AMERICAN WOODCOCK HABITAT SELECTION AND REPRODUCTIVE SUCCESS IN MICHIGAN

By

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ABSTRACT

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A detailed abstract with results is included at the beginning of each chapter as they are intended for separate publication. In chapter one, I evaluated how habitat selection for American woodcock (*Scolopax minor)* nests and broods is affected by local vegetation characteristics. I also assessed changes in earthworm density, an important food source for woodcock, over the course of the breeding season. I hypothesized that habitat selection would be different between nesting and brood-rearing hens, that selection cues would change throughout the breeding season as chicks aged, and that earthworm density would decline throughout the breeding season. I deployed cameras to woodcock nesting sites, captured and marked woodcock broods with telemetry equipment, and measured vegetation around both used and available sites. My results showed that nesting woodcock select different habitat than do brood-rearing birds and that earthworm density in the top layers of soil declines throughout the breeding season, but brood habitat selection did not change as chicks aged.

In chapter 2, I linked nest success and brood survival to local habitat characteristics. I hypothesized that stem density, canopy cover, soil moisture, and soil organic matter would have positive effects on reproductive success. Using Mayfield and known fate analysis methods, I estimated nest success and brood survival from hatch to fledge. My results showed that nest success was not influenced by local habitat characteristics, but that brood survival was influenced by woody ground cover, such as shrubs and seedlings, and soil moisture. My results indicate that understory cover is an important consideration for woodcock habitat management.

This thesis is dedicated to Richard Erickson, the first and best scientist I ever knew. He taught me about the natural world, encouraged me to ask questions, and instilled in me a passion for science that helped lay the foundation for this work.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

While many people appreciate the beauty of old growth forests and undisturbed landscapes, disturbed and early successional forests have inherent value for many wildlife species (Dessecker and McAuley 2001, Litvaitis 2001). Many forms of disturbance that create early successional forest, such as fire and flooding, have been suppressed, leading to steep declines in this type of critical habitat on the landscape (DeGraaf and Yamasaki 2003, Tavernia et al. 2016). Unfortunately, managing for young forest can be challenging due to social perceptions of usual disturbance methods, such as clear cutting and controlled burns (Lorimer 2001). Loss of young forest, however, has resulted in the decline of many different species, especially avian species such as the ruffed grouse (*Bonasa umbellus*), the golden winged warbler (*Vermivora chrysoptera*), the American woodcock (*Scolopax minor*), and many songbird species (Dessecker and McAuley 2001, Bakermans et al. 2015, Masse et al. 2015). American woodcock in particular have declined so steadily since 1970 that they have been designated a species of special conservation need, and habitat loss is thought to be the main driver behind their population decline (Seamans and Rau 2019, Kelley et al. 2008). Answering questions about their relationship to their habitat and creating effective management plans are critical to bolstering their vulnerable population.

American woodcock are a popular game bird in the eastern United States and southeastern Canada (Seamans and Rau 2019). Typically, they are associated with early successional forest, upland shrubland, and wetland shrubland that is maintained by rotating clear cuts in older forests to allow for regeneration of dense stems characteristic to young forests (Donovan et al. 2010). As of 2008, biologists estimated that the woodcock population in the United States had suffered a loss of over 829,000 singing males since 1970, leading to a deficit of over 986,000 males (Kelley et al. 2008). With declining woodcock numbers, woodcock hunting has also decreased, and fewer and fewer birds are seen dancing in the skies each year during the breeding season (Kelley et al. 2008, Seamans and Rau 2019). In response to declining woodcock populations, the Woodcock Task Force, the Migratory Shore and Upland Game Bird Working Group, and the Association of Fish and Wildlife Agencies compiled the American Woodcock Conservation Plan, which delineated a set of goals for woodcock conservation (Kelley et al. 2008). Wildlife managers identified increased understanding of breeding habitat as one of the priority information needs for woodcock (Case and Sanders 2010).

Woodcock breeding habitat has been notoriously difficult to study due to the cryptic nature of the birds and the difficulty associated with locating nesting sites and capturing females with broods in the field (S.R. McWilliams, University of Rhode Island, personal communication, 2018, Masse et al. 2014). Issues with research on female birds has led to a large portion of woodcock research being done with male birds, rather than females (e.g. Hudgins et al. 1985, Brenner et al. 2019). But given that female and juvenile survival, as well as fecundity, are critical factors of woodcock population growth (Saunders et al. 2019), it is essential to study the effects of habitat during the vital period of woodcock nesting and brood-rearing. To gain more information about woodcock breeding habitat, managers were interested in answering questions about how vegetation characteristics affect not only woodcock habitat selection, but also their reproductive success. Information about the habitat that woodcock typically select is useful in creating and revising management strategies, but density alone can be a deceiving metric of habitat quality (Van Horne 1983), and relating the information to an animal's fitness in their environment makes habitat data more advantageous (Aldridge and Boyce 2008). For this reason, I sought to answer questions concerning both habitat selection and survival.

In chapter 1, I evaluated a suite of habitat metrics to determine habitat selection under a use-availability framework. To do this, I located 70 woodcock nesting sites and captured 58 woodcock broods in the spring and early summers of 2018 and 2019. I deployed cameras at as many nesting sites as possible to determine their fates, and I marked woodcock chicks with radio telemetry equipment to allow for relocation and habitat analysis. I measured local-scale habitat measurements such as canopy closure, ground cover, sapling density, basal area, and soil characteristics in both used and available areas once per nest and up to 3 times per brood, to try to evaluate the differences in brood habitat use over time. I hypothesized that I would find differences between habitat selection patterns for nesting versus brood rearing birds, and that I would find differences in selection between young and old chicks. I also sampled earthworm density, an important metric of food availability, and I hypothesized that earthworm density in the top layers of soil would decrease over the course of the breeding season. To identify which habitat characteristics were important for selection, I used conditional logistic regression models to find differences between used and available sites. I also used general linear models to assess the relationships between earthworm density and Julian date, study year, and used and available sites. Nesting birds favored areas of more dense forest closure and drier soils, while brood rearing birds favored areas of wetter soils and more woody ground cover. Stem density was important to both nesting and brood rearing birds. While I did find that earthworm density did indeed decrease over time, I also found that selection did not change for woodcock broods as chicks aged. My results suggest that when creating woodcock management plans, special care must be taken to accommodate the differences between nesting and brood rearing habitat areas. Managers must also consider drier soil conditions in later summer that lead to decreased food availability, and manage for woodcock in areas that have sufficiently wet soil all season long.

In chapter 2, I analyzed both nest success and brood survival and linked them to the same local habitat characteristics that I measured to assess habitat selection in chapter 1. My goal was to determine whether local habitat influenced nest success and chick survival. I used the Mayfield estimator to determine nest success for my study, and used logistic regression to look for habitat differences between successful and failed nesting sites. To assess brood survival, I used a known fate model with staggered entry and right censoring. I hypothesized that sapling density and soil moisture would have the highest impact on woodcock reproductive success. What I found, however, was that habitat characteristics had no discernible effect on nest success at the local scale that I measured. Brood survival was influenced by local habitat characteristics; specifically, woody ground cover such as shrubs and seedling trees <1 m tall had a significant positive effect on brood survival, while excessive soil moisture had a slight negative effect on brood survival. The findings demonstrated the importance of well-developed understory cover in the survival of woodcock broods and the importance of avoiding forest management in areas that are prone to excessive flooding, which can decrease earthworm density (Ausden et al. 2001). The findings also demonstrated the importance of scale considerations when deciding on management plans. Further research on nest success at various spatial scales will be critical in the pursuit of increased understanding of woodcock breeding habitat.

The goal of my research was to increase our understanding of habitat needs for American woodcock and help managers implement more effective forest management and conservation strategies to combat woodcock population declines. Each of these chapters is written for independent publication with coauthors, thus I use the plural “we” instead of the singular “I”.

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CHAPTER 1: HOME SWEET HOME: AMERICAN WOODCOCK NEST AND BROOD SITE CHARACTERISTICS IN MICHIGAN

Abstract

American woodcock *(Scolopax minor)* are a charismatic avian species distributed throughout the eastern United States and southeastern Canada. They are recognized for their value as a game species, especially in Michigan, and for their ecological value as an umbrella species. Woodcock populations have been declining 1% to 1.9% per year or more since 1970 due to habitat loss. Wing collection indices also show a decline in juvenile birds per adult female, suggesting reduced woodcock productivity. Challenges associated with capturing and monitoring breeding females and broods have left our understanding of woodcock breeding habitat incomplete. Our objectives were to assess local scale habitat selection for nests and broods, test for differences in brood habitat selection over time, and determine how availability of woodcock's primary prey varies over the course of the breeding season. We located nest and brood sites in the Lower Peninsula of Michigan and monitored broods 3 times per week by attaching radio transmitters to chicks. We measured habitat variables around all nesting sites and a subset of brood sites. We found that nesting hens select areas with more overstory canopy cover and basal area than hens with broods, while broods use areas with wetter, more organic soils. Probability of site use by woodcock broods doubles with every sapling/m^2 increase, and triples for woodcock nests. We also found that habitat selection within broods does not change over time. Lastly, we determined that earthworm density in the top 10 cm of soil declined by 0.97 worms/m^2/day, possibly because of hotter temperatures and drier soil. Active management that produces forests with high sapling density near wetlands is essential to maintain adequate earthworm abundance in preferred habitat. Effective management must consider soil characteristics and the differences between nesting and brood-rearing habitats.

Introduction

In a world where 3 billion birds have been lost since 1970 (Rosenberg et al. 2019), habitat loss has emerged as one of the critical drivers of wildlife population decline and extinction (Bender et al. 1998, Rappole 1996, Rosenberg et al. 2019). A serious need for effective wildlife management, especially as it pertains to efforts to halt or reverse population declines, is a thorough understanding of species habitat needs and selection, as selection links organisms with the habitat characteristics they need to survive (Leclerc et al. 2016). Given that the survival of females and young and species productivity are especially important to the growth of many populations (e.g. Saunders et al. 2019, Kramer et al. 2019*a)*, it is clear that habitat selection for critical life history stages such as reproduction and rearing young are especially important to understand. The American woodcock (*Scolopax minor*; herein woodcock), an avian game species that inhabits the eastern United States and southeastern Canada, is considered a species of concern across much of its current range, and habitat loss is thought to be the main driver of long-term population declines (Seamans and Rau 2017). Since 1970, woodcock populations have declined between 1% and 1.9% each year across their range, contributing to the catastrophic global loss of avian fauna (Kelley et al. 2008, Seamans and Rau 2017, Rosenberg et al. 2019), and resulting in fewer hunter days afield and fewer woodcock heard singing and seen performing breeding displays (Kelley et al. 2008, Seamans and Rau 2019). Integrated population models that include singing ground surveys, wing collection surveys, band return data, and harvest data from the harvest information program (HIP) show an annual decline of 1% per year since 1963 in both the central and eastern management units, which supports the 1%–1.9% estimates gained from the singing ground survey index alone and shows an even more extensive period of consistent decline (Saunders et al. 2019). In addition to overall population decline, fall wing collection surveys of birds during the woodcock hunting season show a significant decrease in the number of young per adult female (Seamans and Rau 2017). That decrease suggests habitat loss and other sources of mortality are disproportionately impacting woodcock productivity through reduced reproductive success or survival of young.

The decline of woodcock populations has been detrimental to hunters and other enthusiasts who enjoy watching woodcock. Woodcock are a valuable game species; for many years before 1990, woodcock were among the most important avian game species based on numbers harvested in several states east of the Mississippi River, and Michigan has continued to lead the nation in number of woodcock hunters and harvest (McAuley et al. 2005, Cooper et al. 2013). Though over 100,000 woodcock were harvested throughout their range in 2019, the number of woodcock hunters, days spent hunting, and harvest have declined in Michigan and across the U.S. over the last 20 years (Seamans and Rau 2019). Woodcock are also highly appreciated by birders for their unique breeding displays, which have been termed the "sky dance" (Leopold 1949), but fewer woodcock have been seen performing these displays (Seamans and Rau 2019). Aside from the consumptive benefits for conserving woodcock, there are also important ecological incentives for reversing woodcock declines and creating favorable habitat that will ensure their proliferation. Because woodcock are charismatic and sought after by birders and hunters alike, and they share habitat with many other avian species, they are an excellent target species when managers are deciding how to manipulate habitat for the benefit of multiple species (Masse et al. 2015). For example, ruffed grouse (*Bonasa umbellus)*, another popular game species in North America, share habitat requirements with woodcock (Dessecker and McAuley 2001), as does the golden-winged warbler (*Vermivora chrysoptera)*, an avian species that has experienced significant declines in a similar time frame as the woodcock (Bakermans et al. 2015). While the use of woodcock as an umbrella species for the golden-winged warbler has been called into question (Kramer et al. 2019*b*), forests that support woodcock habitat requirements generally contain higher bird diversity because early successional forests support many different species (Masse et al. 2015). Aside from birds alone, a large number of lagomorphs are early successional forest obligates, and black bears *(Ursus americanus)* and little brown bats *(Myotis lucifugus)* utilize early successional forest in addition to mature forest for important foraging areas, especially in early spring (Litvaitis 2001). Even white-tailed deer *(Odocoileus virginianus)* populations, arguably the most important game species in North America, respond positively to creation of early successional forests, though they are not early successional forest obligates (Litvaitis 2001). Managing the landscape for woodcock habitat provides a host of benefits to other wildlife management goals.

We have a good understanding of general habitat requirements for woodcock. Woodcock depend heavily on early successional forest as their primary habitat, and they require moist soils that support healthy earthworm populations, which are their main source of food (Sperry 1940). This type of forest provides higher stem density and greater shrub cover, which is critical in affording woodcock protection from predators, especially during their breeding season (Dessecker and McAuley 2001). Woodcock are often associated with aspen (*Populus* spp.*)* stands, as aspen regenerates from roots underground and can easily create areas of high stem density, but alder management can also create this kind of dense vegetation (Donovan et al. 2010). Essential woodcock habitat is often difficult to maintain, as young forest is transitory by nature and historic natural disturbances have been suppressed, leaving natural forest disturbance unable to create substantial areas of habitat (DeGraaf and Yamasaki 2003). Previously, fire, beavers, windstorms, floods, and Native American agriculture all served as natural disturbance that helped create early successional forest, but most of these phenomena have now been suppressed; indeed, only beavers remain as consequential forest disturbers (DeGraaf and Yamasaki 2003). Forest management is the only realistic way to create extensive woodcock habitat, but management and forest disturbance for woodcock are not appropriate in all types of forest (Donovan et al. 2010). Given the very specific nature of woodcock feeding habits, woodcock need habitat creation in areas with appropriate rich sandy loam or loamy sand soil types (Bourgeois 1976) and near streams, wetlands, and other riparian areas that provide plentiful earthworms throughout the entire breeding season (Donovan et al. 2010). Biologists believe that at least 20 million new acres of woodcock habitat need to be created in appropriate areas to restore woodcock populations to their 1970 population estimates (Kelley et al. 2008, Seamans and Rau 2017).

Woodcock breeding habitat includes their general habitat requirements such as early successional forest, high stem density, forest clearings, and shrub cover, but needs for breeding habitat are more specific. Current knowledge of breeding habitat hinges on previous studies such as McAuley (1996), which showed that woodcock nest sites are often close to edges, in deciduous forest instead of coniferous forest, and in places with shorter and denser trees. In addition, woodcock seem more sensitive to the structure of their habitat than to species composition, and vegetative species vary much more among habitats than do structural components such as stem density and basal area (Gutzwiller et al. 1983, Dessecker and McAuley 2001). Females tend to be especially sensitive to this structure during nesting and select understory cover over moist soils for their nesting sites. Bourgeois (1976) found that after nests hatch, woodcock hens with broods exhibit different habitat selection than those of nesting hens, making use of much wetter areas with higher tree density. While young broods <7 days old make small movements and will often stay within 100 m of their nest site (Kramer et al. 2019*a*), chicks can move great distances after hatching, especially if disturbed (Gregg 1984). Brood movements are affected by earthworm abundance at previous foraging sites and weather patterns, including temperature and precipitation (Doherty et al. 2010). As broods age and move across the landscape, they may exhibit changing habitat selection patterns, which requires consideration when developing management plans to benefit woodcock via habitat manipulation. Changes in habitat selection with brood age could become even more pronounced in dry years, as earthworm abundance is heavily influenced by soil moisture and temperature (Doherty et al. 2010, Rabe et al. 1983*b*). If late season heat causes earthworms to become unavailable, woodcock could face selection choices that prioritize moist soils and earthworm abundance over specific cover types as they age. While some work that shows that older broods may have different habitat preferences than younger broods (Dwyer et al. 1982), the strength of those relationships, and the strength of the relationship between habitat selection and breeding habitat as a whole, has not been quantified. Likewise, while we know that earthworm density is subject to temperature and precipitation, and that light, loamy soils carry higher earthworm populations (Guild 1948), we have not quantified potential changes in earthworm availability in woodcock habitat as the breeding season progresses. Management thrives off clear, quantified results that inform habitat manipulation, and current management strategies might inadequately account for both changing life history traits for woodcock broods and changing food availability in woodcock preferred habitat.

In most cases, habitat management for woodcock includes clearing strips or entire forest stands that simulate natural disturbance. Recent clear cuts serve as forest openings that woodcock use for roosting and displaying, and regenerating areas become young forest habitat on which woodcock and other species depend. Rotating areas of clear cutting is meant to create the kind of varied habitat that woodcock need: clearings for courting and roosting, wetland scrub-shrub habitat for feeding, and drier sites with high sapling density for nesting (Donovan et al. 2010). Despite these management efforts, the amount of young forest and woodcock populations have either declined or remained stagnant in many portions of their range, and rates of young per adult female have continued to fall (Seamans and Rau 2019). In addition, we have a dearth of information specific to breeding habitat due to the challenging nature of capturing and marking females and their broods in the field, as opposed to capturing males at conspicuous display sites (S.R. McWilliams, University of Rhode Island, personal communication, 2018; Gregg and Hale 1977, Masse et al. 2014). Lacking information specific to woodcock nests and broods leads to questions about how habitat selection could be related to chick age and movements, and about how food availability in woodcock breeding habitat may change over time.

Our current understanding of woodcock breeding habitat selection is incomplete. Because very few studies of woodcock chick movements exist, we do not know if recorded habitat differences are strictly between nest and brood sites, or if perhaps subtle differences in habitat selection result in different choices as broods age. The coarse approach that management currently takes to creating young forest may be overlooking the intricacies of local habitat usage by nesting females and their broods, or may be creating habitat in areas suitable to birds in early spring that dry up and leave insufficient food availability. Thus, we sought to answer two important questions about woodcock selection. First, for what local-scale habitat characteristics are woodcock selecting for nesting and brood sites, and how do those characteristics relate to overall habitat selection? Second, how do woodcock habitat needs change through the breeding season, and how does earthworm abundance, and thus woodcock food availability, change over time? We hypothesized that woodcock would show different preferences for nest and brood rearing sites, exhibit changing selections as chicks age, and that earthworm density will decrease throughout the breeding season. Our specific objectives were to: 1) predict probability of habitat use by nesting woodcock and broods based on measured vegetation characteristics, 2) test how habitat selection changes, if at all, as a function of chick age, and 3) analyze changes in earthworm density, and thus food availability, over time. In doing so, we aim to improve the effectiveness of woodcock habitat management by providing insight into the relationship between local habitat characteristics and selections.

Methods

Study area

Our study area spanned the mid- to northern Lower Peninsula of Michigan (Figure 1.1). Most nest and brood sites were in the Boreal Hardwood Transition Bird Conservation Region (BCR), which covers the entire northern Lower Peninsula (Tavernia et al. 2016). In the Boreal Hardwood Transition BCR, we worked in Clare, Crawford, Gladwin, Grand Traverse, Kalkaska, Missaukee, Montmorency, Ogemaw, Roscommon, and Wexford counties. We also worked in the Prairie Hardwood Transition BCR, which covers the southern Lower Peninsula of Michigan (Tavernia et al. 2016). In that area, we worked in Clinton, Gratiot, Isabella, Midland, Oakland, and Osceola counties. We had sites in Mason County that were split between the Prairie and Boreal Hardwood Transition BCRs.

Typical nest and brood sites in the Great Lakes Region consisted of <20-year-old stands of aspen (*Populus* spp.), maple (*Acer* spp.), alder (*Alnus* spp.), or birch (*Betula* spp.) trees (Gregg and Hale 1977, Ammann 1970). Areas were often a mix of dense forest stands, forest openings, and nearby swamps or standing water. Sites contained varying levels of forest versus agricultural areas within 10 km of the nest or brood. For example, Alger State Game Area in Gladwin County, and Wexford State Game area in Wexford County, both in the Boreal Hardwood Transition BCR, contain high levels of forest (80–84%) and low levels of agriculture (1–13%). In the Prairie Hardwood Transition BCR to the south, Gratiot-Saginaw State Game Area, Rose Lake State Game Area, and Holly Recreation Area were all surrounded by higher levels of agriculture, with a 50/50 split between forest and agriculture within 10 km of the areas (Shoffner 2018). The highest density of sites was in Roscommon County and included public land throughout the county, surrounding Houghton Lake, Prudenville, and St. Helen. This region had low levels of agriculture, and was dominated by forest cover. Soils in these areas, and across Michigan, are highly variable. In the northern Lower Peninsula, where most of our study sites were located, sandy soils are dominant (Sommers et al. 1984). Spodosols and histosols, which contain high portions of decaying vegetation and other organic matter, are also prevalent in Roscommon County and other areas where our study sites were concentrated (Sommers et al. 1984). Clay and loam soils dominate the southern Lower Peninsula (Sommers et al. 1984). Based on analysis of our own soil samples, soil types in our study areas, including those in the southern lower peninsula, were predominantly sandy loam or loamy sand, which are the dominant soil types that woodcock use for both nesting and brood-rearing (Bourgeois 1976).

In both years, 2018 and 2019, our study period went from 1 April to 14 July. Average temperatures in northern Michigan during this period in 2018 ranged from 6.38 ℃ to 20.11℃, while in 2019 they ranged from 5.96 ℃ to 18.53℃. Northern Michigan received approximately 268.3 mm of rain and 359 mm of snow during this time in 2018, with the last snow melted in most areas by 20 April. Precipitation in 2019 included 328.8 mm of rain and 251 mm of snow, with snow melted in most areas by 15 April. In southern Michigan, average 2018 temperatures ranged from 9.9℃ to 21.6℃, with precipitation including approximately 303.6 mm rain and 112 mm snow. Snow was melted by 19 April. Average 2019 temperatures in southern Michigan ranged from 9.36℃ to 20.59℃. Rainfall was approximately 332.9 mm, and snowfall was 41 mm. Snow was melted by 15 April. During our 2019 field season, the climate was more moderate, without the extreme high and low temperatures and cold rain events followed by drought that 2018 experienced. All climate data was retrieved from NOAA's database for climate data online (NOAA Climate Data Online 2020).

Woodcock capture and marking

In the summers of 2018 and 2019, we worked with a dozen woodcock banders who volunteered for the Michigan DNR to mark woodcock chicks. We chose sites based on areas that our volunteer banders were familiar with and on our own observations of displaying male woodcock. Most of our sites were on public land, but we used a few areas of private land that were specifically managed for woodcock. We used trained pointing dogs to search for birds in areas of good woodcock habitat, according to accepted capture methods detailed by Ammann (1974) and McAuley et al. (1993). After locating broods, we used hand nets to capture chicks and placed leg bands on all chicks in the brood. We placed radio-transmitters on 2 randomly selected chicks within the brood and used 3 sizes of transmitters depending upon chick weight (Holohil BD-2C, transmitter masses were 0.85, 1.1, and 1.4 g). We attached these transmitters with necklace style collars made of flexible material that was designed to stretch as the chick grew. We custom fit collars by gluing the elastic material into small loops that fit over a chick's head. Each collar was <3% of the chick's overall body weight, which meant that for 9 of our 58 broods, we placed collars on the largest chicks in the brood instead of randomly selecting chicks, as the smaller chicks did not weigh enough to wear transmitters. We used this attachment method in accordance with Daly et al. (2015), who found that this type of collar had no significant impact on the survival of woodcock chicks.

Woodcock nesting sites were also located using pointing dogs. We did not capture hens from nests or float or candle eggs, as nesting woodcock are sensitive and excessive disturbance can induce nest abandonment (McAuley et al. 1993). Instead, we placed trail cameras (Browning BTC-6HD-940) at nesting sites, which took bursts of 5 photos every 30 seconds. In this way, we monitored nests regularly to determine their fate and the date of hatch or failure.

This research was approved by the Michigan State University Institutional Animal Care and Use Committee (Protocol Number 04/18-063-00).

Vegetation surveys

After marking chicks and determining the location of nests, we used these locations to measure vegetation characteristics around selected sites. At each nest site, we measured a suite of characteristics based on methods detailed by Masse et al. (2014) (Table 1.1). With the bird or nest location at the center, we created a circular plot with a 5-m radius. Within this 5-m radius, we chose 4 random points surrounding the center, a random distance from the center in each cardinal direction. At the center of the plot and at each of these 4 random locations, we measured percent canopy closure, counted the number of saplings >1.5 m tall in a square m, and dug a small 10-cm^3 soil pit to count the number of earthworms present (Masse et al. 2014). Finally, we measured ground cover using 1 m square Daubenmire quadrat frames and the Daubenmire class method at the center of the plot and each of the 4 random locations, using cover class intervals of 0–5%, 5–25%, 25–50%, 50–75%, 75–95%, and 95–100% (Bonham 2013). Types of ground cover included litter, bare ground, standing water or puddles, forb, grass, woody shrubs, dead wood, and moss. Finally, we used a soil probe to remove 2 10-cm deep soil samples from the center and each of the 4 random locations. We stored the soil samples in airtight containers in freezers for later analysis in a laboratory after completing all field work responsibilities. We also dug small 10x10 cm soil pits in the center and at each of the 4 random locations, and we counted the number of worms in each pit. We then used the number of worms we counted to estimate the number of worms per square meter in each 15 m diameter plot. We only counted the worms in the top 10 cm of the soil because these are the ones that are available to woodcock; worms in deeper soil will be beyond the reach of a female woodcock's bill, which is typically 72–74 mm in length (Sheldon 1967), and thus not available as a food source.

After finishing the measurements in the 5 sub-quadrats of the vegetation plot, we counted the number of trees present in the entire 5-m radius plot. We counted all trees with a diameter at breast height (DBH) of >10 cm. We measured the DBH of every tree in the plot, and used this information to calculate the basal area of trees in the plot. We then measured the distance from the center of the plot to the nearest forest opening and to the nearest tree, either inside or outside the plot, and we recorded the species of that tree. We recorded the overstory height as one of three categories: 0–3 m tall, 3–9 m, or >9 m.

We performed these same measurements on a subset of brood locations. After marking birds and performing telemetry, we measured vegetation around one diurnal location every 2 weeks, with a goal of performing 3 vegetation surveys per brood. We used this time increment to capture habitat selection at 3 distinct phases of brood maturation. At 0–2 weeks of age woodcock chicks are unable to fly. At 2–4 weeks old they can fly but have not yet separated from their brood. After 4 weeks chicks are often found alone, separated from their brood (Gregg 1984), and we considered them to have fledged. In addition to focusing on these age classes, we kept track of the age in days of each chick, which was calculated by measuring the length of the chicks' bills (Ammann 1977, Gregg 1984). For each used site, both for nesting sites and brood sites, we performed the same set of vegetation measurements on a paired site that we deemed available to the bird at the time they occupied the used site.

Soil analysis

When field data collection was complete, we analyzed all our soil samples to determine moisture and organic content, pH, and inorganic particle components of sand, silt, and clay. Most work was performed by the Plant and Soil Science Nutrient Laboratory at Michigan State University. We performed some work ourselves according to accepted soil analysis procedures laid out by their laboratory protocols. Specifically, we measured soil moisture content by drying samples to a constant weight at 105°C, which is not high enough to burn away any organic matter, and calculating the percent moisture by looking at the differences in weights before and after the drying process (Masse et al. 2013, Pansu and Gautheyrou 2006). After measuring moisture with these oven-dried samples, we further heated the samples to 550°C for 4 hours to burn away organic matter, and weighed the samples again after they had been reduced to inorganic particles. Both soil moisture and organic matter are recorded as a percent by weight (Masse et al. 2013). To measure soil pH, we added distilled water to small soil samples at a 5:1 ratio, and used a glass pH electrode and a pH meter to record pH values of each sample (Masse et al. 2013) using a LabFit AS-3000 pH analyzer. Finally, to determine the percentage amounts of sand, silt, and clay in each soil sample, we used the hydrometer method of particle size analysis (Gee and Bauder 1986). Some of our soil samples were so organic that the sand, silt, and clay they contained was negligible. In these cases, we could not perform full particle size analysis, so after burning off organic particles, we used distilled water to wash smaller particles through a sieve, leaving only sand behind (Gee and Bauder 1986). We could then obtain the percent sand content in the soil, while the leftover non-organic material was considered a mix of silt and clay.

Determining habitat availability

To describe habitat use by nesting woodcock and broods in relation to available habitat, we implemented a use-availability design that allowed us to compare used nest and brood sites with random sites that we deemed available to the bird at the time (Masse et al. 2014, McAuley et al. 1996). Evaluating use and availability is challenging, because we do not know with certainty that a bird never used an available but unoccupied site (Johnson et al. 2006), and it can be difficult to know what scale is appropriate to define available habitat. We informed our decision of habitat availability to woodcock broods based on both literature and our own observations of the daily movements of woodcock broods. During our pilot field season in 2017, the maximum distance that we observed woodcock broods moving between locations during the brood-rearing period was approximately 180 m. These displacements were not daily movements, as we only located broods 3 times a week. Our movement observations agree with previous woodcock literature that describes a woodcock brood’s home range as a space of approximately 200 yards (Gregg 1984). Based on this information, we selected paired available sites by choosing a random direction and distance within 200 m, and using that point as our paired available location. Under this use-availability design, we compared the vegetation characteristics of used sites and random available points. We did not use random sites that fell in open water, directly on roadways, or sites on private land that we did not have permission to access. In these instances, we selected a new random point using the method described previously.

Modeling framework

We modeled habitat use by nesting woodcock and broods based on our vegetation measurements using a conditional logistic regression model, which allowed us to account for our paired used and available sites on the landscape (Duchesne et al. 2010). We performed all our statistical modeling in R using the survival package (Therneau 2015). Paired used and available sites were not independent of one another for either nests or broods, since we determined the location of available sites based on the location of the known used sites. In addition, we performed multiple vegetation surveys on the same brood over time when looking at habitat use in distinct brood maturation phases. The locations of older broods were conditional on the previous locations of those same broods when they were younger, and it is likely that habitat selection was correlated within broods. Conditional logistic regression allowed us to account for pairing of the used and available sites as well as multiple observations per brood, rather than comparing entire groups of used and available sites. We therefore included brood affiliation (i.e., brood identification) as a random explanatory factor in the conditional logistic model.

While conditional logistic regression was useful to allow for pairing of used and available sites, we could not include all 18 of our quantitative habitat variables in one single global model due to a small sample size. To avoid overparameterization, we applied principal components analysis to reduce the dimensionality of the data and produce uncorrelated combinations of these variables (Masse et al. 2014, Johnson and Wichern 2007). In the principal components analysis, we included all variables that measured habitat structure and composition and some soil characteristics, as these factors are directly apparent to the bird and easily attributable to habitat selection (Table 1.1). Since the components of soil (proportions of sand, silt, and clay) are correlated and sum to 1, we used percent sand to characterize soil particle size composition.

Likewise, soil moisture and soil organic matter were also correlated, so we used soil moisture in the principal components analysis to characterize both moisture and organic matter, rather than using both parameters. We did not include earthworm density in our principal components analysis, as it is not a structural component of habitat and it is unlikely birds can use as earthworm abundance directly as a selection criterion. Instead, we analyzed earthworm density and how it changes over time in a separate model, and while we did assess the difference in earthworm density between used and available sites, we did not use earthworm density to predict and quantify habitat selection of woodcock.

Our principal components analysis created 18 components as possible variables, and we retained the first 6 of these components to use in our conditional logistic regression analysis based on their Eigenvalues (Masse et al. 2014). Each principal component also had loadings scores that reflected the weight of each individual variable in the 6 components; by examining these weights, we were able to infer importance of variables each principal component represented, and this helped us to interpret the different components for use in the selection model. We used the individual variables that loaded >0.5 (Table 1.2) in the weights of the components to create and test additional candidate models. We tested candidate models using groups of both individual variables and principal components variables to understand whether principal components or the single variables they represented were a better fit for our data. We tested habitat models for nests and broods separately, which enabled us to see differences in habitat selection for nesting hens and at brood sites. Overall, we tested 17 candidate models to test habitat selection by nesting hens (Table 1.3) and 18 candidate models to test habitat selection by hens with broods (Table 1.4). Our global model for both nests and broods included all 6 of the retained principal components. We used Aikaike's Information Criterion for small sample sizes

(AIC_c) due to small sample size to parameter ratio to rank competing models and select the model of best fit based on a ΔAIC_c of 2 (Burnham and Anderson 2002, Guthery 2008).

To test how habitat selection changes as a function of chick age, we added chick age in days as an explanatory variable interacting with habitat variables and principal component variables in the brood habitat selection models only. We added age in days as an interaction to variables that we specifically hypothesized would change over time: principal components, sapling density, and soil characteristics. Our intent was to test whether selection would change as chicks aged from hatch to fledge during the brood rearing season, while limiting interactions to a priori hypotheses to avoid overparameterizing models or creating an excessively large model set. By adding an interaction of age in days, we tested for differences in habitat use by age class. We did not include age in days as an interaction parameter for nests.

To model earthworm abundance in the top 10 cm of soil over time, we evaluated a suite of 9 linear mixed models designed to estimate the effects of year, Julian date, and used and available sites on earthworm density, as earthworms make up most of a woodcock's diet (Sheldon 1967, Table 1.5). Our global model for this model set included Julian date, year, used and available sites, and the interaction between used and available sites and Julian date. We did not include earthworm density in our habitat selection models because it was not a structural habitat component that could be easily manipulated by management, like sapling density, nor was it a constant indicator that would help make decisions about where to perform management, like soil types. We used brood ID as a random effect in this model to account for multiple observations per brood over time. We did not assume that food availability was constant all season long, as earthworm abundance can be strongly affected by weather patterns such as freezing and drought (Vander Haegan et al. 1993). Once again, we assessed model fit using used

Aikaike's Information Criterion for small sample sizes (AIC_c) due to small sample size to parameter ratio, and we selected the model of best fit based on a ΔAIC_c of 2 (Burnham and Anderson 2002, Guthery 2008).

Results

Summary

In the spring and early summer of 2018 and 2019, we measured vegetation characteristics around 71 nest sites and up to 3 different locations for 58 marked broods. In 2018, we located 27 nesting sites and monitored 17 broods, and in 2019 we located 44 nesting sites and monitored 41 broods. In the 2 years, 5 additional broods were marked but removed from the study because they died or were lost within 24 hours of capture.

We found that woodcock habitat measurements were highly variable at used sites for both nests and broods. Nesting sites ranged from 0.8%–99% canopy closure with an average of 63.1% (Table 1.6); we found nests in both in clearings and in very dense forests. Canopy closure for brood sites ranged from 4.7%–100%, with an average of 74.4%. Sapling density was similar across nest and brood sites, ranging from 0–18 saplings per square meter and averaging approximately 2 saplings per square meter across used sites and 1 sapling per square meter across available sites. While typical brood sites did tend to have higher sapling density than 2 saplings per square meter, we also found broods in small forest openings and swampy areas with more shrubs than saplings. Soil moisture ranged from 5.9%–61% in nesting sites and 0.55–96.1% in brood sites. Brood sites tended to be much wetter than nest sites, and we routinely found broods in swamps and areas of significant standing water, but we did locate 2 nests in unexpectedly swampy areas. Soil moisture was another example of huge variability across used sites. Soil moisture was typically substantially higher in used sites than available sites. Overstory height tended to be similar between nest and brood sites, with a median of about 7 m tall, and ranged from 0–12 m. Overstory height was taller in used sites than available sites for nests, but was not notably different between used and available sites for broods. A complete summary of our vegetation measurements can be found in Table 1.1.

Principal components

Using all the habitat variables listed in Table 1.1, our principal components analysis created 18 components. We retained the first 6 components because their eigenvalues were all >1.0, while the remaining 12 components had eigenvalues of <1.0 (Masse et al. 2014), and tested them in the resource selection models along with individual variables for nests and broods. These 6 components explained 58.9% of the total variance among the variables. We described and named each of these 6 components based on the proportion of each variable in their loadings scores (Table 1.5). Forest closure, component 1, was characterized by a greater percentage of canopy cover, higher overstory height, a higher percentage of leaf litter on the ground, and a decreasing percentage of grassy ground cover. Soil composition, component 2, included higher levels of soil moisture, soil organic content, and mossy ground cover, and a lower percentage of sand in the soil composition. Stem density, component 3, was characterized by an increasing number of saplings per m^2. Components 4, 5, and 6 weighted heavily different aspects of ground cover. We described them as ground cover 1, 2, and 3, respectively. Ground cover 1 was characterized by increasing amounts of open water and decreasing quantities of woody ground cover, such as seedling trees and small shrubs. Ground cover 2 included larger areas of bare ground, and lower amounts of forb ground cover. Finally, ground cover 3 was characterized by higher levels of dead woody ground cover, such as rotting logs and fallen branches.

Nest site selection

We had 5 competing top models for nest site selection, and each of these models included principal components as parameters instead of the individual variables that had loaded heavily into the components (Table 1.2). Together, these 5 top competing models accounted for 0.98 of the overall AIC_c weight (Table 1.2). Forest closure, sapling density, and ground cover 2 were included in all 5 of the competing models and showed strong selection in all of them, while soil composition, ground cover 1, and ground cover 3 were only included in 3 of the top 5 models, and nesting birds did not show strong selection for any of those components. Forest closure and sapling density were positively correlated with nest site selection, while ground over 2 was negatively correlated with nest site selection. Because we had 5 competing models, we performed model averaging to obtain odds ratios and confidence intervals for all components.

Based on odds ratios, the likelihood of a nesting bird selecting an area increased approximately 4 times with each unit increase of forest closure (OR = 4.34, 95% CI = 1.22–15.49, Figure 1.2). Nesting birds also selected strongly for increasing sapling density; with each single unit increase in saplings per sqm, nesting birds were nearly 3 times as likely to select the site (OR = 2.92, 95% CI = 1.23–6.96, Figure 1.2). Ground cover 2, which included more bare ground and less forb cover, was negatively associated with nest site selection. For each unit increase in ground cover 2, nesting birds were <0.2 as likely to choose the associated site (OR = 0.18, 95% CI = 0.04–0.85, Figure 1.2). Though soil composition, ground cover 1, and ground cover 3 were included in some of the top 5 competing models, the 95% confidence intervals around their odds ratios included 1, and their effect on selection for nesting sites was negligible (Soil composition: OR = 2.77, 95% CI = 0.79–9.78. Ground cover 1: OR = 0.49, 95% CI = 0.19–1.25. Ground cover 3: OR = 1.89, 95% CI = 0.82–4.39, Figure 1.2).

Brood site selection

When we evaluated brood site selection, we found that soil composition, sapling density, and ground cover 1 components had the most influence on habitat selection. We had 2 competing top models that had an overall AIC_c weight of 0.59 (Table 1.3). Each of these 2 models included soil composition, sapling density, and ground cover 1. We again used model averaging to calculate averaged coefficients and confidence intervals for the parameters included in the models. Soil composition and sapling density were both positively correlated with selection; with every unit increase in soil composition and sapling density, woodcock were twice as likely to choose that site (Soil composition: OR = 1.99, 95% CI = 1.12–3.52. Sapling density: OR = 2.03, 95% CI = 1.33–3.06, Figure 1.3). Though soil composition included decreasing sand quantity in the soil, we never measured sand in used sites less than 25.2% for brood sites, and most sand percentages were much higher, with an average of 79.3%. Sandy loam was the most common soil type that we observed for brood-rearing sites. Ground cover 1, which included higher levels of open water and lower percentages of woody ground cover, was negatively correlated with selection. For each unit increase in ground cover 1, woodcock were half as likely to use that site (OR = 0.50, 95% CI = 0.26–0.92, Figure 1.3). Forest closure was included in one of the top competing models, not both, but the confidence interval around the odds ratios for that parameter included 1, so the strength of selection for forest closure for broods was minimal (OR = 1.24, 95% CI = 0.83–1.87, Figure 1.3).

Habitat selection change over time

The effect of chick age in days on selection was not included in either of the top 2 competing models (Table 1.3). Odds ratios for the interactions between chick age and soil composition, sapling density, and ground cover 1 were near 1, and therefore showed no support for change in selection of each respective parameter with increasing. Adding age in days as an interaction added extra parameters to the model without improving model fit, and the odds ratios showed that selection for parameters with an age interaction was negligible. We saw no evidence to support our hypothesis that brood habitat selection changes over time as chicks age from hatch to fledge.

Earthworm density

When we evaluated factors affecting earthworm density in the top 10 cm of the soil, we found that the model including Julian date, year, and used and available sites best explained the changes in earthworm density, and this model held a weight of 0.72 in the model set (Table 1.4). Using this model, we were able to predict earthworm density over time, and found that earthworm density was greater at used than available sites, lower in 2019 than in 2018, and that earthworm density decreased with Julian date (Figure 1.4). Earthworm density declined 0.96 worms per sqm per single day increase in Julian date (95% CI = -1.13 – -.80). Available sites typically had approximately 13.13 fewer worms per m^2 than the paired used sites (95% CI = 8.21–18.05). While included in the top model, year had the smallest effect on earthworm density after Julian date and used and available sites, and was not considered to have a significant impact on earthworm density as its confidence interval included 0. Earthworm density in 2019 was approximately 2.28 worms per sqm higher than earthworm density in 2018 (95% CI = -10.21–5.64).

Discussion

Our study provides new information on woodcock breeding habitat, which is considered a priority information need for woodcock management (Case and Sanders 2010). We performed our work in Michigan, a state with a relatively large breeding woodcock population and hunting participation. To improve our understanding of breeding habitat, we assessed selection of nesting females and broods from hatching to fledging. After looking at third order selection (Johnson 1980) under a use-availability framework, we found that nest site selection was influenced by sapling density, forest closure, and leaf litter ground cover; brood habitat selection, while also influenced by sapling density, was more strongly influenced by soil moisture and woody ground cover. Nesting birds selected more strongly for increased sapling density than brood-rearing birds, but sapling density was important for selection throughout the breeding season. Forest closure was the most influential parameter for woodcock nest site selection, while sapling density and soil composition were equally influential for brood site selection. We found differences between habitat selection for nesting hens and hens with broods; specifically, we found that nest sites were in drier areas with ground cover that was dominated by more leaf litter and less forb cover, and that soil composition was not as important for nests as for broods. We found no evidence to support changing intra-brood habitat selection as broods aged, but we saw substantial habitat variability between broods. Finally, we found that earthworm density in the top layers of the soil, an important metric for food availability, declines throughout the breeding season and was higher in used sites than in random available sites.

When we began looking at selection of breeding woodcock, we expected to see differences between habitat choice for nests and broods, especially pertaining to basal area and soil composition (Bourgeois 1976, Rittenhouse et al. 2007), but sapling density emerged as a key similarity for both nest and brood site selection criteria. Increased sapling density was important for both nest site and brood site selection. Current literature agrees, and one previous study about woodcock chick survival found a positive correlation between chick survival and increased sapling density (Daly et al. 2015). Though we used principal components analysis to consolidate variables instead of using individual variables, one of the components was weighted very heavily on a positive relationship with sapling density, while other variables included in the component were negligible (Table 1). High sapling density has long been accepted as a critical component of healthy woodcock habitat, and woodcock Best Management Practices (BMPs) currently in place in the Northeast, Minnesota, and some other areas of woodcock range are focused specifically on increasing areas of young forest with high sapling density (Donovan et al. 2010). In addition to woodcock, many songbird species in need of high sapling density and shrubby forest openings are also in decline, and require increased focus on creating young forest openings and establishing appropriate microhabitat (Roberts and King 2017). A strong focus on increasing sapling density is necessary to promote reestablishment of woodcock populations and achieve conservation goals regarding population declines of other avian fauna.

We expected to find that the distance to the nearest clearing would be as important as sapling density for nest and brood habitat selection, as woodcock use of forest clearings for roosting and courtship behavior has been well documented (Sheldon 1967, Masse et al. 2013). Females often nest in forests that are near clear cuts and other openings (Sheldon 1967, Masse et al. 2013), and brood sites tend to be up to twice as far from clearings as nest sites are (Bourgeois 1967). Despite the documented importance of forest clearings in woodcock habitat, the distance to the nearest clearing was not strongly associated with any of the principal components, and therefore was not included in any of the top models for brood site selection. The soil composition component, which was important for brood habitat selection, included a marginally positive association with the distance to the nearest clearing, but not high enough to be relevant to defining the component. We do not discount the importance of forest clearings to woodcock habitat, but we did not find it to significantly impact habitat selection in our study. We propose several possibilities for the reason behind this. First, while we tried to mitigate bias, our capture method using dogs could have been biased because of the behavior of the dogs during searches. Dog handlers tend to bring dogs to areas that are near forest edges because they are more accessible, and dogs naturally choose the easiest routes to run, which keeps them out of the thickest forest. Most of our random and used sites were relatively close to forest edges, which means that our ability to detect differences in habitat selection based on forest edges was low. Moreover, it could be actively detrimental to woodcock to select areas near forest clearings, since nests near edges may be more vulnerable to predation, the number one source of nest failure both in our study and in general (Hanski et al. 1996). That woodcock nests tend to be associated with forest edges may be more related to their courtship and mating behavior than a specific habitat choice on the part of the female. Finally, it may be that there were enough openings dispersed throughout our study sites that woodcock did not need to be selective about nesting near openings to meet their needs.

While the distance to the nearest clearing was not important to nest site selection in our study, some ground cover characteristics were important; areas with more bare ground and grass were less likely to be chosen, while sites with more litter and forbs were more likely to be chosen. Greater amounts of leaf litter and forb cover, especially later in the year when leaf-out occurs, has been previously documented as important nesting cover (McAuley 1996). Litter and forb cover would be more beneficial to a female woodcock during the nesting phase, when she is sedentary for ~25 days while she is laying and incubating her eggs on the ground. During this period, she relies on cryptic coloration and her ability to remain perfectly still to protect herself from predators - indeed, it is very difficult to locate nesting woodcock in the field, even after it is pointed by a dog. While impractical to simply cover the ground with appropriate substances, promoting forest types that benefit woodcock will ultimately create the thick layer of leaf litter that nesting birds select. Dense stems of aspen, maple, birch, and alder saplings in forest areas <20 years old (Kelley et al. 2008) will create sufficient fall leaf loss to provide a thick layer of leaf litter for nesting areas, while creating enough shade on the forest floor to prevent most grasses from being able to grow. While essential for nesting hens who rely on cryptic coloration to avoid detection, leaf litter was not an important consideration for brood habitat selection, and we found that ground cover was often less in brood sites than nest sites, which has been documented in previous literature (Bourgeois 1976). Differences in ground cover could be a function of different metabolic needs for a nesting hen versus a hen with a brood; while hens typically will not feed within 35 m of their nest sites (Gregg and Hale 1977), during brood-rearing they need to feed up to 4 chicks. Leaf litter around nest sites would not be an impediment to feeding for the nesting hen, but may be a challenge for feeding 4 small chicks at brood sites.

While most aspects of ground cover, including leaf litter, did not significantly affect brood site selection, soil moisture and composition were more important to broods than to nests. Probability of habitat selection increased with additional soil moisture, organic content, and mossy ground cover, while decreasing in areas with higher sand content. Wetter areas with more organic soil may be a necessity for finding enough food, since wet, well-drained soils support higher abundances of earthworms, which are a woodcock's primary prey (Gregg 1984, Reynolds et al. 1977). In both nest and brood sites, earthworm abundances were higher in bird use sites than in available sites. Surprisingly, we often saw higher earthworm abundance at nesting sites than brood-rearing sites, even though nesting woodcock often do not feed near their nests to avoid detection by predators (Greg and Hale 1977). Rather than being a function of selection alone, lower earthworm abundance at brood-rearing sites could be a result of drier soils later in the season, as earthworm densities are affected by several factors related to temperature and weather events (Doherty et al. 2010). Wet areas also typically featured hummocks and low-lying areas, with rotting, dead stems apparent across the areas. These specific features afforded woodcock broods additional cover spaces to hide from predators while remaining in wet, organic soils that support higher earthworm populations. While specific soil characteristics have not been documented as different between woodcock nest and brood sites, previous literature has reported that brood sites are often wet, while nests require dry, well-drained upland areas (Bourgeois 1976, McAuley 1996). Focus on creating habitats that make use of wetland areas near dry, densely forested areas will continue to be essential in woodcock habitat management.

Differences in habitat selection for nest and brood sites were previously documented, but differences in habitat among differently aged chicks, if any, had not been well documented. One study from 1982 suggested that older woodcock broods preferred more mature forest with less dense understory cover and fewer trees and saplings (Dwyer et al. 1982), so we felt it important to test this hypothesis. Older chicks learning to fly may need more open space in the forest to escape predators and provide opportunity for movement, while newly hatched chicks may need more protection provided by a dense understory. After examining this hypothesis, however, we found no evidence that habitat selection changed over time with increasing chick age, which could be caused by several factors. While broods' needs and behavior may change over time, their movements are very localized; chicks one week old or less usually do not move more than 100 m (Kramer et al. 2019*a*), and a woodcock brood's home range during the breeding season is an area with a radius of approximately 180 m (Gregg 1984). In our study, pre-fledged broods never had between-location movements of more than 100 m, and the longest movement we observed for a single post-fledged bird was about 400 m, though movements this large were uncommon in our study even for post-fledged chicks. Broods in our study appeared to concentrate activities within a small area, similar to behavior documented for the daily activity of male woodcock (Hudgins et al. 1985). Given the small area that broods used during the brood-rearing period, it is likely that the habitat did not vary sufficiently to detect significant differences in selection over time.

The transmitters we used for the chicks were so small that we could only pick up their signal from a maximum of approximately 1/3 mile away from the bird's location. In 3 separate instances, we lost older chicks for a few searching periods and found them again later in the vicinity of their original location. They may have remained in the area and we simply did not find them, but they also may have made long distance movements to other areas outside the range of our transmitters. An inability to track long-distance movements of chicks could have affected our study of chick movements and habitat usage. In most cases, however, we were able to track broods from transmitter attachment through their fledge date without any lapse in location record or any failure to locate chicks whose transmitters were still functioning. In post-fledged chicks, we became unable to find birds that we routinely tracked in the same area around the time that we expected their transmitter battery life to end, so we attributed those losses to transmitter failure rather than study area emigration. Because we could successfully track most broods from hatch to fledge, we believe that long-distance movements were not the norm, especially for newly hatched chicks.

In addition to closely centered movements, woodcock broods also use a diversity of habitats in their home range throughout the brood rearing period (Bourgeois, 1976, Gregg 1984, Donovan et al. 2010), which could also add to the difficulty of detecting changes in local scale habitat use from hatch to fledge. Woodcock are more abundant in landscapes that have forest, shrub, and grass covers intermixed, rather than landscapes that have a single type of cover that has aggregated in one area (Thogmartin et al. 2005). Our observations supported those results; we observed birds using areas with multiple types and levels of cover, and areas in which the dominant cover type changed often between forest and shrub. A few birds in our study nested in swamps and open fields, despite most birds nesting in more typical woodcock habitat consisting of dense stems and drier soils. We observed broods living in shrubby wetlands, while also observing them in recent upland aspen cuttings <5 years old and <3 meters tall. Given this variability, it may be difficult to detect changes in brood habitat selection over time. Our sample size was also relatively small, which could have limited our ability to detect differences in brood habitat selection over time. We found many birds that were too small to wear transmitters, and thus were too small to enter our study. Our protocol required woodcock chick transmitters to be <3% of the bird's total body weight (Daly et al. 2015), and for the 3 transmitter sizes that we used (0.85g, 1.1g, and 1.4g), chicks needed to weigh 28.3, 36.6, and 46.6 grams respectively. This meant that, by necessity, we could not put transmitters on chicks younger than 4 days old, and most chicks that we marked with transmitters were at least 7 days old. If chicks were using different habitat when they were newly hatched, we were unable to measure it.

While not an element of habitat structure or vegetation characteristics, we know that earthworm density is an important metric of food availability for woodcock. Sheldon (1967) reported that adult woodcock need to consume their body weight in earthworms each day to maintain their weight. Woodcock cannot directly see earthworm abundance in the soil, which is why we did not include earthworm density in the principal components analyses, but instead may cue in on environmental variables such as soil color as an indicator of earthworm abundance in their selected habitat (Rabe et al.1983*a*). In our research, we found that earthworm density was significantly higher at used sites than available sites for both nesting and brood-rearing birds. We also found that earthworm density was highest at the beginning of the season when birds were nesting, and as the brood-rearing season continued and temperatures rose, we saw earthworm density steadily decline. Prior research that has found earthworm abundance to be highest at the time of peak hatch (Rabe et al. 1983*b*), but our results showed peak earthworm density occurred around 10 April in both years, which was a few weeks before peak hatch in 2019 and over a month before peak hatch in 2018. It is possible that we did not measure earthworm density early enough in the year to know what it was at the time of nest initiation, as we only measured habitat after the nest either hatched or failed. With a 21-day nesting period, however, initiating nests around 10 April would put peak hatch in the last week of April and first week of May, which is what we observed in 2019. In 2018, we found some nests around 10 April, but late snow and freezing rain seemed to cause nest abandonments, and peak hatch did not occur until the third and fourth weeks of May when temperatures were already high, and the ground was very dry.

We know that soil moisture and temperature influence earthworm activity, and that earthworms will move deeper into the soil in unfavorable conditions and thus become unavailable to woodcock (Doherty et al. 2010, Rabe et al. 1983*b*). Woodcock initiate nesting very early in the year, and they are known to initiate nests when snow is still on the ground and temperatures often drop below freezing (McAuley et al. 1990, McAuley 1996). Their early breeding strategy makes them vulnerable to mortality due to excess precipitation and extreme temperatures, which increase the cost of their thermoregulation (Rabe et al. 1983*b*). At the same time, woodcock nesting initiation correlates with increased earthworm activity near the surface of the soil, and peak chick hatch usually occurs in early May when earthworms are still plentiful enough to facilitate successful brood-rearing. Trading off vulnerability to extreme early spring weather with increased earthworm abundance at the time of chick hatching helps ensure that woodcock hens are more likely to be successful when raising a brood (Rabe et al. 1983*b*). In years of excessively cold spring temperatures that push back the date that the growing season commences, woodcock abundance will decrease (Thogmartin et al. 2005), as birds may be hatching their chicks later in the year to avoid adverse conditions and finding decreased food supply available for brood rearing.

Peak hatch does not occur at the same time every year – in our two study years, we saw peak hatch occur during the last week of May in 2018, and during the first week of May in 2019, and yet earthworm density followed the same decreasing pattern in both years and was not significantly impacted between years. In 2018 especially, a late peak hatch led to much lower earthworm density during the brood-rearing period, while earthworm density was much higher during the earlier peak hatch in 2019. The results of our earthworm density model support the hypothesis that timing of woodcock nest initiation has evolved to balance risks of breeding early with benefits of high earthworm abundance in the soil at the time that their chicks hatch. When adverse early spring weather delays woodcock nesting, earthworm density in the soil is lower at the time of peak chick hatch, and woodcock reproductive success could suffer as a result.

Our results show that woodcock habitat selection is complex and cannot be predicted by using only a few metrics. Ground cover, canopy cover, sapling density, food availability, open space, and understory cover are all important elements of woodcock habitat, and woodcock can reproduce under highly variable local habitats in upland deciduous, mixed conifer, and swampy marsh areas. Some habitat aspects, such as soil moisture and percent organic matter, are more important to brood habitat than nesting habitat, due to increased food requirements for hens with broods over hens with nests. Other aspects, such as more leaf litter and less bare ground, are more important for nest sites. Our findings show that management strategies need to consider different requirements for nesting and brood-rearing woodcock, with consideration paid to landscapes with both dry and swampy areas near one another. Woodcock chicks of different ages from hatch to fledge do not exhibit changing habitat selection, but they require much wetter areas than nest sites, especially in the later spring and summer season when earthworm density has begun to wane. Woodcock must constantly balance appropriate cover with food availability, and management for woodcock habitat, while beneficial, will not be appropriate on all landscape types. Wetter areas, dense second-growth upland areas, and forest clearings are all necessary aspects of woodcock habitat, with special attention paid to areas with sandy loam or loamy sand soil (Bourgeois 1976), the most common type of soil we observed in our study sites. In very hot, dry years, proximity to naturally wet, swampy areas with appropriate cover may be even more important to woodcock to ensure continued food supply, though woodcock can make use of other prey items when earthworms are scarce (Vander Haegen et al. 1993).

Management Implications

Current woodcock BMPs for their range throughout North America suggest creation of woodcock habitats that have at least 10,000 stems per acre in feeding areas with moist soils rich with organic matter. Habitats also need to be regenerating clearcuts between 3 and 15 years old for feeding areas, while nesting areas can be slightly older forests (15-20 years) with well-developed understory cover. Historically, these recommendations have been made for landscape level habitat manipulation (Donovan et al. 2010). Our local scale research reinforces current BMPs by confirming that a mosaic of habitat types is necessary to support healthy woodcock populations, and by showing that high stem density is important for both nests and broods. Our findings show that forested wetlands are important parts of woodcock habitat, and management for woodcock in dry areas is unlikely to result in population increases. While we saw definite local habitat preferences for both nesting and brood-rearing areas, we did not find any local-scale differences in habitat selection for broods over time, and variability of choice was much higher between broods than it was within broods. We suggest that further research investigating landscape-scale effects on woodcock habitat selection would be prudent, as a broader scale has been found to have a greater effect on woodcock productivity than local scale habitat characteristics (Kramer et al. 2019*a*). We also recommend that woodcock habitat management focus on areas in proximity to natural forested wetlands, and that managers pay special attention to creating a variety of habitat types that provide clearings, varying ground cover, and differently aged forest to create an array of changing overstory height. Future woodcock management may also need to contend with the effects of climate change on global temperatures and precipitation levels, both of which affect earthworm abundance in the soil (Doherty et al. 2010, Rabe et al. 1983*b*). Hotter, drier late springs and summers could cause earthworm density to decrease during the breeding season even more drastically than we observed in our study.

APPENDICES

APPENDIX I: TABLES

Table 1.1: Explanation of variables measured at American woodcock nesting sites, brood sites, and randomly selected areas and included in a principal components analysis.

Variable	
Distance to Clearing (m)	A measurement in meters from the location point of the nest, bird, or random point to the edge of the nearest forest opening or roadway in which a woodcock could display
Distance to Tree (m)	A measurement in meters from the location point of the nest, bird, or random point to the nearest tree
Overstory Height (m)	A measurement based on size classes 0–3m, 3–9m, and >9m, and values for the size classes were assigned as the midpoint of the size class the height fell into.
Basal Area of trees (ft^2)	Calculated from the diameter at breast height (DBH) of each tree in the plot with a DBH of >10cm.
Water	An ocular estimate of the percent of ground occupied by standing water, based on the Daubenmire method.
Bare	An ocular estimate of the percent of ground occupied by bare areas, based on the Daubenmire method.
Litter	An ocular estimate of the percent of ground occupied by leaf litter, based on the Daubenmire method.
Grass	An ocular estimate of the percent of ground occupied by grass, based on the Daubenmire method.
Forb	An ocular estimate of the percent of ground occupied by forbs, based on the Daubenmire method.
Moss	An ocular estimate of the percent of ground occupied by moss, based on the Daubenmire method.
Woody	An ocular estimate of the percent of ground occupied by small woody vegetation, such as tree seedlings and small shrubs, based on the Daubenmire method.
Dead Woody	An ocular estimate of the percent of ground occupied by dead wood, based on the Daubenmire method.
Saplings/m^2	The number of saplings counted in each square meter sampled per plot, averaged across each of 5 sampling sites.

Table 1.1 (cont'd)

% Canopy Closure	The percent of canopy closure observed at each of 5 locations in each survey plot, averaged across observations.
% Percent Moisture	The percent of soil moisture measured in each soil sample, based on analysis in a soil laboratory
% Organic Matter	The percent of organic matter present in each soil sample, based on analysis in a soil laboratory
Soil pH	The pH of each soil sample, based on analysis in a soil laboratory
% Sand Content	The percent of sand present in each soil sample, based on analysis in a soil laboratory.

Table 1.2: Loadings scores for each variable in the 6 retained principal components. Values in bold indicate variables that loaded highly enough to be considered relevant to defining the component. Variables in italics were reasonably associated with a given component, so we performed t-tests to check for significant differences in these variables between nest and brood sites.

	Forest Closure	**Soil Composition**	**Sapling Density**	**Ground Cover 1**	**Ground Cover 2**	**Ground Cover 3**
Distance to the nearest clearing	0.241	*0.415*	0.017	0.361	-0.11	-0.038
Distance to the nearest tree	*-0.464*	-0.237	0.387	0.213	-0.151	-0.176
Overstory height	**0.792**	0.213	0.007	-0.047	0.175	0.079
Basal area (sqft)	**0.521**	0.305	-0.299	0.106	0.171	-0.096
Open water ground cover	-0.089	0.236	0.264	**0.526**	-0.056	0.085
Bare ground cover	-0.342	-0.036	-0.211	-0.08	**0.609**	-0.314
Litter ground cover	**0.65**	-0.267	0.211	0.223	-0.044	-0.346
Grass ground cover	**-0.656**	0.078	-0.305	-0.108	-0.1	0.27
Forb ground cover	0.154	0.09	-0.386	-0.246	**-0.655**	0.014
Moss ground cover	0.025	**0.586**	0.002	0.174	0.033	-0.148
Woody ground cover	0.085	0.268	0.379	**-0.551**	0.164	0.348
Dead woody ground cover	0.233	0.004	0.065	0.324	0.245	**0.679**
Saplings per square meter	-0.128	0.062	**0.774**	-0.222	-0.125	-0.078
Canopy closure	**0.622**	0.318	0.111	-0.395	0.001	-0.12
Soil moisture	-0.198	**0.727**	0.062	0.167	-0.23	0.054
Soil pH	*-0.493*	*0.452*	0.04	-0.026	0.29	-0.102
Soil sand content	0.293	**-0.615**	0.048	0.137	0.016	0.194

Table 1.3: Akaike Information Criterion (AIC_c) table with variables included in each model considered for nest habitat selection among American woodcock marked in Michigan, 2018-2019.

Model	Variables Included	AIC_c	ΔAIC_c	Weight
13	Forest closure, soil composition, sapling density component, ground cover 1, 2, and 3	55.98	0	0.28
1	Forest closure, soil composition, sapling density component, ground cover 1 and 2	56.54	0.56	0.21
15	Forest closure, sapling density component, ground cover 1, 2, and 3	56.83	0.85	0.18
16	Forest closure, soil composition, sapling density component, ground cover 2 and 3	57.07	1.1	0.16
14	Forest closure, sapling density component, ground cover 2	57.21	1.23	0.15
2	Forest closure, soil composition, sapling density component, ground cover 1	61.84	5.86	0.01
4	Forest closure and sapling density component	63.35	7.37	0.01
3	Soil composition, sapling density component, and ground cover 1	64.89	8.91	<0.001
6	Soil moisture, sapling density, soil sand content	71.23	15.15	<0.001
9	Soil moisture, sapling density, canopy closure, soil sand content	72.17	16.19	<0.001
17	Soil moisture, sapling density, canopy closure	74.84	18.86	<0.001
5	Soil moisture, sapling density, canopy closure, basal area	76.27	20.29	<0.001
10	Basal area, sapling density, distance to clearing, overstory height	77.35	21.37	<0.001
12	Sapling density and canopy closure	80.39	24.42	<0.001
8	Soil sand content and soil moisture	81.27	25.29	<0.001
11	Basal area, sapling density, canopy closure, distance to clearing	81.65	25.67	<0.001
7	Soil moisture, basal area, soil sand content	81.81	25.83	<0.001

Table 1.4: Akaike Information Criterion (AIC_c) table with variables included in each model considered for brood habitat selection among American woodcock marked in Michigan, 2018-2019.

Model	Variables Included	AIC_c	ΔAIC_c	Weight
3	Soil composition, sapling density component, ground cover 1	120.75	0	0.36
2	Forest closure, soil composition, sapling density component, ground cover 1	121.62	0.87	0.23
1	Forest closure, soil composition, sapling density component, ground cover 1 and 2	123.66	2.91	0.08
17	Soil composition*days old, sapling density component, ground cover 1	123.7	2.95	0.08
18	Soil composition, sapling density component, ground cover 1*days old	123.76	3.01	0.08
13	Soil composition, sapling density component*days old, ground cover 1	124.44	3.69	0.06
14	Forest closure, soil composition, and sapling density component	125.16	4.4	0.04
16	Forest closure, soil composition, sapling density component, ground cover 1, 2, and 3	125.47	4.72	0.03
12	Soil composition*days old, sapling density component*days old, ground cover 1*days old	126.08	5.32	0.03
4	Forest closure and sapling density component	131.38	10.62	<0.001
9	Soil moisture, sapling density, canopy closure, soil sand content	133.79	13.04	<0.001
6	Soil moisture, sapling density, soil sand content	142.18	21.42	<0.001
5	Soil moisture, sapling density, canopy closure	142.78	22.03	<0.001
11	Soil Moisture, sapling density*days old, canopy closure	144.15	23.4	<0.001
10	Soil moisture*days old, sapling density, canopy closure	146.93	26.17	<0.001
15	Soil moisture, sapling density, water ground cover, woody ground cover	154.68	33.93	<0.001
8	Soil sand content and soil moisture	155.49	34.74	<0.001
7	Soil moisture, basal area, soil sand content	157.35	36.59	<0.001

Table 1.5: Akaike Information Criterion (AIC_c) table with variables included in each model considered for changes in earthworm density.

Model	Variables Included	AIC_c	ΔAIC_c	Weight
3	Julian date, used and available sites, and year	4361.64	0	0.72
2	Julian date, used and available sites, year, Julian date*used and available sites	4364.53	2.89	0.17
4	Julian date and used and available sites	4365.63	4	0.1
8	Year and Julian date	4371.66	10.02	<0.001
9	Julian date, Julian date squared, used and available sites, and year	4371.96	10.32	<0.001
1	Julian date	4375.66	14.02	<0.001
5	Used and available sites	4391.78	30.14	<0.001
6	Year	4397.37	35.73	<0.001
7	Null	4401.91	40.28	<0.001

Table 1.6: Number of samples, range, median, mean, and SE of all variables included in the 6 retained principal components. Measurements are separated by those taken at used and available sites in both nesting and brood rearing areas. Variables with asterisks indicate ground cover variables that were measured as ocular estimates of percentage of cover in each 15 m diameter plot.

	Used Nests					**Available Nests**				
Variable	n	Range	Median	Mean	SE	n	Range	Median	Mean	SE
Distance to Clearing (m)	70	0–193	11.78	21.74	3.79	70	0–225	10.50	23.83	4.78
Distance to Tree (m)	65	0.19–96	4.22	11.52	2.30	65	0.6–103	6.45	14.43	2.41
Overstory Height (m)	70	1.5–12.5	7.80	9.48	0.34	70	0–10.5	7.80	7.72	0.50
Basal Area of trees (sq. ft)	70	0–5.34	0.11	0.51	0.11	70	0–11.92	0.00	0.67	0.20
Water*	70	2.5–43	2.50	4.04	0.68	70	2.5–43	2.50	3.59	0.61
Bare*	70	2.5–12	2.50	3.03	0.18	70	2.5–90.5	2.50	7.51	1.75
Litter*	70	2.5–97.5	71.25	63.59	2.64	70	2.5–97.5	59.50	55.81	3.36
Grass*	70	2.5–66	9.50	13.41	3.92	70	2.5–97.5	10.00	21.81	3.04
Forb*	70	2.5–76	15.00	19.33	2.05	70	2.5–80.5	12.50	16.11	1.89
Moss*	70	2.5–40.5	2.50	4.47	0.66	70	2.5–14.5	2.50	3.63	0.32
Woody*	70	2.5–38	5.00	7.89	0.89	70	2.5–17	5.00	5.91	0.49
Dead Woody*	70	2.5–62	7.50	8.52	1.10	70	2.5–55	5.00	8.27	0.99
Saplings/sqm	70	0–6.6	1.90	2.17	0.21	70	0–5.6	0.70	1.16	0.16
% Canopy Closure	70	0.76–98.96	68.45	63.07	2.84	70	0–99.6	56.02	49.16	3.82
% Percent Moisture	69	5.9–61	21.50	23.44	1.38	69	3.8–66.1	16.02	18.66	1.29
% Organic Matter	69	2.1–26.1	4.70	7.12	0.67	69	1.2–52.3	4.33	5.78	0.79
Soil pH	66	4.07–8.75	5.70	5.81	0.12	67	4.39–8.37	5.59	5.84	0.11
% Sand Content	68	43.4–88.6	83.85	81.55	0.98	69	24.4–91.7	84.60	80.24	1.42

Table 1.6 (cont'd)

Used Brood Sites					Available Brood Sites				
n	Range	Median	Mean	SE	N	Range	Median	Mean	SE
131	0–439	15.80	34.86	4.85	131	0–321.9	18.10	37.62	4.75
125	0.58–91.2	4.30	9.23	1.29	128	0.33–81	3.60	7.75	1.04
131	1.5–12.5	12.50	9.93	0.27	131	1.5–12.5	12.50	9.30	0.34
131	0–5.78	0.35	0.80	0.10	131	0–7.3	0.38	0.95	0.12
131	2.5–64	2.50	4.22	0.59	131	2.5–73.5	2.50	3.95	0.62
131	2.5–36	2.50	4.86	0.47	131	2.5–87.5	2.50	7.15	1.16
131	2.5–97.5	57.50	54.61	2.37	131	2.5–97.5	57.00	55.64	2.30
131	2.5–85	7.50	15.89	1.56	131	2.5–97.5	9.50	16.68	1.73
131	2.5–81	17.00	22.24	1.53	131	2.5–97.5	17.00	24.08	1.89
131	2.5–71	2.50	6.69	0.88	131	2.5–76	2.50	5.47	0.88
131	2.5–52.5	7.50	12.01	1.08	131	2.5–62	5.00	8.80	0.86
131	2.5–33.5	7.50	9.40	0.62	131	2.5–69	5.00	9.13	0.82
131	0–18	1.00	1.79	0.23	131	0–5.6	0.40	0.80	0.09
131	4.7–100	79.50	74.42	1.82	131	0–100	71.60	62.87	2.59
128	.55–96.1	20.66	27.89	1.81	127	2.56–84.33	19.16	23.31	1.56
128	1.9–88.6	5.53	12.85	2.32	127	0.53–91.1	5.03	9.53	1.31
127	3.96–9.49	5.61	5.70	0.09	125	3.99–9.34	5.39	5.50	0.09
117	21.9–92.9	83.60	79.26	1.18	118	20.9–91.2	84.70	81.04	1.16

APPENDIX II: FIGURES

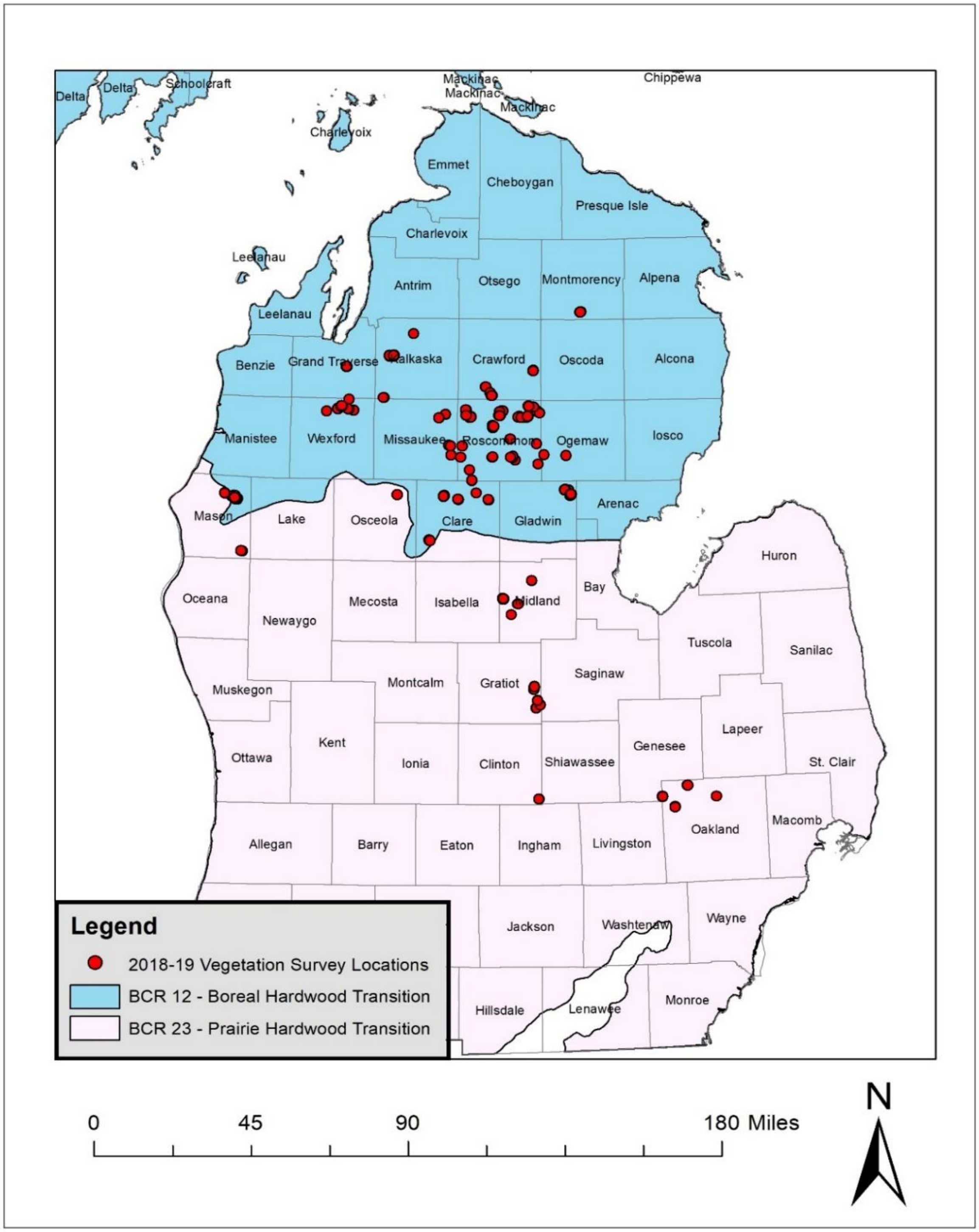

Figure 1.1: Locations in Michigan where woodcock were captured and marked and vegetation surveys were completed at nest and brood sites in 2018 and 2019, with county names for reference. Map colors denote the difference between the Boreal Hardwood Transition and the Prairie Hardwood Transition Bird Conservation Regions.

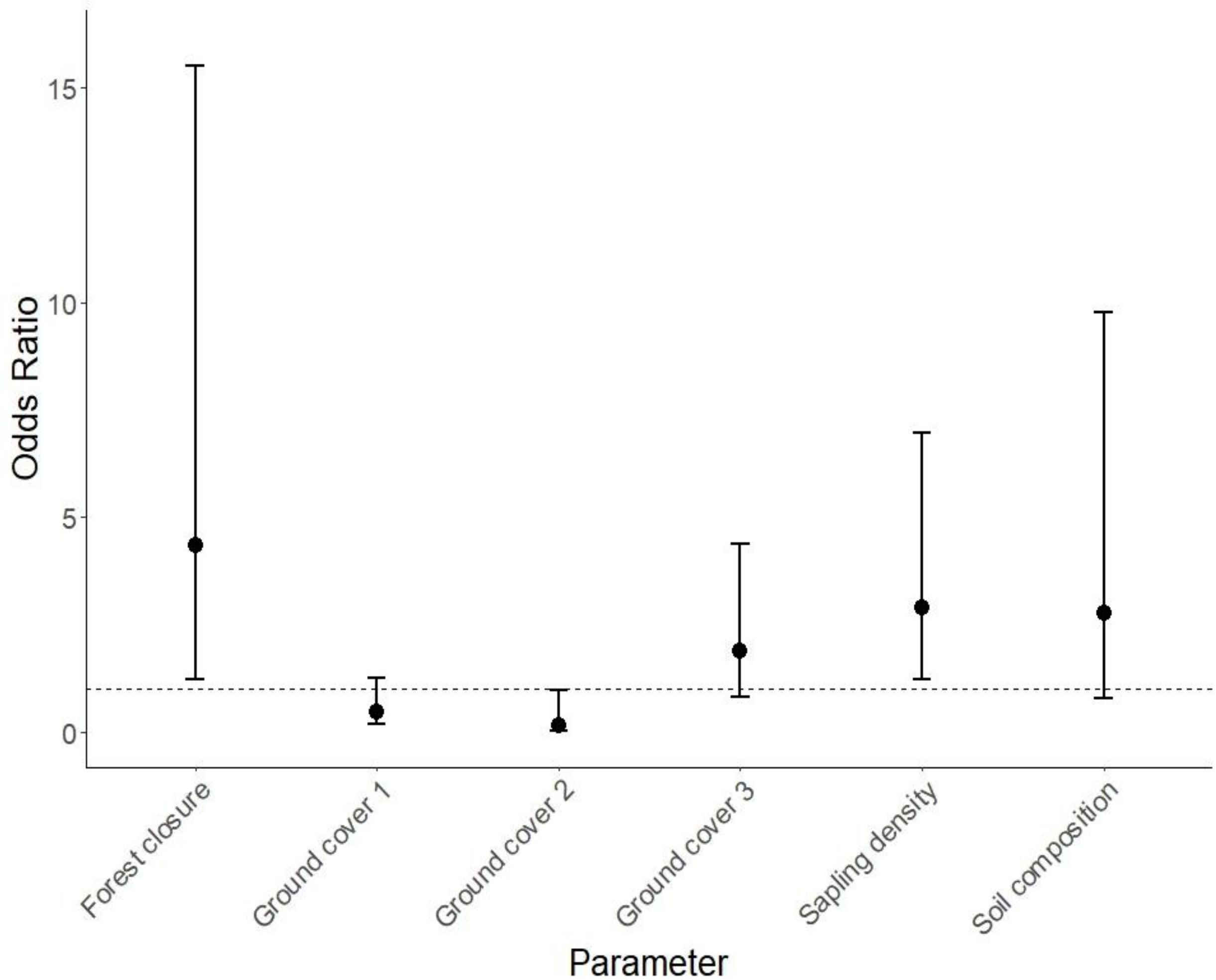

Figure 1.2: Strength of selection of the parameters included in the 5 top models for woodcock nest site selection (see table 1.3). Displayed are the odds ratios and 95% confidence intervals of the parameters in the models, with a dashed line at 1 to represent no selection. Parameters with confidence intervals that overlap 1 show minimal strength of selection, while parameters above 1 show positive selection and parameters below 1 show negative selection.

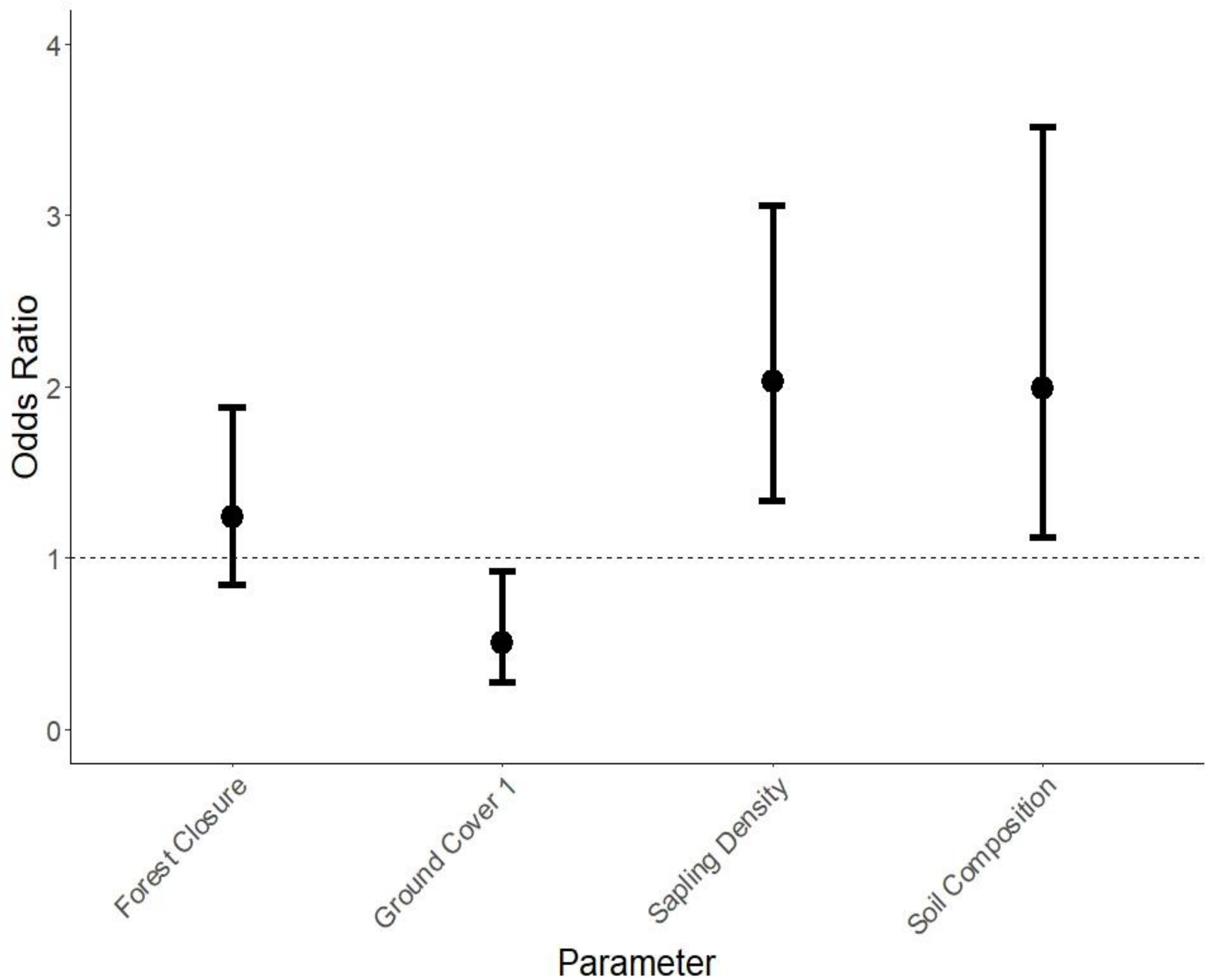

Figure 1.3: Strength of selection of the parameters included in the 2 top models for woodcock brood site selection (see table 1.4). Displayed are the odds ratios and 95% confidence intervals of the parameters in the models, with a dashed line at 1 to represent no selection. Parameters with confidence intervals that overlap 1 show minimal strength of selection, while parameters above 1 show positive selection and parameters below 1 show negative selection.

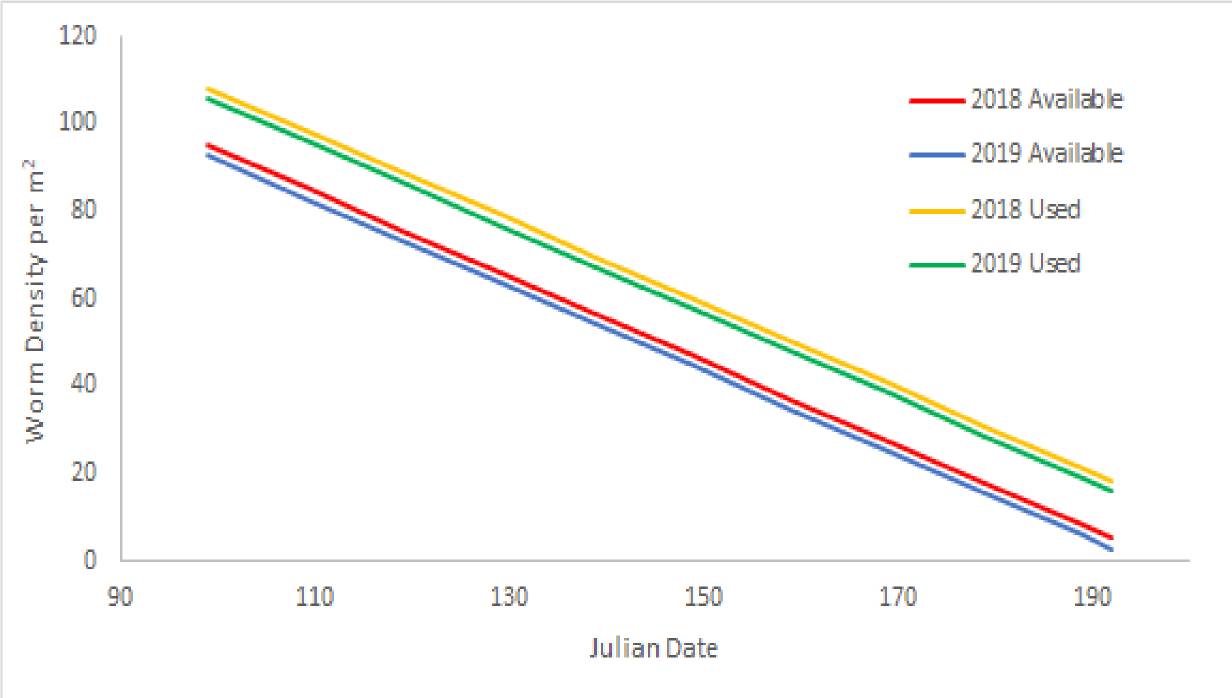

Figure 1.4: Model-based relationships between earthworm density and Julian date on sites used by woodcock and randomly chosen available sites within 200 m in Michigan, 2018 and 2019.

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CHAPTER 2: INFLUENCES OF LOCAL HABITAT CHARACTERISTICS ON AMERICAN WOODCOCK NEST SUCCESS AND BROOD SURVIVAL IN MICHIGAN

Abstract

American woodcock *(Scolopax minor)* are a charismatic avian species distributed throughout the eastern United States and southeastern Canada, and they are recognized for their value as a game species, especially in Michigan, and for their ecological value as an umbrella species. Woodcock populations have been declining 1% to 1.9% per year or more since 1970 due to habitat loss. Wing collection indices also show a decline in juvenile birds per adult female, suggesting reduced woodcock productivity. More targeted research on nesting hens and their broods is necessary to evaluate the effects of breeding habitat on woodcock productivity and create more effective habitat management plans for woodcock. Our objectives were to determine nest success and brood survival rates for breeding American woodcock in Michigan, and link these rates to local habitat characteristics. We located nest and brood sites of woodcock in the lower peninsula of Michigan. Using trail cameras for nests and radio-telemetry for broods, we determined survival or mortality for all nests and broods in the study. We measured local habitat variables around all nest locations and around 1 or 2 locations for each brood. We found that the nest success rate was 0.325, and that nest success was not affected by habitat characteristics at the scale we measured. Brood success from hatching to fledging was 0.827. The likelihood of at least one chick fledging from a brood increased 22% with each percent increase of woody ground cover until woody ground cover reached 20%. Brood survival also declined slightly with each percent increase in soil moisture. Management plans must include provisions for well-developed shrub understory cover in breeding areas, and areas must be wet, but not flooded, to ensure sufficient densities of earthworms for food resources.

Introduction

Wildlife-habitat relationships are a critical piece of conservation research today, and appropriate management decisions must be based on thorough understanding of not only where species occur, but also where they survive and reproduce (Boyce and McDonald 1999, Aldridge and Boyce 2007, Aldridge and Boyce 2008). While challenging to estimate, survival is an important determining factor of the size and trend of various wildlife populations, and it is critical to quantify the parameters that act on survival of individuals to create appropriate management strategies (Murray and Patterson 2006). Productivity is especially important in models of population growth (Kramer et al. 2019*a*), as without sufficient reproduction, new individuals will not be added to the population at a rate high enough to prevent population decline. Species population declines mean that encounters with these populations may become a rare treat, or valuable hunting traditions may come to an end. American woodcock (*Scolopax minor),* a game bird that inhabits eastern North America, populations have been steadily declining at a rate of 1.0% to 1.9% per year for nearly 5 decades. Woodcock population trends are based on singing ground surveys and wing collection surveys and these indices rely on the number of singing males on given survey routes and the number of wings submitted by woodcock hunters in the fall (Seamans and Rau 2017). Wing collection surveys reveal that the number of young per adult female has declined significantly, in addition to the overall population decline (Seamans and Rau 2019), suggesting that recruitment, and therefore juvenile woodcock survival, is also reduced. Given this trend, woodcock are currently considered a species of concern or a species of greatest conservation need in many parts of their current range (Seamans and Rau 2017). Woodcock population growth is sensitive to fecundity and juvenile survival

(Saunders et al. 2019), and without appropriate management to promote increased fecundity and juvenile survival, population numbers may continue to decline.

The ecological and social value of American woodcock cannot be overstated. Throughout their range, woodcock are a valued species for recreational hunting. Woodcock are managed according to 2 regions - the eastern and central regions, which are split by the Appalachian Mountains (Seamans and Rau 2019). Across these 2 regions, thousands of hunters step out each fall to participate in woodcock hunting (Seamans and Rau 2019). Woodcock are lauded as being unique and fun to hunt, a welcomed prize for hunters whose goal it is to enjoy aspects of the hunt beyond filling a bag limit (Liscinsky 1993). In Michigan especially, hunting woodcock is an important pastime; in Michigan's 2019 hunting season, over 29,000 hunters took to the field, and over 59,000 birds were successfully harvested. These harvest numbers are more than double any other state in which people hunt woodcock (Seamans and Rau 2019). For many years before 1990, it was one of the most important migratory game birds based on total numbers harvested (McAuley et al. 2005). Even with woodcock hunting popularity in Michigan remaining much higher than in other states, numbers of successful hunters have fallen drastically over the past several decades, much to the chagrin of those who enjoy the sport (Seamans and Rau 2019). Aside from the more utilitarian purpose of hunting, woodcock are also well-loved by birders and wildlife watchers for their conspicuous mating displays, also called the "sky dance" (Leopold 1949). As woodcock have disappeared from the skies, many of their singing grounds have become silent.

In addition to the consumptive rationale and social pressures to conserve woodcock, we also have important ecological incentives to reverse woodcock declines and improve the habitat on which they depend. Because woodcock are charismatic and sought after by birders and hunters alike, and share habitat requirements with many other species of game animals and songbirds, they are an excellent target species when managers are deciding how to manipulate habitat for the benefit of multiple species (Masse et al. 2015). Ruffed grouse (*Bonasa umbellus*), another popular game species in North America, share habitat requirements with woodcock (Dessecker and McAuley 2001), as does the golden-winged warbler, an avian species that has experienced significant declines in a similar time frame as the woodcock (Bakermans et al. 2015). While the concept of woodcock as an umbrella species for the golden-winged warbler has been called into question, and we cannot assume that species with similar habitats will always benefit similarly from management activities (Kramer et al. 2019*b*), we also see that forests suitable for woodcock habitat contain higher bird diversity (Masse et al. 2015). Ultimately, it is our responsibility as wildlife managers to effectively administer strategies to sustain wildlife populations. Further investigation into the reasons behind woodcock population declines and the factors affecting woodcock survival rates are critical.

Hunting pressure and habitat loss are the two primary hypotheses for the reasons behind declining American woodcock populations, both of which can be manipulated by management activities (Dwyer et al. 1983). Overhunting would, of course, have a dramatic effect on survival rates, which in turn would cause declines in woodcock population numbers. In 1997, bag limits and season lengths in the Central Management Region were curbed to allow for only a 45-day season and a 3-bird bag limit to mitigate the effects of hunting on woodcock population decline (Seamans and Rau 2017, Mayhew and Luukkonen 2006). In Michigan, these changes did not result in significant impacts to woodcock survival rates, and survival remained stable while harvest and hunter numbers declined (Mayhew and Luukkonen 2006). McAuley et al. (2005) found that hunting did not cause significant declines in survival rates. In other areas of the western Great Lakes, woodcock hunting was found to be mostly additive as opposed to compensatory, and had a significant effect on survival rates (Bruggink et al. 2013). Because the effects of hunting on woodcock survival rates vary across regions, it is unlikely that hunting is responsible for range-wide population declines. Meanwhile, during the same period of woodcock population decline, their required young forest habitat has declined precipitously due to the suppression of historical disturbance events such as fire and flooding, agricultural expansion, and changes in land-use practices (King and Schlossberg 2014, Roberts and King 2017). In Michigan's two bird conservation regions (BCRs), the Boreal Hardwood Transition the Prairie Hardwood Transition, only 3.4% and 0.9% respectively are now covered with early successional forest (Tavernia et al. 2016), and maintaining this type of disturbance-dependent landscape is a conservation priority for some conservation agencies in many regions of the woodcock's range (Rosenberg et al. 2016).

Loss of early successional forest is widespread and believed to be the main driver behind declining woodcock recruitment and dwindling population numbers. Biologists estimate that more than 20 million new acres of woodcock habitat need to be added to the landscape to restore woodcock populations to their 1970s levels (Kelley et al. 2008). Determining the best way to create new habitat has led to implementation of American Woodcock Best Management Practices (Donovan et al. 2010), which emphasize creating a mosaic of habitat types to accommodate different life stages and the necessity for woodcock to move between sites to balance metabolic needs and avoid predators (Masse et al. 2013). At a landscape scale, management focuses on clear cutting that stimulates natural disturbance and increases both habitat available to woodcock and woodcock productivity (Kramer et al. 2019*a*). Despite more attention being given to creating habitat, woodcock population numbers have not begun to rise, in Michigan or elsewhere; many states in the Central Management Region show a stable or slightly declining 10-year trend, while some states in the Eastern Management Region continue to show a declining 10-year trend. In both regions, this applies to overall population numbers and recruitment indices (Seamans and Rau 2019).

Given that woodcock population growth is significantly affected by fecundity in the Central Management Region and by juvenile and female survival in the Eastern Management Region (Saunders et al. 2019), it is clear that research into habitat characteristics necessary to promote reproductive success, in terms of both nest and juvenile survival, should be a priority research question for American woodcock. Relative ease of capture of male woodcock has led to much of the body of woodcock research being focused on males, even though male woodcock survival has a weak effect on woodcock population growth (Saunders et al. 2019). Studies concerning survival of woodcock nests and broods have been historically challenging due to the difficulty of capturing females and broods in the field, as opposed to capturing males at conspicuous display sites (S.R. McWilliams, University of Rhode Island, personal communication, 2018; Gregg and Hale 1977, Masse et al. 2014). At a landscape scale, converting grasslands to upland or wetland shrubland increases woodcock productivity (Kramer et al. 2019*a*), and at a local scale, juvenile survival responds positively to increased sapling density and lower rainfall (Daly et al. 2015), but we are still left with questions surrounding the continued decline of woodcock populations and whether or not our management strategies as they currently stand are effective in achieving management goals. The coarse approach that management currently takes to creating young forest may be overlooking the intricacies of local habitat usage by nesting females and their broods, leaving birds vulnerable during a critical portion of the woodcock life cycle.

To gain a better understanding of habitat requirements for woodcock nesting and brood rearing, we sought to measure local habitat characteristics and relate them to woodcock nest success and brood survival. By measuring local habitat and linking it to woodcock reproductive success, we aimed to answer the following questions: in which habitats are woodcock reproductive efforts most likely to be successful, and how can managers adjust their management plans to better support woodcock nesting success and juvenile survival? We hypothesized that high stem density, canopy cover, soil moisture, and soil organic matter would have positive effects on woodcock nesting success and brood survival, and that woodcock brood survival would be higher in older broods than in younger broods. Our specific objectives were to 1) estimate survival rates for woodcock nests and broods and 2) determine which local habitat characteristics have a significant effect on woodcock reproductive success.

Methods

Study area

Our study area spanned the mid- to northern Lower Peninsula of Michigan (Figure 2.1). Most nest and brood sites were in the Boreal Hardwood Transition Bird Conservation Region (BCR), which covers the entire northern Lower Peninsula (Tavernia et al. 2016). In the Boreal Hardwood Transition BCR, we worked in Clare, Crawford, Gladwin, Grand Traverse, Kalkaska, Missaukee, Montmorency, Ogemaw, Roscommon, and Wexford counties. We also worked in the Prairie Hardwood Transition BCR, which covers the southern Lower Peninsula of Michigan (Tavernia et al. 2016). In that area, we worked in Clinton, Gratiot, Isabella, Midland, Oakland, and Osceola counties. We had sites in Mason County that were split between the Prairie and Boreal Hardwood Transition BCRs.

Typical nest and brood sites in the Great Lakes Region consisted of <20-year-old stands of aspen (*Populus* spp.), maple (*Acer* spp.), alder (*Alnus* spp.), or birch (*Betula* spp.) trees (Gregg and Hale 1977, Ammann 1970). Areas were often a mix of dense forest stands, forest openings, and nearby swamps or standing water. Sites contained varying levels of forest versus agricultural areas within 10 km of the nest or brood. For example, Alger State Game Area in Gladwin County, and Wexford State Game area in Wexford County, both in the Boreal Hardwood Transition BCR, contain high levels of forest (80–84%) and low levels of agriculture (1–13%). In the Prairie Hardwood Transition BCR to the south, Gratiot-Saginaw State Game Area, Rose Lake State Game Area, and Holly Recreation Area were all surrounded by higher levels of agriculture, with a 50/50 split between forest and agriculture within 10 km of the areas (Shoffner 2018). The highest density of sites was in Roscommon County and included public land throughout the county, surrounding Houghton Lake, Prudenville, and St. Helen. This region had low levels of agriculture, and was dominated by forest cover. Soils in these areas, and across Michigan, are highly variable. In the northern Lower Peninsula, where most of our study sites were located, sandy soils are dominant (Sommers et al. 1984). Spodosols and histosols, which contain high portions of decaying vegetation and other organic matter, are also prevalent in Roscommon County and other areas where our study sites were concentrated (Sommers et al. 1984). Clay and loam soils dominate the southern Lower Peninsula (Sommers et al. 1984). Based on analysis of our own soil samples, soil types in our study areas, including those in the southern lower peninsula, were predominantly sandy loam or loamy sand, which are the dominant soil types that woodcock use for both nesting and brood-rearing (Bourgeois 1976).

In both years, 2018 and 2019, our study period went from 1 April to 14 July. Average temperatures in northern Michigan during this period in 2018 ranged from 6.38 ℃ to 20.11℃, while in 2019 they ranged from 5.96 °C to 18.53°C. Northern Michigan received approximately 268.3 mm of rain and 359 mm of snow during this time in 2018, with the last snow melted in most areas by 20 April. Precipitation in 2019 included 328.8 mm of rain and 251 mm of snow, with snow melted in most areas by 15 April. In southern Michigan, average 2018 temperatures ranged from 9.9°C to 21.6°C, with precipitation including approximately 303.6 mm rain and 112 mm snow. Snow was melted by 19 April. Average 2019 temperatures in southern Michigan ranged from 9.36°C to 20.59°C. Rainfall was approximately 332.9 mm, and snowfall was 41 mm. Snow was melted by 15 April. During our 2019 field season, the climate was more moderate, without the extreme high and low temperatures and cold rain events followed by drought that 2018 experienced. All climate data was retrieved from NOAA's database for climate data online (NOAA Climate Data Online 2020).

Woodcock capture and marking

In the summers of 2018 and 2019, we worked with a dozen woodcock banders who volunteered for the Michigan DNR to mark woodcock chicks. We chose sites based on areas that our volunteer banders were familiar with and on our own observations of displaying male woodcock. Most of our sites were on public land, but we used a few areas of private land that were specifically managed for woodcock. We used trained pointing dogs to search for birds in areas of good woodcock habitat, according to accepted capture methods detailed by Ammann (1974) and McAuley et al. (1993). After locating broods, we used hand nets to capture chicks and placed leg bands on all chicks in the brood. We placed radio-transmitters on 2 randomly selected chicks within the brood and used 3 sizes of transmitters depending upon chick weight (Holohil BD-2C, transmitter masses were 0.85, 1.1, and 1.4 g). We attached these transmitters with necklace style collars made of flexible material that was designed to stretch as the chick grew. We custom fit collars by gluing the elastic material into small loops that fit over a chick's head. Each collar was <3% of the chick's overall body weight, which meant that for 9 of our 58 broods, we placed collars on the largest chicks in the brood instead of randomly selecting chicks, as the smaller chicks did not weigh enough to wear transmitters. We used this attachment method in accordance with Daly et al. (2015), who found that this type of collar had no significant impact on the survival of woodcock chicks.

After marking chicks, we monitored chicks using radio telemetry equipment. We relocated chicks at least every 3 days and recorded all GPS locations of the chicks. Each time we located chicks, we visually verified whether the broods were alive or dead by either flushing the brood or approaching quietly and locating chicks sitting on the ground. When we observed mortality events, we examined the remains for evidence of what had caused the mortality. When possible, we collected chick remains and had necropsies performed at the Michigan State University Diagnostic Center for Population and Animal Health. Necropsy results were provided to us by Tom Cooley of the MI DNR (Cooley 2019, personal communication). We could not determine a cause of mortality in all instances because of insufficient remains.

Woodcock nesting sites were also located using pointing dogs. We did not capture hens from nests or float or candle eggs, as nesting woodcock are sensitive and excessive disturbance can induce nest abandonment (McAuley et al. 1993). Instead, we placed trail cameras (Browning BTC-6HD-940) at nesting sites, which took bursts of 5 photos every 30 seconds. In this way, we monitored nests regularly to determine their fate and the date of hatch or failure. Predictable break patterns that chicks cause when they hatch from eggs also helped us determine nest fates if camera photos were inconclusive. If eggshells were found mostly intact but split lengthwise, nests were considered to have hatched, as this is consistent with normal hatch patterns for woodcock chicks (Sheldon 1967). If eggshells were smashed or completely missing, nests were considered to have been predated.

This research was approved by the Michigan State University Institutional Animal Care and Use Committee (Protocol Number 04/18-063-00).

Vegetation surveys

After marking chicks and determining the location of nests, we used these locations to measure vegetation characteristics around selected sites. At each nest site, we measured a suite of characteristics based on methods detailed by Masse et al. (2014) (Table 2.1). With the bird or nest's location at the center, we created a circular plot with a 5-m radius. Within this 5-m radius, we chose 4 random points surrounding the center, a random distance from the center in each cardinal direction. At the center of the plot and at each of these 4 random locations, we measured percent canopy closure, counted the number of saplings >1.5 m tall in a square m, and dug a small 10-cm^3 soil pit to count the number of earthworms present (Masse et al. 2014). Finally, we measured ground cover using 1 m square Daubenmire quadrat frames and the Daubenmire class method at the center of the plot and each of the 4 random locations, using cover class intervals of 0–5%, 5–25%, 25–50%, 50–75%, 75–95%, and 95–100% (Bonham 2013). Types of ground cover included litter, bare ground, standing water or puddles, forb, grass, woody shrubs, dead wood, and moss. Finally, we used a soil probe to remove 2 10-cm deep soil samples from the center and each of the 4 random locations. We stored the soil samples in airtight containers in freezers for later analysis in a laboratory after completing all field work.

After finishing the measurements in the 5 sub-quadrats of the vegetation plot, we counted the number of trees present in the entire 5-m radius plot. We counted all trees with a diameter at breast height (DBH) of >10 cm. We measured the DBH of every tree in the plot, and used this information to calculate the basal area of trees in the plot. We then measured the distance from the center of the plot to the nearest forest opening and to the nearest tree, either inside or outside the plot, and we recorded the species of that tree. We recorded the overstory height as one of three categories: 0–3 m tall, 3–9 m, or >9 m.

While we located broods every 3 days, which gave us an average of 10 locations per brood, we only performed these same measurements on up to 2 brood locations. After marking birds and performing telemetry, we measured vegetation around one diurnal location the day after chick capture, and one diurnal location 2 weeks later. We used this time increment to capture habitat usage at 2 distinct phases of brood maturation. At 0–2 weeks of age woodcock chicks are unable to fly. At 2–4 weeks old they can fly but have not yet separated from their brood (Gregg 1984). If chicks did not survive past 2 weeks of age, then the brood only had 1 vegetation survey instead of 2. Our survival analysis was for the period of hatching to fledging, which is approximately 30 days long. We considered woodcock chicks to have fledged when they were routinely found alone, separated from their hen and their brood. All woodcock chicks in our study fledged by 32 days, so our survival analysis ends at 32 days old. We calculated the age in days of each chick by measuring the length of their bills (Ammann 1977, Gregg 1984).

Soil analysis

When field data collection was complete, we analyzed all our soil samples to determine moisture and organic content, pH, and inorganic particle components of sand, silt, and clay. Most work was performed by the Plant and Soil Science Nutrient Laboratory at Michigan State University. We performed some work ourselves according to accepted soil analysis procedures laid out by their laboratory protocols. Specifically, we measured soil moisture content by drying samples to a constant weight at 105℃, which is not high enough to burn away any organic matter, and calculating the percent moisture by looking at the differences in weights before and after the drying process (Masse et al. 2013, Pansu and Gautheyrou 2006). After measuring moisture with these oven-dried samples, we further heated the samples to 550°C for 4 hours to burn away organic matter, and weighed the samples again after they had been reduced to inorganic particles. Both soil moisture and organic matter are recorded as a percent by weight (Masse et al. 2013). To measure soil pH, we added distilled water to small soil samples at a 5:1 ratio, and used a glass pH electrode and a pH meter to record pH values of each sample (Masse et al. 2013) using a LabFit AS-3000 pH analyzer. Finally, to determine the percentage amounts of sand, silt, and clay in each soil sample, we used the hydrometer method of particle size analysis (Gee and Bauder 1986). Some of our soil samples were so organic that the sand, silt, and clay they contained was negligible. In these cases, we could not perform full particle size analysis, so after burning off organic particles, we used distilled water to wash smaller particles through a sieve, leaving only sand behind (Gee and Bauder 1986). We could then obtain the percent sand content in the soil, while the leftover non-organic material was considered a mix of silt and clay.

Nest success analysis

To analyze nesting success, we used the Mayfield method to estimate nesting success (Mayfield 1961) and logistic regression to evaluate habitat differences between failed and successful nests (Hazler 2004). Because we measured 17 different habitat variables during our field study and our sample size was small, we could not include all 17 variables in one global model. To address this, we used principal components analysis to reduce the dimensionality of the data and produce uncorrelated combinations of the habitat variables (Masse et al. 2014, Johnson and Wichern 2007). In the principal components analysis, we used variables that measured both habitat structure and soil characteristics (Table 2.2). The components of soil (proportions of sand, silt, and clay) are correlated and sum to 1, so we used percent sand to characterize soil particle size composition. Likewise, soil moisture and soil organic matter were also correlated, so we used soil moisture in the principal components analysis to characterize both moisture and organic matter. Principal components analysis created 17 components as possible variables, and we retained the first 6 of these components to use in both the general linear model analysis for nests and the known fate analysis for broods based on their Eigenvalues (Masse et al. 2014). Each principal component also had loadings scores that reflected the weight of each individual variable in the 6 components; by examining these weights, we were able to infer importance of variables each principal component represented, which helped us to interpret the different components for use in the selection model. We defined and named each principal component based on which variables they contained that weighted >0.5 (Table 2.3). Using all 6 principal components in one model allowed us to test a model that represented all measured habitat variables.

Because we did not candle or float woodcock eggs, we did not know nest initiation dates for nests that we actively monitored, but our cameras allowed us to record exact hatch and failure dates for nests. Due to the lack of initiation dates, we used a simple Mayfield estimator that used nest exposure days to estimate nest success for American woodcock during our study period (Mayfield 1961). Woodcock typically lay one egg per day, resulting in a laying period of 3–4 days depending on clutch size, and then incubate for a period of approximately 21 days. Chicks leave the nest within hours of hatching (Mendall and Aldous 1943, Sheldon 1967, Liscinsky 1972). We therefore used 25 as the maximum possible number of exposure days for woodcock nests in the Mayfield calculation. Because we could not easily include parameters in the Mayfield estimate to evaluate habitat variables that may influence nest success, we then used logistic regression models to investigate differences between successful and unsuccessful nesting sites.

We developed a priori hypotheses to explain what habitat variables might have an impact on nest success. Using these hypotheses, we developed logistic regression models that used different combinations of both the individual variables and the principal component variables. We evaluated 24 candidate linear regression models to test for differences between successful and unsuccessful nesting sites, including a null model (Table 2.4). Our most complex model included all 6 of the principal components that we retained from the principal components portion of the analysis, which represented all the habitat variables that we measured. We used program R (version 3.6.1, base-package 2019) to run the logistic regression models for nest success. To assess model fit, we used Aikaike's Information Criterion for small sample sizes (AIC_c) due to small sample size to parameter ratio to rank competing models and select the model of best fit based on a ΔAIC_c of 2 (Burnham and Anderson 2002, Guthery 2008).

Brood survival analysis

To analyze brood survival from hatch to fledge, we used a known fate survival framework with staggered entry and right censoring. Staggered entry allowed us to account for the fact that we added new broods to our sample throughout the breeding season (Pollock et al. 1989), and right censoring allowed us to accommodate the broods with unknown fates that were lost due to failed transmitters or emigration from the study area. Our known fate model framework had 10 3-day time intervals which correlated to the age of each brood included in the analysis. The youngest brood captured in our study was 3 days old, so the age time intervals start at 3 days. All our broods fledged, or were found alone, by 32 days, so time intervals end at 32 days old. Birds were located once per interval. We divided our study period into two age sub-periods separated by a biological milestone in woodcock brood growth; from 0–14 days of age, woodcock chicks are unable to fly, while after 14 days of age, chicks are able to fly.

Once again, we could not include all habitat variables in one global model, so we used the same principal components as previously described to reduce dimensionality of the data. We developed candidate models based on a priori hypotheses, and we tested known fate models for individual variables and for principal component variables. We focused our hypotheses and models on habitat variables that would promote high food availability and protection from predators. In some models, we evaluated the interaction between habitat variables and the two age sub-periods in the study. We also tested a null model and a model that used all 6 principal components, which represented all the habitat variables that we measured. Overall, we tested a set of 41 candidate known fate models for brood survival (Table 2.5). All known fate models for brood survival analyses were performed in R using the RMark package (Laake 2013). To assess model fit, we used Aikaike's Information Criterion for small sample sizes (AIC_c) due to small sample size to parameter ratio to rank competing models and select the model of best fit based on a ΔAIC_c of 2 (Burnham and Anderson 2002, Guthery 2008).

In our known fate models, we used the brood as our observation unit, rather than determining survival of individual chicks. Broods were considered successful if at least one chick fledged from the brood. Previous research on juvenile woodcock survival found no evidence for intrabrood dependence and suggested that survival analyses for juvenile woodcock could be performed with individual chicks as the study unit (Daly et al. 2015), but in our study, we saw many occurrences of entire broods being depredated at once, or entire broods dying after the hen was depredated. We did not use chi-square tests to test for intrabrood dependence as suggested by Winterstein (1992), but we chose the brood as our experimental unit to avoid issues of dependency between individuals in our analysis.

In some instances, we were unable to obtain all soil measurements for brood sites on which we measured vegetation characteristics. If sites were under a considerable amount of water, our soil samples were mostly water, or if the water was too deep, we were unable to take them at all. In other instances, the soil samples were made up of mostly organic matter. When the organic matter was burned off the sample during the analysis process, the remaining soil sample was too small to analyze for sand, silt, and clay particles. Because soil measurements were included in the principal components in our analysis, principal component values were necessarily left blank for some broods. Because RMark eliminated entire observations with blank data points, we removed data for 6 broods that lacked principal component values so that models using principal components and individual variables would contain the same data and could be directly compared. Of these 6 removed broods, 3 survived, 2 died, and 1 was censored.

Results

Summary

In our two study years, 2018 and 2019, we recorded vegetation data for 58 active nest locations and 58 used brood sites. Of the 58 broods, we performed only 1 vegetation survey for 24 failed or censored broods, and we performed 2 vegetation surveys for 34 successful broods. In 2018, we located 22 nesting sites and monitored 17 broods, and in 2019 we located 36 nesting sites and monitored 41 broods. In the 2 years, 5 additional broods were marked but removed from the study because all chicks died, or the marked individuals were lost to follow up within 24 hours of capture. Out of 58 nesting sites, 33 successfully hatched at least one chick, and 25 were depredated or abandoned while we were monitoring them. Because of cameras and consistent hatch patterns on woodcock eggs, we knew the fate of each nest with certainty. Because we did not flush birds off nests, we did not know the clutch size of nests on all occasions. Of those that we knew, 12 had 4 eggs, 5 had 3 eggs, and 1 late season nest had 2 eggs. Out of 58 broods, 34 successfully fledged at least one chick, 15 lost all chicks before fledging, and 9 were censored due to transmitter failure or emigration out of the study area, thus causing uncertainty about their fates (Table 2.6).

Predation was the most common reason for both nest and brood failure. Raccoons were most commonly observed depredating nests on our trail cameras; 8 of the 25 failed nests were destroyed by raccoons. We also observed 2 instances of red-tailed hawk predation, 2 of possible deer predation, 1 of weasel predation, 1 of opossum predation, and 1 nest that was located near a popular shooting area and later abandoned. The remaining 10 nests were abandoned or failed due to unknown causes.

We could not identify specific predators of chicks, but in some cases, we were able to discern whether predation was mammalian or avian. When we found nothing left of chicks other than feathers or bloody transmitters, we did not make any judgment about what killed the birds. Of the recovered mortalities, 10 chicks in 3 broods appeared to have died from avian predators, 13 chicks in 4 broods from mammalian predators, and 15 chicks in 9 broods from unknown predators. When we recovered depredated marked chicks, we often recovered other chicks in the brood that had not been marked at the same time. In 2 cases, the hen was predated by a mammal and all chicks in the brood died from exposure, as they were too young to survive on their own. We recovered 4 chicks from 4 broods that had died from apparent exposure, which was determined based on their body and organ condition (Cooley 2019, personal communication), despite their hen and the remainder of their brood still being alive. We recovered 1 chick that died due to drowning after a large rainfall. We collected 7 chicks from 7 different broods that died after becoming tangled in their transmitter. In these cases, one or more of the remaining chicks from the brood survived to fledge, so we still included the brood as successful in our analysis. We never had all marked chicks in a brood die due to an issue with the transmitter becoming tangled. In 19 out of the 34 successful broods, one marked chick died, but other chicks in the brood survived to fledge, so the brood was still considered successful.

Principal components

Using all the habitat variables that are listed in Table 2.2 our principal components analysis created 17 principal components out of the measurements that we took at all the used woodcock sites. We retained the first 6 components because their eigenvalues were all >1.0, while the remaining 11 components had eigenvalues of <1.0 (Masse et al. 2014), and tested them in survival models along with individual variables. We named and described each principal component based on which variables in the component weighted at >0.5 in the component. Component 6 did not have any variables that loaded >0.5, and thus we did not define the component.

Soil composition, or component 1, was characterized by increased soil moisture and organic matter, pH, and sand content. Increased litter ground cover was also included in this component. Forest cover, component 2, was characterized by a declining distance to the nearest tree, increased overstory height, increased basal area, and increased canopy closure. All these characteristics would cause a habitat site to be highly covered and protected from potential predators. Woody ground cover was the only element of component 3 that loaded >0.5, and the component was characterized by decreasing amounts of woody ground cover. Varied ground cover, component 4, contained increasing standing water on the ground and decreasing grass and forb cover. Dead woody, or component 5, was characterized by decreasing amounts of dead woody ground cover such as fallen trees and rotting logs and branches. As stated earlier, component 6 contained no variables that loaded >0.5, but it did include the distance to the nearest clearing, which loaded at 0.485, and soil sand content, which loaded at 0.447. A full list of each variable and their loadings scores in each component is found in Table 2.3.

Nest success

Daily survival rate for nests in our study was 0.956 (95% CI = 0.939–0.973). After accounting for a 4-day egg laying period and a 21-day nesting period typical of American woodcocks (Sheldon 1967, Liscinsky 1972), we calculated an overall Mayfield estimate of nest success rate as 0.325 (95% CI = 0.267–0.567) for the 58 nests in our study. When we used logistic regression to look for habitat differences between successful and unsuccessful nests, the top model was our most complex model that contained all 6 of the components, but none of the components were significantly different between successful and unsuccessful nesting sites. Coefficients for each of the components had 95% confidence intervals that overlapped 0. Though the top model containing all components was a better fit for the data than the null model, and had an area under the curve (AUC) of 0.82, none of the local habitat variables that we measured had a significant effect on woodcock nesting success (Table 2.4).

Brood survival

We found that ground cover, specifically woody ground cover such as shrubs and seedlings up to 1 m tall, had the most significant positive impact on whether at least one chick successfully fledged from a brood. Our top model also included soil moisture, which had a small but negative effect on chick survival. Principal components were not included in the top model – only 2 individual variables. The top model had an overall AIC_c weight of 0.47 (Table 2.5). With each percentage increase in woody ground cover, survival of woodcock broods increased 22% (OR = 1.22, 95% CI = 1.07–1.41, Figures 2.2 and 2.3). Woody ground cover estimates for brood sites ranged from 2.5% to 52.5% with an average of 12.01% (Table 2.6). Increases in woody ground cover had the most significant effect on survival from 0 to 20. When woody ground cover was above 20%, survival was high and did not continue to increase with increasing woody ground cover. Each percent increase in soil moisture had a very small negative effect on brood survival (OR = 0.95, 95% CI = 0.92–0.99, figures 2.2 and 2.4). Soil moisture values ranged from 0.55%–96.1% with an average of 27.89% (Table 2.6). Particularly dry brood sites tended to be late in the season when chicks were older, while particularly wet brood sites were in swamps, and soil samples were mainly water. Such extremely high soil moisture measurements were rare – most soil moisture observations were below 50%. Our data showed a small, consistent decline in survival probability with increasing soil moisture, but the confidence intervals at the highest levels of soil moisture were very wide, indicating a high level of uncertainty around these estimates (Figure 2.4). In the top model, brood survival over the entire observation period, which spanned 3 to 32 days of chick age, was 0.827 (95% CI 0.608 – 0.936). Brood survival during each of the 10 3-day time intervals used in the known fate model was 0.981.

Discussion

Our survival analyses for American woodcock nests and broods provide important information on reproductive success of the species. Our work shows that understory cover is especially important for brood survival, and that nest success is lower and may be more limiting to woodcock productivity and reproductive success than brood survival. All our work was performed in Michigan, which has a large American woodcock population and more participation in woodcock hunting than any other state in the woodcock's range. A better understanding of breeding habitat and how it affects woodcock populations is considered a priority information need for American woodcock (Case and Sanders 2010), so our work was meant to help fill that critical gap. We estimated both nest and brood survival in the lower peninsula of Michigan and assessed differences in local habitat between failed and successful reproductive efforts. We were able to use this information to identify some elements of local-scale breeding habitat that promoted higher survival rates for woodcock nests and broods. For woodcock nesting sites, we were unable to identify any local habitat characteristics that we measured in our study that had a significant impact on nest success. We believe that woodcock nesting success is impacted by habitat characteristics at larger scales than what we measured in our study. When we analyzed brood survival, however, we found that woody ground cover, such as small woody shrubs and tree saplings often found in the understory of young forests, supported higher survival rates for woodcock broods than any other habitat characteristic that we measured. We also found that increasing soil moisture had a small, but significant, negative impact on woodcock brood survival, which we did not expect.

Our Mayfield estimate for nest success, 0.325, was lower than the nest success rate of 50% that was reported over a 12-year study of American woodcock in Wisconsin, but still within the range of 29% to 67% reported by that study (Gregg 1984). Mendall and Aldous (1943) first reported woodcock nesting success at 67%, but as their study occurred prior to the introduction of the Mayfield estimator (Mayfield 1961), their nest success estimate was likely biased high. Our Mayfield estimate also may be biased low due to the low number of exposure days that we were able to observe. In our study, the average number of exposure days across 58 nests was only 9.8, which is less than half of the 21-day incubation period for American woodcock (Mendall and Aldous 1943, Liscinsky 1972). Over half of our nest observations, 55%, had less than 10 exposure days before they either hatched or failed; therefore, our overall number of exposure days could have contributed to a low Mayfield estimate. Despite this possibility, our nest sample was random, and our nest success estimate is consistent with the range of woodcock nest success reported by other longer-term studies (Gregg 1984, Liscinsky 1972, Whitcomb 1974).

We expected that sapling density of deciduous and shrub stems, canopy cover, and some aspects of ground cover would have the most significant effects on nesting success, given the importance of these cover attributes to typical woodcock nesting habitat selection (McAuley et al. 1996, Bourgeois 1976, Chapter 1 of this thesis). Dense saplings and high canopy cover would provide protection from ground and overhead predators, while ground cover such as leaf litter would provide camouflage, given the woodcock's cryptic coloration. Instead, however, we found that none of the local-scale habitat variables we measured influenced nest success. Our sample size was small, which may have contributed to a finding of no significant results. In addition, many of the nests that we found tended to be in areas with similar types of vegetation. With a few exceptions, nests were in mostly dry areas with high sapling density (McAuley et al. 1996). Similarity between sites may have limited our ability to detect differences between successful and unsuccessful nesting sites.

In addition to issues of sample size and similar features among habitats, the scale that we measured in our study was small – our measurements were all within 15 m of nest sites. While vegetation characteristics may impact nest success for woodcock, it may be at a different scale than what we measured. Scale matters when thinking about animals' selection choices and how that impacts their survival (Reidy et al. 2017). Woodcock nests may be more affected by the scale at which predators choose habitat, rather than the scale at which woodcock choose habitat, given that predation is the main cause of nest failure. Woodcock also may choose nest sites at a different scale than they choose brood sites. Adult woodcock are much more mobile than broods, as broods cannot fly for two weeks after hatching. Adult male woodcock, for example, have demonstrated the capacity to assess habitat quality at a landscape scale and select accordingly, even moving a far distance to return to higher quality habitat when artificially moved to a lower quality habitat (Brenner et al. 2019). Though that study was on male woodcock, adult females may follow the same strategy as the adult males in the study. Upon arriving to breeding territories in the spring, females may also demonstrate selection preferences at the landscape scale, leading to their nests being more affected by landscape parameters than local parameters. After chicks hatch, however, the brood is more limited in the scale of habitat they can choose, as they cannot move as far as a hen on her own.

We were able to determine an impact on survival by local habitat characteristics for brood sites. For several ecological reasons, broods have different needs than nesting hens do. More mobility for nesting hens means that they do not need to nest near the best food sources – in fact, hens do not typically feed near their nesting sites (Gregg and Hale 1977). Chicks, with their limited mobility, depend on their mother for food for the first 7 days of their life (McAuley et al. 1990, Gregg 1984), and they need to be in the immediate vicinity of feeding sites. Broods also tend to be farther away from clearings than nests (Bourgeois 1976). Woodcock need clearings for courtship and reproductive behavior, but proximity to edges may also increase the vulnerability of broods to predation as they move about (Andren and Angelstam 1988). Like nests, we did expect that stem density would be the most important factor for brood survival, but instead, we found that woody ground cover had the most significant effect on brood survival at the scale that we measured. Woody ground cover included shrubs and saplings that were <1m tall. Woody ground cover accounted for most of the understory cover in the habitats that we measured, and was variable between brood sites. Stem density was much more uniform across brood sites, which limited our ability to detect an impact of stem density on brood survival. Woody ground cover was also selected for by woodcock broods (Chapter 1 of this thesis), so our finding here of woody ground cover enhancing the probability of survival is consistent with other findings in the study. While our study did evaluate habitat criteria at the local scale, converting grasslands to upland and wetland shrubland at a landscape scale has also been found to significantly increase woodcock productivity (Kramer et al. 2019), which is consistent with our results.

From a management perspective, our results show that the importance of woody ground cover to brood survival is more important to consider if a forest has little or no understory cover. The biggest impact to brood survival comes when the amount of woody cover increases from 0% to 20% (Figure 2.3). Beyond 20% ground cover, survival for each 3-day interval in our analysis is stable and high. If understory cover in an existing landscape is already well-developed and covers at least 20% of the area, our results suggest that woodcock broods will find sufficient cover in those areas, and a focus on increasing woody ground cover would not have a great impact on brood survival. But in areas of young forest that lack shrubby understory cover, adding more available cover could be a way to efficiently increase the odds of woodcock broods successfully fledging at least one chick.

In addition to woody ground cover, our results also showed that soil moisture had a small but negative effect on woodcock survival. A negative effect of soil moisture was surprising, as woodcock broods select for areas with higher soil moisture (Chapter 1 of this thesis), and moist soil is essential to support sufficient quantities of earthworms, which are the main food source for American woodcock (Doherty et al. 2010, Rabe et al. 1983, Sheldon 1967). Indeed, woodcock have been observed frequenting areas with permanent wet spots in late summer when temperatures are high and the ground is dry (Sheldon 1967), and Mendall and Aldous (1943) have reported woodcock seeking shelter in wet thickets for food and cover. We observed many woodcock in swampy areas throughout the course of our study. However, most of our brood sites had soil moisture measurements between 10% and 40%, and our model showed that brood survival decline was more significant after soil moisture percentage was higher than 40%. In addition, beyond soil moisture values of 40%, the confidence interval of our model is very wide (Figure 2.4), indicating uncertainty around the estimates.

Because earthworms are such an important food source for American woodcock, and their abundance is tied to soil conditions, their behavior of may help explain our finding of decreasing survival probability with increasing soil moisture. In areas with soil moisture above 40%, and especially in the few areas with moisture measurements of over 50%, the ground was so wet that broods were usually in standing water, and any soil samples that we collected were mostly water. While earthworms can survive long periods of flooding, they will also often leave flooded areas and congregate in new areas with less water (Plum and Filser 2005, Ausden et al. 2001). High temperatures, like those often seen in the late breeding season, and decaying organic matter deplete oxygen content in standing water, limiting earthworms' ability to survive in such an environment and further necessitating their moves away from water-inundated sites (Plum and Filser 2005). Flooding is not recommended as a way to manage for shorebirds that depend on macroinvertebrates as their primary food source – while the soil needs to be kept moist and easy to probe, flooding will cause a decrease in macroinvertebrate density (Ausden et al. 2001). Without their principal food source, woodcock would have a difficult time foraging enough prey and meeting their metabolic needs to survive. It is critical, therefore, to not negate the importance of soil moisture to appropriate woodcock habitat, but to recognize that habitat should not include too much frequent standing water, and should encompass areas that stay moist, but not flooded, to facilitate favorable conditions for earthworms and other macroinvertebrate prey resources.

Survival estimates for broods in our study based on the top known fate model were high. The likelihood of the brood surviving each 3-day study period was 0.98, while the likelihood of at least one chick successfully fledging, or reaching 32 days of age, from a brood was 0.84. While high, this estimate is consistent with Mayhew and Luukkonen (2006), who reported that the survival rate for local birds during the summer months was 0.848. Daly et al. (2015) also reported high juvenile woodcock survival, with a survival rate of 0.746 in 2011 and 0.843 in 2012 during their two study years for chicks up to 15 days old. In our study, only 15 out of 58 broods lost all chicks before fledging, with 9 broods being censored. Individual chick survival may have been lower, given that many successful broods did lose at least one chick, but our results show that brood success for woodcock is high. Kramer et al. (2019) reported that woodcock nest success has a larger impact on woodcock productivity than brood success. Our nest success estimate was much lower than our brood success estimate, which supports the hypothesis that nest success may be the limiting factor for woodcock reproductive success, rather than brood success. But in the months beyond the spring and summer breeding season, when birds are no longer local, juvenile survival has been reported to be quite low. Mayhew and Luukkonen (2006) reported juvenile survival based on fall band recoveries as 0.273, while Krementz et al. (2003) reported juvenile survival at 0.265. Additional research may be necessary to further evaluate the effects of juvenile survival after fledging on the overall population dynamics of American woodcock.

Our results show that woodcock nesting success is typically lower than brood success during the period of hatching to fledging. Our findings also show that local scale habitat characteristics had no effect on nesting success, meaning that management strategies should address woodcock nesting habitat needs at larger scales. Adult birds can select habitat at a landscape scale (Brenner et al. 2019), meaning that hens may be choosing their nest sites at a vastly different scale than we measured in this study. In addition, spatial scale affects the impact that predators have on prey species (Englund 1997). Nest success may be more strongly impacted by the scale at which predators select habitat, as predation is the most common cause of woodcock nest failure. Further research into the impacts of habitat on nest success at different scales will be imperative to ensure that we have a complete understanding of how best to design management plans to improve woodcock population numbers. Finally, our results show that breeding habitat can be improved to promote higher brood success rates by ensuring more woody ground cover and a well-developed understory, instead of focusing solely on sapling density and proximity to forest openings. Sapling density and other aspects of forest closure will continue to be important for woodcock selection (Chapter 1, this thesis), and indeed, there is evidence that sapling density at the local scale is important for chick survival as well (Daly 2014). Forests suitable for woodcock quickly age out of their preferred early successional forest without intervention to create forest disturbance, and require frequent active management (Masse et al. 2019), and understory cover may age even more quickly into taller trees and shrubs that will have less benefit to woodcock broods. In addition, while broods require wet areas to ensure enough food supply, it is important that areas not be consistently flooded, or wet enough to cause earthworms to leave the area or die due to anoxic soil conditions. Consistent food sources are critical to woodcock broods, and available habitats must allow them to balance their need for cover and protection from predators with their need for plentiful macroinvertebrate prey.

Management Implications

Woodcock habitat management recommendations today include those at the landscape scale. They include recommendations for creating areas with at least 10,000 stems per acre, and they stress the importance of managing for woodcock in areas with moist soils and high amounts of organic matter (Donovan et al. 2010). In this study, we learned that local scale habitat characteristics had no effect on nesting success, and so we recommend that management for woodcock nesting sites focus on strategies based on landscape scale management efforts. We also recommend further research into how habitat characteristics at a landscape scale affect woodcock nesting success, and perhaps how habitat patch sizes affect nest success, especially given that woodcock nests are closely associated with forest edges (Sheldon 1967, Masse et al. 2013). Woody ground cover, however, is an important metric for woodcock brood success, and habitat management should ensure that in addition to promoting early successional forest landscape with dense stems, woodcock habitat should also have seedlings and shrubs in the understory layer to provide additional protection from predators for woodcock broods. We recommend that special attention be paid to ensuring dense shrub thickets are included in forest management plans for woodcock in areas where woody understory cover is sparse. In areas with abundant understory cover, augmenting it will not raise woodcock brood survival rates significantly enough to warrant habitat manipulations. Furthermore, while woodcock broods require moist soils and are often associated with considerably wetter areas than woodcock nests (McAuley 1996, Bourgeois 1976), it is important to manage woodcock habitat in areas that include land that is not too frequently flooded. Dense shrubland near flooded swamps may provide an area for earthworms to move to when they leave flooded areas (Ausden et al. 2001). Areas adjacent to flooding may stay wet enough to avoid a dearth of food resources during dry, late summer periods when woodcock may become more desperate for food (Sheldon 1967). In the future, climate change may cause some areas with frequent floods to dry up, and these areas may become appropriate woodcock management sites as macroinvertebrate prey species recolonize in the drying soil. Young forests with wet, but not flooded, rich soils and well-developed understory cover will provide suitable habitat for woodcock during the breeding season and improve survival of woodcock broods.

APPENDICES

APPENDIX I: TABLES

Table 2.1: Summary of vegetation measurements taken at nest and brood sites, which were used in the principal components and known fate analysis. Variables with asterisks are all ocular estimates of ground cover based on the Daubenmire method.

	Nest Sites					Brood sites				
Variable	n	Range	Median	Mean	SE	n	Range	Median	Mean	SE
Distance to Clearing (m)	58	0–193	10.70	21.35	4.41	131	0–439	15.80	34.86	4.85
Distance to Tree (m)	53	0.19–96	4.20	11.42	2.54	125	0.58–91.2	4.30	9.23	1.29
Overstory Height (m)	58	1.5–12.5	7.80	9.50	0.39	131	1.5–12.5	12.50	9.93	0.27
Basal Area of trees (sq. ft)	58	0–4.33	0.11	0.48	0.10	131	0–5.78	0.35	0.80	0.10
Water*	58	2.5–43	2.50	3.82	0.75	131	2.5–64	2.50	4.22	0.59
Bare*	58	2.5–12	2.50	3.09	0.22	131	2.5–36	2.50	4.86	0.47
Litter*	58	2.5–97.5	71.50	65.05	2.83	131	2.5–97.5	57.50	54.61	2.37
Grass*	58	2.5–66	9.50	13.64	4.11	131	2.5–85	7.50	15.89	1.56
Forb*	58	2.5–76	13.50	17.89	2.10	131	2.5–81	17.00	22.24	1.53
Moss*	58	2.5–40.5	2.50	4.50	0.75	131	2.5–71	2.50	6.69	0.88
Woody*	58	2.5–29	5.00	7.47	0.82	131	2.5–52.5	7.50	12.01	1.08
DeadWoody*	58	2.5–62	7.50	8.86	1.31	131	2.5–33.5	7.50	9.40	0.62
Saplings/sqm	58	0–6.4	1.70	1.96	0.21	131	0–18	1.00	1.79	0.23
% Canopy Closure	58	0.76–97.6	66.30	61.59	3.14	131	4.7–100	79.50	74.42	1.82
% Percent Moisture	57	10–56.9	22.90	24.09	1.43	128	.55–96.1	20.66	27.89	1.81
% Organic Matter	57	2.1–21.48	5.63	7.42	0.74	128	1.9–88.6	5.53	12.85	2.32
Soil pH	54	4.07–8.75	5.77	5.90	0.14	127	3.96–9.49	5.61	5.70	0.09
% Sand Content	56	43.4–88.6	83.70	81.13	1.14	117	21.9–92.9	83.60	79.26	1.18

Table 2.2: Explanation of variables measured at American woodcock nesting and brood sites and included in a principal components analysis**.**

Variable	
Distance to Clearing (m)	A measurement in meters from the location point of the nest, bird, or random point to the edge of the nearest forest opening or roadway in which a woodcock could display
Distance to Tree (m)	A measurement in meters from the location point of the nest, bird, or random point to the nearest tree
Overstory Height (m)	A measurement based on size classes 0–3m, 3–9m, and >9m, and values for the size classes were assigned as the midpoint of the size class the height fell into.
Basal Area of trees (sq. ft)	Calculated from the diameter at breast height (DBH) of each tree in the plot with a DBH of >10cm.
Water	An ocular estimate of the percent of ground occupied by standing water, based on the Daubenmire method.
Bare	An ocular estimate of the percent of ground occupied by bare areas, based on the Daubenmire method.
Litter	An ocular estimate of the percent of ground occupied by leaf litter, based on the Daubenmire method.
Grass	An ocular estimate of the percent of ground occupied by grass, based on the Daubenmire method.
Forb	An ocular estimate of the percent of ground occupied by forbs, based on the Daubenmire method.
Moss	An ocular estimate of the percent of ground occupied by moss, based on the Daubenmire method.
Woody	An ocular estimate of the percent of ground occupied by small woody vegetation, such as tree seedlings and small shrubs, based on the Daubenmire method.
Dead Woody	An ocular estimate of the percent of ground occupied by dead wood, based on the Daubenmire method.
Saplings/sqm	The number of saplings counted in each square meter sampled per plot, averaged across each of 5 sampling sites.
% Canopy Closure	The percent of canopy closure observed at each of 5 locations in each survey plot, averaged across observations.
% Percent Moisture	The percent of soil moisture measured in each soil sample, based on analysis in a soil laboratory

Table 2.2 (cont’d)

Soil pH	The pH of each soil sample, based on analysis in a soil laboratory
% Sand Content	The percent of sand present in each soil sample, based on analysis in a soil laboratory.

Table 2.3: Loadings scores for each variable in the 6 retained principal components. Values in bold indicate variables that loaded highly enough to be considered relevant to component definition and thus to woodcock survival in the known fate analyses models that used these components.

	Soil Composition	Forest Cover	Woody Ground Cover	Varied Ground Cover	Dead Woody Ground Cover	Component 6
Distance to the nearest clearing	0.123	0.446	0.38	0.153	0.221	0.486
Distance to the nearest tree	0.143	**-0.565**	0.202	0.198	0.196	0.014
Overstory height	-0.374	**0.684**	-0.028	0.116	-0.024	0.092
Basal area (sqft)	-0.23	**0.663**	-0.042	0.089	-0.144	0.051
Open water ground cover	0.332	-0.036	0.245	**0.513**	0.2	-0.029
Bare ground cover	0.364	-0.13	-0.35	-0.084	-0.262	0.63
Litter ground cover	**-0.642**	0.003	0.069	0.423	0.062	-0.168
Grass ground cover	0.486	-0.198	0.176	**-0.517**	0.02	-0.007
Forb ground cover	-0.025	0.366	0.035	**-0.589**	0.14	-0.168
Moss ground cover	0.375	0.042	0.042	0.247	-0.122	0.077
Woody ground cover	0.203	0.147	**-0.599**	0.092	0.195	-0.227
Dead woody ground cover	-0.063	0.063	0.308	0.144	**-0.596**	-0.202
Saplings per square meter	0.253	-0.359	-0.383	0.262	0.373	0.097
Canopy closure	-0.143	**0.604**	-0.451	-0.044	0.253	0.045
Soil moisture	**0.77**	0.327	0.282	0.104	0.123	-0.168
Soil pH	**0.558**	0.021	-0.325	0.193	-0.472	0.085
Soil sand content	**-0.505**	-0.122	0.311	-0.113	0.141	0.447

Table 2.4: Akaike Information Criterion (AIC_c) table with variables included in each logistic regression model considered for the differences between successful and unsuccessful nests among American woodcock nesting sites located in Michigan, 2018-2019.

Model	Variables Included	AIC_c	ΔAIC_c	Weight
2	Soil composition, forest cover, woody ground cover, varied ground cover, dead woody ground cover, and component 6 components	68.03	0	0.42
9	Soil composition and forest cover components	69.67	1.63	0.19
22	Forest cover and woody ground cover components	70.33	2.29	0.13
10	Soil composition, forest cover, and varied ground cover components	70.69	2.66	0.11
23	Soil composition and woody ground cover components	71.11	3.08	0.09
21	Soil composition, forest cover, and woody ground cover components	72.01	3.97	0.06
24	Null	81.37	13.34	0
18	Grass and woody ground cover	82.03	14	0
1	Woody ground cover and soil moisture	82.23	14.2	0
7	Distance to nearest tree, basal area, canopy closure, and overstory height	82.75	14.72	0
4	Sapling density	83.24	15.21	0
5	Sapling density and soil moisture	83.41	15.37	0
20	Distance to nearest clearing	83.51	15.48	0
3	Litter ground cover and soil moisture	83.81	15.77	0
12	Litter and woody ground cover	84.72	16.69	0
8	Sapling density and woody ground cover	84.76	16.73	0
15	Distance to nearest clearing and woody ground cover	84.79	16.75	0
6	Litter and sapling density	85.47	17.43	0
14	Litter and canopy closure	85.5	17.47	0
19	Number of trees and overstory height	85.74	17.71	0
16	Litter, woody, and forb ground cover	86	19.97	0
11	Sapling density, canopy closure, and overstory height	86.9	18.87	0
17	Litter, woody, and forb ground cover	88.3	20.26	0
13	Litter and woody ground cover and canopy closure	88.93	20.89	0

Table 2.5: Akaike Information Criterion (AIC_c) table with variables included in each known fate model considered for brood survival among American woodcock marked in Michigan, 2018-2019.

Model	Variables Included	AIC_c	ΔAIC_c	Weight
40	Woody ground cover and soil moisture	97.28	0.00	0.47
39	Woody ground cover and litter ground cover	99.66	2.38	0.14
22	Woody ground cover and grass ground cover	100.26	2.97	0.11
37	Woody ground cover	100.31	3.03	0.10
21	Woody, litter, and forb ground cover	101.35	4.07	0.06
41	Woody ground cover and sapling density	102.20	4.92	0.04
38	Woody ground cover*age period	102.35	5.06	0.04
30	Woody, litter, and forb ground cover and sapling density	103.29	6.00	0.02
15	Woody ground cover*age period and sapling density*age period	106.24	8.96	0.01
23	Age period	108.78	11.50	0.00
5	Woody ground cover component (Component 3)	109.45	12.17	0.00
25	Soil moisture	110.01	12.73	0.00
1	Bare ground cover	110.01	12.73	0.00
12	Soil composition and woody ground cover components (Components 1 and 3)	110.15	12.87	0.00
2	Canopy Closure	110.89	13.61	0.00
33	Sapling density and soil moisture	111.08	13.79	0.00
20	Grass ground cover	111.14	13.86	0.00
18	Null	111.26	13.97	0.00
3	Soil composition component (Component 1)	111.34	14.06	0.00
13	Forest cover and woody ground cover components (Components 2 and 3)	111.36	14.08	0.00
24	Overstory Height	111.60	14.32	0.00
6	Varied ground cover component (Component 4)	111.67	14.38	0.00
9	Soil composition, forest cover, and woody ground cover components (Components 1, 2, and 3)	111.80	14.51	0.00
31	Sapling density*age period	111.86	14.57	0.00
26	Mossy ground cover	112.03	14.75	0.00
8	Component 6	112.32	15.04	0.00

Table 2.5 (cont'd)

32	Sapling density	112.34	15.05	0.00
19	Forb ground cover	112.37	15.09	0.00
17	Distance to nearest tree	112.51	15.22	0.00
16	Dead woody ground cover	112.57	15.29	0.00
36	Standing water ground cover	112.61	15.32	0.00
27	Number of trees	112.69	15.41	0.00
7	Dead woody ground cover component (component 5)	112.81	15.52	0.00
29	Soil sand content	113.00	15.72	0.00
34	Litter ground cover, soil moisture, and soil sand content	113.01	15.72	0.00
10	Soil composition, forest cover, and dead woody ground cover components (Components 1, 2, and 4)	113.10	15.81	0.00
35	Basal area	113.17	15.88	0.00
28	pH	113.25	15.96	0.00
11	Soil composition and forest cover components (Components 1 and 2)	113.26	15.98	0.00
4	Forest cover component (Component 2)	113.28	16.00	0.00
14	Soil composition, forest cover, woody ground cover, varied ground cover, dead woody ground cover, and component 6 components	113.86	16.58	0.00

Table 2.6: A summary of survival information for woodcock nests and broods during the breeding season for 2 study years, 2018 and 2019.

Parameter	2018	2019
Broods captured	19	44
Removed from study	2	3
Broods in study	17	41
Nests Monitored	22	36
Mortality events		
Nest	10	15
Entire brood loss	3	12
Successful nests	12	21
Successful broods		
to 14-days	12	27
to 32-days	11	23
Censored Broods (dropped collar or lost signal)	3	6
Survived study period	11	23

APPENDIX II: FIGURES

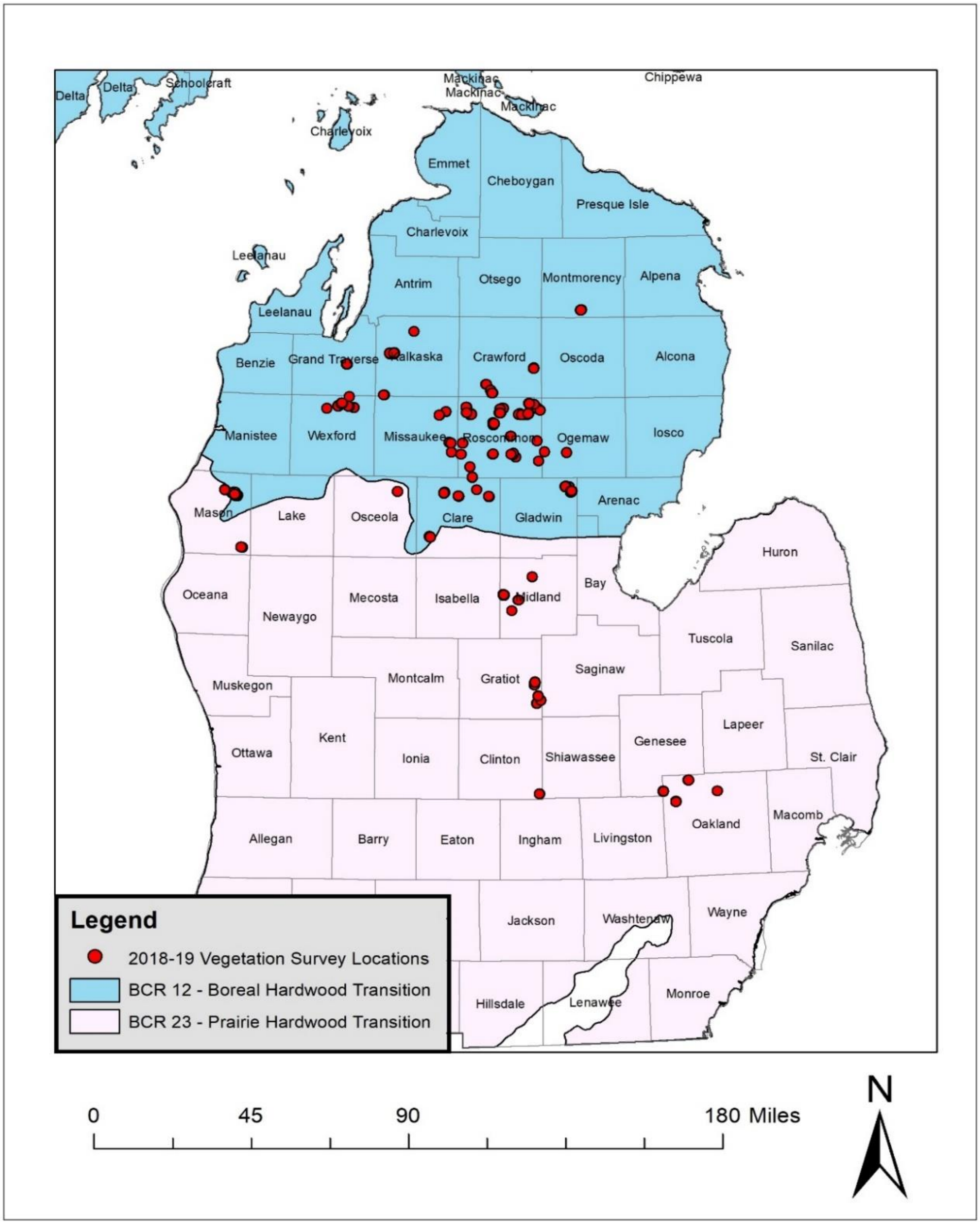

Figure 2.1: Locations in Michigan where woodcock were captured and marked and vegetation surveys were completed at nest and brood sites in 2018 and 2019, with county names for reference. Map colors denote the difference between the Boreal Hardwood Transition and the Prairie Hardwood Transition Bird Conservation Regions

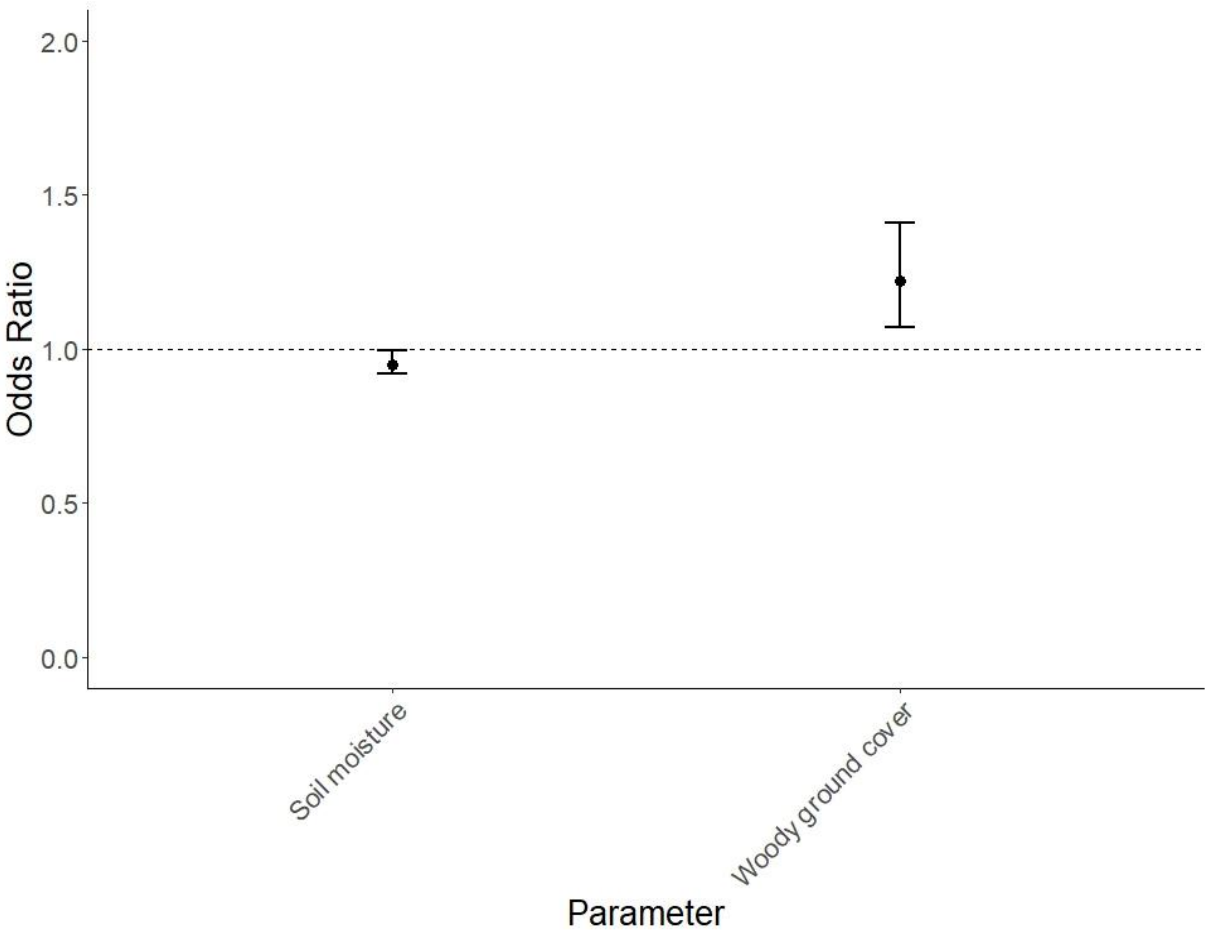

Figure 2.2: Strength of the effect of parameters included in the top model for brood survival (see table 2.5) on brood survival. Displayed are the odds ratios and 95% confidence intervals of the parameters in the models, with a dashed line at 1 to represent no effect on survival. Parameters with confidence intervals that overlap 1 show minimal effect on survival, while parameters above 1 show a positive effect on survival and parameters below 1 show a negative effect on survival

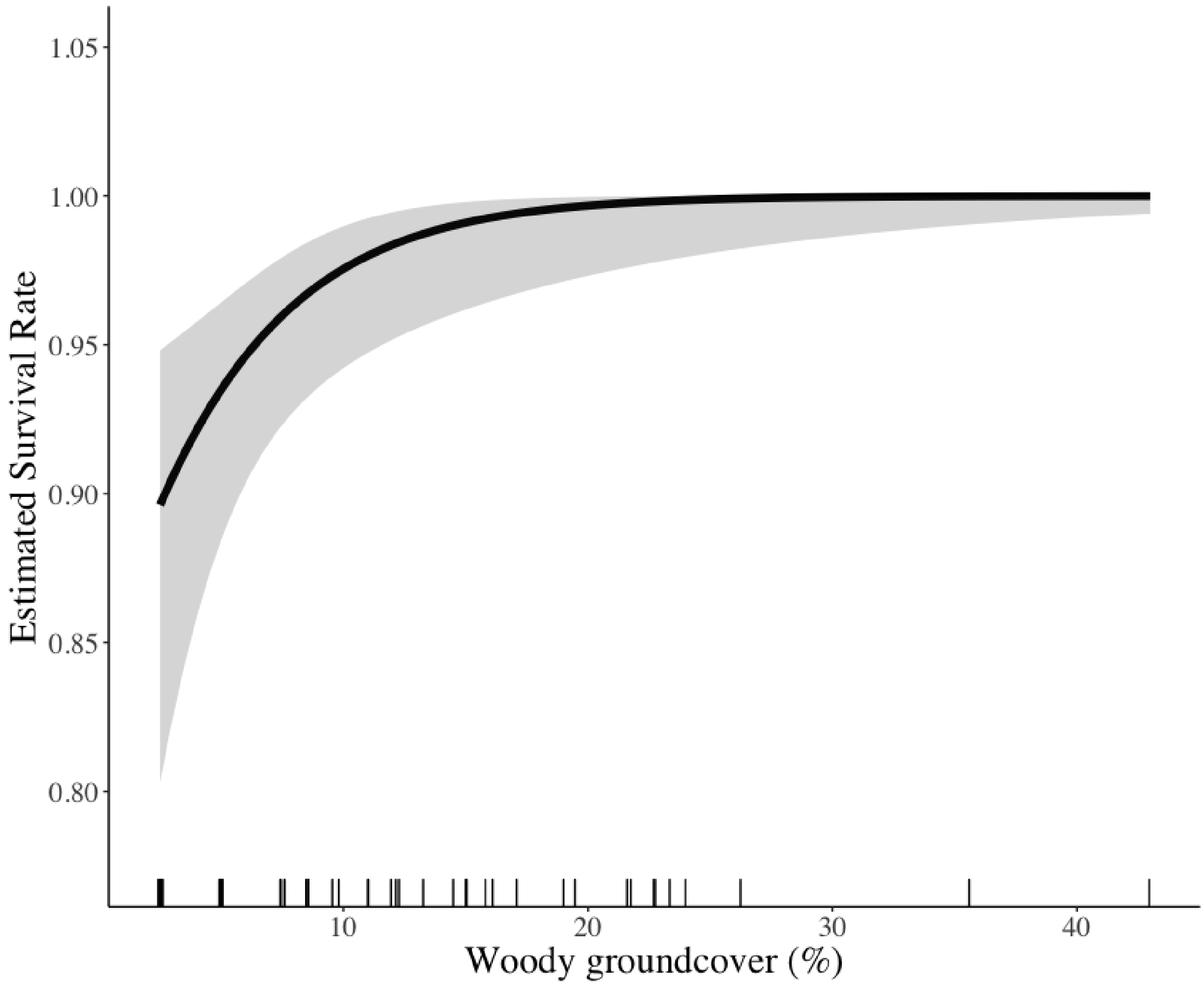

Figure 2.3: Estimated survival rate of woodcock broods for 3-day intervals as included in the known fate models, not the overall survival rate of the entire study period, and how woody ground cover affects that survival rate. Tick marks at the bottom of the graph represent actual data observations.

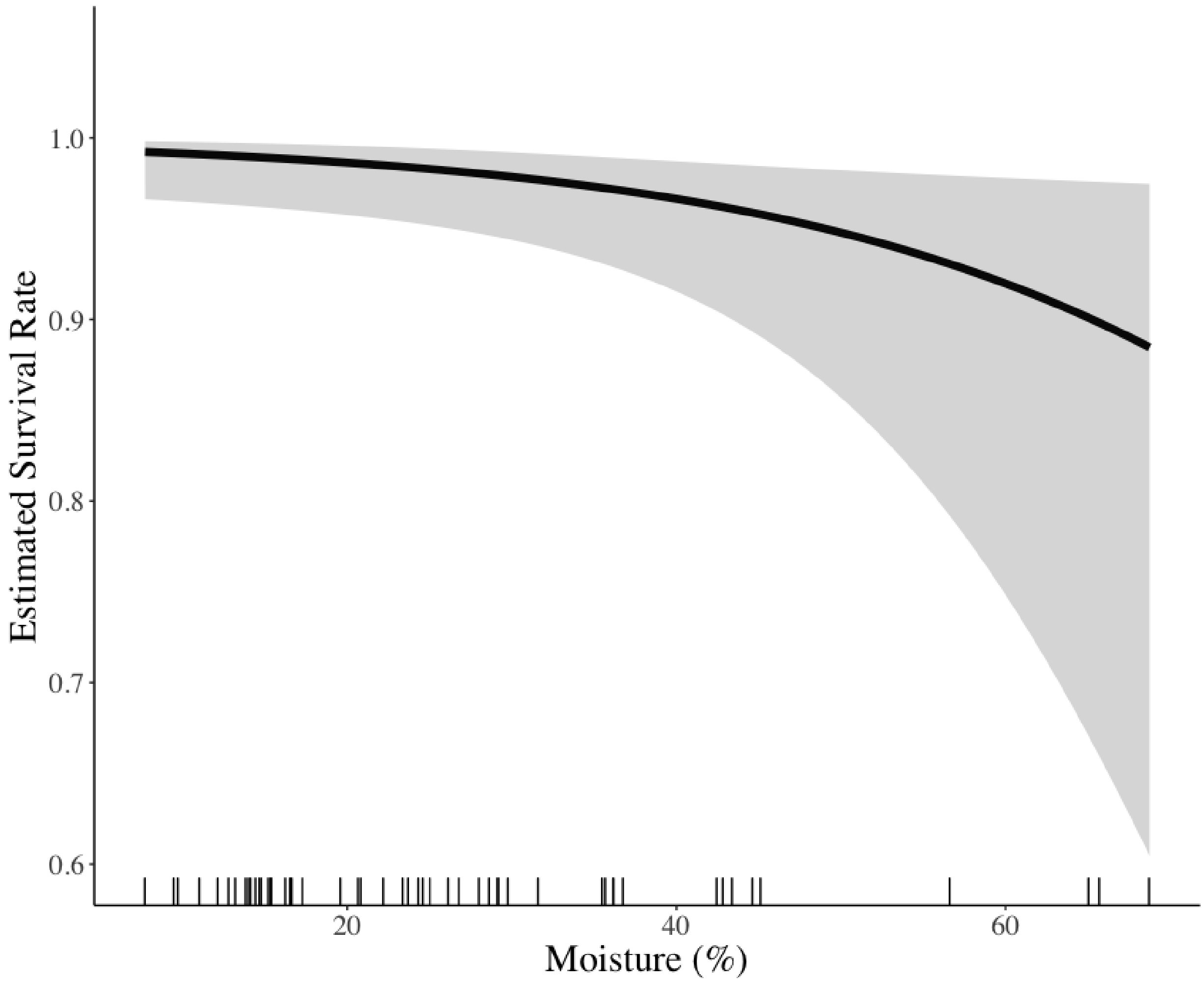

Figure 2.4: Estimated survival rate of woodcock broods for 3-day intervals as included in the known fate models, not the overall survival rate of the entire study period, and how soil moisture affects those survival rates. Tick marks at the bottom of the graph represent actual data observations.

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