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# Foraging and roosting habitat of Eastern Whip-poor-wills in the northeastern United States

## Hábitat de alimentación y percha de Antrostomus vociferus orientales en el noreste de Estados Unidos

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ABSTRACT. The Eastern Whip-poor-will (*Antrostomus vociferus*: hereafter whip-poor-will) has been declining from historical population levels throughout its range in the northeast. Although whip-poor-wills have been reported to use a variety of habitats, most recent studies have associated whip-poor-wills with open canopy habitats, such as early-successional habitats or forest edges. However, there remain substantial gaps in our understanding of whip-poor-wills' habitat associations. For example, historical accounts state that whip-poor-wills roost and nest in forest and forage in openings, and thus, managers advocate the juxtaposition of habitats based on this supposition. Nevertheless, a quantitative evaluation of the habitat used for these activities is lacking. For this reason, we radio-tracked 10 adult whip-poor-wills using radio telemetry in upstate New York and collected vegetation measurements at a subset at these points where the birds were either foraging at night or roosting during the day, as well as at any identified nest sites. Comparisons of the vegetation measurements revealed that foraging habitat was significantly more open than roosting habitat, as foraging habitat had lower tree density, basal area, and understory height. Contrary to historical accounts, the few nest sites found in this study were located in areas that had low basal area, similar to the habitat at foraging locations. These results suggest that although creating more open-canopy habitat may benefit whip-poor-wills by providing suitable foraging habitat, and potentially nesting habitat, maintaining denser forest within proximity to these open areas may also provide valuable cover for roosting whip-poor-wills.

RESUMEN. El pato silbador oriental (*Antrostomus vociferus*) ha disminuido su población comparada con niveles históricos en toda su área de distribución en el noreste. Aunque se ha informado que A. vociferus utilizan diversos hábitats, la mayoría de los estudios recientes han asociado a A. vociferus con hábitats de dosel abierto, como los hábitats de transición temprana o los bordes de los bosques. Sin embargo, siguen existiendo importantes vacíos en nuestro conocimiento de las asociaciones de hábitat por parte de especies de este género. Por ejemplo, los relatos históricos afirman que A. vociferus se perchaba y anidaba en el bosque y se alimentaba en los claros, por lo que los gestores abogan por la yuxtaposición de hábitats basándose en esta suposición. Sin embargo, se carece de una evaluación cuantitativa del uso hábitat para estas actividades. Por este motivo, hemos puesto radios en 10 adultos de A. vociferus para utilizar radiotelemetría en el norte del estado de Nueva York y hemos colectado mediciones de la vegetación en un subconjunto de estos puntos en los que los pájaros buscaban comida por la noche o se perchaban durante el día, así como en los lugares de nidificación identificados. Las comparaciones de las mediciones de la vegetación revelaron que el hábitat de búsqueda de alimento era significativamente más abierto que el hábitat de percha, ya que el hábitat de búsqueda de alimento tenía menor densidad de árboles, área basal y altura del sotobosque. Contrario a los registros histórico, los pocos lugares de nidificación encontrados en este estudio se encontraban en zonas con una baja área basal, similar al hábitat de los lugares de alimentación. Estos resultados sugieren que, aunque la creación de un hábitat de dosel más abierto puede beneficiar a A. Vociferus al proporcionarles un hábitat de alimentación adecuado y, potencialmente, un hábitat de nidificación, el mantenimiento de un bosque más denso en las proximidades de estas zonas abiertas también puede proporcionar una valiosa cobertura para las perchas de A. vociferus.

Key Words: *Antrostomus vociferous; conservation; foraging; nesting; radio telemetry; roosting*

## INTRODUCTION

The Eastern Whip-poor-will (*Antrostomus vociferus*: hereafter whip-poor-will) has been the subject of increasing conservation concern because of significant population decreases in North America. Whip-poor-wills have declined at a rate of 2.76% throughout their range since the 1960s (Sauer et al. 2017). Factors such as food availability and habitat loss may be driving these declines (English et al. 2017, Cink et al. 2020), although landscape-level habitat availability does not seem to influence their breeding distribution (Farrell et al. 2019). However, there is still substantial uncertainty about many aspects of whip-poor-will breeding ecology, such as habitat associations and nest site selection (Cink et al. 2020).

There is a perception in the literature that whip-poor-wills require forested habitat for nesting and open habitat for foraging (Tyler 1940, Wilson and Watts 2008; Hunt 2013, *unpublished manuscript*). The whip-poor-will is a crepuscular species that generally roosts during the day and forages at night near dusk and dawn, and when moonlight is sufficient (Cink et al. 2020). Studies have shown that whip-poor-will foraging activity has been positively associated with increased lunar illumination (Mills

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1986, Wilson and Watts 2006), and increased lunar light in open habitats likely makes it easier for whip-poor-wills to locate back-lit insects (Wilson and Watts 2008, Tozer et al. 2014). Recent studies have associated increased whip-poor-will abundance with openness, whether that comes from proximity to edges (Wilson and Watts 2008, Cink et al. 2020; Hunt 2013, *unpublished manuscript*) or early-successional habitats such as young forest and shrublands (Tozer et al. 2014, Akresh and King 2016, English et al. 2017, Spiller and King 2021; Hunt 2013, *unpublished manuscript*). Although a few older studies found higher whip-poor-will abundance in forested areas when compared with more open areas (Cooper 1981, Bjorklund and Bjorklund 1983), whip-poor-wills generally seem to be absent from areas with extensive and closed forest canopy (Cink et al. 2020).

Nest site selection for whip-poor-wills is also not well understood, but appears to place importance on protecting nests from predation because of their reliance on camouflage, like many nightjar species (Troscianko et al. 2016). Whip-poor-wills lay their eggs on the ground, usually only on the leaf litter, without building a structural nest, and males and females incubate the nest, and young quickly leave the nest after hatching (Tyler 1940, Raynor 1941, Cink et al. 2020). Not only does this make incubating birds difficult to spot because of their cryptic plumage, but incubating birds are very reluctant to flush (Tyler 1940, English et al. 2018) and breeding territories are large (Cink et al. 2020), which makes finding nests and characterizing nest sites challenging. Historical accounts have associated whip-poor-will nesting with forested areas, although they are generally vague about the forest structure (Nauman 1925, Mousley 1937, Fowle and Fowle 1954), such as Clarke's observation that whip-poor-wills "always nests among trees" (Clarke, as cited in Tyler 1940:168) and DuBois's record of a nest in "woods of medium size trees, thickly overgrown" (Du Bois 1911:469, Tyler 1940). Although some studies have reported nests in areas of dense undergrowth (Du Bois 1911, Raynor 1941), others have suggested that little to no undergrowth is preferred (Tyler 1940), and one study found whip-poor-will nests in both dense and sparse understory vegetation (Akresh and King 2016).

To ensure that management practices provide suitable habitat for whip-poor-wills, information is needed to determine whether they require different habitat types for foraging and nesting. Only male whip-poor-wills are known to sing, and they generally appear to call from the same areas in which they forage (Tyler 1940, Cink et al. 2020), so it is likely that aural point counts are biased toward calling males and foraging habitat (Wilson and Watts 2006). If whip-poor-wills do in fact use different habitat types for nesting, that would suggest an information gap in the current literature and that more research will be needed to define nesting habitat and understand nest site selection. In this study, we used radio telemetry to assess whip-poor-will habitat preferences within the home range scale and to compare foraging, roosting, and nesting habitat.

## METHODS

### Study area
We conducted this study at Fort Drum, a U.S. Army installation of over 440 km² located in northwestern New York State. Over 90% of Fort Drum comprises undeveloped training areas, of which approximately 57% is forested land, 14% is grassland, 12%

is shrubland, 4% is surface water, and 1% is forbland (U.S. Army Garrison Fort Drum 2011). The dominant species in mature forests include red and sugar maple (*Acer rubrum, 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*). Fort Drum implements a forest management program that mainly uses silviculture to support training maneuvers, facilitate timber production, and improve forest health (U.S. Army Garrison Fort Drum 2011).

### Radio telemetry
We used 2 m X 12 m 60 mm mesh mist-nets to capture adult whip-poor-wills in May and June 2016, at the beginning of the breeding season. We selected areas for mist-netting where birds had been heard calling and limited our selection to areas that had a high likelihood of continued access throughout the season (because of army training schedules in the surrounding areas). Two standard nylon mist nets were set up at night starting at sunset, in landscape-dependent configurations, on nights with no to minimal wind and no rain, starting 30 minutes before sunset and remaining open for 2–3 hours or until a whip-poor-will was caught. We used playback speakers to project male whip-poor-will calls to lure birds into the nets. We banded each bird with a standard USGS-BBL band, and recorded sex as determined by the presence or absence of extensive white on the outer three rectrices (absent on females; Pyle 1997). We then attached the whip-poor-wills with a radio transmitter (164.00-168.00 Mhz Model 0.5g Blackburn) using a leg-loop harness technique (Naef-Daenzer 2007, Streby et al. 2015). We continued capture of birds throughout the season until we attached all transmitters (10 available for the study).

We tracked the radio-tagged whip-poor-wills on foot using handheld VHF receivers and three-element Yagi antennas. We collected bird locations using both homing and triangulation (White and Garrott 1990), and based on the bird's activity, classified each location as either roosting, foraging, or nesting if the bird was incubating eggs. We aimed to collect a minimum of three visually verified foraging locations per bird, as well as three visually verified roosting locations during the day per bird. For locations when visual verification was not possible, we collected GPS points and bearings during pursuit to triangulate locations. If the adult was found to be incubating eggs or unfledged chicks, we recorded these locations separately as nest locations. We collected foraging locations at night within a few hours after sunset because whip-poor-wills begin feeding about 30 minutes after sunset and may continue as long as light is sufficient (Cink et al. 2020).

For visually verified locations collected at night, we tracked birds with radio telemetry and thus were able to identify them by their individual radio frequencies, and located them using their reflected eye-shine from a high-powered flashlight, which can allow one to locate the bird from a distance (Van Rossem 1927). Most foraging locations were located at perches on tree branches, logs, or the ground; we assumed the birds were sallying from these locations because of their movement before and after. We included "in-flight" locations as the location immediately under where a bird had flown only if we could verify using the radio

transmitters that the bird observed was in fact the one being tracked and had changed locations, with the assumption that they were either in the middle of a sally or moving to a different perch to continue sallying. To compare the perched and flying foraging locations, we conducted the habitat analyses with and without the vegetation measurements that were collected at the flying locations (nine out of the 30 total foraging locations) and found no significant difference, so we included the "in-flight" data in the final analysis.

**Vegetation data**
We collected field vegetation measurements using only visually verified telemetry locations. We measured habitat variables at three visually verified day roosting locations and three visually verified night foraging locations per individual, as well as at five nest locations from five birds. If there were more than three visually verified observations of birds during roosting or foraging, we chose the three locations that represented the broadest variety temporally (date and/or time of day). At each of these location points, we took vegetation measurements using techniques modified from James and Shugart Jr. (1970) and King et al. (2009). We 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 1.5-cm-diameter vertical pole 3-m in height at the location site. We used a 10 BAF cruising prism to select trees in a variable-width radius plot for basal area, recording the dbh and species of each tree in the prism plot. We also collected the same vegetation measurements at five nest locations, resulting in a total of 65 point-intercept measurements and 65 cruising prism plots.

We also analyzed all locations using geographic information system (GIS) technology to determine the proportion of different activities (foraging, roosting, nesting) among discrete habitat classes. We analyzed vegetation cover layers for the study site created by Fort Drum's Natural Resources Branch from digitized 30-cm resolution true color orthoimagery and forest inventory plot data, as well as 2015 0.5-m cell resolution aerial imagery of New York State from the National Agriculture Imagery Program (NAIP) using ArcMap 10.5.1. We used the GIS data to determine the number of locations within each habitat class. The vegetation classes produced by Fort Drum related to the levels of canopy cover (closed tree canopy, open tree canopy, and grassland and shrubland).

**Statistical analysis**
We used the tree dbh and species data from the cruising prism plots to calculate basal area (m²/ha), tree density (trees/ha), and percentage basal area of coniferous trees. We also calculated the basal area of trees (m²/ha) in size classes as defined by DeGraaf and Yamasaki (2001): sapling 2.5–9.9-cm dbh; pole 10–22-cm dbh for softwoods and 10–30 cm for hardwoods; sawtimber > 22–51-cm dbh for softwoods and > 31–61-cm for hardwoods; large sawtimber > 51-cm dbh for softwoods and > 61-cm dbh for hardwoods.

We analyzed the data using multiple methods to account for the fact that there were only vegetation measurements for five of the nine nests located. We first compared the foraging and roosting data using data from all locations where we took vegetation measurements. Because there were three of these locations types per bird per activity, this resulted in a total of 30 foraging and 30

roosting observations for each habitat variable. We used a generalized linear model framework to analyze the data because we were interested in being able to predict differences in the habitat characteristics given the observed activity of the birds. We fit the activity of the bird (foraging or roosting) to each vegetation variable in a univariate generalized linear models. We used a gamma error distribution because of the non-normal distributions of many of the habitat variables (Shapiro-Wilk P < 0.05), which transformations failed to correct. We also included the individual bird as a random effect because there were three vegetation measurements per activity type per bird. Statistical tests were considered significant at p ≤ 0.05 after a Benjamini-Hochberg (1995) correction for multiple comparisons ("BH") was applied to the raw p-values. We then applied a nonparametric multivariate approach using kernel discriminant analysis (KDA), implemented with the ks package (Duong 2018), to find the best combination of habitat variables to predict whip-poor-will behavior. This method involves computing a kernel density across the provided parameters and classifying each observation to the group with the highest local density to predict group membership. We then validated the results using a split-sample validation technique, in which only a percentage of the data (50%) was used to train the kernel algorithm and the derived criterion was used to classify samples from the remaining validation data subset and calculate a more accurate error rate of classification (Duong 2015). Prior to analysis, we assessed variables for collinearity using Kendall rank correlation, and removed one variable from highly correlated pairs (r > 0.6).

We then compared habitat measurements at the nesting locations with habitat measurements at foraging and roosting sites (which were averaged for each individual) using univariate generalized linear models. For the roosting and foraging data, we averaged each of the habitat variables across the three measurements per individual to obtain one measurement per individual per activity type. Using the understory vegetation species data, we also calculated the percentage of roosting and foraging points per bird that had herbaceous or woody understory. This resulted in 10 foraging and 10 roosting observations per each habitat variable, which we compared with the five (unaveraged) nest observations per each habitat variable. Again, we applied a gamma error distribution and a BH correction for multiple comparisons to the raw p-values. We also used KDA to perform a multivariate analysis to find the best combination of habitat variables for this dataset and used split-sample validation (with 70% of data in the training group) to assess the reliability of the results.

Finally, we analyzed all locations, including those where vegetation measurements were not taken, using GIS data to compare the proportions of roosting, foraging, and nesting locations in different discrete habitat types. The habitat classes we compared included "closed tree canopy," "open tree canopy," and "herbaceous vegetation," the last of which included both shrubland and grassland habitats. To compare the results, we performed two-sided Fisher's exact tests (FET) because of the small expected values in many cells of the contingency tables and applied the BH correction to pairwise comparisons.

Based on visual observation data, we also performed FETs to compare substrate type between roosting and foraging locations. We used a chi-square test to determine whether tree composition

used for roosting and foraging differed from the expected proportion based on the tree species data collected in the cruising prism plots. We conducted analyses for the habitat variables in the R software environment, version 3.5.1 (R Core Team 2018).

## RESULTS

In total, we used 133 location points collected from 10 birds in the analyses. Only one of the tracked individuals was female, so we did not factor sex into the analyses. Of all the location points, 49 were classified as foraging locations, 75 as day roosting locations, and nine as nesting locations. One individual was observed double-brooding at two separate nest locations ~70 m apart, but we only recorded vegetation data from one of the nests for statistical analysis. Across the roosting and foraging locations, 77% consisted of visual observations of the bird.

We observed whip-poor-wills roosting on the ground (63.3% of locations), and on perches up to 6 m in height, including on logs/stumps (10.2%), tree branches (24.5%), and snags (2.02%). In 20% of roosting observations, we witnessed the adult roosting with one or two chicks on the ground. While foraging, we observed whip-poor-wills in flight (40%), on the ground (6.67%), as well as on perches up to 3 m in height, including on logs/stumps (13.3%), tree branches (33.3%), and snags (6.67%). The perches whip-poor-wills used while foraging differed from perches used while roosting, with the ground being used significantly less often while foraging (Table 1). Whip-poor-wills used deciduous trees for roosting and foraging less often then coniferous trees (44.4% vs 55.6%, deciduous and coniferous trees, respectively; $\chi^2 = 5.75$, df = 1, p = 0.016).

**Table 1**. Percentage of birds found roosting or foraging at common perch substrates. Common superscripts across rows indicate means that do not differ statistically (p > 0.05) after applying two-sided Fisher's test.

|  | Ground | Logs/ Stumps | Tree Branches | Snags |
|---|---|---|---|---|
| % Foraging | 8.82[a] | 54.6[b] | 55.6[b] | 75[b] |
| % Roosting | 91.2[a] | 45.5[b] | 44.4[b] | 25[b] |

Maximum understory height and tree density were both higher at roosting locations than at foraging locations when comparing only foraging and roosting data (Table 2). When applying the multivariate KDA, the combination of habitat variables that achieved the best group separation and most accurately assigned foraging and roosting activity to the correct habitat values was understory height, tree density, basal area, and percentage of coniferous trees, with a classification error rate of 0.25 after applying split-sample validation (Table 3). Whip-poor-wills foraged in sites with lower understory, tree density, basal area, and percentage of coniferous trees compared to roosting sites.

When comparing the nest data with foraging and roosting data collapsed to the bird level, three additional habitat characteristics were significantly different between foraging and roosting locations, which confirms the need for a bird effect in these models. Maximum understory height, tree density, and basal area were all higher at roosting locations than at foraging locations (Table 4). The maximum understory height was also higher at nesting

locations than foraging locations. The basal area of saplings was higher at roosting sites than at foraging sites, but not significantly different at nesting sites. The percentage of woody understory was lower at foraging locations than at either roosting or nesting locations. When applying the multivariate KDA, the combination of habitat variables that achieved the best group separation and most accurately assigned foraging, roosting, and nesting activity to the correct habitat values was tree density, basal area, and % woody understory, with a classification error rate of 0.375 after applying split-sample validation (Table 5).

**Table 2**. Summary statistics (mean and standard error in parentheses) of habitat variables derived from full set of field measurements taken at 30 foraging and 30 roosting locations, as well as goodness-of-fit statistics derived from analysis of deviance (Type II tests) of the univariate glm models. P-values in bold indicate that 95% confidence intervals did not include zero.

|  | Foraging | Roosting | Df | F | p |
|---|---|---|---|---|---|
| HEI[†] | 69.8(17.4) | 208.1(17.4) | 1 | 13.63 | **0.0043** |
| TPH | 620.9(207.1) | 4910.5(970.6) | 1 | 12.18 | **0.0043** |
| BAS | 13.4(2.05) | 21.7(2.45) | 1 | 0.92 | 0.77 |
| CONI | 23.3(4.86) | 26.5(5.14) | 1 | 0.03 | 0.89 |
| SAP | 1.15(0.49) | 6.20(1.1) | 1 | 4.58 | 0.11 |
| POLE | 3.44(0.78) | 5.59(1.41) | 1 | 0.43 | 0.87 |
| SAW | 7.19(1.33) | 7.89(1.58) | 1 | 0.02 | 0.90 |
| LSAW | 1.61(0.60) | 2.07(0.7) | 1 | 0.08 | 0.90 |

[†]HEI = maximum understory height (cm), TPH = tree density (trees/ha), BAS = basal area (m²/ha), CONI = % basal area of coniferous trees, SAP = basal area of saplings, POLE = basal area of poles, SAW = basal area of sawtimber, LSAW = basal area of large sawtimber.

**Table 3**. Split-sample validation of the kernel discriminant analysis using habitat variables (HEI, TPH, BAS, CONI[†]) derived from full set of field measurements taken at 30 foraging and 30 roosting locations.

|  | F(est.) | R(est.) | Total | error |
|---|---|---|---|---|
| F(true) | 13 | 2 | 15 | 0.13 |
| R(true) | 6 | 11 | 17 | 0.35 |
| Total | 19 | 13 | 32 | 0.25 |

[†]HEI = maximum understory height (cm), TPH = tree density (trees/ha), BAS = basal area (m²/ha), CONI = % basal area of coniferous trees.

When comparing all recorded locations of foraging, roosting, and nesting activity using the GIS-derived cover layer data, there was a significant difference in the proportions of habitat classes between foraging and roosting locations (Fisher's exact test; p < 0.0001), as well as between nesting and roosting locations (p = 0.005), but not between the foraging and nesting locations (p = 0.61; Fig. 1). There were significant differences in the proportions of whip-poor-will activity between closed canopy and herbaceous vegetation (Fisher's exact test; p < 0.0001) and between closed canopy and open canopy conditions (p < 0.0001), but not between herbaceous and open canopy conditions (p = 0.53; Fig. 1). A higher number of the foraging locations and all of the nesting locations were at sites with open canopy conditions, while a higher number of the roosting locations were at sites with closed canopy (Fig. 1).

**Table 4**. Summary statistics (mean and standard error in parentheses) of habitat variables derived from field measurements at nest sites and averaged across birds at foraging and roosting locations, as well as goodness-of-fit statistics derived from analysis of deviance (Type II tests) of the univariate glm models. P-values in bold indicate that 95% confidence intervals did not include zero, while common superscripts across rows indicate means that do not differ statistically (p > 0.05).

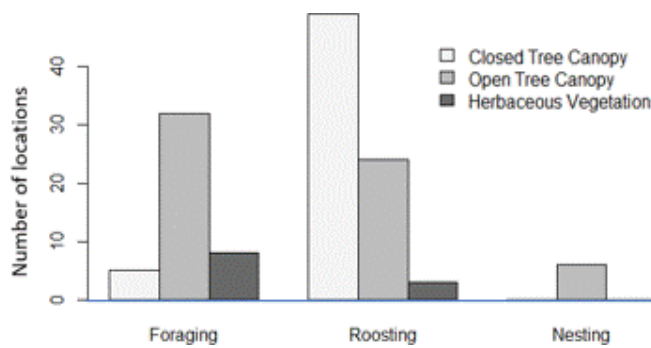| | Foraging | Roosting | Nests | F | Df | p |
|---|---|---|---|---|---|---|
| HEI[†] | 69.8[a](12.4) | 208.1[b](21.8) | 198.0[b](48.0) | 13.7 | 2 | **< 0.001** |
| TPA | 620.9[a](153.1) | 4910.5[b](1467.1) | 2421.8[ab](1115.1) | 11.4 | 2 | **0.002** |
| BAS | 13.4[a](2.26) | 21.7[b](2.57) | 11.5[ab](1.45) | 4.84 | 2 | **0.036** |
| CONI | 23.3(7.31) | 26.5(6.76) | 15.7(10.2) | 0.40 | 2 | 0.75 |
| SAP | 1.15[a](0.4) | 6.20[b](1.62) | 3.67[ab](1.56) | 6.84 | 2 | **0.012** |
| POLE | 3.44(0.87) | 5.59(2.02) | 0.92(0.56) | 3.70 | 2 | 0.059 |
| SAW | 7.191.7 | 7.88(1.87) | 4.59(1.92) | 0.75 | 2 | 0.60 |
| LSAW | 1.610.8 | 2.07(0.74) | 2.3(1.45) | 0.13 | 2 | 0.88 |
| WOOD | 23.3[a](5.09) | 86.7[b](7.37) | 80.0[b](20.0) | 15.4 | 2 | **< 0.001** |

[†]HEI = maximum understory height (cm), TPH = tree density (trees/ha), BAS = basal area (m²/ha), CONI = % basal area of coniferous trees, SAP = basal area of saplings, POLE = basal area of poles, SAW = basal area of sawtimber, LSAW = basal area of large sawtimber, WOOD = % woody vegetation in understory.

**Table 5**. Split-sample validation of the kernel discriminant analysis using habitat variables (TPH, BAS, WOOD[†]) derived from field measurements at nest sites and averaged across birds at foraging and roosting locations.

| | F(est.) | N(est.) | R(est.) | Total | error |
|---|---|---|---|---|---|
| F(true) | 3 | 1 | 0 | 4 | 0.25 |
| N(true) | 0 | 1 | 0 | 1 | 0 |
| R(true) | 0 | 2 | 1 | 3 | 0.667 |
| Total | 3 | 4 | 1 | 8 | 0.375 |

[†]TPH = tree density (trees/ha), BAS = basal area (m²/ha), WOOD = % woody vegetation in understory.

**Fig. 1**. Number of total telemetry locations recorded for foraging, roosting, and nesting Eastern Whip-poor-wills (*Antrostomus vociferus*) by discrete habitat type.



## DISCUSSION

We found that whip-poor-will foraging locations had significantly lower tree density and basal area than roosting locations, consistent with the suggestion of other researchers that habitats with an open canopy may allow for increased penetration of moon light and may provide a richer prey base for foraging (Wilson and Watts 2008, Tozer et al. 2014). This is further supported by our

observation that basal area of saplings—young trees with diameters of 2.5–9.9 cm—was significantly lower at foraging sites than at roosting areas, as a dense midstory would likely decrease visibility. Nevertheless, whip-poor-wills did appear to require some level of tree cover while foraging, as indicated by the greater proportion of foraging locations in open forest relative to grasslands and shrublands. Furthermore, in nearly 40% of the foraging observations, whip-poor-wills used tree branches and snags for perching. These results suggest that although some degree of canopy openness is important for foraging, some level of tree cover is desirable, perhaps because of the extensive use of branches, snags and stumps for foraging perches that we observed in this study.

We also found that there was significantly lower maximum understory vegetation height at foraging locations than at both roosting and nesting locations, which indicates that whip-poor-wills use areas with greater understory openness for foraging. Open understory structure may facilitate foraging for whip-poor-wills by providing a better line of sight to detect prey (Garlapow 2007), whereas too dense of an understory may inhibit their visibility or even maneuverability. The composition of the understory at foraging locations had a lower proportion of woody vegetation than at either roosting or nesting locations, which may also relate to the need for a more open, less shrubby understory while foraging.

In contrast to foraging sites, whip-poor-wills in our study roosted and nested in habitat with more closed canopy-cover and denser understory vegetation. Although little is known about roosting habitat for whip-poor-wills, it was not surprising that habitat characteristics at roost site would be similar to that of nest sites, given that male and female whip-poor-wills are known to roost together before nest site selection (Cink et al. 2020), and males have been reported roosting next to nest sites (Akresh and King 2016). Alternatively, roosting in dense vegetation might confer energetic benefits, as suggested as an explanation for whip-poor-will's selection of nest sites near trees, which might protect them from wind, solar radiation, and precipitation (Fisher et al. 2004, Akresh and King 2016). Although we found few nests, our results that nests were located in sites with higher maximum understory

vegetation and a greater proportion of woody understory is consistent with a number of other studies that have also reported nests in areas of dense understory vegetation (Du Bois 1911, Raynor 1941, Akresh and King 2016). Vegetation density is reported to interfere with nest searching by predators (e.g., Norment 1993), and may enhance the effectiveness of their cryptic coloration for whip-poor-wills that are particularly vulnerable because of their lack of a structural nest and the reluctance of incubating birds to flush (Troscianko et al. 2016, English et al. 2018, Cink et al. 2020). Safety from predation may also explain the association between whip-poor-will roosts and dense vegetation structure. In contrast to the suggestion by other researchers that whip-poor-wills require more densely forested habitat for nesting and open habitat for foraging (Tyler 1940, Wilson and Watts 2008; Hunt 2013, *unpublished manuscript*), all the nests we located were in forests with some degree of canopy openness.

There was no significant difference between foraging, roosting, and nest sites in the percentage of coniferous trees or in the basal area of trees larger than saplings. It has been suggested that forest structure is of more importance than forest composition in whip-poor-will habitat associations (Cink et al. 2020). Notably, whip-poor-wills did use a higher proportion of coniferous trees for perches while both foraging and roosting than would be expected given the surrounding tree composition. In general, however, the results from this study do not suggest that whip-poor-will use habitats with significantly different tree compositions for foraging, roosting, or nesting.

Although differences between habitat and other sites were clear in this project, it would be interesting to see whether these patterns are borne out with a larger sample size of nests. Additionally, whip-poor-wills use other types of forest besides the oak-dominated stands where we worked, and although the association of whip-poor-wills with open-canopy habitats appear to be widespread, whether the differences between foraging, roosting, and nest sites we observed will also be similar in other forest types remains to be determined. Finally, whip-poor-wills are a ground nesting species, and although litter depth did not influence their distribution among habitat types at our study area (Spiller and King 2021), their preference for nest sites may also be influenced by litter depth, which we did not quantify in this study.

## CONCLUSION

Our findings suggest that an interspersion of relatively open canopy conditions for foraging and nesting and more closed forest for roosting will best satisfy the habitat requirements for whip-poor-wills during the breeding season. The average basal area at foraging locations was 13.4 m²/ha, while the average basal area at nest sites was 11.5 m²/ha, both of which correspond to residual basal area following shelterwood treatment (Leak et al. 2014). Roosting sites in our study averaged 21.7 m²/ha of basal area, which is typical of unmanaged closed-canopy forest (Leak et al. 2014). Having breeding and roosting habitat in proximity to suitable foraging habitat has been shown to be beneficial to other nightjar species by decreasing foraging distance and therefore energy expenditure (Evens et al. 2018), so is likely an important factor to whip-poor-wills, as well.

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