

July 2019

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**EASTERN WHIP-POOR-WILL HABITAT ASSOCIATIONS IN  
FORT DRUM, NEW YORK**

A Thesis Presented

by

**KIMBERLY J. SPILLER**

Submitted to the Graduate School of the  
University of Massachusetts Amherst in partial fulfillment  
of the requirements for the degree of

**MASTER OF SCIENCE**

May 2019

Environmental Conservation

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## ACKNOWLEDGMENTS

I would like to express my gratitude to my advisor, Dr. David King, for the opportunity to work on this project. I am grateful for all the support, encouragement, and guidance he has continuously provided throughout this process, and for his ability to secure funding that made this project possible. I would also like to express my thanks to Dr. Kevin McGarigal, for all the statistical support, and to Jeff Bolsinger, for all the assistance in the field and arranging so many logistics at Fort Drum. I am grateful to everyone in my committee for their valuable comments and insightful input on this thesis.

Support for this project was provided by the US Army at Fort Drum, New York, and I would like to express my thanks to Fort Drum's Natural Resources Branch, especially Raymond Rainbolt. I would also like to thank the service members and veterans working at Range Control at Fort Drum for always being incredibly helpful and good-natured. I am grateful to the USDA Forest Service Northern Research Station for allowing me use of a field vehicle for two summers. I would like to sincerely thank my field assistants, Leah Klehn and Drew Eline, for all their hard work and dedication during challenging field seasons. I am also grateful to the many people who answered questions and provided statistical guidance for my thesis, including Michael Akresh, Dr. Christopher Sutherland, Dr. Jack Finn, and Javan Bauder.

Finally, I would like to express my gratitude to my family and friends. To my parents, for always supporting me, and my sister, who has always been and always will be my best friend. I would like to thank my partner for his endless love, encouragement, and patience throughout this process, and for enduring many field seasons apart. I am grateful to all my friends and especially grateful for the many new friendships I forged here at UMass – thanks for being there and for enriching my life.

Thanks to the New York State Breeding Bird Atlas for supplying Atlas data, and to the volunteer participants who gathered data for the project. Thanks to the official sponsors of the Ontario Breeding Bird Atlas (Bird Studies Canada, Canadian Wildlife Service, Federation of Ontario Naturalists, Ontario Field Ornithologists, and Ontario Ministry of Natural Resources) for supplying Atlas data, and to the thousands of volunteer participants who gathered data for the project.

## **ABSTRACT**

### **EASTERN WHIP-POOR-WILL HABITAT ASSOCIATIONS IN FORT DRUM, NEW YORK**

MAY 2019

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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 habitat, such as early-successional habitats or forest edges. Population declines of other early-successional bird species have been attributed to the loss of early-successional disturbance-dependent habitats in the northeast, and it has been suggested that habitat loss is a significant factor in whip-poor-will population declines, as well. However, there remain substantial gaps in our understanding of whip-poor-will habitat associations, and quantitative habitat data in the literature are lacking. As forest management plays an important role in creating and maintaining habitat for many disturbance-dependent bird species, further characterization of whip-poor-will habitat preferences is necessary to determine whether management efforts may benefit this species as well. In order to derive quantitative estimates of habitat requirements, I studied whip-poor-will habitat associations at Fort Drum in upstate New York.

In 2015 and 2016, whip-poor-wills were surveyed at night at randomly-selected point count locations and vegetation measurements were collected in the point count radii to relate whip-poor-will occupancy with structural and compositional habitat variables. Whip-poor-will occupancy was strongly related to intermediate amounts of basal area, with values that generally correspond to forest denser than most shrublands, but more open than closed-canopy forest. Occupancy was also related to lower understory height values, which supports evidence that whip-poor-wills may prefer habitat with a relatively open understory.

In 2016, I also measured habitat at locations where whip-poor-wills were foraging, roosting, and nesting, to investigate the theory that whip-poor-wills require open habitat for foraging, but more closed habitat for nesting. Ten adult whip-poor-wills were tracked using radio telemetry and vegetation measurements were collected at a subset at these points where the birds were either foraging 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 conventional thought, the few nest sites found in this study were in areas that had low basal area, similar to the habitat at foraging locations. The results suggest that while 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.

In conclusion, I suggest that landowners looking to create or maintain suitable habitat for whip-poor-wills apply forest management treatments that create openings but still maintain intermediate levels of basal area, such as shelterwood or group tree selection. Foraging habitat for whip-poor-wills appears to be generally more open than roosting habitat, both in terms of lower basal area and a more open understory, so having areas where tree and understory removal is concentrated in proximity to areas that are denser may also benefit this species.



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# CHAPTER 1

## LITERATURE REVIEW

### 1.1 Introduction

The eastern whip-poor-will (*Antrostomus vociferus*: hereafter whip-poor-will) is a crepuscular and nocturnal migratory bird of the Nightjar family (*Caprimulgidae*). Their breeding range extends through the eastern half of the US and southeastern Canada, while their winter range spans from southern Florida to at least Honduras, but possibly farther south (Cink et al. 2017). An aerial insectivore, these birds feed on insects while in flight by sallying from nearby perches (Cink et al. 2017). Recently, whip-poor-wills have been the focus of increasing conservation concern due to their declining population numbers (Sauer et al. 2017). In this review, I will examine and synthesize the current state of knowledge on this species of bird, including their population status, hypothesized causes of declines, and conservation recommendations.

### 1.2 Population Status

One of the principal sources of data on whip-poor-will population trends is the North American Breeding Bird Survey (BBS), which consists of roadside surveys conducted annually during the breeding season in the US and Canada (Sauer et al. 2017). Survey data collected by the BBS from 1966 to 2015 have revealed significant declines in whip-poor-will populations at a rate of 2.76% per year throughout their range (Sauer et al. 2017). Of the 30 US states and three Canadian provinces that have recorded whip-poor-will survey data in the BBS, 21 states show significant population decreases and 11 show non-significantly decreasing or stable population trends, with only Oklahoma showing a significant increase in whip-poor-will populations.

However, only the data from Missouri were robust enough to be considered as having regional credibility; the remaining states and provinces reflect “data with a deficiency” or “data with an important deficiency” (Sauer et al. 2017). These data deficiencies are likely due to the fact that the BBS employs an early-morning census method, and whip-poor-wills vocalize most frequently outside the time interval during which BBS surveys are conducted (Cink et al. 2017). Such methods are generally not well-suited for nocturnal and crepuscular species such as whip-poor-wills, contributing to low sample sizes and higher uncertainty around these trends. Despite these deficiencies in the data, however, the population trends for whip-poor-wills have exhibited widespread declines across their range and in most individual states, along with steady declines since the inception of the BBS in the late 1960s (Sauer et al. 2017).

State-level Breeding Bird Atlases (BBAs) are another source of population data for many bird species, including whip-poor-wills. These atlases use grid-based systems to determine the amount of breeding evidence for each bird species at a state or provincial level (U.S. Geological Survey Patuxent Wildlife Research Center 2018). While most states and provinces have completed at least one atlas, a number have also completed a more recent second-generation atlas, and comparisons of the two atlases can reveal changes in the ranges of breeding bird species over time. Each atlas reports whether breeding evidence for a particular species was “confirmed,” “probable,” or “possible” in each square or block of the grid, and the amount of effort required to collect these data usually takes several years. Second-generation breeding bird atlases from Delaware, Iowa, Indiana, Massachusetts, Maryland & DC, Michigan, New York, Ontario, Pennsylvania, and Vermont have all showed declines of 28-80% in the number of squares or blocks with breeding evidence of whip-poor-wills from 20-30 years ago (Table 1). On average, whip-poor-wills have disappeared from 49% of their ranges from these states (Table 1).

The BBS and BBAs are the main sources of data on the decline of whip-poor-will populations, with considerably less information having been published on this species from other sources. Along with the declines reported by various BBAs, Cink et al. (2017) also noted the disappearance of whip-poor-wills from certain regions in a number of state breeding bird lists, including North Dakota, northern West Virginia, southeastern Pennsylvania, and northern Texas. Even an account from 1925 noted that whip-poor-will numbers in southern Iowa “steadily decreased” from the late 1800s (Nauman 1925). The New Hampshire Audubon uses nighttime roadside survey data from volunteer observers for the Northeast Nightjar Survey, which collects nightjar data with a focus on whip-poor-wills. A report with the 2007 whip-poor-will survey results was published in 2008, covering states in the northeast, as well as North Carolina and Wisconsin (Hunt 2008). The Center for Conservation Biology has also been collecting citizen science data on whip-poor-wills and other nightjars for the Nightjar Survey Network since 2007, covering survey routes in states not included in the Northeast Nightjar Survey (Center for Conservation Biology 2018). Although population trend data have not yet been published from these sources, these citizen science nightjar projects are relatively young compared to datasets such as the BBS, and in time they will surely become invaluable sources of whip-poor-will population data as they are more suitable for nocturnal species.

Partners in Flight (PIF), a landbird conservation network, has analyzed BBS data to create population and trend estimates for landbird species in North America. PIF estimates the global breeding population of whip-poor-wills to be about 2 million individuals, based on the 1998-2007 BBS data and using estimates from part of their range extrapolated to the remainder of their range (PIF Science Committee 2013). Other insectivorous birds with similar ranges, such as the wood thrush (*Hylocichla mustelina*) or Baltimore oriole (*Icterus galbula*), have much



higher population estimates at 11 million and 12 million individuals, respectively, although these estimates are not intended to be direct comparisons (PIF Science Committee 2013). The PIF North American Landbird Plan 2016 also used data from the BBS to estimate a 69% global population loss for whip-poor-wills from 1970-2014 (Rosenberg et al. 2016).

Due to their declining numbers, whip-poor-wills have been listed as threatened in Vermont and as a species of concern/special concern for many states in the northeastern US (Table 2). They have also been identified as a species of concern in multiple conservation priority lists, such as the PIF Landbird Conservation Plan Watch List (Rosenberg et al. 2016), the North American Bird Conservation Initiative (NABCI) “State of the Birds 2016” Watch List (NABCI 2016), and in numerous State Wildlife Action Plans (Table 2). Climate models created by National Audubon predict that this species will lose 78% of its breeding range and 55% of its non-breeding range by 2080 (National Audubon Society 2014), which may also exacerbate population declines.

### **1.3 Habitat Associations**

Historically, whip-poor-wills have been reported to use a variety of habitats throughout their breeding range, including mixed, deciduous, and coniferous forested areas, wetlands and riparian woodlands, pasture and fields, and even suburban areas (Cooper 1981, Bjorklund and Bjorklund 1983, Buck et al. 2001, Hunt 2013, Cink et al. 2017). They are also often associated with scrub oak-pitch pine barrens (Garlapow 2007, Akresh and King 2016, Cink et al. 2017). While some older studies did find higher whip-poor-will abundance in forested areas (Cooper 1981, Bjorklund and Bjorklund 1983), more recent research suggests that whip-poor-wills prefer proximity to open areas and/or early-successional habitats (Wilson and Watts 2008, Hunt 2013, Tozer et al. 2014, Akresh and King 2016, Cink et al. 2017, English et al. 2017b). Whip-poor-will

territories appear to be relatively large, with one study measuring territories from 2.8 to 11.1 ha and another finding an average of 5.1 ha (Fitch 1958 in Cink et al. 2017, Cink et al. 2017). A study of 43 whip-poor-will territories over five years found a range of 0.77 – 12.98 ha, with an average territory size of 4.82 ha (Hunt 2013).

Nest site selection for whip-poor-wills is not well-understood, but appears to place importance on protecting nests from predation due to 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 (Tyler 1940, Raynor 1941, Cink et al. 2017). Not only does this make incubating birds difficult to spot due to 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. 2017), which makes finding nests and characterizing nest sites challenging. While some studies suggest that whip-poor-wills nest in forested habitat and forage in open habitat (Wilson and Watts 2008, Hunt 2013), many accounts of whip-poor-wills nesting in forested areas are vague about the forest structure and are somewhat outdated (Nauman 1925, Mousley 1937, Fowle and Fowle 1954), such as Clarke’s observation that whip-poor-wills “always nests among trees” (Tyler 1940). Some studies have reported nests in areas of dense undergrowth (Du Bois 1911, Raynor 1941), while others in areas of little to no undergrowth (Tyler 1940). Akresh and King (2016) compared whip-poor-will nesting success in a variety of habitats and found the majority of nests in early-successional forest, under both dense and sparse understory vegetation.

Recent studies conclude that whip-poor-wills do appear to require some form of openness for foraging. This is presumably because open habitats receive increased lunar illumination and make it easier for these birds to locate back-lit insects, evidenced by the positive association

between whip-poor-will foraging activity and lunar illumination (Mills 1986, Wilson and Watts 2006). In North Carolina, whip-poor-will abundance was dramatically higher along the edges of regenerating loblolly pine clearcuts than within forests (Wilson and Watts 2008). Similarly, whip-poor-will occupancy increased 3.3 times in red pine-dominated stands harvested using clearcuts (younger than 16 years) with seed trees compared to stands without clearcuts in Ontario. However, shelterwood harvesting in white pine-dominated stands did not affect occupancy in the same study (Tozer et al. 2014). Whip-poor-will abundance was higher in early-successional forests in Massachusetts, such as scrub oak barrens and thinned pitch pine stands, compared to closed-canopy coniferous and deciduous forests (Akresh and King 2016). Hunt (2013) concluded that whip-poor-will home ranges require some form of openness, whether that includes shrubland with regenerating openings, thinned mature forest, or forested areas with a hard edge, such as a clearcut. In general, whip-poor-wills appear to be absent from areas of dense uninterrupted forest or where the forest canopy is extensive and closed (Cink et al. 2017). A study of presence at multiple spatial scales found that whip-poor-wills were positively associated with forest area at broad scales yet were positively associated with open-canopy habitat at finer scales. This result suggests that they do require forest cover, but some degree of openness is important to allow the penetration of moonlight for foraging (English et al. 2017b).

There remain substantial gaps in our understanding of whip-poor-will habitat associations. While many studies suggest that proximity to open areas for foraging is important for this species, and that early-succession is probably preferred to late, there is no data on preferred forest structure and size (Cink et al. 2017). The degree of undergrowth typically associated with whip-poor-wills is also uncertain, with some evidence for whip-poor-wills being more likely to occupy sites with open understory (Tyler 1940, Garlapow 2007, Cink et al. 2017),

but other studies finding whip-poor-will nests in dense understory vegetation (Du Bois 1911, Raynor 1941, Akresh and King 2016). Since whip-poor-wills have been found in a wide variety of forest types, it is also suggested that understory structure may be of greater importance to breeding habitat than forest composition, though no data exist to confirm this (Cink et al. 2017). There is also very little information on the habitat associations of whip-poor-wills during migration and in the overwintering range (Cink et al. 2017).

#### **1.4 Potential Causes of Decline**

As aerial insectivores, whip-poor-wills are part of a diverse guild of birds that also includes swallows, swifts, other nightjars, and flycatchers. Aerial insectivores are also experiencing significant guild-wide population declines in North America, with these losses appearing greater in the northeast and starting in at least the 1980s (Nebel et al. 2010). According to the 2012 NABCI Canada “The State of Canada’s Birds” report, aerial insectivores have been decreasing more significantly than any other bird group, and possibly since before the 1980s (NABCI Canada 2012). It is unclear as to what is causing these population declines, although multiple hypotheses exist.

One leading theory is that the declines of aerial insectivores are related to their communal food source of aerial insects. Whip-poor-wills mainly feed on moths and beetles, but also consume flying ants, flies, grasshoppers, mosquitos, and other flying insects (Garlapow 2007, Cink et al. 2017). However, worldwide declines in insect populations may be affecting the food supply of whip-poor-wills and other insectivorous birds. Multiple studies from Europe have found significant insect declines, such as a loss of two thirds of moth species over 35 years in Britain (Conrad et al. 2006), a 30% loss of bee and hoverfly species in Britain and the Netherlands (Biesmeijer et al. 2006), and a seasonal decline of 76% in flying insect biomass over

27 years in Germany (Hallmann et al. 2017). Although there is less data available on insect trends in North America, studies have found losses in species richness, abundance, and geographic range of bees in the US (Gixti et al. 2009, Cameron et al. 2011) and declines in moth species in the northeastern US (Wagner 2012, Young et al. 2017), so it is likely that insect populations are declining in North America as well. In Ontario, Canada, whip-poor-will abundance was associated with both habitat and food supply across multiple spatial scales (English et al. 2017b), and moth abundance was found to have a positive influence on daily chick survival rates (English et al. 2018), which suggests that such insect losses may negatively impact whip-poor-will populations. While the cause of insect declines is also uncertain, declines in insectivorous birds have been correlated with the use of pesticides such as neonicotinoids (Hallmann et al. 2014).

Habitat loss on the breeding grounds has also been considered as a potential factor influencing whip-poor-will declines (Mills 2007, Cink et al. 2017). Whip-poor-wills have more recently been associated with early-successional habitat and open forest (Hunt 2013, Tozer et al. 2014, Akresh and King 2016, Cink et al. 2017). However, numerous regions in the eastern and central US have shown declines in early-successional habitat, especially in the northeast where the percentage of seedling-sapling timberlands in New England fell from over 30% in the 1960-1970s to only 7.9% by the late 1990s (Trani et al. 2001). While the historical natural range of early-successional habitat varies considerably depending on the region and timescale examined, recent early-successional habitat loss has been primarily due to intensive agriculture or forest succession due to a lack of natural disturbance (Foster et al. 2002, Lorimer and White 2003, Mills 2007). Many species reliant on these habitats have experienced severe declines, and

shrubland birds were found to require more long-term conservation planning and monitoring than other bird species (Askins 2001, Dettmers 2003).

Other proposed factors that may be contributing to whip-poor-will population declines include vehicle collisions and non-breeding ground factors, but more data are needed in these areas (Cink et al. 2017). While not much is known about whip-poor-wills' migration routes, a study from Ontario found that whip-poor-wills exhibited both sex-differential migration as well as "leapfrog" migration, where northern birds appeared to migrate farther than southern birds, indicating that more northern populations of whip-poor-wills could have higher migratory costs than southern populations (English et al. 2017a).

More study is needed not only on the discussed potential causes of decline, but also to determine where the demographic limitation is in the life cycle of whip-poor-wills. While Akresh and King (2016) found a relatively high nest survival rate of 63% from 26 nests over six years, English et al. (2018) found a nest survival rate of only 40% from 26 nests over three years. Chick survival varied annually, with rates of 91%, 40%, and 70% over three years (English et al. 2018). Very little information is available on lifespan, adult survivorship, and juvenile survivorship (Cink et al. 2017).

## **1.5 Conservation Recommendations**

While there is strong evidence of declines in whip-poor-wills' prey base of flying insects, it is difficult to suggest conservation recommendations until more research is done on what factors are contributing to insect declines and how these declines may be influencing whip-poor-will populations. Similarly, more information is needed on whip-poor-will migratory routes and wintering grounds to determine the impact of non-breeding ground factors.

Habitat loss on the breeding grounds, however, is a factor that is likely to be contributing to whip-poor-will declines and can be addressed directly. Forest management, such as the use of silvicultural methods, has been effectively used to create and maintain habitat for early-successional species (Thompson III and DeGraaf 2001). Many studies on whip-poor-will abundance recommend forest management in order to increase populations (Wilson and Watts 2008, Hunt 2013, Tozer et al. 2014, Akresh and King 2016). Radio-tracking data of whip-poor-wills over broad habitat types in New Hampshire showed that whip-poor-wills not only used shrubland areas, with variable regeneration as would be found in early-successional habitat, but they also used thinned mature forest and edges along clear cuts and a powerline right-of-way (Hunt 2013). These results indicate that whip-poor-wills preferred the thinned areas and edges over unmanaged mature forest (Hunt 2013). Clear-cuts with and without seed trees and of varying sizes have been suggested for whip-poor-will management, as well as overstory and understory removal and crop tree release (Garlapow 2007, Wilson and Watts 2008, Hunt 2013, Tozer et al. 2014).

## **1.6 Conclusion**

Much about the biology and habitat associations of whip-poor-wills remains not well-studied and poorly understood, due to the combination of their crepuscular and nocturnal behavior, their cryptic eggs and plumage, and their large territories (Cink et al. 2017). However, it appears clear from the information available that whip-poor-wills are undergoing significant population declines throughout their breeding range. More study is needed on whip-poor-will habitat selection, including forest structure and composition, to make more effective management recommendations and to determine whether efforts to maintain early-successional

habitat suitable for disturbance-dependent birds may also benefit whip-poor-wills (Thompson III and DeGraaf 2001, King and Schlossberg 2014). In the following chapters, I will describe the results of my studies on habitat associations of whip-poor-wills in upstate New York, with the hopes that such information will help researchers to understand more about these birds and help managers create and maintain suitable habitat for this charismatic species.



Table 1. Change in number of blocks with breeding evidence (confirmed, probable, or possible) of eastern whip-poor-wills for states with second-generation breeding bird atlases (includes all blocks if states also had “priority” blocks).

State/Province	Atlas Year	Block size	Total blocks with breeding evidence	Decrease in range	Data Source
Delaware	1983 - 1987	1/6 of a USGS 7.5 minute topographic quad	129	80%	Breeding Bird Atlas Explorer*
	2008 - 2012		26		Breeding Bird Atlas Explorer
Iowa	1985 - 1990	3 x 3 mi	167	42%	Breeding Bird Atlas Explorer
	2008 - 2012		97		Iowa Ornithologists' Union 2018
Indiana	1985 - 1990	1/6 of a USGS 7.5 minute topographic quad	224	28%	Breeding Bird Atlas Explorer
	2005 - 2011		161		Breeding Bird Atlas Explorer
Massachusetts	1974 - 1979	1/6 of a USGS 7.5 minute topographic quad	215	44%	Breeding Bird Atlas Explorer
	2007 - 2011		121		Breeding Bird Atlas Explorer
Maryland & DC	1983 - 1987	1/6 of a USGS 7.5 minute topographic quad	423	56%	Breeding Bird Atlas Explorer
	2002 - 2006		185		Breeding Bird Atlas Explorer
Michigan	1983 - 1988	3 x 3 mi	627	56%	Breeding Bird Atlas Explorer
	2002 - 2008		277		Chartier et al. 2011
New York	1980 - 1985	5 x 5 km	564	57%	Breeding Bird Atlas Explorer
	2000 - 2005		241		New York State Department of Environmental Conservation 2007
Ontario	1981 - 1985	10 x 10 km	884	37%	Breeding Bird Atlas Explorer
	2001 - 2005		559		Bird Studies Canada et al. 2006
Pennsylvania	1983 - 1989	1/6 of a USGS 7.5 minute topographic quad	862	42%	Wilson et al. 2012
	2004 - 2008		496		Breeding Bird Atlas Explorer
Vermont	1976 - 1981	1/6 of a USGS 7.5 minute topographic quad	69	46%	Breeding Bird Atlas Explorer
	2003 - 2007		37		Breeding Bird Atlas Explorer
Overall average				49%	

\*Citation: (U.S. Geological Survey Patuxent Wildlife Research Center 2018)

Table 2. Conservation status of eastern whip-poor-wills in the US

<b>State Endangered</b>	<b>State Threatened</b>	<b>Species of Concern/ Special Concern</b>	<b>State Wildlife Action Plan “Species of Greatest Conservation Need”</b>
None	VT	CT, IN, KS, ME, MA, MI, NH, NJ, NY, OH, WI	AR, CT, DE, DC, FL, IL, IN, IA, KS, KY, ME, MD, MA, MI, MN, MO, NE, NH, NJ, NY, OH, OK, PA, RI, SC, TN, VT, VA, WV, WI

## CHAPTER 2

### OCCUPANCY ANALYSIS OF EASTERN WHIP-POOR-WILL HABITAT ASSOCIATIONS

#### 2.1 Introduction

The eastern whip-poor-will (*Antrostomus vociferus*: hereafter whip-poor-will) 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 (Sauer et al. 2017), and multiple second-generation breeding bird atlases have shown disappearances of these birds in an average of about 50% of their breeding ranges compared to 20-30 years prior (Table 1; Sauer et al. 2017). Various hypotheses have been suggested as to what may be causing population declines among insectivorous birds, including food availability, pesticide use, climate change, and wintering ground conditions (Grüebler et al. 2010, Nebel et al. 2010, Mineau and Palmer 2013, Hallmann et al. 2014). Habitat loss has also been suggested as a potential factor in whip-poor-will declines (Mills 2007, Cink et al. 2017, English et al. 2017b).

Although whip-poor-wills have been known to use a variety of habitats (Cooper 1981, Bjorklund and Bjorklund 1983, Garlapow 2007, Hunt 2013, Cink et al. 2017), they have most recently been associated with early-successional habitat or open areas (Hunt 2013, Tozer et al. 2014, Akresh and King 2016, English et al. 2017b). Multiple studies have found an increased presence of whip-poor-wills in young forests or forest edges compared to closed-canopy forest or areas without clearcuts (Wilson and Watts 2008, Tozer et al. 2014, Akresh and King 2016). It is suggested that whip-poor-wills require at least some form of openness in their territories, whether that come from managed shrublands, thinned mature forest, or forest edges (Hunt 2013). Whip-poor-will nests and roosts have been found in managed shrublands, as well (Akresh and

King 2016). However, whip-poor-wills have also been found in a variety of other habitat types, and there is uncertainty regarding many preferred habitat characteristics, such as degree of openness or forest composition (Cink et al. 2017).

Early-successional habitat has also significantly declined over the past century, resulting in habitat loss being suggested as a cause of decline for whip-poor-wills (Mills 2007, Cink et al. 2017). Declines in young forest have occurred throughout the whip-poor-will's range, but are especially noticeable in the northeast, where the proportion of seedling-sapling timberlands in New England fell from over 30% in the 1960-1970s to only 7.9% by the late 1990s (Trani et al. 2001). These losses in early-successional habitat, primarily attributed to increases in intensive agriculture or maturation of forests (Lorimer and White 2003, Mills 2007), have been associated with the population declines of many shrubland bird species (Litvaitis 1993, Askins 2001, Thompson III and DeGraaf 2001). As a result, the maintenance of early-successional disturbance-dependent habitat has become a subject of conservation concern in the northeast (Askins 2001).

Forest management such as silviculture can be used to provide habitat for disturbance-dependent species, both by creating new habitat or maintaining existing suitable habitat (Thompson III and DeGraaf 2001, DeGraaf and Yamasaki 2003). To be most effective, silvicultural prescriptions need to consider factors such as the size of regenerating clearcuts, the frequency of disturbance, and patch isolation (DeGraaf and Yamasaki 2003). Many studies have recommended forest management practices in order to maintain or increase whip-poor-will populations, including 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). While forest management for other early-successional bird species may also

benefit whip-poor-wills (King and Schlossberg 2014), more data is necessary to characterize whip-poor-will habitat, including forest structure and composition. In this study, I will investigate the habitat associations of a population of whip-poor-wills in Fort Drum, New York, using an occupancy analysis to relate habitat variables with whip-poor-will presence.

## **2.2 Methods**

### **2.2.1 Study Area**

Fort Drum is a US Army installation comprising over 44,000 ha in northwestern New York State in Jefferson and Lewis counties. Though the installation includes a cantonment area and an airfield, over 90% of the installation is composed of training areas. About 10% of Fort Drum is developed, mostly within the 4,500 ha cantonment area and the airfield, with about 3% of this development accounted for by paved roads. The majority of land throughout the installation is undeveloped, with approximately 57% forested land, 14% grasslands, 12% shrublands, 4% surface water, and 1% forblands. Mature forests are dominated by 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*). Elevations range from 125 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 (US Army Garrison Fort Drum 2011).

### 2.2.2 Bird Surveys

Fort Drum's Natural Resources Branch has conducted whip-poor-will and common nighthawk (*Chordeiles minor*) surveys since 2008. Six survey routes were established along systematic transects starting at road intersections and extending along the trails and roads of the training areas. Each route is comprised of 10 survey points spaced one mile apart, for a total of 60 survey points that provide representative coverage of the training areas (Fig. 1). I surveyed nightjars at these locations in 2015 and 2016 using a protocol modified from the New Hampshire Audubon's Northeast Nightjar Survey (New Hampshire Audubon 2015). Surveys occurred three times per year (May-July) in 2015, but each point was only surveyed one or two times in 2016 due to logistical constraints. Surveys were conducted using a removal sampling design consisting of six successive 1-minute intervals in which all new and repeat detections of individual birds were recorded (Chandler et al. 2011). All surveys were conducted between 30 minutes after sunset and 30 minutes before sunrise (Mills 1986). Time, wind speed, cloud cover, and background noise were recorded before each survey, and the estimated distance and compass bearing of each bird from the observer as well as the number of passing cars were recorded during the survey. Surveys were only conducted on nights with little wind, no precipitation, and temperatures above 40° Fahrenheit. In 2015, when surveys occurred three times, at least two of these times occurred when the moon was at least 50% illuminated, since whip-poor-wills have been shown to be most vocal with higher amounts of moonlight (Mills 1986, Wilson and Watts 2006). In 2016, all surveys occurred when the moon was at least 50% illuminated. Detected birds that were estimated to be within 100 m of the survey point location were considered “present.”

### **2.2.3 Vegetation Surveys**

Habitat characteristics at the 60 surveys points were quantified by taking vegetation measurements in 100-m radius plots centered on each survey point location. Vegetation measurements were taken in 2016 using techniques modified from James and Shugart Jr. (1970) and King et al. (2009). Four transects were established in each of the cardinal directions from the survey point location. 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 was recorded at 10-m intervals along each transect. This resulted in a total of 40 measurements per survey point, although measurements 10 m from the plot center were removed during analysis to eliminate any road-shoulder bias. At the midpoint of each of these four transects (i.e., 50 m in each of the cardinal directions from the plot center), a 10 BAF cruising prism was used to select trees in a variable-width radius plot for basal area. The diameter at breast height (dbh) and species of each tree in the prism plot was recorded.

High spatial resolution vegetation cover layers for the study site provided by Fort Drum's Natural Resources Branch were analyzed using geographic information system (GIS) technology to calculate the proportion of discrete habitat classes within the 100-m radius vegetation plots. The habitat classes used included closed-canopy forest, open-canopy forest, grassland, and disturbed/developed habitat.

### **2.2.4 Statistical Analysis**

Analyses for the habitat variables were conducted in R 3.5.1 (R Core Team 2018) and calculation of proportions of cover types were conducted in ArcMap 10.5.1. The point-intercept data was used to calculate average maximum height of understory (cm), coefficient of variation (CV) of understory height, and percentage of understory cover that was herbaceous, woody, or

litter. The cruising prism plots were used to calculate tree density (trees/ha), basal area ( $\text{m}^2/\text{ha}$ ), CV of basal area, and percentage basal area of coniferous trees. I also calculated the basal area of trees ( $\text{m}^2/\text{ha}$ ) 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 (Table 3). Measurements of each variable were averaged for each survey point. As the basal area of large sawtimber only represented >0.25 relative proportion of basal area at two of the 60 sample sites, trees of this size appeared to represent relatively rare characterizations of the vegetation community among the study plots and this variable was dropped from the analysis. Detection variables included observer, Julian date, time (minutes from midnight, due to whip-poor-wills being most active around dawn and dusk), wind speed (0-3), cloud cover (0-3), noise (0-3), and number of passing cars. The relative amount of moonlight potentially available during each survey was also calculated using the lunar package in R (Lazaridis 2014). All continuous variables were standardized to  $x = 0$  and  $SD = 1$  to facilitate model convergence. Quadratic terms were included for variables that appeared to have a non-linear relationship to the occupancy data, such as basal area and % litter.

Single-season occupancy models that incorporate detection probability by using replicated surveys were used to model the data (MacKenzie et al. 2017). In my study, I used both the replicated counts over the course of the breeding season as well as subintervals during the surveys to help estimate detection probability (Alldredge et al. 2007, Chandler et al. 2011). Whip-poor-wills appear to exhibit high site fidelity (Cink et al. 2017, English et al. 2017a), and because I was interested in occupancy determinants rather than dynamic components (such as extinction/colonization), I modeled the two 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. I accommodated the yearly variation in site occupancy by “stacking” the data so each site-year combination represented a unique site, for a total of 120 sites (with three visits in 2015 and one or two visits in 2016) as in Bauder et al. (2017). A logit link was used to relate occupancy and detection probability to respective covariates.

Variables were assessed for collinearity using both Pearson correlation ( $r > 0.6$ ) and variance inflation factors ( $VIF > 3$ ), and highly correlated covariates were not included in the same models. Prior to model fitting, the overdispersion parameter ( $c$ -hat) was estimated using a parametric bootstrap (MacKenzie and Bailey 2004) with 1000 iterations of a global model containing all detection and occupancy covariates using the AICcmodavg package in R 3.4.1 (Mazerolle 2017). Based on the results, I used Akaike's Information Criterion adjusted for overdispersion and small sample size ( $QAIC_c$ ) to compare candidate models. The  $c$ -hat parameter ( $c$ -hat = 1.75) was used in the model selection process and to inflate standard errors (MacKenzie and Bailey 2004).

I began the model selection process by selecting the best detection covariates to include in subsequent candidate models. Due to the small sample size, I used a forward selection approach to compare competing detection models with the intention of minimizing model overfitting (Burnham and Anderson 2002), by starting with univariate detection models that included all occupancy variables and building up from the top performing models. The detection covariates that were statistically significant at  $p \leq 0.05$  and that were in models with  $\Delta QAIC_c \leq 2$  were retained (Burnham and Anderson 2002). With these fixed detection covariates, I then selected the occupancy covariates using the same forward selection method, starting with univariate occupancy models that contained the chosen detection covariates. Occupancy

covariates were considered supported if included in models with a  $\Delta\text{QAIC}_c \leq 2$  and strongly supported if statistically significant at  $p \leq 0.05$  (Burnham and Anderson 2002). I then plotted the relationships between occurrence and habitat variables by using the top models to plot model-averaged predictions of the focal variable while holding all the other variables at their mean (Fiske and Chandler 2011). Occupancy models were fit using the unmarked package (Fiske and Chandler 2011) and QAIC<sub>c</sub> assessments were conducted using the AICcmodavg 2.1-1 package (Mazerolle 2017) in the R software environment, version 3.5.1 (R Core Team 2018).

### **2.3 Results**

In total, there were 297 individual detections of whip-poor-wills in 2015, 52 of which were within 100 m of the plot center, and 189 individual detections of whip-poor-wills in 2016, 27 of which were within 100 m of the plot center. In 2015, 25 of the 60 sites had at least one detection, while in 2016, 15 of the 60 sites had at least one detection; for the “stacked” analysis, 40 of 120 unique site-year combinations had at least one detection.

Of the ten detection covariates considered, lunar illumination and year were included in the top models (Table 4). In exploratory analysis, the observer covariate was dropped because it was found to be highly correlated with year as a detection covariate; 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. The top models indicated a relationship between occupancy of whip-poor-wills and average basal area, average understory height, tree density (trees/ha), and CV of basal area (Table 4). Occupancy showed a negative relationship average understory height and tree density, but a positive relationship with CV of basal area. Basal area was positively associated with occupancy at moderate levels, but probability of occupancy decreased as basal area reached low or high levels, with a peak at 13.1 m<sup>2</sup>/ha (Figure 2). Basal

area and average understory height were strongly supported, but the relationship between occupancy and tree density or CV of basal area was not statistically significant.

## **2.4 Discussion**

Despite increasing conservation concern for the whip-poor-will, there remains considerable uncertainty as to some fundamental aspects of its breeding habitat requirements. For example, the whip-poor-will has been considered by some as a shrubland bird (Schlossberg and King 2007, Gifford et al. 2010, Tozer et al. 2014), with shrubland habitats being typically characterized as open-canopy habitats with little or no tree cover (Lorimer 2001); on Fort Drum, shrublands are defined as having less than 25% tree species cover (US Army Garrison Fort Drum 2011). In contrast, other accounts have described whip-poor-wills as being associated with forested habitat or woodlands with openings (DeGraaf and Yamasaki 2001, Hunt 2013, Cink et al. 2017).

Due to the wide variety of habitat types represented at Fort Drum, I was able to study whip-poor-will occupancy along a gradient of forest cover, which allowed me to detect an association with intermediate levels of basal area that were not apparent in previous studies. Several older studies compared whip-poor-will abundance between discrete habitat types that were broadly characterized. For instance, Cooper (1981) found that calling whip-poor-wills were more numerous in forested habitat than in pasture or suburban habitats, and Bjorklund and Bjorklund (1983) found that out of seven stations, whip-poor-wills were most abundant at a site that included mixed forest and openings and least abundant at a pine plantation. However, quantitative habitat measurements such as tree density or basal area were not analyzed in these studies. Garlapow (2007) did not find an association between whip-poor-will occupancy and canopy cover, but the habitat sampled in that study was characterized by relatively open canopy

conditions of about 50% canopy cover, so there may not have been enough variation present to detect significant associations.

The results of my study indicate that whip-poor-will presence was positively associated with intermediate basal area measurements. Whip-poor-will occupancy was most highly associated with basal areas between 7.5 to 18.7 m<sup>2</sup>/ha, which correspond to the range of residual basal area of forest following shelterwood (low and high density) and tree selection treatment (Thompson III and DeGraaf 2001). These results indicate that although whip-poor-wills are associated with disturbance, they are also associated with habitat that had higher basal areas than would be typically associated with shrublands. This is consistent with the species account by Cink et al. (2017), who list a wide variety of forest conditions and cover types as suitable habitat for whip-poor-wills, as well as studies that have associated whip-poor-will presence with habitats such as thinned mature forest (Hunt 2013). Multiple studies have suggested that more open areas with higher amounts of associated backlighting will have superior foraging conditions for aerial insects (Tozer et al. 2014, Akresh and King 2016), and English et al. (2017b) concluded that forest cover cannot be dense enough to prevent penetration of moonlight for foraging. In contrast, having some forest cover is likely beneficial in providing perches for roosting and foraging, as well as providing shade and cover for nests, which have often been found at the base of deciduous cover (Akresh and King 2016, Cink et al. 2017). Whip-poor-will nests were found in forested areas with frequent gaps (English et al. 2018), as well as on the edge of closed-canopy forests (Akresh and King 2016), which suggests that some amount of tree cover may be beneficial for nest sites.

Although not statistically significant, I also found that occupancy was positively associated with variation in basal area throughout the vegetation plots, which suggests that whip-

poor-wills may prefer habitat characterized by variable basal area rather than uniform basal area. The appearance of high CV of basal area in the top models could potentially mean that whip-poor-wills actually require patches of denser forest cover and openings that average out to basal area values within the intermediate range I found to be most suitable, but the fact that this variable was not statistically significant in our models suggests more evidence would be needed to make such a conclusion. Although our results suggest a strong relationship between whip-poor-will occupancy and basal areas in the range of 7.5 to 18.7 m<sup>2</sup>/ha, further research focusing on habitat patchiness and variable tree density would help clarify this question. The negative association between occupancy and tree density, though appearing in the top models, was also not statistically significant. This suggests that while whip-poor-wills may be found in areas with lower levels of tree density, this correlation was not as strong as the relationship between occupancy and basal area or understory height.

Whip-poor-will occupancy was also strongly associated with lower maximum understory height, which suggests that whip-poor-wills are more often found in areas with greater understory openness. This finding 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*), they stay much closer to the ground (Tyler 1940), and whip-poor-wills have been observed using 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 forest (Garlapow 2007). Furthermore, whip-poor-wills have been observed nesting in areas characterized by having an open understory (Tyler 1940, Akresh and King 2016). Thus, is it

possible that having greater understory openness would be beneficial to whip-poor-wills while both foraging and nesting.

The percentage of coniferous trees did not appear in the top models, which supports the theory that forest composition may not be significant to whip-poor-will habitat preferences (Cink et al. 2017). As all point counts consisted of roadside surveys, the plots were characterized by varying amounts of disturbed or developed habitat, which included roads, trails, and structures. There was also no evidence that occupancy was related to the amount of disturbed or developed habitat within the plot areas.

## **2.5 Management Implications**

While previous research has established that whip-poor-wills are associated with some form of openness for foraging, many were not specific on the degree of preferred openness (Wilson and Watts 2008, Hunt 2013, Tozer et al. 2014, Akresh and King 2016, Cink et al. 2017, English et al. 2017*b*). In this study, by relating whip-poor-will occupancy to habitat characteristics derived from field measurements across a gradient of forest openness, I was able to derive quantitative estimates of habitat requirements. The results of this study indicate that whip-poor-wills are most frequently encountered at intermediate levels of forest openness and in areas with greater understory openness.

The results of this study suggest that the basal area target condition of 7.5 to 18.7 m<sup>2</sup>/ha can explicitly be incorporated into forest management planning for the conservation of whip-poor-wills. Although the stocking percent of a forest is related to several factors, including average tree diameter and tree density, this range of basal area could generally be associated with an understocked forest, or the lower end of a fully-stocked forest (Ginrich 1967). Such levels of basal area can be created using silvicultural systems such as shelterwood or even tree selection in

small groups (Thompson III and DeGraaf 2001). I also suggest forest management that maintains low understory height, such as understory removal, which may be beneficial to whip-poor-wills for both foraging and nesting. My finding that they possibly use patchy areas with variability in canopy cover also supports the suggestions of others that whip-poor-wills may benefit from the creation and maintenance of early-successional or open-canopy habitat in proximity to denser, more closed-canopy forest (Hunt 2013, Akresh and King 2016). These forest management suggestions will hopefully prove beneficial to forest managers and landowners who want to create and maintain suitable habitat for whip-poor-wills, while the information collected in this study further contributes to the growing body of data on whip-poor-will habitat associations.

Table 3. Summary statistics (mean  $\pm$  standard deviation) for habitat variables derived from field measurements taken around 60 point count locations and from GIS analyses of discrete cover type layers of Fort Drum, NY.

Measurement Type	Variable	Abbreviation	Mean $\pm$ SD
<i>Field</i>	Herbaceous (%)	HERB	45.02 $\pm$ 21.77
	Litter (%)	LIT	4.81 $\pm$ 7.52
	Woody (%)	WOOD	50.17 $\pm$ 21.45
	Average maximum understory height (cm)	HEI	113.14 $\pm$ 45.99
	CV understory height	CVH	93.25 $\pm$ 41.79
	Average tree density (trees/ha)	TPH	3716.96 $\pm$ 3734.71
	Average basal area (m <sup>2</sup> /ha)	BAS	14.91 $\pm$ 9.43
	CV basal area	CVB	82.62 $\pm$ 49.55
	Basal area of saplings (m <sup>2</sup> /ha) <sup>a</sup>	SAP	4.31 $\pm$ 4.17
	Basal area of pole timber (m <sup>2</sup> /ha) <sup>a</sup>	POLE	6.29 $\pm$ 4.39
	Basal area of saw timber (m <sup>2</sup> /ha) <sup>a</sup>	SAW	3.43 $\pm$ 4.55
	% basal area of coniferous trees	CONI	15.49 $\pm$ 26.59
<i>Cover types</i>	Closed-canopy forest (%)	CLOS	34.27 $\pm$ 32.75
	Open-canopy forest (%)	OPEN	17.74 $\pm$ 25.33
	Grassland (%)	GRAS	20.03 $\pm$ 26.31
	Disturbed/developed areas (%)	DIST	8.9 $\pm$ 7.12

<sup>a</sup> Size class definitions referenced from DeGraaf and Yamasaki (2001)



Table 4. Parameter estimates and associated standard error values (in parentheses) of detection and state covariates for occupancy models of eastern whip-poor-will occurrence with  $\Delta\text{QAIC}_c \leq 2$ . Coefficients in bold indicate that 95% confidence intervals did not include zero.

Model	Detection			Occupancy							Model Selection	
	Intercept (2015)	Year (2016)	Lunar Illumination	Intercept (2015)	BAS	BAS <sup>2</sup>	HEI	TPH	CVB	Year (2016)	$\Delta\text{QAIC}_c$	$\text{QAIC}_c \text{ Wt}$
BAS, HEI	<b>-0.76</b> <b>(0.1)</b>	<b>1.24</b> <b>(0.2)</b>	<b>0.2 (0.08)</b>	0.52 (0.37)	-0.72 (0.43)	<b>-1.45</b> <b>(0.46)</b>	<b>-0.74</b> <b>(0.26)</b>	-	-	-0.94 (0.44)	0.00	0.29
BAS, HEI, TPH	<b>-0.76</b> <b>(0.1)</b>	<b>1.24</b> <b>(0.2)</b>	<b>0.2 (0.08)</b>	0.53 (0.37)	-0.52 (0.44)	<b>-1.44</b> <b>(0.45)</b>	<b>-0.65</b> <b>(0.27)</b>	-0.44 (0.31)	-	-0.96 (0.45)	1.15	0.16
BAS, HEI, CVB	<b>-0.76</b> <b>(0.1)</b>	<b>1.24</b> <b>(0.2)</b>	<b>0.2 (0.08)</b>	0.52 (0.37)	-0.43 (0.48)	<b>-1.5</b> <b>(0.5)</b>	<b>-0.7</b> <b>(0.26)</b>	-	0.41 (0.32)	-0.95 (0.45)	1.35	0.15

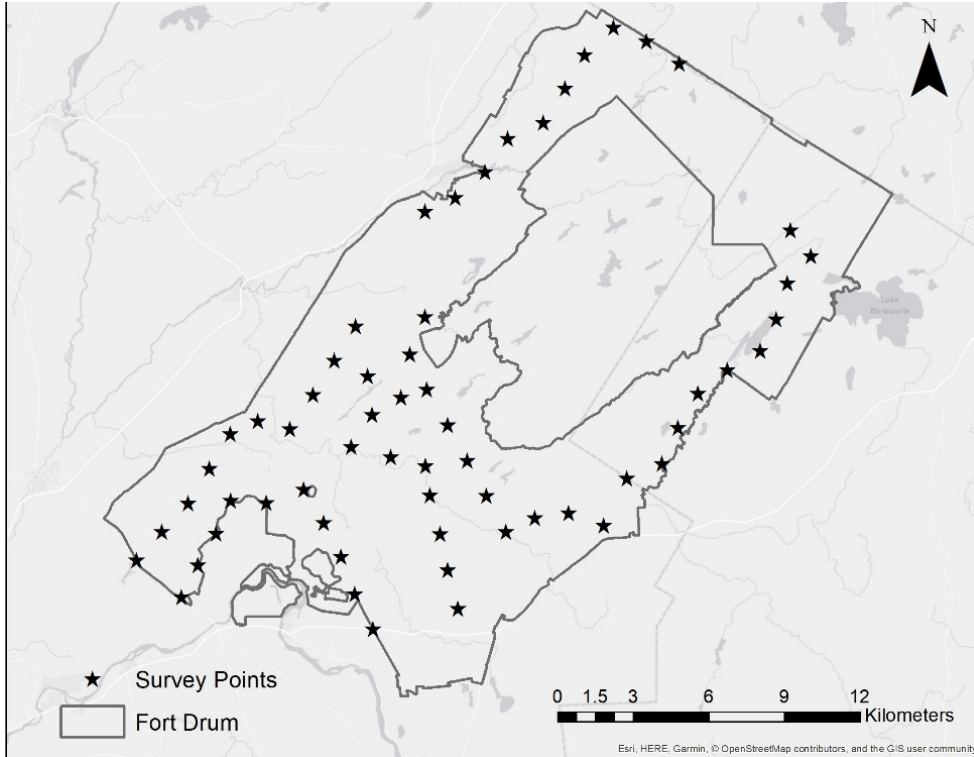


Figure 1. Map of the study area at Fort Drum in northwestern New York State. Black stars represent location of point counts and centroids of vegetation plots.

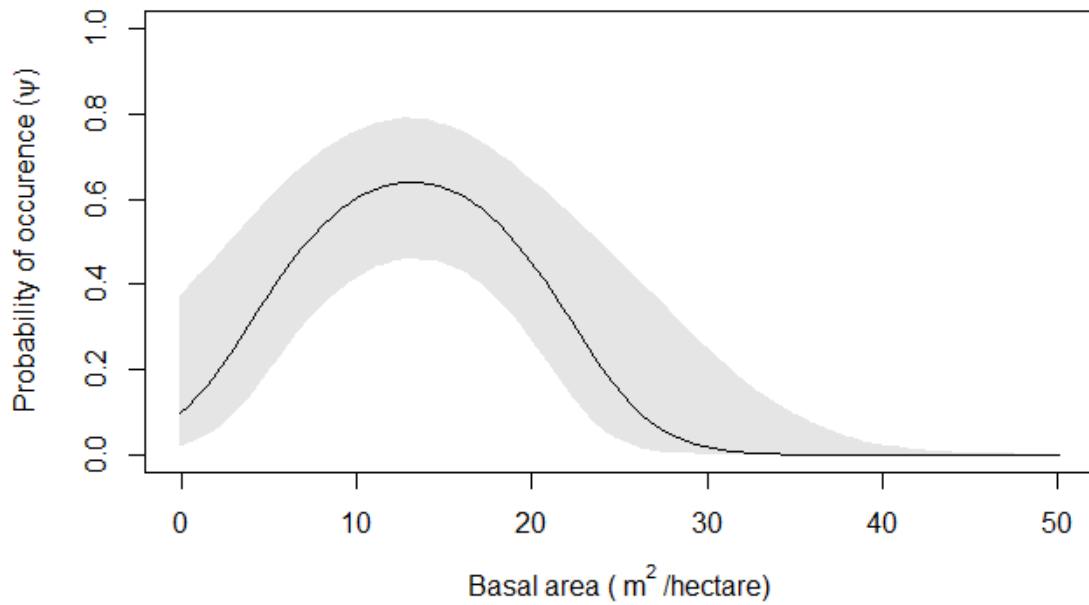


Figure 2. Relationship between eastern whip-poor-will occurrence ( $\psi$ ) and average basal area ( $\text{m}^2/\text{ha}$ ) from the best supported ( $\Delta\text{QAIC}_c \leq 2$ ) models. The solid line represents the model-averaged predicted values and the gray shaded band represents the 95% confidence interval.

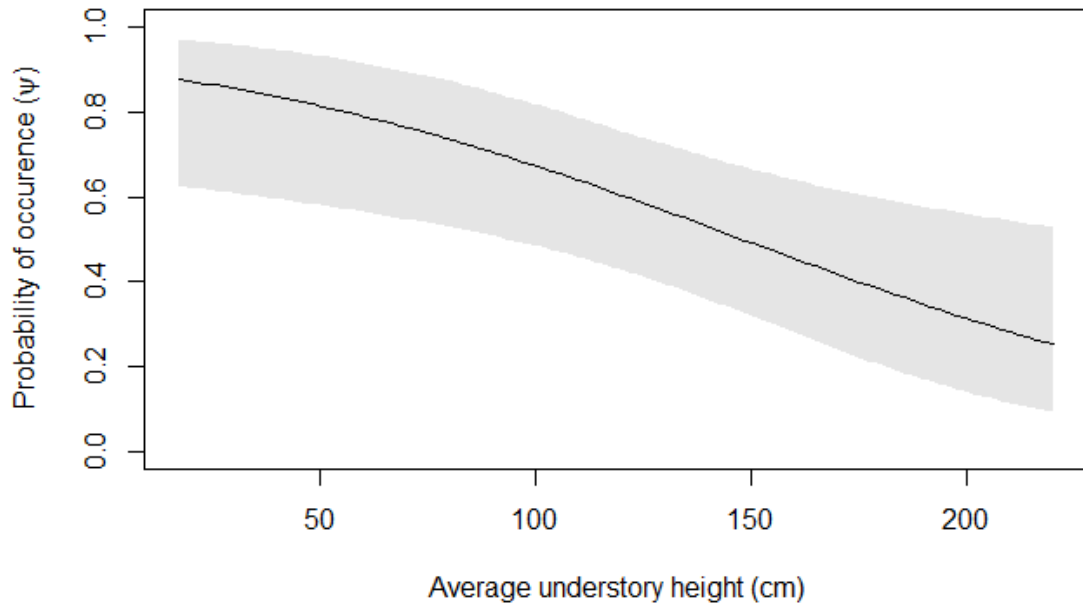


Figure 3. Relationship between eastern whip-poor-will occurrence ( $\psi$ ) and average maximum understory height ( $m^2/ha$ ) from the best supported ( $\Delta QAIC_c \leq 2$ ) models. The solid line represents the model-averaged predicted values and the gray shaded band represents the 95% confidence interval.

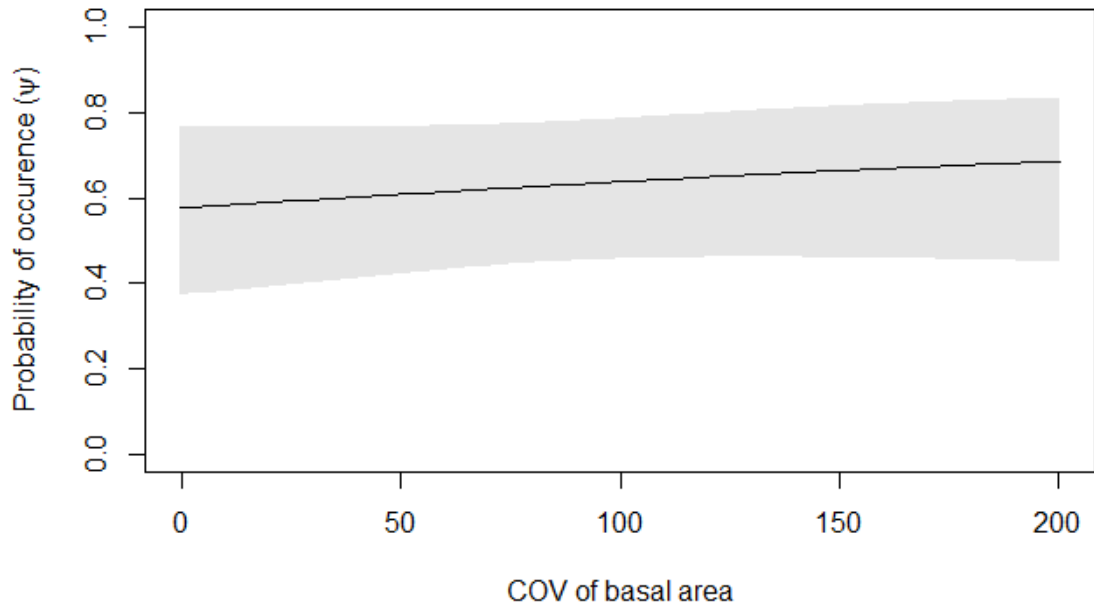


Figure 4. Relationship between eastern whip-poor-will occurrence ( $\psi$ ) and CV of basal area from the best supported ( $\Delta\text{QAIC}_c \leq 2$ ) models. The solid line represents the model-averaged predicted values and the gray shaded band represents the 95% confidence interval.

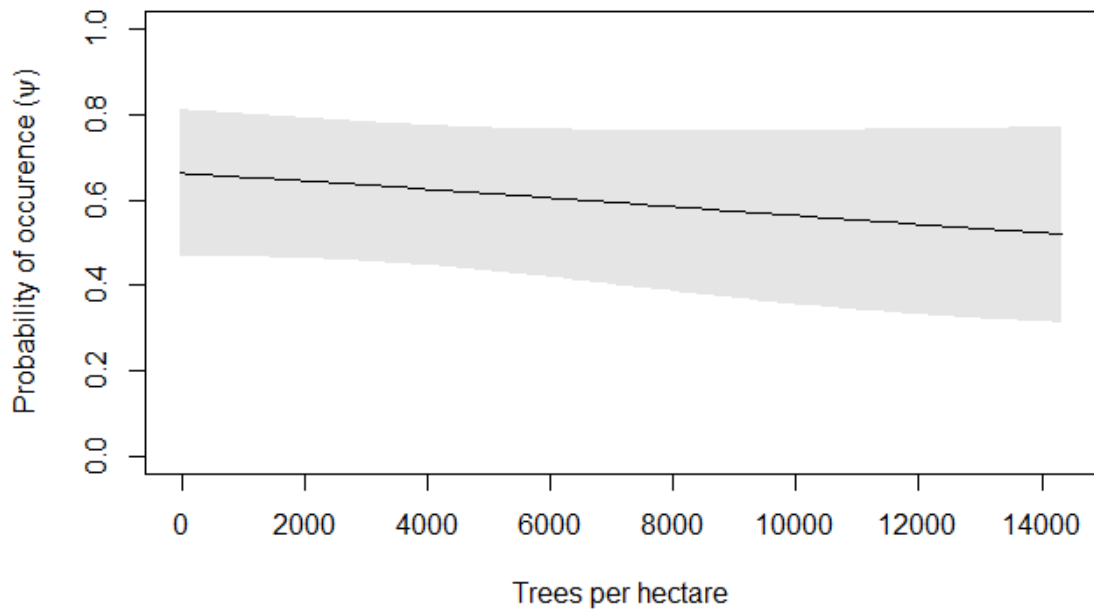


Figure 5. Relationship between eastern whip-poor-will occurrence ( $\psi$ ) and average tree density (trees/ha) from the best supported ( $\Delta\text{QAICc} \leq 2$ ) models. The solid line represents the model-averaged predicted values and the gray shaded band represents the 95% confidence interval.

## CHAPTER 3

### HABITAT CHARACTERISTICS AT FORAGING, ROOSTING, AND NESTING RELOCATIONS OF EASTERN WHIP-POOR-WILLS

#### 3.1 Introduction

The eastern whip-poor-will (*Antrostomus vociferus*: hereafter whip-poor-will) has been the subject of increasing conservation concern due to significant population decreases in North America. Whip-poor-wills have been declining at a rate of 2.76% throughout their range since the 1960s and have disappeared from an average of about 50% of their range compared to 20-30 years ago (Table 2, Sauer et al. 2017). It is unclear as to what is causing these population declines for whip-poor-wills, with hypotheses such as food availability and habitat loss being potential factors (Cink et al. 2017, English et al. 2017b). 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. 2017).

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). 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. 2017). As such, whip-poor-will foraging activity has been positively associated with increased lunar illumination (Mills 1986, Wilson and Watts 2006). It is generally believed that the increased lunar light in open habitats 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, Hunt 2013, Cink et al. 2017) or early-successional habitats such as young forest and shrublands (Hunt 2013, Tozer et al. 2014, Akresh and King 2016, English et al. 2017*b*). While a few older studies found higher whip-poor-will abundance in “forested” areas when compared to 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. 2017). Other species of birds have similarly been shown to select habitat in order to optimize foraging opportunities, such as golden-cheeked warblers and golden-winged warblers (Rappole et al. 1999, Chandler and King 2011).

Due to a lack of data in the literature, nest site selection for whip-poor-wills is not well-understood. Some 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” and DuBois’s record of a nest in “woods of medium size trees, thickly overgrown” (Du Bois 1911, 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). Akresh and King (2016) studied whip-poor-will nesting in Massachusetts and found almost all nests in managed shrublands such as heavily thinned



pitch pine and scrub oak barrens, with only two nests located in closed-canopy forest, but within 50-m of more open-canopy habitat.

In order to make the most effective management recommendations for whip-poor-will conservation, more data 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. 2017), 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, I used radio telemetry to assess whip-poor-will habitat preferences within the home range scale and to compare foraging, roosting, and nesting habitat.

## **3.2 Methods**

### **3.2.1 Study Area**

This study was conducted at Fort Drum, an US Army installation of over 44,000 ha located in northwestern New York state. The majority of land in Fort Drum is comprised of undeveloped training areas accessible by both paved and unpaved roads. Of the over 90% undeveloped land in Fort Drum, approximately 57% is forested land, 14% is grassland, 12% is shrubland, 4% is surface water, and 1% is forbland. 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 has a forest management program that mainly uses silviculture to support training maneuvers, facilitate timber production, and improve forest health (US Army Garrison Fort Drum 2011).

### **3.2.2 Radio Telemetry**

Mist-netting for adult whip-poor-wills was conducted in May and June 2016, at the beginning of the breeding season. I selected areas for mist-netting where birds had been heard calling and limited my selection to areas that had a high likelihood of continued access throughout the season (due to 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. Playback speakers were used to project male whip-poor-will calls to lure birds into the nets. Each whip-poor-will was weighed and banded with a standard USGS-BBL band on one tarsus. Sex and standard morphological measurements were recorded for each bird. The whip-poor-wills were then attached with a radio transmitter (164.00-168.00 Mhz Model 0.5g Blackburn) using a leg-loop harness technique (Streby et al. 2015). Capture of birds continued throughout the season until all transmitters (10 available for the study) were attached.

The radio-tagged whip-poor-wills were tracked on foot using handheld VHF receivers and three-element Yagi antennas. Bird relocations were collected using both homing and triangulation (White and Garrott 1990), and based on the bird's activity, each relocation was classified as either roosting during the day (R), foraging (F), or nesting if the bird was incubating eggs (N). I aimed to collect a minimum of three visually-verified foraging relocations per bird, as well as three visually-verified roosting relocations during the day per bird. For relocations when visual verification was not possible, GPS points and bearings were collected during pursuit to triangulate locations. Any identified nest locations were recorded separately.

The foraging relocations were collected at night within a few hours after sunset. Whip-poor-wills begin feeding about 30 minutes after sunset and may continue as long as light is sufficient, adopting a sit-and-wait foraging strategy known as "sallying" where they make short flights from a perch to catch prey, often returning to the same perch multiple times (Hersey 1923, Cink et al. 2017). Although whip-poor-wills also roost at night when not active, they remain motionless while roosting and are not known to sing at these sites (Cink et al. 2017), so I no longer considered relocations as representative of foraging activity when radio transmitter feedback indicated that the birds had stopped actively moving and I could hear no whip-poor-wills calling nearby. Any relocations collected after this point were considered roosting locations. Roosting relocations collected at night were less robust than the day roosting data, and there was uncertainty regarding whether roosting relocations taken at night were truly representative of roosting behavior of the studied birds (or if the birds may have resumed foraging after the

relocation was taken). To test this, I conducted analyses both with and without the night roosting data being combined with the day roosting data for the GIS-derived habitat distributions. There was no significant difference in results when combining all roosting relocations, but due to the uncertainty the following results are reported without the night roosting data.

For visually-verified relocations collected at night, birds were identified using the radio transmitters and were located 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 relocations were located at perches on tree branches, logs, or the ground – it was assumed the birds were sallying from these locations due to their movement before and after. I included “in-flight” relocations as the location immediately under where a bird had flown only if I 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 relocations, I conducted the habitat analyses with and without the vegetation measurements that were collected at the flying relocations (nine out of the 30 total foraging relocations) and found no significant difference, so the “in-flight” data were included in the final analysis.

### **3.2.3 Vegetation Data**

I collected field vegetation measurements using only visually-verified telemetry relocations. Habitat variables were measured at three visually-verified day roosting

relocations and three visually-verified night foraging relocations 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, I chose the three locations that represented the broadest variety temporally (date and/or time of day). At each of these relocation points, vegetation measurements were taken using techniques modified from James and Shugart Jr. (1970) and King et al. (2009). 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 was recorded at the relocation site. A 10 BAF cruising prism was used to select trees in a variable-width radius plot for basal area, with the dbh and species of each tree in the prism plot being recorded. The same vegetation measurements were also collected at the five nest locations, resulting in a total of 65 point-intercept measurements and 65 cruising prism plots.

I also analyzed all relocations using geographic information system (GIS) technology to determine the proportion of different activities (foraging, roosting, nesting) among discrete habitat classes. I used both vegetation cover layers for the study site provided by Fort Drum's Natural Resources Branch and 2015 0.5-m cell resolution aerial imagery of New York State from the National Agriculture Imagery Program (NAIP) to determine the number of relocations within each habitat class. The habitat classes were related to the levels of canopy cover (closed tree canopy, open tree canopy, and grassland and shrubland).

### 3.2.4 Statistical Analysis

Analyses for the habitat variables were conducted in R 3.5.1 (R Core Team 2018). I used the tree dbh and species data from the cruising prism plots to calculate basal area ( $\text{m}^2/\text{ha}$ ), tree density (trees/ha) and percentage basal area of coniferous trees. I also calculated the basal area of trees ( $\text{m}^2/\text{ha}$ ) 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.

Mapping of the relocations and GIS analyses were conducted in ArcMap 10.5.1. Due to the explicit focus on specific activities and behavior of the bird during the telemetry data collection, the data is not representative of animal movement and therefore not suitable for mapping home ranges for whip-poor-wills. As a result, I did not calculate available habitat or analyze habitat selection in this study.

I analyzed the data using multiple methods to account for the fact that there were only vegetation measurements for five nest sites. I first compared just the foraging and roosting data using data from all relocations where I took vegetation measurements. As there were three of these relocations types per bird per activity, this resulted in a total of 30 foraging and 30 roosting observations for each habitat variable. A generalized linear model framework was used to analyze the data because I was interested in being able to predict differences in the habitat characteristics given the observed activity of the birds. The activity of the bird (foraging or roosting) was fit to each vegetation variable in a univariate generalized linear models. A gamma error distribution was used due to the

non-normal distributions of many of the habitat variables (Shapiro-Wilk  $P < 0.05$ ), which transformations failed to correct. The individual bird was also included as a random effect, as there were three vegetation measurements per activity type per bird. Statistical tests were considered significant at  $p \leq 0.05$  after a Benjamini-Hochberg (BH) correction for multiple comparisons (Benjamini and Hochberg 1995) was applied to the raw  $p$ -values. I 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. The results were then validated 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, variables were assessed for collinearity using Kendall rank correlation, and one variable was removed from highly correlated pairs ( $r > 0.6$ ).

I then included the nesting relocations and used univariate generalized linear models to compare this data with averaged roosting and foraging data, collapsed to the bird level. For the roosting and foraging data, each of the habitat variables was averaged across the three measurements per individual to obtain one measurement per individual per activity type. Using the understory vegetation species data, I 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 I compared with the five (unaveraged) nest observations per each habitat variable. Again, a gamma error distribution was used and a BH correction for multiple comparisons was applied to the raw p-values. I 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, I analyzed all relocations, including those where vegetation measurements were not taken, using GIS data to compare the proportions of roosting, foraging, and nesting relocations in different discrete habitat types. The habitat classes compared were “closed tree canopy,” “open tree canopy,” and “herbaceous vegetation,” the last of which included both shrubland and grassland habitats. To compare the results, Fisher’s exact tests were performed due to the small expected values in many cells of the contingency tables, and the BH correction was applied to pairwise comparisons.

Based on visual observation data, Fisher’s exact tests were also performed to compare substrate type between roosting and foraging relocations. A chi-square test was used 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. Analyses were conducted in the R software environment, version 3.5.1 (R Core Team 2018).



### 3.3 Results

In total, 133 relocation points collected from 10 birds were used in the analyses. Only one of the tracked individuals was female, so sex was not factored into the analyses. Of all the relocation points, 49 were classified as foraging relocations, 75 as day roosting relocations, and nine as nesting relocations (six nests from five individuals). Across the roosting and foraging relocations, 95 included visual observations of the bird. Whip-poor-wills were observed roosting on the ground (63.27% of relocations), and on perches up to 6 m in height, including on logs/stumps (10.2%), tree branches (24.49%), and snags (2.02%). In 20% of roosting observations, the adult was witnessed roosting with one or two chicks on the ground. While foraging, whip-poor-wills were observed in flight (40%), on the ground (6.67%), as well as on perches up to 3 m in height, including on logs/stumps (13.33%), tree branches (33.33%), and snags (6.67%). The perches whip-poor-wills used while foraging differed from perches used while roosting ( $p < 0.0001$ ), with the ground being used significantly less often while foraging (Table 5). Whip-poor-wills used 44.44% deciduous and 55.56% coniferous trees as perches while both roosting and foraging, which differed from the expected proportion given the observed tree composition calculated from the vegetation measurements ( $\chi^2 = 5.754$ ,  $df = 1$ ,  $p = 0.016$ ).

Of the eight habitat variables that were analyzed when comparing only foraging and roosting data, two were effective in explaining the difference between foraging and roosting relocations (Table 6). Maximum understory height ( $p < 0.005$ ) and tree density ( $p < 0.005$ ) were both higher at roosting locations than at foraging locations. 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 % of coniferous trees, with a classification error rate of 0.25 after applying split-sample validation (Table 7).

When comparing the nest data with the averaged foraging and roosting data, five of the habitat variables were effective in explaining the difference between the activity types (Table 8). Maximum understory height ( $p < 0.005$ ), tree density ( $p = 0.016$ ), and basal area ( $p = 0.048$ ) were all higher at roosting locations than at foraging locations. The maximum understory height was also higher at nesting locations than foraging locations ( $p < 0.005$ ). The basal area of saplings ( $p = 0.034$ ) was higher at roosting sites than at foraging sites, but not significantly different at nesting sites. The amount of woody understory was higher at foraging locations than at either roosting ( $p < 0.005$ ) and nesting locations ( $p < 0.005$ ). 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 9).

When comparing all recorded relocations of foraging, roosting and nesting activity using the GIS-derived cover layer data, there appeared to be a significant difference in the proportions of habitat classes between foraging and roosting relocations ( $p < 0.0001$ ), as well as between nesting and roosting relocations ( $p = 0.005$ ), but not between the foraging and nesting relocations ( $p = 0.613$ ). A significantly higher number

of the foraging relocations and all of the nesting relocations were in open tree canopy habitat, while a higher number of the roosting relocations were in closed tree canopy habitat (Figure 6).

### **3.4 Discussion**

I used multiple methods to analyze the data to account for the small number of nests that were found and to establish whether there was a significant bird effect in the habitat data derived from field measurements. Using the full set of foraging and roosting locations where vegetation measurements were recorded, I found two habitat variables (maximum understory height and tree density) that were significantly different between foraging and roosting locations. However, comparing the foraging and roosting data collapsed to the bird level also revealed three additional habitat characteristics (basal area, basal area of saplings, and % woody understory) that were significantly different between foraging and roosting locations, which confirms the need for a bird effect in these models.

Whip-poor-wills appeared to generally use more open habitat for foraging. My observation that foraging relocations had significantly lower tree density and basal area than roosting locations is consistent with the suggestion of other researchers that habitats with an open canopy may allow for increased penetration of lunar illumination and may provide a richer prey base for foraging (Wilson and Watts 2008, Tozer et al. 2014). This is further supported by the fact 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 having

areas dense with small trees would likely decrease visibility and the penetration of lunar illumination. However, whip-poor-wills did appear to require some level of tree cover while foraging. The average basal area measured at foraging locations was 13.39 m<sup>2</sup>/ha, and there was a significantly higher number of foraging relocations located in open tree canopy habitat than in either closed-canopy habitat or in 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 while forest spacing is important for foraging, with more open canopy habitat being preferred, whip-poor-wills do still use areas with moderate tree cover when foraging.

I also found that there was significantly lower maximum understory vegetation height at foraging relocations 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 amount 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, whip-poor-wills often appeared to roost in habitat that was denser, both in terms of canopy-cover and understory vegetation. I found that roosting habitat had significantly higher understory height, tree density, overall basal area, and basal area of saplings than foraging habitat. A high proportion of all recorded roosting relocations

were found in habitat defined as “closed tree canopy” (Figure 6). Although little is known about roosting habitat for whip-poor-wills, one can assume that habitat characteristics at roost site would be similar to that of nest sites. Male and female whip-poor-wills are known to roost together before nest site selection (Cink et al. 2017), and male roost sites generally appear to be close to the nest (Akresh and King 2016). Similar to their nesting strategy, whip-poor-wills appear to rely on camouflage to protect themselves from predation while they roost during the day and when not active at night; they have cryptic plumage, remain motionless at their roost sites, and often roost on limbs close to the ground with their body parallel to the branch (Troschianko et al. 2016, Cink et al. 2017). It is possible that whip-poor-wills roost in more densely forested habitat for protection and shade, or to indirectly reduce energetic costs (Fisher et al. 2004, Akresh and King 2016). Denser understory habitat may provide more cover for ground roost sites and higher tree density may provide greater availability or variety in tree branch roost sites.

These habitat associations, as well as the effect of forest management, were also noticeable in our observations of whip-poor-wills in the field. Whip-poor-wills were observed using areas approximately 1.5 – 3 ha in size that had been clearcut between one and two years prior. Many of these regenerating clearcuts were adjacent to the open road and in proximity to thinned forest and/or dense, closed-canopy forest. For example, one whip-poor-will was observed foraging within an approximately 1.5 ha regenerating clearcut that was bordered by road, forest that had been thinned (parcels about 1.4 and 2.5 ha in size), and large expanse of mature forest, but was found roosting at multiple locations within the adjacent mature forest. Another whip-poor-will used a slightly

shrubber regenerating clearcut surrounded mostly by grassland and thinned forest for both foraging and roosting, but was also found both foraging and roosting in the thinned forest nearby.

Although only a few nests were found in this study, there was a significant difference in the understory vegetation between nest sites and foraging sites. Nest sites in this study had significantly higher maximum understory vegetation height than foraging sites, and a greater proportion of the understory vegetation was woody. As ground-nesting birds, whip-poor-wills rely on camouflage to protect their nests from predation, evidenced by their lack of a structural nest, the cryptic plumage of adult birds, and the reluctance of incubating birds to flush (Troscianko et al. 2016, Cink et al. 2017, English et al. 2018). While the literature is inconclusive on whether whip-poor-wills prefer dense or sparse undergrowth surrounding their nests, a number have studies have also found nests in areas of dense understory vegetation (Du Bois 1911, Raynor 1941, Akresh and King 2016). Whip-poor-will nests are also often found at the base of deciduous cover, as woody cover can provide shade and cover (Akresh and King 2016, Cink et al. 2017). Five nests found in this study were found under deciduous understory vegetation while only one was found under herbaceous cover (ferns), which supports the theory that nest sites are selected on account of the presence of cover at the nest-site spatial scale (Akresh and King 2016).

When examining six total nest sites using the GIS-derived data, all were found in open-canopy mixed or deciduous forest habitat. These results support the findings of Akresh and King (2016), who also found many whip-poor-will nests in open-canopy,

early-successional forest, although they acknowledge that closed-canopy habitat was not extensively searched. I did not find any significant difference in field vegetation measurements such as tree density between roosting and nest sites, although this may have been a result of the small sample size ( $n=5$ ) of nests where field measurements were taken. The average tree density at the nest sites was between that of the foraging and roosting sites and the average basal area of nest sites was lower than at either foraging and roosting sites, and in previous studies, whip-poor-will nests have been found in forested areas with openings and at the edge of closed-canopy forests (English et al. 2018, Akresh and King 2016). This could suggest that whip-poor-wills use habitat characterized by intermediate openness for nesting, though the results from this study were not statistically significant. Nevertheless, the fact that all nests were found in open-canopy forest provides further evidence that the paradigm of whip-poor-wills mainly using closed-canopy forest for nesting may not be entirely accurate.

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. 2017). Interestingly, 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.

In conclusion, it appears that forest structure is a crucial factor in habitat associations for whip-poor-wills at both the canopy level and the understory level, with openness being preferred at both levels for foraging. In the multivariate analysis of foraging, roosting, and nest sites, the combination of variables that best predicted whip-poor-will behavior were tree density, basal area, and the percentage of woody understory, which suggests that both the tree level and understory level are important. The results from this study demonstrate that foraging behavior, roosting behavior, and nesting behavior exert unique influences on habitat selection of whip-poor-wills and support a growing body of evidence that whip-poor-wills require open habitat for foraging, due to their specialized foraging behavior.

### **3.5 Management Implications**

Many studies on whip-poor-will abundance recommend forest management to increase shrubland or open-canopy habitat (Wilson and Watts 2008, Hunt 2013, Tozer et al. 2014, Akresh and King 2016). In this study, whip-poor-wills appeared to generally use more open habitat for foraging and denser habitat for roosting. Although the data at nest sites was limited, all identified whip-poor-will nests were located in habitat with low basal area and that was characterized as “open tree canopy,” so it appears that whip-poor-wills may use habitat that is more open than closed-canopy forest for nesting.

Both the data collected in this study and observations in the field support the theory that increased open habitat, such as early-successional forest or even thinned mature forest, may benefit whip-poor-wills by providing more areas for foraging and,



potentially, nesting (Hunt 2013, Akresh and King 2016). The average basal area at foraging locations was 13.39 m<sup>2</sup>/ha, while the average basal area at nest sites was 11.48 m<sup>2</sup>/ha, both of which correspond to residual basal area following low-to high density shelterwood treatment (Thompson III and DeGraaf 2001), suggesting that such treatments and residual basal area targets may be suitable when managing for foraging and nesting habitat. Foraging habitat also appeared to have a low number of saplings and a generally open understory, which can also be addressed through forest management techniques such as understory removal. Nesting habitat had a higher maximum understory height than foraging habitat, which may be due to the fact that whip-poor-will appear to prefer nesting under deciduous understory vegetation (Akresh and King 2016, Cink et al. 2017). Therefore, our results suggest that while whip-poor-wills may prefer nesting in habitat that has a lower overall basal area, similar to their foraging habitat, such habitat would require more understory deciduous cover to provide shade and protection.

In contrast to previous theories, the results from this study suggest that while whip-poor-wills do likely require open areas for foraging, they may prefer more forested areas for roosting rather than nesting. As a result of my findings, I would encourage maintaining closed-canopy forest within proximity to these thinned and more open areas, as other studies have suggested (Akresh and King 2016), because more densely forested habitat may also provide important roosting habitat for whip-poor-wills. The average basal area at roosting locations was almost twice as high as foraging locations at 21.74 m<sup>2</sup>/ha, which is representative of closed-canopy forest that has not been treated through

forest management (Thompson III and DeGraaf 2001). 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. Furthermore, studies have shown that species diversity increases in response to both uneven-aged and even-aged harvests (Annand and Thompson III 1997), so efforts to create and maintain patchy habitat with variable levels of openness for whip-poor-wills may also benefit other disturbance-dependent species.

Table 5. Perch substrate at roosting and foraging sites. Common superscripts across rows indicate means that do not differ statistically ( $p > 0.05$ ) after applying Fisher's test.

	Ground	Logs/Stumps	Tree Branches	Snags
% Foraging	8.82 <sup>a</sup>	54.55 <sup>b</sup>	55.56 <sup>b</sup>	75 <sup>b</sup>
% Roosting	91.18 <sup>a</sup>	45.45 <sup>b</sup>	44.44 <sup>b</sup>	25 <sup>b</sup>

Table 6. 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*	69.83 (17.4)	208.07 (17.36)	1	13.63	<b>0.0043</b>
TPH	620.91 (207.1)	4910.48 (970.59)	1	12.18	<b>0.0043</b>
BAS	13.39 (2.05)	21.74 (2.45)	1	0.92	0.7702
CONI	23.25 (4.86)	26.46 (5.14)	1	0.03	0.8937
SAP	1.15 (0.49)	6.2 (1.1)	1	4.58	0.1104
POLE	3.44 (0.78)	5.59 (1.41)	1	0.43	0.8717
SAW	7.19 (1.33)	7.89 (1.58)	1	0.02	0.8937
LSAW	1.61 (0.6)	2.07 (0.7)	1	0.08	0.8937

\*HEI = maximum understory height (cm), TPH = tree density (trees/ha), BAS = basal area (m<sup>2</sup>/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 7. 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

Table 8. 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	Df	F	Sum of Squares	p
HEI*	69.83 <sup>a</sup> (12.42)	208.07 <sup>b</sup> (21.79)	198 <sup>b</sup> (48.02)	2	13.67	6.2224	<b>0.0007</b>
TPA	620.92 <sup>a</sup> (153.14)	4910.48 <sup>b</sup> (1467.12)	2421.8 <sup>ab</sup> (1115.11)	2	11.44	18.464	<b>0.0013</b>
BAS	13.39 <sup>a</sup> (2.26)	21.74 <sup>b</sup> (2.57)	11.48 <sup>ab</sup> (1.45)	2	4.84	1.8237	<b>0.0363</b>
CONI	23.25 (7.31)	26.46 (6.76)	15.71 (10.2)	2	0.40	0.8481	0.7485
SAP	1.15 <sup>a</sup> (0.4)	6.2 <sup>b</sup> (1.62)	3.67 <sup>ab</sup> (1.56)	2	6.84	12.798	<b>0.0123</b>
POLE	3.44 (0.87)	5.59 (2.02)	0.92 (0.56)	2	3.7	8.408	0.0586
SAW	7.19 1.69	7.88 (1.87)	4.59 (1.92)	2	0.75	0.929	0.6029
LSAW	1.61 0.83	2.07 (0.74)	2.3 (1.45)	2	0.13	0.523	0.8763
WOOD	23.33 <sup>a</sup> (5.09)	86.67 <sup>b</sup> (7.37)	80 <sup>b</sup> (20)	2	15.39	8.6579	<b>0.0007</b>

\*HEI = maximum understory height (cm), TPH = tree density (trees/ha), BAS = basal area (m<sup>2</sup>/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 9. 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

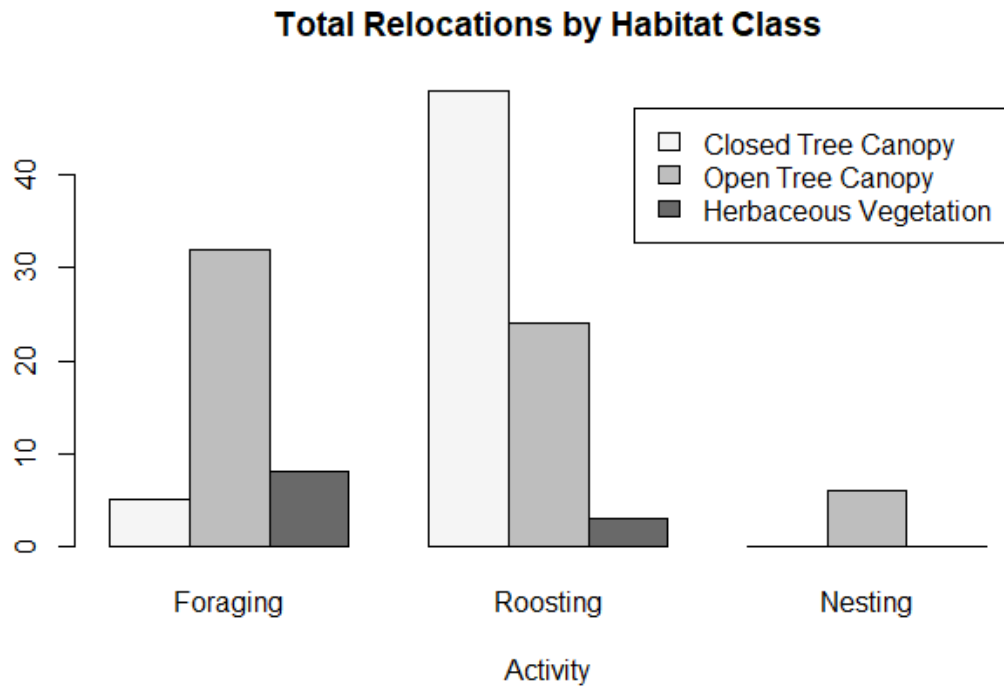


Figure 6. Number of total telemetry relocations recorded for foraging, roosting, and nesting eastern whip-poor-wills by discrete habitat type.

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