to the nest.

Point Counts

We surveyed abundance by point counts. We located points by randomly placing a 250-m grid across a site so that 9-14 points fell within the site and points were >50 m from the edge of a site. We conducted 10-minute unlimited-radius point counts between sunrise and 1000. We did not conduct surveys in precipitation, winds above roughly 13 kph, or in temperatures below 10° Celsius. We measured the distance to each bird detection with a Bushnell Yardage Pro laser range-finder (Bushnell, Overland Park, KS, USA) or estimated distance when obstructions existed between the observer and the bird. We recorded the temperature, wind speed, cloud cover, and precipitation at the beginning of each count. Each point was surveyed once by one of five observers to maximize the number of points and study areas.

Vegetation Measurements

We recorded Universal Transverse Mercator coordinates at points and nests with a handheld geographic positioning system (Garmin, GPCMAP76S, Olathe, KS). We measured diameters at breast height (DBH) of all trees in an 11.3 m radius of the nest and point count locations, and calculated percent tree stocking based on trees > 4 cm DBH. Percent tree stocking is a measure of the amount of growing space occupied by trees based on basal area, tree diameters, and stems/ha (Johnson et al. 2009). We classified points as savanna, woodland, or forest if percent stocking was < 50%, 50-80%, or > 80%, respectively. These stocking-level categories are similar to categories based on canopy closure used to classify these vegetation types (Nelson 1985), however, we believed percent stocking was a better measure of the dominance of trees on a site. We measured nest height with a clinometer. We used ArcMap 10 (ESRI 2011) to create a 10-km buffer around each nest and calculated the percent forest in the buffer using the 2006 National Land Cover Dataset (Fry et al. 2011); we reclassified all land cover types as either forest (deciduous, evergreen, and mixed forest) or non-forest (all other land cover types; Fig. 1).

Data Analysis

We used the logistic exposure method to estimate daily nest survival and the effects of covariates (Shaffer 2004; Shaffer and Thompson III 2007) using the GENMOD procedure in SAS (SAS Institute Inc., Cary, NC). The logistic exposure method considers nest fate during each nest check interval and models the effects of time-varying (e.g. nest stage, date) and habitat covariates on survival (Shaffer 2004). We constructed a set of a priori candidate models and evaluated model support with Akaike's Information Criteria adjusted for small sample sizes (AIC_c) in an information theoretic framework (Burnham and Anderson 2002). We ran an initial set of temporal models including all singular and additive combinations of stage (incubation or nestling stage), year (2009, 2010, or 2011), and linear, quadratic, cubic, and quartic forms of ordinal date (ordinal date, ordinal date^2, ordinal date^3, and ordinal date^4). We did not consider nests in the laying stage, because the last days of the building stage and the first days of laying stage were difficult to determine because we did not use the video pole on sequential days for fear of affecting nest survival. We then controlled for the most-supported temporal effects by including variables from the models with a ΔAIC < 2 in all habitat models. Habitat models consisted of all combinations of nest height, percent stocking, and percent forest. We checked for a difference in survival between young and old nestlings by comparing survival in incubation stage and two stages of nestling stage: an early stage (≤ 8 days old) and a late stage (> 8 days old) using logistic exposure models on nests with survival data during incubation stage and a confirmed number of nestlings per nest. We similarly used a model selection approach to evaluate support for the effects of date and stocking on the number of eggs in a nest (clutch size) and the number of young fledged (fledge rate) using regression models (McDonald and White 2010; Proc GLIMMIX, SAS Institute Inc., Cary, NC). In exploratory analyses, we also examined effects of quadratic and cubic date and found that the linear date variable was most-supported. We also ran a simple univariate regression on parental feeding visits per hour to determine if nestling age affected the frequency of visits to the nest.

We estimated detection probabilities and Pewee density using distance models in Program Distance 6.0 (Thomas et al. 2010). We truncated the plot radius at the 90th percentile of distances to detections (Buckland et al. 2001). Distance sampling estimates density based on distance to detected individuals and assumes detectability decreases with increasing distance from the observer (Buckland et al. 2001). This method assumes: 1) objects at a distance of zero are always detected, 2) objects are detected at their initial location (no movement in response to the observer or other influences), and 3) distances are measured accurately (Buckland et al. 2001). We first fit null models with hazard-rate and half-normal key functions with manual selection of zero model parameters to determine which key function best fit the data using model-selection criteria, and built further models using the most-supported key function. We ran a conventional distance sampling model using a global detection function and a conventional distance sampling model with separate detection functions for each vegetation type. We fit multiple covariate distance models with observer, type of detection (aural, visual, or both), minutes since sunrise, day of year, and vegetation type singly and in all additive combinations. We manually selected starting points for parameter adjustments, based on the parameter point estimates of the null model. We assessed model fit using Kolmogorov-Smirnov goodness-of-fit and ranked model support using AIC_c. We present estimates of Pewee density for savanna, woodland, and forest from the most-supported model that fit the data.

RESULTS

Thirty-two nests were found in 2009, 69 in 2010, and 218 in 2011. Three-hundred and ten nests were used in the analyses because some nests could not be used due to missing vegetation measurements, final fate was unknown, or the nest failed in building or laying stages. Nest contents were recorded for 167 nests. Nest predation was the most common cause of nest failure and accounted for 96% of failures. The top logistic exposure models for temporal effects were stage and year + stage (Table 2), so we included these two covariates in all subsequent habitat models. Results of model selection for nest survival models with habitat effects included the most support for the model stage + perforest, with 43% of the model weight, followed by models with weak effects of stocking, nest height, and year (Table 3 and 4). Overall daily survival rate was 0.977 (95% CI: 0.972, 0.981), and period survival was 0.505 (95% CI: 0.436, 0.597). Daily nest survival was greater in incubation than nestling stage (0.989, 95% CI: 0.0.984, 0.992 and 0.962, 95% CI: 0.955, 0.969, respectively) and nest survival increased substantially with a decrease in percent forest in a 10-km radius (Fig. 2). Nest height and stocking had very weak effects (Fig. 2).

We determined clutch size for 111 nests. Model selection indicated support for a model with stocking and linear date + stocking (Table 5). Average clutch size was 2.568 (95% CI: 2.454, 2.681; Table 6) based on the average date and stocking level. Predicted clutch size in areas with 8% stocking was 2.839 (95% CI: 2.588, 3.09), whereas clutch size in areas with 131% stocking was 2.211 (95% CI: 1.922, 2.501; Fig. 3). We determined the number of young fledged from 65 nests. The null model was the most-supported model but there was some support for a negative linear effect of date (Table 5). Nests fledged an average of 2.2 young (95% CI: 2.031, 2.369; Table 6). Four nests (1.25% of nest attempts) were parasitized by Cowbirds, and only one Cowbird young fledged from a Pewee nest in the three years of this study. We recorded parental feeding visits for 56 nests with nestlings ranging in age from 1-15 days. The mean feeding rate frequency was 7.893 visits per hour and mean duration of nest visits was 1.336 min (Table 6). We determined that nestling age significantly affected the number of feeding visits to the nest ($p=0.049$). Average nest height was 12.239 m (Table 6). We recorded 20 instances of double brooding, 9 of which reused the same nest for a second brood.

Five observers surveyed 320, 235, 173, 106, and 72 points in 2009-2011, respectively, between 29 May and 7 July. We classified 197 points savanna, 263 woodland, and 446 forest. We report detection probability and density estimates of Pewees for the most-supported models with a ΔAIC < 4 (Table 7). The top-ranked model included observer, type of detection, and minutes since sunrise and had the largest effect on detection probability, and all competing models (ΔAIC < 2) included observer and type of detection (Table 7). Estimated densities of Pewees were lower in savanna (0.278 ± 0.025 birds/ha) than nearly equal densities in woodland and forest (0.416 ± 0.033 and 0.428 ± 0.021 birds/ha, respectively). Kolmogorov-Smirnov goodness of fit ranged from 0.053 to 0.251 for the top 5 models, though density estimates of the top-ranked models were very similar.

DISCUSSION

Ours is the first study to examine the breeding demography of the Pewee with a large sample of nests across several habitats. We found support for a temporal effect of nest stage and a landscape effect of percent forest in a 10-km radius on nest survival, but we did not find support for other nest or habitat effects such as nest height or stocking. Therefore, we found no evidence of negative effects of savanna or woodland restoration on nest success of pewees.

Top-ranked temporal models included stage and year + stage. Survival during the nestling stage was much lower than during the incubation stage, which is similar to other studies in the Midwest (Burhans et al. 2002; Cox et al. In Press-b). Increased predation rates during the nestling stage may be a result of increased parental activity at the nest (Martin et al. 2000; Stake et al. 2005). In Ohio, daily survival rates of Cerulean Warbler, another canopy-nesting passerine, were found to decrease with nest age, comparable to our results (Newell and Rodewald 2011b). Some studies, however, found greater survival or lower predation rates in the nestling stage (Roper and Goldstein 1997; Cottam et al. 2009) or survival in incubation and nestling stages were not different (Farnsworth and Simons 1999; Peak et al. 2004; Grant et al. 2005; Peak 2007) in other passerine species. Survival may differ between species and nest stages due to variation in predator guilds, conspicuousness of the parents or nestlings, or the date of each stage in the breeding season, since predation rates have been shown to vary within a season (Benson et al. 2010; Cox et al. In Press-b).

Nest survival was similar to that reported by other studies that included Pewees. For example, Pewee daily survival was 0.974 ± 0.006 in Minnesota, Wisconsin, and Iowa (Knutson et al. 2004), 0.983 in Illinois (Brawn 2006), and 0.97 ± 0.002 in southeast Ohio (n=263; Newell and Rodewald 2011b). Percent stocking did not significantly affect estimates of period survival for Pewees (Fig. 2). Our findings are similar to other studies of Pewee nest success across varying vegetation or management types. Brawn (2006) compared the nest success of Pewees and other birds in savanna and closed-canopy forest in Illinois and also found Pewee daily survival rate to be marginally higher in savanna than closed-canopy forest. Newell and Rodewald (2011a) also compared survival of Pewee nests found in shelterwood harvested sites compared to those in unharvested sites in southeastern Ohio and found daily survival rate to be marginally lower in shelterwood sites than unharvested sites. Our weak effects of vegetation type are similar to past studies in that Pewee daily survival does not differ greatly between different vegetation types.

We predicted that nest survival would increase with an increase in percent forest in a 10-km radius, but we found strong support for the opposite trend. Period survival decreased from 64% to 39% over a range of 25% to 92% forest cover. This pattern is contrary to most Midwestern studies where, in general, nest survival of Midwestern songbirds increases with forest cover, as predation and nest parasitism increase with forest fragmentation (Donovan et al. 1995; Robinson et al. 1995; Thompson III et al. 2000). Brood parasitism (hereafter parasitism) is a primary driver of fragmentation effects, because Cowbird abundance and parasitism are negatively correlated with percent forest cover in the landscape (Robinson et al. 1995; Thompson III et al. 2000). However, Cowbirds had little effect on Pewees in our study, which may partly explain the lack of a fragmentation effect. Underwood et al. (2004) reviewed the literature for cases of parasitism in the Pewee and experimentally parasitized nests to check for acceptance and found 5.4% of 354 nests in 7 studies were parasitized and described the Pewee as infrequently parasitized but an acceptor of Cowbird eggs. Brawn (2006), however, found 68% of 34 Pewee nests found in savanna to be parasitized and 100% of 12 nests found in closed-canopy forest to be parasitized in Illinois. Illinois, however, is a highly fragmented and more hostile environment with high predation rates, Cowbird abundance, and parasitism (> 75% of open-cup nests found were parasitized in central Illinois; (Robinson 1992). Cowbirds have also been found to predate nests (Arcese et al. 1996; Hoover and Robinson 2007) and are more frequent predators in less-forested landscapes (Cox et al. In Press-a). Pewees in the Missouri Ozarks appear to be less susceptible to these effects of fragmentation than other passerines in the Midwest, potentially because of low levels of forest fragmentation in the Missouri Ozarks compared to other highly fragmented states like Illinois. Pewees may also be less susceptible to forest-specific predators compared to savanna or woodland-specific predators, though no data exist on these predators or to what extent they differ from forest predators. More information is needed to draw further conclusions about the lack of fragmentation effects on Pewee nest survival.

Clutch size and fledge rate were affected differently by date and stocking. Clutch size ranged from 2.839 eggs to 2.211 eggs over a range of 8% to 131% stocking, a different of about 0.6 egg. Areas with high stocking (forest) generally have a greater number of stems per acre, and stocking values > 100 are considered overstocked. Overstocked or heavily forested areas provide fewer open foraging sites than areas with low stocking (savanna). This may result in a food limitation in forest and prevent Pewees from laying clutches as large as those in savanna. Food has been thought to limit clutch size (Lack 1954), and food has been found to be a limiting factor in avian fecundity (Martin 1995), but not necessarily clutch size (Martin 1987; Ferretti et al. 2005). Pewee densities were also higher in forest compared to savanna. Increased density may create increased competition for resources and foraging areas and limit clutch size in forest. Fledge rate was not strongly affected by date or stocking, as the null model was most-supported. These results are similar to overall period survival, which was very weakly affected by stocking.

Descriptive statistics provided here, such as fledge rate, brood parasitism, and feeding rate, provide the largest known dataset available for the Pewee and fill knowledge gaps in the species' breeding biology. Nest heights were similar to an average height of 17.3 m for Pewee nests in southeastern Ohio (n=236; Newell and Rodewald 2011b). We provide the first published data on Pewee fledge rate and feeding rate, as well as the first nearly definitive cases of double brooding in the Pewee. Although we did not mark birds, we are confident in our observations of double broods because of multiple observations of fledglings remaining in a territory under the care of one parent while the second parent constructed a nest, incubated, and, in some cases, raised a second brood to fledge. Double brooding also occurs in the Western Wood-Pewee (*Contopus sordidulus*; Curson et al. 1996).

Pewee density increased with percent stocking, though marginally between woodland and forest (Table 3). Pewees nest in mature trees, and woodland and forest habitats provide more nesting substrate than open savannas with few trees, potentially explaining higher detected densities in woodland and forest. Pewees were detected in all three wooded habitats, and did not seem to avoid managed restoration sites. Newell and Rodewald (2011a) found little difference in Pewee territories/ha when comparing areas with shelterwood harvest to unharvested areas. However, based on 25 transects, Brawn (2006) found a difference in abundance when comparing average Pewee detections per 10 points in savanna and closed-canopy forest (6.9 ± 1.12 and 5.6 ± 0.6 avg/10 pts ± SE, respectively). Previously reported densities range from 0.03-0.2 birds/ha (McCarty 1996), which was substantially lower than our density estimates (Table 7). We found no strong effect of savanna or woodland restoration on

Pewee breeding density, other than providing alternative habitat. Overall, we found higher density, lower clutch size, and marginally lower nest survival in forested areas with high stocking compared to areas with low stocking. Overstocked forest may have fewer open areas that Pewees use for foraging strategies like hawking and sallying and increase competition for food resources. This foraging site or food limitation may have an effect on clutch size and nest success, as food has been found to limit fecundity in passerines (Nagy and Holmes 2005), though we found a minimal effect of stocking on nest success.

Contrary to previous studies examining fragmentation effects, nest survival may not always decrease with fragmentation or less forest cover. Fragmentation effects are likely dependent on certain key predators like Cowbirds, which highlights the need to identify important predators for different species, habitats, and landscapes (Burhans et al. 2002; Reidy and Thompson III 2012; Cox et al. In Press-b). Further analysis and research are needed to understand trade-offs between higher Pewee abundance in woodland and forest habitats and lower Pewee nest survival in more forested landscapes. However, Pewees appear to be best-adapted to woodland habitats, given lower abundance in savanna, and lower clutch size and marginally lower nest survival in forest.

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Figure 1. Study areas on which we searched for Eastern Wood-Pewee nests and determined breeding season densities of Pewees in savanna, woodland, and forest, in Missouri, 2009-2011. Non-forest and forest land covers classified using the 2006 National Land Cover Dataset. Northern Arkansas included to show land cover used in 10-km radii of nests in southern Missouri.

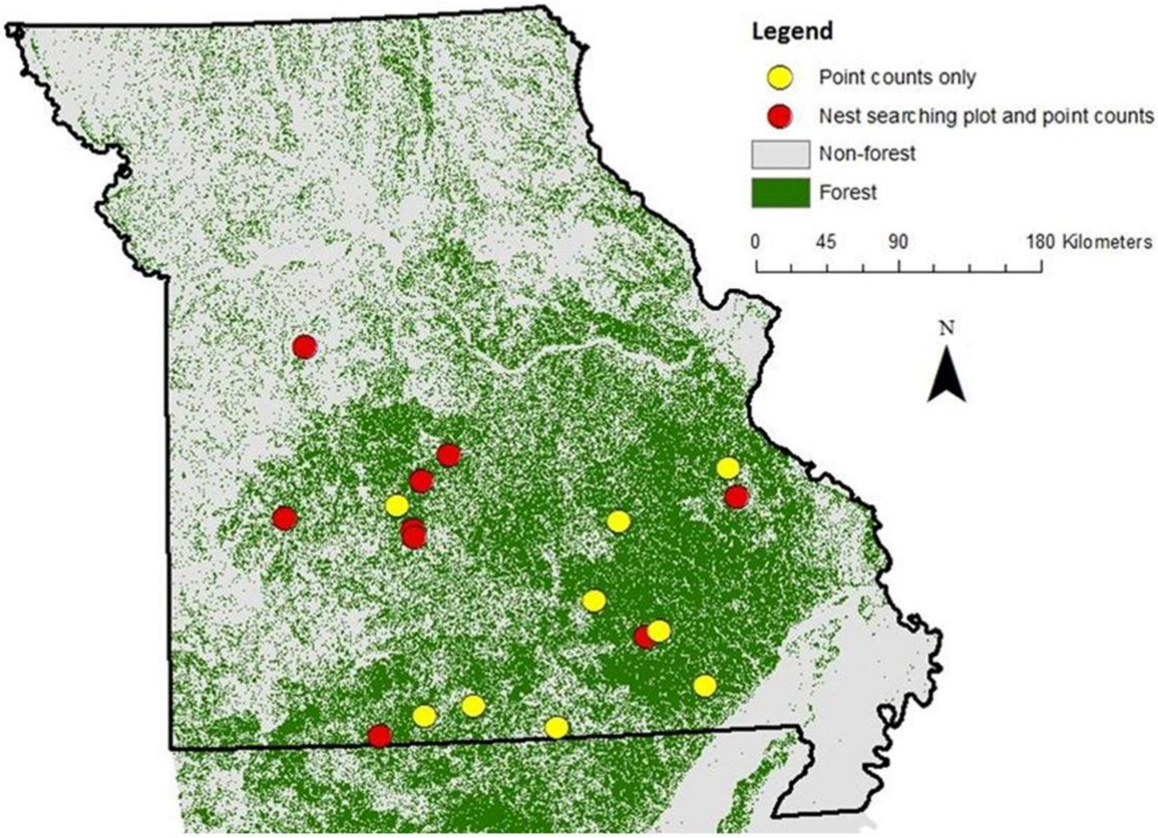

Figure 2. Relationships between (a) nest height, (b) stocking, and (c) percent forest in a 10-km radius on period survival (model-averaged mean ± 95% confidence intervals; based on a 30-day nesting cycle; n=2386) of Eastern Wood-Pewee nests found in savanna, woodland, and forest in the Missouri Ozarks, 2009-2011.

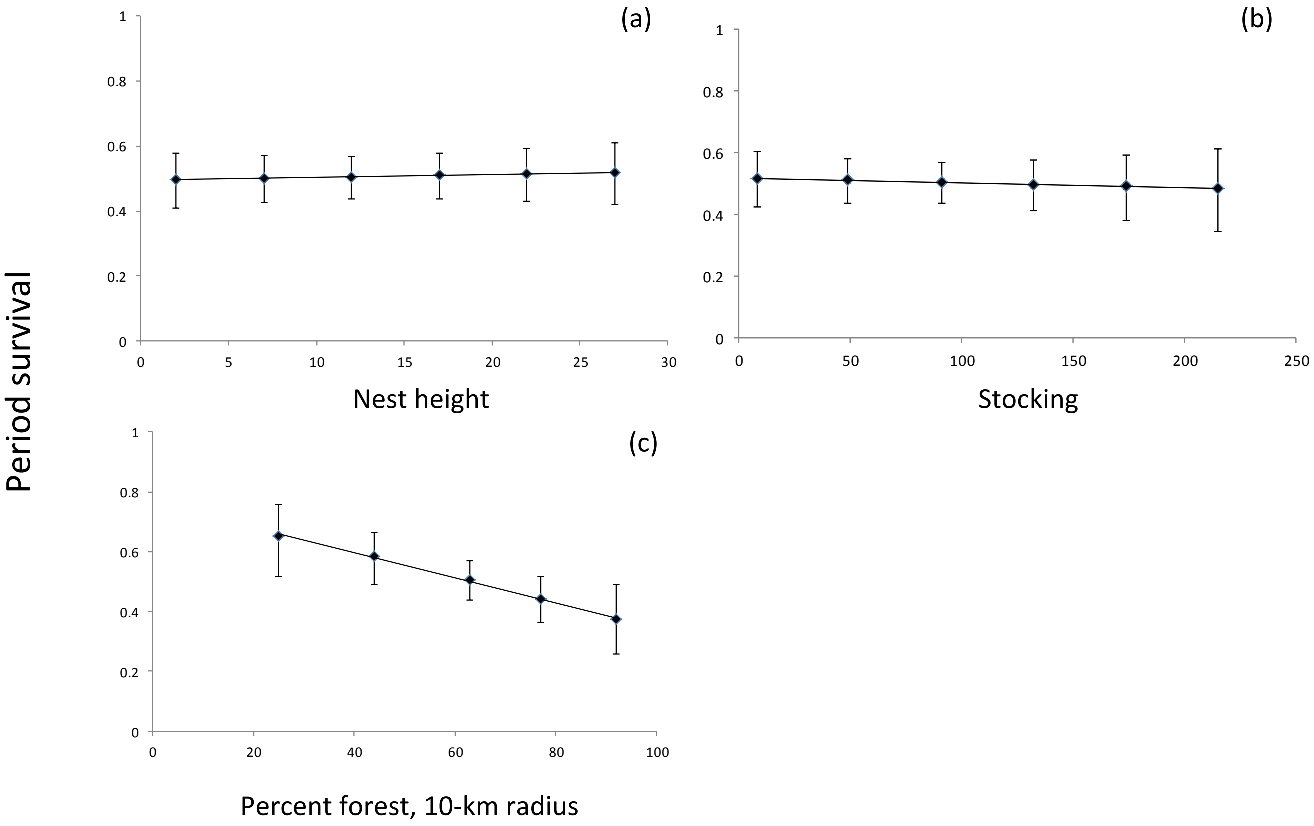

Figure 3. Relationship between percent tree stocking and clutch size (model-averaged mean ± 95% confidence intervals) of Eastern Wood-Pewee nests found in savanna, woodland, and forest in the Missouri Ozarks, 2009-2011 (n=111).

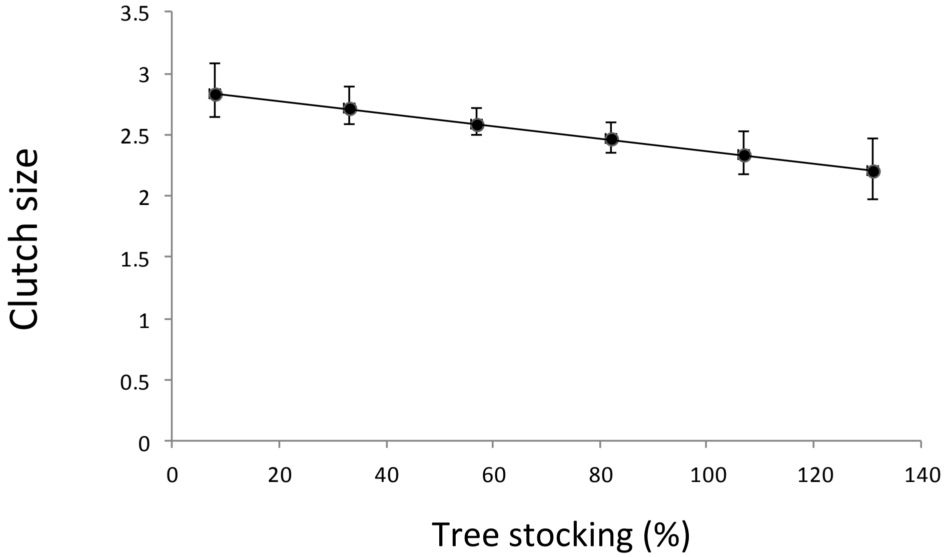

Table 1. Study areas on which we determined breeding season densities and nest monitoring of Eastern Wood-Pewees in savanna, woodland, and forest in the Missouri Ozarks, 2009-2011. All sites were used for point counts.

Site name	County	Total area (ha)	Nest monitoring
Bennett Spring State Park	Dallas	1301	Yes
Bennett Spring Savanna (TNC)	Dallas	372	Yes
Bluff Springs Conservation Area	Cedar	167	Yes
Caney Mountain Conservation Area	Ozark	3196	
Chilton Creek (TNC)	Carter, Shannon	2277	
Drury-Mincy Conservation Area	Taney	1654	Yes
Ha Ha Tonka State Park	Camden	384	Yes
Indian Trail Conservation Area	Dent	5464	
Knob Noster State Park	Johnson	1550	Yes
Lake of the Ozarks State Park	Miller	7133	Yes
Lead Mine Conservation Area	Dallas	255	
Little Black Conservation Area	Ripley	162	
Mark Twain Glade Top	Douglas	408	
Peck Ranch Conservation Area	Carter, Shannon	9328	Yes
Rocky Creek Conservation Area	Shannon	15378	Yes
Sunklands Conservation Area	Shannon	2327	
St. Joe State Park	St. Francois	3334	Yes
St. Francois State Park	St. Francois	1050	
White Ranch Conservation Area	Howard, Howell	2676	

Table 2. Results of model selection for most-supported nest survival models and temporal variables for Eastern Wood-Pewee nests found in savanna, woodland, and forest in the Missouri Ozarks, 2009-2011.

Model [a]	Log (L)	K	AICc	ΔAIC	wi
STAGE	-552.005	2	1108.012	0	0.534
YEAR + STAGE	-550.697	4	1109.4	1.389	0.266
STAGE + DATE	-549.376	6	1110.766	2.755	0.135

[a] STAGE is nest stage.

Table 3. Support for models predicting nest survival based on nest and habitat characteristics while controlling for nest stage and year for Eastern Wood-Pewee nests in savanna, woodland, and forest in the Missouri Ozarks, 2009-2011.

Model [a]	$\mathrm{Log}_e(L)$	K	AIC_c	ΔAIC	w_i
STAGE PERFOREST	-548.623	3	1103.249	0	0.474
STAGE PERFOREST STOCK	-548.474	4	1104.954	1.705	0.202
STAGE PERFOREST NEST_HT STOCK	-547.961	5	1105.932	2.682	0.124
STAGE YEAR PERFOREST	-548.595	5	1107.199	3.95	0.066
STAGE YEAR PERFOREST STOCK	-548.44	6	1108.894	5.645	0.028
STAGE NEST_HT	-551.898	3	1109.799	6.55	0.018
STAGE YEAR PERFOREST NEST_HT STOCK	-547.932	7	1109.882	6.633	0.017
STAGE STOCK	-551.984	3	1109.973	6.724	0.016
STAGE PERFOREST NEST_HT	-551.984	3	1109.973	6.724	0.016
STAGE YEAR NEST_HT	-550.486	5	1110.981	7.732	0.01
STAGE YEAR STOCK	-550.667	5	1111.344	8.095	0.008
STAGE YEAR PERFOREST NEST_HT	-550.667	5	1111.344	8.095	0.008
STAGE NEST_HT STOCK	-551.875	4	1111.757	8.508	0.007
STAGE YEAR NEST_HT STOCK	-550.454	6	1112.921	9.672	0.004

[a] STAGE is nest stage, PERFOREST is percent forest in a 10-km radius, STOCK is percent tree stocking, and NEST_HT is nest height.

Table 4. Model-averaged coefficients and 95% confidence intervals from the top 4 nest survival models of Eastern Wood-Pewee nests found in savanna, woodland, and forest in the Missouri Ozarks, 2009-2011.

Parameter [a]	Model-averaged estimate	95% Confidence Interval
STAGE, Incubation	1.274	0.871, 1.678
PERFOREST	-1.256	-2.242, -0.27
NEST_HT	0.003	-0.009, 0.015
STOCK	-0.001	-0.003, 0.002

[a] PERFOREST is percent forest in a 10-km radius, NEST_HT is nest height, and STOCK is percent tree stocking.

Table 5. Support for models predicting clutch size and fledge rate of Eastern Wood-Pewees based on percent tree stocking and date in savanna, woodland, and forest in the Missouri Ozarks, 2009-2011.

Model [a]	Clutch size		Fledge rate	
	ΔAIC	w_i	ΔAIC	w_i
NULL	7.395	0.017	0	0.509
STOCK	0	0.693	2.058	0.182
DATE	9.423	0.006	1.58	0.231
STOCK DATE	1.791	0.283	3.76	0.078

[a] STOCK is percent tree stocking and DATE is ordinal date.

Table 6. Descriptive statistics for Eastern Wood-Pewee nests found in savanna, woodland, and forest in the Missouri Ozarks, 2009-2011.

Variable	n	Mean	Mean SE	95% CI	Min	Max
Clutch size	111	2.568	0.057	2.454, 2.681	1	3
Fledge rate	65	2.2	0.085	2.031, 2.369	1	3
Feeding rate						
Visits per hour	65	7.893	0.61	6.671, 9.115	1	21
Visit duration (min)	65	1.336	0.214	0.915, 1.758	< 1	57
Nest height (m)	310	12.239	0.248	11.751, 12.727	2.5	26.62

Table 7. Estimates of detection probability and density of Eastern Wood-Pewees in savanna, woodland, and forest from the most-supported distance-sampling models (ΔAIC < 4), in the Missouri Ozarks, 2009-2011.

Model [a]	Detection probability (SE)	K-S GOF [b]	Vegetation type	Density estimate (birds/ha)	Density SE	95% confidence interval	K	Δ AIC
OBS TYPE MINS	0.642 (0.025)	0.06	Savanna	0.2780	0.027	0.229, 0.337	9	0
			Woodland	0.4160	0.033	0.13, 0.23		
			Forest	0.428	0.021	0.388, 0.471		
OBS TYPE	0.656 (0.025)	0.143	Savanna	0.273	0.026	0.226, 0.328	8	0.16
			Woodland	0.406	0.031	0.349, 0.472		
			Forest	0.419	0.02	0.381, 0.460		
OBS TYPE MINS DOY	0.666 (0.025)	0.224	Savanna	0.268	0.025	0.223, 0.321	10	1.33
			Woodland	0.397	0.03	0.343, 0.460		
			Forest	0.415	0.02	0.378, 0.455		
OBS TYPE DOY	0.673 (0.024)	0.251	Savanna	0.266	0.024	0.222,0.317	9	2.62
			Woodland	0.39156	0.028	0.340, 0.451		
			Forest	0.41093	0.019	0.376, 0.449		

Model [a]	Detection probability (SE)	K-S GOF [b]	Vegetation type	Density estimate (birds/ha)	Density SE	95% confidence interval	K	Δ AIC
TYPE DOY HAB	0.60495 (0.028)	0.053	Savanna	0.255	0.028	0.205, 0.316	7	3.61
			Woodland	0.428	0.038	0.359, 0.511		
			Forest	0.479	0.029	0.425, 0.541		

[a] OBS is observer, TYPE is type of detection, MINS is minutes since sunrise, DOY is day of year, and HAB is habitat type.

[b] Kolmogorov-Smirnov goodness of fit