A Multi-Regional Assessment of Eastern Whip-poor-will (Antrostomus vociferus) Occupancy in Managed and Unmanaged Forests Using Autonomous Recording Units

A Multi-Regional Assessment of Eastern Whip-poor-will (*Antrostomus vociferus*) Occupancy in Managed and Unmanaged Forests Using Autonomous Recording Units

A Thesis Presented

by

Jeffery T. Larkin

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DEDICATION

This thesis is dedicated to all my friends and family members who are no longer with us, but played an instrumental role in getting me to where I am today.

"Perhaps the greatest value in studying endangered species is what we learn about ourselves in our haphazard efforts to save them." -David S. Maehr

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ABSTRACT

A MULTI-REGIONAL ASSESSMENT OF EASTERN WHIP-POOR-WILL (*ANTROSTOMUS VOCIFERUS*) OCCUPANCY IN MANAGED AND UNMANAGED FORESTS USING AUTONOMOUS RECORDING UNITS

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State and federal agencies spend considerable time and resources to enhance and create habitat for wildlife. Understanding how target and non-target species respond to these efforts can help direct the allocation of limited conservation resources. However, monitoring species response to habitat management comes with several logistical challenges that are exacerbated as the area of geographic focus increases. I used autonomous recording units (ARUs) to mitigate these challenges when assessing Eastern Whip-poor-will (*Antrostomus vociferus*) response to forest management. I deployed 1,265 ARUs across managed and unmanaged public and private forests from western North Carolina to southern Maine. I then applied a machine learned classifier to all recordings to create whip-poor-will daily detection histories for each survey location. I used detection data and generalized linear models to examine regional, landscape, and site factors that influenced whip-poor-will occurrence. Whip-poor-wills were detected at 399 (35%) survey locations. At the regional scale, occupancy decreased with latitude and elevation. At the landscape scale, occupancy was negatively associated with the amount of impervious cover within 500m, and was positively associated with the amount of oak forest and evergreen forest cover within 1,750m. Additionally, whip-poor-will occupancy exhibited a quadratic relationship with the amount of shrub/scrub cover within 1,500m. At the site-level, occupancy was negatively associated with increased basal area and exhibited a quadratic relationship with woody stem density. Whip-poor-will populations can benefit from the implementation of forestry practices that create and sustain early successional forests within forested landscapes, especially those dominated by oak forest types. The use of ARUs helped overcome several challenges associated with intensive broad-scale monitoring efforts for a species with a limited survey window, but also presented new challenges associated with data management, storage, and analyses.

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CHAPTER 1

LITERATURE REVIEW

1.1 Eastern Whip-poor-will Species Description and Ecology

The Eastern Whip-poor-will is a nocturnal aerial insectivore within the family *Caprimulgidae* (nightjars or goatsuckers; Cink 2020). The core breeding season distribution of this species ranges from eastern Minnesota, south to central Arkansas, and east to the Atlantic coast and north to southern Ontario (Cink et al. 2020). The species overwinters from Florida west to Texas and south to Panama (Cink et al. 2020, Korpach et al. 2022, Skinner et al. 2022). Adult whip-poor-will weigh between 43-63 g (Cink et al. 2020). Plumages of males and females are similar, with exception for white collar and patches that adorn the corners of the tail, which is tan on females (Peterson 2008). Like many other nightjar species, the whip-poor-will is difficult to detect visually due to its cryptic coloration that is well suited for blending in with its forested surroundings. Specifically, the species' broken brown and black plumage, beige to off-white collar, and black throat enhance its concealment in leaf litter or on tree limbs. The whip-poor-will has an elongated flattened stature with large eyes, a small beak that opens into a disproportionately large mouth, and whiskers which are used when aerially capturing prey. Females typically produce a clutch of two eggs which are laid directly on leaf litter (Akresh and King 2016, Cink et al. 2020). Perhaps its most well-known characteristic, which gave rise to its name, is its repetitive and incessant 3-part song: "whip poor will, whip poor will, …, whip poor will". This nocturnal songster has several other vocalizations: the quirt, growl and hiss, and growl-cluck (Cink et al. 2020).

Whip-poor-will, and other nightjars, are unique in that most aspects of their life history can be tied to the lunar cycle (Cink et al. 2020, Bjorklund and Bjorklund 1983, Mills 1986,

Wilson and Watts 2006). A study conducted in Illinois found that increasing lunar illumination positively influenced the number of individuals singing and the vigor of their songs (Bjorklund and Bjorklund 1983). Similarly, a study from North Carolina found that whip-poor-will detection was more than doubled when lunar illumination was >50% (Wilson and Watts 2006). This same study also observed that whip-poor-will singing was greatest when the moon was above the horizon (Wilson and Watts 2006). Whip-poor-will foraging, nest departure rates, and reproductive cycle have also been found to be influenced by the lunar cycle. A study in eastern Ontario found a positive relationship in singing, foraging, and nest departure rates as lunar illumination increased and suggested that whip-poor-will use the moon to backlight their prey (Mills 1986). Moreover, they found a synchrony between the whip-poor-wills reproductive cycle and the lunar cycle with their hatching date occurring approximately 10 days before a full moon (Mills 1986). This suggests that whip-poor-wills time their young to hatch as prey is becoming most abundant and easiest to capture. Chick survival was found to be lowest when there was a mismatch between hatching, prey abundance, and potentially the lunar cycle (English et al. 2018a).

To date, little research has examined breeding whip-poor-will territory and home range size. In Kansas, early estimates of the species territory size examining singing birds ranged from 2.8-11.1 hectares (Fitch 1958). Subsequent research found whip-poor-will territory size to be 5.1 ha on average (Cink 2020). Breeding season home range size, quantified by radio-telemetry and spot mapping, range from 0.77-282 ha (Wilson 2003, Hunt 2013). A study in pine dominated forest of North Carolina collected nocturnal locations from 27 radio-tagged male whip-poor-wills (Wilson 2003). Home range size in homogeneous, forested landscapes averaged 25 ha (range: 1.7 to 154.4 ha) and 19 ha (range: 1.1 to 94.2 ha) in heterogeneous, forested landscapes

using a 50% probability kernel utilization distribution (Wilson 2003). Home range size at the 75% probability distribution averaged 50 ha (range: 5.1 to 282.8 ha) in homogeneous, forested landscapes and 40 ha (range: 2.3 to 165.6 ha) in heterogeneous, forested landscapes (Wilson 2003). Another study, which used spot-mapping locations from 43 individuals in pine-oak dominated forests of New Hampshire, found home range size (based on minimum convex polygons) to average 4.8 ha (range: 0.77 to 12.98 ha; Hunt 2013). Furthermore, individuals are rarely known to forage >500m from their nest site (home range = <79 ha) (Cink 2020).

Similar to home range and territory size, there exists relatively little published research regarding diet and foraging behaviors of whip-poor-will, and most of what is known is from anecdotal historical accounts. For example, in one account the observer deduced that whip-poor-will were aerial feeders after encounters with 25 individuals (Van Rossem 1927). Similarly, another observer reported following an individual and watching it fly into the air to capture insects (Heresy 1923). Whip-poor-will were assumed to forage on a variety of flying insects including moths, beetles, grasshoppers, flying ants, and mosquitos (Martin et al. 1951). More recently, there have been quantitative analyses of whip-poor-will diet confirming and refining what was previously reported. A study in pitch pine-scrub oak communities in Massachusetts collected 70 fecal samples from 10 whip-poor-will and found that 98% of prey items were moths (Lepidoptera; 61%) and beetles (Coleoptera; 37%) (Garlapow 2007). Similarly, another study in Illinois used DNA metabarcoding to conclude that whip-poor-will diet primarily consisted of moths (86%), with a lesser component of cockroaches (Blattodea; 9%) and beetles (6%) (Souza-Cole et al. 2022). This latter study using DNA metabarcoding is likely the most accurate assessment of whip-poor-will diet, given Lepidoptera parts may more likely dissolve and become

unrecognizable in fecal samples compare to harder-bodies taxa like beetles (Clare et al. 2009, Rytkönen et al. 2019).

1.2 Eastern Whip-poor-will Surveys

Whip-poor-will life history is closely tied to the lunar cycle. Thus, it is recommended that surveys for this species occur during the 5th and 6th full moons of the annual lunar cycle when lunar illumination is ≥50%, as activity is highest during this time (between the first quarter and the last quarter) (nightjars.org, Mills 1986, Wilson and Watts 2006). When surveying for whip-poor-will, observers typically follow a protocol similar to that of the Center for Conservation Biology's Nightjar Survey Network (nightjars.org)(Tozer et al. 2014, Palumbo et al. 2021, Spiller and King 2021, Souza-Cole et al. 2022). While research not adhering strictly to this protocol has yielded useful results, it is typically constrained to small sample sizes and/or limited spatial extents (Wilson and Watts 2008, Akresh and King 2016). The Nightjar Survey Network is a volunteer-based survey that monitors nightjars across the continental US. This monitoring protocol employs road-based surveys, meaning all counts occur on navigable roads along designated routes. Each route is 10-miles long and has 10 roadside stops that are spaced ~1-mile apart. At each stop, a 6-minute, passive count is conducted once annually. Similar to diurnal bird surveys, whip-poor-will counts should not occur during precipitation or high winds. Additionally, surveys should be avoided on nights with dense cloud cover and should only occur at night when the moon is above the horizon when the probability of detection is highest (>30 min after sunset) (Mills 1986, Wilson and Watts 2006).

The Nightjar Survey Network survey protocol was developed to monitor whip-poor-will, and other nightjars, safely and efficiently across a large spatial extent. However, as with most survey methods, this protocol has several shortcomings. The brief survey period for whip-poor-

will limits the number of surveys that can be completed in a given season. This brief survey period is further constrained by weather limitations. The minimal amount of time spent at a survey location each breeding season leads to high probability of false negatives. Granted, false negatives can be accounted for in a typical occupancy modeling framework (Fiske and Chandler 2011). However, accounting for imperfect detection in an occupancy modeling framework uses statistical power that could otherwise be used to better evaluate how species occurrence is influenced by habitat variables (MacKenzie et al. 2017). Furthermore, road-based survey efforts can result in several biases, such as disproportional sampling of habitat types (Lawler and O'Connor 2004, Harris and Haskell 2007, Matsuoka et al. 2011) and inaccurate estimates of population size (Hanowski and Niemi 1995). Also, road-based surveys often do not monitor forest management well, as management footprints are not centered along navigable roads. Thus, inferences regarding the species response to management efforts, abundance estimates, and habitat associations are limited.

1.3 Eastern Whip-poor-will Habitat Associations

1.3.1 Site Level

Whip-poor-wills are considered a forest dependent species and are known to use a variety of successional conditions (Wilson and Watts 2008, Akresh and King 2016, Cink 2020, Spiller and King 2021) and forest types (Wilson and Watts 2008, Akresh and King 2016, Palumbo et al. 2021). Early accounts of the species noted that they invariably foraged in and on the edges of open areas (Van Rossem 1927). Subsequent research has further re-enforced whip-poor-wills strong association with young seral forest patches in all forest types found across its range (Wilson and Watts 2008, Hunt 2013, Tozer et al. 2014, Akresh and King 2016, Farrell et al.

2017, Spiller and King 2021). A study in the pine dominated forests of coastal North Carolina found a greater abundance of whip-poor-will in regenerating stands compared to mature forests (Wilson and Watts 2008). Similarly, in northern New York, whip-poor-will had associations with shorter understory, lower tree density, and reduced basal area (Spiller and King 2021). In boreal forests, located on the northern periphery of the species range, a study did not find a strong association of whip-poor-will to either clearcut or burned stands compared to open-canopy wetlands (Farrell et al. 2017). However, although not significant, they did find occupancy was higher in burned stands (Farrell et al. 2017). Moreover, survey locations proximate to young forest patches and shrublands have been shown to have higher whip-poor-will occupancy than those near mature unmanaged forests (Tozer et al. 2014, Grahame et al. 2021). Whip-poor-will dependence on young forest is attributed to its foraging technique where birds are able to backlight and capture their prey (Mills 1986, Cink 2020). There is evidence that suggests whip-poor-will use young forest and shrubland for nesting and roosting more than previously understood (Akresh and King 2016, Grahame et al. 2021).

There is mixed evidence on whip-poor-will use of mature forest and associated edge (Bent 1940, Wilson and Watts 2008, Akresh and King 2016, Grahame et al. 2021). Early species accounts noted that whip-poor-will nest in the mature portion of edge habitats where the larger trees cast patchy shade on the forest floor thus enhancing the effectiveness of their cryptic coloration (Bent 1940). Additionally, whip-poor-will distribution in young forests has been found to be skewed toward mature forest edges with detection more likely within 200m of an edge (Wilson and Watts 2008). A similar result was found in New Hampshire, where whip-poor-will selected for edge habitats (Hunt 2013). It has been hypothesized that young forests proximate to mature stands may provide opportunity to exploit foraging and nesting habitats

(Wilson and Watts 2008). More recently, whip-poor-will have been found to also roost and nest in young forest and shrubland habitats (Akresh and King 2016, Spiller 2019, Grahame et al. 2021). A study in pine-oak barrens in Massachusetts located 26 nests with 17 in thinned pitch pine, 7 in scrub-oak, and 2 in closed canopy areas within 50m of a young forest/shrubland edge (Akresh and King 2016). In this same study, nearly all roost sites were within thinned pitch pine and scrub-oak with only 3 of the 59 roosts in closed canopy forests, though closed-canopy forests were not surveyed extensively in the study. Similarly, a study in Ontario found that whip-poor-will predominately roosted in shrublands (Grahame et al. 2021). Collectively, past research has indicated that mature forest and ecotones are used by whip-poor-will (Wilson and Watts 2008, Spiller and King 2021). Thus, forest management practices targeting whip-poor-will should create and maintain patches of regenerating forest proximate to mature forests (Wilson and Watts 2008, Spiller 2019, Spiller and King 2021).

Other factors known to influence whip-poor-will use of a site are wetlands and rock barrens. A study that looked at small scale habitat associations of whip-poor-will in Ontario found a positive association with rock barrens at night (Grahame et al. 2021), which is likely attributed to the species foraging ability in openings (Mills 1986). Additionally, this same study found a negative relationship with the use of wetlands, which is contrary to what has been found at larger spatial extents (Vala et al. 2020, Farrell et al. 2019). However, Grahame et al. 2021 investigated the landcover within 15m of a known whip-poor-will location rather than the 1,000m and 6,000m spatial extents that have been found to be significant in landscape scale studies (Grahame et al. 2021, Vala et al. 2020, Farrell et al. 2019). Forest type may also influence whip-poor-will occupancy. Whip-poor-will are typically associated with dry, pine dominated sites such as pine-oak barrens (Akresh and King 2016), loblolly pine plantations

(Wilson and Watts 2008), or white/red pine forests (Tozer et al. 2014). However, whip-poor-will have been found to occupy other forest types as well (Farrell et al. 2017, Palumbo et al. 2021, Spiller and King 2021). One study in Ontario found that whip-poor-will used deciduous and mixed forests at night more than expected based on available cover (Grahame et al. 2021). Yet, limited research has been conducted in the core of the species range, which is largely dominated by deciduous forest (Dyer 2006). Furthermore, the vast majority of whip-poor-will research has been conducted in pine dominated or heavily mixed forest landscapes (Wilson and Watts 2008, Hunt 2013, Tozer et al. 2014, Akresh and King 2016, Farrell et al. 2019). Recent efforts to better understand whip-poor-will habitat associations on the breeding grounds are instrumental for informing conservation and management for this rapidly declining species. Nonetheless, relative to the large size of the species breeding distribution, there remains a paucity of information regarding breeding season habitat preferences. For example, the 2015-2025 Pennsylvania State Wildlife Action plan also lists the Eastern Whip-poor-will as a Species of Greatest Conservation Need and explicitly highlights the following two research needs for the species: 1) Determine the key features that constitute high quality whip-poor-will habitat in Pennsylvania, and 2) Determine response of this species and others to silvicultural treatments especially for young forest/early successional habitats.

1.3.2 Landscape Level

Whip-poor-will occupancy is also influenced by factors beyond the site level (Cink 2020, Vala et al. 2020, Wilson and Watts 2008). Indeed, research conducted across the species range indicates that whip-poor-will occupancy is also influenced by landscape level features such as land cover composition, elevation, and intensity of forest management (Wilson and Watts 2008,

Vala et al. 2020, Palumbo et al. 2021). The spatial extent at which landscape features and whip-poor-will have been investigated varies between 500m and 10km around survey locations (Farrell et al. 2019, Vala et al. 2020). Whip-poor-will occupancy and abundance appears to be influenced by the amount of forest, associated management, and edge habitat in the landscape (Hunt 2013, Tozer et al. 2014, Vala et al. 2020), and highest in forested landscapes with a mosaic of age class and structural diversity (Wilson and Watts 2008, English et al. 2016, Farrell et al. 2017). Specifically, forested landscapes with diverse successional stages, including regenerating forest and ecotones provide the most benefit to whip-poor-will (Wilson and Watts 2008, Akresh and King 2016, English et al. 2016, Farrell et al. 2019).

Beyond forest cover and community type, whip-poor-will occupancy and abundance has been linked to other landscape attributes. Several studies found a negative relationship between whip-poor-will abundance and occupancy and urban landcover (English et al. 2016, Vala et al. 2020, Souza-Cole et al. 2022). Also, contrary to what is discussed at the site level, there is evidence that whip-poor-will may have positive association with the extent of wetlands at larger spatial scales (Farrell et al. 2019, Vala et al. 2020). Moreover, a study in Nebraska found a negative association with increasing amounts of row-crops at both one and four kilometers around a survey location (Brenner and Jorgensen 2020). However, in New York, occupancy was found to be positively related to increased hay/pasture in the local landscape, although the authors provided no proportional values for context (Palumbo et al. 2021). This same study found that whip-poor-will occupancy increased with lower elevations (Palumbo et al. 2021). Site level management intended to benefit whip-poor-will could be futile, or at least limited in effectiveness, if it is embedded in landscape contexts that are unsuitable for the species. As such,

it is important to consider landscape context when planning and implementing habitat management for whip-poor-will (Wilson and Watts 2008, Vala et al. 2020).

1.4 Eastern Whip-poor-will Conservation Status and Population Declines

The steady long-term decline of whip-poor-will populations has led to its status as a continental watchlist species (Rosenberg et al. 2016). Over the past half century, whip-poor-will have been experiencing significant population declines, with an estimated 64% overall population decline (Rosenberg et al. 2019, Pardieck et al. 2020). In the late 1800s to early 1900s, there were accounts of the species being common across its historic range. One account from southern Iowa stated that whip-poor-will were as "common as Robins" (*Turdus migratorius*) with many being flushed throughout the day (Nauman 1925). Another account from Massachusetts during migration was quoted as saying:

> "There were numbers of birds about the house, on the door-step and ridge-pole, others singing from the road or stone walls along the road side, while still others could be heard down in the pastures- often 8 or 10 were singing in the same instant. I walked down the road for a half mile and the birds seemed equally as abundant on neighbor's farms" (Heresy 1923).

However, since the time of these early accounts the species has become increasingly uncommon or absent across large portions of its historic range (Cink 2020, Pardieck et al. 2020). Whip-poor-will have been extirpated from North Dakota, southeastern Saskatchewan, and portions of Michigan's upper peninsula (Stewart 1975, Eastman 1991, Smith 1996) and experienced significant declines across most of their range (Hall 1983, McGowan and Corwin 2008, Wilson et al. 2012, Rodewald et al. 2016, Pardieck et al. 2020). There are two primary factors suspected

to be contributing most substantially to whip-poor-will decline, decreases in prey abundance (English et al. 2018b) and breeding habitat loss and degradation (Purves 2015).

Insect populations are known to have been declining globally for the past several decades (Dirzo et al. 2014, Hallman et al. 2017, Vogel 2017, Wagner 2020), which have been tied to numerous stressors such as habitat loss and degradation, climate change, intensive agriculture, non-native species, urbanization, insecticides, light pollution, and herbicides (Boettner et al. 2000, Wilson and Maclean 2011, Hallman et al. 2014, Vogel 2017, Piano et al. 2019, Eggleton 2020, Wagner 2020, Wagner et al. 2021). A study conducted at sites within landscapes dominated by agriculture, urban, and forest in Ohio found a 30% decline in butterflies (Lepidoptera) across a 20-year study (Wepprich et al. 2019). Monarch butterflies (*Danaus plexippus*) are also known to be declining with an expected population reduction of an additional 14% over the next 100 years (Flockhart et al. 2015). Similarly, a long-term study in Germany found a 75% decline in insect biomass over 27-years in 63 forested nature preserves (Hallman et al. 2017). Thus, it is not surprising that species in higher trophic levels that depend on insects as prey are also declining (Hallman et al. 2017, Rosenberg et al. 2019). A study that used isotopes to assess the connection between whip-poor-will and insect declines, found a significant change in dietary isotopes over the past 130 years (English et al. 2018b). These findings suggest whip-poor-will are foraging on lower order flying insects and that their decline may be exacerbated by reductions in prey populations. Contrary, and although a different species, a study on European Nightjars in Switzerland found that moth abundances had not changed significantly over 30 years of data and that light pollution was a significant cause of decline (Sierro and Erhardt 2019). Light pollution was 2-5 times greater at abandoned sites compared to occupied sites, suggesting light pollution exceeded tolerable levels for nightjars (Sierro and Erhardt 2019).

Collectively, habitat loss, fragmentation, and degradation is the single most contributing factor to wildlife population declines globally (Fahrig 2003, Ewers and Didham 2006, Buchmann et al. 2013, Rosenberg et al. 2019), and is thought to be the case for whip-poor-will (Purves 2015). Forest succession, coupled with reduced frequency and intensity of disturbance, is the primary driver of habitat loss for species that require grassland and young seral communities (Rosenberg et al. 2019). Urbanization and land conversion are factors that reduce and degrade the availability of forests in eastern North America (Marzluff 1997, Aronson et al. 2015, Atasoy et al. 2018), and are thought to further contribute to whip-poor-will habitat loss (Vala 2020, Souza-Cole et al. 2022). Prior to European settlement, North American forests were vast with approximately one third of forest cover falling in the eastern portion of the continent (MacCleery 2011, Blondel 2018). Eastern forests were remarkably dynamic with an array of natural and anthropogenic disturbances that contributed to forest complexity (Bormann and Likens 1979, Clawson 1979, Nowacki and Abrams 2008, MacCleery 2011, Abrams et al. 2021). The great diversity of mammals and avifauna that European settlers wrote about can largely be attributed to the complexity of the forest at this time (MacCleery 2011, Blondel 2018). This would have included young seral communities that were created and maintained on the landscape through keystone wildlife species such as beavers (*Castor canadensis*), wildfires (more so in Appalachia), and high wind events such as tornados and hurricanes (Bormann and Likens 1979, Clawson 1979, Nowacki and Abrams 2008, MacCleery 2011, Abrams et al. 2021). From the mid-1800s to early 1900s, over two centuries after European settlers arrived, eastern North America experienced unprecedented land clearing for agriculture, exploitative logging, and hunting that had impacts, which can still be seen today (Clawson 1979, MacCleery 2011). Farm abandonment quickly followed due to the more productive farmlands in the Midwest (Whitney

and Foster 1988, Litvaitis 1993, MacCleery 2011). These abandoned farms led to an increase in young seral forests, which greatly benefited wildlife (Litvaitis 1993, Askins 1998, Askins 2001). Today, these abandoned farms have reverted to mature forests, which are becoming older and more uniform in composition and structure (Litvaitis 1993, Shifley 2014). As a result, it has been argued that the amount of young seral communities in North America is at historically low levels (King and Schlossberg 2014, Shifley et al. 2014). Thus, it is not surprising that the greatest contributor to whip-poor-will population declines, along with those of many other species, is suggested to be reductions in the amount of young seral communities (King and Schlossberg 2014).

1.5 Autonomous Recording Units

Autonomous Recording Units (ARUs) are small, battery powered recording devices that can be programed to collect acoustic data during specified dates and times (Hill et al. 2019). Since their development, ARUs have been attractive to many conservation professionals who monitor species that make auditory cues, such as insects, amphibians, birds, and mammals (Adams 2013, Jeliazkov et al. 2016, Shonfield and Bayne 2017, Lapp et al. 2021, Maegawa et al. 2021). However, the cost of recording units and the associated acoustic data's size and processing has limited ARU use (Hill et al. 2019, Sugai et al. 2019). The recent availability of low-cost ARUs, and efforts to make data processing easier have revitalized ARU based monitoring efforts (Hill et al. 2019, Kahl et al. 2021). ARUs are known to be particularly useful for monitoring species that are difficult to detect with diurnal human-based point counts, such as nocturnal and secretive bird species (Bobay et al. 2018, Knight et al. 2022).

Traditional whip-poor-will monitoring protocols have several shortcomings that ARU-based monitoring efforts have the potential to overcome (Knight et al. 2022). For example, units can be deployed at offroad sites to passively record for weeks on end. Thus, more sites can be safely monitored, and surveyed for a greater amount of time. This in turn, limits the likelihood of false negatives and potentially eliminates the need to account for imperfect detection and its associated drain on statistical power by adding additional parameters (MacKenzie et al. 2017). Another advantage to using ARUs is the ability to monitor larger spatial extents (Hill et al. 2019, Vala et al. 2020, Knight et al. 2022). Human-based monitoring efforts are often limited to small geographic extents for a multitude of reasons which include, but not limited to, funding, number of technicians, small survey windows, and weather conditions (Wilson and Watts 2008, Akresh and King 2016). ARUs help overcome these challenges as a single technician can deploy hundreds prior to the start of a survey window, capturing all days with adequate survey conditions.

Although ARUs help overcome many shortcomings of traditional monitoring protocols, the use of this technology comes with a new set of challenges. Still today, the quantity of data collected over a single season and its associated processing requires significant computing power and knowledge. Indeed, there are programs intended to make data processing easier (e.g., BirdNET by Cornell), however the ability of these programs to detect focal species varies considerably (Kahl et al. 2021, Lapp et al. 2022, Pérez-Granados 2023). Thus, creating a well-trained machine learned classifier appears to be the best option when analyzing acoustic data (Lapp et al. 2022, Maegawa et al. 2021). Post processing, there is still much debate on how ARU-generated data should be analyzed and how occupancy should be defined (Wood and Peery 2022). Given the considerable amount of recording data collected, a more conservative definition

of occupancy is likely warranted (Wood and Peery 2022). Nonetheless, ARU-generated data have significant potential to augment those collected by human observers to research and monitor whip-poor-will or many other species that produce auditory cues.

CHAPTER 2

A MULTI-REGIONAL ASSESSMENT OF EASTERN WHIP-POOR-WILL (*ANTROSTOMUS VOCIFERUS*) OCCUPANCY IN MANAGED AND UNMANAGED FORESTS USING AUTONOMOUS RECORDING UNITS

2.1 Introduction

North American birds are experiencing significant population declines, with an estimated loss of nearly three billion individuals over the past half-century (1970-2017; Rosenberg et al. 2019). Eastern forest birds and aerial insectivores are among the most strongly declining groups of birds with an estimated loss of nearly 170 million individuals (15-19%) and 160 million individuals (26-36%), respectively (Rosenberg et al. 2019). Thus, it is not surprising that species belonging to both groups are some of the most imperiled. One such species, the Eastern whip-poor-will (*Antrostomus vociferus*; hereafter whip-poor-will), is a nocturnal aerial insectivore that inhabits forests of eastern North America (Cink et al. 2020), which has experienced an estimated 64% population reduction (1.9% loss/year) from 1966-2017 (Pardieck et al. 2020). Possible factors contributing to whip-poor-will population declines include reduced food availability related to pesticides and climate change, but also habitat loss and degradation (Spiller and Dettmers 2019).

Whip-poor-wills use a variety of forest conditions and appear to be influenced by landscape context during the breeding season (Wilson and Watts 2008, Cink 2020, Vala et al. 2020). The species relies on early successional communities for foraging, however there is mixed evidence suggesting they are influenced by conditions beyond the stand level, such as the proximity of mature forests or forest ecotones for diurnal roosting and nesting (Wilson and Watts 2008, Akresh and King 2016). Forest management is known to be an important tool for creating

and maintaining stand- and landscape-scale conditions that are attractive to whip-poor-will (Wilson and Watts 2008, Farrell et al. 2017, Spiller and King 2021). A study conducted in pine dominated forests of North Carolina concluded that forest management practices targeting whip-poor-will should create and maintain patches of regenerating forest proximate to mature forests (Wilson and Watts 2008). Similarly, studies conducted in the northern portion of the species range found that sites proximate to young forest patches and shrublands had higher occupancy than sites in landscapes with only shelterwood harvests or mature unmanaged forests (Tozer et al. 2014, Grahame et al. 2021). Additionally, whip-poor-will occupancy was positively correlated with forest patch size and amount of wetland cover in the landscape, yet was unaffected by the type of agriculture present in the landscape (hay/pasture vs cropland; Vala et al. 2020). Given its ongoing population decline, broad breeding season distribution, and documented stand and landscape context dependencies, there is a need for additional studies that further inform our understanding of whip-poor-will ecology relative to forest type, management practices, and landscape land use patterns (Akresh and King 2016). Moreover, the core of the whip-poor-will's breeding distribution falls within landscapes heavily dominated by eastern deciduous forests (Cink 2020), yet to my knowledge no studies have investigated factors that influence broad scale patterns of whip-poor-will distribution within this forest type and associated landscape contexts.

Deciduous forests of the eastern US are dominated by uniformly mid-aged, closed canopy forests (80-100 years old; Shifley et al. 2014). As such, many species that require more diverse young and old forest structural conditions are in decline (Anders et al. 1998, Litvaitis 2001, Boves et al. 2013, King and Schlossberg 2014, Fiss et al. 2020). Numerous conservation efforts are underway on public and private lands to address the need for creating and sustaining

diverse forest conditions that promote the recovery of many declining forest wildlife (Bauer 2018, Nareff et al. 2019, Litvaitis et al. 2021). While assessments of focal species response to these efforts have been completed (*i.e.*, Golden-winged Warbler [*Vermivora chrysoptera*; McNeil et al. 2020], New England Cottontail [*Sylvilagus transitionalis*; Bauer 2018] and Cerulean Warbler [*Setophaga cerulea*; Nareff et al. 2019, Shaffer 2022]), an assessment of how whip-poor-will respond to these forest management efforts has not been undertaken.

The very specific nocturnal and lunar phases suitable for surveying breeding whip-poor-will has limited biologists' ability to evaluate the potential benefits of forest management across large geographic extents. Because they are nocturnal, most surveys for whip-poor-will are conducted from roads (*i.e.*, Nightjar Survey Network) to avoid the challenges of navigating through off-road areas at night. Since managed forests are poorly represented by roadside surveys, the inferences that can be made to the species response to stand-level forest management may be limited (Betts et al. 2007). This is compounded by the limited temporal window for surveying whip-poor-wills, which sing reliably on nights with minimal cloud cover with the moon at least 50% illuminated (Wilson and Watts 2006, Souza-Cole et al. 2022), a period less than a month in duration (~30 survey days). When factoring in weather conditions, the number of actual survey nights in a breeding season can decline considerably.

Recently available low-cost autonomous recording units (ARUs) can overcome monitoring challenges for nocturnal species such as the whip-poor-will (Knight et al. 2022). ARUs can be deployed prior to the onset of a survey window and left in place for the duration of a breeding season, and thus can facilitate off-road, nocturnal surveys during optimal lunar conditions at scales sufficient to capture regional variation and landscape factors that influence whip-poor-will occurrence (Hill et al. 2019). Thus, the deployment of hundreds of ARUs across

managed landscapes has significant potential to increase our understanding of whip-poor-will habitat associations, regional population trends, behavior, response to forest management, and detectability.

Forest management that targets whip-poor-will could be futile, or at least limited in effectiveness, if it is embedded in landscape contexts that are unsuitable for the species. As such, it is important to understand the extent to which stand-level forest management practices satisfy the habitat needs of whip-poor-wills and to identify landscape contexts associated with high occupancy. In this study, I developed and implemented an ARU-based regional monitoring protocol to assess whip-poor-will occupancy across various silvicultural treatments, landscape contexts, and forest types across the Appalachian Mountains and New England. The objective of this study was two-fold; 1) to assess whip-poor-will occupancy across a gradient of forest management intensity from clearcut to intact closed canopy forest, and 2) to identify within stand and landscape level factors that influence whip-poor-will site occupancy and range-wide distribution. Based on past research, I predicted factors influencing whip-poor-will occupancy would include amount of scrub-shrub landcover (with a positive influence on occupancy; +), impervious cover (-), forest area (+), and forest type (+ dry forest types) at the landscape level, and basal area (-) and small diameter woody stem density (high to intermediate amounts of saplings or shrubs) at the stand level. This study improves our understanding of whip-poor-will ecology and its response to conservation efforts that target other species like Cerulean Warbler, Golden-winged Warbler, and New England cottontail. Moreover, it serves as a case study for implementing ARU-based surveys across a large spatial extent that would not be logistically feasible using human observers.

2.2 Methods

2.2.1 Study Area

This study included survey locations in forests ranging from western North Carolina to southern Maine. I selected this geography to represent a latitudinal extent that ranges from the 'core' to the 'periphery' of the whip-poor-will's breeding range in the eastern US, in addition to encompassing a range of eastern forest types. I placed all survey locations within the Eastern Temperate Forest ecoregion or the Northern Forests ecoregion (US EPA 2006). The forest stands I monitored were all between 0-110 years post-disturbance. Tree species composition varied across survey locations; however, most study sites were predominantly comprised of deciduous tree species (e.g. *Acer* spp., *Betula* spp., *Carya* spp., and *Quercus* spp.), with few (<8%, n = 103) sites having a significant evergreen component (>10% within 250m; *Pinus* spp., *Picea* spp., and *Tsuga canadensis*). Understory vegetation composition and heights also varied across sites, ranging from low (<2 m) herbaceous vegetation, shrubs, saplings, and *Rubus* spp. to tall (>2 m), dense, regenerating closed-canopy sapling stands. Elevation at sites ranged between 6 and 1,199 meters above sea level.

2.2.2 Forest Management Treatments

Survey locations were located on public and private lands and represented a continuum of forest disturbance intensities ranging from recent regeneration and partial timber harvest to closed-canopy forest. Closed canopy forest (hereafter "unmanaged"; Figure 1a) included stands that were 21-110 years old. Basal area, tree size/spacing, and under-/mid-story structure varied among unmanaged forest stands depending on human and natural disturbance history and site conditions. Shelterwoods (Figure 1b and 1c), the primary silvicultural treatment employed when managing nesting habitat for Cerulean Warblers (Wood et al. 2013), included commercial and

non-commercial harvest that partially reduced stand basal area (ranging from 9-21 m^2/ha [40-90 ft^2/ac]) with the purpose of controlling light levels to favor the establishment of desired tree species in a regeneration layer. All shelterwoods included in this study were treated within 10 years of whip-poor-will monitoring. The interplay between residual basal area, time since treatment, site class, and browsing pressure by deer influenced the mid- and understory structure within each shelterwood stand. Lastly, overstory removals Figure 1d and 1e), the primary silvicultural treatment employed when managing for Golden-winged warblers and New England Cottontails (Bakermans et al. 2011, Bauer 2018), included commercial and non-commercial harvests that resulted in stands with 0-7 m^2/ha (0-30 ft^2/ac) of residual basal area. Stands within this treatment category were either in 1) the stand initiation stage (i.e., <10 years post-treatment) with a mix of herbaceous, shrub, saplings, and scattered residual trees, or 2) the early stem exclusion phase (i.e., 10-20 years post-treatment) with an intact canopy of saplings and shrubs (<5m tall) and minimal herbaceous component.

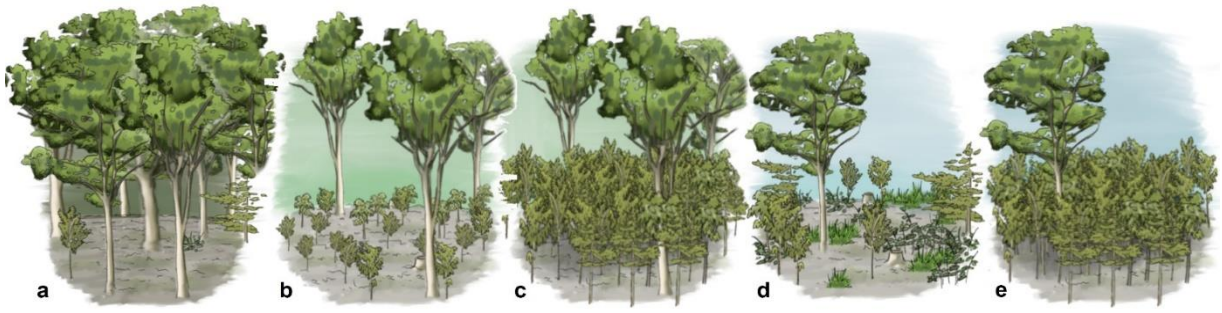

Figure 1. Graphic displaying 3 stand conditions that were monitored for Eastern Whip-poor-will at sites ranging from western North Carolina to southern Maine from April-July 2020 and 2021. a) Unmanaged; b/c) Shelterwood harvest at varying times since treatment (b more recent than c); d/e) Regeneration harvest at varying times since treatment (d more recent than e).

2.2.3 Whip-poor-will Survey Locations

I used ArcGIS Pro Version 2.9.1 (ESRI 2021) and the "Create Random Points" tool to randomly plot whip-poor-will survey locations within forest stands that represented a gradient of management intensity (Figure 1). I ensured that all survey locations were spaced a minimum of 500m apart to reduce the likelihood of double counting individual whip-poor-will and maintain their spatial independence (Ruff et al. 2020); past studies have reported whip-poor-will home range size to average 5 ha (~128m radius circle) (Cink et al. 2020, Hunt 2013). Thus, a 250m radius buffer around each survey location resulted in a 19.6 ha area that did not overlap with another survey location's buffer. Additionally, survey locations in managed stands (regeneration cuts and shelterwoods) were restricted to $\geq$50m from the treatment edges to limit edge effects. If an unmanaged site was scheduled for management at a later time, I placed survey points within the planned management boundary. Based on the above criteria, 1,265 unique survey locations were selected for monitoring (Figure 2).

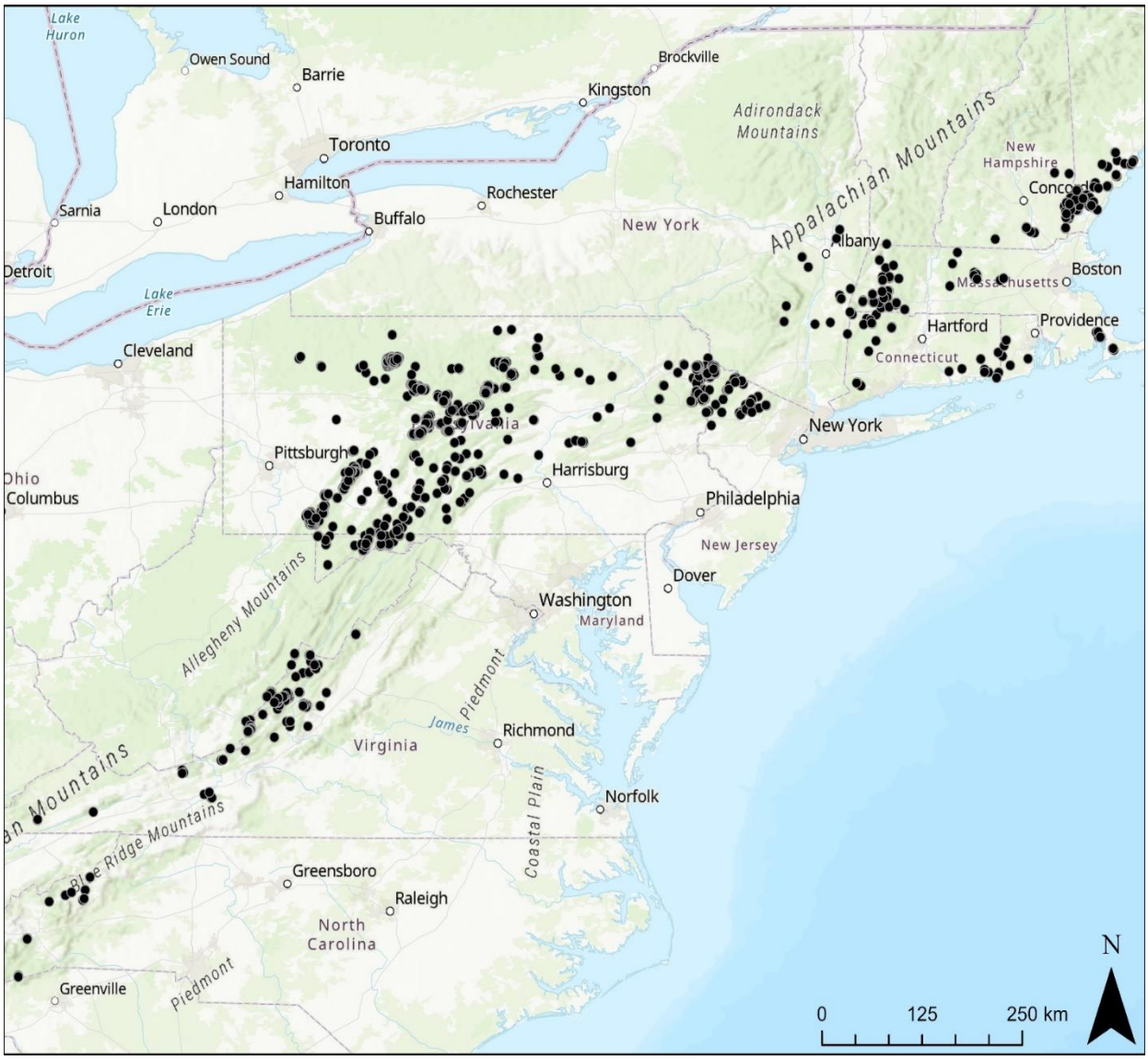

Figure 2. Locations of autonomous recording units (n=1,265) deployed to monitor Eastern Whip-poor-wills within managed and unmanaged forest communities ranging from western North Carolina to southern Maine from April-July 2020 and 2021. Note: Each private land survey location was shifted in a random direction 0-25km to preserve landowner privacy.

2.2.4 Autonomous Recording Units and Whip-poor-will Surveys

I used ARUs (AudioMoths, developed by Open Acoustic Devices) to collect audio recordings at each survey location from April-July 2020 and 2021 (Hill et al. 2019). I deployed ARUs at 294 locations in 2020 and 971 locations in 2021. Ninety-four locations were on private

forests in Pennsylvania and Maryland enrolled in Natural Resource Conservation Service's (NRCS) Regional Conservation Partnership Program to benefit Cerulean Warbler (*Setophaga cerulea*); 271 locations were in private forests enrolled in the NRCS's Working Lands For Wildlife (WLFW) program to create habitat for the Golden-winged Warbler in North Carolina, Virginia, Maryland, Pennsylvania, and New Jersey; 139 locations in private forests enrolled in WLFW to create habitat for New England Cottontail (*Sylvilagus transitionalis*) in New York, Connecticut, Rhode Island, Massachusetts, New Hampshire and Maine; and 642 locations on public forests administered by the Pennsylvania Game Commission (n= 403), Department of Conservation and Natural Resources-Bureau of State Parks (n=230), and Department of Conservation and Natural Resources-Bureau of State Forests (n=9); Virginia Department of Game and Inland Fisheries (n=9); New Jersey Division of Fish and Wildlife (n=8); Massachusetts Division of Fisheries and Wildlife (n=7), Massachusetts Department of Conservation and Recreation (n=10), New Hampshire Fish and Game (n=18), Maine Department of Inland Fisheries and Wildlife (n=2), US Forest Service (VA; n=61), and US Fish and Wildlife Service (ME; n=2), National Oceanic and Atmospheric Administration National Estuarine Research Reserve (ME; n=2).

I followed ARU setup and deployment guidance from a protocol developed by the University of Pittsburgh (Rhinehart 2019). ARUs were updated to AudioMoth firmware version 1.5.0 and equipped with a 64 gigabyte micro- Secure Digital (SD) card. Additionally, each ARU was programed to record for 2 hours after sunset (9-11 pm EST). Each ARU was placed in a quart-sized Ziploc freezer bag containing silica desiccant to absorb potential moisture. A zip tie was used to attach each ARU to a sapling (>3 cm in diameter) or tree closest to the randomly generated survey location at a height of 1.5-2m from the ground. ARUs were programed to

capture at least one of the 2-week whip-poor-will survey windows during which whip-poor-will singing behavior is elevated due to illumination of the moon delineated in the nightjar survey network protocol to enhance detections (nightjars.org, Wilson and Watts 2006). In 2020, nightjar survey windows were: a) 30 April to 14 May and b) 29 May to 13 June. In 2021, the nightjar survey windows were: a) 19 May to 2 June and b) 17 June to 1 July (nightjars.org). All ARUs were deployed during April and mid-May and recovered by early July.

2.2.5 Vegetation Sampling

I sampled site level vegetation at most survey locations immediately after ARU recovery. I used a single bi-radial vegetation survey centered on each ARU location to quantify several vegetation metrics during June 1-July 15, 2020 and 2021 (Figure 3). The vegetation survey had three main components: 1) basal area prism sweeps, 2) $1m^2$ ground cover plots, and 3) woody regeneration belt transects. Specifically, a 35-m radial transect was oriented in 2 of 3 bearings, 0°, 120°, and 240°, radiating from point center (Figure 3). At each plot's center and the end of each transect, a 10-factor wedge prism was used to estimate basal area. The three resulting estimates were averaged to produce a basal area (m^2/ha) estimate for the survey location. To assess ground cover, I sampled within three $1m^2$ plots, located at plot center and one at the end of each transect. Within each $1m^2$ plot, I recorded the presence of the following: woody seedlings (<0.5m tall), herbaceous cover, leaf litter, bare ground/rock, *Rubus* spp., and fern. Lastly, along each 35-m transect all woody stems >0.5m in height and <10cm DBH were counted within a 1x10-m wide belt transect that ran from 15-25m from point center. No site level vegetation data were collected at 127 sites (70 sites in Virginia, 53 sites in Pennsylvania, 3 sites in North

Carolina, and 1 site in Massachusetts). Thus, 1,138 of 1,265 survey locations had associated site level vegetation data.

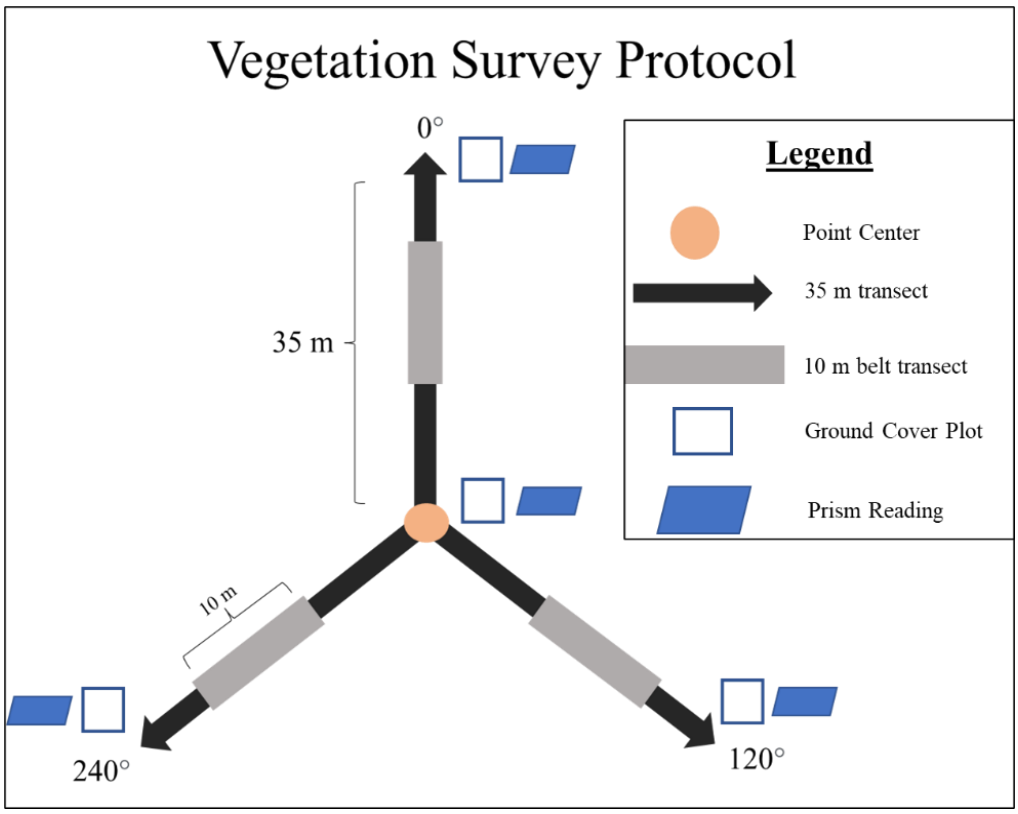

Figure 3. Layout of the vegetation surveys, including locations of 10m transects, ground cover plots, and prism readings. Observers randomly selected 2 of the 3 transect directions, thus the number of measurements was one less than those shown. The vegetation survey was completed within managed forest communities surveyed for Eastern Whip-poor-wills ranging from western North Carolina to southern Maine from April-July 2020 and 2021.

2.2.6 Landscape Assessment

I used the "summarize categorical raster" tool in ArcGIS Pro 2.9.1, and the *extract* function in the "raster" package in program R (Hijmans et al. 2015, R Core Team 2020), to characterize the local landscapes surrounding each ARU location at the following spatial extents reported to be relevant to whip-poor-will habitat associations: 250, 500, 750, 1,000, 1,250, 1,500, and 1,750m (Vala et al. 2020, Hunt 2013, Tozer et al. 2014). I used the National Land Cover Dataset (NLCD 2019; Dewitz 2021) raster to quantify the percent composition of various land

cover classes, discussed below. I used the NLCD "Urban Imperviousness" layer to quantify human development (NLCD Impervious Surface 2019; Dewitz 2021). Finally, I used the US Forest Service's Forest Inventory and Analysis dataset (USDA Forest Service 2019) to assess forest community types, and the United States Geological Survey's Global Multi-resolution Terrain Elevation Data (GMTED 2010; Danielson and Gesch 2011) to estimate elevation around each survey location.

2.2.7 Acoustical Processing

After I collected ARUs from the field, I downloaded their recordings to an external hard drive and a cloud-based server. I then split recordings into 5-second clips (e.g., 1 hour of recording = 720, 5-second clips) using python coding and ran them through an automated whip-poor-will classifier which was developed using whip-poor-will songs from recordings I collected and from Xeno-Canto (xeno-canto.org). The classifier assessed each 5-second clip for the presence of whip-poor-will song and then assigned the clip a score, with higher scores indicating increased likelihood that the clip contains whip-poor-will song. To assess the accuracy of my classifier, I listened to the three top scoring 5-sec clips from each survey location across both survey windows (3,465 clips). This process enabled me to determine a threshold score for which there were no detected false positives. After determining the threshold score of 4.3 (Figure 4), I randomly selected and listened to an additional 2,500 clips with scores >4.3 to further ensure no false positives. I assessed site occupancy by referring to the daily top scoring clip for each survey location. If the clip score was higher than the 4.3 threshold, I considered the site to be occupied for the given day. If the clip score was equal to or lower than the threshold, it was considered

unoccupied. Using these data, I was able to create a daily occurrence history for each survey location whereby "1" denoted a whip-poor-will was present and "0" denoted a non-detection.

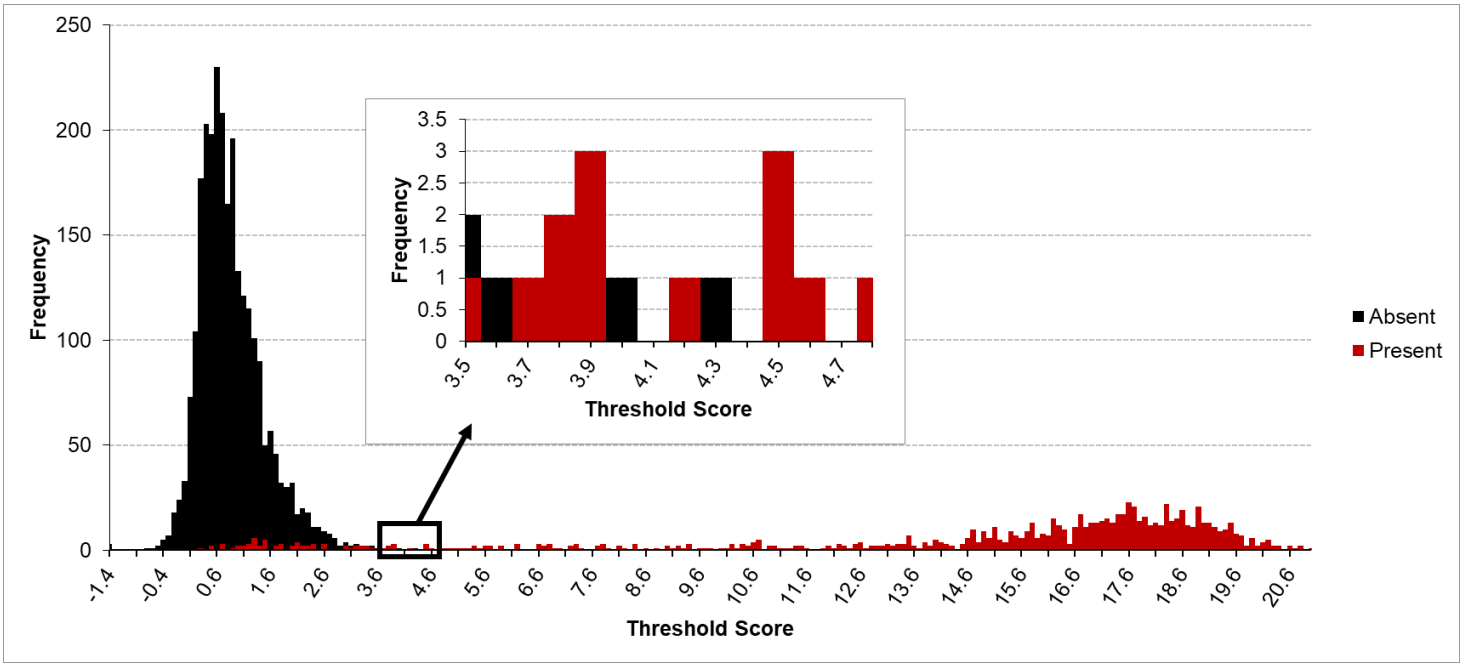

Figure 4. A) Histogram displaying the critical threshold score of 4.3 for the Eastern Whip-poor-will classifier created in collaboration with the University of Pittsburgh. The x-axis in the histogram is threshold score, and the y-axis is frequency of recording clips. In black, is the data from all clips where whip-poor-will song was absent. In red, is the data from where whip-poor-will songs were present. The inset barplot is displaying a subset of the data from histogram "A", whereby the critical threshold of 4.3 is apparent. Whip-poor-will were considered present in all clips scoring above 4.3. Clips used to create this histogram where from ARUs deployed to monitor Eastern Whip-poor-will within managed and unmanaged forest communities ranging from western North Carolina to southern Maine from April-July 2020 and 2021.

2.2.8 Data Analysis

I considered a site to be occupied by a territorial whip-poor-will if 2 detections were registered at least 10 days apart (Bibby 2000). As such, all survey locations with fewer than 10 days of recording were excluded from my analyses. I modeled whip-poor-will occupancy using Generalized Linear Models (GLM) fit to a binomial distribution with program R (R Core Team 2020). I chose to use GLM over occupancy modeling because preliminary review of my final 10-

day whip-poor-will occupancy dataset revealed that cumulative detection probability approached 1 after only four nights of recording (daily detection probability = 0.54), thus eliminating the need to account for imperfect detection in my analyses.

I created three separate model sets: regional, landscape, and site-level; and compared models within each of these sets using an information-theoretic framework (Burnham and Anderson 2002). I considered the following potential predictor variables for inclusion in my "regional" model set: days of recording, latitude, longitude, and elevation (Table 1). 'Days of recording' tested whether the duration of recording at each survey location had an influence on occupancy probability. Prior to constructing my "landscape" model set I first removed from further consideration any landscape variable that occurred at <10% of my survey locations. Then, I ran univariate models for each of the remaining landscape variables to determine the spatial extent (250, 500, 750, 1,000, 1,250, 1,500, and 1,750m radius around each survey location) that best predicted whip-poor-will occupancy. Univariate models were ranked using Akaike's Information Criterion adjusted for small sample size (AICc, Burnham and Anderson 2002), and I carried the spatial extent contained in the top model into my "landscape" model set (Willey et al. 2022). Lastly, I included quadratic terms of three variables that previous research found to influence whip-poor-will occupancy to potentially identify values that result in highest occupancy: shrub/scrub (Akresh and King 2016), wetland (Farrell et al. 2019), and barren land (Grahame et al. 2021). I considered the following potential predictor variables for inclusion in my "landscape" model set: % barren land (1,500m), % barren land^2 (1,500m), % cultivated crops (1,750m), % hay/pasture (1,250m), % shrub/scrub (1,500m), % shrub/scrub^2 (1,500m), % herbaceous (750m), % evergreen forest (1,750m), % deciduous forest (250m), % mixed forest (250m), % wetland (250m), % wetland^2 (250m), % mean imperviousness (500m), and % Oak

(1,750m), % Maple-Beech-Birch (1,500m), and % Red-White-Jack pine (250m) (Table 1). Due to logistics and lack of resources no site-level vegetation data were collected at 69 survey locations. I considered the following potential predictor variables for inclusion in my "site-level" model set: presence/absence of leaf litter, woody seedlings, herbaceous, fern, brambles, and bare ground, and basal area (m^2/ha), basal area^2 (m^2/ha), woody stem density (stems/10m^2), and woody stem density^2 (stems/10m^2) (Table 1). I decided to include quadratic terms for basal area and woody stem density because forest managers manipulate these two features most often to attain desired structural conditions, and thus I wanted to have the greatest potential for identifying optimal values for these features relative to whip-poor-will occupancy. Before creating the final regional, landscape and site-level model sets, I tested for correlation among all variables within each model set by calculating pairwise Pearson's Correlation Coefficients. Variables that had correlation coefficients >±0.6 were considered correlated (Sokal and Rohlf 1969). If two variables were correlated, I excluded the one with the least potential influence on whip-poor-will ecology from further analyses. The following terms were included in my final model sets: Regional [n=3; days of recording, latitude, and elevation); Landscape [n=13; % barren land (1,500m), % barren land^2 (1,500m), % cultivated crops (1,750m), % hay/pasture (1,250m), % shrub/scrub (1,500m), % shrub/scrub^2 (1,500m), % herbaceous (750m), % evergreen forest (1,750m), % mixed forest (250m), % wetland (250m), % wetland^2 (250m), % mean imperviousness (500m), and % Oak (1,750m)]; and Site-level [n=10; leaf litter, woody seedlings, herbaceous, fern, brambles, bare ground, basal area (m^2/ha), basal area^2 (m^2/ha), woody stem density (stems/10m^2), and woody stem density^2 (stems/10m^2)].

I created all possible combinations of variables for the regional model set, and all possible combinations of 5 or less variables within the landscape and site- level model sets using the function dredge in the package "MuMIn" (Burnham and Anderson 2002, Bartoń 2022). I restricted the number of variables the landscape and site level model-sets contained to limit model complexity and to adhere to the rules of parsimony (Burnham and Anderson 2002). Additionally, the objective of my research was to identify the most important factors influencing whip-poor-will occupancy, and thus constraining models helped identify the most influential variables within each model-set. Models within two ΔAICc of the top model were considered competing (Burnham and Anderson 2002), and variables in competing models were further investigated to determine if they significantly predicted whip-poor-will occupancy. The variables contained in top ranked models that did not have 95% confidence intervals overlapping 0 were considered significant. Lastly, to assess model fit I calculated Area Under the Curve (receiver operating characteristic; AUC) and Briers Score for each model-set (Hijmans et al. 2017, R Core Team 2020).

Table 1. Meta-data on the 3 model-sets (regional, site, and landscape) included in an analysis that examined Eastern Whip-poor-will habitat associations at 1,265 public and private land sites ranging from western North Carolina to southern Maine in 2020 and 2021. The "Removed" column indicates variables that were removed from analyses due to correlation.

Model Set	# of survey locs	Variables	Data source	Unit	Removed
Regional	1,265	Latitude	Field Collected	Decimal Degrees	Y
		Longitude	Field Collected	Decimal Degrees	
		Elevation	GMTED2010: Mean 7.5 arc-sec	Meters	
		Days surveyed	Field Collected	Days	
Landscape	1,265	Maple, Beech, Birch	USFS	%	Y
		Red, White, Jack Pine	USFS	%	Y
		Oak (Oak-Hickory & Oak-Pine)	USFS	%	
		Barren Land	NLCD: Landcover	%	
		Barren Land^2	NLCD: Landcover	%	
		Wetland (Herbaceous & Woody)	NLCD: Landcover	%	
		Wetland^2 (Herbaceous & Woody)	NLCD: Landcover	%	
		Cultivated Crops	NLCD: Landcover	%	
		Hay/Pasture	NLCD: Landcover	%	
		Scrub/shrub	NLCD: Landcover	%	
		Scrub/shrub^2	NLCD: Landcover	%	
		Herbaceous	NLCD: Landcover	%	
		Herbaceous^2	NLCD: Landcover	%	
		Evergreen Forest	NLCD: Landcover	%	
		Deciduous Forest	NLCD: Landcover	%	Y
		Mixed Forest	NLCD: Landcover	%	
		Impervious	NLCD: Imperviousness	%	
Site	1,180	Basal Area	Field Collected	m^2/ha	
		Basal Area^2	Field Collected	m^2/ha	
		Woody Stem Density	Field Collected	#/10m^2	
		Woody Stem Density^2	Field Collected	#/10m^2	
		Leaf litter	Field Collected	Presence	
		Woody	Field Collected	Presence	
		Herbaceous	Field Collected	Presence	
		Fern	Field Collected	Presence	
		Rubus spp.	Field Collected	Presence	
		Bare ground	Field Collected	Presence	

2.3 Results

Of the 1,265 locations surveyed, 76 had fewer than 10 days of recording due to ARU failure caused by bear or water damage. Thus, data from 1,189 survey locations were included in my analyses. These survey locations represented a continuum of canopy disturbance conditions (Figure 5). Based on the criteria of a) detection threshold score of >4.3 and b) at least two detections >10 days apart, 399 of 1,189 locations were considered occupied by whip-poor-will (naïve occupancy of territorial birds = 34%). Whip-poor-wills were detected at an additional 78 sites (6.2%) that had at least two whip-poor-will detections, but not ≥10 days apart, and thus were classified as 'unoccupied' for my analyses. Of the survey locations on private lands enrolled in NRCS conservation programs that had >10 days of ARU recordings and were post-treatment, I detected whip-poor-will at 33 of 129 (26%) WLFW-NEC sites, 139 of 246 (57%) WLFW-GWWA sites, and 36 of 66 (55%) RCPP-CERW sites.

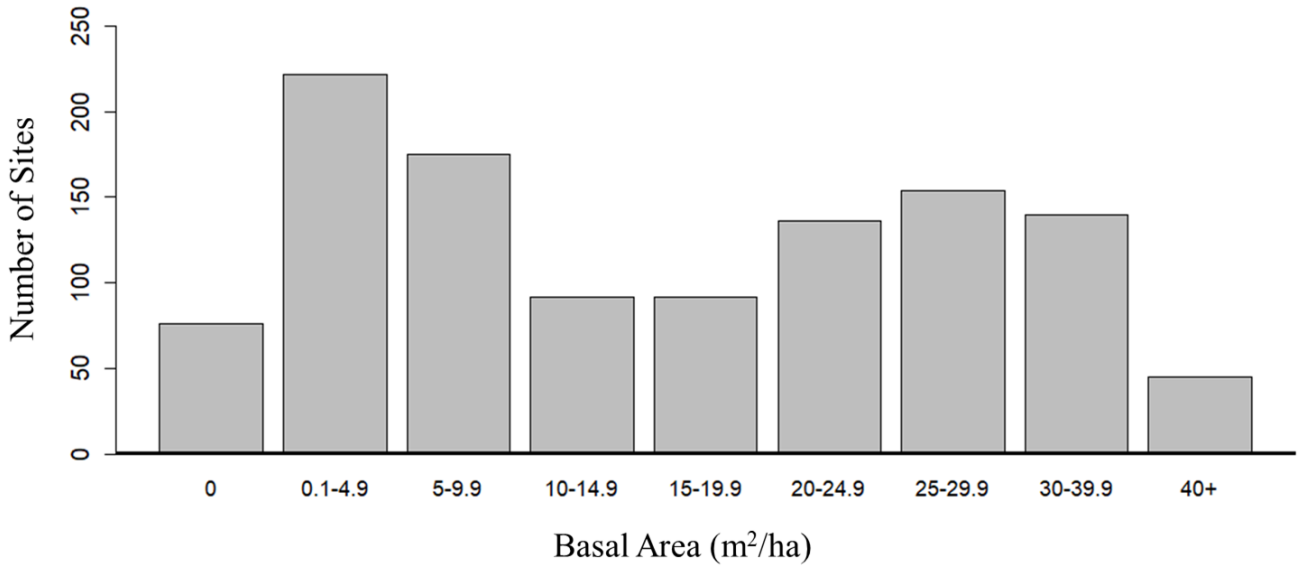

Figure 5. Barplot displaying the number of autonomous recording units deployed within each basal area range. Units were deployed to monitor Eastern Whip-poor-will within managed and unmanaged forest communities ranging from western North Carolina to southern Maine from April-July 2020 and 2021.

At the regional scale, the best approximating model contained elevation and latitude (AUC= 0.58, Brier score= 0.22; Table 2). Whip-poor-will occupancy probability decreased with elevation (β = -0.001 [95% CI: -0.002 – -0.001]; Figure 6A) and latitude (β = -0.32 [95% CI: -0.44 – -0.21]; Figure 6B). A model also with support (i.e. within 2 AIC of the top model) in the regional model set also contained days of recording, however there was no significant relationship between the number of days of recordings at a location and whip-poor-will occupancy probability (95% CI: -0.03 – 0.01).

At the landscape scale, the best approximating model contained the percentage of imperviousness, oak forest, evergreen forest cover, and scrub-shrub at different spatial extents around the survey location (AUC= 0.76, Brier score = 0.18; Table 2). Occupancy probability decreased with the amount of imperviousness cover within 500m of the survey location (β = -0.35 [95% CI: -0.56 – -0.19]; Figure 6C), and increased with the amount of oak forest (β = 3.02 [95% CI: 2.40 – 3.68]; Figure 6D) and evergreen forest cover (β = 8.40 [95% CI: 5.61 – 11.35]; Figure 6E) within 1,750m. Additionally, whip-poor-will occupancy probability exhibited a quadratic relationship with the amount of scrub-shrub cover within 1,500m, which was maximized at 9.1% (β = 82.40 [95% CI: 66.06 – 99.64], β_2 [quadratic parameter estimate] = -453.00 [95% CI: -622.80 – -309.40]; Figure 6F).

At the site-level, my top model contained basal area, woody stem density, and woody stem density^2 (AUC= 0.69, Brier score= 0.20; Table 2). Occupancy probability decreased with increasing basal area (β = -0.05 [95% CI: -0.06 – -0.04]; Figure 6G) and exhibited a quadratic relationship with woody stem density which was maximized at 8.8 stems/m^2 (87,900 stems/ha; β = 0.02 [95% CI: 0.01 – 0.03]), β2 = -0.0001 [95% CI: -0.0002 – -0.00004]; Figure 6H). *Rubus* (β = -0.28 [95% CI: -0.57 – 0.02]) and herbaceous (β = -0.40 [95% CI: -0.86 – 0.07]) presence were

both in the top site level model, however both variables had 95% CIs that overlapped zero, and thus were interpreted as weak biological effects. No competing site level models contained new variables that significantly predicted whip-poor-will occupancy. However, *Rubus* presence did become a significant predictor in some of the competing models (biologically meaningful negative relationship in 3 of 4 competing models), but was still interpreted as a weak biological effect given its inconsistency.

Table 2. AIC tables displaying top and competing models from generalized linear models within three model-sets. This analysis investigated Eastern Whip-poor-will occupancy in relation to regional, site, and landscape level variables at locations which ranged from western North Carolina to southern Maine in 2020 and 2021.

Model set	Model	K	AIC	ΔAIC	w_i
Regional	Latitude + Elevation	3	1489.00	0.00	0.53
	Latitude + Elevation + Days Surveyed	4	1489.20	0.21	0.47
Landscape	Evergreen Forest + Imperviousness + Oak Forest + Shrub Scrub + Shrub Scrub^2	6	1290.30	0.00	1.00
Site-level	Basal Area + Herbaceous + *Rubus* + Woody Stem Density + Woody Stem Density^2	6	1318.10	0.00	0.11
	Basal Area + *Rubus* + Woody Stem Density + Woody Stem Density^2	5	1318.90	0.76	0.08
	Basal Area + Fern + *Rubus* + Woody Stem Density + Woody Stem Density^2	6	1319.20	1.09	0.07
	Basal Area + Herbaceous + Woody Stem Density + Woody Stem Density^2	5	1319.50	1.36	0.06
	Basal Area + Leaf Litter + *Rubus* + Woody Stem Density + Woody Stem Density^2	6	1319.60	1.50	0.05
	Basal Area + Bare Ground + *Rubus* + Woody Stem Density + Woody Stem Density^2	6	1319.90	1.80	0.05
	Basal Area + Fern + Herbaceous + Woody Stem Density + Woody Stem Density^2	6	1319.90	1.80	0.05
	Basal Area + Herbaceous + Leaf Litter + Woody Stem Density + Woody Stem Density^2	6	1320.10	1.98	0.04

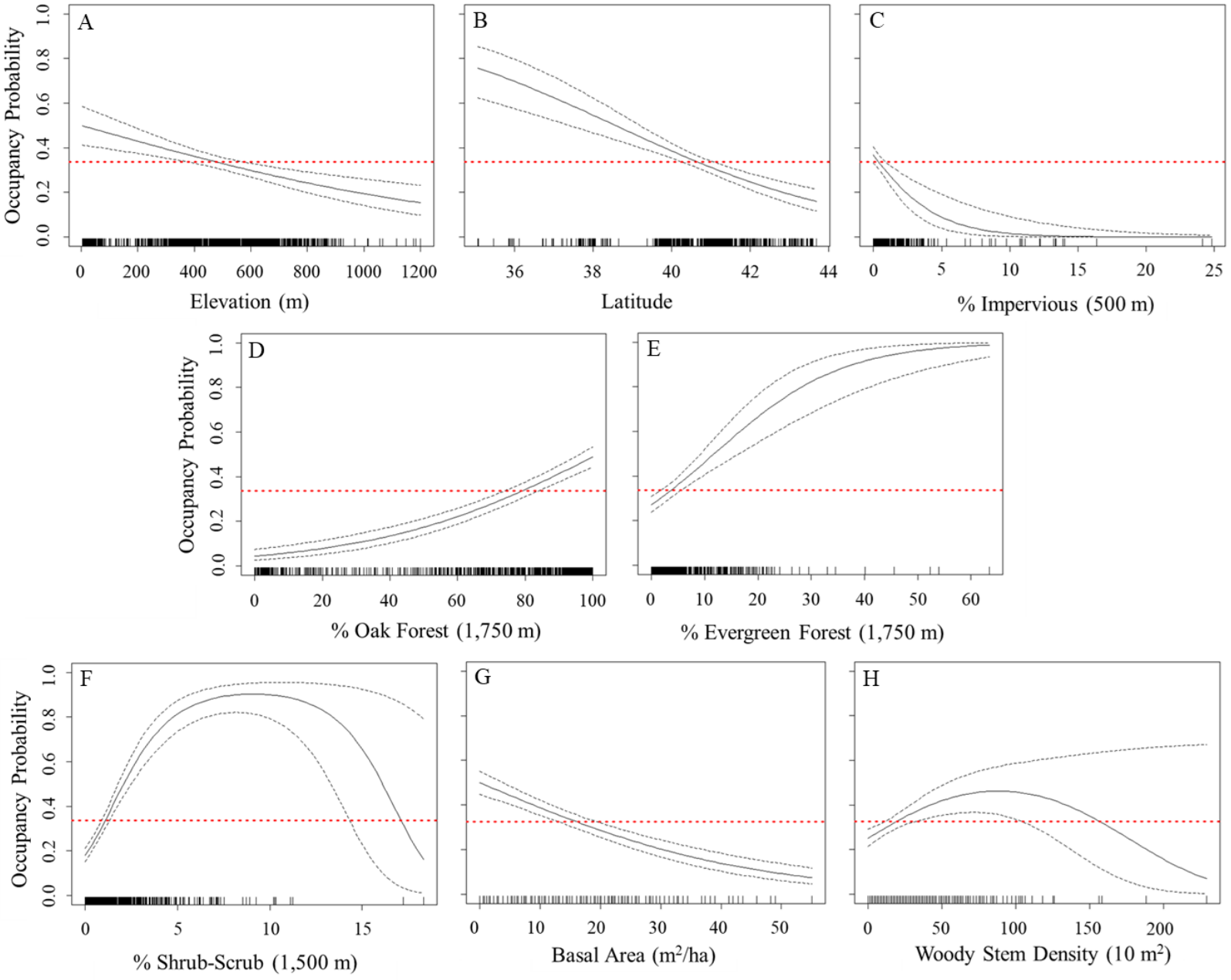

Figure 6. Plots, with 95% confidence intervals (CI), of the significant variables from the regional (A & B), landscape (C-F), and site-level (G-H) model sets in the analysis which required 2 eastern whip-poor-will detections at least 10 days apart for occupancy. Occupancy probability is on the y-axis and the predictor variable is on the x-axis in all plots. Additionally, in all plots there is a red dashed line that represents the mean occupancy probability (A-F: 34%; G-H: 33%) and along the x-axis in plots "A" through "H" are rugs that display the spread of the data.

2.4 Discussion

My analyses provide insight into whip-poor-will ecology across a large, understudied portion of the species breeding range that is dominated by deciduous forest. Unlike past research efforts that were conducted at smaller geographic extents, with more limited sample sizes, fewer nights surveyed per location, and often using road-based surveys, my ARU-based protocol allowed us to sample more than 1,250 off-road locations in forests that represented a continuum of management intensity and variation in local landscapes context (i.e., landcover, forest type, and elevation) across portions of eleven states. Moreover, my research also demonstrated the benefits conferred to whip-poor-will by conservation efforts that target other disturbance-dependent at-risk forest wildlife such as Cerulean Warbler, Golden-winged Warbler, and New England Cottontail.

Given the large geographic extent and variation in forest structure and composition represented by my sampling locations, I identified novel habitat associations for whip-poor-will and reaffirmed findings from previous studies. For example, whip-poor-will occupancy in my study, like elsewhere, was a) positively associated with forest disturbance (Wilson and Watts 2008, Tozer et al. 2014, Akresh and King 2016, Spiller and King 2022), b) influenced by factors beyond the stand scale (Brenner and Jorgensen 2020, Vala et al 2020, Souza-Cole et al. 2022), and c) positively associated with evergreen forest and oak communities (Akresh and King 2016, Cink 2020, Thompson et al. 2022). Most previous whip-poor-will research was conducted in regions dominated by pine and pine-oak communities (Garlapow 2007, Wilson and Watts 2008, Hunt 2013, Tozer 2014, Akresh and King 2016). In contrast, most of the oak forests in my study were of the oak-hickory type with very few survey locations having oak-pine forests in their surrounding landscapes. A study in New Hampshire suggested that habitat management for

whip-poor-will should be discouraged at sites dominated by hardwoods due to the species' affinity for forests with a strong pine component (Hunt 2013). My findings, however, suggest that across a large portion of the whip-poor-will breeding distribution, the species should benefit from management practices that target sites dominated by oak communities, even those with limited pine components. Given the strong negative correlation between northern hardwoods (maple-beech-birch) and oak forests (r= -0.93) in my dataset, I know that the probability of whip-poor-will occupancy has a negative relationship with the northern hardwood forest type. Thus, habitat management for whip-poor-will in landscapes dominated by northern hardwoods would likely be less effective.

The strong association whip-poor-will have with oak forests in my study may be best explained by differences in Lepidopteran prey availability among forest types. Adult Lepidopterans (moths) are a major component of whip-poor-will diets (Garlapow 2007, Souza-Cole et al. 2022). In eastern forests, it is known that deciduous trees host greater Lepidopteran species diversity than coniferous species (Powell 1980, Maier and Davis 1989, Hammond and Miller 1998) and oak communities support among the highest Lepidopteran densities (Summerville and Crist 2008, Narango et al. 2020, Tallamy 2021). Moreover, other plant species that commonly co-occur within oak-dominated forests (such as *Prunus* spp. and *Vaccinium* spp.) also support a high diversity of moth species (Wagner et al. 1995, Summerville and Crist 2008). Therefore, it is not surprising that whip-poor-will occupancy in my study was driven by the proportion of oak forest types in the local landscape, where nocturnal aerial insect prey may be most abundant (Summerville and Crist 2008, Garlapow 2007, Souza-Cole et al. 2022, Tallamy 2021). Unfortunately, oak forests of the eastern US are experiencing unprecedented challenges (Knoot et al 2010, Shifley et al. 2014). Insect pests (e.g., spongy moth [*Lymantria dispar*]; Morin

and Liebhold 2016), intense browsing by white-tailed deer (*Odocoileus virginianus;* Rooney and Waller 2003, Parker et al. 2020) and anthropogenic factors (e.g., high grading and fire suppression; Curtze et al. 2022, Nowacki and Abrams 2008) are major contributors to the degradation and mesophication of oak forests (Shifley et al. 2014, Dey 2014, Nowacki and Abrams 2008). Conservation of viable whip-poor-will populations across my study regions will be undoubtably linked to management decisions that promote the resilience and recovery of oak-dominated communities.

Beyond forest type, my analyses demonstrate how within-stand and landscape scale forest structure also influence whip-poor-will occupancy. Specifically, the amount of shrub-scrub cover (i.e., young forest) in the local landscape, as well as basal area and woody stem density at the site-level, were important predictors of whip-poor-will occupancy and represent characteristics driven by forest disturbances. Whip-poor-will require young forest for foraging (Cink 2020, Mills 1986), roosting, and nesting (Akresh and King 2016, Grahame et al. 2021, Spiller 2019). Additionally, the species can be associated with older forests and ecotones during the breeding season (Wilson and Watts 2008, Hunt 2013, Akresh and King 2016). Given the species use of both young and older forests, I postulated that there would be an area of shrub-scrub cover at which whip-poor-will occupancy probability would be maximized. Indeed, my results indicate a quadratic relationship between whip-poor-will occupancy and shrub-scrub cover, that was maximized at 9.1% (87.5 ha) within 1,500m of a survey location (Figure 4F). However, this estimated value is likely lower than the true value at which whip-poor-will occupancy is maximized because the NLCD data layer I used is known to underestimate shrub-scrub cover (Bulluck et al. 2022). Nonetheless, the quadratic relationship identified in my study demonstrates that while breeding whip-poor-will use young forests, the availability of ample

amounts of older forests and associated edge habitats is an important characteristic of sites occupied by the species in my study area. This finding corroborates with those from studies elsewhere (Wilson and Watts 2008, Hunt 2013, Spiller and King 2021), and highlights how long-term forest management planning that creates and perpetuates landscapes with a continuum of diverse forest successional stages will be needed to recover and sustain whip-poorwill populations.

Site-level vegetation structure also influenced whip-poorwill occupancy probability in my study which further provides evidence of the reliance whip-poor-will populations have on forest disturbance. Specifically, occupancy was highest at sites with lower basal area and moderate woody stem densities. Basal area is a measure of the total cross-sectional area occupied by tree stems (m^2/ha) and is usually positively correlated with canopy cover (Cade 1997, Ashton and Kelty 2018). Many practices implemented by forest managers modify basal area to influence light levels, which in turn, drives understory stem density and species composition (Oliver and Larson 1996, Ashton and Kelty 2018). My analysis found whip-poor-will occupancy probability was highest at sites with a basal area of 0 m^2/ha and dropped below mean occupancy at 15 m^2/ha. While my analysis indicates a negative linear relationship between occupancy and basal area, a study in New York reported a quadratic relationship for which whip-poor-will occupancy peaked at 13.8 m^2/ha (Spiller and King 2021). Regardless, the basal area values associated with high whip-poor-will occupancy in both studies are much lower than those of typical mature eastern deciduous forests (i.e., 27±1 [SE] m^2/ha; Boves et al 2013). Sites with low basal area in my study were usually the result of forest management practices that leave varying amounts of residual canopy trees to promote the establishment and growth of woody regeneration, which I also found to be an important predictor of whip-poor-will occupancy. Indeed, I found whip-poor-will

occupancy exhibited a quadratic relationship with small diameter woody stem density that peaked at 8.8 stems/m^2. While previous research has reported whip-poor-will nest associations with dense woody understories (Akresh and King 2016), it has also been postulated that the species does not occupy stands with overly dense woody understories due to reduced foraging ability (Mills 1986, Garlapow 2007, Spiller et al. 2022). Ultimately, my site level model corroborates findings from more localized studies that suggested whip-poor-will require open canopied forests with variation in understory density to balance roosting, nesting, and foraging requirements.

My work also echoes the findings of past research regrading a negative relationship with whip-poor-will occupancy probability and impervious cover (English et al. 2016, Vala et al. 2020, Souza-Cole et al. 2022). At 2.5% impervious cover within 500m of a survey location, occupancy probability fell below the mean (34%) and approached zero at 10% imperviousness (7.8 ha within 500m). This result is similar to that from a study in Illinois that found whip-poor-will occupancy was nearly zero when 1% medium/high intensity development occurred within 5km of a survey location (Souza-Cole et al. 2022). Additionally, findings from a study in Canada reported a weak negative relationship between whip-poor-will occupancy and urban landcover (Vala et al. 2020). Impervious cover is heavily correlated with light pollution (Sutton 2003, Bennie et al. 2014), which is known to have negative effects on insect populations (Vogel 2017, Piano et al. 2019). Additionally, it has been suggested that light pollution may be a significant cause of decline to the European nightjar (*Caprimulgus europaeus*), as it potentially negatively affects the species' ability to forage (Sierro and Erhardt 2019). Given these two species are closely related, it is reasonable to postulate that whip-poor-will may be similarly affected by light pollution. Further research that assesses whip-poor-will presence, foraging behavior, and

prey availability in landscapes with a gradient of imperviousness cover would be worthwhile.

Beyond gaining new insight into factors that influence whip-poor-will occupancy, my study also provides a powerful example of the tremendous potential passive acoustical methods have for large scale wildlife monitoring efforts. My use of ARUs and a machine learned classifier proved to be an effective strategy to assess occupancy of a nocturnally active species at more than 1,200 off-road locations, and to my knowledge is the single largest attempt to use passive acoustical surveys to monitor wildlife. ARU-based monitoring efforts are very enticing to researchers due to their cost effectiveness and the quantity of recording data they can collect (Sugai et al. 2019). My study demonstrates how ARUs can be used to survey several hundred sampling locations nightly across a large spatial extent in a single breeding season with minimal personnel. The number of nights of recording did not predict occupancy probability in my study, which is likely due to my high-performing machine learned classifier coupled with the high detectability of whip-poor-will (0.54 after one night of sampling and 0.996 after 10 nights). Because detection probability was so high in my study, I was able to use an analytical approach that did not account for imperfect detection. Other ARU-based survey efforts that target species with low detectability have used occupancy analyses that account for imperfect detection to gain conservation insight (i.e., Campos-Cerqueira and Aide 2016, Appel et al. 2023). Indeed, conservation scientists that desire to implement ARU-based monitoring should carefully consider a species' detectability and rigorously assess machine-leaned classifier performance when designing sampling protocols and selecting subsequent analyses.

While there are certainly many benefits associated with ARU-based monitoring programs, there are also many logistical challenges of which users should be aware. For example, organization, meticulous record keeping, and attention to detail are critical during mass

ARU deployment and recovery efforts to ensure audio data from each ARU are correctly paired with their deployment location. Following the retrieval of ARUs from the field, users need to download and organize substantial amounts of audio recording data often measured in terabytes, which requires appropriate allocation of staff time to download and organize data and a thoughtful strategy for long-term storage and analysis. The most significant challenges perhaps are associated with processing the recording data into usable information. First, the creation of a highly functioning machine learned classifier is critical for maximizing the use of copious amounts of recording data ARUs collect. Poor classifier performance can result in inaccurate detection histories and in turn erroneous inferences on species-habitat associations. Ultimately, it is relatively easy to quickly deploy hundreds of ARUs and amass a considerable quantity of recording data in a single field season, but users should be aware of the time it can take to rigorously process those recordings into reliable species occurrence data. Indeed, unlike observer-based point counts where collected data are readily available for analysis at the end of a field season, the time it takes to convert audio recordings into usable data can be lengthy depending on the amount of data collected, the questions sought to be answered, number of target species, existence of automated classifiers for each target species, and available computing power. Thus, professionals who depend on the timely delivery of survey results to help guide conservation efforts should be aware of potential delays associated with ARU data processing. Nonetheless, the various challenges associated with ARU-based surveys can be mitigated through careful planning, detailed record keeping, and clear communication with data end-users about potential delays in obtaining survey results due to organizing and processing large amounts of recording data.

2.4.1 Conservation Implications

My findings reveal that in regions dominated by eastern deciduous forest whip-poor-will occupancy was highest at sites that were recently managed using sustainable timber harvest practices that resulted in moderate to severe canopy disturbance. Implementing management practices that reduce tree basal area to <15 m^2/ha and create small-diameter woody stem densities between 3-15 stems/m^2 at low elevation sites (<475 m) in local landscapes dominated by oak forests and having limited impervious cover (<2.5%) should maximize the probability of whip-poor-will occupancy. Management that targets whip-poor-will should also aim to create and sustain a diversity of forest age classes (including at least 10% young forest conditions within 1,500 m) while also retaining and enhancing evergreen cover (4-25% within 1,750 m) to meet the species roosting, nesting, and foraging needs. It is imperative that land managers implement pre- and post-harvest practices, that create conditions best suited for whip-poor-will and perpetuate the persistence of oak forest types long into the future (i.e., Dey 2014).

Fortunately, there are silvicultural practices that can achieve the site-level and landscape conditions my study found to be important to whip-poor-will occupancy. One method is a shelterwood system which is an even-aged prescription often used to regenerate oak forests (Loftis 1990). A shelterwood system involves multiple (2-3) entries into a stand to gradually reduce canopy cover through a series of partial harvests, and therefore manipulate light conditions to levels that promote the establishment and growth of desired shade tolerant to mid-tolerant species (e.g., oaks) (Loftis 1990, Ashton and Kelty 2018). Once advanced regeneration of desired species becomes established, a final overstory removal harvest is implemented which leaves a residual basal area between 0-7 m^2/ha. As such, forest stands treated with shelterwood harvests achieve basal area and small diameter woody stem density values, in addition to the

species composition that were important to whip-poor-will occupancy in my study. Moreover, the final removal harvest of a shelterwood system contributes toward the 10% young forest age class within a local landscape that my study also revealed to be important to whip-poor-will occupancy. However, it should be noted that because the goal of a shelterwood system is to regenerate a stand into a mature forest, the young forest conditions created by a shelterwood system are ephemeral. Thus, planning and implementing a complex of several shelterwood systems in varying phases across a landscape ensures both the health and perpetuity of oak forests (Dey 2014, Ashton and Kelty 2018), and increases age-class diversity and structural heterogeneity that is important to whip-poor-will and many other wildlife (Wilson and Watts 2008, Sheehan et al. 2014, Silvis et al. 2016). Restoration of open forest ecosystems is also a management strategy that can be used to create the stand and landscape conditions attractive to whip-poor-wills. Open forest conditions in the form of savannahs and woodlands dominated by oak and pine are estimated to have historically covered more than 100 million hectares of eastern North America (Hanberry et al. 2020). These communities are characterized by having an open structure with variable basal areas between 5-30m^2/ha and understories comprised of both herbaceous and woody stems, the proportions of which depend upon the frequency of fire (Burger et al. 2018, Hanberry et al. 2018, Hanberry et al. 2020). The restoration and maintenance of open forest ecosystems is perhaps the most viable conservation strategy for creating whip-poor-will breeding habitat when overall forest management objectives are ecologically driven. Ultimately, the site and landscape conditions important to whip-poor-will occupancy that were identified in my study are attainable through conservation practices that are grounded in responsible forest management.

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