HABITAT ASSOCIATIONS AND RESOURCE SELECTION OF CHUCK-WILL'S-WIDOWS (*ANTROSTOMUS CAROLINENSIS*) ACROSS THE ANNUAL CYCLE

by

NATALIE RAMOS

(Under the Direction of Clark Rushing)

ABSTRACT

Chuck-will's-widows (*Antrostomus carolinensis*), the largest North American aerial insectivore, have declined by 1.6% annually since 1970. Habitat loss and pesticide use likely drive these declines, though the primary threats to the species are poorly understood. As long-distance migratory birds, Chuck-will's-widows face threats throughout the annual cycle. Understanding their habitat needs and how they respond to habitat management is essential for conservation. Currently, tracking studies on this species are lacking, and their migration phenology remains poorly described. Detailed information about habitat requirements across the annual cycle and responses to management practices are also needed. This project aimed to fill knowledge gaps on Chuck-will's-widow migration patterns and habitat associations across the annual cycle. In Chapter 2, I examined the effect of land cover and habitat management on breeding density, revealing a positive effect of landscape heterogeneity and prescribed fire on breeding density. In Chapter 3, I used GPS tracking data from one male Chuck-will's-widow to provide the first data on migration behavior and non-breeding habitat selection for this species, revealing preferences for forested habitats in proximity to more open habitats throughout the annual cycle. Continued tracking efforts are needed to inform habitat management and conservation strategies.

INDEX WORDS: Chuck-will's-widow, *Antrostomus carolinensis*, Caprimulgidae, Aerial Insectivores, Resource Selection Function, Migration, Migratory Connectivity, Habitat Selection, Distance sampling, Prescribed fire, Habitat Management

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DEDICATION

This thesis is dedicated to my remarkable mommy, Martha. Your unwavering belief in my abilities has been a beacon of strength and motivation throughout this journey. In moments of uncertainty, you have seamlessly provided words of encouragement and wisdom that have pushed me forward. Your support has been an immeasurable gift, shaping every step of this endeavor. To my best friend, my pal, my good time boy, Chase, I am at a loss for words to express what your support has meant to me. Through the late nights, the moments of doubt, and the triumphs, your presence in my life has brought me so much security, and I will never be able to thank you enough. To my friends and family, your boundless love, encouragement, and understanding has carried me through every obstacle. This achievement would not have been possible with your steadfast support and belief in me, and I am deeply grateful for every one of you.

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INTRODUCTION

Introduction

Migratory bird species across North America are experiencing rapid population declines, resulting in a collective loss of nearly 3 billion birds and marking a 29% decrease in abundance since 1970 (Rosenberg et al. 2019; Ziolkowski et al. 2023). The decline of migratory bird populations represents a critical ecological issue, with significant implications for biodiversity and ecosystem health (Bauer and Hoye 2014). Migrants embark on journeys spanning thousands of kilometers, often navigating across multiple countries, exposing individuals to threats that include habitat loss and degradation, prey decline, climate change, and predation (Cox 2010). Across their annual cycle, migratory birds inhabit diverse geographic regions, experiencing variation in resource availability and land use patterns. This variation makes it particularly challenging to understand migration patterns and the drivers of migratory bird population declines.

During their travels between breeding, migration, and wintering grounds, migratory birds encounter various hazards, including habitat destruction, increased predation, and adverse weather conditions, with the degree of risk varying across seasons (Newton 2004). Species that depend on a limited number of specific habitats for migration, breeding, or wintering are particularly vulnerable to overexploitation, disturbance, and habitat loss or destruction (Wilcove and Wikelski 2008). The loss of habitat can result in smaller territories and increased breeding densities, reducing reproductive success through factors such as competition, territory disputes, or heightened susceptibility to diseases, ultimately leading to a decrease in the overall population (Lambert and Hannon 2000). Furthermore, long-distance migrants demonstrate less flexibility in their migration timing than short-distance migrants, indicating that they may struggle to synchronize their migration as effectively with environmental conditions, which can impact survival and reproductive success (Møller et al. 2008). Despite the need for conservation efforts, 91% of migratory bird species lack adequate protected area coverage for at least one part of their annual cycle, with only 10% of full migrant species having sufficient protection across all stages of migration (Runge et al. 2015). Developing accurate models that predict ecological responses to landscape changes across various geographical areas and seasons requires a comprehensive understanding of the factors influencing migration behavior throughout their annual cycle (Webster et al. 2002).

Conservation efforts for migratory bird species rely on understanding how habitat characteristics, such as suitability and resource availability, influence population dynamics across the annual cycle, with threats and drivers of decline varying by season and geographic location (Alerstam 2003; Sherry and Holmes 1995; Sheehy et al. 2010). Anthropogenic impacts on natural systems are of immediate concern to all seasonal migrants, and evidence suggests that managing habitats throughout the annual cycle is critical for maintaining positive population growth (Calvert et al. 2009). Changes in habitat conditions are strongly associated with population trends among neotropical migrant bird species (Robbins et al. 1989). These birds face threats at multiple spatial scales throughout the annual cycle, which also contribute to their population declines (Faaborg et al. 2010). The multiple threats across different spatial scales highlight the need for comprehensive conservation strategies that address threats across their entire annual cycle.

Aerial insectivores, a group of birds that includes swifts, swallows, flycatchers, and nightjars, are among the fastest-declining avian guilds across North America, experiencing a decline of approximately 30% since 1970 (Rosenberg et al. 2019). The rates of decline vary among species within this group and across various regions, highlighting the complexity of factors influencing population trends (Michel et al. 2015). Widespread declines among aerial insectivores suggest a link between declining insect populations and the decline of insectivorous birds (Tallamy and Shriver 2021). Overuse of non-selective pesticides driving prey declines (Møller 2019) and loss and degradation of suitable habitat are hypothesized to contribute to the decimation of aerial insectivore populations (Straight and Cooper 2020). Variation in habitat associations and resource use throughout the annual cycle remains poorly understood for many aerial insectivores, complicating the identification of specific threats and focal areas for conservation interventions such as habitat management.

Nightjars (family Caprimulgidae), a family of nocturnal and crepuscular aerial insectivores known for their cryptic plumage and elusive behavior, present challenges in studying and tracking efforts. Little is known on the migratory connectivity, range, and population status of many nightjar species (Noble-Dalton and Knight 2020). Research efforts have documented the habitat requirements of nightjars to better understand their ecology and inform conservation strategies. For example, European Nightjars (*Caprimulgus europaeu*) require diverse habitat structures, such as pre-thicket stage forests and grazed grass-health areas, to support nesting and foraging activities (Sharps 2015), possibly because moonlight can penetrate areas with more open canopy, potentially facilitating foraging for insects back-lit by the moonlight (Wilson and Watts 2008). Eastern Whip-poor-wills (*Antrostomus vociferus*) select nest sites in proximity to deciduous trees and roost in shrubby clearings, emphasizing the importance of maintaining suitable early successional habitats (Akresh and King 2016). The strong site fidelity of Common Nighthawks (*Chordeiles minor*) to breeding sites suggest vulnerability to local events and broader potential population threats, emphasizing the need to understand their migratory connectivity across various periods for effective conservation strategies (Ng et al. 2018).

Chuck-will's-widows (*Antrostomus carolinensis*) are an understudied, declining species of nightjar native to the southeastern United States. Chuck-will's-widows are the largest North American nocturnal aerial insectivore, and during the breeding season they are generally found in open deciduous, coniferous, and mixed woodlands, often near forest edges (Straight and Cooper 2000). They spend most of the day roosting on horizontal tree limbs or on the ground where camouflage makes detection difficult. Though Chuck-will's-widows may occasionally eat small bats and birds, their diet primarily consists of nocturnal flying insects, mainly from the order Lepidoptera (moths and butterflies; Owre 1967). Long-term monitoring data indicates that Chuck-will's-widow populations have declined by at least 69% since 1966 (Hayes et al. 2010), though the causes of these declines are not well understood. Their nocturnal and secretive nature have made it difficult to study the species, limiting answers to important habitat questions (Straight and Cooper 2020). Information on nesting ecology, habitat selection, and space use is needed to understand breeding habitat requirements for this species. Research has indicated that Chuck-will's-widow abundance may increase in heterogeneous landscapes and be positively linked to burning and thinning of forests. Fire can increase insect prey abundance, as adult moths prefer to lay their eggs on regrowth provided after burning, while still retaining adequate dense cover for nesting and roosting (Thompson et al. 2022). However, the effects of landscape composition on Chuck-will's-widow density and space use remain poorly understood, especially outside of the breeding season. Quantitative monitoring data are necessary to understand responses to landscape characteristics, which can be used to inform management decisions to maximize Chuck-will's-widow populations (Hudson et al. 2017).

The primary objectives of this project were to fill knowledge gaps regarding Chuck-will's-widow breeding season habitat use, full annual cycle roost site selection, and migration phenology to inform decisions about how best to manage habitat for Chuck-will's-widows. In Chapter 2, I quantified the effects of landscape characteristics (e.g., habitat type) and prescribed fire on Chuck-will's-widow breeding density. I hypothesized that breeding Chuck-will's-widows would select forested areas adjacent to open habitats, where prey availability is predicted to be higher, thereby offering suitable foraging grounds. I also predicted a higher abundance of Chuck-will's-widows in recently burned forest landscapes, because such areas typically support higher prey densities due to the regenerative effects of fire (Koltz 2018; Swengel 2001). In chapter 3, I quantified seasonal variation in roost site selection throughout the annual cycle using GPS tracking data. By analyzing roost site selection across breeding, post-breeding, and stationary non-breeding periods, I sought to determine potential variation in habitat selection during different periods of the year. I predicted that Chuck-will's-widows would occupy forested landscapes while avoiding developed areas. Additionally, considering the habitat preferences of other nightjar species, known for selecting diverse environments facilitating foraging opportunities, I predicted Chuck-will's-widows would choose locations near landscapes with abundant food resources. Given the consistent roost site selection patterns observed in closely related nightjar species throughout the annual cycle, I predicted that Chuck-will's-widows would exhibit similar habitat preferences across all stages of their annual cycle.

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CHAPTER 2

HABITAT ASSOCIATIONS AND ABUNDANCE OF CHUCK-WILL'S-WIDOWS (*ANTROSTOMUS CAROLINENSIS*) IN COASTAL GEORGIA

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Abstract

Chuck-will's-widows (*Antrostomus carolinensis*) are the largest North American nocturnal aerial insectivore. Although specific threats are not entirely understood, habitat loss and pesticide use are the most likely drivers of this species' decline. Habitat management practices that reduce woody understory vegetation, such as prescribed fire, may provide breeding habitat for Chuck-will's-widows. The primary objectives of this project were to fill knowledge gaps regarding breeding density and habitat selection to inform decisions about how best to manage breeding habitats for Chuck-will's-widows. This work was conducted at three sites in coastal Georgia, characterized by a variety of intact terrestrial habitats that support Chuck-will's-widow breeding populations. Data from point count surveys were used to quantify Chuck-will's-widow abundance as a function of habitat type and fire history using hierarchical distance sampling models. Our findings reveal a significant increase in Chuck-will's-widow density 1-2 years post-burn, followed by a decline, indicating that prescribed fire initially creates favorable conditions for the species, but these benefits diminish over time.

Introduction

Aerial insectivores are experiencing greater declines than any other group of birds in North America, with over 60% of species currently in decline (Rosenberg et al. 2019). Once abundant across the continent, this taxonomically diverse group, which includes swifts, swallows, flycatchers, and nightjars, feeds mainly on flying insects that are captured during flight. The decline of aerial insectivore populations has raised concerns regarding potential shifts in food availability and the underlying drivers of these declines (English et al. 2018). Proposed hypotheses to explain this decline include decreases in insect prey availability, habitat loss, and the impacts of climate change (Nebel 2010; Straight and Cooper 2020). The lack of knowledge of habitat associations and response to habitat management practices complicates efforts to identify the primary drivers behind the decline of many aerial insectivores. This challenge is true for many species of aerial insectivores belonging to the nightjar family (family Caprimulgidae), which are elusive and hard to observe for most of the year. However, recent research efforts on this group, which includes multiple species of conservation concern in North America, have begun to shed light on their habitat needs during the breeding season, as well as their response to active conservation efforts.

Previous studies have highlighted the importance of active management in maintaining nocturnal insect biodiversity to maximize nightjar populations, (Thompson et al. 2022). Research on the dietary preferences of the Eastern Whip-poor-will (*Antrostomus vociferus*) revealed 92% of samples contained moth DNA sequences, indicating moths are likely their primary prey (Souza-Cole et al. 2022). This finding suggests a positive correlation with Whip-poor-will abundance and insect availability, emphasizing the connection between prey availability and bird population dynamics. Observations from breeding point count surveys of Whip-poor-wills indicate higher abundances in areas where clearcutting has created open areas within forests. These open areas improve foraging conditions by providing better visibility and access to flying insects (Tozer 2014). Understanding the combined effects of habitat and landscape regeneration practices on nightjars could lead to effective management strategies for conservation of insect biodiversity and nightjar populations.

The Chuck-will's-widow (*Antrostomus carolinensis*) is a nocturnal aerial insectivore belonging to the nightjar family that has experienced significant declines across its range (Straight and Cooper 2020; Ziolkowski et al. 2023). Despite concern about the rate of decline in this species, our understanding of the Chuck-will's-widow ecology, including detailed aspects of distribution, density, and habitat selection, remains limited. This limitation is attributed, in part, to the species' cryptic behavior, characterized by their nocturnal activity patterns, highly effective camouflage, and tendency to exhibit lower activity levels during the day, all of which pose challenges to studying the species. During the breeding season, many aerial insectivores, including Chuck-will's-widows, Whip-poor-wills, and Common Nighthawks (*Chordeiles minor*), have demonstrated a preference for restored forest stands including areas that are regularly subject to prescribed fire and manual thinning of trees (Farrel et al. 2017; Thompson et al. 2022). However, one study on the effects of landscape characteristics on Chuck-will's-widow density showed no difference between the number of Chuck-will's-widows detected in pastureland, suburban, and forested areas (Cooper 1981). Another study demonstrated that Chuck-will's-widows were present in various habitats including rural residential areas and forested landscapes (Hayes et al. 2010). Although these studies provide some insights, more research is needed to refine our understanding of habitat associations and abundance of Chuck-will's-widows, particularly across a broader range of habitat types and geographical areas.

Rigorous monitoring data are needed to understand the response of Chuck-will's-widow populations to landscape and environmental processes, including human-induced habitat alteration. A better understanding of these responses will allow management decisions to more effectively target Chuck-will's-widow habitat requirements to increase conservation success (Hudson et al. 2017).

My study aimed to quantify the effects of land cover characteristics and prescribed fire on habitat selection of breeding Chuck-will's-widows in coastal Georgia. Based on previous research, I hypothesized that breeding Chuck-will's-widows would maximize foraging opportunities by selecting forested areas near open habitats, which have higher prey availability than areas near development. I also hypothesized that prescribed fire creates open habitats preferred by Chuck-will's-widows and therefore predicted that breeding density would be higher in recently burned areas than unburned or distantly burned areas.

Methods

Study Sites

During the summers of 2022 and 2023, I conducted point count surveys for breeding Chuck-will's-widows at three sites in coastal Georgia (Fig. 1). Little St. Simons Island is a privately-owned barrier island located in Glynn County, Georgia. The island is located at the mouth of the Altamaha River, edging the Atlantic Ocean on the east and the Hampton River along the south and west end. Measuring approximately 10-km x 5-km, the island is a mostly undeveloped landscape of over 4500 hectares, consisting of approximately 3000 hectares of salt marshes and 1500 hectares of upland habitats (mature maritime forests, shrub/scrub communities, and maritime grasslands). Salt marsh habitats consist primarily of smooth cordgrass (*Spartina alternaflora*) and saltgrass (*Distichlis spicata*). Maritime forests on the island are dominated by live oak (*Quercus virginiana*) and laurel oak (*Quercus laurifolia*). Maritime shrub communities on the island are dominated by wax myrtles (*Myrica cerifera*) and saw palmettos (*Serenoa repens*). Maritime grassland habitats, characterized by lush muhly grasses (*Muhlenbergia capillaris*), are actively planted to help restore this rare and endangered ecosystem. For several decades, prescribed burning has been applied to 120 hectares of maritime grasslands on the island as a management technique to maintain open areas and prevent the encroachment of woody vegetation. Patches of varying size are burned in the maritime grasslands on a 4-year rotation. Altama Plantation Wildlife Management Area (hereafter Altama WMA) is a 1600-hectare property located in northwest Glynn County, Georgia, approximately 25-km inland from the Little St. Simons study site. Management decisions on the property have resulted in the landscape being dominated by approximately 620 hectares of tidal freshwater floodplain forest, 120 hectares of upland hardwood forest, and a 600-hectare area of pine stands under intense silviculture management. The Georgia Department of Natural Resources actively manages the property through practices including prescribed fire, logging, and thinning to restore longleaf pine (*Pinus palustris*), which currently encompasses one-fourth of the property. Other portions of Altama WMA are composed of planted loblolly (*Pinus taeda*) and slash pine (*Pinus elliottii*), which undergo regular thinning as part of restoration efforts. Annual prescribed burns promote a nutrient-rich understory of wiregrass (*Aristida stricta*) and saw palmettos (*Serenoa repens*). Harris Neck National Wildlife Refuge is a 1200-hectare public access refuge located in McIntosh County, Georgia. The refuge consists of six man-made freshwater impoundments, 300 hectares of coastal plain maritime forest and woodlands of live oak (*Quercus virginiana*), cedar (*Cedrus spp.*) and cabbage palmetto (*Sabal palmetto*), 200 hectares of planted and regenerated loblolly (*Pinus taeda*) and sweetgum (*Liquidambar styraciflua*) pine stands and is surrounded by 430 hectares of salt marshes and tidal creeks, with 24 kilometers of paved roads and trails.

Point count surveys

I conducted point count surveys on Little St. Simons Island at 28 sites (Fig. 1), visiting each site three times (once per month) during the 2022 breeding season (May- July) and twice during the 2023 breeding season (May and June). I also conducted point counts at 24 sites at Altama WMA and 16 sites at Harris Neck, which I visited twice during 2023 (May and June). At each study site, point count locations were randomly stratified within land cover types and spaced apart by at least 500 meters to avoid overlap, consistent with the 250-meter radius buffer used for the point count surveys conducted during sampling. Chuck-will's-widows are the most vocal within 1-2 after sunset (Cooper 1981). Therefore, all surveys were conducted between sunset and approximately 22:30. To maximize survey efficiency within this limited window, survey points were restricted within 20 meters of existing roads or trails. Point-count surveys consisted of a single observer conducting an initial 3-minute passive point-count survey followed by a series of 3, 1-minute segments of broadcasted Chuck-will's-widow calls. During the survey, all Chuck-will's-widow detections within a 250-meter radius were recorded, as well as the detection cue (singing, visual), detection time, and wind speed at the start of each count. Wind intensity was recorded on a scale ranging from 0 to 4, where 0 represented no wind, 1 indicated movement of leaves and twigs, 2 denoted movement of small branches, 3 represented movement of small trees and/or branches, and 4 indicated strong wind.

Covariates and Data Processing

I used the National Land Cover Database 2021 dataset (Dewitz and USGS 2021) to classify land cover types at a 30 m resolution within a 250-meter radius buffer surrounding each point count location. Weather data, including temperature (°C) and cloud cover, for each survey period at each survey location were downloaded using the RNCEP package in R (Kemp 2011). Moon phase and illumination for each survey period were computed using the package moonlit in R (Śmielak 2023). Moon phase refers to the fraction of the moon's surface that is illuminated by the sun as observed from Earth, though is not directly related to moonlight intensity on the ground due to the orbit of the moon. Illumination denotes the combined intensity of moon and twilight, measured in lux, which refers to the actual brightness of the moon and sun's light as it reaches the Earth's surface, considering the angle of the moon in the sky and atmospheric conditions. For points located at Little St. Simons and Altama, I also recorded the time since the most recent prescribed fire, with sites that had not been burned in at least 10 years recorded as "unburned".

Prior to analysis, I removed land cover types that accounted for less than 5% of total land cover within the point count circles. I also tested for correlation among covariates and if any covariates were highly correlated (Pearson correlation coefficient > 0.7), I removed ones that were *a priori* predicted to have less influence of Chuck-will's-widow breeding density or behavior. Specifically, I hypothesized that certain land cover types, such as urban areas, would have less influence on breeding density of Chuck-will's-widows compared to areas adjacent to open habitats and recently burned landscapes where I predicted higher insect availability After applying this criterion, distance metrics for six land cover types remained: evergreen forest, developed area, woody wetlands, barren land, and herbaceous grasslands. Start times were converted to minutes after sunset. Temperature values for each survey period were standardized to be relative to a reference value of 24 degrees Celsius, as this was the lowest temperature recorded during the surveys. Cloud cover estimates were standardized relative to a reference value of 50% cloud cover, as surveys were not conducted if cloud cover exceeded 50%. Illumination values were transformed using a logarithmic scale to accommodate the wide range of values (0 - 2000 lx).

Data Analysis

To quantify the influence of land cover and fire history on breeding density, I used a hierarchical distance-sampling model, implemented using the "gdistsamp" function in the "unmarked" package in R. This approach allowed me to estimate the effects of habitat covariates on breeding density, correcting for survey-specific variability in availability and detection probability (Fiske and Chandler 2011; Royle et al. 2004). Because most detections (>87%) were auditory, accounting for availability (i.e., the probability that a Chuck-will's-widow vocalizes during the point count) was critical to estimating both detection probability and density. To assess habitat diversity at each point count site, I calculated the Shannon Diversity Index using land cover proportion data within the 250-meter radius circle within a given point count site (Shannon 1948). This index measures the uncertainty in predicting that habitat cover type of a randomly chosen point within the study area. Higher values of the Shannon Diversity Index indicate greater diversity of habitat types, reflecting both a wider variety of habitats and a more balanced distribution among them. The calculation was performed by applying the Shannon Index formula to the proportions of land cover types extracted from our dataset for each point count site. To quantify the direct effects of land cover, I modeled breeding density as a function of the proportion of each land cover type within the 250-meter radius circle around each point. I modeled Chuck-will's-widow availability as a function of covariates that I hypothesized influence the singing behavior of Chuck-will's-widows, including temperature, start time (relative to sunset time), cloud cover, illumination, and the interaction between cloud cover and illumination. The interaction was included to account for the fact that the illumination experienced by the birds is influenced by cloud cover. I modeled detection probability as a function of wind speed, based on the hypothesis that windy conditions make it more difficult to hear birds singing. I constructed a single model encompassing all covariates hypothesized to influence density, availability, and detection probability and interpreted p-values associated with each covariate as evidence of support for each hypothesis (Trennedick et al. 2021). To model the effect of prescribed fire on Chuck-will's-widow breeding density, I fit a second model that only included points located in forested habitats (the only habitat type with consistent fire history data). Density was modeled as a function of time since fire (treated as a categorical predictor with levels: unburned or 1, 2, 3, 4+ years since burn). Availability and detection probabilities were modeled as described above.

Results

Over the course of the study, I conducted 204 point count surveys at 96 points. Estimates for Chuck-will's-widow density, availability, and detection modeling are presented in Table 1 and 2. Among the habitat covariates included in the model, there was strong evidence that density increased with the proportion of grassland and moderate evidence that density was positively associated with proportion of woody wetlands and proportion barren land (Fig. 2).

However, there was no evidence of significant effects for Shannon Diversity Index, proportion of evergreen forest, or proportion of developed area on Chuck-will's-widow density. Within forested points, prescribed fire had a significant effect on the density of Chuck-will's-widows (Table 4), though the effect varied as a function of time since burn. There was strong evidence of higher density 1-2 years after burning relative to unburned locations, but within 3 years post-burn, there was no significant difference in density between burned and unburned sites (Fig. 3). There was no evidence that cloud cover, moon phase, start time or temperature influenced availability. There was weak evidence suggesting that illumination positively affects availability, indicating that Chuck-will's-widows vocalized more when conditions were brighter; however, there was a significant negative interaction between cloud cover and illumination. Specifically, as cloud cover increases, the effect of illumination on availability decreases (Fig. 4). This suggests that when cloud cover is higher, illumination has less of an effect on availability than under low cloud cover conditions. There was no evidence indicating that Chuck-will's-widow detection probability was influenced by wind speed.

Discussion

Results from this study provide valuable information regarding the association between habitat characteristics and Chuck-will's-widow breeding density. Within our study areas, Chuck-will's-widows exhibited a strong preference for areas with high percentages of grasslands, evergreen forests, barren lands, and woody wetlands. These results are consistent with previous work showing that nightjars generally prefer heterogeneous landscapes with a variety of habitat types (Camacho et al. 2014; Evens et al. 2018). For Chuck-will's-widows, forests provide essential roosting and nesting sites, offering protection from predators and environmental stressors. Similarly, open habitats like grasslands, woody wetlands, and barren land offer open areas that increase foraging opportunities by providing abundant prey items (Farrel et al. 2017; Thompson et al. 2022). Conversely, the negative association between density and developed areas suggest the adverse impacts of urban encroachment and habitat fragmentation on habitat suitability for the species. Urbanization not only reduces availability of suitable nesting and foraging habitats (Souza-Cole et al. 2022), but also introduces various anthropogenic disturbances that disrupt breeding behaviors and decrease aerial insect populations (Merckx and Dyck 2019). These findings emphasize the need for targeted conservation efforts in regions undergoing urban development during the breeding season. They highlight the importance of prioritizing the preservation of large, contiguous natural habitats, while also maintaining a mix of different habitat types within these areas to maximize Chuck-will's-widow populations.

In addition to the positive effect of heterogeneous land cover, these results suggest that prescribed fire can have a strong positive influence on breeding densities of Chuck-will's-widows. The observed higher density at sites 1-2 years post-burn, followed by a gradual decline, suggests that prescribed fire may initially create favorable foraging and nesting conditions for Chuck-will's-widows, due to the enhanced availability of open understory and increased insect density in burned areas (Thompson et al. 2022). However, the subsequent gradual decline in density in sites 3-5 years post-burn indicates a potential negative shift in habitat use or resource availability over time. These findings highlight the importance of incorporating burn regimes in habitat management strategies, as the ecological effects of prescribed fire may vary depending on post-fire succession and habitat recovery processes. Exploring how vegetation and prey availability change following prescribed burns may help explain the factors driving fluctuations in Chuck-will's-widow density. Additionally, integrating long term-monitoring data with spatially explicit models could reveal how Chuck-will's-widows use landscapes post-burn in different areas over time. Effective conservation strategies should consider the connection between burning regimes, habitat structure, and species response to disturbance, emphasizing the importance of promoting and maintaining landscape heterogeneity.

These results also have important implications for the design of sampling protocols for not only Chuck-will's-widows but potentially other nightjars as well. Although our results did not show a significant correlation between start time, temperature, and availability, previous studies suggest that Chuck-will's-widow activity patterns can vary throughout the night (Souza-Cole 2022; Witynski 2023). Other environmental factors influence nocturnal activity patterns and foraging behavior. For instance, previous studies have suggested that higher temperatures can increase insect activity (Mellanby 1939), thereby potentially increasing prey availability for Chuck-will's-widows and promoting greater foraging activity as well as singing behavior. Singing serves a crucial cue for availability, utilized by males to defend their territories and by females to locate potential mates (Hall 2004). Nesting cycles and territoriality are closely linked to environmental factors such as temperature, time, and illumination (Ardia et al. 2006). During the breeding season, higher temperatures and longer daylight hours may accelerate the development of eggs and chicks, possibly influencing the timing and success of nests (Zuckerberg et al. 2018). Males may adjust their singing behavior to link with optimal conditions for attracting mates and defending territories.

Illumination levels can influence nocturnal activities (Jetz et al. 2003), potentially enhancing visibility for both nightjars and their prey, thereby affecting foraging and singing behavior. However, the relationship between moon phase and nocturnal singing behavior is nuanced. Earlier studies suggested that Chuck-will's-widows were more likely to be detected when the moon was more than half full, with their likelihood of detection increasing with moon illumination (Cooper 1981). The association between availability and cloud cover, along with moon illumination, suggests that Chuck-will's-widows may exhibit reduced activity under adverse weather conditions. This deepens our understanding of light as a cue for nocturnal activities, particularly singing behavior (Wilson and Watts 2000). Moon phase alone might not reliably predict singing behavior on a given night, as factors such as cloud cover and moon rise time can significantly influence nocturnal behavior. On cloudy nights, the influence of moon illumination on Chuck-will's-widows' behavior may diminish, highlighting the combined effect of cloud cover and moon phase in determining nocturnal activity levels. For instance, on cloudy nights with minimal moonlight, these birds might reduce their singing and foraging activities due to decreased visibility and prey availability.

For designing effective sampling protocols for surveying Chuck-will's-widows, these findings have practical implications. Surveys should ideally be conducted during nights with moderate to high illumination and clear skies to maximize detection rates. Specifically, periods around the first and last quarters of the moon phase, when illumination is moderate and less likely to be affected by cloud cover, might be best for conducting surveys. Additionally, survey efforts should account for moon rise and set times to ensure sampling occurs when the moon is visible, and illumination is consistent. Incorporating audio recording units (ARUs) into these protocols can further enhance detection accuracy by capturing vocalizations over extended periods, reducing the influence of availability, and leading to more accurate estimates of density and habitat relationships (Knight et al. 2017). This approach reduces under or overestimation of density and ensures more robust data collection (Marques et al. 2012; Priyadarshani et al. 2018). Given the renewed interest in large-scale nightjar surveys in Georgia, these recommendations can help optimize survey efforts and ensure more accurate monitoring of Chuck-will's-widow populations. By selecting survey nights based on these environmental factors and utilizing ARUs, data quality can improve, and we can better understand the behavior and distribution of Chuck-will's-widows.

Several limitations could influence the interpretation and applicability of these results. Robust estimates of population density require accounting for imperfect detection through appropriate sampling designs and modeling frameworks, particularly for a nocturnal species like Chuck-will's-widows that primarily rely on auditory cues for communication and detection. While point count surveys may capture vocalizations to some extent, other factors still limit generalizability. One significant limitation is the geographic scope of my study. The focus on Chuck-will's-widows in coastal Georgia during the breeding season may not fully capture the species' distribution and behavior across broader geographic ranges. Habitats and environmental conditions in coastal regions can differ significantly from those inland or in other parts of the species' range. For instance, other nightjars, such as Whip-poor-will's, are known to exhibit regional variation in habitat use and behavior (Tonra 2019), and additional research in different regions across the annual cycle is needed to generalize these findings. Additionally, specific attributes of our study sites, such as the rare and endangered grasslands found on Little St. Simons Island may not be representative of habitats elsewhere. The sample size within different burn intervals and habitat types could also impact the robustness of our conclusions. Ensuring a larger and more diverse sample size across various habitats and management practices would strengthen the applicability of our results. By addressing these limitations in future studies, we can improve our understanding of Chuck-will's-widow ecology and enhance conservation efforts across their range.

Further research incorporating long-term monitoring data and spatially explicit habitat modeling approaches will be essential for developing conservation strategies and ensuring the effective management of critical habitats for this species. Collaborative initiatives, such as the integration of Chuck-will's-widow surveys into nightjar survey networks, offer opportunities to maximize resources and expand geographic coverage. By standardizing survey protocols and data collection methods, researchers can generate large-scale datasets that facilitate population assessments and trend analyses. Targeted studies on habitat use, breeding biology, and migratory connectivity, coupled with incorporating climate change projections into habitat models, will advance our understanding of the species' ecological requirements and inform proactive conservation measures. Outreach and education initiatives are crucial for raising awareness and nurturing community stewardship among local communities, ultimately contributing to the long-term monitoring and conservation of Chuck-will's-widow populations and their habitats.

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Table 1. Models and number of parameters (K) used to quantify the effects of landscape covariates on breeding density of Chuck-will's-widows (*Antrostomus carolinensis*) in coastal Georgia. The first model included all surveys of the 96 point count locations. The second model included only counts from 80 points located within forest areas and for which information on prescribed fire history was available.

Model	**K**
λ(Shannon Index + Proportion Evergreen Forest + Proportion Developed + Proportion Woody Wetlands + Proportion Barren Land + Proportion Grassland) φ(Start time + Cloud*Illumination + Cloud*Moon Phase + Temperature) p(Wind)	12
λ(Burn) φ(Start time + Cloud*Illumination + Cloud*Moon Phase + Temperature) p(Wind)	12

Table 2. Estimated effects of covariates on density, availability, and detection modeling for Chuck-will's-widows (*Antrostomus carolinensis*).

Category	**Covariate**	**β**	**SE**	**p-value**
Density	Intercept	-3.754	0.739	**<0.001**
	Shannon Index	0.159	0.378	0.675
	Proportion evergreen forest	1.411	0.747	0.0587
	Proportion developed area	-4.939	3.261	0.131
	Proportion woody wetlands	1.814	0.680	0.00766
	Proportion barren land	2.164	0.811	0.00760
	Proportion grassland	9.766	3.132	**<0.001**
Availability	Intercept	2.497	1.562	0.110
	Start time	0.00286	0.0238	0.905
	Cloud	-0.0858	0.0579	0.138
	Illumination	0.646	0.403	0.109
	Moon Phase	-0.830	1.300	0.523
	Temperature	0.000701	0.0864	0.994
	Cloud*Illumination	-0.0263	0.0134	0.0498
	Cloud*Moon Phase	0.0184	0.0646	0.776
Detection	Intercept	5.0557	0.130	<0.001
	Wind	-0.0732	0.0691	0.289

Table 4. Estimated effects of covariates on density modeling for Chuck-will's-widows (*Antrostomus carolinensis*), with the intercept corresponding to the unburned condition. Availability and detection effects are not reported as the full model was used to estimate the strength of these covariates.

Category	**Covariate**	**β**	**SE**	**p-value**
Density	Intercept	-2.969	0.212	**<0.001**
	1 year since burn	1.234	0.382	0.00124
	2 years since burn	1.0583	0.348	0.00238
	3 years since burn	0.0489	0.595	0.935
	4+ years since burn	0.605	0.503	0.229

Figure 1. Point count survey locations for Chuck-will's-widows (*Antrostomus carolinensis*) conducted at three sites: Altama Plantation Wildlife Management Area (24 points), Harris Neck National Wildlife Refuge (18 points), and Little St. Simons Island (28 points).

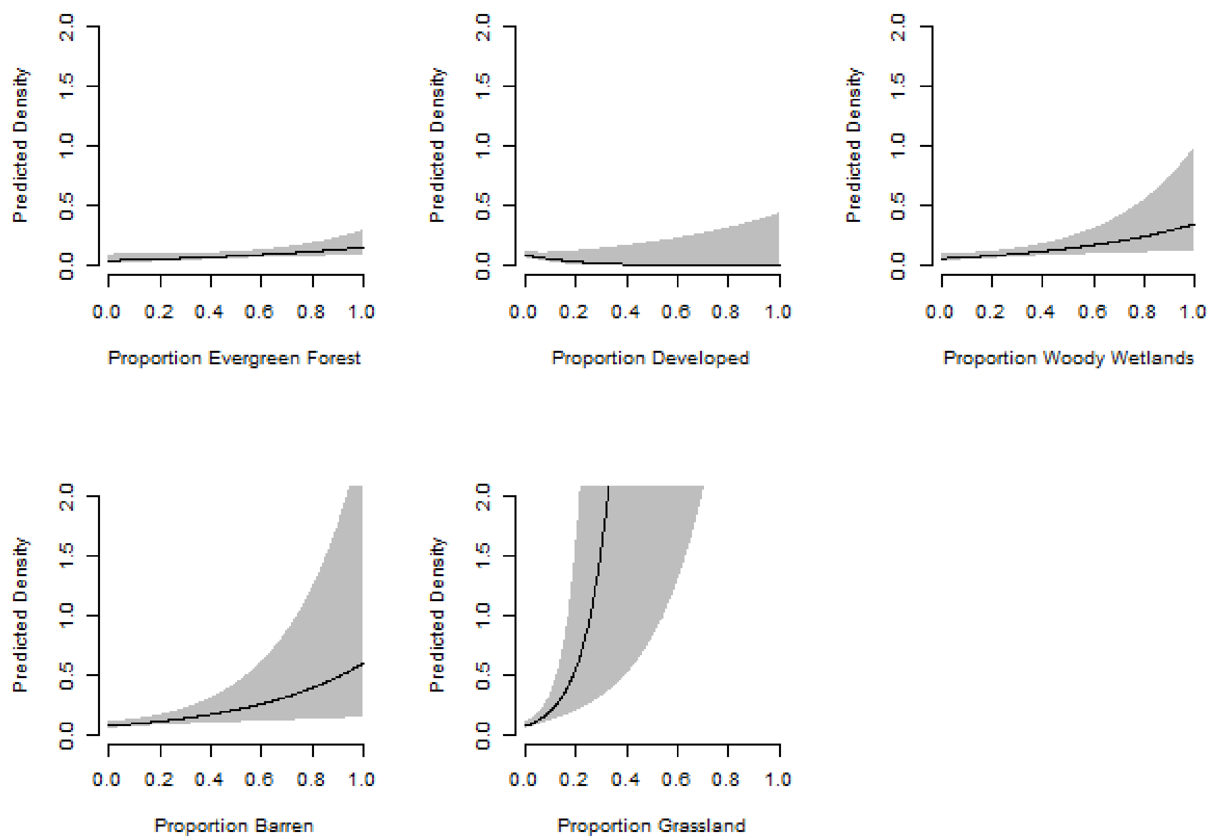

Figure 2. Predicted density of Chuck-will's-widows (*Antrostomus carolinensis*) in relation to the proportion of land cover types within a 250-meter radius circle. The gray denotes the 95% confidence intervals.

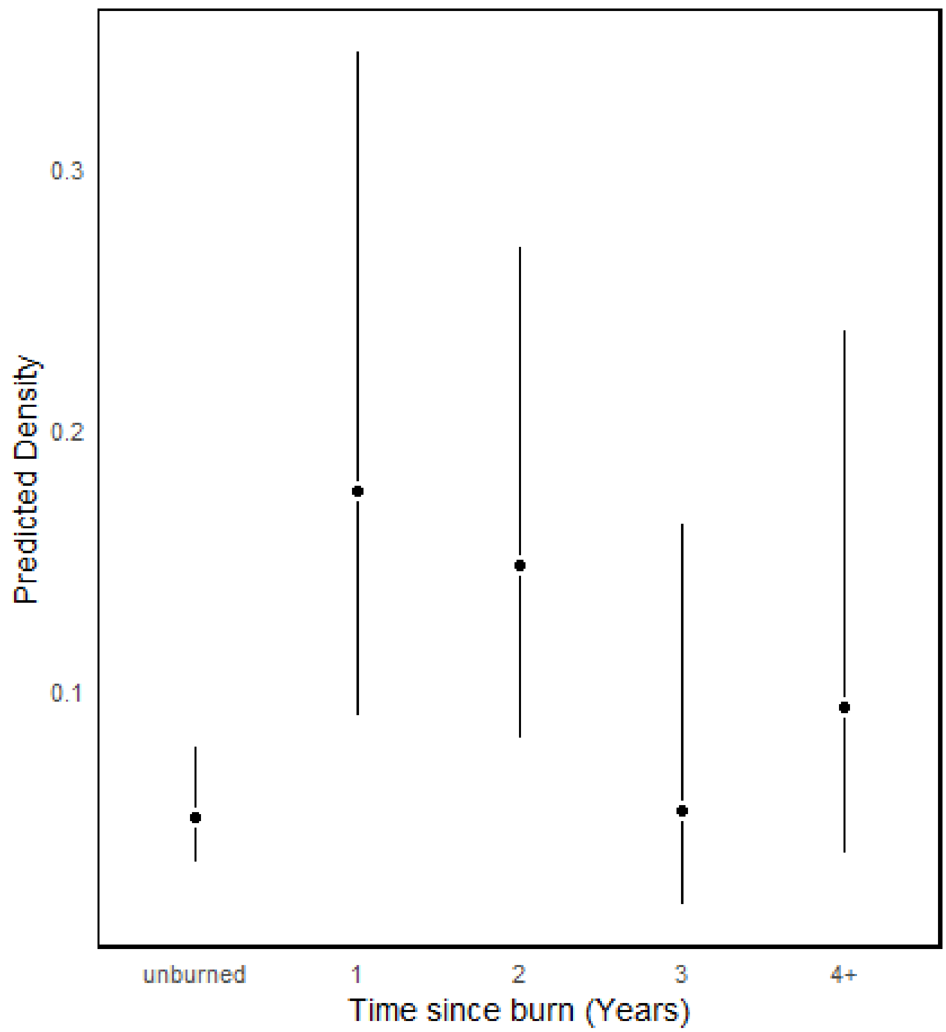

Figure 3. Predicted density of Chuck-will's-widows (*Antrostomus carolinensis*) in forested areas as a function of time since prescribed fire. Points that had not been burned in > 10 years were categorized as "unburned". 8 points were 5-years post burn and were lumped with 4 years since burn points to increase statistical power. Error bars show 95% confidence intervals.

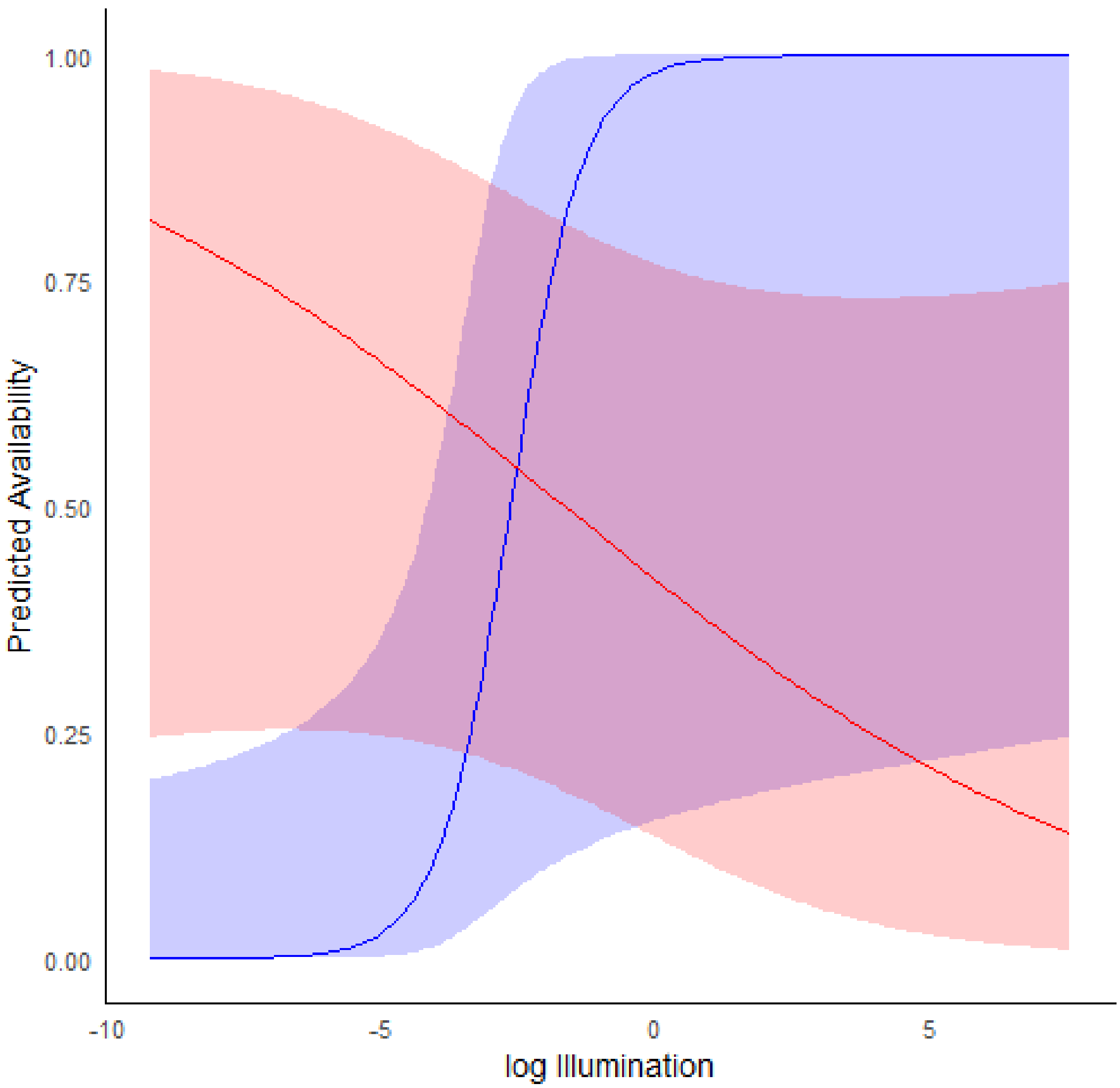

Figure 4. Predicted availability of Chuck-will's-widow (*Antrostomus carolinensis*) as a function of illumination. Solid lines represent fitted values and dashed lines represent 95% confidence bands. Predictions shown for two values of cloud cover: highest observed (81%; red line) and lowest observed (15%; blue line).

CHAPTER 3

BREEDING AND POST-BREEDING RESOURCE SELECTION FOR A CHUCK-WILL'S-WIDOW (*ANTROSTOMUS CAROLINENSIS*) ACROSS THE ANNUAL CYCLE

Ramos, N., Cox, C., and C. Rushing. To be submitted to a peer-reviewed journal.

Abstract

Long-distance migratory birds rely on high-quality habitat throughout their annual cycles, including breeding, wintering, and stopover sites. Identifying habitat requirements and use across the full annual cycle is critical to understanding the ecological requirements needed to maximize conservation decisions. Chuck-will's-widows (*Antrostomus carolinensis*) are the largest North American aerial insectivore and have experienced sustained declines of 1.6% per year since 1970. As a long-distance migratory bird, Chuck-will's-widow population declines may be driven by threats experienced during breeding, migration, or on the wintering grounds. At present, there have been no tracking studies on this species and the phenology, migration routes, winter distribution and habitat requirements during different periods of the annual cycle are not well described. The primary objectives of this project were to fill knowledge gaps regarding movement and resource selection to inform decisions about how best to manage habitats for Chuck-will's-widows throughout the annual cycle. Using high-resolution GPS tracking data from one male Chuck-will's-widow from coastal Georgia, USA, we provide the first description of migration behavior and non-breeding habitat selection of this species. After breeding, this individual moved northward and spent 8 weeks in a mostly suburban landscape approximately 15 km from its breeding site. After this post-breeding period, the individual migrated through eastern Florida, wintered within a small area of central Cuba, and followed a similar route back to its original breeding site. We used resource selection functions to characterize habitat used by the individual during its stationary breeding, post-breeding, and wintering periods. This analysis indicated that the individual selected forested habitats during each stationary period, though the landscape features surrounding used locations differed across seasons. Continued efforts to gather tracking data from more individuals across the breeding range will help improve our understanding of the

landscape features that drive habitat use and selection in breeding and non-breeding grounds and inform habitat management plans to help conserve Chuck-will's-widow populations.

Introduction

Migratory aerial insectivores are among the fastest-declining avian guilds in North America (Rosenberg et al. 2019). This taxonomically diverse group, which includes swifts, swallows, flycatchers, and nightjars, feeds almost entirely on flying insects and was once abundant across the continent. Since the 1970's, aerial insectivores, especially those that migrate to Central and South America, have experienced steep population declines (Michel et al. 2015; Nebel et al. 2010; Smith et al. 2015). Although downward trends are hypothesized to be the result of habitat loss and degradation, other threats may include insect declines, climate change, disease, predation, and pesticide overuse (Straight and Cooper 2020; Stanton et al. 2017; Imlay et al. 2022; Møller 2019). Habitat selection is not well understood for many aerial insectivores, particularly outside of the breeding season, which makes identifying the primary threats driving population declines difficult. This is especially true for nightjars (family Caprimulgidae), which are cryptic and difficult to study throughout most of the year. Recent focus on this group, which includes several species of conservation concern in North America, has begun to document habitat requirements across the annual cycle.

Previous studies on nightjars suggest some species may avoid areas with high levels of human development and select habitats with interspersed forest and open areas (Sharps 2015; Souza-Cole et al. 2022; Thompson et al. 2022). Evidence from breeding point count surveys indicates that Eastern Whip-poor-wills (*Antrostomus vociferus*), for example, are more likely to be detected near forest edges. In addition, they strategically place their territories near forest openings created by forest regeneration practices, such as logging and prescribed fire (Wilson and Watts 2008), or in areas with lower maximum understory height, possibly facilitating foraging opportunities (Tozer 2014). Archival GPS tag studies on Whip-poor-wills have revealed that habitat selection may be consistent across different stages of the annual cycle, with responses to forest conditions remaining consistent throughout their range (Spiller and King 2021; Tonra 2019). Research on another North American nightjar, the Common Nighthawk (*Chordeiles minor*), suggests this species relies heavily on open landscapes that provide abundant insect populations across all stages of their annual cycle (Vala et al. 2020). Although research on these two species has shed light on nightjar habitat selection, basic information about habitat use throughout the annual cycle is lacking for many other species.

The Chuck-will's-widow (*Antrostomus carolinensis*) is a nightjar species that breeds in the southeastern United States and winters in the Caribbean and Central America. The species is of high conservation concern due to population declines of at least 66% over the past half century (Hayes et al. 2010). Like other aerial insectivores, the causes of these declines are not well understood, in part because their nocturnal and secretive nature make it difficult to conduct detailed field studies, especially outside of the breeding season (Straight and Cooper 2020). At present, no tracking studies have documented the routes, timing, nor phenology of Chuck-will's-widow migration and basic information on resource selection outside of the breeding season is unavailable. Threats to this species are hypothesized to include breeding and wintering habitat loss and degradation including development, agriculture, and other anthropogenic disturbances (Straight and Cooper 2020; Nebel 2010). As a long-distance migratory bird, Chuck-will's-widow population declines might be attributed to threats experienced during the breeding season, migration, or on their wintering grounds. Declines in insect abundance and diversity restrict foraging opportunities for this species, and a decrease in food availability could contribute to their decline (Nebel 2010). Point count surveys suggest that breeding Chuck-will's-widows are generally most abundant in open deciduous, coniferous, and mixed woodlands (Straight and

Cooper 2000; Hayes et al. 2010). However, information on many aspects of their natural history and ecology, including habitat requirements outside of the breeding season, migration phenology, routes, and winter distribution, are lacking (Straight and Cooper 2020).

My study aimed to fill a significant gap regarding routes, phenology, and duration of Chuck-will's-widow migration. Additionally, I aimed to quantify seasonal variation in roost site selection across the annual cycle using GPS tracking data. By examining roost site selection across the annual cycle, this study aimed to uncover whether roost site selection varies across the breeding, post-breeding, and stationary non-breeding periods. Based on previous research showing that singing male Chuck-will's-widows are most abundant in open forests, I predicted that birds would most often be found in forested landscapes and would avoid open or developed habitats. Furthermore, because other nightjar species have been shown to select heterogeneous habitats that provide access to open habitats used for foraging, I predicted that birds would select locations closer to habitat types thought to have higher food availability. Finally, because closely related nightjar species show consistent patterns of roost site selection across the annual cycle, I predicted the Chuck-will's-widows would select similar habitat types for roosting during the breeding, post-breeding, and stationary non-breeding periods.

Methods

Study Site

I captured and tagged Chuck-will's-widows during the summer of 2022 at Altama Plantation Wildlife Management Area (hereafter Altama WMA), Glynn County, Georgia, USA. Altama WMA is an approximately 1,600-hectare property ca. 25 kilometers from the coast, located on the south bank of the Altamaha River. In the early 1880's, rice impoundments were the primary land cover type within the study area. The Georgia Department of Natural Resources (DNR) employs active management strategies on the property, which include prescribed fire and logging. As a result, the landscape is now dominated by approximately 620 hectares of tidal freshwater floodplain forest, 120 hectares of upland hardwood forest, and a 600-hectare area under intense silviculture management. The Georgia DNR is engaged to restore a longleaf pine forest that takes up one-fourth of the property. Planted loblolly (*Pinus taeda*), longleaf (*Pinus palustris*), and slash pine (*Pinus elliottii*) undergo regular thinning as part of restoration efforts, while prescribed burning of approximately 100 hectares of pine annually promotes a nutrient-rich understory of wiregrass (*Aristida stricta*) and saw palmettos (*Serenoa repens*).

Tag deployment and recovery

During the summer of 2022, Chuck-will's-widows were lured into mist nets using recorded calls of conspecifics and a decoy made of corrugated plastic. Upon capture, I took standard morphological measurements (e.g. mass, wing chord and tail length), aged and sexed individuals based on plumage characteristics, and attached a uniquely numbered U.S. Geological Survey aluminum band. Individuals that weighed more than 110g were also given an archival GPS tag (3.5-gram Lotek PinPoint GPS VHF), attached using a wing loop harness constructed from elastic cord. Tag weight (including harness) did not exceed 3% of the individual's body weight. All capture and tagging methods were approved by the USGS Bird Banding Laboratory (permit # 24181) and the University of Georgia Institutional Animal Care and Use Committee (protocol #A2022 01-020-Y3-A0). The GPS tags were scheduled to record the individual's location from June 10, 2022, to June 1, 2023, at variable intervals designed to collect more detailed information during periods when birds were expected to be migrating (Table A1). All points were recorded at 12:00 UTC, at which time all birds should be using their daytime roosts (Table A2). Tags were also equipped with a VHF beacon to allow birds to be relocated upon their return in 2023 so that GPS points could be remotely downloaded using a handheld receiver (Lotek PinPoint Commander). Beacons were scheduled to be active every day from 13:00 to 18:00 UTC during three periods: May 22-25, June 5-8, and June 19-22, 2023. During these intervals, I searched the study area using a directional antenna to locate tagged individuals and download the data.

Data analysis

Based on initial inspection of the location data, I divided the annual cycle into three distinct periods: breeding season (defined as time spent at the initial tagging site, both during the year of tagging and upon return the following year), post-breeding season (defined as the period of time after a bird left the initial tagging site but before sustained southward migration in fall), and the stationary non-breeding season (defined as the period after the end of southward migration in fall and before northward migration in spring).

Within each period, I used a resource selection function (Manly 2002) to quantify third-order habitat selection (Johnson 1980) and to characterize roost-site site selection based on remote-sensing data. To compare roost-site selection across the full annual cycle, I used the ESRI Sentinel-2, 10m-resolution land use dataset (Karra et al. 2021), which represented the highest-resolution data available across each of the three stationary periods. For each "used" roost location, I characterized the land cover type based on the Sentinel-2 data. I also characterized the habitat type of all raster cells within a 2-km buffer around all used points using GIS software for spatial analysis of land cover data. The 2-km buffer was chosen based on previous research on closely related species, which indicated that Whip-poor-wills have small but variable home range sizes ranging up to 155 hectares and Common Nighthawks averaging 10.4 hectares (Armstrong 1965; Wilson 2003). Radio-tracked European Nightjars traveled a mean maximum distance of 747 meters from territory center during foraging activities (Sharps et al. 2015).

Land cover classes that accounted for less than 1% of the area of the 2-km buffer in each period were excluded from analysis (Tables A3-7). Initial inspection of the GPS locations indicated that all used roost sites were located within forested habitats, as classified by the Sentinel-2 data. For this reason, I focused my analysis on the landscape characteristics surrounding forest points by restricting selection of random "available" points to forested cells within each 2-km buffer, at a ratio of 10 available locations to 1 used location. For each used and available location, I calculated the Euclidean distance to the closest cell of each non-forest land cover type (Hesselbarth et al. 2019). To avoid highly correlated land cover types, I also calculated pairwise correlations between the distances to each land cover type. For any land cover classes with correlations above 70%, I prioritized those that were predicted to have the greatest impact on Chuck-will's-widow abundance (Tables A8-12) and removed the others. After applying this criterion, distance metrics for six land cover types remained: bare ground, built area, cropland, flooded vegetation, rangeland, and water. I then used a logistic regression model to test hypotheses regarding whether forested locations used by Chuck-will's-widows as roost sites differed from randomly available points in their relation to their proximity to other land cover classes. I included the distance to various land cover types as predictor variables in the model and compared these distances between used roost sites and available points.

Although the Sentinel-2 data provided consistent land cover classification to compare roost site selection across the full annual cycle, I also conducted a more comprehensive analysis of land cover characteristics during the breeding and post-breeding periods using the National Land Cover Database 2021 dataset (Dewitz and USGS 2021). Although coarser than the Sentinel-2 dataset, the 30m NLCD dataset includes more detailed land cover classes, which allowed me to better understand roost site selection during these periods. Based on the NLCD classification, all used locations during the breeding season were within evergreen forest and all used locations during the post-breeding period were within woody wetlands. I followed the same procedure as described above to investigate the landscape context for roost site selection during these periods, again eliminating highly correlated (< 0.7) or rare (less than 1% of the area within each 2-km buffer) land cover types and calculating distances to the closest cells of each of the remaining habitat types. Based on the filter criteria, the NLCD analysis included distance to six land cover types: developed areas, evergreen forest (post-breeding only), grasslands, herbaceous wetlands, shrublands, and woody wetlands (breeding only). As described above, I used logistic regression to compare the landscape features surrounding used and available points.

Results

In June 2022, GPS tags were deployed on six adult male Chuck-will's-widows, and I recovered data from one male bird that returned in May 2023. This individual remained at the study site for 61 days after tagging (June 10, 2022 - August 11, 2022), before moving approximately 15 kilometers northward to McIntosh County, Georgia (Fig. 1). After spending 59 days in the post-breeding area, the bird departed on southward migration on October 9, 2022, traversing eastern Florida to reach its wintering grounds in central Cienfuegos, Cuba on October

16, 2022. Following a similar migration route, it returned to coastal Georgia in early March 2023, spending the breeding season at its original site at Altama WMA. In total, I obtained 55 locations during the breeding season (combining data from 2022 and 2023), 48 locations during the post-breeding period, and 13 locations during the stationary non-breeding period.

During all three periods of the annual cycle, this individual only roosted in forested areas, as classified by the Sentinel-2 data. However, there were differences across the annual cycle in the landscape context surrounding used points. During the breeding season, this individual selected for areas closer to cropland (β = −0.049, 95% CI [−0.070, −0.034]) and flooded vegetation (β = −0.027, 95% CI [−0.040, −0.033]) (Table 3). Contrary to my prediction, however, I found no evidence that the bird selected sites in relation to bare ground (β = 0.0051, 95% CI [0.0027, 0.0080]), built area (β = 0.042, 95% CI [0.026, 0.064]), rangeland (β = 0.022, 95% CI [0.012, 0.034]), or water (β = 0.00029, 95% CI [−0.0037,0.0043]). Similar to the breeding period, this individual used areas closer to cropland during the post-breeding period (β = −0.0019, 95% CI [−0.0036, −0.00052]), but also used areas closer to built (β = −0.0030, 95% CI [−0.0045, −0.0017]), bare ground (β = −0.0048, 95% CI [−0.0070, −0.0029]), and rangeland (β = −0.00071, 95% CI [−0.0040, 0.0026]). Although the relationship with distance to water was statistically significant (β = 0.0031, 95% CI [0.0012, 0.0053]), the effect size on roost site selection was small, and there was no flooded vegetation within the 2-km buffer around post-breeding points. During the stationary winter period, this individual selected land cover types closer to cropland (β = −0.090, 95% CI [−0.26, −0.027]) and water (β = −0.0047, 95% CI [−0.032, 0.022]). Distance to built areas shows a marginally significant positive effect (β = 0.073, 95% CI [0.018, 0.22]), and distance to rangeland shows a positive effect (β = 0.063, 95%

CI [0.0069, 0.18]) on roost site selection during the non-breeding season. There was no flooded vegetation or bare ground within the 2-km buffer in the non-breeding region.

Detailed analyses of the breeding and post-breeding stationary periods using the NLCD land cover dataset revealed further differences in roost site selection during these two periods. During the breeding season, the individual only used points classified as evergreen forest and selected areas closer to grasslands ($\beta = -0.0017$, 95% CI [−0.0029, −0.00058]), herbaceous wetlands ($\beta = -0.0021$, 95% CI [−0.0030, −0.0012]), and shrub ($\beta = -0.0011$, 95% CI [−0.0023, −0.000023]). I found no evidence that distance to developed areas ($\beta = 0.00076$, 95% CI [−0.00030, 0.0010]) or woody wetlands ($\beta = 0.0088$, 95% CI [0.0061, 0.012]) influenced roost site selection. In contrast, during the post-breeding season, all used points were within the woody wetlands land cover class. During this period, the individual selected areas closer to the developed areas ($\beta = -0.011$, 95% CI [−0.020, −0.0070]), evergreen forest ($\beta = -0.015$, 95% CI [−0.032, −0.00059]), grasslands ($\beta = -0.0034$, 95% CI [−0.0071, −0.000080]) and shrublands ($\beta = -0.0073$, 95% CI [−0.014, −0.0038]). I found no evidence that distance to herbaceous wetlands ($\beta = 0.024$, 95% CI [0.016, 0.034]) influenced post-breeding roost site selection.

Discussion

In this study, I tracked the movements of a single Chuck-will’s-widow throughout its annual cycle, utilizing multiple land cover datasets to examine roost site selection patterns during the breeding, post-breeding, and stationary non-breeding periods. This study marks the first tracking of Chuck-will’s-widow migration, improving our understanding of their annual movements and roost site selection. Similar to Whip-poor-will’s (Tonra 2019), Chuck-will’s-widow roosting sites were exclusively located within forested habitats throughout the annual cycle, though there was seasonal variation in both the type of forest used by the individual and the composition of the surrounding landscape. Consistent with the hypothesis of habitat selection from breeding season point count surveys (Straight and Cooper 2000; Hayes et al. 2010), during the breeding season this individual roosted in evergreen forest in proximity to grasslands, cropland and floodland vegetation. Contrary to initial hypotheses, the bird did not select areas near rangeland or water, but as predicted, avoided sites near bare ground and built areas. During the post-breeding period, the individual used sites closer to developed areas, grasslands, and shrublands. Although detailed land cover data is not currently available for Cuba, Sentinel-2 data indicated that during the winter, the bird roosted exclusively in forested areas in proximity to cropland and water. These findings highlight both consistency and variation in seasonal roost site selection throughout the annual cycle, which has important implications for the management strategies aimed at conserving this species.

These results suggest that protection of forested landscapes is critical for providing roost sites for Chuck-will's-widows across their annual cycle. Furthermore, the results from the Resource Selection Function (RSF) analysis indicate that conservation efforts focusing on landscape-level prioritization, including proximity to various vegetation communities such as cropland, flooded vegetation, and grasslands, may also be important during different parts of the annual cycle. Chuck-will’s-widows, like other nightjars, select landscapes characterized by a mix of forested and open areas, which aligns with findings from previous studies (Sharps 2015; Thompson et al. 2022; Tonra 2019). Roosting in sites situated within the forest offers camouflage and protection from predators and are adjacent to open land cover types that offer visibility for detecting nocturnal flying insects (Thompson et al. 2022). By integrating these findings into conservation planning, efforts can be made to mitigate the adverse impacts of anthropogenic threats, focusing development planning on minimizing forest loss and maintaining landscape heterogeneity to maintain the integrity of essential Chuck-will's-widow habitats.

In interpreting my findings, several caveats and limitations must be considered. This tracking study involved GPS tracking data from a single individual Chuck-will's-widow. This limited sample size restricts the extent to which these findings can be applied to the entire population of this species and potentially to other individuals within the same population (Lakens 2022). In total, I obtained 123 daytime location points, which provided valuable information on roost site selection but may not fully capture the details of fine-scale movements and habitat use. Therefore, the findings presented provide only a partial understanding of the species' overall habitat requirements. Further, it remains unclear whether the findings accurately reflect roost site selection or if proximity to different land cover types was merely a result of landscape context. Future research should aim to gather additional data and increase sample size to capture a more comprehensive understanding of various aspects of movement and habitat use, including foraging behavior, throughout the annual cycle for this species (Straight and Cooper 2020). It is important to be cautious when making inferences on observed roost site selection patterns to other individuals or populations of Chuck-will's-widows, as the migration behavior of this individual may not accurately represent the variability within the species. Roost site selection patterns may vary across different geographic regions, seasons, and years (Camacho et al. 2014), potentially influenced by environmental factors not considered in this study. Chuck-will's-widows may also exhibit individual variation in roost site selection, with factors such as age, sex, and reproductive status potentially influencing their choices (O'Connor 2013). Further research with larger sample sizes, spanning multiple individuals and locations, is needed to expand upon the findings of this study. Long-term Chuck-will's-widow GPS tracking studies are essential to understand the variability of roost site selection patterns over time across different spatial scales.

Nocturnal aerial insectivores, including Chuck-will's-widows, are generally understudied compared to other avian species, leading to significant knowledge gaps about their ecology and habitat requirements for conservation (Bracken 2024; Straight and Cooper 2020). These findings offer a foundational understanding of the roost site selection and migration behavior of Chuck-will's-widows, guiding future research on this species and other aerial insectivores. Incorporating the information of Chuck-will's-widow migration route and stopover sites to selection improves the understanding of their response to environmental changes throughout the annual cycle. By acknowledging how distance to various land cover types influences roost site selection, policymakers and managers can work towards mitigating the adverse effects of urbanization, agricultural expansion, and other anthropogenic activities that might impact the habitat use of Chuck-will's-widows. Additionally, this study highlights the need for collaborative tracking efforts to develop effective management strategies to address the variation in roost site selection across nightjar species (Thompson et al. 2022; Tonra 2019). Long term monitoring studies and larger-scale tracking efforts across multiple regions can provide a deeper understanding of the factors that drive roost site selection and migration patterns of Chuck-will's-widows. Future research can contribute to the development of more robust conservation strategies and management practices aimed at maximizing Chuck-will's-widow populations.

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Table 1. Covariates considered from the ESRI Sentinel-2 Land Cover Explorer database for resource selection functions used to assess patterns of use for a Chuck-will's-widow (*Antrostomus carolinensis*) in coastal Georgia (June 2022 - May 2023). Positive (+) and negative (−) predictions indicated these covariates were expected to be positively and negatively associated with use, respectively, whereas 0 indicated that I expected these covariates may influence use but could have positive or negative associations.

Category	**Covariate**	**Prediction**	**Unit**
Land cover			
	Distance to bare ground	0	m
	Distance to built	+	m
	Distance to cropland	-	m
	Distance to flooded vegetation	-	m
	Distance to rangeland	-	m
	Distance to water	-	m

Table 2. Covariates considered from the U.S. Geological Survey National Land Cover Database for resource selection functions used to assess patterns of use for a Chuck-will's-widow (*Antrostomus carolinensis*) in coastal Georgia (June 2022 - May 2023). Positive (+) and negative (−) predictions indicated these covariates were expected to be positively and negatively associated with use, respectively, whereas 0 indicated that I expected these covariates may influence use but could have positive or negative associations.

Category	**Covariate**	**Prediction**	**Unit**
Land cover			
	Distance to developed	+	m
	Distance to grassland	-	m
	Distance to herbaceous wetlands	-	m
	Distance to shrub	-	m
	Distance to woody wetlands	-	m

Table 3. Estimated seasonal effects of landscape features on roost site selection by one male Chuck-will's-widow (*Antrostomus carolinensis*) during the breeding, post-breeding, and winter periods. Landscape classifications were based on the ESRI Sentinel-2 satellite imagery to allow consistent comparison across all three stationary periods. NA indicates the land cover was not present within the 2-km buffer places around used points.

Category	**Covariate**	**Season**	**β**	**SE**	**p-value**
Land cover	Distance to bare ground	Breeding	0.00510	0.00133	**<0.001**
		Post-breeding	-0.00478	0.00105	**<0.001**
		Non-breeding	NA	NA	NA
	Distance to built	Breeding	0.0423	0.00944	**<0.001**
		Post-breeding	0.00298	0.000708	**<0.001**
		Non-breeding	0.0729	0.0438	0.0959
	Distance to cropland	Breeding	-0.0492	0.00943	**<0.001**
		Post-breeding	0.00193	0.000786	0.01422
		Non-breeding	0.0898	0.0504	0.0744
	Distance to flooded vegetation	Breeding	0.0271	0.00566	**<0.001**
		Post-breeding	NA	NA	NA
		Non-breeding	NA	NA	NA
	Distance to rangeland	Breeding	0.0221	**0.00535**	**<0.001**
		Post-breeding	0.000712	0.00168	0.671
		Non-breeding	0.0630	0.0404	0.119
	Distance to water	Breeding	0.000291	0.00202	0.885
		Post-breeding	0.00308	0.00105	0.00326
		Non-breeding	0.00470	0.0125	0.707

Table 4. Estimated seasonal effects of landscape features on roost site selection by one male Chuck-will's-widow (*Antrostomus carolinensis*) during the breeding and post-breeding periods. Landscape classifications were based on the U.S. Geological Survey National Land Cover Database to provide more detailed inference about roost site selection during the periods of the annual cycle when the individual remained within the United States. See text for description of the breeding and post-breeding areas used by this individual. NA indicates the land cover was not present within the 2-km buffer places around used points.

Category	**Covariate**	**Season**	**β**	**SE**	**p-value**
Land cover	Distance to developed	Breeding	0.000761	0.000530	0.151
		Post-breeding	0.0114	0.00280	**<0.001**
	Distance to evergreen	Breeding	NA	NA	NA
		Post-breeding	0.0152	0.00794	0.0552
	Distance to grassland	Breeding	0.00168	0.000578	0.00362
		Post-breeding	0.00338	0.00176	0.0556
	Distance to herbaceous wetlands	Breeding	0.00206	0.000430	**<0.001**
		Post-breeding	NA	NA	NA
	Distance to shrub	Breeding	0.00112	0.000580	0.0529
		Post-breeding	0.00730	0.00223	0.00105
	Distance to woody wetlands	Breeding	0.00879	0.00143	**<0.001**

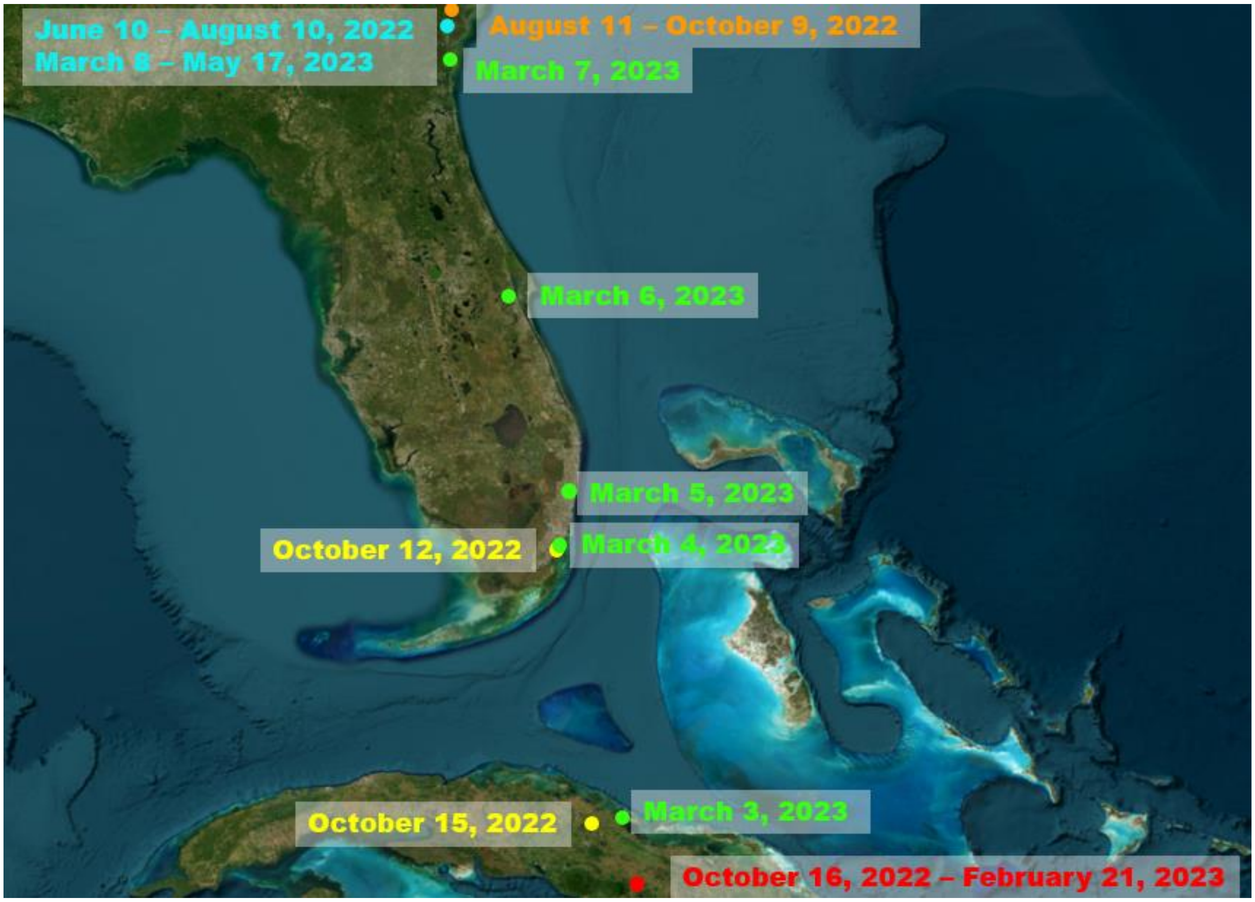

Figure 1. Movement pattern of a Chuck-will's-widow (*Antrostomus carolinensis*) individual tagged on June 10, 2022, at Altama Plantation Wildlife Management Area. The bird remained in its breeding territory at Altama for 62 days post-capture before migrating 15 kilometers northward for 59 days. Following this post-breeding period, it migrated through eastern Florida, reaching its wintering grounds in central Cuba by October 16, 2022, where it spent 128 days. The bird then retracted a similar route back to coastal Georgia, returning to Altama in early March 2023 for the subsequent breeding season. Data collection concluded on May 22, 2023.

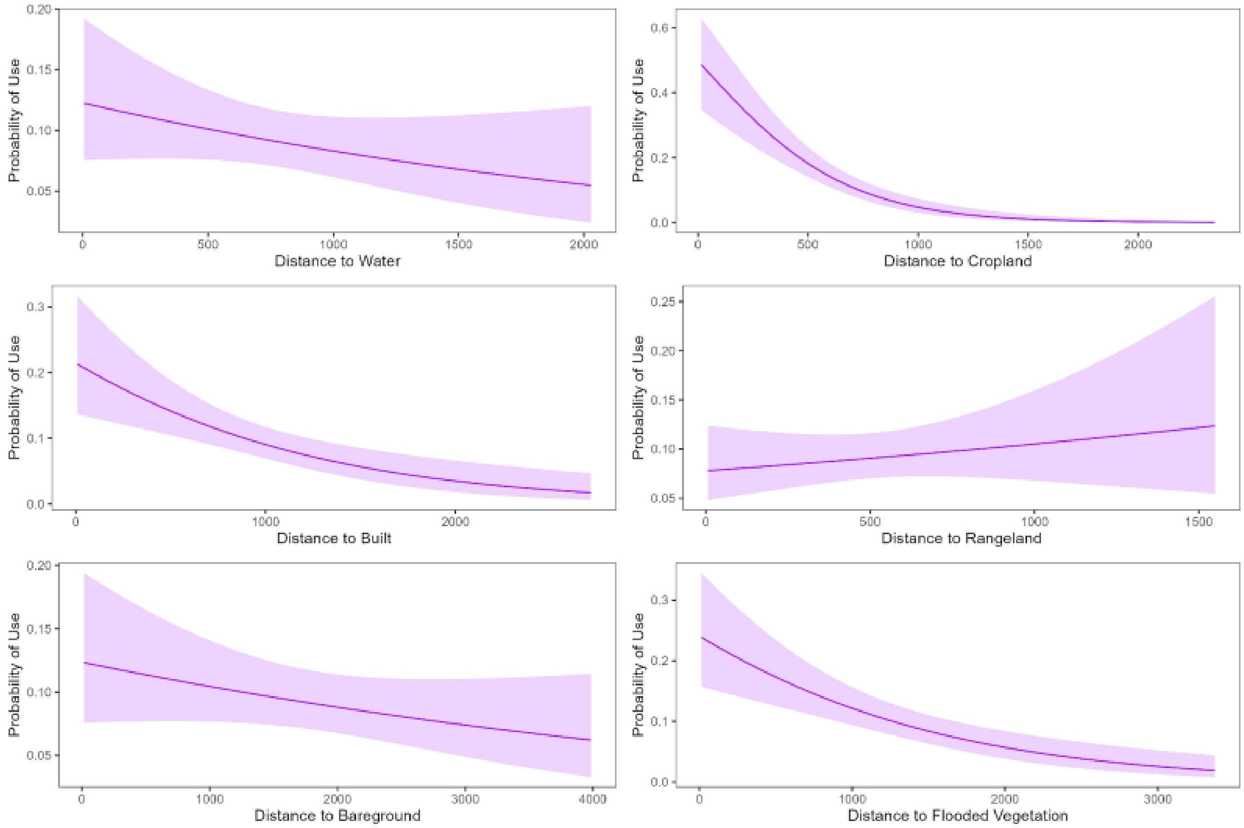

Figure 2. Probability of Chuck-will's-widow (*Antrostomus carolinensis*) breeding-season use as a function of distance to land cover using the ESRI Sentinel-2 Land Cover Explorer Database.

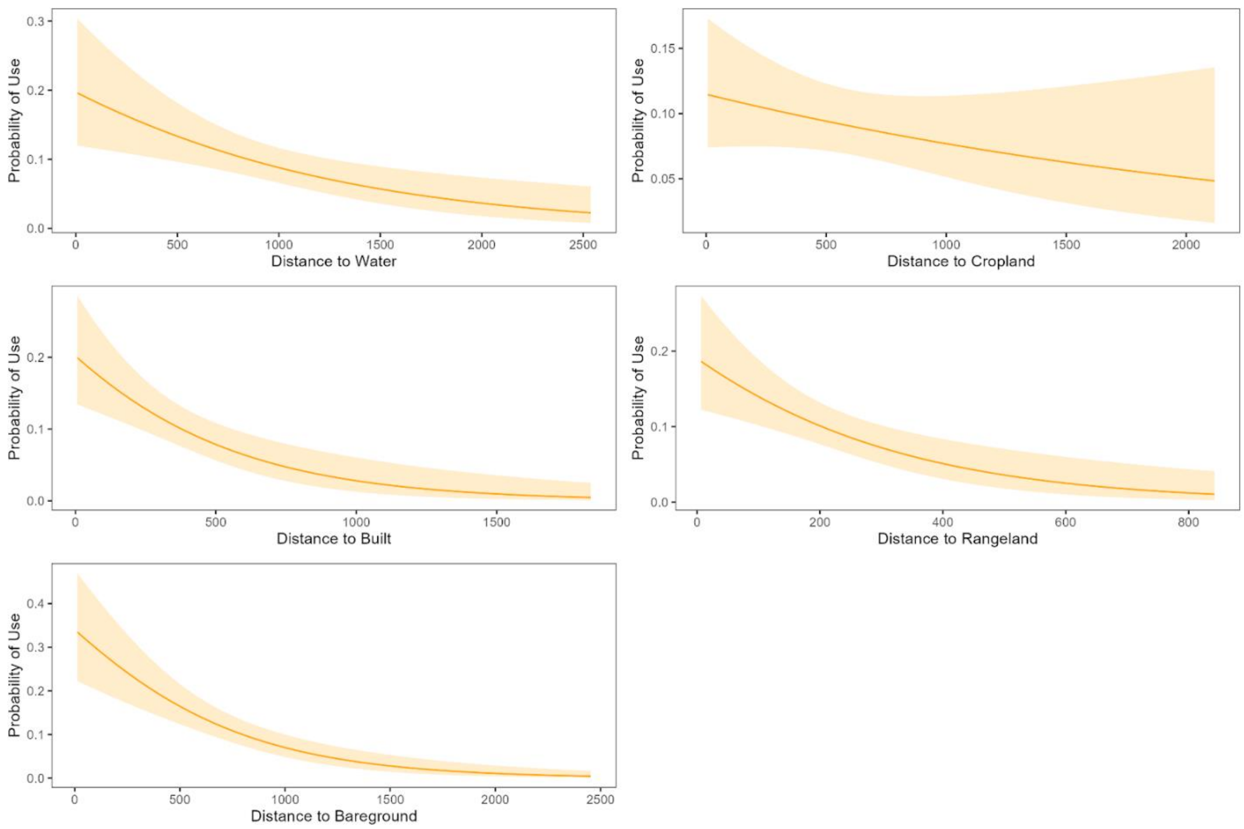

Figure 3. Probability of Chuck-will's-widow (*Antrostomus carolinensis*) post-breeding-season use as a function of distance to land cover using the ESRI Sentinel-2 Land Cover Explorer Database.

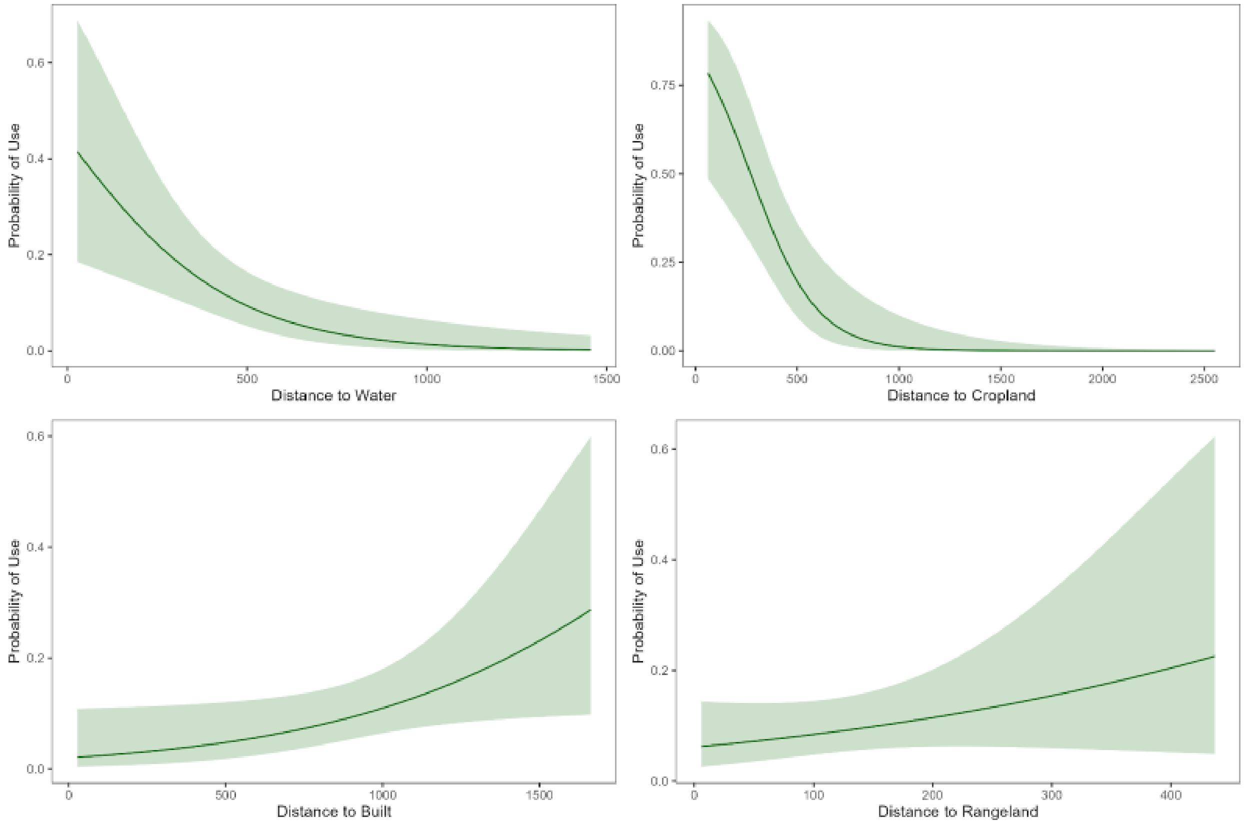

Figure 4. Probability of Chuck-will's-widow (*Antrostomus carolinensis*) winter-season use as a function of distance to land cover using the ESRI Sentinel-2 Land Cover Explorer Databases.

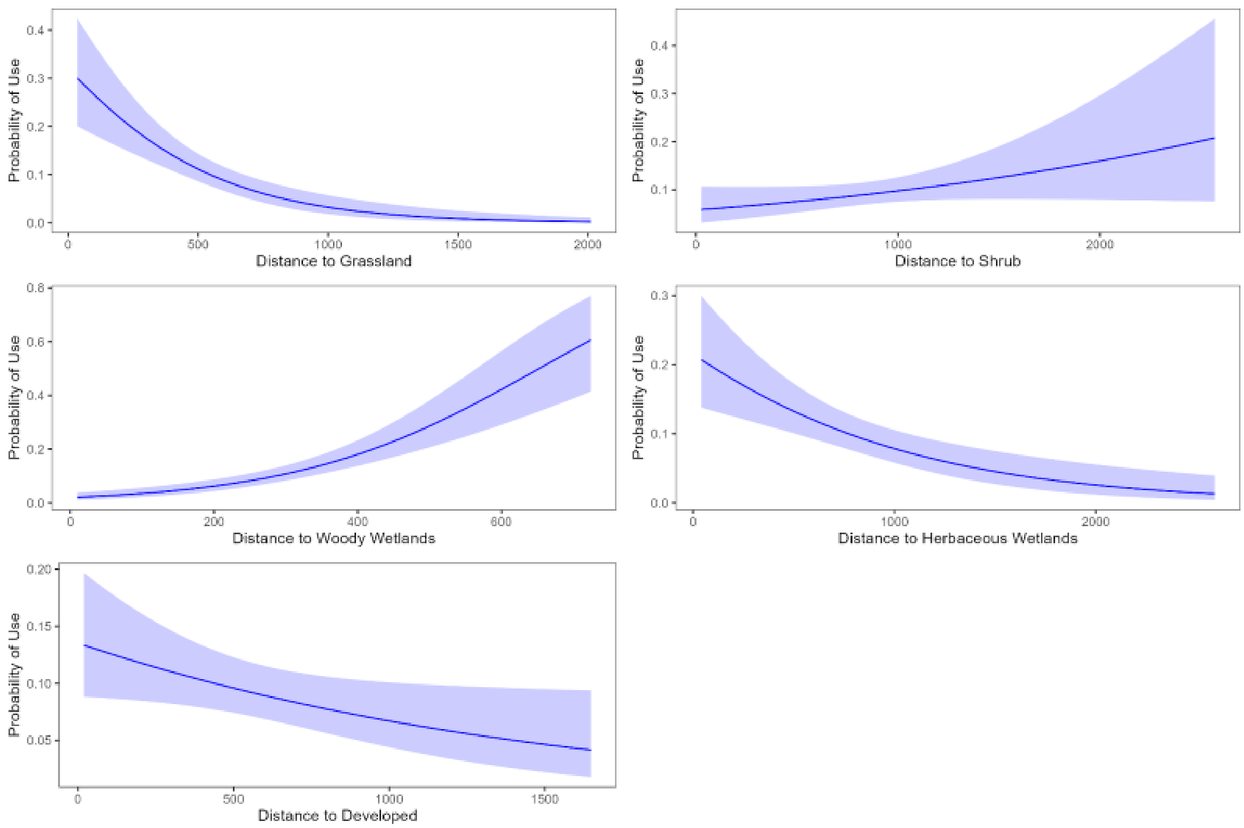

Figure 5. Probability of Chuck-will's-widow (*Antrostomus carolinensis*) breeding-season use as a function of distance to land cover using the U.S. Geological Survey National Land Cover Database.

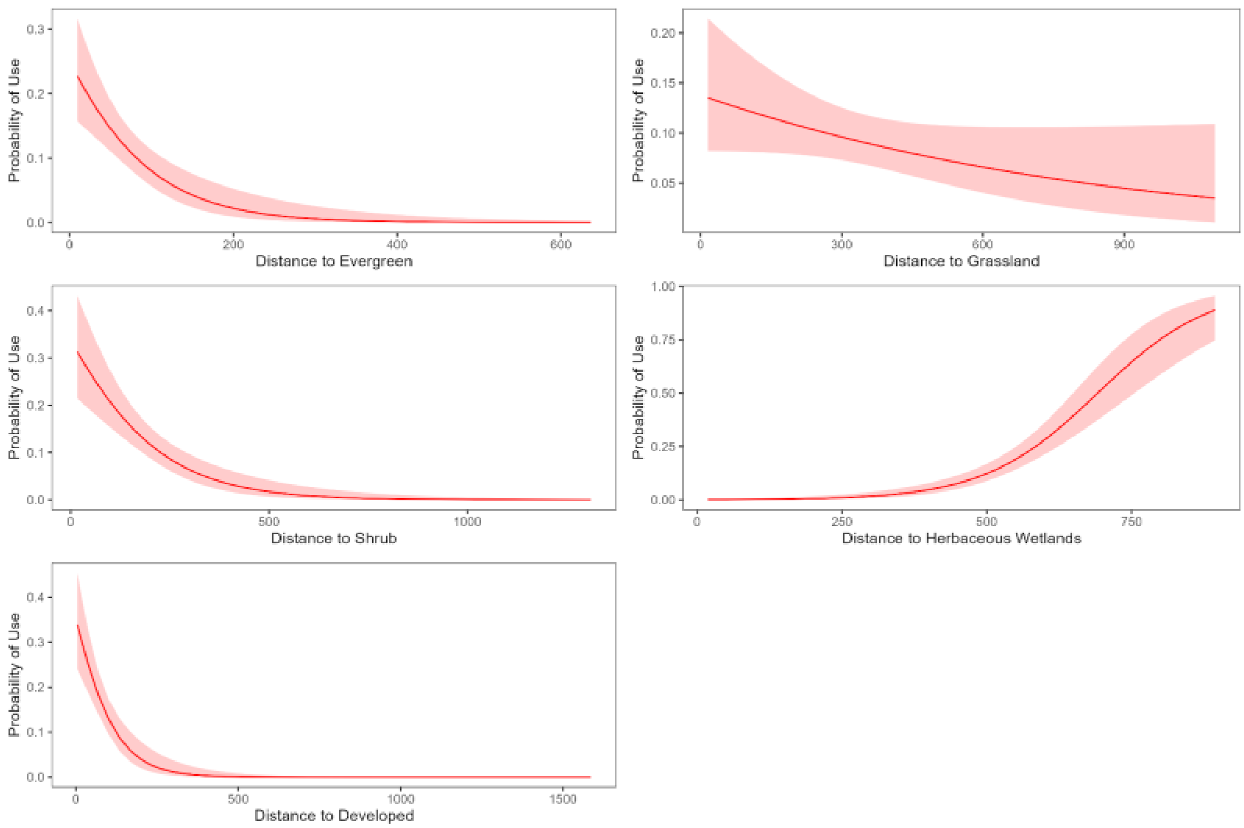

Figure 6. Probability of Chuck-will's-widow (*Antrostomus carolinensis*) post-breeding-season use as a function of distance to land cover using the U.S. Geological Survey National Land Cover Database.

Table A1. GPS schedule for a Chuck-will's-widow (*Antrostomus carolinensis*) tagged on June 10, 2022, at Altama Wildlife Management Area.

GPS Fix Schedule	**Interval**	**Observation Period (UTC)**
6/10/22 - 7/15/22	15 days	12:00
7/16/22 - 8/1/22	3 days	12:00
8/2/22 - 9/20/22	1 day	12:00
9/21/22 - 10/15/22	3 days	12:00
10/16/22 - 2/5/23	15 days	12:00
2/6/23 - 3/1/23	3 days	12:00
3/2/23 - 4/1/23	1 day	12:00
4/2/23 - 5/1/23	3 days	12:00
5/2/23 - 6/9/23	15 days	12:00

Table A2. Beacon schedule for a Chuck-will's-widow (*Antrostomus carolinensis*) tagged on June 10, 2022, at Altama WMA.

Beacon Schedule	**Observation Period (UTC)**
5/22/23 - 5/25/23	13:00 - 18:00
6/5/23 - 6/8/23	13:00 - 18:00
6/19/23 - 6/22/23	13:00 - 18:00

Table A3. Land cover percentage in the 2-kilometer buffer area around Chuck-will's-widow (*Antrostomus carolinensis*) used locations during the breeding season using the ESRI Sentinel-2 Land Cover Explorer Database.

Land Cover Type	**Percentage**
Water	7.98
Forest	67.60
Flooded Vegetation	9.83
Cropland	2.83
Built	0.94
Bare Ground	0.64
Rangeland	10.20

Table A4. Land cover percentage in the 2-kilometer buffer area around Chuck-will's-widow (*Antrostomus carolinensis*) used locations during the post-breeding season using the ESRI Sentinel-2 Land Cover Explorer Database.

Land Cover Type	**Percentage**
Water	0.83
Forest	79.90
Cropland	3.27
Built	2.92
Bare Ground	0.09
Rangeland	13.00

Table A5. Land cover percentage in the 2-kilometer buffer area around Chuck-will's-widow (*Antrostomus carolinensis*) used locations during the winter season using the ESRI Sentinel-2 Land Cover Explorer Database.

Land Cover Type	**Percentage**
Water	0.56
Forest	31.40
Cropland	0.48
Built	10.20
Rangeland	57.40

Table A6. Land cover percentage in the 2-kilometer buffer area around Chuck-will's-widow (*Antrostomus carolinensis*) used locations during the breeding season using the U.S. Geological Survey National Land Cover Database.

Land Cover Type	**Percentage**
Open Water	6.63
Developed Area	2.75
Barren Land	0.03
Shrub/Scrub	40.20
Grassland/Herbaceous	0.36
Deciduous Forest	0.27
Evergreen Forest	0.39
Mixed Forest	39.60
Emergent Herbaceous Wetland	9.73

Table A7. Land cover percentage in the 2-kilometer buffer area around Chuck-will's-widow (*Antrostomus carolinensis*) used locations during the post-breeding season using the U.S. Geological Survey National Land Cover Database.

Land Cover Type	**Percentage**
Open Water	0.54
Developed Area	5.84
Barren Land	0.44
Shrub/Scrub	0.13
Grassland/Herbaceous	NA
Deciduous Forest	32.70
Evergreen Forest	0.01
Mixed Forest	7.03
Emergent Herbaceous Wetland	5.01

Table A8. Correlation of land cover types in the 2-kilometer buffer area around Chuck-will's-widow (*Antrostomus carolinensis*) used locations during the breeding season using the ESRI Sentinel-2 Land Cover Explorer Database.

	Distance to water	Distance to forest	Distance to flooded vegetation	Distance to cropland	Distance to built area	Distance to bare ground	Distance to rangeland
Distance to water	1	-0.07393323	0.04432465	0.33536928	0.3912832	-0.1497067	0.5528112
Distance to forest	-0.07393323	1	-0.03005059	0.16502192	0.1106846	-0.1628874	0.1355949
Distance to flooded vegetation	0.04432465	-0.03005059	1	-0.09765998	0.4307729	0.5090493	0.1174444
Distance to cropland	0.33536928	0.16502192	-0.09765998	1	0.8508098	-0.8858238	0.9376127
Distance to built	0.39128322	0.11068459	0.43077295	0.8508098	1	-0.5256341	0.9257377
Distance to bare ground	-0.14970671	-0.1628874	0.50904929	-0.88582381	-0.5256341	1	-0.7243856
Distance to rangeland	0.55281121	0.13559494	0.11744436	0.93761271	0.9257377	-0.7243856	1

Table A9. Correlation of land cover types in the 2-kilometer buffer area around Chuck-will's-widow (*Antrostomus carolinensis*) used locations during the post-breeding season using the ESRI Sentinel-2 Land Cover Explorer Database.

	Distance to water	Distance to forest	Distance to cropland	Distance to built area	Distance to bare ground	Distance to rangeland
Distance to water	1	0.1458044	-0.9322115	-0.5556439	0.9790388	-0.892388
Distance to forest	0.1458044	1	-0.1046403	-0.1607061	0.1398092	-0.1150182
Distance to cropland	-0.9322115	-0.1046403	1	0.501359	-0.8711026	0.9644935
Distance to built	-0.5556439	-0.1607061	0.501359	1	-0.4155552	0.6790232
Distance to bare ground	0.9790388	0.1398092	-0.8711026	-0.4155552	1	-0.7938364
Distance to rangeland	-0.892388	-0.1150182	0.9644935	0.6790232	-0.7938364	1

Table A10. Correlation of land cover types in the 2-kilometer buffer area around Chuck-will's-widow (*Antrostomus carolinensis*) used locations during the winter season using the ESRI Sentinel-2 Land Cover Explorer Database.

	Distance to water	Distance to forest	Distance to cropland	Distance to built area	Distance to rangeland
Distance to water	1	-0.32884079	-0.2376289	-0.2390675	0.36483388
Distance to forest	-0.3288408	1	0.1673872	0.195808	0.04670358
Distance to cropland	-0.2376289	0.1673872	1	0.9696687	0.36241324
Distance to built	-0.2390675	0.19580802	0.9696687	1	0.21873408
Distance to rangeland	0.3648339	0.04670358	0.3624132	0.2187341	1

Table A11. Correlation of land cover types in the 2-kilometer buffer area around Chuck-will's-widow (*Antrostomus carolinensis*) used locations during the breeding season using the U.S. Geological Survey National Land Cover Database.

	Distance to Water	Distance to Evergreen	Distance to Shrub	Distance to Grassland	Distance to Pasture	Distance to Woody Wetlands	Distance to Herbaceous Wetlands	Distance to Developed Area
Distance to Water	1	-0.25403603	-0.56712409	-0.92012623	-0.76751578	-0.30648394	0.09832007	0.07127753
Distance to Evergreen	-0.25403603	1	-0.46700346	0.33719307	0.64555103	-0.02045603	0.21922177	-0.6304028
Distance to Shrub	-0.56712409	-0.46700346	1	0.43667259	0.03348844	0.38978285	-0.47987774	0.50651392
Distance to Grassland	-0.92012623	0.33719307	0.43667259	1	0.90253895	0.04135132	0.22534668	-0.40071504
Distance to Pasture	-0.76751578	0.64555103	0.03348844	0.90253895	1	-0.0606227	0.44076934	-0.67584303
Distance to Woody Wetlands	-0.30648394	-0.02045603	0.38978285	0.04135132	-0.0606227	1	-0.58799613	0.45724289
Distance to Herbaceous Wetlands	0.09832007	0.21922177	-0.47987774	0.22534668	0.44076934	-0.58799613	1	-0.82505162
Distance to Developed Area	0.07127753	-0.6304028	0.50651392	-0.40071504	-0.67584303	0.45724289	-0.82505162	1

Table A12. Correlation of land cover types in the 2-kilometer buffer area around Chuck-will's-widow (*Antrostomus carolinensis*) used locations during the post-breeding season using the U.S. Geological Survey National Land Cover Database.

	Distance to Water	Distance to Evergreen	Distance to Shrub	Distance to Grassland	Distance to Pasture	Distance to Woody Wetlands	Distance to Herbaceous Wetlands	Distance to Development
Distance to Water	1	-0.25403603	-0.56712409	-0.92012623	-0.76751578	-0.30648394	0.09832007	0.07127753
Distance to Evergreen	-0.25403603	1	-0.46700346	0.33719307	0.64555103	-0.02045603	0.21922177	-0.6304028
Distance to Shrub	-0.56712409	-0.46700346	1	0.43667259	0.03348844	0.38978285	-0.47987774	0.50651392
Distance to Grassland	-0.92012623	0.33719307	0.43667259	1	0.90253895	0.04135132	0.22534668	-0.40071504
Distance to Pasture	-0.76751578	0.64555103	0.03348844	0.90253895	1	-0.0606227	0.44076934	-0.67584303
Distance to Woody Wetlands	-0.30648394	-0.02045603	0.38978285	0.04135132	-0.0606227	1	-0.58799613	0.45724289
Distance to Herbaceous Wetlands	0.09832007	0.21922177	-0.47987774	0.22534668	0.44076934	-0.58799613	1	-0.82505162
Distance to Development	0.07127753	-0.6304028	0.50651392	-0.40071504	-0.67584303	0.45724289	-0.82505162	1