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Research Article

Breeding Habitat Associations of Eastern Whip-Poor-Wills in Managed Forests

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ABSTRACT Populations of the eastern whip-poor-will (*Antrostomus vociferus*; whip-poor-will) have declined throughout most of its range, making it a species of high conservation concern in nearly every state and province where it occurs. Researchers have reported whip-poor-wills are associated with forest stands with open canopies, and thus silviculture may be a promising means for promoting their populations, yet the ecological literature does not quantify fine-scale habitat relationships capable of assisting with silviculture prescriptions. Our objective was to quantify the associations between whip-poor-wills, canopy openness, and other vegetation characteristics to provide managers with guidance for whip-poor-will management. Based on prior research, we hypothesized that whip-poor-wills may be associated with intermediate levels of canopy retention and that their numbers would also be affected by understory characteristics. We surveyed whip-poor-wills with point counts in managed forest at the Fort Drum Army installation in New York, USA, during 2015 and 2016 and collected vegetation measurements at each point count location to relate whip-poor-will occupancy with vegetation structure and composition. Whip-poor-will occupancy was strongly related to intermediate levels of basal area, with peak occupancy at 13.8 m^2/ha, a value that corresponds to forest denser than most shrublands but more open than closed-canopy forest. Whip-poor-will presence was negatively related to understory height, which is consistent with prior studies. These findings provide managers with quantitative targets that can be used to increase or maintain whip-poor-will numbers and abundance of other disturbance-associated species similarly unable to persist in unmanaged forests stands.

KEY WORDS *Antrostomus vociferus*, conservation, disturbance, management, point count.

The eastern whip-poor-will (*Antrostomus vociferus*; whip-poor-will) is a nocturnal, insectivorous bird species that has been experiencing significant population declines in North America. Since the 1960s, whip-poor-wills have been decreasing at a rate of 2.76% per year throughout their range in the United States and Canada (Sauer et al. 2017), and a synthesis of second-generation breeding bird atlases from 9 states and 1 Canadian province indicated a 50% breeding range contraction over 20–30 years (Spiller 2019). In response to these declines, 11 states have identified whip-poor-wills as a species of concern, and 30 of the 32 states in which whip-poor-wills breed have designated them as a species of greatest conservation need (Spiller 2019). The whip-poor-will is listed as threatened under Canada's Species at Risk Act (Nature Canada 2009).

Many researchers suggest breeding habitat loss as a contributing factor to population declines of the whip-poor-will (Mills 2007, Cink et al. 2017, English et al. 2017*b*). Whip-poor-wills favor early-successional or open sites and are scarce or absent from closed-canopy forest (Wilson and Watts 2008, Hunt 2013, Tozer et al. 2014, Akresh and King 2016). Sites with open canopy receive increased lunar illumination that may facilitate foraging for back-lit insect prey (Mills 1986, Wilson and Watts 2006). Whip-poor-will nests and roosts have been found in managed shrublands also (Akresh and King 2016).

Early-successional shrublands used by whip-poor-wills have significantly declined over the past century. In the Northeast, the proportion of forest in the seedling-sapling stage thought to be suitable for whip-poor-wills has declined to approximately 6% of the forested area, an average loss of 2.38% per year (King and Schlossberg 2014). These losses of early-successional vegetation, primarily resulting from increases in intensive agriculture or maturation of forests (Lorimer and White 2003, Mills 2007), have likely caused or exacerbated the population declines of other shrubland bird species besides whip-poor-wills (Litvaitis 1993, Askins 2001, Thompson and DeGraaf 2001). Therefore, forest managers are concerned with maintaining early-successional disturbance-dependent shrubland vegetation in the Northeast to support conditions suitable for a suite of declining species (Askins 2001).

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Forest management can provide habitat for shrubland birds and other wildlife by creating the open-canopy conditions and dense brushy structure preferred by these species (Thompson and DeGraaf 2001, DeGraaf and Yamasaki 2003). Recommended forest management to maintain or increase whip-poor-will populations include clear-cuts with and without seed trees and of varying sizes, overstory and understory removal, and crop tree release (Garlapow 2007, Wilson and Watts 2008, Hunt 2013, Tozer et al. 2014). In addition to whip-poor-wills, these forest management practices benefit a suite of other declining early-successional bird species that are of concern to managers and conservationists (Askins 2001, Thompson and DeGraaf 2001, Dettmers 2003, Greenberg et al. 2011, King and Schlossberg 2014). Despite this well-established association, how much canopy cover maximizes whip-poor-will numbers remains unclear.

In this study, we related whip-poor-will occurrence with a continuous measure of canopy openness (as indicated by basal area) instead of discrete classes (e.g., open-canopy forest vs. closed-canopy forest). We hypothesized there would be a level of canopy openness at which occupancy of whip-poor-wills peaked, which could serve as a management target (Villard and Jonsson 2009). Furthermore, other features besides canopy conditions, such as understory structure, could influence whip-poor-will abundance (Garlapow 2007, Cink et al. 2017), so we included a standard suite of understory structural variables (James and Shugart 1970) to test whether they influence whip-poor-wills, as has been reported in other studies (Garlapow 2007, Cink et al. 2017).

STUDY AREA

Fort Drum is a United States Army installation comprising over 440 km^2 in northwestern New York in Jefferson and Lewis counties. Though the installation includes a cantonment area and an airfield, >90% of the installation is composed of training areas that are relatively undeveloped, consisting of approximately 57% forested land, 14% grasslands, 12% shrublands, 4% surface water, and 1% forblands (U.S. Army Garrison Fort Drum 2011). Fort Drum experiences a humid continental climate characterized by cold (−23°C) and snowy winters and warm to hot (31°C) summers. Mature forests are dominated by red (*Acer rubrum*) and sugar maple (*A. saccharum*), black cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), and poplar (*Populus* spp.); early successional forests are dominated by gray birch (*Betula populifolia*), quaking aspen (*Populus tremuloides*), and poplars; and conifer forests are dominated by eastern hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*). Representative fauna includes white-tailed deer (*Odocoileus virginianus*), red fox (*Vulpes vulpes*), and eastern gray squirrel (*Sciurus carolinensis*). The topography of Fort Drum varies from flat terrain to small hills, with elevations ranging from 125 m to 278 m. Fort Drum has a forest management program that uses mainly silviculture for the purposes of training support, timber production, and to improve forest health (U.S. Army Garrison Fort Drum 2011).

METHODS

Bird Surveys

We surveyed whip-poor-wills at sampling points distributed along survey routes that followed trails and roads traversing the training area (Fig. 1). Because whip-poor-wills are sparsely distributed, covering a large enough survey area to encompass a sufficient sample of individuals is challenging, especially at night when whip-poor-wills are vocalizing. Thus, we employed roadside surveys, which are the standard means to monitor whip-poor-wills in continent-wide monitoring programs (e.g., Bird Studies Canada 2011, Center for Conservation Biology 2019).

Each route was composed of 10 survey points spaced 1.61 km apart, for 60 survey points across the training area (Fig. 1). We surveyed whip-poor-wills at these locations in 2015 and 2016 using the protocol employed in continent-wide whip-poor-will monitoring programs (Bird Studies Canada 2011, Center for Conservation Biology 2019) that has been used previously at Fort Drum. We surveyed each point 3 times between May and July in 2015, but in 2016 we sampled 50% of points twice and 50% of points only once because of logistical constraints. We conducted all surveys between 30 minutes after sunset and 30 minutes before sunrise (Mills 1986). We recorded start time, wind speed, cloud cover, and background noise on a scale of 0–3 (Table S1, available online in Supporting Information) before each survey. We estimated distance of each bird to ensure they were within the count radius of 100 m, and the number of cars passing during each survey. We followed Scott et al. (1981) to ensure that errors in distance estimation, and variations among observers in distance estimation, were minimized. We hired observers with previous experience surveying birds using point counts, and we emphasized the importance of correct distance estimation during the interview and subsequently in the field. Before surveys began, observers practiced distance estimation using visual markers at known distances until they were able to consistently assign markers to within and beyond 100 m. During a subset of surveys, a second observer stood at the point count perimeter to validate the estimated distances of vocalizing whip-poor-wills from the person conducting the point count. When possible, observers validated estimated distances after actual point counts by walking to the location of vocalizing whip-poorwills and comparing their estimated distance with the distance estimated with a handheld global positioning system.

We conducted surveys only on nights with little wind, no precipitation, and temperatures >4.4°C. In 2015, when surveys occurred 3 times, ≥2 of these times occurred when the moon was ≥50% illuminated because whip-poor-wills are most vocal with greater amounts of moonlight (Mills 1986, Wilson and Watts 2006). In 2016, all surveys occurred when the moon was ≥50% illuminated. We recorded detections of whip-poor-wills ≤100 m from point

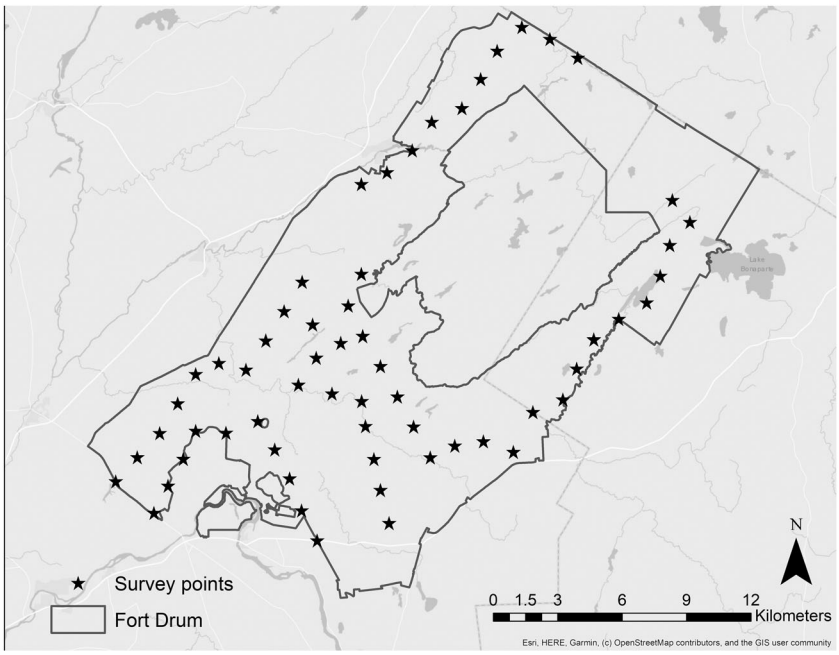

Figure 1. Study area at the Fort Drum Army installation in New York, USA, 2015–2016. Black stars represent location of point counts and centroids of vegetation plots. Map created by K. J. Spiller.

count locations. This survey protocol was reviewed and approved by the Institutional Animal Care and Review Committees (IACUC) at the University of Massachusetts Amherst (protocol 2016-0025).

Vegetation Data

We quantified site characteristics at each of the 60 survey points to provide a continuous measure of basal area retention, a surrogate for canopy coverage more easily employed by the land managers responsible for whip-poor-will populations at Fort Drum, and to investigate whether variables other than canopy closure influenced whip-poor-will occupancy. We measured site characteristics on 100-m-radius plots centered on each survey point location using methods modified from James and Shugart (1970) and King et al. (2011). We established 4 transects in each of the cardinal directions from the survey point location. We then recorded the species and maximum height of understory vegetation, or type of ground cover in the absence of vegetation, that came in contact with a 3-m vertical pole at 10-m intervals along each transect. This resulted in 40 measurements/survey point, although we removed measurements 10 m from the plot center during analysis to eliminate any measurements taken on roads or road shoulders. King and DeGraaf (2002) reported that this distance was sufficient to avoid the influence of roads on vegetation. At the midpoint of each of these 4 transects (i.e., 50 m in each of the cardinal directions from the plot center), we used a 10 basal area factor cruising prism to select trees in a variable-width radius plot for basal area, and recorded the diameter at breast height (dbh) and species of each tree within the prism plot.

We analyzed vegetation cover layers for the study site created by Fort Drum's Natural Resources Branch from digitized 30-cm resolution true color ortho-imagery and forest inventory plot data (U.S. Army Garrison Fort Drum 2011). We used ArcMap 10.5.1 (Esri, Redlands, CA, USA) to calculate the proportion of discrete vegetation classes within each of the 100-m-radius vegetation plots. The vegetation classes produced by Fort Drum included closed-canopy forest, open-canopy forest, grassland, and disturbed or developed sites (Table 1).

We used the point-intercept data to calculate understory height, the coefficient of variation (CV) of understory height, and percentage of understory cover that was herbaceous, woody, or litter. We used the cruising prism plots

Table 1. Summary statistics ($\bar{x} \pm$ SD) for site variables derived from field measurements taken at 60 sample locations of eastern whip-poor-will survey points and from geographic information system analyses of discrete cover type layers of the Fort Drum Army installation, New York, USA, 2015–2016.

	Variable	$\bar{x}$	SD
Field	Herbaceous (%)	43.7	20.3
	Litter (%)	6.1	8.0
	Woody (%)	50.2	21.5
	Understory height (cm)	113.1	46.0
	CV understory height	93.3	41.8
	Tree density (trees/ha)	2,211.9	2,101.8
	Basal area (m^2/ha)	14.1	9.2
	CV basal area	84.3	51.6
	Basal area of saplings (m^2/ha)[a]	3.6	3.4
	Basal area of pole timber (m^2/ha)[a]	6.3	4.4
	Basal area of saw timber (m^2/ha)[a]	3.4	4.4
	% basal area of coniferous trees	15.5	26.6
Cover types	Closed-canopy forest (%)	34.3	32.8
	Open-canopy forest (%)	17.7	25.3
	Grassland (%)	20.0	26.3
	Disturbed or developed areas (%)	8.9	7.1

[a] Size class definitions referenced from DeGraaf and Yamasaki (2001).

to calculate tree density (trees/ha), basal area (m^2/ha), CV of basal area, and percentage basal area of coniferous trees. We also calculated the basal area of trees (m^2/ha) in size classes as defined by DeGraaf and Yamasaki (2001) based on dbh: sapling (2.5–9.9 cm), pole (10–22 cm for softwoods and 10–30 cm for hardwoods), sawtimber (>22–51 cm for softwoods and >31–61 cm for hardwoods), and large sawtimber (>51 cm for softwoods and >61 cm for hardwoods). We averaged measurements of each variable for each survey point. Because the basal area of large sawtimber only represented >0.25 relative proportion of basal area at 2 of the 60 sample sites, trees of this size appeared to represent relatively rare characterizations of the vegetation community among the study plots and we dropped this variable from the analysis.

Statistical Analysis

Because counts of whip-poor-wills are a function of their abundance and the probability of detection, we corrected our point count surveys for detectability using occupancy analysis (MacKenzie et al. 2018). We chose this approach because whip-poor-wills occur at low densities (Cink et al. 2017), so we anticipated the data would take the form of presence–absence, and thus that occupancy analysis would be suitable (MacKenzie 2005). We used single-season occupancy models that incorporate detection probability from replicated surveys to model the data (MacKenzie et al. 2018). These repeat surveys across a season assisted with detection probability; because this detection probability includes availability, occupancy is therefore the probability of ≥1 whip-poor-will's home range intersecting the survey unit (Latif et al. 2016). Whip-poor-wills appear to exhibit high site fidelity (Cink et al. 2017, English et al. 2017*a*), and because we were interested in occupancy determinants rather than dynamic components (e.g., extinction, colonization), we modeled the 2 years together as a single-season model with a year term on the state side of all candidate models to account for inter-year variation in occupancy. We accommodated the yearly variation in site occupancy by stacking the data so each site-year combination represented a unique site, for 120 sites (with 3 visits in 2015 and 1–2 visits in 2016) as in Bauder et al. (2017). We used a logit link to relate occupancy and detection probability to respective covariates.

To facilitate computation, we standardized all continuous variables to mean = 0 and standard deviation = 1. There were 12 occupancy variables derived from the field measurements and 4 variables from the geographic information system cover type analysis. We included quadratic terms for basal area and other variables that appeared to exhibit a nonlinear relationship because it seemed reasonable that the occupancy of whip-poor-wills would be lowest at extreme values, as observed for other bird species in relation to basal area (King et al. 2012) or shrubland birds and vegetation succession (Schlossberg and King 2009). Detection variables included observer, ordinal date, year, time (min. from midnight because whip-poor-wills are most active around dawn and dusk), wind speed, cloud cover, noise, and number of passing cars (Bird Studies Canada 2011, Center for Conservation Biology 2019). Using the lunar package in R (Lazaridis 2014), we calculated the relative amount of moonlight potentially available during each survey, which we also used as a detection variable.

We assessed variables for collinearity using Pearson correlation ($|r| > 0.6$) and removed 1 covariate of highly correlated pairs from any given model (Zar 1984:338). Prior to model fitting, we estimated the overdispersion parameter ($\hat{c}$) using a parametric bootstrap (MacKenzie and Bailey 2004) with 1,000 iterations of a global model containing all detection and occupancy covariates using the AICcmodavg 2.1-1 package in R (Mazerolle 2017). Based on the results, we used Akaike's Information Criterion adjusted for overdispersion and small sample size ($QAIC_c$) to compare candidate models. We used the $\hat{c}$ parameter ($\hat{c} = 1.72$) in the model selection process and to inflate standard errors (MacKenzie and Bailey 2004).

We selected detection covariates by adding each detection variable to a model that included all occupancy variables and retaining the detection covariates or combination of detection covariates that increased model performance as indicated by a $\Delta QAIC_c$ less than the intercept-only model (Burnham and Anderson 2002). We then selected occupancy covariates by modeling each individually, including the selected detection covariates, and retaining those that increased model performance relative to the intercept-only model. We then created all possible combinations of these retained occupancy covariates. We considered occupancy covariates supported if they were included in models with a $\Delta QAIC_c \leq 2$, and strongly supported if 95% confidence intervals of coefficients did not include zero (Burnham and Anderson 2002). We visualized the relationships between occupancy and site variables by plotting model-averaged occupancy estimates along covariate gradients. Model-averaged estimates represented occupancy probabilities averaged across top models (those with a $\Delta QAIC_c \leq 2$). When plotting a relationship, we estimated occupancy at varying levels of the focal variable while holding all the other variables at their mean (Fiske and Chandler 2011). We fit occupancy models using the occu function in unmarked (version 0.12-0; Fiske and Chandler 2011) in the R software environment, version 3.5.1 (R Core Team 2018).

RESULTS

We detected 52 whip-poor-wills in 2015, and 27 whip-poor-wills in 2016. We detected whip-poor-wills at 40 of the 120 unique site-year combinations over the 2-year study. Of the 9 detection covariates considered, lunar illumination and year were included in the top models. In exploratory analysis, we dropped the observer covariate because it was highly correlated with year; therefore, it is possible that year is also representing an observer effect, resulting in its significance in the models. Both detection covariates were strongly supported. Overall detection probability was 0.39 ± 0.02 (SE).

We evaluated 26 occupancy models; 13 performed better than the intercept-only model and 4 were supported

Table 2. Parameter estimates and associated standard error values of occupancy covariates for models of eastern whip-poor-will occurrence from point count data collected at the Fort Drum Army installation in New York, USA, 2015–2016. Only models with Akaike's Information Criterion for overdispersed count data corrected for small sample sizes ($\Delta QAIC_c$) ≤ 2 are discussed. Coefficients with an asterisk (*) indicate that 95% confidence intervals did not include zero.

Model[a]	Intercept (2015)	Basal	Basal^2	Height	Trees	CV basal	Year (2016)	K[b]	$\Delta QAIC_c$	Weight
Basal^2, height	0.38 (0.35)	−0.31 (0.37)	−1.11 (0.39)*	−0.68 (0.25)*			−0.9 (0.44)*	9	0.00	0.22
Basal^2, height, CV basal	0.37 (0.36)	0.11 (0.47)	−1.12 (0.41)*	−0.67 (0.25)*		0.49 (0.33)	−0.92 (0.44)*	10	0.87	0.14
Basal^2, height, trees	0.39 (0.36)	−0.14 (0.39)	−1.13 (0.39)*	−0.57 (0.26)*	−0.45 (0.33)		−0.92 (0.44)*	10	1.23	0.12
Basal^2, trees	0.23 (0.34)	−0.27 (0.38)	−0.96 (0.37)*		−0.68 (0.32)*		−0.87 (0.43)*	9	1.86	0.09
Basal^2, height, CV basal, trees	0.37 (0.36)	0.25 (0.48)	−1.12 (0.41)*	−0.56 (0.26)*	−0.44 (0.34)	0.47 (0.32)	−0.93 (0.44)*	11	2.23	0.07
Basal^2, CV basal, trees	0.2 (0.34)	0.11 (0.45)	−0.9 (0.37)*		−0.67 (0.32)*	0.47 (0.29)	−0.89 (0.43)*	10	2.55	0.06
Basal^2	0.16 (0.33)	−0.57 (0.34)	−0.83 (0.35)*				−0.83 (0.42)*	8	2.58	0.06
Basal^2, CV basal	0.14 (0.33)	−0.18 (0.42)	−0.79 (0.35)*			0.48 (0.29)	−0.85 (0.42)*	9	3.06	0.05
CV basal	−0.35 (0.27)					0.53 (0.21)*	−0.81 (0.41)*	7	3.23	0.04
Height, CV basal	−0.35 (0.27)			−0.32 (0.21)		0.47 (0.21)	−0.83 (0.42)*	8	3.93	0.03
CV basal, trees	−0.35 (0.28)				−0.39 (0.25)	0.45 (0.21)*	−0.83 (0.42)*	8	4.16	0.03
Trees	−0.37 (0.27)				−0.5 (0.24)*		−0.79 (0.41)	7	4.45	0.02
Height	−0.35 (0.27)			−0.42 (0.21)*			−0.79 (0.41)	7	4.85	0.02
Intercept only	−0.667 (0.2)							6	5.1	0.02

[a] Covariates include basal area (basal; m^2/ha), understory height (height; cm), tree density (trees; trees/ha), and coefficient of variation of basal area (CV basal).
[b] Number of parameters.

($\Delta QAIC_c \leq 2$; Table 2). A quadratic relationship of basal area was included in all supported models and was strongly supported in all cases. There was a >50% probability of whip-poor-will occupancy with basal areas ranging from 8.4–18.7 m^2/ha, with a peak at 13.8 m^2/ha (Fig. 2A). Understory vegetation height was included in 3 of the supported models and was strongly supported in all cases. Whip-poor-will occupancy decreased with increasing understory height (Fig. 2B). Tree density was included in 2 supported models, and was strongly supported in 1 case, suggesting that whip-poor-will occupancy decreased with increasing tree density (Fig. 2C). Finally, CV of

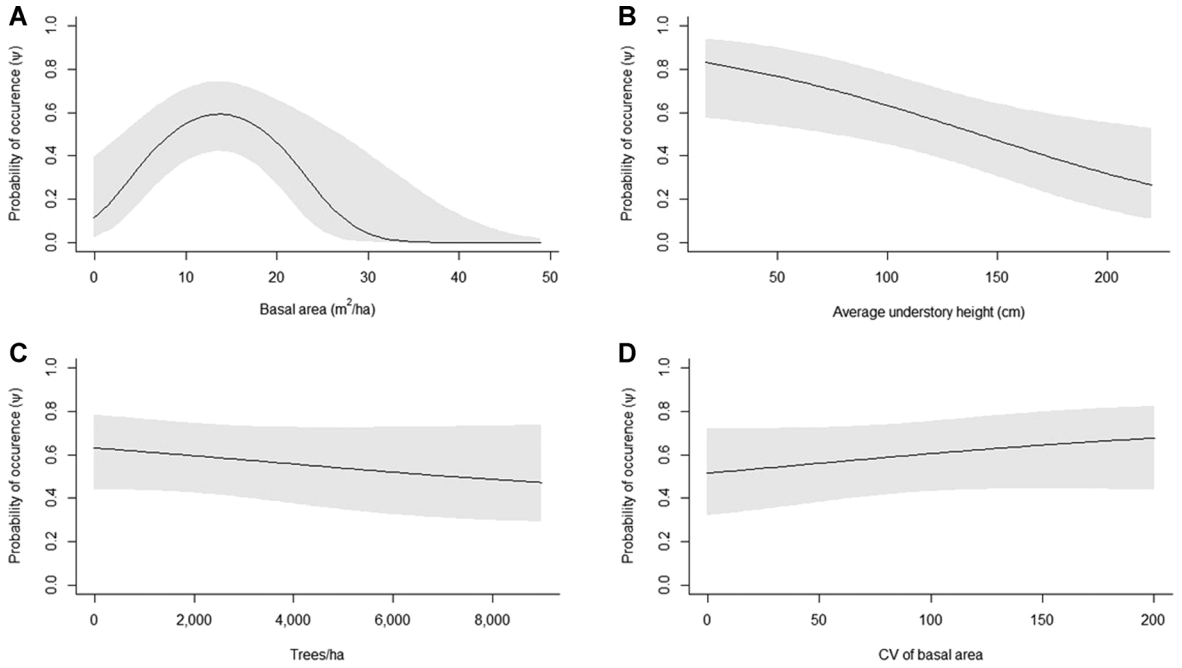

Figure 2. Relationship between eastern whip-poor-will occurrence (ψ) and basal area (m^2/ha; A), understory height (cm; B), tree density (trees/ha; C), and coefficient of variation (CV) of basal area (D) from the best supported models with Akaike's Information Criterion for overdispersed count data corrected for small sample sizes ($\Delta QAIC_c$) ≤2. The solid line represents the model-averaged predicted values and the gray shaded band represents the 95% confidence interval. Data are from point count data collected during 2015 and 2016 at the Fort Drum Army installation in New York, USA, 2015–2016.

basal area was included in only 1 supported model, and was not strongly supported, yet this relationship suggests whip-poor-will occupancy increased with increased variability in basal area (Fig. 2D). Models with tree density and CV of basal area were ranked lower than equivalent models without these variables, indicating weak support for these variables (Arnold 2010). No other additional variables were supported in models with $\Delta QAIC_c > 2$ (Table 2).

DISCUSSION

Our findings are consistent with reports that whip-poor-wills are scarce in closed-canopy forest but contrast with their characterization as a shrubland bird because whip-poor-wills at Fort Drum were associated with intermediate levels of basal area, and shrublands typically have little or no forest cover (Greenberg et al. 2011, King and Schlossberg 2014). Some accounts have identified the whip-poor-will as a shrubland species based on their presence in open sites with little or no canopy cover, such as regenerating clearcuts or pitch-pine scrub-oak (*Quercus* spp.) barrens (Schlossberg and King 2007, Gifford et al. 2010, Tozer et al. 2014). Other researchers have described whip-poor-wills as being associated with forest or woodlands with openings (DeGraaf and Yamasaki 2001, Cink et al. 2017). Based on our results, we consider the whip-poor-will a disturbance-dependent species but not necessarily a shrubland species.

Because we analyzed whip-poor-wills along a gradient of forest cover, we were able to identify an association with intermediate levels of basal area that were not apparent in previous studies that compared whip-poor-will use among discrete management categories or treatments. Bjorklund and Bjorklund (1983) reported that whip-poor-wills were most abundant at a site that included mixed forest and openings, and least abundant at an unmanaged pine plantation. Hunt (2013) reported that whip-poor-wills were associated with thickets and managed forest in New Hampshire, USA, and Tozer et al. (2014) reported that whip-poor-wills were more abundant at sites where clearcuts were present in the landscape than sites where clearcuts were absent. These studies report an association between whip-poor-wills and forest management but do not specify a treatment level most suitable for supporting their numbers. We found that whip-poor-will occupancy peaked at 13.8 m^2/ha, a value typical of an understocked forest, or the lower end of a fully stocked forest (Ginrich 1967), and which corresponds to the residual basal area levels created by a shelterwood harvest (Leak et al. 2014). Thus, we are able to provide managers with a specific level of basal area retention to employ as a management target for this species, which increases the precision of management activities and the rigor and transparency of conservation planning and evaluation (Villard and Jonsson 2009).

Whip-poor-will occupancy was also strongly associated with lower maximum understory height, which supports the suggestions by others that whip-poor-wills are more likely to occupy sites with a relatively open understory (Garlapow 2007, Cink et al. 2017). Clark reported that although whip-poor-wills feed in the open like common nighthawks (*Chordeiles minor*), whip-poor-wills stay much closer to the ground (Tyler 1940), and employ upward-directed sallies to forage on backlit aerial insect prey (Mills 1986). As a result, it has been suggested that open understory structure could facilitate foraging for whip-poor-wills by providing a better line of sight to detect prey when compared to denser understories (Garlapow 2007).

Similarly, the positive association between whip-poor-will occupancy and the CV of basal area might also be associated with whip-poor-will foraging behavior. Although this relationship was not strongly supported, it suggests that whip-poor-wills may prefer sites characterized by variable basal area rather than uniform basal area, such as clumps of trees interspersed with openings. English et al. (2017*b*) suggested an open canopy allows the penetration of moonlight, and thus forest openings could facilitate the location and capture of flying insect prey. In contrast, whip-poor-will nests are typically located at the base of trees, although frequently within open area (Akresh and King 2016, Cink et al. 2017), which would account for the association of whip-poor-wills with some tree cover.

The percentage of coniferous trees did not appear in any supported models, which supports the hypothesis that whip-poor-wills occur in a wide range of forest cover types (Cink et al. 2017). Furthermore, there was also no support for models of whip-poor-will occupancy and the amount of disturbed or developed conditions within the plot areas. This contrasts with the findings of Cooper (1981) who reported that calling whip-poor-wills were scarce in suburban areas in Georgia, USA, and Hunt (2013) who reported whip-poor-wills rarely used un-vegetated portions of their study sites in New Hampshire. The lack of relationships between whip-poor-wills and developed areas at Fort Drum might be because a relatively small portion of the study area (8.9%) was disturbed or developed.

Although our sampling was restricted to a relatively small (440 km^2) area, the northern hardwoods forests that occur on Fort Drum extend throughout the eastern United States and southeastern Canada, and the forest management practices on Fort Drum are commonly applied in these forest types throughout their extent (Leak et al. 2014). Furthermore, studies of whip-poor-wills throughout this region all show the same general patterns with respect to the gross effects of forest management; that is, they are more abundant in open forest than unmanaged forests (Hunt 2013, Tozer et al. 2014, Akresh and King 2016, English et al. 2017*b*). Because the conditions on Fort Drum represent conditions throughout eastern managed deciduous forests and the responses of whip-poor-wills to forest conditions appear to be consistent across their range, we expect our results are applicable throughout the forested portions of the range of this species.

Furthermore, our study points were located along roads to facilitate nocturnal access, in conformity with continent-wide whip-poor-will monitoring programs (Bird Studies Canada 2011, Center for Conservation Biology 2019). We assumed that any effect from roads that might have been present would be common to all survey points; however, we suggest critically examining this assumption in future studies.

MANAGEMENT IMPLICATIONS

Occupancy of whip-poor-wills is greatest at sites with intermediate levels of basal area, with peak occupancy at 13.8 m^2/ha. These values can serve as a quantitative target for management planning for the conservation of whip-poor-wills. This range of values of basal area is typical of an understocked forest, or the lower end of a fully stocked forest, and could be achieved using silvicultural systems such as shelterwood harvests.

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