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EASTERN WOOD-PEWEE (*CONTOPUS VIRENS*) BREEDING DEMOGRAPHY ACROSS A GRADIENT OF SAVANNA, WOODLAND, AND FOREST IN THE MISSOURI OZARKS

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Abstract.—Better knowledge of bird response to savanna and woodland restoration is needed to inform management of these communities. We related temporal and habitat variables to breeding demography and densities of the Eastern Wood-Pewee (*Contopus virens*) across a gradient of savanna, woodland, and forest. We determined nest success, clutch size, young fledged, and breeding densities and evaluated support for relationships with year, nest stage, date, nest height, tree cover, and percent forest in a 10-km radius. One hundred and twenty-eight of 310 nests (41.3%) fledged young. The most supported nest-survival model included nest stage and percent forest in the landscape. Daily nest survival was greater in the incubation than in the nestling stage and increased substantially with decreasing forest in the landscape. Four nests (1.3%) were parasitized by Brown-headed Cowbirds (*Molothrus ater*). Eastern Wood-Pewee density increased 83% over a range of 10–170% tree cover (percent tree stocking). Increased nest success with decreasing forest in the landscape indicates that Eastern Wood-Pewees are not highly susceptible to forest-fragmentation effects in the Missouri Ozarks, probably because they were not very susceptible to brood parasitism. The absence of any strong relationships between habitat measures and nest success, clutch size, or young fledged is in contrast to the large increase in density over the range of tree cover and is further evidence that variation in bird density does not always correspond to similar patterns in productivity. *Received 2 November 2012, accepted 11 February 2013.*

Key words: breeding demography, *Contopus virens*, density, Eastern Wood-Pewee, fragmentation, parasitism, restoration, savanna, woodland.

Demografía Reproductiva de *Contopus virens* en un Gradiente de Sabanas, Áreas Arboladas y Bosques en los Ozarks de Missouri

Resumen.—Se necesita un mejor conocimiento de la respuesta de la aves a la restauración de sabanas y bosques para informar el manejo de sus comunidades. Relacionamos variables temporales y del hábitat con la demografía reproductiva y las densidades de *Contopus virens* a través de un gradiente de sabanas, áreas arboladas y bosques. Determinamos el éxito de los nidos, el tamaño de las nidadas, la cantidad de pichones emplumados y la densidad reproductiva, y evaluamos las relaciones de estas variables con el año, la etapa de anidación, la fecha, la altura del nido, la cobertura de árboles y el porcentaje de bosque en un radio de 10 km. Los polluelos de 128 de 310 nidos (41.3%) emplumaron. El modelo de supervivencia de nidos mejor apoyado incluyó la etapa del nido y el porcentaje de bosque en el paisaje. La supervivencia diaria de los nidos fue mayor durante la incubación que en la etapa de polluelos, y se incrementó sustancialmente con menor cantidad de bosque en el paisaje. Cuatro nidos (1.3%) sufrieron parasitismo por parte de *Molothrus ater*. La densidad de *C. virens* aumentó un 83% a través de un rango de 10–170% de cobertura de árboles (porcentaje de repoblamiento de árboles). El incremento en el éxito de los nidos con la disminución del porcentaje de bosque en el paisaje indica que *C. virens* no es áltamente susceptible a los efectos de la fragmentación de los bosques en los Ozarks de Missouri, probablemente debido a la baja susceptibilidad al parasitismo de cría observada. La ausencia de cualquier relación fuerte entre las medidas del hábitat y el éxito de los nidos, el tamaño de las nidadas o la cantidad de polluelos emplumados contrasta con el gran incremento en densidad en relación con la cobertura de árboles y provee más evidencia de que la variación en la densidad de las aves no siempre corresponde a patrones similares en la productividad.

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SAVANNAS AND WOODLANDS are natural communities that were historically prevalent across the Midwestern United States. Oak savanna covered 11–13 million ha prior to European settlement, but only 2,607 ha remained in the Midwest by 1985 (Nuzzo 1986). Land-use changes associated 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). Land management agencies have great interest in restoring these communities, and ~24,000 ha are being restored in Missouri by the Missouri Department of Conservation, the Missouri Department of Natural Resources, and The Nature Conservancy (K. Borisenko, K. McCarty, and D. Ladd pers. comm.). Mechanical tree thinning and prescribed fire are commonly used to restore or manage savanna and woodland. Mechanical thinning reduces tree density and canopy closure and allows more sunlight to reach the ground. Prescribed fire maintains an open understory by killing shrubs and small trees.

Savanna and woodland restoration can increase the availability of breeding habitat and promote increased avian breeding-season diversity, density, and nest survival in the Midwest. Savanna and woodland may provide additional habitat for some species that now occupy forest or grassland (Davis et al. 2000). Species richness and density tend to be greater in savanna managed with prescribed fire than in unburned, nonmanaged areas. Bird species richness and density were 1.65× and 1.80× greater, respectively, on burned than on unburned savanna restoration sites in central Minnesota (Davis et al. 2000). In Indiana, frequent fires in restored savanna and woodland were positively correlated with bird species diversity and with the density of the most-threatened species (Grundel and Pavlovic 2007b). Ten of 13 species, including the Eastern Wood-Pewee (*Contopus virens*; hereafter "pewee"), had greater daily nest survival in restored savanna than in closed-canopy forest in Illinois (Brawn 2006).

Understanding the effects of ecosystem restoration on birds is important in balancing multiple conservation goals that include desired plant community composition and structure in addition to wildlife abundance or viability. Studying a species across a wide habitat gradient can also identify factors that affect a species' demography. Pewees offer an excellent opportunity to address both of these objectives because they breed across a wide range of tree cover or percent tree stocking. Percent tree stocking is a measure of the percent of an area covered by tree canopies and is estimated from the tree diameters on a plot (Johnson et al. 2009); stocking can be >100%, because canopies can overlap. Definitions of savanna, woodland, and forest vary, but they are generally characterized as having <50%, 50–80%, or >80% canopy cover, respectively (Nelson 2002, U.S. Department of Agriculture Forest Service 2005). We used percent tree stocking as our measure of tree cover and as a continuous covariate, because it more precisely measures the extent to which a site is occupied by trees than field measurements of canopy cover and should be directly affected by tree thinning and prescribed fire.

The 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 north into the southern regions of Canada (McCarty 1996). Despite being widespread and abundant, pewees are a species of regional conservation concern in the Central Hardwoods Region because of the great reduction in the areal extent of woodlands (Fitzgerald and Nigh 2005). Because pewees often place nests high in the canopy and far out on horizontal limbs (Newell and Rodewald 2011b), relatively little is known about their breeding ecology. Newell and Rodewald (2011b) found marginally greater pewee nest survival on unharvested forest plots than on thinned shelterwood plots (similar canopy closure to savannas), but density was lower in unharvested forest, providing evidence that pewee abundance may not be coupled with productivity in different habitats.

Our objectives were to (1) evaluate how breeding demography (i.e., nest success, clutch size, young fledged, brood parasitism rate, and breeding density) varied across a gradient of tree cover represented by savanna, woodland, and forest communities; and (2) provide information on pewee breeding ecology such as nest success, clutch size, young fledged, brood parasitism rate, and breeding density. The pewee's use of a wide range of tree cover across savanna, woodland, and forest enabled us to consider the effects of a large ecological gradient on multiple aspects of the species' breeding demography, and we hypothesized that restoration would affect pewee productivity and density. If pewees are adapted to savanna and woodland, then productivity and density should peak at low or intermediate tree cover; but if they are better adapted to forest, these measures should increase with tree cover. Nest survival might also increase with tree cover, because nests in areas with higher tree cover (forest) may be more difficult to detect, given the number of trees for predators to search compared with savanna, or because these areas may support lower overall numbers of nest predators. Previous studies in the Midwest found pewee densities to be greatest at intermediate tree density (Grundel and Pavlovic 2007b) and in forest when a gradient of wooded habitats were sampled (Grundel and Pavlovic 2007a). We predicted that nest survival would (1) be greater in the incubation stage than in the nestling stage, (2) increase with percent forest in the landscape, and (3) increase with nest height. Nest survival is often greater in the incubation stage than in the nestling stage for passerines, potentially because of decreased activity at the nest and fewer parental visits during incubation (Martin et al. 2000). Nest survival has been positively correlated with percent forest in the landscape because of fragmentation effects such as increased nest predation and nest parasitism (Donovan et al. 1995, Robinson et al. 1995). Increased nest height can decrease the probability of predation (Wilson and Cooper 1998, Burhans et al. 2002), and higher pewee nests may be more difficult for predators, such as terrestrial snakes or mammals, to detect or access.

METHODS

Study sites.—We studied pewees in the Ozark Highlands of Missouri. The region is equally divided between steep and rolling hills and gently rolling plains, ranging in elevation from 100 to 600 m (McNab and Avers 1994). The region includes oak–hickory and oak–hickory–pine forest, bluestem (*Andropogon gerardii* and *Schizachyrium scoparium*) prairie, and Eastern Redcedar (*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 the 20 years preceding our study.

We selected 19 point-count sites across the region, of which 13 were also used as nest-monitoring sites (Fig. 1) on lands owned by the Missouri Department of Conservation, Missouri Department of Natural Resources, The Nature Conservancy, and the U.S. Department of Agriculture Forest Service. We selected sites by contacting land managers and asking them to identify managed savanna or woodland sites of >30 ha that had achieved the desired vegetative composition and structure for these communities or showed a positive response to restoration efforts. A second condition was that we could identify a forested site within 1 km on similar landforms that had not undergone any forest management or harvesting in >20 years, although most had not been managed in >50 years.

Nest searching and monitoring.—We searched for pewee nests between early May and mid-August, 2009–2011, using parental behavior within a territory. Nests were monitored every 3–4 days, or daily near predicted fledging date, to determine whether nests were active, the stage of the nest, and nest contents. We considered a nest successful if we verified at least one host fledgling. If we determined that a nest had failed, we attempted to locate a renesting attempt by the pair in that territory. We also continued monitoring territories with successful nests to determine whether the pair attempted a second brood. In 2010 and 2011, we intensified our focus on pewees and became much better at finding nests, which led to an increase in the number of nests monitored during those years.

Pewees nest at heights of 1.8–21 m (Peck and James 1987), so we constructed a telescoping video pole composed of a Spiderbeam antenna pole (WiMo, Herxheim, Germany) and a wireless camera and monitor (Defender Phoenix surveillance system; Defender, Niagara Falls, Ontario) to view nest contents ≤16.5 m high in 2010 and 2011. A two-person team used the video pole to determine the contents of nests once per nest stage (incubation and nestling stages). We did not use the video pole if we detected Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), or Brown-headed Cowbirds (*Molothrus ater*; hereafter "cowbirds") in the area, to minimize time around the nest and attention drawn to the nest. We also did not use the video pole if we could visually confirm the number of young in the nest with binoculars, because older pewee nestlings were usually conspicuous and easy to count, even in high nests, and we did not want to risk force-fledging young.

Point counts.—We conducted point counts in late May through early July, 2009–2011. First, we randomly placed a grid of points 250 m apart over a site and randomly selected a starting point and direction for each transect. We then selected 9–14 points within the managed and nonmanaged areas that were >50 m from the edge of the site. We conducted 10-min unlimited-radius point counts between sunrise and 1000 hours and did not conduct surveys in precipitation, in winds >13 km h^{-1}, or when temperatures were <10°C. We measured the distance between the observer and the location of the bird's initial detection location or a reference object near the bird with a Bushnell Yardage Pro laser range-finder (Bushnell, Overland Park, Kansas) but sometimes had to estimate distance when we could not focus the rangefinder on or near the bird because of vegetation or topography. We also recorded the temperature, wind speed (measured as 0–3 on the Beaufort scale), cloud cover, and precipitation at the beginning of each count. Each point was surveyed one time by one of five observers to maximize the number of points and study areas we could cover.

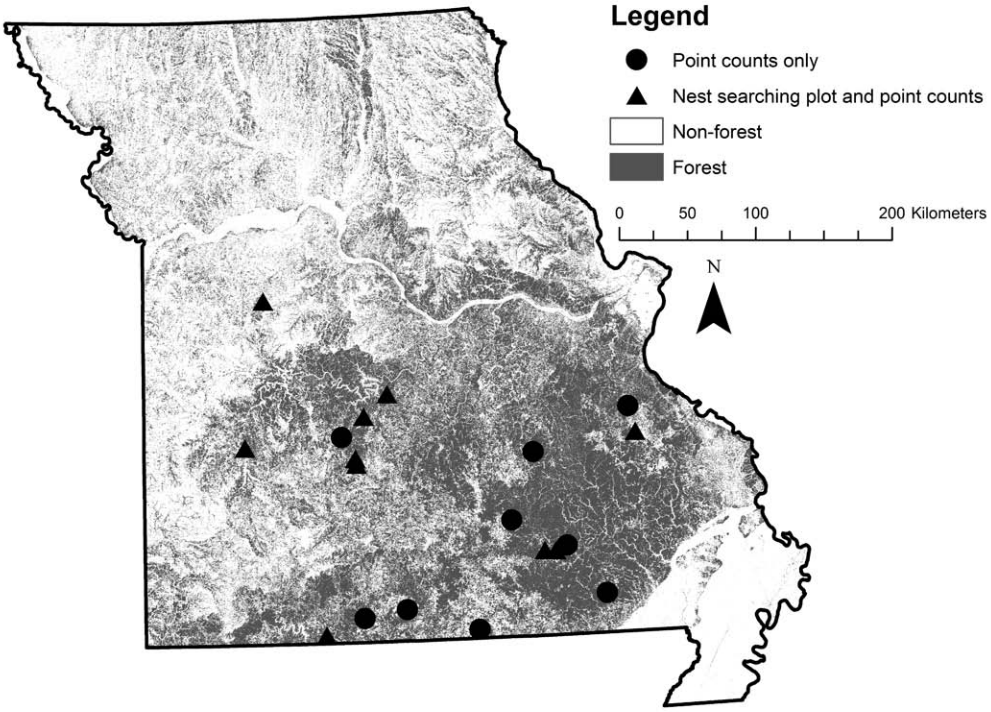

Fig. 1. Study areas on which we surveyed abundance and monitored nests of Eastern Wood-Pewees in savanna, woodland, and forest in the Missouri Ozarks, 2009–2011.

Vegetation and landscape measurements.—We recorded Universal Transverse Mercator coordinates at nests and survey points using a handheld global positioning system (Garmin, GPCMAP76S, Olathe, Kansas). We measured diameters at breast height (DBH) of all trees with DBH >2.5 cm in an 11.3-m radius of the nest and point-count locations. We measured tree cover using percent tree stocking, which we calculated from DBH of all live trees on a plot—using equations for upland oaks and hickories for deciduous trees, and the equation for short-leaf pine for all conifers—and summed these values for total percent tree stocking (Johnson et al. 2009). We measured nest height with a clinometer. We used ARCMAP, version 10 (ESRI, Redlands, California), 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 forest (deciduous, evergreen, and mixed forest) or nonforest (all other land cover types; Fig. 1). We chose a 10-km buffer, because past studies have successfully used this measure to identify landscape relationships (Donovan et al. 1995, Robinson et al. 1995, Cox et al. 2013).

Analysis of nest survival, clutch size, and young fledged.—We used the logistic exposure method to estimate daily nest survival and relationships with covariates (Shaffer 2004, Shaffer and Thompson 2007) using the GENMOD procedure in SAS (SAS Institute, Cary, North Carolina). The logistic exposure method considers nest fate during each monitoring interval and models the relationships with time varying (e.g., nest stage, date) and habitat covariates on survival (Shaffer 2004). We assigned values for nest stage and age, date, and nest status to a nest interval on the basis of the observed condition at the time of the nest check defining the end of each interval. We constructed a set of *a priori* candidate models and evaluated model support with Akaike's information criterion 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 nest stage (incubation or nestling stage), year (2009, 2010, or 2011), and four forms of ordinal date (ordinal date, ordinal date+ordinal date^2, ordinal date+ordinal date^2+ordinal date^3, and ordinal date+ordinal date^2+ordinal date^3+ordinal date^4). We did not consider nests in the laying stage in the survival analysis; it was difficult to determine when laying began, because we did not use the video pole on sequential days, to minimize adversely affecting egg laying or nest survival.

We then controlled for the most-supported temporal relationships by including variables from the top-ranked model in all habitat models. Habitat models consisted of all combinations of nest height, percent forest, and linear, quadratic, and cubic forms of tree cover (tree cover, tree cover+tree cover^2, and tree cover+tree cover^2+tree cover^3). We calculated period survival based on a 32-day nesting cycle with 14.5 incubation days (includes 2 laying days) and 17.5 nestling days. We excluded the upper and lower 1% of tree cover values to eliminate outliers. We also evaluated the relationship between nestling age and nest survival by comparing survival in the incubation stage and two nestling-stage age groups (<8 days old and ≥8 days old). Pewees typically fledged 15–18 days after hatching (S. W. Kendrick pers. obs.). We analyzed nestling age separate from overall nest success because we could confirm nestling age for only a subset of nests. We incorporated site as a random effect in models for nest survival, clutch size, and young fledged to account for variation among sites if it was supported by a likelihood ratio test of the global model with and without the random effect.

We similarly used a model-selection approach to evaluate support for the relationships with date and tree cover on the number of eggs in a nest (clutch size) and the number of young fledged (young fledged) using regression models with a normal distribution using Proc GENMOD or GLIMMIX in SAS, an approach that is robust to deviations from an assumed distribution when analyzing egg or nestling count data (McDonald and White 2010). In exploratory analyses, we also examined relationships with linear, quadratic, and cubic date and found that the linear date variable was the most supported. We excluded the upper and lower 1% of tree cover values to eliminate outliers when generating model predictions.

Analysis of density.—We determined relationships between tree cover and density and estimated density of pewees using hierarchical distance-based abundance models in the R package "unmarked" (Royle et al. 2004, Fiske and Chandler 2011). We used distance sampling to estimate a detection function and a Poisson distribution for the local abundance model that included covariate relationships on density. The unmarked hierarchical models used a site-specific likelihood for data gathered at each point as a function of local abundance around that point; abundance was treated as a random effect, and analysis was based on the integrated likelihood or on a function of the parameters of the detection function, density, and density covariates (Royle et al. 2004). Distance sampling assumes that (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 excluded observations with distances >90th percentile to minimize the effects of outliers (Buckland et al. 2001).

We fit models in a three-stage process and evaluated model support at each step using AIC_c. We first determined whether a uniform, half-normal, or hazard-rate key function was the most supported for the detection function. We used the most-supported key function and evaluated candidate models for detection probability in relation to observer, minutes since sunrise, ordinal date, and tree cover, singly and in all additive combinations. We considered observer because detectability can vary with degrees of skill, hearing, or experience (Alldredge et al. 2007); minutes since sunrise because of a potential decline in singing throughout the morning; day of year because birds may sing more earlier in the breeding season to defend and claim territories and to attract females; and tree cover because greater cover could make birds more difficult to detect or localize (Alldredge et al. 2007). We hypothesized that these covariates could influence detectability individually or in any additive combination.

We then included detection covariates from the most-supported detection model and evaluated support for four models predicting density: (1) a null model, (2) tree cover, (3) tree cover+tree cover^2, and (4) tree cover+tree cover^2+tree cover^3. Quadratic and cubic forms of tree cover suggest that bird density could peak in a nonlinear fashion or at some intermediate level of tree cover. We excluded the upper and lower 1% of tree cover values to eliminate outliers. We assessed the fit of the most-supported model with a Freeman-Tukey test based on a parametric bootstrap of the top-ranked model (Fiske and Chandler 2011). We estimated

TABLE 1. Descriptive statistics for Eastern Wood-Pewee nests found in savanna, woodland, and forest in the Missouri Ozarks, 2009–2011. Reported means are arithmetic means from the data.

Variable	*n*	Mean	SD	95% CI	Minimum	Maximum
Clutch size	111	2.57	0.63	2.45–2.69	1.00	3.00
Young fledged	64	2.20	0.61	2.03–2.38	1.00	3.00
Date of point counts	921	18 June	9.76	31 May–7 July	29 May	8 July
Nest height (m)	310	12.24	4.37	11.75–12.73	2.50	26.62
Tree cover at nests	310	76.62	33.64	72.86–80.38	8.72	209.84
Tree cover at points	921	78.58	37.25	76.17–80.99	0.00	237.39
Percent forest	310	62.29	17.76	60.32–64.27	24.88	92.10
Minutes since sunrise [a]	921	129.80	69.30	125.32–134.27	1.0	256.00

[a] From start of point count.

density over the range of observed tree cover by deriving predicted densities from the top-ranked density model.

RESULTS

We used 31, 63, and 216 nests monitored in 2009, 2010, and 2011, respectively, in the nest survival analysis. Nest predation was the most common cause of nest failure and accounted for 96% of failures. Ranges for nest height, tree cover, and percent forest were 2.5–26.6 m, 8.7–209.8%, and 24.8–92.1%, respectively, across the sample of nests (Table 1). Preliminary analyses indicated no support for inclusion of a young and old nestling-age category, so we proceeded with only incubation and nestling nest stages in our candidate models, and site was not supported as a random effect ($\chi^2 = 0.00$, df = 1, $P = 1.0$). Nest stage was the most-supported temporal variable (Table 2), and additional parameters were uninformative on the basis of ΔAIC_c values of 0–2 (Burnham and Anderson 2002, Arnold 2010); therefore, we included nest stage in all subsequent habitat models. Nest stage+percent forest was the most-supported nest survival model for habitat relationships and had 39% of the model weight (Table 2). There was some support for nest height and tree cover but, because the addition of these variables resulted in ΔAIC_c values of 0–2, we did not consider them further. Parameter estimates for the top model were as follows: intercept, 3.99 (95% CI: 3.36–4.62); nest stage (incubation vs. nesting), 1.28 (95% CI: 0.88–1.68); and percent forest, –1.21 (95% CI: –2.16 to –0.26). Mean daily survival rate was 0.9786 (95% CI: 0.9742–0.9823), resulting in period survival of 0.50 (95% CI: 0.43–0.56). Daily nest survival was greater in the incubation (0.9892 [95% CI: 0.9846–0.9925]) than in the nestling stage (0.9623 [95% CI: 0.9552–0.9684]). Period survival decreased from 64% to 37% over a range of 25% to 92% forest cover in the landscape (Fig. 2).

We confirmed the contents of 167 nests using the video pole and clutch size for 111 nests. Average clutch size was 2.57 (Table 1). Site was not supported as a random effect ($\chi^2 = 0.00$, df = 1, $P = 1.0$) for the clutch-size analysis. We found support for a linear relationship of clutch size with date (Table 3), and predicted clutch size declined from 2.83 (95% CI: 2.66–3.01) on 31 May to 2.03 (95% CI: 1.73–2.33) on 10 August. We determined the number of young fledged from 64 nests. Successful nests fledged an average of 2.20 young (95% CI: 2.03–2.38; Table 1). Site was supported as a random effect ($\chi^2 = 6.32$, df = 1, $P = 0.006$) for analysis of young fledged, and the estimated site variance was 0.1492. The null model was the most-supported model predicting number of young fledged (Table 3). Four nests (1.3% of nest attempts) were parasitized by cowbirds, and only one fledged a cowbird; the other three parasitized nests failed. However, we observed an additional cowbird fledgling tended by adult pewees for which we did not locate the nest.

TABLE 2. Support for logistic-exposure nest-survival models representing temporal and temporal + habitat effects on nest survival of Eastern Wood-Pewees in savanna, woodland, and forest in the Missouri Ozarks, 2009–2011. Models are ranked in decreasing order of support, and only models with $\Delta\text{AIC}_c < 4$ are shown.

Model [a]	–2Log(L)	*K*	ΔAIC_c	w_i
Temporal models				
Stage	1,102.78	2	0.00 [b]	0.36
Stage + date	1,102.19	4	1.41	0.18
Stage + date + date^2	1,100.96	6	2.19	0.12
Stage + year + date	1,099.56	5	2.78	0.09
Temporal + habitat models				
Stage + percent forest	1,096.15	3	0.00 [c]	0.39
Stage + percent forest + nest height	1,095.24	4	1.09	0.23
Stage + percent forest + tree cover	1,095.59	4	1.44	0.19
Stage + percent forest + nest height + tree cover	1,094.63	5	2.49	0.11

[a] Percent forest = percent forest in a 10-km radius of the nest.

[b] $\text{AIC}_c = 1{,}106.79$.

[c] $\text{AIC}_c = 1{,}102.15$.

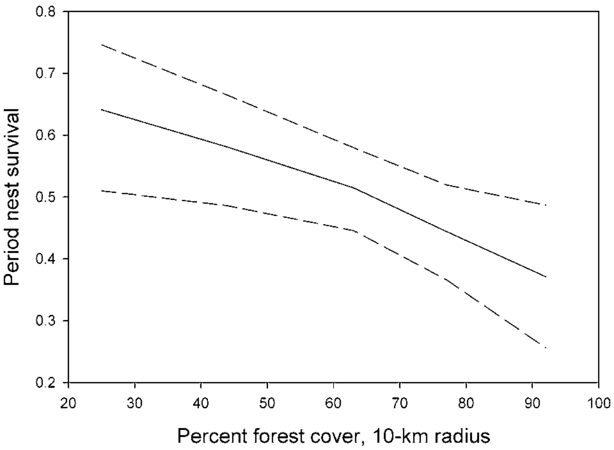

FIG. 2. Relationship between percent forest in a 10-km radius and period nest survival ± 95% confidence intervals based on the most-supported survival model by Eastern Wood-Pewee nests in savanna, woodland, and forest in the Missouri Ozarks, 2009–2011.

Table 3. Support for models predicting clutch size and number of young fledged of Eastern Wood-Pewees in savanna, woodland, and forest in the Missouri Ozarks, 2009–2011. Models with $\Delta AIC_c = 0$ have the most support, and models with greater values of ΔAIC_c and lesser values of w_i have less support.

	Clutch size			Young fledged		
Model	K	ΔAIC_c [a]	w_i	K	ΔAIC_c [b]	w_i
Null	1	12.28	0.00	3	0.00	0.46
Tree cover	2	14.35	0.00	4	2.26	0.15
Date	2	0.00	0.47	4	2.10	0.16
Date2	3	1.77	0.19	5	2.87	0.11
Date3	4	3.54	0.08	6	5.22	0.03
Tree cover + date	3	2.09	0.17	5	4.44	0.05
Tree cover + date2	4	3.91	0.07	6	5.30	0.03
Tree cover + date 3	5	5.73	0.03	7	7.70	0.01

[a] $AIC_c = 200.13$.
[b] $AIC_c = 135.47$.

Five observers surveyed 328, 238, 175, 103, and 77 points, respectively, between 29 May and 7 July, 2009–2011, and detected 866 singing pewees. We excluded from analysis 61 detections at distances >105 m. The most-supported detectability model included observer, day of year, and minutes since sunrise, and all competing models (ΔAIC_c <4) included day of year and observer (Table 4). The probability of detection was 0.65, based on the top model. The most-supported density model included a quadratic form of tree cover (Table 4), and there was no evidence of lack-of-fit based on the Freeman-Tukey test ($P = 0.851$). Estimated densities of pewees increased from 0.22 birds ha^{-1} (95% CI: 0.18–0.27) to 0.40 birds ha^{-1} (95% CI: 0.35–0.46) in areas with 10% and 170% tree cover, respectively; this is an 83% difference between areas with the greatest and lowest density (Fig. 3).

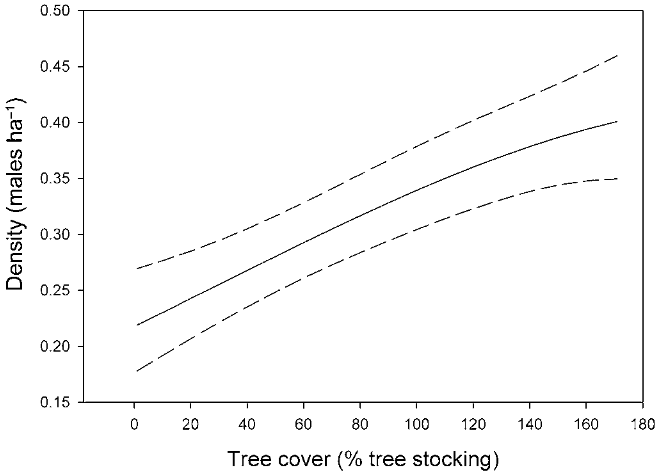

Fig. 3. Eastern Wood-Pewee predicted breeding density and 95% confidence intervals based on the most-supported detectability and density model across a range of tree cover based on distance modeling of point count data from savanna, woodland, and forest in the Missouri Ozarks, 2009–2011.

Discussion

Ours is the first study to examine effects of management across a wide habitat and landscape gradient on breeding demography of the Eastern Wood-Pewee. We found strong support for a temporal relationship of nest stage and a landscape relationship of percent forest with nest survival. Daily nest survival was similar to that reported by others, ranging from 0.969 to 0.983 in Midwestern states (Knutson et al. 2004, Brawn 2006, Newell and Rodewald 2011a). Nest survival was substantially lower during the nestling stage than during the incubation stage, which is similar to results for other forest and shrubland birds in the Midwest (Burhans et al. 2002, Newell and Rodewald 2011b, Cox et al. 2012b) and for Western Wood-Pewees (*Contopus sordidulus*; Chace et al. 1997). Increased predation rates during the nestling stage may be a result of increased parental and nestling activity at the nest, which potentially attracts visual predators (Martin et al. 2000, Stake et al. 2005). Blue Jays and cowbirds were common on our sites, and we observed adult pewees aggressively defending nests against both of these predators. A decrease in nest attendance and potential nest defense during the nestling stage, because adults are gathering food, might also be responsible for greater predation during the nestling stage. However, nest survival of some songbirds is greater in the nestling stage (Roper and Goldstein 1997, Cottam

Table 4. Support for top models ($\Delta AIC_c < 4$) predicting Eastern Wood-Pewee density in the Missouri Ozarks, 2009–2011. In step 1, only covariates affecting detectability (ρ) were considered, and in step 2, the most-supported covariates affecting detectability were included in candidate models for effects on density (λ).

Model	K	AIC_c	ΔAIC_c	w_i
Effects on detectability				
$\lambda(.)\ \rho(\text{Date + Obs + MSS})$	9	4,165.48	0.00	0.47
$\lambda(.)\ \rho(\text{Date + Obs})$	8	4,166.75	1.27	0.25
$\lambda(.)\ \rho(\text{Date + Obs + Tree Cover + MSS})$	10	4,167.33	1.85	0.19
$\lambda(.)\ \rho(\text{Date + Obs + Stock})$	9	4,168.72	3.23	0.09
Effects on detectability and density				
$\lambda(\text{Tree Cover + Tree Cover}^2)\ \rho(\text{Date + Obs + MSS})$	11	4,145.05	0.00	0.44
$\lambda(\text{Tree Cover})\ \rho(\text{Date + Obs + MSS})$	10	4,145.25	0.20	0.40
$\lambda(\text{Tree Cover + Tree Cover}^2\text{ + Tree Cover}^3)\ \rho(\text{Date + Obs + MSS})$	12	4,147.04	1.99	0.16
$\lambda(.)\ \rho(\text{Date + Obs + MSS})$	9	4,165.48	20.43	0.00

[a] Date = day of year, Obs = observer, MSS = minutes since sunrise.

et al. 2009) or not different among stages (Farnsworth and Simons 1999, Peak et al. 2004, Grant et al. 2005, Peak 2007). Survival may differ among species and between nest stages because of variation in predators, conspicuousness of the parents or nestlings, or the timing of nesting, given that predation may vary within a season (Benson et al. 2010, Cox et al. 2012b).

Percent forest cover in the landscape had the greatest influence on nest survival. We predicted that nest survival would increase with an increase in percent forest in a 10-km radius because of the relationship between forest fragmentation and nest success (e.g., Robinson et al. 1995); however, we found strong support for the opposite trend. Knutson et al. (2007) also found that pewee nest survival decreased with increasing forest in a 5-km radius in portions of Iowa, Minnesota, and Wisconsin. This pattern is contrary to that found in most Midwestern shrubland and forest songbirds, in which nest survival generally increases with forest cover because predation and nest parasitism increase with forest fragmentation (Donovan et al. 1995, Robinson et al. 1995, Thompson et al. 2000). Brood parasitism (hereafter "parasitism") is a primary driver of fragmentation effects on songbird productivity in the Midwest because their abundance increases in disturbed ecosystems and, consequently, rates of parasitism and cowbird-induced nest predation are higher in areas with lower percent forest cover in the landscape (Robinson et al. 1995, Thompson et al. 2000, Cox et al. 2012a). Despite cowbird presence on most of our sites, we observed very few parasitized pewee nests; therefore, we believe that predation by cowbirds was also likely low, which at least partially explains the lack of a fragmentation effect. Only 5.4% of 354 pewee nests from seven studies were parasitized, and pewees are infrequent acceptors of cowbird eggs (Underwood et al. 2004). Sixty-eight percent of 34 pewee nests in savanna and 100% of 12 nests in closed-canopy forest were parasitized in Illinois (Brawn 2006); however, Illinois is a highly fragmented and more hostile environment with greater predation rates, higher cowbird abundance, and more frequent parasitism than many other forested landscapes (>75% of open-cup nests found were parasitized in central Illinois; Robinson 1992). Cowbirds also depredate nests (Arcese et al. 1996, Hoover and Robinson 2007) and are more frequent predators in less-forested landscapes (Cox et al. 2012a). Pewees in the Missouri Ozarks seem less susceptible to these effects of fragmentation than other passerines in the Midwest, potentially because of lower levels of forest fragmentation in the Missouri Ozarks compared with other highly fragmented areas of the Midwest like Illinois. Pewees are also different from many other forest or shrubland birds that are affected by fragmentation in that they are high-canopy nesters and, therefore, may be affected by different predators. Research of subcanopy-nesting flycatchers in similar landscapes, however, indicates that possible predators include raptors, rodents, and Black Rat Snakes (*Elaphe obsolete*; Cox et al. 2012b). We know little about nest predators of canopy nests in general, and our study is another example of how knowledge of nest-predator species is needed to understand factors that affect songbird productivity among species and sites (Benson et al. 2010, Cox et al. 2012a, Reidy and Thompson 2012).

The weak relationships of tree cover and nest height with nest survival are similar to those reported in past studies in which pewee daily nest survival did not differ greatly across different vegetation types (Brawn 2006, Newell and Rodewald 2011a) or with nest height (Newell and Rodewald 2011b). Our findings suggest that pewee nest survival is influenced more by large-scale landscape factors than by small-scale nest-patch or nest-site measures. Nest heights were fairly similar to an average nest height of 18 m for pewee nests in southeastern Ohio ($n = 236$; Table 1). The small effect of nest height on survival is consistent with reports of nest success of pewees in Iowa, Minnesota, and Wisconsin (Knutson et al. 2007). Most support for an effect of nest height on nest survival is for understory or shrub-nesting species (Wilson and Cooper 1998, Burhans et al. 2002), and pewee nests in our study were very high.

Patterns in clutch size were similar to those reported in past studies in which passerine clutch size decreased as the breeding season progressed (Slagsvold 1982, Perrins and McCleery 1989, Skwarska et al. 2012). For species that undergo relatively little nest predation, one advantage to decreasing clutch size later in the breeding season, before migration, is that smaller clutches require less parental time and effort before and after fledging (Slagsvold 1982). This may especially apply to the pewee, because pairs initiated renesting attempts after nest failures throughout July; one pair was confirmed incubating three eggs as late as 3 August (S. W. Kendrick pers. obs.).

Pewees occurred across savanna, woodland, and forest, but density increased by 83% across our observed range of tree cover. Pewees nest in mature trees, and areas with greater tree cover provide more nesting substrate than open savannas with few trees, which potentially results in greater densities. Newell and Rodewald (2011a) found little difference in pewee density between forest with no timber harvest and forest with shelterwood harvest. However, Brawn (2006) detected slightly more pewees in savanna than in closed-canopy forest. The lack of any substantial relationship between tree cover and clutch size, young fledged, or nest survival was in stark contrast to the substantial variation in density in relation to tree cover. However, although pewees were equally productive across the gradient, a greater breeding density at greater levels of tree cover would mean more young produced per unit area at greater tree cover.

Further study to identify nest predators of pewees and other high-canopy nesters across varied landscapes is needed to tease out potential drivers of landscape relationships with pewee nest survival. We suggest that savanna and woodland restoration provide productive alternative habitat for the pewee, but densities will be less than in forest with greater tree cover. We provide further evidence that variation in abundance does not necessarily correspond to variation in productivity (Van Horne 1983, Perlut et al. 2006) and emphasize the need to consider all aspects of species demography when assessing habitat quality or effects of land management practices. A more complete understanding of the demography of the pewee will require additional intensive study of marked individuals to investigate dispersal, survival, and productivity across age classes and sexes.

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