*The Wilson Journal of Ornithology* 128(4):846–856, 2016

# EASTERN WHIP-POOR-WILLS (*ANTROSTOMUS VOCIFERUS*) ARE POSITIVELY ASSOCIATED WITH LOW ELEVATION FOREST IN THE CENTRAL APPALACHIANS

CHRISTINA L. SLOVER[1,3,4] AND TODD E. KATZNER[1,2,5]

ABSTRACT.—Populations of the Eastern Whip-poor-will (*Antrostomus vociferus*) are thought to be declining because of a range of potential factors including habitat loss, pesticide use, and predation. However, this species is nocturnal and, as a consequence, it is poorly studied, and its population status is not well assessed by traditional diurnal bird surveys. We used nocturnal road surveys to study habitat associations and distribution of Eastern Whip-poor-wills to better understand and contextualize their population status and to provide a framework for subsequent research and management. We used occupancy models to associate presence of Eastern Whip-poor-wills with habitat characteristics. Global models with habitat associations at a radius of 1600 m (1.0-ha area) were the best supported by the data, suggesting that this was the scale at which the species responded to the habitat parameters we measured. At this scale, Eastern Whip-poor-wills most frequently occupied areas lower in elevation and characterized by forested, herbaceous, and wetland cover types. In contrast, high elevation conifer forest communities had substantially fewer Eastern Whip-poor-wills. Detection rates were positively correlated with moon visibility and negatively correlated with noise. We used the results of our surveys to generate a regional model to predict distributions of Eastern Whip-poor-wills and that can be used as a framework for future management. Our results suggest that succession of agricultural fields and other clearings into forested habitats with dense understory may be a contributing factor to ongoing declines of Eastern Whip-poor-wills. *Received 22 September 2015. Accepted 1 March 2016.*

Key words: *Antrostomus vociferus,* Eastern Whip-poor-will, elevation, forest edge, land cover types, occupancy modeling, predictive map.

Populations of avian aerial insectivores are declining (Sauer et al. 2014), often more rapidly than those of many other birds of great conservation concern (Nebel et al. 2010). These declines are of particular note because variation in numbers of aerial insectivores may indicate underlying ecosystem changes (Nebel et al. 2010, Hobson et al. 2015). In the northeastern United States, populations of aerial insectivore species began to decline around the late 1970s (Smith et al. 2015). Putative causes for these declines include predation, pesticide use for Lepidopterans, climate change, and loss of habitat (Cink 2002a, b; Nebel et al. 2010; Dunn et al. 2011; Hunt 2013).

Declines in this guild are prominent in the Family Caprimulgidae, a group characterized by cryptic coloration, wide mouths, large eyes, and the ability to take insects on the wing (Cink 2002b). North American species in this family include the Common Nighthawk (*Chordeiles minor*), Lesser Nighthawk (*C. acutipennis*), Chuck-will's-widow (*Antrostomus carolinensis*), Mexican Whip-poor-will (*A. arizonae*), Common Poorwill (*Phalaenoptilus nuttallii*), and Eastern Whip-poor-will (*A. vociferus*). These species are generally not active during the day, making them difficult to survey. Nevertheless, there is documentation from limited Breeding Bird Survey (BBS) data that populations of several of these species are experiencing significant declines; for others, the data show no survey-wide trend or provide imprecise population estimates (Sauer et al. 2014). As such, there is an important need to evaluate these populations to understand how they are faring and to identify potential steps towards their conservation and management.

Eastern Whip-poor-wills are thought to have specific habitat associations. Historic accounts suggest that this species breeds on dry, well-drained ground at the edge of mixed oak (*Quercus* spp.), beech (*Fagus* spp.), and pine (*Pinus* spp.) forest with little to no underbrush and uncrowded trees (Tyler 1940). In some reports, the openness of forest understory is more important in determining appropriate nesting habitat than is the composition of the forest (Wilson 1985). More

[1] West Virginia University Division of Forestry and Natural Resources, P.O. Box 6125, Morgantown, WV 26506-6125, USA.

[2] U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 970 Lusk Street, Boise, ID 83706, USA.

[3] Current address: West Virginia University Department of Biology, P.O. Box 6057, Morgantown, WV 26506-6057, USA.

[4] Corresponding author; e-mail: sloverc524@gmail.com

[5] Corresponding author; e-mail: tkatzner@usgs.gov

recent literature also suggests that Eastern Whip-poor-wills prefer areas with dry soils in pine, beech, or oak forests for nesting (Cink 2002b), and that presence of these birds is positively correlated with pine forests and large clearcuts and negatively associated with high elevation dense forest cover and developed landscapes (Hunt 2006). Finally, it is not clear at what scale this species responds to the habitats it uses (Cink 2002b) or the state of the habitat it prefers, with contrasting reports suggesting preference for both pristine (Hunt 2013) and impacted (Reese 1996) habitats.

We studied occupancy and distribution of Eastern Whip-poor-wills to better understand their habitat associations in the central Appalachians and to gain insight into how their populations may be responding to modern land use practices. In particular, we sought to answer the following questions a) at what scale do Eastern Whip-poor-wills respond to the habitat variables we measured?; b) what land cover types are associated with the presence of Eastern Whip-poor-wills?; and c) what is the expected distribution of the species within our focal study area, the Monongahela National Forest (MNF), in the central Appalachian Mountains?

## METHODS

*Study Area*.—We collected data on Eastern Whip-poor-wills within the MNF and surrounding lands of West Virginia, USA (Fig. 1). The MNF stretches over 305,538 ha within the Central Allegheny Mountain province of the Appalachian Plateau in West Virginia (Ferguson 1964). Elevation within the MNF ranges from 305–1,482 m above sea level (USDA 2013). The western side of the MNF receives ~152 cm of rain per year while the eastern side receives ~76 cm (USDA 2013). Some of our transect routes followed the border between the MNF and heavily impacted land not managed by the United States Forest Service. These properties often included houses, pastures, and forests.

*Focal Species*.—Eastern Whip-poor-wills are migratory ground-nesting birds distributed across most of eastern North America. Once they arrive on breeding grounds, male Eastern Whip-poor-wills establish territories that apparently include both nesting and foraging habitat (Cink 2002b); males vocalize throughout these territories. Intensity of calling is the greatest during the breeding season but occurs throughout the year, primarily at dusk and dawn and on moonlit nights (Mills 1986, Cink 2002b). The species is depredated by a range of reptilian, avian, and mammalian species (Santner 1992, Cink 2002a). In West Virginia, historic accounts suggest that Eastern Whip-poor-wills are present in forests of oak-hickory (*Carya* spp.), white pine (*Pinus alba*), or hardwood-hemlock (*Tsuga canadensis*) and occasionally in northern hardwood forest (Hall 1983).

*Sampling Strategy.*—We surveyed for singing Eastern Whip-poor-wills along marked paved and dirt roads. With GIS (ArcMap 10.1; ESRI 2012), we selected roads that ran through or were close to habitat thought to be preferred by the species, including burned forest, conifer stands, and agricultural lands (Cink 2002b). We targeted roads at least ~16 km in length so that we would be able to place 10 point count locations at 1.6-km intervals along the road. From over 70 roads that ran through appropriate habitat, we randomly chose 10 that were close enough to each other and to our field camp to allow for ease of access. Five of the roads were located in the northern portion of the forest and the other five were in the southern portion of the forest (Fig. 1). Although the distribution of roads we selected did not include middle and southwestern portions of the MNF, these roads were broadly representative of the habitats within the forest.

We conducted surveys using protocols from The Center for Conservation Biology's (CCB) United States Nightjar Survey (CCB 2012). CCB protocols suggest that the approximate best time periods for sampling during our two summer field seasons were during full moons in late May and early June and then again in late June and early July. These periods corresponded with the periods of brightest moonlight, the time when detection rates of Eastern Whip-poor-wills are thought to be highest (Wilson and Watts 2006). Roads were each surveyed twice in 2012 and 2013. Surveys began 30 mins after sunset and ended 15 mins before sunrise. At each point, we also recorded cloud cover (%), wind (0–3), noise levels (0–2), and moon visibility (0–1), all per CCB (2012) protocols. Surveys were not conducted in rain, if winds exceeded 24 km/hr, or if dense cloud cover obscured the sky.

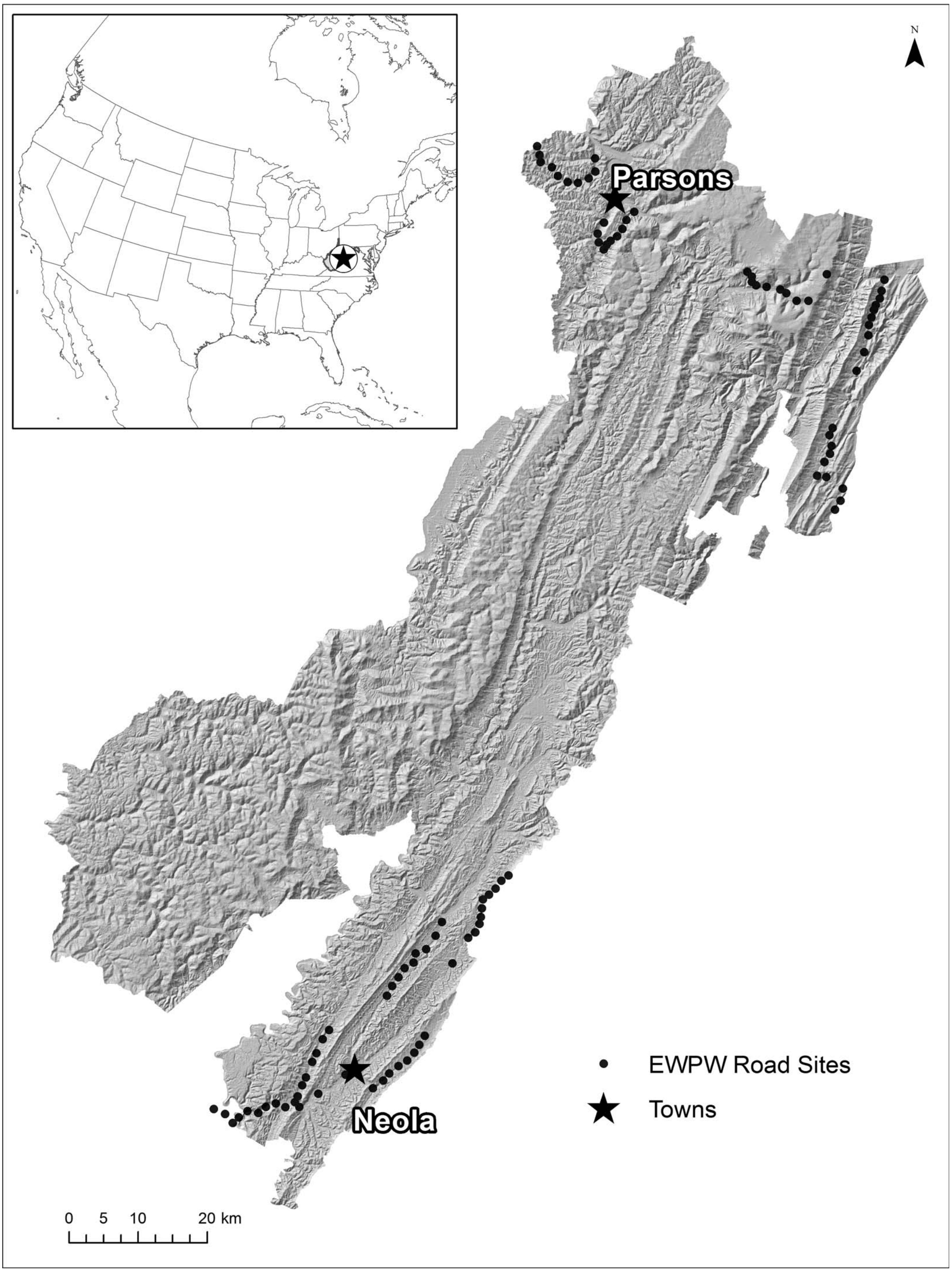


FIG. 1. Grayscale topographic relief of the study area in Monongahela National Forest (MNF) in eastern West Virginia. Nocturnal surveys of Eastern Whip-poor-wills (EWPW) were conducted at the 95 points shown along 10 roads. Stars show the location of important towns within the MNF and the inset shows the location of the MNF within North America (see Fig. 2 inset for location of MNF within West Virginia).

On each transect, we stopped 10 times, once every 1.6 km (1 odometer mile) per CCB protocols, to survey for nocturnally calling birds. Because some points were located at noisy intersections unsuitable for aural surveys, two roads only had 8–9 points. In total, we aimed to survey 95 points twice each per year. We surveyed each transect twice each year, traveling in opposite directions on the two surveys. There were two observers present throughout the surveys, and they shared information on the number and location of birds heard during each survey (i.e., we did not use a double observer framework; Nichols et al. 2000). Each point location was surveyed for 6 mins, and we recorded all individual birds heard. Two or three transects were generally completed each night, and we varied order of transects within each year so that the second visit to survey points did not occur at the same time of the day as the first visit.

*Data Associations*.—At each survey point, we used GIS to create circular plots with radii of 800 m, 1600 m, 2400 m, 3200 m, 4000 m, and 4800 m (see below for data analysis). We then used zonal statistics to tabulate the area ($m^2$) of the following NLCD (National Land Cover Database; Fry et al. 2011) land cover types within each plot: developed (includes all four NLCD developed classes), deciduous forest, evergreen forest, mixed forest, herbaceous/hay/pasture/shrub (includes shrub/scrub, grassland/herbaceous, sedge/herbaceous and pasture/hay), cultivated crops, and wetland (includes both NLCD wetland types). Within each plot, we also calculated the total length of forest edge, as defined by the habitat classes above. Although newer data exist today, the NLCD 2006 land cover data were the most current available when transects were selected, and thus the choice of transects is based on those data. We averaged elevation across each plot using a 2003 USGS and WV SAMB digital elevation model (USGS and SAMB 2005). All spatial data collection and interpretation were conducted within ArcMap10.1 (ESRI 2012).

*Occupancy Modeling*.—To determine patterns of occupancy by whip-poor-wills, we used single-species multiple season occupancy modeling in program PRESENCE (MacKenzie 2012), using survey stops as our unit of measure. The assumptions of this model include independence of survey stops within years, no colonization or extinction within years, the potential for heterogeneity between survey stops across years, and no false detections (MacKenzie et al. 2006). Model parameters included the occupancy rate by year (i.e., probability of Eastern Whip-poor-wills being present; $\Psi$), the rate of occupancy change, designated as $\lambda_t$ and estimated as $\Psi_{t+1}/\Psi_t$, the between-year extinction probability at survey stops ($\varepsilon_t = P(absence\ at\ time\ t+1 |\ presence\ at\ t)$), the colonization probability at survey stops (($\gamma_t = P(presence\ at\ time\ t+1 |\ absence\ at\ t)$), and the detection probability (i.e., the probability of detecting an Eastern Whip-poor-will that is present, $p$; MacKenzie et al. 2006).

We converted survey data into detection histories for each point using the presence (1) and absence (0) data we collected (MacKenzie 2012). Data from both surveys in a year were combined additively to ensure that we were accurately able to determine presence of whip-poor-wills. We used logistic regression with a logit link to model the probability that a survey stop would be occupied by whip-poor-wills and we included as covariates the elevation, edge, and land cover variables noted previously. Year, moon visibility, and noise level (0–2) were similarly used as covariates but only to calculate detection probabilities. The untransformed beta values in the PRESENCE output were used to calculate an odds ratio (i.e., the odds of a whip-poor-will being present in comparison to the odds of one being absent) and then transformed with an inverse logit to estimate the percent occupancy at the survey points (MacKenzie et al. 2006).

To rank and evaluate models in the model set, we used quasi-Akaike's Information Criterion values (QAICc) and QAICc weights, both provided in PRESENCE outputs (Burnham and Anderson 2002, MacKenzie et al. 2012).

*Modeling Occupancy of Eastern Whip-poor-wills*.—There is uncertainty as to the amount of space Eastern Whip-poor-wills use on the breeding grounds and as to how far their song will travel (CCB 2012, Hunt 2013). Consequently, there is no firmly established protocol for associating external data sets with observations of this species. To determine the best scale to estimate occupancy of Eastern Whip-poor-wills in the MNF, we created global models of Eastern Whip-poor-wills' habitat associations within circles of 800 m, 1600 m, 2400 m, 3200 m, 4000 m, and 4800 m (0.5

TABLE 1. Site and sampling covariates used in models of occupancy and habitat associations of Eastern Whip-poor-wills in the Monongahela National Forest of West Virginia. Site covariates were used to estimate probability of occupancy while the sampling covariates were used to estimate probability of detection.

| Site covariate | Metric (units) |
|---|---|
| Land cover class | |
| Herbaceous/shrub/pasture | Area (km$^2$) |
| Deciduous forest | Area (km$^2$) |
| Evergreen forest | Area (km$^2$) |
| Mixed forest | Area (km$^2$) |
| Developed | Area (km$^2$) |
| Wetland | Area (km$^2$) |
| Open water | Area (km$^2$) |
| Cultivated crops | Area (km$^2$) |
| Other | |
| Elevation | Mean/plot (m) |
| Edge | Distance (km) |

| Sampling covariate | Metric (units) |
|---|---|
| Environmental parameters | |
| Moon | Visible (1), not visible (0) |
| Noise level 1 | No noise (1), noise 2 or 3 (0) |
| Noise level 2 | Slight noise (1), noise 1 or 3 (0) |
| Noise level 3 | Moderate noise (1), noise 1 or 2 (0) |
| Year | |
| 2012 | First survey year (1), second year (0) |
| 2013 | Second survey year (1), first year (0) |

ha,1.0,. . .,3.0 ha) centered around each survey point. Each global model incorporated the same survey data (i.e., the same sample size $n = 95$ and the same 16 covariates; Table 1). Therefore, we interpreted the global model with the lowest AIC value as indicative of the best scale at which to model occupancy of Eastern Whip-poor-wills in the MNF (Burnham and Anderson 2002, Symonds and Moussalli 2011).

Once we identified the most appropriate spatial scale at which to evaluate our survey data, we then built, in PRESENCE, a series of sub-models, all at that most appropriate spatial scale. These models evaluated the effects of site covariates (elevation, forest edge, area open water, area cultivated crops, area herbaceous/shrub/pasture land, area deciduous forest, area evergreen forest, area mixed forest, area developed, and area wetland) on occupancy and the effects of sampling covariates (moon visibility, noise, and year) on detection (Table 1). In each model, colonization and emigration were held constant and equal. Site and sampling covariates were converted to *Z*-scores to reduce the influence of variables that had larger ranges (Donovan and Hines 2007). We used model averaging to account for model selection uncertainty. After model averaging, we calculated odds ratios and percent occupancy using untransformed beta values provided by PRESENCE.

To predict the distribution of the Eastern Whip-poor-wills within the MNF, we used the raster calculator tool (ESRI 2012) to apply the averaged model built above to USGS NLCD 2006 and elevational data for the entire MNF. The output layer included a map of areas describing the predicted probability of occupancy of whip-poor-wills based on modeled covariates.

## RESULTS

We recorded 181 vocalizing Eastern Whip-poor-wills between 29 May–5 June and 26 June–July in 2012 (1.9/point) and 101 between 21–27 May and 25–27 June in 2013 (1.0/point). Weather constrained our ability to complete all planned surveys. In 2012, one transect was impacted by weather, with 4 of 95 points only sampled once. In 2013, three transects were impacted by weather, with 30 of 95 points only sampled once. Missing data were accounted for in program PRESENCE (MacKenzie et al. 2006).

*Scale Dependence in Habitat Associations*.—Occupancy of whip-poor-wills was best predicted by global models with habitat associations within 1600-m circles (i.e., those models were best supported by the data; Table 2). Other models that reasonably predicted occupancy of whip-poor-wills were those based on data at 800 and 2400 m. Models based on data at a scale >2400 m all performed poorly.

Support for the models at 1600 m is a possible indicator of the amount of space that these birds use in the MNF. At this scale, deciduous forest was the most common land cover type surrounding the transects, comprising 78% of all the land cover at all survey points, and wetlands were the least common land cover type comprising <1% of the total cover.

*Elevation, Forest Edge, and Landscape Associations*.—We compared models based on habitat

TABLE 2. Global models for Eastern Whip-poor-will occupancy and QAICc scores for those models. Models were built to describe habitat associations at six different spatial scales within the Monongahela National Forest of West Virginia. Covariates are described in Table 1 and details of model construction are given in the text (Methods).

| Circle radius (area) | Global models | QAICc |
|---|---|---|
| 800 m (0.5 ha) | Occupancy (elevation+edge+land cover classes), detection (year+moon+noise) | 473.01 |
| 1600 m (1.0 ha) | | 467.11 |
| 2400 m (1.5 ha) | | 477.36 |
| 3200 m (2.0 ha) | | 698.54 |
| 4000 m (2.5 ha) | | 704.13 |
| 4800 m (3.0 ha) | | 708.06 |

parameters within 1600-m circles to understand selection by Eastern Whip-poor-wills of habitat parameters. The most highly supported model described occupancy of whip-poor-wills as a function of elevation and edge, and detection rates as a function of year, moon visibility, and noise. This model had 1.6 times more support than the next best model (different from the first in that occupancy was constant) and much more support than the third-ranked model (the first which included land cover class; Table 3). The first two models, which together had 99% of the support in the data, suggest that elevation and edge were highly influential in determining occupancy of Eastern Whip-poor-wills; other variables in Table 1 which were not included in the final model were not in any supported model.

Because there was some minimal support for the model that included land cover covariates in addition to elevation, we averaged models to assess the role of those covariates on probability of occupancy (Table 4). Beyond the strong positive associations with edge and negative associations with elevation, model averaged results suggested (a) weak negative associations of Eastern Whip-poor-wills' occupancy with increasing open water, conifer forest, and herbaceous/shrub/pasture cover; and (b) weak positive associations between Eastern Whip-poor-wills' occupancy and increasing mixed and deciduous forest, cultivated crops, and wetland cover (Table 4). Finally, detection of Eastern Whip-poor-wills was strongly positively correlated to moon visibility and negatively correlated to increasing noise levels.

*Distribution of Eastern Whip-poor-wills within the Monongahela National Forest*.—We applied our model averaged occupancy rates to the entire MNF, using elevation and land cover data to estimate probability of Eastern Whip-poor-wills' occupancy. The model predicts multiple locations throughout the MNF that would be suitable for occupancy of Eastern Whip-poor-wills (Fig. 2). As might be expected based on the input model, our

TABLE 3. Candidate models describing habitat associations of Eastern Whip-poor-wills within a 1600-m (1.0-ha) radius circle of survey points within the Monongahela National Forest, West Virginia. Colonization and emigration were held constant and equal in all models. Covariates used in these models are those listed in Table 1; because some AICc weights are small, we provide three significant digits.

| Model | QAICc | ΔQAICc | AICc Weight | Parameters | Log Likelihood |
|---|---|---|---|---|---|
| Occupancy (elevation+edge), detection (year+moon+noise) | 458.63 | 0 | 0.608 | 10 | 1359.76 |
| Occupancy (constant), detection (year+moon+noise) | 459.59 | 0.96 | 0.376 | 8 | 1375.12 |
| Occupancy (elevation+edge+land cover classes), detection (year+moon+noise) | 467.11 | 8.48 | 0.009 | 15 | 1342.64 |
| Occupancy (land cover classes), detection (year+moon+noise) | 467.51 | 8.88 | 0.007 | 17 | 1356.29 |
| Occupancy (constant), detection (constant) | 478.24 | 19.61 | 0 | 4 | 1457.74 |
| Occupancy (constant), detection (year) | 479.50 | 20.87 | 0 | 5 | 1455.44 |

TABLE 4. Model averaged parameter estimates for occupancy, colonization, emigration, and detection probabilities for surveys of Eastern Whip-poor-wills in the Monongahela National Forest of West Virginia. The intercept term includes deciduous forest. Covariate (Beta) estimates and their standard errors are untransformed. Estimated occupancy probabilities as a function of each beta parameter were used to weight raster maps to create Figure 2. Because some of the beta estimates were small, all numbers in this table are to four significant digits.

| Parameter | Variable | Beta estimate | SE | Occupancy probability | SE | Odds ratio |
|---|---|---|---|---|---|---|
| Occupancy | Intercept (deciduous forest) | 0.3239 | 1.6536 | 0.5803 | 3.9254 | 1.3826 |
| | Edge | 0.0407 | 0.2546 | 0.5102 | 0.6200 | 1.0415 |
| | Mixed forest | 0.0034 | 0.3917 | 0.5009 | 0.9544 | 1.0034 |
| | Cultivated crops | 0.0012 | 0.3030 | 0.5003 | 0.7383 | 1.0012 |
| | Wetlands | 0.0004 | 0.2590 | 0.5001 | 0.6312 | 1.0004 |
| | Developed | 0.0000 | 0.3079 | 0.5000 | 0.7503 | 1.0000 |
| | Shrub/grassland | –0.0001 | 0.2235 | 0.5000 | 0.5445 | 0.9999 |
| | Evergreen forest | –0.0025 | 0.4112 | 0.4994 | 1.0020 | 0.9975 |
| | Open water | –0.0173 | 1.0322 | 0.4957 | 2.5149 | 0.9829 |
| | Elevation | –0.2266 | 0.4187 | 0.4436 | 1.0072 | 0.7972 |
| Colonization | (colonization) | –0.1515 | 0.6078 | 0.4622 | 1.4724 | 0.8594 |
| Emigration | (emigration) | –0.6065 | 1.0812 | 0.3528 | 2.4064 | 0.5452 |
| Detection | Moon visibility | 0.2927 | 0.3615 | 0.5727 | 0.8622 | 1.3400 |
| | 2013 | –0.0079 | 0.3255 | 0.4980 | 0.7931 | 0.9921 |
| | 2012 | –0.0685 | 0.3468 | 0.4829 | 0.8441 | 0.9338 |
| | Noise 1 | –0.1758 | 0.3444 | 0.4562 | 0.8327 | 0.8388 |
| | Noise 2 | –0.3616 | 0.4004 | 0.4106 | 0.9445 | 0.6966 |

map predicts that areas with lower elevation and edge are most likely to support Eastern Whip-poor-wills.

## DISCUSSION

Our data and models suggest that within the MNF, distribution of Eastern Whip-poor-wills is determined by a combination of elevation and habitat components and that the CCB survey protocols are effective at detecting these birds. These findings have a suite of implications for our understanding of the biology and management of this species.

Our best global model for predicting occupancy of whip-poor-wills included covariates at a range of 1600 m around point counts, a finding on the low side of the range of previous telemetry-based estimates of home range size (Hunt 2013). Not only is it reassuring that our results are consistent with those from previous studies that used different analytical approaches, but this consistency provides a useful framework for understanding Eastern Whip-poor-wills' habitat associations.

Studies in New Hampshire found that Eastern Whip-poor-wills were much more likely to be detected at elevations $<$180 m above sea level (ASL; Hunt 2006). Likewise, the species is absent above ~300 m in the Adirondack and Catskill Mountains of New York (Sibley 1988). The lowest elevation of our survey plots was ~305 m asl, but we never detected Eastern Whip-poor-wills at our highest elevation sites (Dolly Sods, 900 m). These patterns suggest that this species has specific habitat preferences related to elevation and that occupancy may show dramatic variation in the diverse habitats of the Appalachians. Thus, because the birds we found were at relatively low elevations, it may be that these habitat preferences also correspond to latitude and that birds farther south are found at still higher elevations.

We found weak support in models for effects of edge areas and deciduous forest and mixed forest land cover types on occupancy patterns of Eastern Whip-poor-wills. This is consistent with studies suggesting that these birds require a mosaic of young forest and open areas for nesting and foraging (Wilson and Watts 2008, Hunt 2013). However, the negative association we observed with conifer forest is inconsistent with those previous studies. This may be because elevation is the principal effect in our models and because

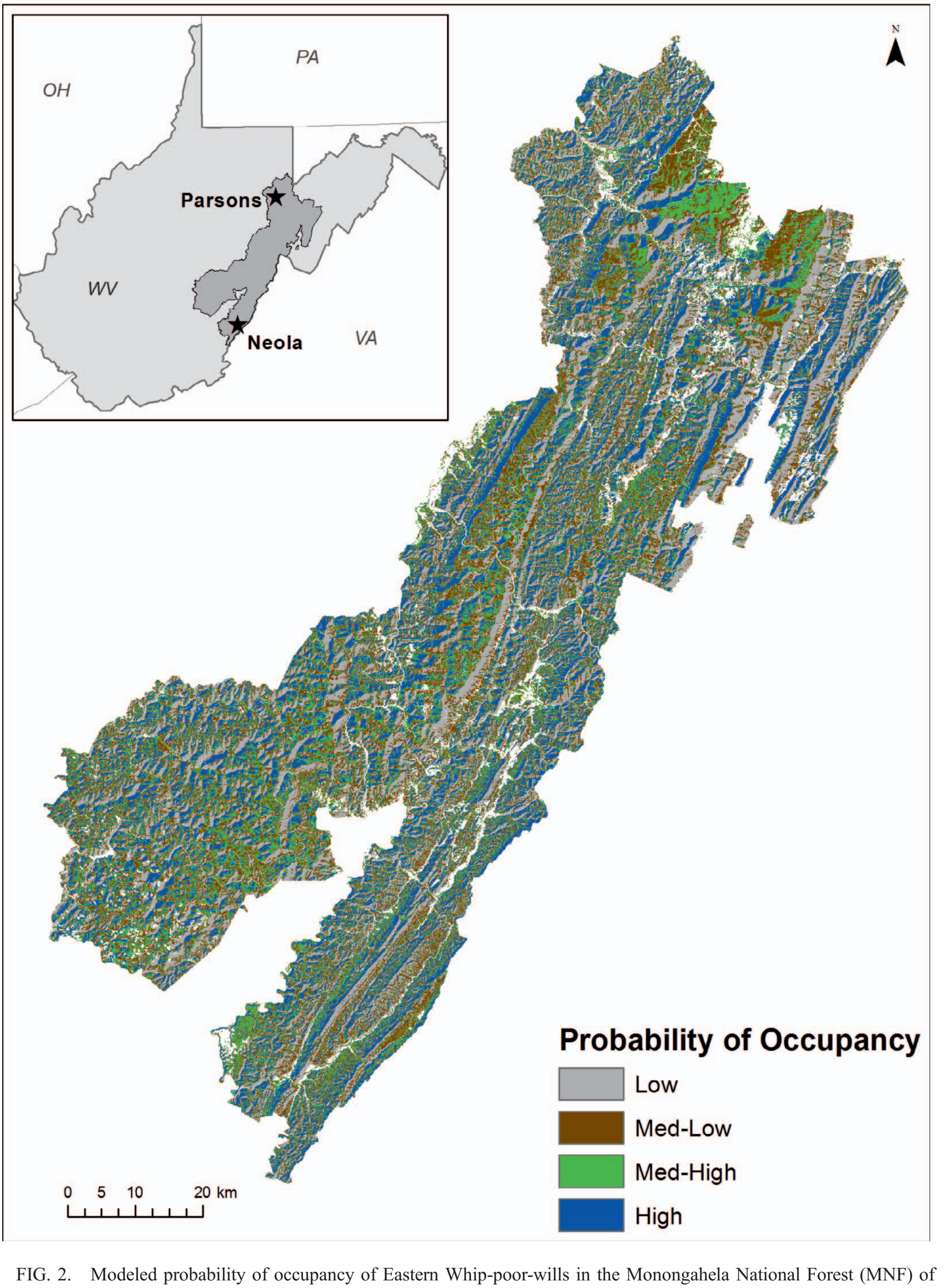


FIG. 2. Modeled probability of occupancy of Eastern Whip-poor-wills in the Monongahela National Forest (MNF) of West Virginia. Occupancy models are derived from the averaged model describing habitat (elevation, edge, landcover) associations of the species (see text for details). Inset shows the location of the MNF within West Virginia and the location of WV relative to neighboring US states.

the little conifer forest that occurs on the MNF is found only at high elevations and is predominantly spruce-fir. In contrast, in New Hampshire and North Carolina, forest classified as "conifers" are predominantly composed of pines.

Published literature suggests that Eastern Whip-poor-wills prefer managed forest areas (Hunt 2013). Neither maps from the Forest Service nor the land cover dataset that we used allowed us to differentiate between managed and unmanaged forest types, and we were unable to accurately measure size and boundaries of management areas from the road. Nevertheless, our analysis points to use and avoidance of specific habitat associations that are useful in predicting distributions and in developing potential conservation measures for this and related species. Future studies could incorporate managed forest plots to determine to what extent management approaches influence occupancy of Eastern Whip-poor-wills (recently accomplished in Akresh and King 2016).

One of the goals of this study was to use a survey protocol designed specifically for nightjars to create a MNF-scale map of Eastern Whip-poor-wills' occupancy. To our knowledge, this approach has never been attempted with data collected via the CCB Nightjar Survey Protocol. Use of occupancy models, first to identify a relevant scale and subsequently to characterize habitat associations, produced a validation-ready map that provides (a) detailed predictions on where Eastern Whip-poor-wills may be found in the MNF; (b) insight into unsurveyed areas within the MNF that may be well suited to new nightjar survey routes; and (c) a framework that could be developed for similar work in other National Forests with different land cover compositions.

Eastern Whip-poor-wills were present in every West Virginia County during the 1920s, a period that followed heavy settlement and logging (Hall 1983). However, numbers of Eastern Whip-poor-wills in the state are thought to have steadily decreased since the 1950s (Hall 1983, Buckelew and Hall 1994), and the species has declined in or disappeared from many other parts of the United States (e.g., NY, PA; Santner 1992, New York State Department of Environmental Conservation 2007, Wilson et al. 2012). These declines are thought to be because of loss of habitat to urbanization, grazing, and succession of open habitat to dense forest (Hall 1983, Buckelew and Hall 1994, Cink 2002b).

Because of the likely effects of past habitat change on this species, it is reasonable to speculate about how future change may influence populations of Eastern Whip-poor-wills. The severity of storms the MNF experiences appears to be increasing (Simmonds and Keay 2009, Tang et al. 2014). These severe storms cause widespread damage to forests, including felling of overstory trees and gap creation, all of which may create forest more suitable for whip-poor-wills. Other environmental changes may have different consequences for this species. The monitoring tool our study provides should be a useful mechanism to track the occupancy of Eastern Whip-poor-wills and their potential response to these ongoing and future changes.

## ACKNOWLEDGMENTS

Funding for this project was provided by the United States Forest Service. T. Schuler and the staff at the USFS Northern Research Station provided access and logistical support for the research, and J. Phillips and K. Pangman assisted with data collection. M. Braham assisted with mapping. P.B. Wood, J. Edwards, S. Stoleson, J. Hagar, P. Hunt, and an anonymous reviewer provided helpful comments on early drafts of the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Statement of author contributions: CLS and TEK designed the study and wrote the manuscript, CLS led data collection and analysis. This is Scientific Article No. 3284 of the West Virginia Agricultural and Forestry Experiment Station, Morgantown.

## LITERATURE CITED

Akresh, M. E. and D. I. King. 2016. Eastern Whip-poor-will breeding ecology in relation to habitat management in a pitch pine–scrub oak barren. Wildlife Society Bulletin 40:97–105. doi:10.1002/wsb.621

Buckelew Jr., A. R. and G. A. Hall. 1994. The West Virginia Breeding Bird Atlas. University of Pittsburgh Press, Pittsburgh, Pennsylvania, USA.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition. Springer-Verlag, New York, USA.

Center for Conservation Biology (CCB). 2012. Survey instructions. Nightjar Survey Network, Williamsburg, Virginia, USA. www.nightjars.org/participate/survey-instructions/ (accessed 3 Jan 2012).

Cink, C. L. 2002a. Avian predation on the eggs of the whip-poor-will. Kansas Ornithological Society Bulletin 53:23–24.

Cink, C. L. 2002b. Eastern Whip-poor-will (*Antrostomus vociferus*). The birds of North America online. Number 620.

Donovan, T. M. and J. Hines. 2007. Exercises in occupancy modeling and estimation. Vermont Cooperative Fish and Wildlife Research Unit, Burlington, USA. www.uvm.edu/rsenr/vtcfwru/spreadsheets/occupancy/occupancy.htm (accessed 3 May 2014).

Dunn, P. O., D. W. Winkler, L. A. Whittingham, S. J. Hannon, and R. J. Robertson. 2011. A test of the mismatch hypothesis: how is timing of reproduction related to food abundance in an aerial insectivore? Ecology 92:450–461.

Environmental Systems Research Institute (ESRI). 2012. ArcMap. Version 10.1. ESRI, Redlands, California, USA.

Ferguson, R. H. 1964. The timber resources of West Virginia. USDA, Forest Service, Resource Bulletin NE-2. Northeastern Forest Experiment Station, Upper Darby, Pennsylvania, USA.

Fry, J. A., G. Xian, S. Jin, J. A. Dewitz, C. G. Homer, L. Yang, C. A. Barnes, N. D. Herold, and J. D. Wickham. 2011. Completion of the 2006 National Land Cover Database for the conterminous United States. Photogrammetric Engineering and Remote Sensing 77:858–864.

Hall, G. A. 1983. West Virginia birds: distribution and ecology. Carnegie Museum of Natural History Special Publication 7:1–180.

Hobson, K. A., K. J. Kardynal, S. L. Van Wilgenburg, G. Albrecht, A. Salvadori, M. D. Cadman, F. Liechti, and J. W. Fox. 2015. A continent-wide migratory divide in North American breeding Barn Swallows (*Hirundo rustica*). PLoS ONE 10:e0129340.

Hunt, P. D. 2006. An analysis of whip-poor-will habitat use in the Piscataquog River watershed: 2003–2005, with notes on statewide comparisons. Report to the Piscataquog Watershed Association and Russell Piscataquog River Watershed Foundation. New Hampshire Audubon, Concord, USA.

Hunt, P. D. 2013. Habitat use by the Eastern Whip-poor-will (*Antrostomus vociferus*) in New Hampshire, with recommendations for management. Report to the New Hampshire Fish and Game Department Nongame and Endangered Wildlife Program. New Hampshire Audubon, Concord, USA.

MacKenzie, D. I. 2012. PRESENCE user manual. Clark County Desert Conservation Program, Las Vegas, Nevada, USA. www.clarkcountynv.gov/airquality/dcp/Documents/Library/dcp%20reports/2012/PRESENCE_Occupancy_Statistics%20_Software_Manual_20121112.pdf (accessed 1 Sep 2015).

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Burlington, Massachusetts, USA.

Mills, A. M. 1986. The influence of moonlight on the behavior of goatsuckers (Caprimulgidae). The Auk 103:370–378.

Nebel, S., A. Mills, J. D. McCracken, and P. D Taylor. 2010. Declines of aerial insectivores in North America follow a geographic gradient. Avian Conservation and Ecology 5(2):1.

New York State Department of Environmental Conservation. 2007. New York State Breeding Bird Atlas 2000. Release 1.0. New York State Department of Environmental Conservation, Albany, USA. www.dec.ny.gov/animals/7312.html (accessed 24 Jan 2016).

Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. The Auk 117:393–408.

Reese, J. G. 1996. Whip-poor-will. Pages 194–195 *in* Atlas of the breeding birds of Maryland and the District of Columbia (C. S. Robbins, Editor). University of Pittsburgh Press, Pittsburgh, Pennsylvania, USA.

Santner, S. 1992. Whip-poor-will. Pages 172–173 *in* Atlas of breeding birds in Pennsylvania (D.W. Brauning, Editor). University of Pittsburgh Press, Pittsburgh, Pennsylvania, USA.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski Jr., and W. A. Link. 2014. The North American Breeding Bird Survey, results and analysis 1966–2013. Version 01.30.2015. USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Sibley, S. C. 1988. Whip-poor-will *Caprimulgus vociferus*. Pages 218–219 *in* The atlas of breeding birds in New York State (R. F. Andrle and J. R. Carroll, Editors). Cornell University Press, Ithaca, New York, USA.

Simmonds, I. and K. Keay. 2009. Extraordinary September Arctic sea ice reductions and their relationships with storm behavior over 1979–2008. Geophysical Research Letters 36:L19715.

Smith, A. C., M.-A. R. Hudson, C. M. Downes, and C. M. Francis. 2015. Change points in the population trends of aerial-insectivorous birds in North America: synchronized in time across species and regions. PLoS ONE 10:e0130768.

Symonds, M. R. E. and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65:13–21.

Tang, Q., X. Zhang, and J. A. Francis. 2014. Extreme summer weather in northern mid-latitudes linked to a vanishing cryosphere. Nature Climate Change 4:45–50.

Tyler, W. M. 1940. *Antrostomus vociferus vociferus* (Wilson): Eastern Whippoorwill. Pages 163–183 *in* Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies: orders Psittaciformes, Cuculiformes, Trogoniformes, Coraciiformes, Caprimulgiformes, and Micropodiiformes (A. C. Bent, Editor). United States National Museum Bulletin 176:1–506.

U. S. Department of Agriculture (USDA). 2013. About the forest. USDA, Forest Service, Monongahela National Forest, Elkins, West Virginia, USA. www.fs.usda.gov/main/mnf/about-forest (accessed 6 Oct 2013).

U. S. Geological Survey (USGS) and West Virginia State Addressing and Mapping Board (SAMB). 2005. West Virginia statewide digital elevation models. USDI, Geological Survey, Rolla, Missouri, USA. wvgis.wvu.edu/data/fullmetadata/3MeterDEM_SAMB_2003_utm83.htm (accessed 18 Feb 2014).

Wilson, S. G. 1985. Summer distribution of whip-poor-wills in Minnesota. Loon 57:6–8.

Wilson, A. M., D. W. Brauning, and R. S. Mulvihill (Editors). 2012. Second atlas of breeding birds in Pennsylvania. Pennsylvania State University Press, University Park, USA.

Wilson, M. D. and B. D. Watts. 2006. Effect of moonlight on detection of whip-poor-wills: implications for long-term monitoring strategies. Journal of Field Ornithology 77:207–211.

Wilson, M. D. and B. D. Watts. 2008. Landscape configuration effects on distribution and abundance of whip-poor-wills. Wilson Journal of Ornithology 120:778–783.