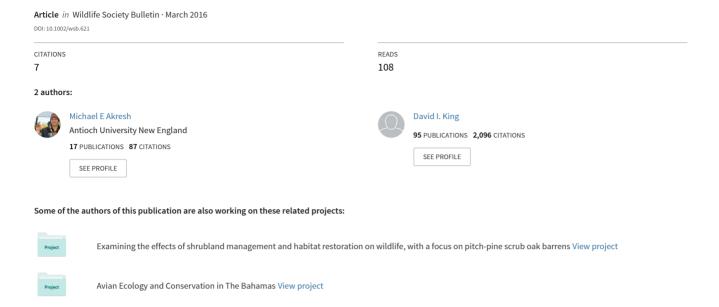
Eastern whip-poor-will breeding ecology in relation to habitat management in a pitch pine-scrub oak barren



Original Article



Eastern Whip-Poor-Will Breeding Ecology in Relation to Habitat Management in a Pitch Pine-Scrub Oak Barren

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ABSTRACT Numerous wildlife species are dependent on the creation and maintenance of early successional forests, yet little is known about the effects of habitat management on some threatened species. One such species is the eastern whip-poor-will (Antrostomus vociferous), a nocturnal bird of conservation concern. We examined the effects of heavy thinning, mowing, burning, and herbicide treatments on this species by conducting point counts and nest searches on a pitch pine-scrub oak (Pinus rigida-Quercus ilicifolia) barren in western Massachusetts, USA, between 2006 and 2013. Our point-count data showed that the abundance of calling birds was greater in managed shrublands such as scrub oak barrens and heavily thinned pitch pine stands, compared to closed-canopy pitch pine and deciduous forest. We found a high number of whip-poorwill nests (n = 26) and roosts (n = 59), which we located primarily within managed shrublands. We did not search for nests in closed-canopy forests, and we were unable to determine the extent of their use of the forest edge for nesting. Nevertheless, birds selected nest sites under residual deciduous trees within the early successional forests; therefore, canopy cover appears to be important for nest placement at the nest-patch spatial scale, but not necessarily at a broader scale. Nests were found in both dense and sparse understory vegetation; none were found in vegetation patches that were <2 years since treatment. Estimated nest survival was 63% through incubation (daily survival rate = 0.977, n = 21), consistent with other published studies of nightjars in the United States and Canada. Creating and maintaining open-canopy early successional forests in pitch pine-scrub oak barrens, with the retention of some residual deciduous trees, should increase the amount of habitat suitable for courtship, roosting, and nesting by eastern whip-poorwills. © 2016 The Wildlife Society.

KEY WORDS aerial insectivore, *Antrostomus vociferous*, Caprimulgiformes, fire, nest survival, nightjar, population limitation, shrubland, thinning.

Understanding breeding ecology and habitat use of species of conservation concern is important to inform wildlife management and prevent population declines. The eastern whip-poor-will (Antrostomus vociferous), a species in the nightjar family (Caprimulgidae), is a nocturnal and crepuscular, aerial insectivorous, migratory bird that has dramatically declined throughout its range (MassAudubon 2011, Sauer et al. 2014). Proposed reasons for the decline of whip-poor-wills include diminishing insect food resources (Boettner et al. 2000, Hallmann et al. 2014), wintering ground factors, decreases in breeding season productivity (Santner 1992 in Cink 2002), and declines in the amount of suitable breeding habitat (Tozer et al. 2014). Eastern whip-poor-wills have been reported to use many vegetation cover

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types such as conifer, deciduous and mixed forests, pasture, and even suburban areas (Cooper 1981, Bjorklund and Bjorklund 1983, Cink 2002). Recent studies in the past decade have found that eastern whip-poor-wills prefer large areas of early successional forest such as regenerating clearcuts (Wilson and Watts 2008, Hunt 2013, Tozer et al. 2014), which may provide suitable habitat for foraging (Tyler 1940, Cink 2002, Garlapow 2007). Active forest management plays an important role in creating and maintaining early successional forests for eastern whip-poor-wills and other declining early successional bird species (Thompson and DeGraaf 2001). Nevertheless, little is known about key aspects of whip-poor-will breeding ecology, including abundance, nest site characteristics, and nesting success, particularly in relation to these forest management practices (Cink 2002).

Other bird species require specific habitats and nesting sites (Bulluck and Buehler 2008, King and Schlossberg 2014), and nest survival can be affected by habitat features such as forest

type or distance to forest edge (Fink et al. 2006, King et al. 2009). There is a perception in the literature that whip-poor-wills may nest in closed canopy, forested areas adjacent to early successional foraging sites (Wilson and Watts 2008, Hunt 2013). However, because whip-poor-wills are nocturnal and nests are very inconspicuous, few nests have actually been described, especially in a single study area (Raynor 1941, Mills 1986, Cink 2002). A better understanding of whip-poor-wills' selection of nest sites and reproductive success is critical in determining whether management efforts are successful in providing productive breeding habitat (Sallabanks et al. 2000, Donovan et al. 2002).

We studied whip-poor-wills in a managed pitch pine-scrub oak (*Pinus rigida-Quercus ilicifolia*) barren to determine the effects of fuels reduction and habitat restoration on their abundance and nesting success. Our objectives were to 1) assess whether whip-poor-wills have higher abundance in managed shrublands in our study site; 2) determine whip-poor-will nest and roosting site selection and nest survival in relation to habitat management; and 3) address knowledge gaps in the natural history of this threatened yet little-studied species.

STUDY AREA

We conducted the study in the Montague Plains Wildlife Management Area, an approximately 600-hectare managed pitch pine-scrub oak barren in western Massachusetts, USA (N $42^{\circ}34'$, W $72^{\circ}31'$). The majority of the study area consisted of closed-canopy pitch pine stands, heavily thinned pitch pine stands, and open-canopy scrub oak barrens (Motzkin et al. 1996). Deciduous closed-canopy forest (>90% canopy cover, King et al. 2011) and a few power-line corridors were also present in the study site. The Montague Plains were managed by the Massachusetts Division of Fisheries and Wildlife, which had been logging pitch pine and conducting prescribed burns to restore the pitch pinescrub oak barren natural community and reduce the amount of wildfire fuels at the site. Starting in 2000, patches of scrub oak stands were treated with mowing and/or burning, and treatments continued during the study. Active cutting of some of the pitch pine stands occurred between 2004 and 2008, in which 70% of the basal area of overstory pitch pine was removed and the understory was mowed. Power-line corridors were treated with selective herbicide, specifically targeting the removal of saplings and trees. These practices resulted in a reduction of tree canopy cover from >80% to <40% in treated pitch pine forests, the maintenance of low tree canopy cover in scrub oak barrens (<22%), and a complete lack of tree canopy cover in power-line corridors (King et al. 2011, Akresh 2012).

METHODS

Sampling

We conducted nocturnal point counts for whip-poor-wills at 24 survey points located throughout the study site in 4 forest types (6 points in each): closed-canopy deciduous forest, closed-canopy pitch pine forest, open-canopy-treated pitch

pine, and open-canopy scrub oak. Distance between points was >250 m, which is greater than the average diameter of a whip-poor-will territory (Hunt 2013). Thus, the likelihood of double-counting the same bird at multiple points was probably low. We visited each point 3 times/season, at 15-200 min after sunset between 16 June and 13 July in 2006, and between 29 May and 29 June in 2007. We surveyed most points in both 2006 and 2007 (92%); we moved 2 point locations between years, but the new points were located in the same forest type. One observer (D.I. King) conducted all the point counts, recording the number of whip-poor-wills estimated to be singing within 100 m during a 10-minute survey period. We conducted counts during conditions of little wind (<10 miles/hr [16 km/hr]) and no precipitation. Although some of our surveys in 2006 were conducted when the moon-face illumination was low and eastern whip-poorwills may have been less detectable (Wilson and Watts 2006), we believe that this did not bias our results. We surveyed every location in 2006 at least once when the moon-face illumination was >50%, and we found similar results in 2007 when all surveys were conducted with a moon-face illumination percentage of \geq 65%.

We located nests and roosting sites primarily by incidentally flushing whip-poor-wills while searching for prairie warbler (Setophaga discolor) nests as part of a separate study (Akresh et al. 2015). Prairie warblers are shrubland specialists; therefore, we only searched treated pitch pine, scrub oak, and power-line corridors. We surveyed study plots intensively while mapping prairie warblers and searching for their nests (every week in 2008 and every 2-4 days in 2009-2013) from late April through July (Akresh et al. 2015). We surveyed 5 plots in treated pitch pine, totaling 83.7 ha; 2 plots in scrub oak, totaling 34.7 ha; and 2 plots in power-line corridors, totaling 9.9 ha (see Akresh et al. [2015] for a map of the plots; the ninth plot was the northern-treated pitch pine area). A few plots were not surveyed extensively in some years of the study (a 27.5-hectare plot in treated pitch pine, and a 6-hectare plot in scrub oak). The study plots comprised most of the early successional, managed area within this pitch pine-scrub oak barren. Between 2008 and 2013, we estimated that we surveyed more treated pitch pine that was relatively older: approximately 10% of the treated pitch pine surveyed was 0-1 years since treatment, 45% was 2-4 years since treatment, and 45% was 5-9 years since treatment. Furthermore, approximately 20% of the scrub oak barrens surveyed was 0–1 years since treatment and 80% was >1 years since treatment.

We marked eastern whip-poor-will nests with flagging 15–20 m from the nest, and we checked nests every 2–4 days. Whip-poor-wills are semiprecocial and nestlings can move from the original nest site after hatching (Cink 2002). These movements typically increase in frequency and distance with nestling age; younger nestlings are usually within 0–5 m of the original nest site (Kramer and Chalfoun 2012). When we did not locate eggs or nestlings during a nest check, we searched an area of 10–15 m around the original nest location. Additionally, we often conducted another search of the area during the next nest check (Allen and Peters 2012).

We classified nest failure by the disappearance of adults and eggs, in addition to sometimes finding cracked, broken eggs but no nestlings. We found no signs of eggshells after eggs successfully hatched (Raynor 1941). For a few nests, we were unsure if one or both of the nestlings hatched and fledged because of the difficulty in locating both nestlings after they quickly fled under thick vegetation (Dyer 1977). Nevertheless, flushed adults were often conspicuous and conducted broken-wing displays, allowing us to determine whether the nest was still active, even if only one nestling was observed.

We recorded a Global Positioning System point using a handheld receiver (Garmin Ltd., Olathe, KS) for all nests and almost all roosting sites found. For 10% of roosting sites, we did not record the coordinates; however, we still recorded the forest type. We defined roosting sites as locations where birds were flushed and we did not observe eggs or nestlings. From 2011 to 2013, when possible, we recorded the sex of the roosting bird, based on observations of white on the outer rectrices of the bird in flight (Cink 2002). For most of the nests, we recorded the distance to the nearest tree trunk (tree defined as vegetation >4 m tall), and recorded the tree species.

During the final year of the study, we measured canopy cover at all nests for which the canopy was unchanged since the time of nesting. This included all nests found in 2013 (n=5), and some nests found in previous years (n=6). We defined canopy cover as any vegetation taller than 3 m seen directly over the nest location (Akresh et al. 2015). To do this, M.E. Akresh held a 3-meter pole vertically above the nest, and used this pole and corresponding sightline to determine whether canopy was present or absent directly above the nest. We classified the canopy cover as consisting of either predominantly deciduous or coniferous foliage. We also measured canopy cover at the nest patch. Using the same method, we recorded whether canopy cover was present or absent at locations 5 m from the nest in each cardinal direction. We then defined nest patch cover as the proportion of canopy presence at the 5 locations surveyed (N, E, S, W, and at the nest). We assessed total canopy cover at the nest patch, as well as cover by only deciduous foliage.

Statistical Analysis

We conducted Generalized Linear Models to examine the relative abundance of eastern whip-poor-wills among forest types. Given our small number of point-count locations, we could not analyze the data with N-mixture models that would more directly account for detection probability (Royle 2004). Instead, we took the maximum count for each point from the 3 surveys in a given year, and fit these data to a Poisson distribution with a log link (King et al. 2011). Taking the maximum count from the 3 surveys should help in preventing the possible effect of moonlight on the detection of birds, because every point was surveyed at least once per year when the moon-face illumination was high. We included 2 predictor variables in our model: forest type and year. We examined the differences in abundance among closed-canopy forest (pitch pine and deciduous forest combined), treated pitch pine, and scrub oak. We initially

tested for a difference in abundance between closed-canopy pitch pine and deciduous forest; however, whip-poor-wills were nearly absent from both of these forest types, so we lumped these closed-canopy forests together to simplify the model and reduce the number of parameters. We also fit a model with a random effect of point location, but the random effect did not converge well, and we therefore examined the simpler, fixed-effect model. Parameters were considered significant if the 95% confidence interval of the parameter estimate did not include 0. The model fit well with a dispersion parameter of 0.83 and a McFadden's Pseudo R^2 of 0.25 (McFadden 1974). We used the R statistical program version 3.1.1 to conduct all analyses (R Core Team 2014).

We plotted roosting and nest site locations on Geographic Information System (GIS) layers of management treatments and aerial photos (MassGIS 2008/2009). We created a GIS layer defining the forest edge, classified as the edge of closed-canopy forest with early successional forest. We then computed the distance to the closest forest edge for each nest and roost site using the "spatstat" package in R (Baddeley and Turner 2005). With the management-treatment GIS layer, we determined the years since treatment and the forest type for each nest and roost location. One nest in our nest survival analysis was located in a closed-canopy forest in which the understory had been previously burned; we lumped this nest with those found in treated pitch pine. We therefore had 2 forest types in our nest survival analysis: scrub oak and treated pitch pine.

To analyze nest survival rates, we used Program MARK version 8.0, run through the R package "RMark" (White and Burnham 1999, Dinsmore et al. 2002). Given our knowledge of nestling movements, we were confident that we were able to locate the nestlings during the first nest check after hatching. We determined nest survival up until the date of the nest check where we first saw nestlings. This analytical method has been used by other studies assessing nightjar nest survival (Allen and Peters 2012). Although a few nests were placed in similar locations (within 10 m of each other) in consecutive years, we believe multiple factors could have affected these nests differently among years, and we thus classified each nest as an independent sample in our analysis.

We examined the daily nest survival rate and 95% confidence intervals, as well as the estimated survival rate for 20 days—the approximate length of the laying and incubation period (Cink 2002). In addition to the null survival model, we examined a number of single-covariate models in which we tested the effects of forest type (Table 1), time since treatment, distance to the nearest forest edge, distance to the nearest tree, and a linear and quadratic effect of ordinal day of season. We determined whether predictor variables significantly affected nest survival by examining the 95% confidence intervals of the parameter estimates. The effect was deemed insignificant if the 95% confidence interval included 0. We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) and Akaike's model weights (w_i) to rank the candidate models and determine the top models that described nest survival (Burnham and Anderson 2002).

Table 1. Candidate models in the eastern whip-poor-will nest-survival analysis (data obtained from nest searches on a pitch pine–scrub oak barren in western MA, USA, between 2008 and 2013). Presented are the models, number of parameters (K), Akaike's Information Criterion corrected for small sample sizes (AIC_c), change in AIC_c from the top model (Δ AIC_c), and Akaike's model weights (w_i).

Model	K	AIC _c	ΔAIC_c	w_i
$S_{ m (Null)}$	1	50.71	0.00	0.29
S(Distance to Tree)	2	51.97	1.26	0.16
S _(Day of Season)	2	52.18	1.47	0.14
S _(Forest Type)	2	52.44	1.73	0.12
S(Distance to Forest Edge)	2	52.65	1.95	0.11
S(Years Since Treatment)	2	52.72	2.01	0.11
S(Quadratic Day Of Season)	3	53.53	2.83	0.07

Little data exist concerning whip-poor-will nests; therefore, we also present data on clutch size, incubation period, and nesting phenology. We recorded clutch size for nests visited before hatching. We classified nests found during the laying period as nests found initially with one egg, and found with a second egg on the next nest check. For a subset of nests, we determined the nest initiation date by either finding the nest during egg-laying (n=3), or by observing the nest before and after the hatch date and back-estimating the nest initiation date assuming a 20-day incubation cycle (n=13; Cink 2002).

RESULTS

We recorded 54 detections of eastern whip-poor-wills during the point-count surveys in 2006 and 2007. Combining the 3 surveys/point, we heard ≥ 1 eastern whip-poor-will at 12 (50%) of the points in 2006, and 9 (38%) of the points in 2007. Whip-poor-wills were significantly less abundant in closed-canopy forest compared with both scrub oak barrens ($\beta = 2.30$, 95% CI = 1.33–3.54), and thinned pitch pine ($\beta = 1.39$, 95% CI = 0.23–2.71; Fig. 1), and significantly more abundant in scrub oak than thinned pitch pine

 $(\beta = -0.92, 95\% \text{ CI} = -1.80 \text{ to } -0.13)$. There was no significant variation in abundance between years $(\beta = -0.51, 95\% \text{ CI} = -1.26 \text{ to } 0.19)$.

We found 26 eastern whip-poor-will nests—17 in thinned pitch pine and 7 in scrub oak (Fig. 2). We found 2 nests in closed-canopy forest, but within 50 m of open-canopy areas. We did not find any nests in the interior areas of power-line corridors. Vegetation in which we found nests had been treated with mowing or burning 2-7 years previously (median = 4), with an exception of one nest found in untreated closed-canopy forest. Nests in shrublands averaged 83 m from the forest edge (range = 4–191 m). All nests that we examined (n = 23) were within 10 m of a tree trunk (mean distance = 3 m, range = 0.5-10 m), and the closest tree to the nest was almost always deciduous (91% of the nests; Fig. 3). For the 11 nests for which we measured canopy coverage, all had deciduous canopy present directly above the nest. Additionally, deciduous canopy coverage directly above the 5-m-radius nest patch averaged 58% (SD = 21%), with the total canopy cover (including conifers) directly above the nest patch averaging 69% (SD = 14%). Nests were usually placed on dried oak leaves or other leaf litter. Nests were found in a wide range of understory vegetation densities; some were in patches of relatively few woody shrubs with open understory, whereas others were in small openings ($<1 \text{ m}^2$) of open ground within areas of thick understory vegetation (Fig. 3).

We located 59 roost sites, detecting 15 males, 13 females, 5 adult pairs, 22 birds of unknown sex, 1 juvenile (incomplete tail but old enough to fly), and 3 adult–juvenile pairs. To the best of our knowledge, all roosting sites were on the ground, although some birds were first seen flying midair after being flushed. We found roosting locations primarily in treated pitch pine (n = 45) and scrub oak (n = 11); a few roosts were found in closed-canopy forest (n = 3). We did not find any roosting sites within the interior areas of power-line corridors. Roosting locations were in a large range of

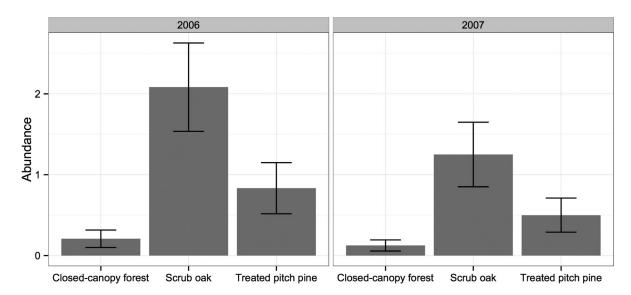


Figure 1. Predicted eastern whip-poor-will abundance estimates among forest types based on point counts conducted in the study site in western Massachusetts, USA, during 2006 and 2007. Closed-canopy forest consists of closed-canopy deciduous and pitch pine stands combined, whereas scrub oak and treated pitch pine are open-canopy shrublands. Error bars are ±1 standard error.

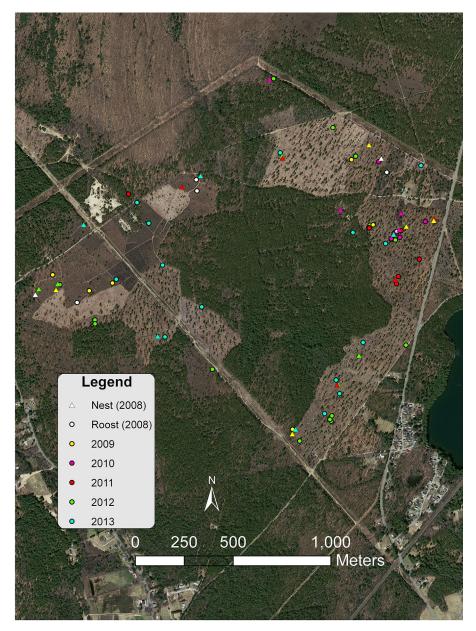


Figure 2. An aerial map of the Montague Plains, Massachusetts, USA, in April 2009 (MassGIS 2008/2009), with nesting and roosting locations of eastern whip-poor-wills found during 2008–2013. Note the aerial photo was taken before deciduous vegetation leafed out, and the dark green areas are closed-canopy pitch pine forest. The dark green spots are residual pine trees. Roost sites are depicted as circles, and nests are triangles. Different colors indicate nests or roosts found during different years.

treatment ages (1–9 yr since treatment, median = 5), and in patches that were treated with mowing or burning. Roosts in shrublands were, on average, 89 m to the closest forest edge (range = 3–212 m), and the 3 roosts found in closed-canopy forest were within 50 m of the forest edge.

Of the 26 nests, we located 5 after the young hatched, and we excluded these nests from the nest survival analyses. Therefore, we included 21 nests for 301 total observation days in the nest survival models. For the nests found during incubation, 14 of 21 (67%) survived until hatching. Sample sizes within years were small, and apparent survival varied among years: 2 of 2 nests survived in 2008, 2 of 4 in 2009, 1 of 1 in 2010, 4 of 4 in 2011, 2 of 5 in 2012, and 3 of 5 in 2013. From our nest survival analysis in MARK, the daily nest

survival rate was 0.977 (95% CI = 0.954–0.989). Using this daily survival rate, the nest survival rate during a 20-day incubation period was calculated to be 63% (95% CI = 39–81%). The null model was the best-supported model based on AIC_c values (Table 1). We found no predictor variables that significantly affected nest survival rates (the 95% CI of the parameter estimates of all the predictor variables included 0).

For the 14 nests that survived until hatching, we found and observed the young for an additional 3–5 days for 21% (3) of the nests, 6–10 days for 43% (6) of the nests, and 11–17 days for 21% (3) of the nests. For one nest, we did not search for the nestlings in a subsequent check after they hatched; and for one nest we found a dead, abandoned nestling a few days



Figure 3. (a) A typical eastern whip-poor-will nest site in scrub oak in western Massachusetts, USA (nest present but not visible). Note the presence of deciduous canopy cover and dense understory vegetation. (b) The same nest site as shown in "a" with eggs partially visible (in circle). (c) A typical eastern whip-poor-will nest site and brooding adult (in circle) in treated pitch pine, with less understory vegetation. (d) The same nest as shown in "c" with an egg and a camouflaged nestling. Photos taken by M. E. Akresh (a and b) and B. Kramer (c and d).

after hatching, but we do not know what happened to the second nestling. Overall, we were unable to determine whether nestlings that disappeared were depredated or if we just could not locate them after they moved.

All 21 nests observed before hatching had a clutch size of 2 eggs. We found 3 nests during the laying period, and 2 survived to hatching. The adults incubated these 2 nests for \geq 20 and 21 days, respectively, after which we found nestlings at the next nest checks 3–4 days later. We also found one nest after laying (with 2 eggs), which was incubated for \geq 22 days; but the nest was depredated by the next nest check. Nest initiation dates ranged from 9 May to 2 July (n = 16). The majority of active nesting (adults on eggs) that we found occurred between mid-May and mid-June, with apparently fewer adults incubating eggs in July.

DISCUSSION

Despite ongoing forest management for wildlife species of conservation concern, the effects of management on some threatened species, such as the eastern whip-poor-will, are not well known. Previous accounts indicate that eastern whip-poor-wills are present in a wide range of forest types during the breeding season (Cooper 1981, Cink 2002); however, our results are more consistent with recent studies reporting that whip-poor-will numbers are highest in shrublands and early successional forests (Wilson and Watts 2008, Hunt 2013, Tozer et al. 2014). Recent studies have noted that whip-poor-wills' preference for open canopy, early successional forests could be due to the admission of more moonlight in these forests, which can provide higher visibility compared with closed-canopy forests and may facilitate whip-poor-will's ability to forage and back-light prey (Mills 1986).

Despite recent studies that show whip-poor-will abundance is typically higher in shrublands compared with closedcanopy forests, there is a perception in the recent literature that eastern whip-poor-wills nest primarily in closed-canopy forest next to large early successional areas (Wilson and Watts 2008, MassAudubon 2011, Hunt 2013). However, this assumption appears to be unwarranted; large shrublands have not been adequately surveyed for nests and few eastern whip-poor-will nest sites have actually been described (Cink 2002). We did not search extensively for nests or roost sites in closed-canopy forest, so we cannot assert that whip-poorwills do not nest in unthinned forest. Indeed, we found a few nests on the edge of closed-canopy forest. However, the fact that we did find numerous nests within shrublands, including some nests that were >150 m away from the forest edge, demonstrates this species does not exclusively nest in closedcanopy forest. Furthermore, nests in shrublands were mostly successful; the estimated daily nest survival rate for whippoor-wills was high (0.977) compared with the estimated daily nest survival rate of another shrubland bird, the prairie warbler, that nested in the same areas (0.958; Akresh 2012).

Nest sites were not selected specifically in large areas of closed-canopy forest, but rather, sites appeared to be selected on account of the presence of deciduous canopy at the nest-site spatial scale. We observed many nests placed under residual trees, specifically deciduous trees, despite the low density of these trees in the surveyed early successional areas (King et al. 2011, Akresh et al. 2015). For 11 nests that we found, both the deciduous canopy coverage directly above the nest (100%) and the average deciduous canopy coverage directly above the 5-m-radius nest patch (58%) were substantially higher than the amount of deciduous canopy coverage within these shrublands (<17%; King et al.

2011, Akresh 2012). We did not find nests in the interior areas of power-line corridors, which lacked taller deciduous trees and canopy cover. Our observations are consistent with previous qualitative descriptions of whip-poor-will nest sites. For instance, Terrill in Tyler (1940:166) found a nest in a "patch of deciduous trees" and Clarke in Tyler (1940:168) reported that "the whippoorwill always nests among trees . . . and seems to avoid extensive areas of conifers." Other accounts include a nest in a "semi-open glade" of predominantly white oak (Quercus alba) trees near an agricultural field (Kent and Vane 1958:72), a nest in a red maple (Acer rubrum) thicket (Fowle and Fowle 1954), and a nest under a 2-meter sapling in a regenerating strip mine (Wood 1982). Deciduous trees provide a bed of deciduous leaf litter that serves as excellent camouflage for the brooding adult and mobile nestlings (Tyler 1940). Additionally, the canopy cover provides uneven shade, which can further enhance the concealment of the brooding adult and nestlings. Cover from the sun could potentially also help in thermoregulation by keeping birds cooler during hot days (Fisher et al. 2004), although adults of many nightjar species are known to tolerate high temperatures through a number of unique physiological mechanisms such as gular fluttering and maintaining a low metabolic rate (Dawson and Fisher 1969, Lane et al. 2004).

Whip-poor-wills may be more likely to occupy sites that have areas of open understory (Cink 2002, Garlapow 2007), but whip-poor-wills do not appear to specifically need large, open understory areas for nesting. We observed a number of nests in areas with dense understory vegetation. Similarly, Raynor (1941:98) reports finding nests in habitat with "rather dense undergrowth," and DuBois (1911:469) found a nest "in a strip of medium size trees, thickly undergrown." We did not find any nests in early successional vegetation 0–1 years since treatment, although we acknowledge that much of the area surveyed during nest searching was older in age. Nevertheless, birds may prefer to nest in slightly older shrublands, at which point the vegetation grows back and provides some understory structure and cover in the form of taller saplings. In addition, suitable leaf litter may not be present in burned vegetation patches until a few years after

During the point counts, we recorded lower eastern whippoor-will abundance in treated pitch pine compared with the scrub oak barrens. In 2006 and 2007, when we conducted point counts, the treated pitch pine was relatively young, at 0-3 years since treatment. In contrast, point-count locations in scrub oak had generally older vegetation, more understory cover, and more vegetation structure than in treated pitch pine during this time (King et al. 2011). As we observed with nesting sites, it is possible that eastern whip-poor-wills prefer to occupy slightly older shrublands that are at least a few years after treatment (note that we could not precisely quantify years since treatment at scrub oak point-count locations because of small treatment patches within this forest type). In New Hampshire, USA, Hunt (2013) also found that radiotracked and spot-mapped whip-poor-wills tended to avoid large, interior areas of recent clearcuts that had little

understory vegetation. Although preference for slightly older and thicker understory vegetation is contrary to the notion that eastern whip-poor-wills need areas of open understory for foraging (Cink 2002, Garlapow 2007), we did observe eastern whip-poor-wills foraging before dawn in the many dirt roads and fire breaks in our study site. This is consistent with observations of birds foraging on logging roads in North Carolina (Wilson 2003) and Kansas, USA (Cink 2002). These areas in our study site may have provided small gaps of open understory that could be important for foraging habitat (Cink 2002).

Selection of preferred daytime roosting sites of eastern whip-poor-wills can be important by directly minimizing adult mortality due to predation, or more indirectly by reducing energetic costs that could otherwise be used to improve reproduction efforts (Fisher et al. 2004). We found a number of roosting sites within shrublands; many of these were located close to, and in similar areas as, nests. We often found roosting locations under the shaded cover of understory shrubs or overstory trees, which could be important in providing concealment from predators and possibly to a lesser extent to keep birds cooler on hot days. Similar to our findings, Hunt (2013) found more than half of whip-poor-will roosting sites of radiotracked birds were located in shrubby clearings. Interestingly, Wilson and Watts (2008) noted high use of closed-canopy-forested areas during the day in a study with radiotracked birds, but the adjacent regenerating forest in their study had a complete lack of canopy cover. In contrast, scrub oak and treated pitch pine in our study had at least some residual trees, and we found birds selected to roost in these early-successional forests, although additional roosts may have been present in closed-canopy forests that we did not extensively search.

We estimated a relatively high nest survival rate (0.63) during the incubation period in our study site. This is consistent with the findings of a study in Kansas, in which apparently 70% of 100 eastern whip-poor-will nests fledged young successfully (Cink 2002). Studies of 3 other nightjar species that reside in the United States and Canada also report high rates of nest success. Allen and Peters (2012) reported an estimated nest survival rate through incubation of 0.79 for 16 common nighthawk (Chordeiles minor) nests in a New Jersey, USA, pine barren. In the Great Plains, 93% of 14 common nighthawk nests were successful (Kantrud and Higgins 1992). At least 75% of 8 common nighthawk nests found in Wyoming, USA, survived to hatching (Kramer and Chalfoun 2012). O'Connor and Ritchison (2013) observed 67% of 6 Chuck-will's-widows' (Antrostomus carolinensis) nests in Ohio were successful to hatching. Csada and Brigham (1994) studied common poorwills (Phalaenoptilus nuttallii) and observed a hatching success rate of 65% for 26 nests found in British Columbia and Saskatchewan, Canada. In contrast, only one study computed a low nest-survival rate through incubation: 0.28 of 14 common nighthawk nests in Florida (Perkins and Vickery 2007). Nightjars in North America are declining in abundance and have recently been highlighted as threatened species by many conservation organizations (North American Bird Conservation Initiative [U.S. Committee] 2010, MassAudubon 2011). A number of possible explanations for declines of nightjars have been proposed, including decreases in breeding-season productivity or nest survival (Santner 1992 in Cink 2002, MassAudubon 2011). Our study supports a growing literature base suggesting that reduced nest survival may not represent a major threat to these declining species.

MANAGEMENT IMPLICATIONS

Our observation that eastern whip-poor-wills are most abundant in shrublands suggests that current efforts to create and maintain these habitats for other shrubland birds (King and Schlossberg 2014) will also benefit whip-poor-wills. We rarely detected whip-poor-wills in the interior closed-canopy forest, although we were not able to determine the full extent of their use of closed-canopy forest edge for nesting or other activities. Nevertheless, we found that whip-poor-wills roosted and nested successfully in shrublands, particularly under or near residual deciduous trees. Given our uncertainty about the use of closed-canopy forest at the edge of shrublands, we suggest that managers consider maintaining closed-canopy forest within proximity to shrubland areas, especially if there are few residual deciduous trees in the shrubland area. Because nesting success was not negatively affected by distance to forest edge, this practice should not negatively affect whip-poor-wills. In large early successional areas, we recommend that some deciduous trees be retained, to the extent that they do not interfere with the settlement of other shrubland-dependent species (Smetzer et al. 2014). Lastly, whip-poor-wills may prefer to nest and occupy early successional vegetation a few years after treatment and can readily nest in vegetation with a dense understory, although some gaps of open ground cover may be beneficial in providing better foraging habitat (Garlapow 2007). To stop the decline of this unique, charismatic species, we hope there will be an increased effort for managers to create and maintain suitable early successional forests and shrublands.

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