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Woodland restoration and forest structure affect nightjar abundance in the Ozark Highlands

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Abstract

Chuck-will's-widow (*Antrostomus carolinensis*) and eastern whip-poor-will (*Antrostomus vociferus*) are nightjars in eastern North America that have declined 69% and 67%, respectively, in abundance since 1966, resulting in conservation concerns for these species. We investigated relationships between nightjar abundance and landscape composition, forest structure, and application of tree thinning and prescribed fire because of regional interest in woodland restoration and nightjar conservation. We conducted nocturnal nightjar surveys at 385 points in southern Missouri, USA, in 2014 and 2015 and related counts to pine (*Pinus* spp.) and hardwood basal area, canopy closure, percent forest cover, and percent of area thinned or burned within 500 m of survey points. We modeled abundance of chuck-will's-widow and eastern whip-poor-will using time-removal models that included a detection process and an abundance process within a hierarchical Bayesian framework. We detected 534 eastern whip-poor-will and 186 chuck-will's-widow during surveys. Our data supported global models that included all 6 vegetation and management variables for both species. Chuck-will's-widow abundance was negatively related to hardwood basal area and peaked at intermediate values of percent area burned and percent forest cover. Eastern whip-poor-will abundance was negatively related to hardwood basal area and canopy cover, positively related to percent forest cover and percent of area burned, and peaked at low to moderate levels of percent of area thinned.

Relationships to forest structure and management activities generally supported the conclusion that woodland restoration benefits nightjars and that chuck-will's-widow select landscapes with less forest cover than eastern whip-poor-will.

KEYWORDS

Antrostomus carolinensis, *Antrostomus vociferu*, basal area, canopy cover, chuck-will's-widow, eastern whip-poor-will, forest cover, Missouri, prescribed fire

Nightjars are nocturnal aerial insectivores in the family Caprimulgidae. Greater than 70% of aerial insectivores in North America are declining in abundance, with an overall decline of 31.8% since 1970 (Rosenberg et al. 2019). Chuck-will's-widow (*Antrostomus carolinensis*) and eastern whip-poor-will (*Antrostomus vociferus*) are nightjars that breed in forests and woodlands of southeastern and eastern North America, respectively. Chuck-will's-widow and eastern whip-poor-will declined 69% and 67%, respectively, in abundance since 1966 (Sauer et al. 2017) and as a result, there are conservation concerns for these species. Eastern whip-poor-will is listed as a species with population declines and moderate to high threats and chuck-will's-widow is categorized as a common bird in steep decline by the Partners in Flight Landbird Conservation Plan (Rosenberg et al. 2016). There is no consensus on the cause of declines but potential factors on the breeding grounds include landscape change such as urbanization, habitat degradation such as forest succession that results in more closed-canopy and dense forest, and declines in nocturnal insect prey (English et al. 2017, Spiller and Dettmers 2019, Cink et al. 2020, Straight and Cooper 2020, Tallamy and Shriver 2021).

Chuck-will's-widow and eastern whip-poor-will nest directly on the ground in leaf litter or pine (*Pinus* spp.) needles in deciduous, mixed, or pine forest. An open forest understory and proximity to openings can be important for both species because they facilitate aerial foraging for moths and beetles on moonlit nights and they may be absent from areas of extensive closed forest (Tozer et al. 2014, English et al. 2017, Cink et al. 2020, Straight and Cooper 2020). Eastern whip-poor-will are more abundant or have greater occupancy in heavily thinned pines, managed barrens, and forest with intermediate basal area than closed-canopy pine and deciduous forest (Akresh and King 2016, Spiller and King 2021) and in forested landscapes with clearcuts or other open-canopy vegetation types present (Tozer et al. 2014, English et al. 2017). Eastern whip-poor-will tend to be more abundant in landscapes with greater forest cover and larger forest patch size (English et al. 2017, Vala et al. 2020), while chuck-will's-widow are more abundant in landscapes with 50% forest cover and 50% agriculture than those with 90% forest cover (Cooper 1982).

Pine and pine-oak (*Quercus* spp.) woodlands are vegetation communities in the southeastern United States characterized by moderate canopy cover of 30–90%, little or no midstory, and a diverse ground cover of grasses, forbs, and shrubs that are maintained by fire and grazing (Nelson 2005). Woodlands now occur at a small fraction of their historical extent because of extensive timber harvest in the late 1800s and early 1900s, conversion to agricultural land, and succession to closed-canopy forest due to fire suppression and mesophication (i.e., succession to shade-tolerant mesophytic species) in eastern forests (Schroeder 1981, Nuzzo 1986, Cutter and Guyette 1994, Cunningham 2007, Nowacki and Abrams 2008). The loss of savannas and woodlands has likely contributed to the decline of many disturbance-dependent and open-forest bird species (Brawn et al. 2001, Hunter et al. 2001, Hanberry and Thompson 2019).

There is growing interest in restoring woodlands and open forest communities because of their contribution to biodiversity and habitat for early successional or disturbance-dependent birds (Thompson et al. 2018, Hanberry and Thompson 2019). The Collaborative Forest Landscape Restoration Program (CFLRP) is a national program to encourage the collaborative, science-based ecosystem restoration of priority forest landscapes (CFLRP 2021). Goals of the program include encouraging ecological, economic, and social sustainability of forest resources and reducing wildfire management costs by reestablishing natural fire regimes that preempt catastrophic wildfires. The Mark

Twain National Forest (MTNF) in Missouri received funding under this program to work with 7 collaborating natural resource agencies and non-government organizations to restore pine-oak woodlands in Missouri. Management is focused on opening the forest overstory and removing midstory trees through thinning to bring more light to the forest floor. Periodically burning the understory favors fire-adapted herbaceous species and reduces competition from woody species. Since 2012, 24,129 ha on the MTNF CFLRP have received mechanical overstory treatments and ≥2 prescribed fire treatments and are considered restored to their desired structure (B. K. Davidson, MTNF, personal communication). Restoration efforts to retore and sustain pine woodlands are occurring throughout the southeastern United States (CFLRP 2021). A better understanding of relationships between nightjar abundance and woodland restoration will allow for more effective woodland restoration and nightjar conservation efforts.

We investigated relationships between nightjar abundance and landscape composition, forest structure and composition, and application of tree thinning and prescribed fire given the current interest and efforts in restoring pine woodlands and in conservation of nightjars. We hypothesized abundance of chuck-will's-widow and eastern whip-poor-will would be non-linearly related to percent forest cover in the surrounding landscape, tree basal area, and canopy cover within forest, such that abundances peaked at intermediate values of these variables. We also hypothesized abundances would be positively or non-linearly related to the amount of tree thinning and area burned by prescribed fire because these practices maintain an open midstory, which is consistent with our understanding of these species' breeding habitat preferences.

STUDY AREA

This study occurred from April to July in 2014 and 2015 primarily on the 139,903-ha Collaborative Forest Landscape Restoration Project in the MTNF. The area is within the Ozark Highlands of Missouri and included portions of Butler, Carter, Howell, Oregon, Reynolds, Ripley, Shannon, and Wayne counties. Elevation ranged 112–386 m and topography was characterized by rolling to rugged terrain with diverse karst landscapes resulting in an abundance of exposed rock, caves, and spring systems amid the steep hills and valleys (The Nature Conservancy Ozarks Ecoregional Assessment Team 2003, Missouri Department of Natural Resources 2016). Climate was characterized by hot, humid summers and cool, relatively dry winters. Thirty-year average annual precipitation was 116.0 cm and mean monthly temperatures ranged from 0.4°C in January to 25.4°C in August (PRISM Climate Group 2021). Land use included forest products, cattle grazing, recreation on federal and state lands, and small towns and low-density rural development. Forests were dominated by oak-hickory, pine-oak, and mixed-oak woodland communities. Common upland tree species included post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*), white oak (*Q. alba*), northern red oak (*Q. rubra*), hickory (*Carya* spp.), shortleaf pine (*Pinus echinata*), and flowering dogwood (*Cornus florida*) with open woodland and savanna containing bluestem grasses (big bluestem [*Andropogon gerardii*], little bluestem [*Schizachyrium scoparium*]), sedges (*Cyperaceae* spp.), woody shrubs such as fragrant sumac (*Rhus aromatica*) and blackberry (*Rubus* spp.), and saplings (Nelson 2012). Non-forested areas were primarily cool-season grassland. The Ozark region has approximately 148 breeding bird species dominated by migrant and resident forest and woodland birds (Jacobs and Wilson 1997).

METHODS

Survey methods

We located 385 survey points primarily within the MTNF CFLRP boundaries and a subset outside the CFLRP boundary to sample a wider range of landscape conditions (Figure 1). Points were spaced every 1.6 km along Forest Service and county roads within the area of interest. We chose to survey along roads to facilitate surveying a large number points.

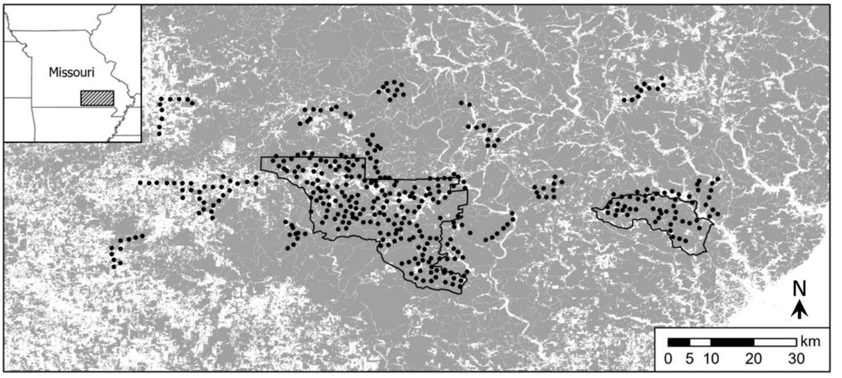

FIGURE 1 Locations of points surveyed for chuck-will's-widow and eastern whip-poor-will in 2014–2015, forest land cover (in gray), and boundaries of the Mark Twain National Forest Collaborative Forest Landscape Restoration Project (CFLRP) in Missouri, USA

We acknowledge the potential biases of surveying along roads, but we believe they were minor compared to the benefits of surveying more points. These were minimally improved roads that often had tree canopies overhead and the large detection radius for nightjars included substantial area away from roads. We conducted 6-minute unlimited-radius point-count surveys (Ralph et al. 1995) to determine abundances of chuck-will's-widow and eastern whip-poor-will. We visited each point once in either 2014 or 2015. We generally followed the survey guidelines for the Nightjar Survey Network (<www.nightjars.org/>, accessed 15 Nov 2021). We conducted surveys between 30 minutes post-sunset and 15 minutes pre-sunrise and only during peak moon cycles from April through July (i.e., face of moon >50%). We recorded each individual nightjar and whether they were audibly detected during each of the 6 1-minute intervals of the count. We did not conduct surveys during overcast skies, precipitation, or strong winds (>30 km/hr). Our survey design allowed us to estimate detectability based on time of detection, increased detectability by surveying when nightjars were most actively calling, and allowed us to visit more points than would be possible with multiple visits to a point. We believe it was more important to survey a greater range and have better replication of habitat conditions than to visit points more than once.

Forest and landscape variables

We sampled forest landscape and structural characteristics around survey points from national layers produced by integrating remotely sensed data. We obtained data on land cover and canopy cover at 30-m resolution from the National Land Cover Dataset (NLCD; Homer et al. 2015). We used maps of basal area created at a 250-m resolution using imputation of Forest Inventory and Analysis data based on moderate resolution imaging spectroradiometer imagery and re-sampled these to 30-m resolution to be consistent with the land cover and canopy cover layers (Wilson et al. 2012). We estimated nightjars could be detected at distances approaching 500 m so we calculated mean canopy cover, basal area of hardwoods, and basal area of pine within a 500-m radius of each survey point as a measure of forest structure within the area a nightjar was likely detected. We used ArcGIS Desktop 10.7 (Esri, Redlands, CA, USA) to calculate these focal statistics across all 30-m cells in the layers that were classified as forest by NLCD within 500 m of each point. We calculated the percent forest within 1 km of survey points to characterize the interspersion of forest and non-forested openings within the larger landscape. Habitat selection in birds is generally considered a hierarchical process whereby individuals first consider large-scale patterns when selecting a landscape and finer-scale patterns when selecting a territory or nest site (Hilden 1965, Johnson 1980, Jones 2001). Therefore, we measured the percent forest cover within a 1-km radius as a landscape-scale measure and forest structure and management within a 500-m radius as finer-scale measures that may reflect where birds locate territories. Given points were spaced 1.6 km apart, we acknowledge some overlap in the 1-km radii used to assess percent forest cover around points, but given the large number of points and range of landscape conditions, we believe any resulting spatial autocorrelation had minimal effect on the analysis.

We obtained spatially explicit data on management treatments (i.e., records of burning and thinning treatments) up to 10 years prior to surveys for points within the CFLRP area from the MTNF. From these data, we determined the percent of the area within a 500-m radius of survey points that had been thinned or burned within the last 10 years as measures of management activity in the area the bird was likely detected. We focused on management in the previous 10 years because the effects of thinning and fire diminish over time (Johnson et al. 2009).

Data analysis

We modeled abundance of chuck-will's-widow and eastern whip-poor-will and their relationships to 1 landscape, 3 forest structure, and 2 management variables using time-removal models within a hierarchical Bayesian framework (Kéry and Royle 2016). All models included a detection process in addition to the abundance process to account for individuals present but not detected, and thus estimate the overall number of individuals present at a point. We used a conditional, multinomial (3-part) model (Kéry and Royle 2016) and treated counts in the 6 separate 1-minute intervals y_i as a multinomial observation process integrated with a binomial availability process that ultimately stemmed from a Poisson abundance (ecological) process. Thus, the model was expressed by the 3 component models:

$$y_i \mid n_i \sim \text{Multinomial}(n_i, \pi_i^c),$$

$$n_i \sim \text{Binomial}(N_i, 1 - \pi_0),$$

$$N_i \sim \text{Poisson}(\lambda_i),$$

where N_i was the latent number of birds estimated at the ith point, n_i was the number of birds actually detected at the point, and y_i was the individual counts of birds detected among the time intervals with probabilities π_i^c based on the length of the intervals and the detection rate at the ith point. We modeled abundance for each species at a point by allowing N_i to follow a Poisson distribution with a mean abundance λ_i equal to a log-linear link that incorporated values at the ith point for the predictive variables in each model. We modeled detection probability based on day of year and time of day to account for a potential change in bird calling over the breeding season and throughout the night. We specified a random effect for observer to estimate the overall marginal effect and the variance among the observers around that mean but also to sample and report levels for each observer, which are drawn from that mean. For prediction, including abundance graphs, we used the overall grand mean as it reflects the effects of observers in general. We used vague normal priors and hyperpriors for detection effects and centered and scaled all predictor variables. The point counts had an unlimited detection radius; therefore, we did not sample a fixed area. Thus, abundances represent the number of birds at a point and were not converted to density. We fit models using Markov chain Monte Carlo analysis in JAGS (Plummer 2003) via the package jagsUI 1.5.0 in R version 3.6.0 (R Core Team 2019). We simulated 3 chains of 20,000 samples. We used a burn-in of 10,000 samples and a thinning rate of 5. We required a Gelman-Rubin diagnostic <1.1 for model convergence and evaluated posterior predictive checks and overdispersion on all models (Plummer 2003, Kéry and Royle 2016).

The 1 landscape and 3 forest structure variables were available for points inside and outside the CFLRP, but the 2 management variables were only available for points inside the CFLRP. Therefore, we took a 3-stage approach to model fitting that used informative Bayesian priors to derive a model that captured the structural and landscape patterns important across all points but also incorporated management effects for points inside the CFLRP (Gelman and Hill 2007). In the first stage, we fit 5 *a priori* models that considered the 1 landscape and 3 forest structure variables fit to all points outside and inside the CFLRP. We included a null model with no covariates and a global model with the

1 landscape and 3 forest structure variables in quadratic form to examine non-linear patterns between variables and abundance. We also considered 3 reduced versions of the global model that considered only the 3 forest structure variables, only the 1 landscape variable, and only the linear forms of the forest structure and landscape variables. We used vague normal priors for all parameter effects. We compared support for models based on values of the expected log pointwise predictive density (elpd) of the posterior distributions, estimated through leave-one-out cross-validation in the loo package (Vehtari et al. 2016, 2017). Higher densities indicate better prediction for withheld data. Vehtari et al. (2017) suggested differences in elpd >4 are potentially large and should be evaluated in terms of the standard error of the difference. Cross validation as measured by elpd identifies models that would perform well with new data, describe the data well and are generalizable, and are not overfit, which is what measures like Akaike's Information Criterion approximate based on the log likelihood and a fixed penalty for the number of parameters to guard against over-fitting.

In the second stage, we refit the most supported model for each species to the subset of data outside the CFLRP and calculated the mean and standard deviation of the posterior distribution of the estimated effects to be used in the third stage. We again used vague normal priors for all parameter effects.

In the third stage, we fit models to the points inside the CFLRP that included the supported forest structure and landscape variables from stage 2 and the management variables. We incorporated the posterior estimates for the forest structure and landscape variables from the second stage as informative priors and used vague normal priors for the additional management variables. Because the posterior distribution for model parameters is proportional to the combination of prior and likelihood distributions, this approach allowed us to combine the knowledge gained from modeling the data outside of the CLFRP with the information contained in the data from within the CFLRP area. We interpreted results from the final stage because it included all variables and was informed by all stages of model fitting. We report the mean, standard deviation, 95% credible interval, and proportion of the posterior distribution with the same sign as the mean for variables in the most supported models as measures of effect size and uncertainty. We present plots of the relationship between predicted abundance across the ranges of variables with meaningful effects while holding other variables in the model at their mean. Computer code for our abundance model is available online (Supporting Information) and data used in the analysis are available from the authors on request.

RESULTS

We surveyed 150 and 235 points outside and inside the CFLRP, respectively, over 2014–2015. We detected 0–5 and 0–4 eastern whip-poor-will and chuck-will's-widow per point, respectively, for 534 eastern whip-poor-will and 186 chuck-will's-widow detections (Table 1). We conducted surveys between 2029 and 0523 central daylight time from 30 April to 10 July. Survey points spanned a wide range of vegetation and landscape conditions. Mean pine and hardwood basal area ranged 0.04–12.89 and 0.44–9.78 m^2/ha, respectively. Mean canopy cover ranged 23–82%. The percent area burned or thinned around points ranged from 0–100% and percent forest cover within 1 km ranged 12–98% (Table 1). Correlations among predictor variables ranged from −0.11 to 0.75. The greatest correlations were between percent forest cover and hardwood basal area and canopy cover (0.64, 0.75, respectively) and between percent area thinned and burned (0.60); all other correlations were ≤0.50 (Table 2). Variance inflation factors were <3.0 except for percent forest cover, which was 3.62, indicating low multicollinearity (Table 2). These levels of multicollinearity generally do not require corrective action, but the observed variable correlations potentially had some effect on parameter estimates (Allison 1999).

We successfully fit the initial set of candidate models for chuck-will's-widow and eastern whip-poor-will to all points and, based on differences in the elpd, we selected the global model in the first stage for both species. The global models produced the highest elpd values under cross-validation, followed by the structural model for chuck-will's-widow and the linear model for eastern whip-poor-will (Table 3). Although those models showed similar predictive performance for each species, we selected to move forward with the global models given their ability to address landscape and structural aspects of habitat for nightjars and identify important ranges of these

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TABLE 1 Descriptive statistics for detections per point, survey time, and forest management and vegetation variables measured in a 500-m or 1-km radius around survey points for chuck-will's-widow and eastern whip-poor-will in Missouri, USA, 2014–2015

Variable	*n*	$\bar{x}$	SE	Min.	25th percentile	50th percentile	75th percentile	Max.
Chuck-will's-widow detections	385	0.48	0.04	0.00	0.00	0.00	1.00	4.00
Eastern whip-poor-will detections	385	1.39	0.07	0.00	0.00	1.00	2.00	5.00
Start time	385	2248	446	2029	2129	2227	2341	0523
Day of year	385	159.41	1.24	120.00	141.00	162.00	188.00	191.00
Burned 500 m (%)	235	16.73	2.09	0.00	0.00	0.00	8.93	100.02
Thinned 500 m (%)	235	14.76	1.51	0.00	0.00	0.00	25.89	99.95
Forest 1 km (%)	385	79	1	12	69	86	94	98
Canopy cover 500 m (%)	385	66.48	0.52	23.00	60.00	69.00	75.00	82.00
Pine basal area 500 m (m^2/ha)	385	4.33	0.14	0.04	2.25	3.70	5.91	12.89
Hardwood basal area 500 m (m^2/ha)	385	4.85	0.08	0.44	3.71	4.96	6.12	9.78
Total basal area 500 m (m^2/ha)	385	9.18	0.16	0.58	7.52	9.44	11.17	16.73

TABLE 2 Pearson correlation coefficients between predictor variables and tolerance and variance inflation factor (VIF) values for diagnosing multicollinearity for models in a study of chuck-will's-widow and eastern whip-poor-will abundance in Missouri, USA, 2014–2015

	Pearson correlation coefficient							
Variable	% forest	% burned	% thinned	Pine basal area	Hardwood basal area	Canopy cover	Tolerance	VIF
% forest	1.00	0.30	0.33	0.43	0.64	0.75	0.28	3.62
% burned	0.30	1.00	0.60	0.26	0.08	0.30	0.62	1.61
% thinned	0.33	0.60	1.00	0.27	0.11	0.30	0.61	1.64
Pine basal area	0.43	0.26	0.27	1.00	−0.11	0.46	0.51	1.95
Hardwood basal area	0.64	0.08	0.11	−0.11	1.00	0.50	0.39	2.56
Canopy cover	0.75	0.30	0.30	0.46	0.50	1.00	0.39	2.60

factors for increased abundance. We refit the global models to points outside the CFLRP and used the posterior estimates as informative priors for the final models for the 250 points inside the CFLRP that included management variables. The models for the 250 points inside the CFLRP that included management variables converged and were supported based on a lack of overdispersion for both models ($\hat{c}$ < 1.06) and Bayesian posterior predictive checks of 0.5 and 0.53, for eastern whip-poor-will and chuck-will's-widow models, respectively. Thus, our interpretations follow from the final model fits.

Detectability of chuck-will's-widow varied with observer and declined with day of year as indicated by 95% credible intervals (CRIs) that did not overlap zero (Table 4). The most supported relationships to abundance were hardwood basal area, percent forest cover, and percent area burned (Table 4). Chuck-will's-widow abundance

TABLE 3 Support for candidate models predicting abundance of chuck-will's-widow and eastern whip-poor-will in relation to forest, landscape, and management covariates in Missouri, USA, 2014–2015 based on expected log pointwise predictive density (elpd) and its standard error (SE elpd), the difference in elpd from the top model (elpd diff) and its standard error (SE diff), overdispersion ($\hat{c}$) and Bayesian P-values (Bayes P-value). Models with greater elpd have more support and can be further assessed for adequate fit based on overdispersion ($\hat{c}$; values close to 1 indicate good fit) and Bayes P-values (values close to 0.5 indicate good fit)

Species, model	elpd diff	SE diff	elpd	SE elpd	$\hat{c}$	Bayes P-value
Chuck-will's-widow						
Global	0.0	0.0	−141.7	7.5	1.11	0.69
Structural	−2.7	3.1	−144.4	7.6	1.10	0.68
Landscape	−8.1	3.8	−149.9	7.9	1.09	0.65
Linear	−11.2	4.6	−152.9	8.2	1.08	0.65
Null	−30.1	6.7	−171.8	9.3	1.02	0.53
Eastern whip-poor-will						
Global	0.0	0.0	−279.1	9.9	0.92	0.29
Linear	−0.9	7.6	−280.0	9.8	0.91	0.28
Landscape	−11.5	8.4	−290.6	9.5	0.88	0.23
Structural	−24.3	9.7	−303.3	9.2	0.82	0.13
Null	−34.4	10.7	−313.5	9.4	0.83	0.15

decreased from 2.6 birds/point to 0.2 birds/point as hardwood basal area ranged from 0.4 m^2/ha to 9.3 m^2/ha (Figure 2). Chuck-will's-widow reached its highest abundance (>2 birds/point) in landscapes with 50–70% forest cover and decreased to <0.6 birds/point as forest cover approached 0% and 100% (Figure 2). Chuck-will's-widow abundance increased from 1.4 birds/point to 2 birds/point as the percent area burned increased from 0% to 25%, but then declined as the percent area burned increased to 100% (Figure 2).

Detectability of eastern whip-poor-will also varied with observer, but effects of time and day of year were not supported (Table 4). The most supported effects on abundance were hardwood basal area, canopy cover, and percent forest cover based on mean effects with 95% CRIs that did not overlap zero (Table 4; Figure 2). Abundance decreased from 2 birds/point to 0.4 birds/point as hardwood basal area ranged from 0.3 m^2/ha to 9.3 m^2/ha. Abundance decreased from 1.8 birds/point to 0.7 birds/point as canopy cover increased from 23% to 82%. Abundance increased from 0 birds/point to 3.1 birds/point as percent forest cover ranged from 12% to 98% (Figure 2). There was also some support for effects of burning and thinning based on proportions of the posterior distribution that were greater or less than zero (0.733–0.971; Table 4). Eastern whip-poor-will abundance increased from 1.3 to 2.7 birds/point as the percent area burned increased from 0 to 100%. Eastern whip-poor-will abundance increased from 1.2 to 1.3 birds/point as the percent area thinned increased from 0% to 30%, and then declined to 0.6 birds/point as percent area thinned increased to 100% (Figure 2).

DISCUSSION

Our data generally supported our hypotheses that chuck-will's-widow and eastern whip-poor-will abundance was positively related to woodland restoration, moderate tree basal area and canopy cover, and some degree of interspersion between forest and open areas at the landscape scale. Open areas consisted primarily of pastures but

TABLE 4 Mean, standard deviation (SD), 95% credible interval (CRI), and proportion of the posterior distribution with the same sign as the mean (Propn) for parameters in hierarchical time-removal models with a detection process and an abundance process for predicting abundance of chuck-will's-widow and eastern whip-poor-will in Missouri, USA, 2014–2015

	Chuck-will's-widow				Eastern whip-poor-will			
Process, parameter	$\bar{x}$	**SD**	**95% CRI**	**Propn**	$\bar{x}$	**SD**	**95% CRI**	**Propn**
Detection								
Observer mean	−3.09	1.20	−6.19, −1.23	0.99	−1.52	1.31	−4.50, 1.01	0.91
Observer variance	1.98	1.74	0.07, 6.97	1	3.14	1.43	1.36, 6.95	1
Day of year	−1.55	0.24	−2.02, −1.08	1	0.04	0.14	−0.24, 0.31	0.62
Time	0.05	0.34	−0.62, 0.73	0.56	0.05	0.18	−0.30, 0.40	0.60
Time^2	0.28	0.22	−0.06, 0.85	0.94	−0.01	0.07	−0.14, 0.12	0.55
Intercept	0.62	0.33	−0.01, 1.29	0.97	0.26	0.14	−0.01, 0.53	0.97
Observer 1	−2.42	1.28	−4.41, 0.60	0.94	−2.14	0.71	−3.30, −0.35	0.99
Observer 2	−4.04	2.60	−11.14, −1.13	1	−5.61	2.47	−11.93, −2.43	1
Observer 3	−5.51	2.93	−13.71, −2.25	1	0.50	0.28	−0.05, 1.05	0.96
Observer 4	−2.32	0.92	−4.02, −0.33	0.99	0.06	0.35	−0.68, 0.71	0.59
Observer 5	−2.25	0.43	−3.09, −1.43	1	0.46	0.18	0.10, 0.80	0.99
Observer 6	−2.12	0.37	−2.85, −1.41	1	−0.30	0.22	−0.74, 0.12	0.92
Observer 7	−3.19	1.01	−5.54, −1.62	1	−3.74	0.59	−4.98, −2.63	1
Abundance								
Percent burned	0.57	0.42	−0.25, 1.38	0.92	−0.15	0.16	−0.46, 0.15	0.83
Percent burned^2	−0.71	0.32	−1.37, −0.10	0.99	0.14	0.08	0.00, 0.30	0.97
Percent thinned	−0.02	0.26	−0.55, 0.48	0.53	0.07	0.11	−0.15, 0.29	0.73
Percent thinned^2	−0.06	0.19	−0.48, 0.30	0.59	−0.07	0.06	−0.18, 0.04	0.89
Pine basal area	0.09	0.16	−0.21, 0.40	0.71	0.06	0.11	−0.14, 0.28	0.70
Pine basal area^2	−0.09	0.12	−0.34, 0.14	0.79	−0.01	0.06	−0.13, 0.11	0.53
Hardwood basal area	−0.42	0.20	−0.82, −0.05	0.99	−0.28	0.10	−0.47, −0.07	1
Hardwood basal area^2	−0.11	0.14	−0.40, 0.15	0.77	−0.04	0.07	−0.17, 0.09	0.72
Canopy cover	0.19	0.25	−0.30, 0.68	0.78	−0.31	0.11	−0.53, −0.09	1
Canopy cover^2	0.03	0.10	−0.17, 0.22	0.62	−0.07	0.06	−0.20, 0.04	0.89
Percent forest	−0.67	0.29	−1.26, −0.12	0.99	0.88	0.16	0.57, 1.20	1
Percent forest^2	−0.37	0.15	−0.69, −0.10	1	−0.01	0.09	−0.20, 0.17	0.53

included a limited number of wildlife openings and timber harvests. One of the most strongly supported relationships was the negative relationship of both species' abundances to hardwood basal area. Lower hardwood basal area is typical of pine and pine-oak woodlands because these ecosystems typically have lower tree density and basal area than closed canopy pine and oak forest. Management to restore woodlands typically uses tree thinning to remove mid-story trees and some overstory trees to create basal areas in the range of 2.8–7.4 m^2/ha

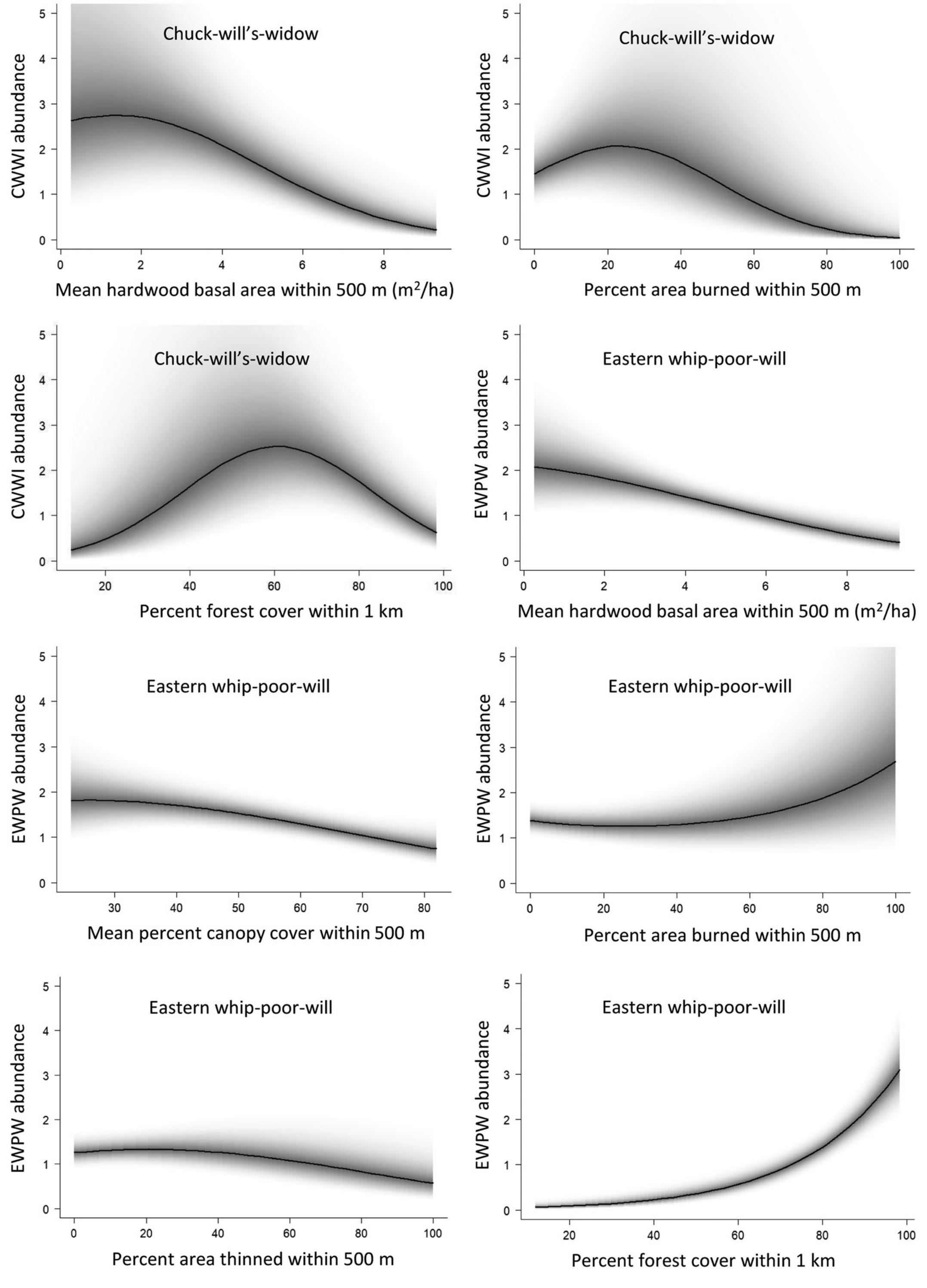

FIGURE 2 Predicted abundances of chuck-will's-widow (CWWI) and eastern whip-poor-will (EWPW) in relation to landscape composition, forest structure, and management in Missouri, USA, 2014–2015. The black line represents the mean and uncertainty in predictions is conveyed by the full posterior of Monte Carlo samples in gray

and 30–80% stocking (Dey et al. 2017, Bragg et al. 2020) and pine-woodland restoration specifically targets hardwoods for removals.

Thinned stands with lower basal areas also tend to have lower canopy cover, and our data revealed a negative relationship of eastern whip-poor-will abundance and canopy cover but no supported relationship for chuck-will's-widow. The weaker and inconsistent relationship between species with canopy cover, in contrast to basal area, could be because canopies quickly respond to thinning and begin to close again (Johnson et al. 2009), whereas an open midstory and reduced basal area can be maintained by periodic fire.

While abundance for both species was negatively related to hardwood basal area, our data had little support for a relationship to pine basal area. This could be because management in the study area was focused on pine woodland restoration and thinning generally removed hardwoods while favoring pines. Therefore, restored pine woodlands tended to have low hardwood basal area, moderate pine basal area, and a total basal area lower then closed forest. Spiller and King (2021) similarly found that occurrence of eastern whip-poor-will peaked at an intermediate basal area of 13.8 m^2/ha; however, basal areas of northeastern forests are generally higher than forests in the Ozark Highlands. Total basal area in our study averaged 9.2 m^2/ha and reached a maximum of 16.7 m^2/ha; nightjar abundances reached a peak where hardwood basal area approached zero and total basal area was around 9–10 m^2/ha.

Our data also had some support for direct relationships with management. Chuck-will's-widow abundance was greatest at intermediate levels of percent forest burned and eastern whip-poor-will abundance increased as area burned increased from 0% to 100%. Periodic burning is used in woodland management to kill small trees and shrubs and prevent the redevelopment of an understory and midstory (Dey et al. 2017, Bragg et al. 2020). In the interval between fires, the understory rapidly redevelops by sprouting and can be dense until the next fire sets it back again, typically before it gets taller than 1–2 m. Spiller and King (2021) did not examine burning as a management practice but did report the occurrence of eastern whip-poor-will was negatively related to understory height, which is consistent with effects of fire in our study. Eastern whip-poor-will abundance was greater in pitch pine (*Pinus rigida*)–scrub oak (*Quercus ilicifolia*) barrens managed by thinning, mowing, burning, and herbicide than in closed canopy forest, and nests were found in both dense and sparse understories in Massachusetts, USA (Akresh and King 2016). Burning also stimulates new growth of vegetative ground cover that can result in greater insect abundance and potential prey for nightjars. Forests in Kentucky, USA, managed with prescribed fire had greater insect abundances and foraging activity by bats, another nocturnal aerial insectivore (Lacki et al. 2009). The combination of thinning and repeated prescribed fire resulted in greater abundances and diversity of flower-visiting insects in forest in North Carolina, USA (Campbell et al. 2018).

Given the strong negative relationships between abundance and hardwood basal area, and positive relationship to moderate or high levels of precent area burned, we expected more support for a positive effect of percent area thinned. There was a positive correlation of 0.6 between burning and thinning, which is likely because prescribed fire is frequently used to prevent the redevelopment of a midstory after a thinning. We suggest the lack of a stronger relationship with thinning is in part because many areas had low hardwood basal area and woodland structure due to earlier thinnings (i.e., >10 years ago, thus not counted by us), and woodland structure was now maintained by prescribed fire; hence, we detected a stronger effect of fire and hardwood basal area. In Massachusetts, eastern whip-poor-will were more abundant in scrub oak barrens (<22% canopy cover) and recently thinned pitch pine forest (<40% canopy cover) than forest (>80% canopy cover; Akresh and King 2016).

Our data had some evidence for slightly lower abundances of chuck-will's-widow and eastern whip-poor-will if >40% of the landscape was burned or was thinned within the last 10 years, respectively. These results seem inconsistent with other stronger effects, such as a positive relationship with lower hardwood basal area for both species, and with percent area burned for eastern whip-poor-will, and are in the opposite direction hypothesized. The non-linear nature of these relationships suggests some benefit to heterogeneity in the landscape with managed and non-managed areas, perhaps because fire can have positive (Lacki et al. 2009, Campbell et al. 2018) and negative effects (Thom et al. 2015) on potential insect prey of nightjars. Given that burning and thinning are constrained to modest portions of the landscape and that current landscape burning practices result in natural heterogeneity of burned and unburned areas in burn units, we do not think this is a concern, and suggest these practices are needed because of their greater benefit in restoring and sustaining woodland structure.

Our findings are consistent with results from Georgia, USA, that chuck-will's-widow are more abundant than eastern whip-poor-will in landscapes with 50% forest cover and 50% agriculture, whereas eastern whip-poor-will are more abundant in landscapes that were 90% forest and 10% agriculture (Cooper 1982). In our study, chuck-will's-widow reached their greatest abundance in landscapes with 60% forest cover and 40% pasture, wildlife openings, or openings created by recent timber harvest, while eastern whip-poor-will reached its greatest abundance at sites approaching 100% forest in a 1-km radius. English et al. (2017) similarly reported the probability of detecting eastern whip-poor-will in breeding bird atlas blocks in Ontario, Canada, increased as the percent forest cover increased from 4% to 96%. In Ontario, Vala et al. (2020) reported eastern whip-poor-will occupancy was positively related to forest patch size and negatively related to urban land cover. Also in Ontario, Tozer et al. (2014) reported eastern whip-poor-will site occupancy is positively related to the occurrence of clearcuts in forest landscapes, and Farrell et al. (2019) reported a positive relationship with the percent of open wetland in the landscape (up to 15%) but no relationship with percent of area in clearcuts. Eastern whip-poor-will are more abundant in Illinois, USA, forests where openings are present (Bjorklund and Bjorklund 1983). While abundance of eastern whip-poor-will increased as percent forest cover approached 100%, much of this forest cover is woodland managed by thinning and fire and has many small canopy gaps and an open midstory. The combination of a moderate canopy closure, no midstory, and a variable understory resulting from thinning and periodic prescribed fire supports high abundances of other early successional birds (Hanberry and Thompson 2019), so we do not think it should be surprising woodland restoration and management is related to nightjar abundance. We are not aware of any suggested reasons for why chuck-will's-widow preferred landscape with more open land than eastern whip-poor-will, but perhaps they make greater use of open land for foraging.

There were a couple of differences between species in factors affecting abundance besides greater abundances of chuck-will's-widow at moderate levels of percent forest cover and eastern whip-poor-will at high levels of forest cover. Eastern whip-poor-will abundance increased with decreasing canopy cover, while there was no such relationship for chuck-will's-widow. We suggest both species are responding to heterogeneity in tree cover, but chuck-will's-widow may prefer heterogeneity at a coarser scale such as between forest or woodland and non-forest openings. Eastern whip-poor-will may prefer heterogeneity at a finer scale created by lower canopy cover within woodlands. Their relationships with percent area burned were also consistent with this idea. Eastern whip-poor-will abundance peaked at 100% of area burned, but there was still heterogeneity within burned areas because of topography and fire behavior. Chuck-will's-widow abundance peaked at 25% area burned, which would result in coarser-scale heterogeneity between burned and non-burned areas.

Chuck-will's-widow and eastern whip-poor-will inhabit barrens, savannas, woodlands, and other forms of open forests throughout the eastern United States. We concur with others who suggest eastern whip-poor-will is a disturbance-dependent species and we suggest the same is true for chuck-will's-widow (Tozer et al. 2014, Akresh and King 2016, Farrell et al. 2017, Spiller and King 2021). Some combination of tree cover with open to dense understory, open midstory, low to moderate tree density and canopy cover, and openings in the landscape seem to be important structural components for breeding habitat. This structure likely facilitates penetration of the canopy by moonlight, the location and capture of prey (English et al. 2017, Spiller and King 2021), and perhaps increased food resources for their insect prey. Disturbance is required to prevent the succession and densification of these open forests to closed canopy forests and redevelopment of the midstory.

MANAGEMENT IMPLICATIONS

Management to restore and sustain woodlands that reduces basal areas to 9–10 m^2/ha by thinning and uses periodic prescribed fire to prevent the redevelopment of the understory and midstory should create conditions to support high abundances of chuck-will's-widow and eastern whip-poor-will in the Ozark Highlands. Thinning and fire are essential tools for restoring and sustaining woodland structure that benefits nightjars. We suggest planning should also ensure there is some heterogeneity in the larger landscape created by sites managed with thinning and fire and those not thinned or burned. In the Ozark Highlands, this heterogeneity can occur across land types when they are managed for the communities they are most suited for (i.e., prairie, glade, savanna, woodland, forest) or because of the effects of topographic diversity on fire behavior.

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CONFLICT OF INTERESTS

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

We followed recommendations for the use of wild birds in research by the Ornithological Council (Fair et al. 2010).

DATA AVAILABILITY STATEMENT

The computer code that support the findings of this study are available in the supporting information and the data are available from the corresponding author upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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