Fall 12-2021

American Woodcock (Scolopax minor) Migration Ecology in Eastern North America

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Recommended Citation

Fish, Alexander, "American Woodcock (Scolopax minor) Migration Ecology in Eastern North America" (2021). *Electronic Theses and Dissertations*. 3522.
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AMERICAN WOODCOCK (*SCOLOPAX MINOR*) MIGRATION ECOLOGY IN EASTERN NORTH AMERICA

By

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A DISSERTATION

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Wildlife Ecology)

The Graduate School

The University of Maine

December 2021

Advisory Committee:

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AMERICAN WOODCOCK (*SCOLOPAX MINOR*) MIGRATION ECOLOGY IN EASTERN NORTH AMERICA

By Alexander C. Fish

Dissertation Advisors: Dr. Erik J. Blomberg and Dr. Amber M. Roth

An Abstract of the Dissertation Presented
in Partial Fulfillment of the Requirements for the
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Across temperate regions of North America, migrating animals must contend with seasonally influenced thermal extremes, changing food abundance, and stochastic weather events. Migrating individuals must locate suitable areas, termed stopover locations, to rest and rebuild energy reserves needed to continue migration (Rodewald and Brittingham 2004, Taylor et al. 2011). The American Woodcock (*Scolopax minor*; woodcock hereinafter) is a migratory forest bird that has experienced long-term population declines (Seamans and Rau 2019). We created the Eastern Woodcock Migration Research Cooperative, including 34 provincial, federal, state, and non-governmental partners, with the goal of describing the migration ecology of woodcock in the eastern portion of its range. We were primarily interested in understanding migration phenology, identifying weather conditions that were associated with migratory departure events, and quantifying survival during migration.

Recent advances in transmitter design allowed the cooperative to remotely obtain high resolution locations of migrating woodcock. We deployed 304 satellite-gps transmitters in three provinces and 12 states and collected movement data from 1 October 2017 to 18 June 2020. We begin by describing the phenology associated with migration initiation, timing of stopovers, and termination of migration during fall migration, and the initiation of spring migration and describe the spatial, demographic, and body-conditions based variation in these events. We then built predictive models to estimate the dates associated with fall and spring migration and provide a framework for wildlife managers to evaluate the timing of hunting seasons under current and future harvest regulations. Next, we evaluate the environmental cues associated with migratory departure events and found that age influenced cue selection in the fall and sex in the spring. Furthermore, the specific conditions in which an individual initiated migration could influence the distance an individual traveled in a single migratory flight, but not the pace of migration which was more spported by spatial features. Lastly, we quantified survival of woodcock during migratory periods and found that survival varied by migratory behavioral state, through time, and depending on the season, but was not influenced by age or sex.

DEDICATION

To my parents Jon Fish and Kristine Kondrak-Fish for teaching me to love the natural world as a child, continually demonstrating what hard work can achieve, and for their ceaseless love and support throughout this journey. I cannot thank you enough.

ACKNOWLEDGEMENTS

I'd like to begin by thanking the incredible cooperators that contributed to the Eastern Woodcock Migration Research Cooperative, and thereby contributed most of the data used in my dissertation. I would also like to thank the dedicated biologists, technicians, and volunteers that gave up their evenings, often accompanied by freezing temperatures, rain, and or snow, as we attempted to capture woodcock until the early morning hours. I will never forget the sleep deprivation, and general misery you endured to make this project a success. A special thank you to D. McAuley, T. McAuley, and R. Brown for teaching me how to capture woodcock and to D. McAuley and the United State Geological Survey Patuxent Wildlife Research Center for lending me woodcock capture equipment. I would also like to thank J. Hately for access at the J. F. Witter Teaching and Research Center, M. Potiska for access to the University of Maine's Hackerspace laboratory and for teaching me everything necessary to successful 3D print, and the volunteers, A. Barnes, E. Carvalo, D. Donadio, K. Lima, K. Overturf, M. Turso and K. Wilson, all of whom made my fourth chapter possible.

Support was provided in part by the Alabama Department of Conservation and Natural Resources, American Woodcock Society, Association des Savaginiers du Saguenay-Lac-St-Jean, Canaan Valley National Wildlife Refuge, Club des Becassiers du Quebec, Eastern Bird Banding Association, Environment and Climate Change Canada, Florida Fish and Wildlife Conservation Commission, Friends of the 500th, Georgia Department of Natural Resources, Maine Department of Inland Fisheries and Wildlife, Maryland Department of Natural Resources, Moosehorn National Wildlife Refuge, New Jersey Department of Environmental Protection, New York Department of Environmental Conservation, North Carolina Wildlife Resources Commission, Old Hemlock Foundation, Pennsylvania Game Commission, Penobscot Valley Chapter – Maine Audubon, Rhode Island Department of Environmental Management, Ruffed Grouse Society, State University of New York – Cobleskill, South Carolina Department of Natural

Resources, United States Fish and Wildlife Service, USFWS Webless Migratory Game Bird Program, USGS Patuxent Wildlife Research Center, University of Maine, University of Maine Canadian-American Center, University of Rhode Island, Virginia Department of Wildlife Resources, West Virginia Highlands Conservancy, Wildlife Management Institute, and the Woodcock Conservation Society. This project was supported by the USDA National Institute of Food and Agriculture, McIntire-Stennis project number ME0-21422 and ME0-42108 through the Maine Agricultural and Forest Experiment Station.

I would also like to recognize the amazing community that has supported me throughout this journey. Your friendship, encouragement, and commiseration at local breweries, while playing nerdy board games, sitting next to the bonfire, or partaking in one of my hair-brained outdoor adventures that often resulted in copious amounts of blood loss due to Maine's abundance blood-sucking insects, has been integral to my success. A special thanks to A. Barnes, L. Berigan, N. Bieber, J. Boone, S. Boone, S. Chen, O. Choi, B. Evans, M. Gonnerman, C. Heilakka, M. Hess, M. Mensinger, A. O'Malley, B. O'Malley, B. Peterson, C. Pohlman, J. Rodriquez, S. Shea, S. Snyder, J. Tebbenkamp, O. Tumendemberel, S. Vogel, S. Welsch, K. Whittum, and K. Wilson, for the unforgettable memories! I need to extend a tremendous thank you to my housemates, L. Berigan, C. Heilakka, M. Mensinger, C. Pohlman, S. Welsch, and K. Whittum, because let's face it… being locked inside together for COVID was difficult, but I couldn't imagine of a better group of people to quarantine alongside. A special thank you to my lab and office mates for continually providing honest, thoughtful, and pragmatic feedback. I would also like to thank my family for their continued support both before and while attending the University of Maine. You are all the hidden figures in my life and I would never have made it this far without you. Thank you.

I would lastly like to thank my graduate committee. Beginning with my advisors Erik Blomberg and Amber Roth. You both have pushed me beyond my comfort zone, have been my harshest critics, and greatest cheerleaders. You and your families have welcomed me into you homes, encouraged me to strike a healthy work-life balance, and have always treated me with respect and as a peer, rather than a subordinate. I cannot thank you enough for this experience and all that I have become with your mentorship and support. To my committee Erin Simons-Legaard, Joe Zydlewski, and Brian Olsen, you have been fantastic to work with. You have treated me with honesty and respect, offered direct feedback, were generous with your time, and have approached everything with positive, proactive, can-do attitudes. Thank you for your support and encouragement for the past four years.

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CHAPTER 1

AMERICAN WOODCOCK (*SCOLOPAX MINOR*) FALL AND SPRING MIGRATION PHENOLOGY IN EASTERN NORTH AMERICA; IMPLICATIONS FOR HUNTING SEASON TIMING

Abstract

Understanding the timing of migration is fundamental to migratory bird management throughout the annual cycle. For migratory gamebirds, management goals focus on ensuring the conservation of local breeding and migrant populations using detailed spatial and temporal information for each segment of the population. We used GPS transmitters to track American Woodcock (*Scolopax minor*), a medium-bodied migratory gamebird, during their fall departure from breeding areas until the initiation of spring migration from the wintering grounds. We captured 304 woodcock in three Canadian provinces and ten US states in eastern North American from 2017 to 2020. Using locations collected every 1.7 days on average, we assessed whether migration initiation, termination, or stopover timing of woodcock migration varied geographically, differed among age and sex classes, or was based on individual body condition. Using general linear and linear mixed effect models, we found support for geographic variation in every migration stage. During fall, woodcock migrating from areas farther north and west (e.g., Ontario, Quebec) in the study area initiated migration and made stopovers earlier than woodcock migrating from areas farther south and east (e.g., Rhode Island). Woodcock migrating from farther north and west also terminated migration earlier. Adult woodcock initiated fall migration four days before young woodcock, and during migration adult females progressed through migration prior to young birds (5 days), and adult males (9 days). During spring migration, woodcock farther west initiated migration before birds farther east, and males initiated migration on average six days before females.

Wildlife managers may use the phenological data we present to evaluate the timing of hunting seasons with respect to local breeding and migrant populations.

Introduction

Understanding the phenology of migration is central to the conservation of migratory birds. During migration individuals travel between areas of breeding and winter residency, and often must navigate threats or challenges encountered. Knowledge of the timing and spatial characteristics of migration enables a greater insight into potential threats (Belaire et al. 2014), or mismatch of resource availability and use timing. For example, timing of the red knot (*Calidris canutus rufa*) spring migration coincides stopover with mass breeding events of the horseshoe crab (*Limulus polyphemus*) in Delaware Bay (Clark et al. 1993, Walls et al. 2002, Karpanty et al. 2006). The energy that horseshoe crab eggs provide has been linked to red knot reproductive success on the breeding grounds (Guy Morrison et al. 2007), and a mismatch or reduction in availability of horseshoe crab eggs can result in red knot declines (Baker et al. 2004). In addition to carry over effects on populations stemming from resource availability, direct threats to individual survival in the form of collision with anthropogenic structures (e.g., wind turbines, buildings, cell towers) also occur (Barclay et al. 2007, Gehring et al. 2011, Loss et al. 2019, 2020). Mitigation strategies often include slowing or shutting down wind turbines, and encouraging participation in lights out programs during specific time periods or conditions when there is the greatest opportunity to prevent bird mortality or injury (Loss et al. 2020). Because such mitigation activities incur a financial cost, it is important to understand the timing and locations of potential conflicts to ensure maximum benefit while minimizing costs.

Effective harvest management for migratory gamebirds similarly requires an understanding of migration phenology. Hunting season structure is often variable across a species' range, and harvest management strategies may target a mix of both local and migrant individuals within an administrative division boundary (e.g. state or province). Managers typically establish the timing, duration, and bag limits of hunting seasons based on when birds are most likely to be available for harvest in a given area in order to maximize hunter opportunity. By understanding phenology of local breeding and migrant populations, managers can modify hunting season structure within their administrative division to meet local management goals. For example, local wildlife managers may set hunting seasons and harvest limits to prevent overexploitation of local resident populations, while increasing hunting opportunities by targeting larger numbers of migrant individuals. If hunting seasons are misaligned with migratory phenology, however, local breeding populations or certain age and sex classes may be disproportionately harvested.

The timing of bird migration often differs among age (Francis and Cooke 1986, Lozano et al. 1996, Shamoun-Baranes et al. 2017) or sex classes (Moore et al. 1990, Shamoun-Baranes et al. 2017), with many species exhibiting spring protandry (Wobker et al. 2021). Males of many species typically initiate and complete spring migration prior to females but not always (Rubolini et al. 2004, Pedersen et al. 2019, Krietsch et al. 2020). Similarly, various age cohorts may have different migration phenology due to prior migratory experience or navigation naivety. For example, young birds are often recorded in higher densities compared to adults birds on geographic features that concentrate birds during migration, such as the Cape May Peninsula in New Jersey (Krohn et al. 1977, Allen et al. 2020). Observations like this suggest distinct cohorts of birds may migrate at different times, or exhibit distinct spatial patterns, which may cause segments of the population may be exposed to variable environmental or anthropogenic threats (Francis and Cooke 1986, Lerche-Jørgensen et al. 2018, Rousseau et al. 2020). Understanding the potential for variable risk of harvest requires disentangling these sources of variation in migration timing, which has traditionally been limited by available technology.

Recent advances in satellite transmitter technology have revolutionized tracking individual animals throughout migration (Bridge et al. 2011). GPS-based satellite tracking tags recently became small enough for use on the American woodcock (*Scolopax minor*; hereafter, woodcock), a migratory gamebird native to eastern North American, improving resolution and tracking of individuals throughout migration (Moore et al. 2019). Woodcock breed from southern Canada to the southeastern US, with the highest breeding densities in the northern portions of the breeding range (Seamans and Rau 2019). The highest overwintering densities occur in mid-Atlantic, southeastern US, and Gulf Coast states, with some birds overwintering in coastal southern New England (McAuley et al. 2020). Because the woodcock range spans most of eastern North America, managers must be cognizant of migration timing as they set hunting seasons, where the relative abundance of local breeding residents to migrant birds may vary considerably among administrative divisions. Hunter harvest data for woodcock indicate a proportionally greater harvest of adult females compared to other age and sex classes (Seamans and Rau 2019). Adult females are important for regulating population growth, and higher harvest of this cohort may be concerning in the context of prolonged woodcock population declines (Seamans and Rau 2019). The underlying factors contributing to greater harvest of adult females are poorly understood, particularly when paired with limited information on migratory phenology. A better understanding of the timing of woodcock migration, and how it varies by demographic cohorts and locations across the range, can better inform harvest management of the species.

Our goal was to describe American Woodcock migratory phenology during the time periods of migration that overlap with current woodcock hunting seasons (e.g. fall and early spring). Specifically, we sought to provide managers with information to estimate local timing of migration for resident and migrant woodcock within administrative units relevant to woodcock harvest management. In pursuit of this goal, our objectives were to 1) describe spatial variability in the timing of migration events (i.e., initiation, stopover, termination) among administrative division boundaries, 2) understand variation in migration timing among age and sex classes, and 3) evaluate the contribution of individual body condition to migration timing. We used GPS transmitters on woodcock marked throughout eastern North American to track woodcock during fall and early spring migratory periods.

Study Area

Our research focused on the Eastern Woodcock Management Region, one of two spatial units by which the United States Fish and Wildlife Service and Environment and Climate Change Canada managed woodcock populations (Seamans and Rau 2019; Figure 1.1). The Eastern Woodcock Management Region included US states located east of the Appalachian Mountains, as well as the Canadian provinces of New Brunswick, Newfoundland, Nova Scotia, Prince Edward Island, and Quebec. We included several sites from the Central Woodcock Management Region (eastern Ontario and Alabama) due to their close proximity to the Eastern Woodcock Management Region and the potential for woodcock to migrate across management region boundaries (Moore et al. 2019). The Eastern and Central Woodcock Management Regions generally corresponded with the Atlantic and Mississippi flyways (Seamans and Rau 2019). During fall (September-October), our capture efforts targeted breeding populations in Maine, New York, Nova Scotia, Ontario, Pennsylvania, Quebec, Rhode Island, Virginia, and West Virginia (Figure 1.1). In the winter (December-March), our capture efforts shifted to overwintering areas including Alabama, Florida, Georgia, Maryland, New Jersey, North Carolina, South Carolina, and Virginia (Figure 1.1).

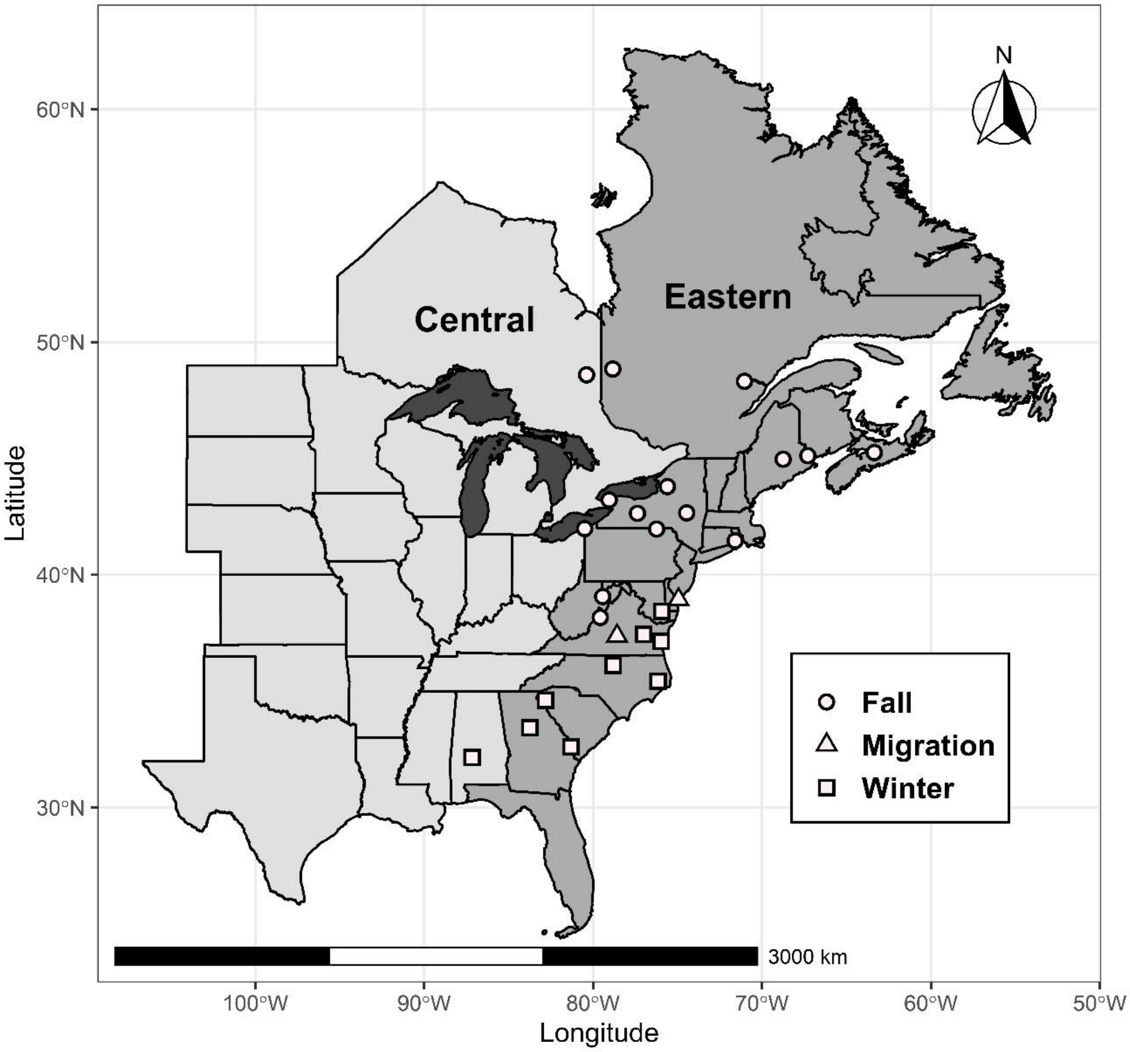

Figure 1.1. Distribution of capture locations in 2017-2020 and delineation of American Woodcock Central and Eastern Management Regions, which generally covers the species distribution in eastern North America. Capture sites were generally distributed within the Eastern Woodcock Management Region, with two sites in the Central Woodcock Management Region (Ontario and Alabama). Captures primarily occurred in fall and winter prior to migration initiation, however some captures in the mid-Atlantic Region occurred during migration.

Methods

Capture and Marking

Woodcock were captured just prior to the onset of migration to maximize GPS tag life during migration and the number of individuals available to migrate. The range of capture dates generally included 27 August to 30 October during falls 2017 to 2019, and 3 January to 29 February during winters

2019 to 2020, however, some individuals were also captured during migratory periods (18 November to 14 December, 2018 to 2019). Capture sites were within cooperating states or provinces based on prior expert knowledge to identify areas near young forest management (e.g., harvest) where woodcock densities are known to be highest (Dessecker and McAuley 2001). We captured woodcock using mist nets during crepuscular flights (Sheldon 1960) by setting mist net arrays near known roosting fields, travel corridors, and forested wetlands to capture birds as they left diurnal use areas and flew to night roosts. Additionally, we used spotlights and thermal imaging scopes to locate night-roosting woodcock and captured them with hand nets (Rieffenberger and Kletzly 1966, McAuley et al. 1993, Moore et al. 2019).

We aged captured woodcock to two age classes including adult (after hatch year or after second year; > 1 year old) or young (hatch year or second year; < 1 year old), based on wing plumage characteristics, and determined sex (male or female) using a combination of wing plumage and bill length (Mendall and Aldous 1943, Martin 1964). We also recorded the mass of each individual using a spring scale 300 ± 2 g (Pesola Präzisionswaagen AG, Schindellegi, Schwitzerland) and the lower leg length using either a dial caliper (± 0.1 mm) or metric ruler (± 1 mm). The lower leg length comprised the intertarsal joint to the end of the foot excluding the toes (Blomberg et al. 2014). Woodcock were fitted with a Lotek PinPoint GPS transmitter (Model 75 or Model 120; Lotek Wireless Inc., Newmarket, Ontario, CA) enabled with a Platform Transmitter Terminal (PTT) for transmitting locational data to the ARGOS satellite network. Satellite transmitters were attached with a leg-loop style harness (Moore et al. 2019). Transmitter weight in combination with the harness did not exceed 4% of an individual's body mass. Mean male (μ ± SD) mass was 152 ± 14 g and mean female mass was 196 ± 18 g, resulting in 3.06 ± 0.44% body mass for the PinPoint 75 model and 3.68 ± 0.25% for the PinPoint 120 model. (All capture and marking procedures were approved by the University of Maine Institutional Animal Care and Use Committee Protocol A2017-05-02).

Woodcock Location Data Collection

Transmitters collected GPS locations on pre-programmed schedules and transmitted data to a central database using the ARGOS satellite system. We programmed transmitters to collect locations every 1-2 days during likely periods of migration using LOTEK PinPoint Host software (LOTEK Wireless Inc., Newmarket, Ontario, CA). During likely non-migratory periods, we collected locations less frequently (e.g., one location every 5-7 days) to extend battery life. This approach allowed for collection of one seasonal (e.g. fall or spring) migratory track for all birds, with the potential to collect a second migration. Transmitters primarily collected locations during diurnal periods, however some schedules contained nocturnal locations depending on objectives unrelated to this study. We stopped receiving locations when birds either died or dropped their transmitter, causing the transmitter to rest on the ground and attenuate the signal, or if the transmitter failed.

We manually downloaded woodcock locations from the ARGOS website every 1 to 5 days, and used Movebank (Kranstauber et al. 2011) to store location data. We did not recover every location that was programmed in the transmitter, as satellite uploads sometimes failed due to a variety of factors (e.g., poor satellite configuration, local topography). Hence, recovered data contained at least one interval greater than 1 day between successive locations for most individuals, and these non-recovered locations occurred throughout the monitoring period. Overall, this programming schedule resulted in an average of 1.74 days between relocations of marked individuals during migratory periods, which we consider our mean precision of migration timing estimates.

Movement Modeling

We identified migratory behavioral states for each marked woodcock location using Multivariate Hidden Markov Models (MHMM), implemented with the momentuHMM package (McClintock and Michelot 2018) in program R (R version 3.6.3, www.r-project.org, accessed 1 Dec 2020). The MHMMs identify latent behavioral states within animal movement trajectories, where probabilities of transitions among states are inferred from movement data streams and their underlying distributions (McClintock and Michelot 2018). We used two data streams, step length (Euclidean distance) and turning angle (bearing) between each successive location in an individual's track, and specified a gamma distribution for step length and a wrapped Cauchy distribution for turn angle. We developed a model to identify three migratory behavioral states: pre-migration, migration, and post-migration. We constrained transition between states such that 1) individuals in the pre-migration state could only transition to migration, and 2) once in the migration state, individuals could either remain or transition into post-migration. Post-migration was specified as a terminal behavioral state, where once an individual had entered post-migration it could not transition to another state. We specified state-specific initial values for step length (mean, SD, and zeromass) and turn angle (mean and concentration) following the recommended procedure outlines by Michelot et al. (2016; Appendix A).

We subset woodcock location data into fall (1 October to 14 January) and spring (15 January to 18 June) migratory periods for each study year, and conducted a separate analysis for each of the 5 migratory periods (three years for fall and two years for spring). We removed individuals with three or fewer locations during each seasonal period prior to analysis, as a minimum of three locations is required by momentuHMM. We used the resulting distribution of step lengths and turning angles to predict the behavioral state associated with each location using the viterbi function in momentuHMM.

For each woodcock included in the MHMM analysis, we manually validated the state assignments and transitions from pre-migration to migration and migration to post-migration. Individuals that stopped transmitting locations prior to transitioning into the migration behavioral state provided us no information on timing of migration, so we did not consider them further. Between marking and migration initiation, a subset of woodcock exhibited long-distance ranging movements that caused premature entry into the migration state (e.g., migration initiation) but did not reflect a clear transition to a directional migratory path. Because this complicated our ability to identify the onset of migration, we excluded these individuals from analysis. Similarly, a combination of ranging movements after migration termination, or persistent movement between wintering sites, resulted in delayed identification of migration termination date for a subset of birds, and these were subsequently removed from the migration termination analysis. Generally, these birds were few (~6 % for fall initiation, ~21 % for fall termination, and ~19 % for spring initiation), and we assume their exclusion does not bias the more general patterns within the dataset.

When state transitions (e.g., initiation or termination events) were identified but had greater than one day between successive locations and the exact date of departure or arrival could not be verified, we used the mean date between locations as an approximation. While this does yield some ambiguity, conceivably the migration events were just as likely to occur earlier or later than the mean date, and thus this would reflect latent variation in the data but would not result in bias. We consider all locations associated with the migratory behavioral state to reflect migratory stopovers, and will refer to them as stopover locations hereafter. Lastly, for every state or province with a stopover location, we reviewed 2020-2021 hunting regulations and collected the daily bag limit, dates associated with woodcock hunting seasons, and the total number of days hunters can pursue woodcock. These dates were then used to compare the timing of migration to the most recent hunting season structure.

Statistical Analysis

We developed a multi-tier modelling approach to explore the effects of spatial variation, demographic characteristics, and body condition on migration phenology, using general linear or linear mixed effects models, where appropriate. We replicated this general approach to describe migration initiation, termination, and stopover timing, with modifications for each migratory state as described below. First, we constructed a priori spatial models, evaluating how latitude, longitude, and administrative divisions influenced date of migration initiation, termination, or stopover. We considered additive effects of latitude, longitude, and their interaction to explore general spatial variation in migration timing throughout the Eastern Woodcock Management Region, and we contrasted this with a competing model based on administrative divisions. While the later models required far more parameters, it provided a useful contrast to the more general model based on spatial coordinates and was also directly relevant to interests of woodcock managers within the region. Each US state and Canadian province has the authority to manage woodcock populations within their boundaries, and administrative divisions are often the spatial unit in which management decisions (e.g., hunting season dates) are based.

Using the best-supported model from the first tier of analysis, we proceeded to evaluate demographic influences on migration phenology by adding age and sex covariates in the second analytical tier. We tested additive effects, as well as interactions between age and sex. Woodcock are sexually dimorphic, with females being larger. Conceivably, a larger body size may increase cold tolerance (Prescott 1994, Macdonald et al. 2016), and influence migration timing. We included an interaction effect between age and sex to investigate differences among the four age-sex cohorts, with a particular interest in adult females. Migratory timing relative to the hunting season timing could explain the disproportionately high rate of adult females harvested relative to the other age-sex cohorts. Hence, comparing adult females to other cohorts may provide insight for managers interested in reducing adult female harvest.

For the third analytical tier, we evaluated individual condition using the best-supported model from the first two tiers. We created a priori models including condition as an additive effect and as an interaction with age or sex and spatial predictors, as supported during earlier tiers of analysis. To characterize the condition of woodcock, we developed a general linear model using the stats package (Bolar 2019) in Program R to relate body mass with body size (as indexed by leg length), sex, and age (Blomberg et al. 2014). This model confirmed a positive association between body mass and size (β = 0.38 ± 0.25), as well as a generally higher body mass for females (β = 42.73 ± 1.85) and lower body mass for adults (β = -2.35 ± 1.72) and had a strong fit to the data (R^2 = 0.74, model intercept: β_0 = 139 ± 9.34). Once the model was fit, we extracted individual residuals using the modelr package (Wickman 2020). A positive residual score indicated those individuals that were heavier than expected (i.e., above-average condition) given their size, age, and sex, while individuals with a negative residual score were those lighter than expected (below-average condition; Blomberg et al. 2014). Woodcock in below-average condition would be expected to have lower energy reserves for migration, and this relationship may be more pronounced for certain age and sex classes, or individuals originating from specific locations. We were only able to include condition on a subset of individuals, as some birds had missing biometric data and others were marked prior to a focal migratory period (e.g., marked in fall, but still transmitting data during spring migration) thus, we assumed their condition score was no longer representative. Similarly, we did not include condition as a predictor in stopover timing, as an individual's condition continually changes during migration and we were unable to monitor changes in condition.

For models of migration initiation (fall and spring) and termination (fall only), we used general linear models, as each individual was represented in a given analysis by one data point. For models of stopover timing, we used linear mixed effect models implemented with the lme4 package (Bates et al. 2015). We created an individual random intercept term, which allowed us to account for variation in mean stopover timing among individuals. This was important because individual woodcock varied in the number of stopover locations collected due to either differences in transmitter schedules, or individual variation in the pace and distance of migration. We set the Restricted Maximum Likelihood (REML) to 'false' for all linear mixed effect models so we could perform model selection.

We used Akaike's Information Criterion corrected for small sample size (AIC$_c$) to rank models for each step in the tiered modeling approach. We chose the model with the lowest AIC$_c$ score that contained no parameter(s) with 95% confidence interval(s) that overlapped zero as the most parsimonious model, and used this for further inference during the next tier of the analysis. For the categorical covariates age and sex, we coded young birds and males as zero and adults and females as 1. Beta coefficients produced from linear modeling must be interpreted with this understanding. We used the predict function in the car package (Fox and Weisberg 2019) to compare predictions of spatial models based on latitude and longitude to those built using administrative divisions, which allowed us to further evaluate model fit and identify any outlier regions within the dataset.

Results

We captured and marked 304 woodcock including 6 in 2017, 75 in 2018, 163 in 2019, and 60 in 2020. Of these, 153 were males (69 adults and 84 young) and 151 were females (72 adults and 79 young; Table 1.1). We collected 18,074 GPS locations between 01 October 2017 – 18 June 2020 including 179 in 2017, 2,584 in 2018, 9,306 in 2019, and 5,909 in 2020. Seventy-five woodcock were removed from the movement models due to failure to upload any locations post-capture (n = 14), termination data transmission prior to initiating migration (n = 44), or uploading 3 or fewer locations during a focal period(s) (e.g., 15 Jan – 18 June [spring] and 1 Oct – 14 January [fall]; n = 17). Thirty-one woodcock marked in the fall were included in the spring initiation analysis (12 in 2019, and 19 in 2020). The remaining 229 birds provided 260 migration attempts included in the movement models and subsequently had migratory behaviors assigned to their respective locations (Table 1.2). A complete list of parameter outputs (e.g., step length and turning angle) from the movement models used to assign migratory behavioral states to locations and transition probability matrices can be viewed in Appendix A.1.

Table 1.1. The total number of American Woodcock (*Scolopax minor*) with GPS transmitters attached between September 2017 and March 2020, prior to fall and spring migration respectively. Woodcock were aged either as adults (> 1 year old) or young (< 1 year old) and sexed based on plumage characteristics.

	Male		**Female**		
	Young	**Adult**	**Young**	**Adult**	**Total**
Alabama	1	2	2	2	7
Georgia	3	3	1	5	12
Maine	5	1	3	4	13
Maryland	1	6	9	3	19
New Jersey	14	0	16	0	30
New York	8	7	12	12	39
North Carolina	9	3	4	5	21
Nova Scotia	3	0	4	0	7
Ontario	1	1	1	2	5
Pennsylvania	5	5	3	11	24
Quebec	7	0	4	4	15
Rhode Island	0	24	0	6	30
South Carolina	4	4	6	3	17
Virginia	21	12	13	15	61
West Virginia	2	1	1	0	4
Total	**84**	**69**	**79**	**72**	**304**

Table 1.2. The number of American Woodcock (*Scolopax minor*) with migratory behaviors classified from Multivariate Hidden Markov Models and individuals that transitioned into a migratory behavior state (initiation), out of a migratory state (termination), and the number of individual locations recorded in a migratory state (stopover locations). Capture periods occurred during August to October for fall migration, and November to December and January to March for spring migration. Woodcock captured during November and December primarily occurred in the mid-Atlantic during fall migration but were only considered for the spring analysis.

	Fall (Oct-Jan)				**Spring (Jan-Apr)**		
	2017	**2018**	**2019**	**Total**	**2019**	**2020**	**Total**
Individuals	6	40	80	126	52	82	134
Migration initiation	6	38	73	117	37	71	108
Migration termination	3	29	61	93	–	–	–
Stopover locations	23	838	1207	2068	–	–	–

Fall Migration Initiation

The best-supported spatial model for the date of fall migration initiation included an additive effect of longitude and latitude (Table 1.3). One other competitive model with a lower AIC_c score contained an interaction between latitude and longitude, however the confidence intervals overlapped zero and the model was not included in the next analysis tier. The best supported demographic model included an additive effect of age, whereas the null model received the most support in the condition modeling tier. Initially an additive effect of condition and an interaction effect between condition and age were included in the competitive model set, however, both contained parameters estimates with confidence intervals that overlapped zero. Hence the best-supported model for fall initiation of migration was the demographic model, which explained 60% of the variation within the data ($R^2 = 0.60$), and included a combination of latitude ($\beta = -3.95 \pm 0.30$), longitude ($\beta = 0.85 \pm 0.18$), and age ($\beta = -4.07 \pm 1.77$). Woodcock marked farther north and west (e.g., Ontario, western Quebec) initiated migration before birds farther south and east (e.g., Rhode Island). For every 1° decrease in latitude or longitude, woodcock initiated migration 4.0 days (latitude) and 0.9 days (longitude) earlier, on average. Additionally, given a constant latitude and longitude, adults initiated migration an average of 4.1 days earlier than young birds (Table 1.3, Appendix B.1).

Table 1.3. Beta coefficients for the top supported general linear models describing American woodcock (*Scolopax minor*) migratory phenology based on AIC_c. Coefficients that were significant predictors in the model are denoted by an asterisk and only significant predictors were included in subsequent models. Models used males and young birds as reference (coded at intercept) for sex and age respectively. Standard error is provided in parentheses.

		Spatial			Demographic		Body Condition		
	N	Lat[a]	Long[b]	Lat× Long	Age	Sex	Cond[c]	Cond× Age	Cond× Sex
Fall initiation									
Spatial	117	-13.76 (5.31)*	6.57 (3.06)*	-0.13 (0.07)					
Demographic	117	-3.95 (0.30)*	0.85 (0.18)*		-4.07 (1.77)*				
Body condition	97	-3.52 (0.30)*	0.64 (0.19)*		-5.85 (1.82)*		-0.25 (0.10)*	0.26 (0.13)	
Fall termination[d]									
Spatial	93	12.20 (9.06)[e]	-6.95 (5.22)[e]	0.17 (0.12)					
Demographic	93	-1.46 (0.49)*	0.81 (0.32)*		-5.07 (3.06)				
Body condition	78	-1.21 (0.53)*	0.79 (0.36)*						
Spring initiation									
Spatial	108		1.01 (0.31)*						
Demographic	106		1.09 (0.31)*			5.91 (2.73)*			
Body condition	63		1.53 (0.39)*			2.47 (2.66)	-0.34 (0.14)*		0.59 (0.18)*

[a] latitude

[b] longitude

[c] body condition

[d] both latitude and longitude for initiation and termination were included in the model, but only latitude and longitude from initiation location received support

[e] covariates were non-significant when included in a model with an interaction effect, the inference model contained an additive effect of latitude and longitude and were included in subsequent models

Fall Migration Termination

The best-supported spatial model for termination of fall migration (Table 1.3) included additive effects of latitude and longitude for location of migration initiation (hereafter, starting latitude and starting longitude). One other competitive model included an interactive effect of starting latitude and starting longitude, however the interaction had confidence intervals overlapping zero. The base spatial models were best supported for both the demographic and condition modeling tiers, indicating that no additional parameters were significant predictors of migration termination. Age was included in one competitive demographic model, but the confidence intervals overlapped zero and was not retained. The best-supported final model was the spatial model explaining 8% of the variance ($R^2 = 0.08$) and included additive effects of starting latitude ($\beta = -1.25 \pm 0.48$) and starting longitude ($\beta = 0.79 \pm 0.32$; Table 1.3; Appendix B.1). Woodcock that initiated migration farther north and west in our sample (e.g., Ontario and western Quebec) terminated earlier than woodcock marked farther south and east (e.g., Rhode Island). On average, for every 1°decrease in starting latitude and starting longitude, woodcock terminated migration 1.3 days (latitude) and 0.8 days (longitude) earlier. Ending latitude and longitude did not have an influence on migration termination date and no age, sex, or condition covariates were supported (Figure 1.2).

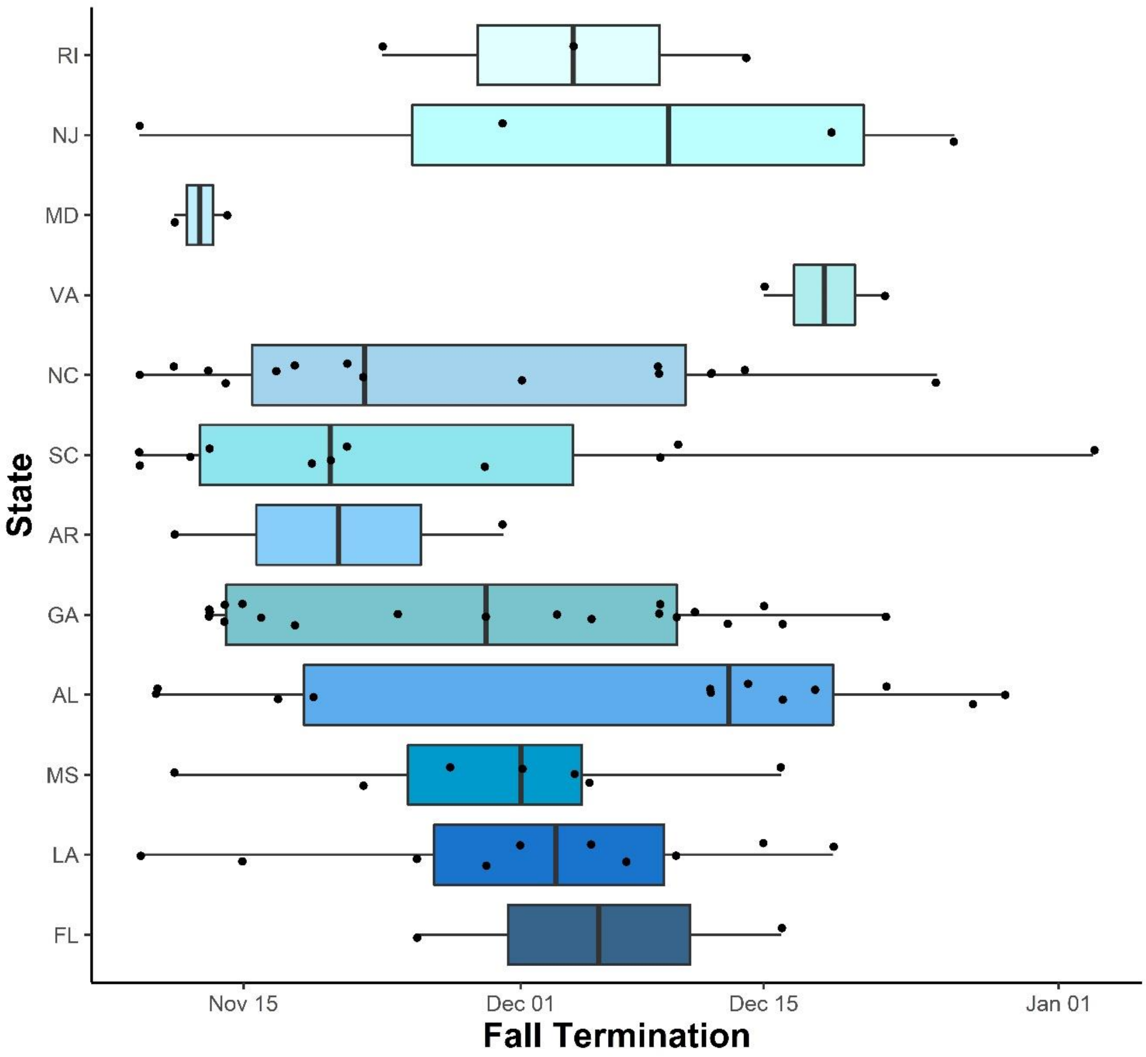

Figure 1.2. Termination of fall migrating American Woodcock (*Scolopax minor*) marked in Eastern North America, 2017-2019, by administrative division of migration destination. Black circles represent individual observations.

Spring Migration Initiation

The best-supported model for initiation of spring migration included a combination of longitude (β = 1.53 ± 0.39), sex (β = 2.47 ± 2.66), condition (β = -0.34 ± 0.16), and an interaction between condition and sex (β = 0.59 ± 0.18; Table 1.3; Appendix B.1). This model explained 24% of the observed variance in the data (R^2 = 0.24). Additive effects of sex from the demographic tier of analysis (β = 5.91 ± 2.73) indicated that males initiated spring migration 5.9 days before females, and woodcock wintering farther west initiated migration an average of 1.5 days earlier for every 1° decrease in longitude. The interaction between sex and condition suggested that males in above-average condition initiated migration earlier, while females in above average condition initiated migration later (Figure 1.3). Hence, condition had an inverse relationship to migration initiation date depending on the sex of the individual.

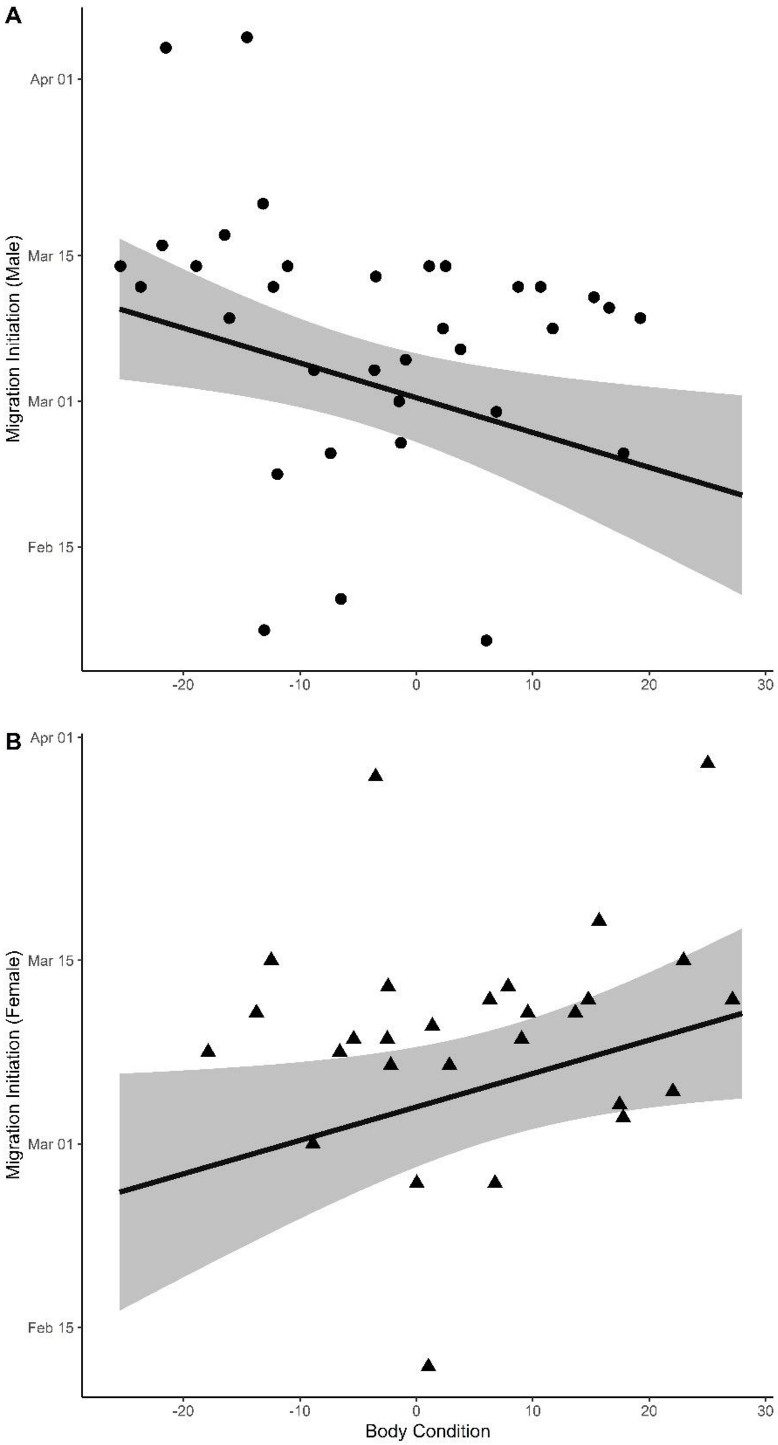

Figure 1.3. Predicted spring migration initiation date for American Woodcock in eastern North America (*Scolopax minor*) captured on the wintering grounds prior to spring migration (January-March). Males (a) and females (b) showed inverse influences of condition on the timing of migration initiation. One adult female was removed from the plot with a condition score of 53.

Fall Migration Stopover Timing

The best-supported fall stopover spatial model included an additive effect of administrative divisions (Figure 1.4), and was better-supported and captured a greater amount of variance in the data compared with latitude and longitude (Tables 1.S4 and 1.S6). The demographic model identified both age and sex as influencing stopover timing. One competitive model also contained only sex with a confidence interval that did not overlap zero. However, when we further investigated the second best-supported model, which contained an interaction between sex and age, we found that timing of stopover for adult females differed fundamentally from the other three age classes, and we selected this as the best-supported model. Therefore, the best-supported model, which explained 73% of the observed variance ($R^2 = 0.73$), included administrative division, age ($\beta = 3.88 \pm 3.77$), sex ($\beta = -0.42 \pm 3.90$), and an interaction between age and sex ($\beta = -8.56 \pm 5.30$; Table 1.4; Appendix B.1). The beta coefficients for each administrative division covariate were highly variable (Appendix C.1). Adult males ($\beta = 8.99 \pm 3.59$), young females ($\beta = 4.68 \pm 3.73$), and young males ($\beta = 5.11 \pm 3.49$) had later stopover events than adult females, although 95% confidence intervals overlapped for each pairwise comparison among groups with the exception of adult males and adult females. Adult females performed stopover events an average of 9 days earlier than adult males, indicating a more rapid pace of migration in general for adult females.

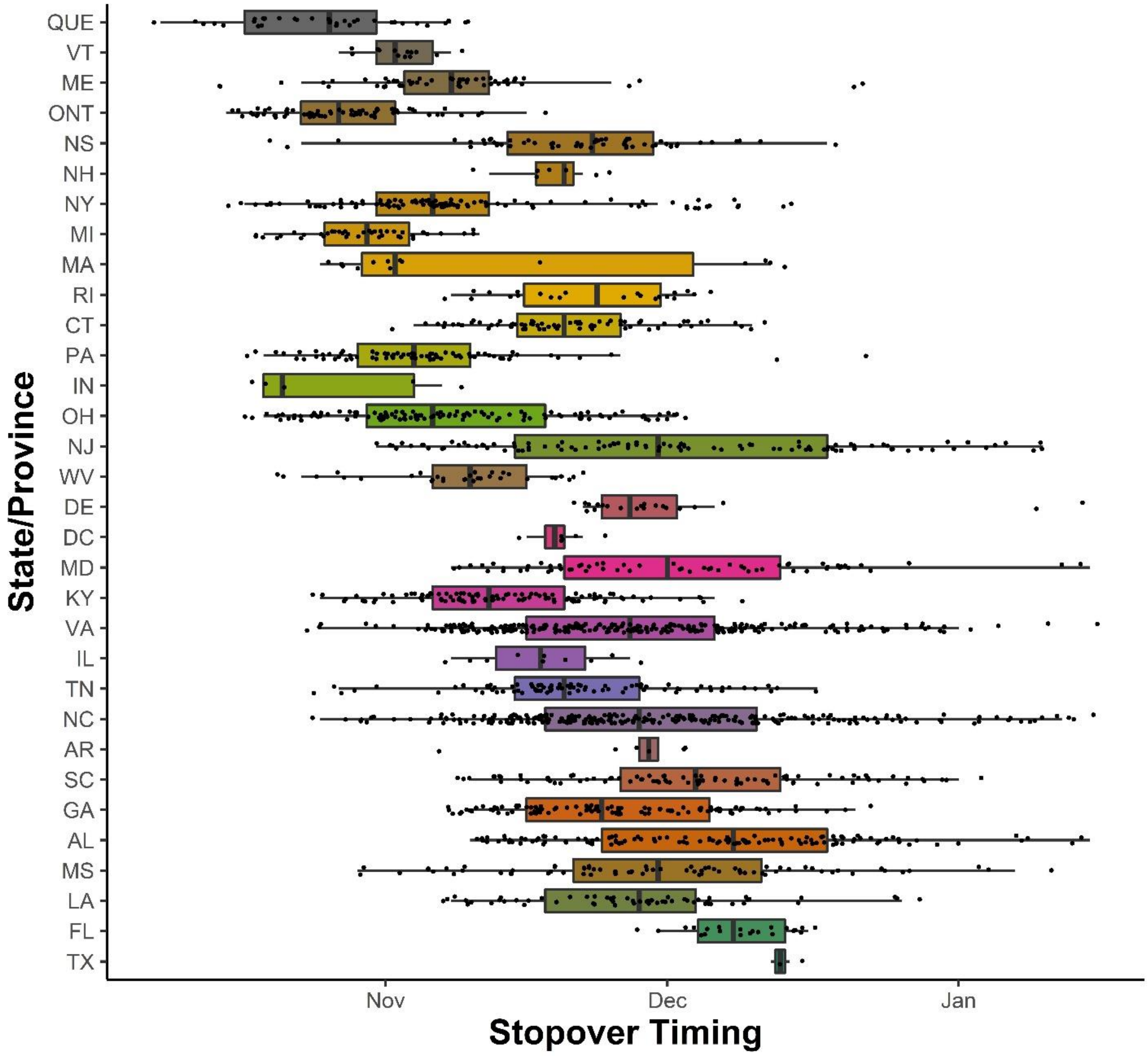

Figure 1.4. Timing of fall migration stopovers by state or province collected from American Woodcock (*Scolopax minor*) marked in in Eastern North America, 2017-2019.

Table 1.4. Beta coefficients for the top supported linear mixed effect model describing American Woodcock (*Scolopax minor*) migratory stopover phenology based on AIC_c. Coefficients that were significant predictors in the model were denoted by an asterisk and only significant predictors were included in subsequent models. Models used males and young birds as reference (coded at intercept) for sex and age respectively. Standard error is provided in parentheses.

	n	**Intercept**	**State/ Province**	**Age**	**Sex**	**Age×Sex**
Spatial	2068	70.487 (1.769)	Varies by state[a]			
Demographic	2068	71.224 (2.830)	Varies by state[a]	3.883 (3.770)[b]	-0.424 (3.901)[b]	-8.5644 (5.302)

Model Spatial Predictions

Model spatial predictions for the timing of fall migration initiation were generally well fit to the data (Figure 1.5), with most predicted mean initiation dates falling within the range of the observed values. The only division for which the model predicted later initiation dates compared to the observations was for woodcock marked in Pennsylvania. Predictions for fall migration termination also fit the data generally well (Figure 1.6); the two exceptions were that woodcock from Ontario, which terminated migration earlier than model predictions, and woodcock from Nova Scotia, which terminated migration later. Lastly, predictions for spring migration initiation performed relatively well, with the exception of Louisiana and Rhode Island (Figure 1.7). Woodcock wintering in Louisiana initiated spring migration later than model predictions, while woodcock wintering in Rhode Island initiated migration earlier than the model predicted. In all cases, model predictions seemed less reliable at the longitudinal extremes of the data, and in some cases, may have related to relatively small sample sizes.

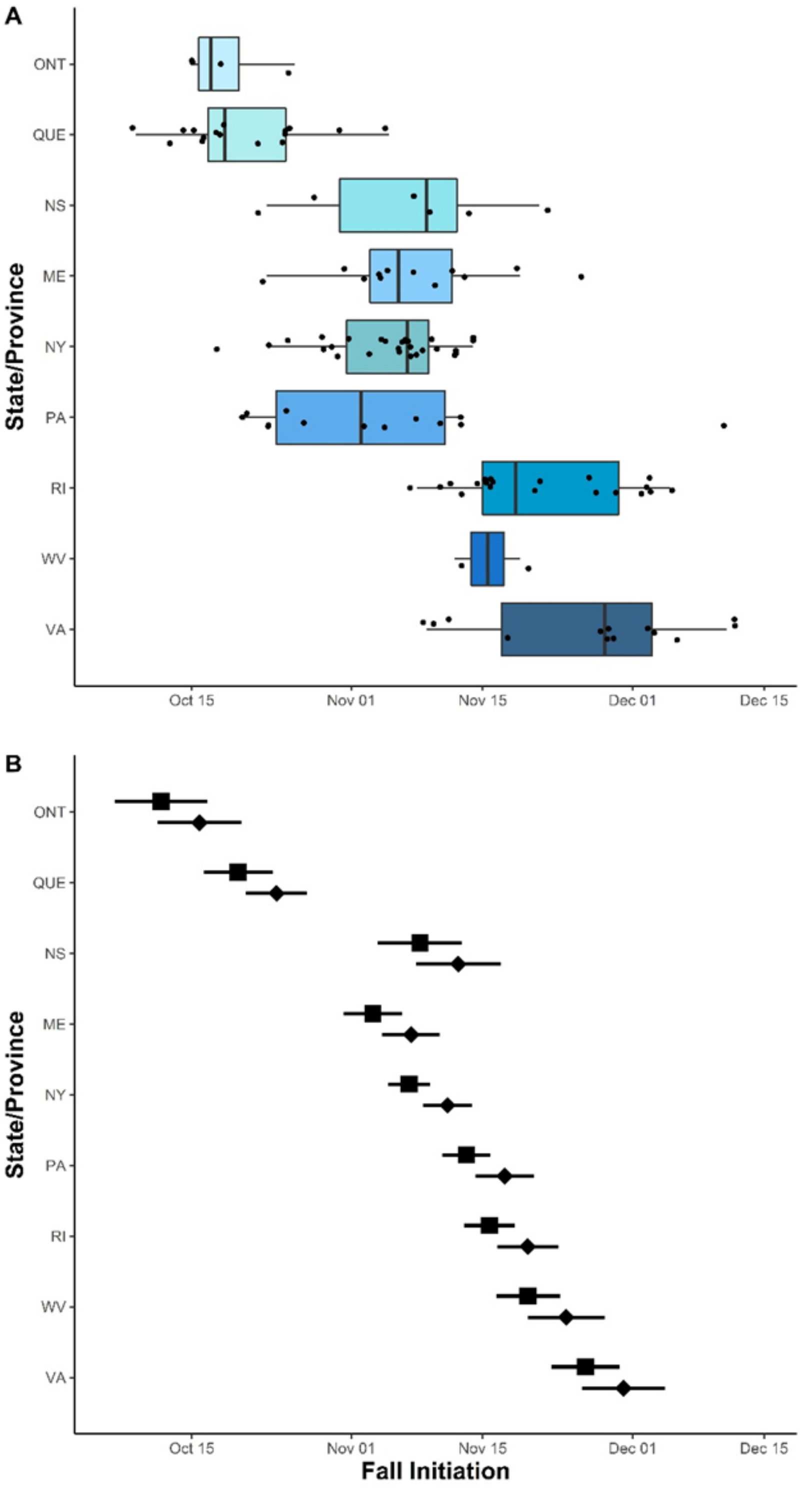

Figure 1.5. Initiation of fall migration for American Woodcock (*Scolopax minor*) marked in Eastern North America, 2017-2019. The distribution of migration initiation dates by administrative division (A), and the predicted initiation of fall migration while accounting for spatial distribution and age (B). Squares represent adults >1 year of age and diamonds reflect young woodcock <1 year of age.

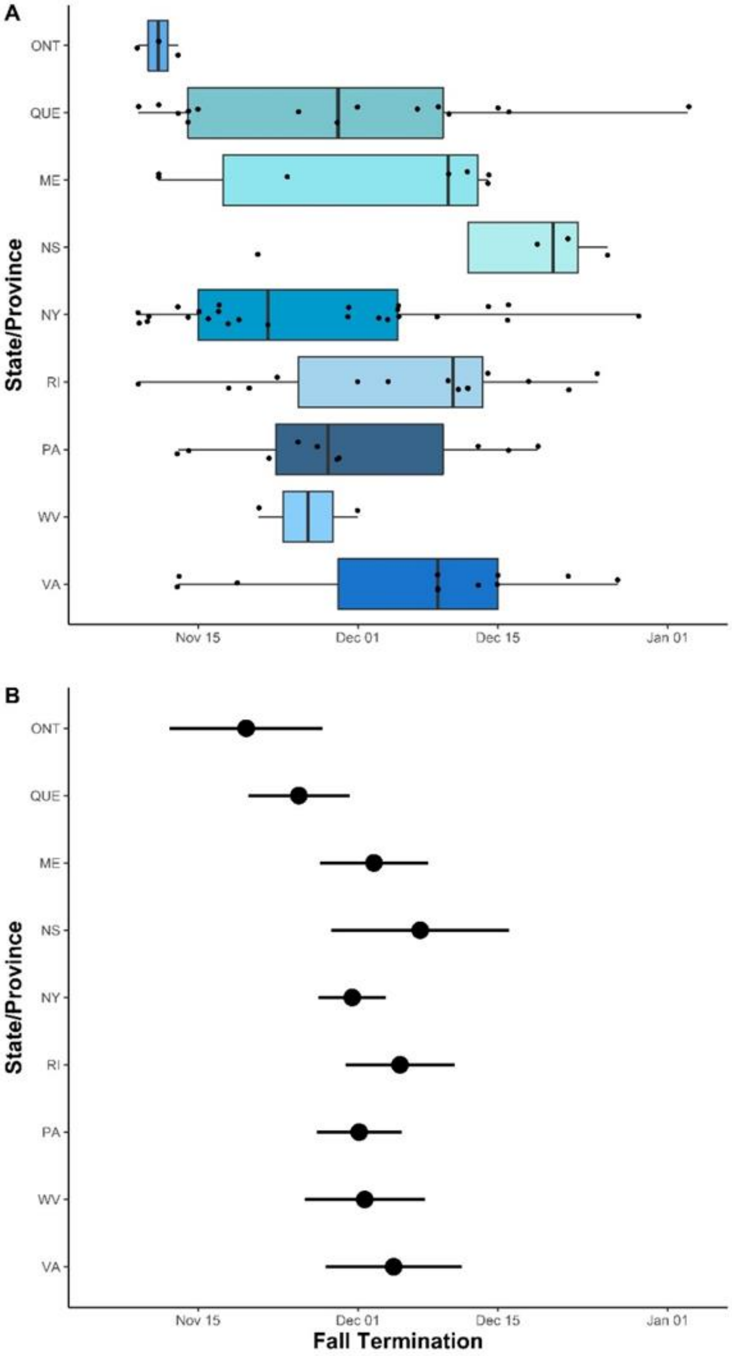

Figure 1.6. Termination of fall migration for American Woodcock (*Scolopax minor*) marked in Eastern North America, 2017-2019, by administrative division of migration initiation. The distribution of termination dates by initiation administrative division (A), and the predicted termination of fall migration while accounting for initiation latitude and longitude (B).

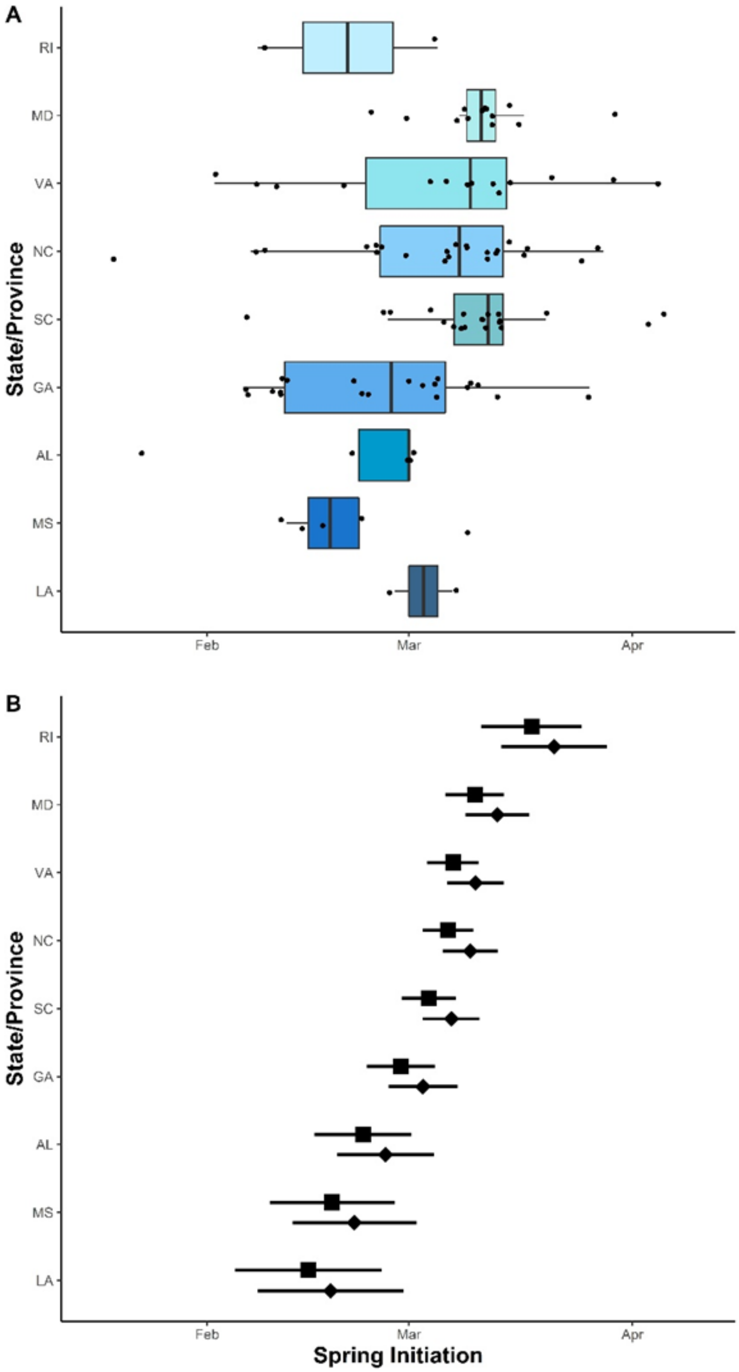

Figure 1.7. Initiation of spring migration for American Woodcock (*Scolopax minor*) marked in Eastern North America 2018-2020. The distribution of initiation dates by administrative division (A), and the predicted initiation of fall migration while accounting for longitude and sex (B). Boxes represent males and diamonds females.

Discussion

We were able to track both spring and fall migration for woodcock in eastern North America, showing that the timing of migration was influenced by a combination of spatial, demographic, and condition-based factors. While spatial factors received support in each analysis preformed, demographic- and condition-based factors were also important in explaining the timing of fall and spring migration events. Age influenced fall migration initiation and timing of stopover events, while sex influenced spring migration initiation. While the patterns described were based on range-wide observations, we generated predictions by administrative division boundaries to facilitate interpretation at scales relevant to harvest management. When possible, we predicted demographic effects (e.g., age and sex) to facilitate interpretation at local scales.

We found a clear spatial pattern throughout our data that was generally well-captured by latitude and longitude, but the specific relationship varied across migratory events. Woodcock marked farther north initiated and terminated fall migration earlier than woodcock marked farther south, and termination timing was independent of termination location. This pattern indicated an earlier fall migration strategy for northern-marked woodcock compared to southern-marked individuals, irrespective of their ultimate wintering area. A similar spatial pattern was observed with earlier peaks for stopover events in administrative divisions farther north and west. However, administrative divisions that bordered the Atlantic Coast tended to have a greater range of dates associated with stopover timing. We attributed this primarily to birds initiating fall migration later from coastal areas (e.g., Nova Scotia, Rhode Island), with those birds then migrating near the Atlantic Coast. Occasionally, woodcock marked farther inland adopted similar coastal migratory routes, but this was less common.

The influence of latitude and longitude on fall migration initiation makes intuitive sense, as woodcock farther north and west may have experienced colder temperatures and snowfall earlier in the fall than woodcock marked farther south and east. Administrative divisions along the Atlantic Ocean likely experienced more moderate temperatures and delayed freezing relative to inland areas at the same latitude. These spatial patterns suggested that woodcock may receive unequal harvest exposure due to breeding location origin, other aspects of geography, timing of migration, and hunting season dates. Generally, we would anticipate that hunting season dates earlier in fall migration would likely produce higher harvests of individuals from inland woodcock populations, while later hunting seasons would contain higher proportions from coastal woodcock populations. Thus, the proportion of migrating woodcock from coastal to inland populations within each administrative division will influence susceptibility of different source breeding populations to harvest.

Conversely to fall migration, spring migration initiation was more influenced by longitude. This relationship was likely due to the more latitudinally-restricted wintering range of woodcock compared to the species' breeding range, which reduced the possible range of latitudes of wintering woodcock. While we observed some woodcock overwintering in southern New England and the mid-Atlantic, these cases were relatively infrequent, and most transmitters failed prior to initiation of spring migration. Our limited sample in the northern portion of the wintering range likely reflects lower over-wintering densities in this region (McAuley et al. 2020). Initiation of spring migration occurred in February through April, with mean initiation dates for most administrative divisions occurring in March (Figure 1.5). Most hunting seasons ended November to January, with seasons farther south generally terminating during January, and all terminated prior to the start of February (Table 1.5). Only two woodcock initiated spring migration during January, whereas the remainder initiated spring migration after the termination of hunting seasons. As a consequence, timing of spring migration initiation is unlikely to influence harvest framework decisions throughout the winter unless seasons are extended significantly later (e.g., into February) than present (Table 1.5).

Table 1.5. American Woodcock (*Scolopax minor*) hunting season dates in Eastern North America based on the 2020-2021 hunting season. Only divisions with fall migration locations were included in the table, and divisions were generally organized by observed stopover latitudes. Most divisions had seasons open for a continuous period, but some divisions contained split seasons partitioned by temporal or spatial features.

Administrative Divisions	**Bag Limit**[a]	**Season Length**[b]	**Season Dates**			
			Open	**Close**	**Reopen**	**Close**
Quebec - District A	8	107	1-Sep	16-Dec	-	-
Quebec - District B	8	106	12-Sep	26-Dec	-	-
Quebec - District C-F	8	99	19-Sep	26-Dec	-	-
Quebec - District G	8	92	26-Sep	26-Dec	-	-
Vermont	3	45	1-Oct	14-Nov	-	-
Maine	3	52[c]	1-Oct	21-Nov	-	-
Ontario[d]	8	93	15-Sep	16-Dec	-	-
Ontario - Southern District H	8	97	15-Sep	20-Dec	-	-
Ontario - Southern District I	8	87	25-Sep	20-Dec	-	-
Nova Scotia	8	61[c]	1-Oct	30-Nov	-	-
New Hampshire	3	45	1-Oct	14-Nov	-	-
New York	3	45	1-Oct	14-Nov	-	-
Michigan	3	45	25-Sep	8-Nov	-	-
Massachusetts	3	52[c]	1-Oct	21-Nov	-	-
Rhode Island	3	45	17-Oct	30-Nov	-	-
Connecticut	3	51[c]	21-Oct	14-Nov	17-Nov	12-Dec
Pennsylvania	3	52[c]	17-Oct	27-Nov	14-Dec	23-Dec
Indiana	3	45	15-Oct	28-Nov	-	-
Ohio	3	45	10-Oct	23-Nov	-	-
New Jersey (North)	3	41	17-Oct	31-Oct	3-Nov	28-Nov
New Jersey (South)	3	42	7-Nov	1-Dec	17-Dec	2-Jan
West Virginia	3	45	15-Oct	19-Nov	28-Nov	6-Dec
Delaware	3	52[c]	23-Nov	28-Nov	5-Dec	19-Jan
District of Columbia	-	-	-	-	-	-
Maryland	3	51[c]	21-Oct	27-Nov	11-Jan	23-Jan
Kentucky	3	45	24-Oct	13-Nov	16-Nov	9-Dec
Virginia	3	45	7-Nov	30-Nov	24-Dec	13-Jan
Illinois	3	45	17-Oct	30-Nov	-	-
Tennessee	3	45	14-Nov	6-Dec	10-Jan	31-Jan
North Carolina	3	52[c]	10-Dec	30-Jan	-	-
Arkansas	3	45	7-Nov	21-Dec	-	-
South Carolina	3	45	18-Dec	31-Jan	-	-

Table 1.5 continued.

Georgia	3	45	5-Dec	18-Jan	-	-
Alabama	3	45	18-Dec	31-Jan	-	-
Mississippi	3	45	18-Dec	31-Jan	-	-
Louisiana	3	45	18-Dec	31-Jan	-	-
Texas	3	45	18-Dec	31-Jan	-	-
Florida	3	45	18-Dec	31-Jan	-	-

[a] Maximum number of birds harvested per hunter per day
[b] Number of days between hunting season open and close dates
[c] Includes days hunters cannot harvest woodcock, typically Sunday(s)
[d] Includes the Hudson-James Bay, Northern, and Central Districts

During fall migration, age was an important predictor of migratory initiation and thus timing of migration, with adults initiating fall migration earlier than young birds. Adult woodcock may have used experience gained from previous migrations to select weather conditions that optimize migratory efficiency (e.g., tailwind; Mitchell et al. 2015). In contrast, young birds were presumably naive to the weather cues associated with migration, having no prior migration experience, and were less able to preemptively initiate migration under optimal conditions (Mitchell et al. 2015). Alternatively, woodcock making poor migratory timing decisions may not survive to repeat another migration, and thus failure to recognize deadly weather conditions would be limited in the population (Newton 2006). The interaction of age and sex influenced fall stopover timing during migration, with adult females making stopovers earlier than both young birds and adult males. It is possible that adult females migrated more energetically efficient than other cohorts, allowing them to more rapidly complete migration, but additional investigation into migration efficiency is needed to understand this dynamic (Ellegren 1991). No demographic effect explained termination of fall migration and the predictive strength of the spatial covariates was low, indicating that termination of migration was largely dependent on variables not included in our analysis. The dates associated with termination of migration and initiation of spring migration provide a comprehensive picture of when woodcock were on the wintering grounds. These dates can be used by wildlife managers on the southern range to evaluate hunting season timing to coincide with woodcock overwinter residency.

Differential fall stopover timing among cohorts could result in cohorts having differential exposure to harvest or mortality (Newton 2006, 2007). While there was a significant difference between adult female and adult male stopover timing, there was considerable overlap between young and adult birds. Adult females are particularly important for population growth, therefore if harvest management strategies could be implemented to reduce adult female harvest, there may be population growth benefits (Sæther and Bakke 2000). For example, coastal states with relatively longer migration periods may be able to delay the hunting season so that later migrating young and male woodcock were more likely to be targeted. However, for most inland and northern administrative divisions, there may not be the flexibility in migration timing to modify season dates to target specific cohorts, because allowable season lengths (45 days for both management regions in 2020; Table 1.5) are sufficiently long to encompass the entire migration period. Furthermore, hunting seasons on the southern range extent primarily target overwintering woodcock, and the timing of fall migration termination did not appear to vary among age or sex classes. Therefore, modifying hunting season dates to target specific age or sex classes in southern administrative divisions may not be an effective management strategy.

Individual condition was only important in predicting spring migration initiation, with the effect of condition dependent on sex. Males in below-average condition likely spent more time building energy reserves and, therefore, delayed migration initiation relative to above-average males (Cooper et al. 2015). Owen and Krohn (1973) suggested woodcock gained weight prior to initiating migration, lost weight during migration, and were at their lowest weight when they arrived on the breeding grounds in late spring. Therefore, securing energy reserves prior to initiating migration provides an important energetic buffer during migration. The condition-migration initiation relationship for female woodcock was opposite of males, with females in below-average condition initiating migration before above-average females. This surprising result may relate to breeding attempts on the winter grounds, which are a well-documented but poorly understood aspect of woodcock ecology (Roboski and Causey 1981, Wiley and Causey 1987, Whiting et al. 2005). Females gain mass prior to initiating nests (Wendeln and Becker 1996, Smith and Moore 2003) and therefore would likely be in an above-average condition at the time of capture. Some female woodcock are known to complete migration following nest failure in their wintering areas (Gary Costanzo, Virginia Department of Fish and Game, unpublished data), but the frequency with which this strategy occurs is unknown. Alternatively, if greater body reserves facilitate a more rapid pace of migration, females in better condition may delay departure to avoid threats associated with early migration (e.g., encountering early spring storm events). A greater understanding of female woodcock reproductive ecology would provide useful insights into the mechanisms governing the patterns we found.

Our ability to predict migratory phenology, as indicated by model R^2 values, varied widely among stages of migration. The high R^2 values associated with initiation of fall migration, and to a lesser extent the timing of stopover, indicated the timing of these events was more predictable than those associated with termination of fall migration, likely due to a shared cue (e.g., temperature or photoperiod) that all birds are acting upon. However termination is dependent on a variable suite of environmental conditions encountered during migration (e.g., wind, temperature) that impact departure decisions from stopover sites, the pace of migration, and subsequently the timing of migration termination (Zehnder et al. 2001, Shamoun-Baranes et al. 2017, Haest et al. 2019, Bradarić et al. 2020). If termination of migration relies on environmental conditions and individual migration decisions, the variable nature of these events likely results in lower predictability. We had a moderate ability to predict the timing of spring migration, indicating some consistency between years, but additional environmental variables also likely influenced migration timing during spring (Hagan et al.

1991, Marra et al. 2005, Palm et al. 2009, Tøttrup et al. 2010). The environmental cues associated with woodcock migration decisions have received some attention, but most prior work focused on single sites (Coon et al. 1976, Krementz et al. 1994b, Allen 2017), with limited ability to follow individual birds throughout their migration cycle. Therefore, additional investigation into these cues is necessary to better understand the mechanisms influencing our ability to predict spring migratory timing.

Given the predictable nature of fall initiation and stopover timing, our models provide reliable tools to evaluate the timing of hunting seasons and inform the management decision process. The data and models we present provide an unbiased description of fall migration phenology that can be used to ensure hunting seasons coincide with the presence of woodcock in a particular area, thereby maximizing opportunity (Table 5). How this information is applied in the decision-making process is likely to vary by administrative division or region. For example, for the most northern populations, there may be a relatively short window in which migrants are available for harvest and residents are primarily harvested. Conversely, managers in more southern breeding areas may have small residential populations, with the greatest local woodcock abundance occurring during migratory or over-winter periods. Depending on where administrative divisions are located, agencies can weigh options over the relative harvest of local versus migrant populations. Conceptually, hunting opportunity would be maximized when hunting seasons co-occur with the greatest abundance of individuals, which will inherently vary depending on spatial location and date. Lastly, we demonstrated how emerging animal tracking technologies can inform management of migratory gamebirds by providing unbiased metrics of migratory movements.

Management Implications

We provided detailed American woodcock migratory phenology metrics for the Eastern Woodcock Management Region to aid wildlife managers with evaluation of harvest management, hunting season timing in particular. This data in combination with migratory phenology data from the Central Woodcock Management Region (Moore et al. 2021) can be used to inform range-wide harvest management. Managers may use the dates provided (e.g., migration timing, initiation, termination) to ensure they balance hunting pressure according to local management objectives and stakeholder values. Furthermore, the predictive models and descriptive data we present can be used to evaluate current but also future hunting season timing as management frameworks change. For example, if the woodcock hunting season length were shortened as a result of future population declines, managers would need to modify their current season structure and determine when to remove dates.

CHAPTER 2

INTRASPECIFIC VARIATION IN USE OF MIGRATION CUES BY A MEDIUM-DISTANCE MIGRANT, THE AMERICAN WOODCOCK (*SCOLOPAX MINOR*)

Abstract

Migration, the travel between seasonally available resources in predictive cyclic movements, is a trait that has arisen independently in numerous taxa throughout the animal world. Migratory animals rely on external cues to make decisions about the timing of migratory departures, however individuals response to specific cues often varies interspecifically by age or sex class. We were interested in understanding how a medium-distance migrant bird, the American Woodcock (*Scolopax minor*), used environmental cues to make migratory departure decisions. We were also interested in exploring patterns of intraspecific variation in these decisions and how these decisions influenced migratory efficiency. Between 2017-2020, we captured and attached satellite transmitter to 304 pre-migratory woodcock throughout eastern North America, and obtained location data as they migrated between breeding and wintering areas. We used conditional logistic regression and general linear models to explore effects of weather and lunar variables on woodcock departure from breeding, wintering, and stopover sites, and asked how these relationships varied between age and sex classes. We further explored how an individual's use of specific wind conditions influenced flight distance and how the overall pace of migration varied with geography and interspecific characteristics. Woodcock responded to barometric pressure, moon illumination, temperature, wind assistance, and wind speed when making departure decisions, but selection often varied by season, age, and sex. In the autumn, adult woodcock generally showed greater selection for wind assistance compared to young birds. During spring migration, female woodcock showed a greater selection for wind assistance and barometric pressure but males showing stronger response to temperature and moon illumination. Woodcock that departed using tailwinds generally had longer flight distances, which we assume reflected a more efficient flight.

Woodcock that wintered in the southeastern United States had the lowest pace of migration and migrated more efficiently overall. In this study we demonstrate how emerging satellite transmitters can be used to evaluate migratory departure decisions across a large spatial area (e.g., eastern North America), using remotely transmitted location data. We found intraspecific variation in cue selection that was dependent on age during autumn migration and sex during the spring, which provides an example of the variation that can exist within a species.

Introduction

Many species of animals exhibit migratory movements (Thorpe 1988, Sawyer et al. 2005, Egevang et al. 2010, Inamine et al. 2016), and many migratory species have experienced substantial population declines (Wilcove and Wikelski 2008, Gilroy et al. 2016). Migratory birds may be particularly suseptable, as many migratory bird species in North America have experienced population declines (Rosenberg et al. 2019). Approximately 2.5 billion of the estimated 2.9 billion North American birds lost in the past 50 years have been migratory birds (Rosenberg et al. 2019). Most migratory birds rely on spatially disjunct seasonal-use areas and move between these areas in predictive patterns (Dingle 2014). However, individual species exhibit considerable variation in migratory strategies (Egevang et al. 2010, Pratt et al. 2017, Moore et al. 2019, Carneiro et al. 2020), and even within species there can be considerable variation (Ely and Meixell 2016, Moore et al. 2019). Individuals or subpopulations may over-winter in spatially disjunct regions, often with demographic consequences (Ely and Meixell 2016). Significant intra-specific variation in migration indicates that individual birds respond differently to a variety of extrinsic cues during migratory periods. Understanding this variability is fundamental to our knowledge of the ecology of migration, which is important for both our general knowledge of avian ecology as well as in crafting strategies for migratory bird conservation (Martin et al. 2007).

Efforts to understand which cues migratory birds respond to have received considerable attention over the past few decades. Migratory bird departure decisions are commonly associated with wind (Deppe et al. 2015, Manola et al. 2020, Van Den Broeke and Gunkel 2021, Roques et al. 2021), changes in barometric pressure (Morganti et al. 2011, Manola et al. 2020, Literák et al. 2021), temperature (Morganti et al. 2011, Kelly et al. 2016, Pratt et al. 2017, Xu and Si 2019, Klinner and Schmaljohann 2020), cloud cover or fog (Panuccio et al. 2019, Packmor et al. 2020), photoperiod (Schwemmer et al. 2021), moon light (Coon et al. 1976, Krementz et al. 1994b, Meunier et al. 2008), or precipitation (Morganti et al. 2011, O'Neal et al. 2018, Literák et al. 2021). However, cue selection can vary widely in the directionality and magnitude of a specific response, and sources of such variability are less well-understood. For example, while some studies report species select for strong tailwinds believed to increase migratory efficiency (Roques et al. 2021), especially when crossing large inhospitable regions (Santos et al. 2020), others species select for low wind conditions or show no selection at all (Karlsson et al. 2011, Carneiro et al. 2020, Schwemmer et al. 2021). Clearly wind can be an important cue influencing migratory departure decisions, and there is variability in the specific wind conditions individuals use to make departure decisions. Migration theory assumes that individuals select wind conditions that strike a balance of energy conservation and the need to reach a destination (Alerstam 2011). However, individuals do not always make optimal departure decisions, which can reduce overall migration efficiency or result in mortality (Literák et al. 2021).

The specific environmental cues associated with migration may vary by age or sex class, or may change seasonally (Morganti et al. 2011), or may exhibit no intraspecific variation at all (Schwemmer et al. 2021). Adult birds typically show a greater selection for tailwinds compared to young birds, likely due to prior migratory experience (Monti et al. 2018), and in autumn strong tailwinds are typically associated with migratory movements whereas in the spring low wind speeds may be selected for (Morganti et al. 2011). These patterns can be difficult to disentangle from research conducted at single sites or using sampling techniques that do not allow long-distance tracking of individuals (e.g., Doppler radar, banding station counts), but can more comprehensively be obtained from continuous tracking of individuals throughout migration. Hence, emergent satellite tracking technology that records an individual's complete migratory path has the potential to shape our understanding of how departure decisions are made during the entire migratory period (Klaassen et al. 2014, Baert et al. 2018, Schwemmer et al. 2021). Furthermore, we can subdivide and compare decisions among the initial departure from the wintering grounds (migration initiation) and departures from stopover sites to determine how cue selection varies among different stages of migration. Satellite tracking data can also improve our ability to draw inference about migratory efficiency associated with intraspecific variation in departure decisions (e.g., wind selection) by exploring the outcomes of particular decisions on individuals' pace of migration. For example, in bird species exhibiting protandry, males that arrive on the breeding grounds earlier in the spring have a fitness advantage (Lozano et al. 1996), and this fitness advantage may drive males to advance spring migration more rapidly than females (Pedersen et al. 2019). In contrast, female's delayed arrival on the breeding grounds may allow greater choice in selecting migratory conditions that maximize migratory efficiency.

We were interested in understanding how a medium-distance migrant, the American woodcock (*Scolopax minor*) used environmental cues when making migratory departure decisions. Woodcock have undergone range wide declines for the past 50 years and there is growing interest in understanding the species' full season phenology, especially during migration. Woodcock departure decisions have been associated with moon phase (Coon et al. 1976, Krementz et al. 1994b, Meunier et al. 2008) and changing barometric pressure associated with weather fronts (Krementz et al. 1994b, Meunier et al. 2008, Allen 2017). However, these associations have only been investigated at single sites (Coon et al. 1976, Allen 2017), or over a regional spatial scope (Krementz et al. 1994b, Meunier et al. 2008). Furthermore, most investigations have been associated with migration initiation (Coon et al. 1976, Krementz et al. 1994b, Meunier et al. 2008), with only limited investigation into departure from stopover sites (Allen 2017). While these investigations are useful in understanding how woodcock make departure decisions, they predominately used tracking technology that had limited ability to relocate individual's post-departure (Myatt and Krementz 2010) and thus cover only a single stage of migration (Coon et al. 1976, Krementz et al. 1994b, Meunier et al. 2008, Allen 2017). With the use of emergent tracking technologies, Moore et al. (2019) demonstrated that woodcock could be tracked throughout migration using satellite transmitters, thereby considerably expanding the potential scope of migration investigations for the species.

Our goal for this study was to understand the environmental conditions that woodcock use as cues when making migratory decisions, and to understand how those cues varied geographically, among age and sex classes, and during different stages of migration. We created the Eastern Woodcock Migration Research Cooperative to capture, mark, and track migrant woodcock throughout the species' eastern range in North America. These efforts yielded a multi-year dataset containing detailed tracks of individual woodcock migrating between breeding and wintering areas. To that end, our objectives were to 1) identify extrinsic factors (e.g., environmental cues) that influenced migration initiation and departure from stopover sites, 2) evaluate patterns of intraspecific variation within these departure decisions, and 3) understand how these decisions influenced the efficiency of both single migratory flights and the entirety of an individual's migration. Our investigation sought to provide unique insights into how environmental cues influence departure decisions by migrating American woodcock.

Materials and Methods

Study Area

We focused our work on the eastern extent of the woodcock's distribution in North America (Figure 2.1). We primarily captured woodcock in eastern Canada, and in US states east of the Appalachian Mountains, but also included some provinces and states west of the Appalachian Mountains proximate to the woodcock eastern range extent (Figure 2.1). In autumn, we concentrated capture efforts in Maine, New York, Nova Scotia, Ontario, Pennsylvania, Quebec, Rhode Island, Virginia, and West Virginia. Throughout the winter, we concentrated capture efforts in Alabama, Florida, Georgia, Maryland, New Jersey, North Carolina, South Carolina, and Virginia. While our marking efforts were focused on the eastern portion of the range, some woodcock migrated throughout eastern North America; thus, our dataset contained locations from throughout the species' range extent.

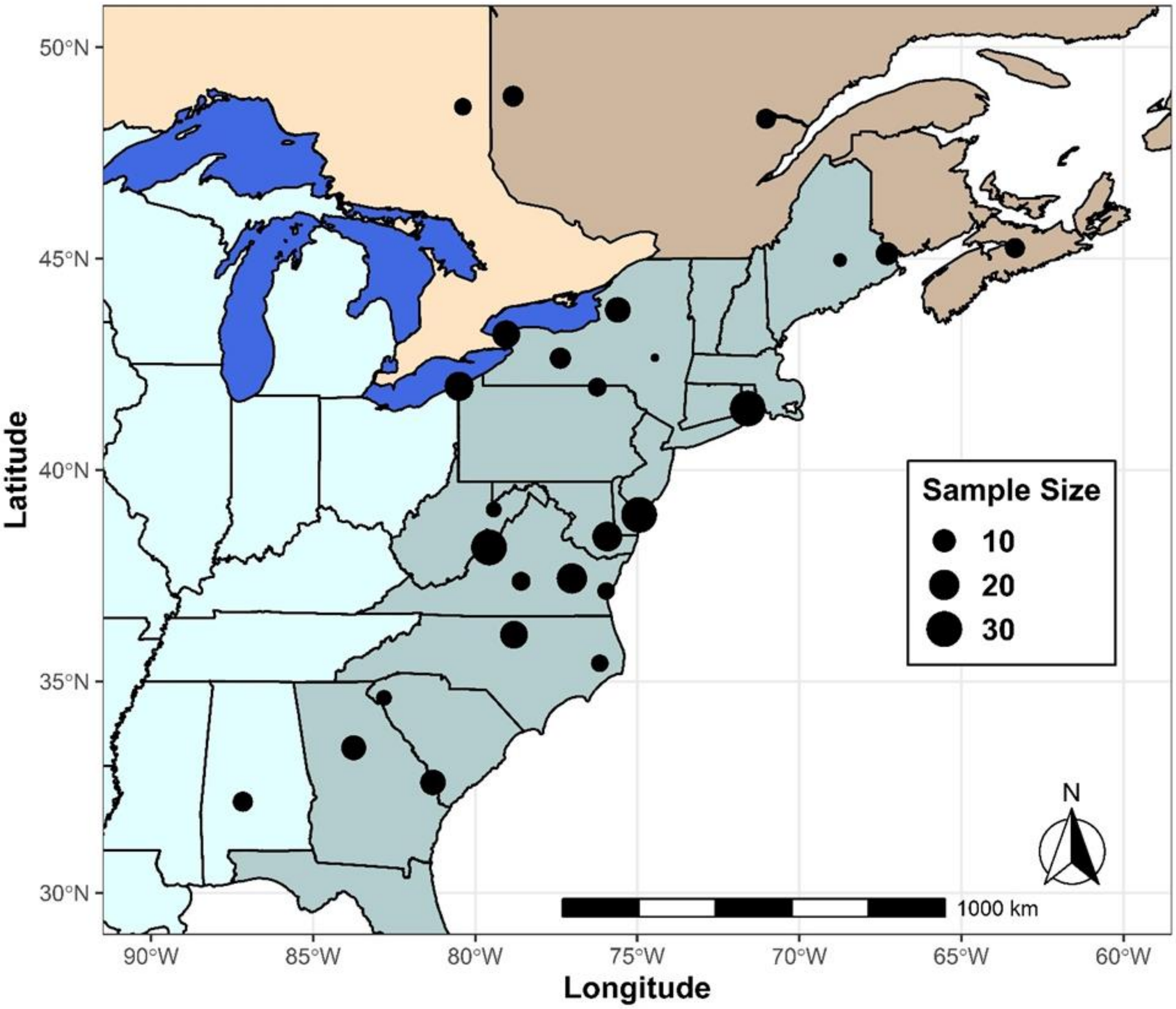

Figure 2.1. We captured American Woodcock (*Scolopax minor*) in eastern North America 2017 - 2020, concentrating on the species eastern range extent (darker shaded regions) of Canada (brown) and the United States (gray). The distribution of capture sites and samples sizes depended on cooperator locations and commitment.

Capture and Marking

We captured woodcock near the onset of migration to maximize the number of locations collected by each transmitter. Woodcock were captured between 27 August and 30 October during autumn 2017, 2018, and 2019, and between 3 January and 29 February during winters 2019 and 2020, using mist nets (Sheldon 1960) or spotlights and hand nets (Rieffenberger and Kletzly 1966, McAuley et al. 1993, Moore et al. 2019). Once captured, woodcock were ringed, and aged as either adult (after hatch year or after second year; > 1 year old) or young (hatch year or second year; < 1 year old) using a combination of wing plumage, bill length, and mass (Mendall and Aldous 1943, Martin 1964). We recorded unflattened wing chord length and lower leg length (Blomberg et al. 2014) using either a metric ruler (± 1 mm) or dial caliper (± 0.1 mm), and recorded the mass of each individual using a 300 ± 2 g spring scale (Pesola Präzisionswaagen AG, Schindellegi, Schwitzerland). Lastly, woodcock were fitted with a rump-mounted Lotek Pinpoint GPS transmitter (model 75 or 120; Lotek Wireless INC., Newmarket, Ontario, CA) enabled with a Platform Transmitter Terminal (PTT). The PTT facilitated remote uploads of GPS location data using the ARGOS satellite network. Transmitters and harness weight did not exceed 4% of an individual's body mass, and in general comprised 3.06 ± 0.44% body mass (mean ± SD) for PinPoint 75 and 3.68 ± 0.25% for the PinPoint 120 models (Chapter 1). All capture and marking procedures were approved by the University of Maine Institutional Animal Care and Use Committee (protocol A2017-05-02).

Location Collection

PinPoint transmitters collected GPS locations at pre-programmed intervals and periodically uploaded locations to a central database using the ARGOS satellite system. The transmission process required the transmitter antenna to be elevated above the ground, therefore we stopped receiving locations due to either dropped transmitters or mortalities, which caused signal attenuation, or if the transmitter otherwise failed. Transmitters were programmed using LOTEK PinPoint Host Software

(LOTEK Wireless Inc., Newmarket, Ontario, CA) under one of three location collection schedules. The schedules generally collected one location every day (frequent), one location every few days (infrequent) or contained periods of frequent and infrequent location collection (hybrid) during migratory periods (autumn [15 October to 31 December] and spring [1 March to 15 May]). Generally, the three schedules were constructed to maximize the number of locations collected during the migration following capture. During non-migratory periods (winter [January to February] and summer [15 May to 15 October), transmitters collected locations once every 5-7 days to extend battery life. We did not recover every programmed location from each transmitter, due to poor satellite connection or signal attenuation. Every individual had at least one instance with multiple days between locations. Locations were primarily programmed to be collected during daytime, however some objectives, not related to this study, required nocturnal locations. Overall, we had data precision of ± 1.74 days between relocations of woodcock during migratory periods. In some cases, we further subset data to only that with finer levels of precision (i.e., +/- 1.0 day) based on the level of inference required for specific questions, as described below. We downloaded woodcock locations from the ARGOS website, and used Movebank (Kranstauber et al. 2011) to store all location data.

Movement Modeling

We used Multivariate Hidden Markov Models (MHMM), implemented with the momentuHMM package (McClintock and Michelot 2018) in program R (R version 3.6.3, www.r-project.org, accessed 1 Dec 2020) to identify behavioral states related to migratory movements for each individual (Chapter 1). The MHMM used the distribution of two data streams, distance between subsequent locations (step distance) and turning angles, to delineate three behavioral states: pre-migration, migration, and post-migration (Chapter 1). We constrained transition between behavioral states such that pre-migration could only transition to migration, and migration could only transition to post-migration. Post-migration was a terminal state and once an individual transitioned into post-migration it could not transition to another behavioral state. We extracted woodcock locations from Movebank (Kranstauber et al. 2011) collected in spring (15 January to 18 June) and autumn (1 October to 14 January) and assigned migratory movements following the model and procedures outlined in Chapter 1.

Environmental Data Collection

We compiled environmental data previously described as influencing migratory bird movements (Morganti et al. 2011, Haest et al. 2020, Klinner and Schmaljohann 2020, Manola et al. 2020) to intersect with each woodcock location in our database, including barometric pressure, moon illumination, moon phase, temperature, wind direction and wind speed. We retrieved environmental data using the Environmental Data Automated Track Annotation System (Env-DATA; Dodge et al. 2013), which allowed for spatial and temporal data to be annotated and downloaded directly through Movebank, with original source databases described further below as appropriate. Most of these datasets were interpolated based on regional reanalysis. Barometric pressure (surface air pressure) data were gathered from the European Centre for Medium-Range Weather Forecasts Reanalysis ERA5 and was recorded at a 0.25-degree spatial scape collected at hourly intervals. Surface air pressure has increased variation at higher altitudes, however other mean sea level barometric pressure datasets failed to cover the spatial and temporal extant of our data, therefore we used the surface air pressure. We obtained U and V (east-west and north-south) wind velocity components, and potential temperature from the National Centers for Environmental Prediction North American Regional Reanalysis produced by the National Oceanic and Atmospheric Administration. Temperature and wind components were collected at a 0.75-degree spatial range every six hours.

Migratory birds often select for wind assistance (tailwind) during migratory movements (O’Neal et al. 2018, Roques et al. 2021), and wind assistance is thought to decrease energy expenditure while migrating (Alerstam 2011). However, the optimal direction of wind assistance likely varies by geographic region based on local geography, regional wind patterns, and variation in the realized trajectories of birds traveling between different seasonal use areas (e.g. breeding to wintering grounds). To account for this variation across all capture sites, we calculated a site-specific migration bearing to compare with prevailing wind directions. We first converted the U and V wind velocity metrics to wind speed and wind bearing using the uv2wdws function in the Rsenal package (Appelhans et al. 2021). For each state and province where we captured woodcock, we calculated the mean bearing of all migration paths from our GPS-marked woodcock, and used the resulting central tendency to describe state- or province-specific migration directional tendencies. We calculated the absolute difference between the wind bearing at the time of location collection and this state/province-specific mean migration bearing. A score of ‘0’ would represent optimal flight assistance (i.e., a tailwind at departure, given the mean trajectory of all birds from the site) and ‘180’ would result in maximum impedance, i.e., departing into a headwind. Importantly, this approach removed the circularity inherent to measures of wind directionality while also retaining greater interpretability than alternative transformations.

Moon phase has been associated with the initiation of woodcock migration at regional scales, but it is unknown how the moon influences the onset of migration across the larger species’ range, or how its influence differs among age and sex classes or stages of migration (Coon et al. 1976, Krementz et al. 1994b, Meunier et al. 2008). Therefore, we used the lunar package (Lazaridis 2015) in program R to extract moon illumination and moon phase associated with each GPS location. Moon illumination was the percent of the moon illuminated when visible, whereas moon phase accounted for illumination and visibility, given that different stages (new, waxing, full, or waning) varied in timing of moonset and moonrise. We choose to test for the effects of moon illumination, moon phase, and their interactions to explore how the moon influenced migration departures.

We tested for covariance among all environmental variables, with the exception of moon phase because it was not a numeric covariate, by performing a Pearson’s Correlation Coefficient test. No correlations were greater than 0.41, therefore we concluded that the selected environmental variables lacked significant collinearity, and included them all in the analyses. We scaled all covariates around the mean, such that the regression coefficients were comparable among all variables and analyses.

Statistical Analysis

Migration Initiation

One of our key objectives was to better understand how woodcock use environmental cues when initiating spring and autumn migration, as well as departing from spring and autumn stopover sites. Migration initiation was defined as the date a woodcock transitioned from pre-migration to migration behavioral states, and departure from stopover sites was any movement in which an individual traveled greater than 11.54 km while in the migratory behavioral state. We chose 11.54 km because it was twice the longest observed local movement between diurnal and nocturnal use areas in our dataset. By setting this distance threshold, we reduced the potential to misclassify ranging movement within stopover sites as migratory departures. Most woodcock also had at least one interval with multiple days between subsequent locations, which reduced our ability to determine the exact date of departure. To account for this, we subset the data such that we only considered departure events where the previous day's status was known; this ensured we evaluated environmental conditions individuals experienced the day of migration initiation or stopover site departure.

Once we had isolated known departure events, we developed conditional logistic regression models using the survival package in program R (Therneau et al. 2021) to evaluate factors that contributed to migratory decision making. The conditional regression allowed us to compare the conditions experienced by an individual woodcock for each migratory decision (i.e., a date of departure, or the 'case' observation) by the same bird on the previous days during which it did not depart (controls). To define a range of control dates, we first needed to determine the period during which individuals were otherwise likely to initiate migration. We calculated the earliest migration initiation from each state or province where woodcock were captured, and set the first available migratory day two days prior. In practice this allowed for at least one case and one control point for each bird, the minimum required to fit a conditional logistic regression, with the exact number of control points varying among birds. This approach also effectively accounted for the intrinsic factors governing the onset of migration (i.e., migratory restlessness in response to changing photoperiod) by focusing the analysis only on ranges of dates where migration was likely to occur within a particular state or province. We included barometric pressure, temperature, moon illumination, moon phase, wind assistance, and wind speed as potential covariates explaining migration initiation decisions. We used individual bird ID as the condition (e.g., grouping) in the migration initiation analysis, and applied weights to locations so that each individual contributed equally to the case and control components of the model. Each case was given a weight of one and the weight for each control point was calculated as the reciprocal of the number of control locations for each individual. The resulting model returned the expected probability of departure, given the environmental variables experienced by each bird on any given day.

Departure from Stopover Site

We similarly used a conditional logistic regression framework to evaluate the extrinsic factors associated with departure from stopover sites. As with migration initiation, we only used data spanning one-day intervals. We also used the combination of unique stopover site and individual as the conditional specification, such that departure decisions were only compared to the range of dates individual woodcock experienced while at a particular stopover site, and not those experienced at previous or subsequent stopovers. We removed all single day stopover events, as only multi-day stopover events provided the necessary two locations to be included in the conditional logistic regression framework. We included barometric pressure, temperature, wind assistance, and wind speed as possible explanations of stopover departure. For the spring departure analysis, we removed dates after 1 April, as migrating woodcock generally had progressed to snow covered areas, where migratory decisions were likely based on a combination of snow melt and weather conditions, which would have confounded our analysis in two ways. First snow cover would have prevented north-ward movement independent of weather cues, and second migratory movements often stopped being directional as individuals began ranging in and out (north and south) of snow-covered areas. We applied a similar weighting process to migration initiation, where control points were weighted by the reciprocal of the number of non-departure days for each individual at each stopover site.

Demographic Effects

Related to demographic differences in woodcock migratory phenology, we wanted to investigate how age influenced autumn migration decisions and how sex influenced spring migration. Our previous research demonstrated that adult woodcock initiated autumn migration earlier than young woodcock, and in spring males initiated migration prior to females (Chapter 1). Thus, we expected that woodcock of differing age and sex cohorts may rely on fundamentally different environmental cues. To evaluate how these demographic factors influenced migratory decisions in the conditional logistic regression framework, we subset the data by age or sex, and conducted separate analyses for each demographic component. Age and sex could not be included as predictive covariates in the models because individuals, on which the model was conditioned, maintained the same age or sex class throughout the analysis. Hence, conducting separate analyses for each age or sex class was the only feasible way to evaluate variable patterns among different demographic groups. We compared differences in model selection results and regression coefficients between each analysis to evaluate the differences among age and sex classes.

Migration Efficiency

We expected that a woodcock's ability to take advantage of favorable flight conditions, given their decision making related to departure, would influence how efficiently they migrated. Conceptually, woodcock that performed longer distance movements between stopover sites, or completed migration in the shortest amount of time, would have maximized energy conservation and thus migrated more efficiently. We thus investigated factors that influenced the migratory flight distances (e.g., distance between stopover sites) and the pace of woodcock migration. We used either linear mixed effect models using the lme4 package (Bates et al. 2015) or general linear models using the stats package (Bolar 2019) in R. Linear mixed effect models allowed us to account for repeated sampling and individual variation in distance traveled by including a random intercept for each individual woodcock. However, the individual random intercept term failed to converge when modeling spring migration data, likely due to insufficient repeated sampling of unique individuals. Thus, we used general linear models for spring, and assumed that all flight distances were independent. We explored how various combination of additive and interactive effects of age, sex, wind assistance, and wind speed influenced migratory distance. We included age and sex as an interaction in the model set, but also explored additive effects of just age or sex post-hoc when the confidence interval for a particular demographic cohort (e.g., adult females) did not overlap zero.

To evaluate how migratory decisions affected the efficiency of migration overall, we developed a multi-tiered modeling approach to evaluate the pace of woodcock autumn migration. We only calculated pace of migration for individuals with a full migration path (i.e., those that transitioned from pre-migration to migration to post-migration behavioral states). When uncertainty existed for departure or arrival dates (multiple days between locations), we selected the mean date between locations when the transition could have occurred. While this approach introduced some uncertainty in the date of departure or arrival, error was equally likely to occur before or after the mean transition date, and therefore would not be considered directional bias. For each woodcock, we summed the length (e.g., Euclidean distance) of all migratory steps to provide a total net migratory distance. We then calculated the pace of migration by dividing net migration distance by the number of days between the initiation and termination of migration.

We used general linear models to evaluate variation in the pace of migration under a three-tiered approach to analysis. In the first tier of the analysis, we evaluated how initiation latitude and longitude, termination latitude and longitude, and state/province of origin influenced pace of migration. We selected the top-supported (inference) model and added demographic covariates in the second tier of the analysis. We added additive and interactive effects of age and sex, and the top supported model from this stage became the next inference model. In the third modeling tier, we evaluated how pre-migratory body condition influenced the pace of migration. Body condition was included as a standalone covariate and as an interactive term with age, sex, and migration initiation latitude, where condition scores were the residuals of a linear model describing the relationship between the lower leg length and body mass, while controlling for differences between age and sex classes (Chapter 1).

Approach to Inference

We used Akaike's Information Criterion corrected for small sample size (AIC_c) to rank models and select inference models. For all conditional logistic regressions, and for assessing the distance traveled between migratory steps, we constructed a list of a priori models and used AIC_c to rank model fit. For models evaluating total migratory distance, we used the tiered approach to model selection described above. We selected the model with the lowest AIC_c score that contained no parameter(s) with 95% confidence intervals that overlapped zero as the most parsimonious model. We considered models within two AIC_c of the top model competitive for the conditional logistic regression models, and model less than two AIC_c unit for every additional model parameter competitive for migratory flight distance. We extracted the odds ratio for covariates in the conditional logistic regression models, which provide the log odds of an event occurring. An odds ratio with a confidence interval overlapping one indicates equal probability of an event occurring and would conceptually be described as a null relationship. The odds ratio is on the log scale and values cannot be less than zero.

Results

We captured and marked 304 woodcock between 2017 and 2020; 6 in 2017, 75 in 2018, 163 in 2019, and 60 in 2020. Of these, 153 were males (69 adults and 84 young) and 151 were females (72 adults and 79 young). We collected 18,074 locations from these birds between 01 October 2017 and 18 June 2020 (Chapter 1). Most of the 304 woodcock captured were included in at least one analysis, with inclusion depending on location upload frequency and timing.

Initiation of Autumn Migration

Sixty-two individuals (32 adults and 30 young woodcock) provided 998 locations to evaluate factors that influenced initiation of autumn migration, including 62 departure events and 936 control days. Of 32 a priori models, six were considered competitive for adults and nine for young woodcock (Table 2.1). The top supported models indicated that migration initiation had a negative relationship with temperature for both adult and young woodcock, but young woodcock responded more strongly to temperature (based on the strength of regression coefficients; Table 2.1, Figure 2.2). Similarly, woodcock initiated migration using tailwinds (negative selection for wind assistance) and under greater wind speeds, with adults showing a stronger selection for wind assistance (Figure 2.2). Woodcock also selected for lower barometric pressure, which is commonly associated with lower temperatures and higher wind speeds. Woodcock selected for lower levels of moon illumination, although this relationship was only significant for young birds (Table 2.1). Lastly young woodcock responded to an interaction between temperature and barometric pressure, indicating they were most likely to initiate migration under a combination of low temperature and decreasing barometric pressure. While most extrinsic factors received some level of support, generally lower temperature and wind assistance had the greatest influence on initiation of migration, with age having a moderating effect on the magnitude to which individuals responded to these variables. See Table D.1 for a complete list of ranked models.

Table 2.1. Competing conditional logistic regression models and regression coefficients explaining which extrinsic factors are most important for autumn migration initiation in American Woodcock (*Scolopax minor*), 2017-2019. Of the 34 a priori models included in the analysis only models ≤ 2 AIC_c units of the top model were considered competitive. Five covariates were included; optimal wind assistance (wind.assist), temperature (temp), barometric pressure (b.pres), wind speed (wind.spd), and moon illumination (m.illum). Regression coefficients were z-standardized with standard errors in parentheses. An asterisk indicates a covariates with confidence intervals that do no overlap zero. Initiation events for adults (32) and for young birds (30) were included in the models. Samples sizes below indicate number of case and control points.

Model	**K**	**Delta AIC_c**	**wind. assist**	**temp**	**b.pres**	**wind. spd**	**m. illum**	**Interaction**
Adult (n = 454)								
wind.assist + temp	2	0[a]	-0.65 (0.13)*	-0.95 (0.19)*				
wind.assist + temp + b.pres	3	0.32	-0.65 (0.13)	-1.26 (0.18)*	-0.93 (0.26)*			
wind.assist + temp + wind.spd	3	0.77	-0.65 (0.30)*	-0.95 (0.20)*		0.30 (0.13)*		
wind.assist + temp + b.pres + m.illum	4	1.64	-0.67 (0.15)*	-1.34 (0.24)*	-1.21 (0.21)*		-0.29 (0.20)	
wind.assist + temp + wind.assist×temp	3	1.76	-0.72 (0.16)*	-1.04 (0.26)*				-0.15 (0.10)[b]
wind.assist + temp + m.illum	3	1.89	-0.65 (0.13)*	-0.95 (0.21)*			-0.11 (0.18)	
Young (n = 544)								
temp	1	0[c]		-1.15 (0.13)*				
temp + b.pres	2	0.63		-1.36 (0.16)*	-0.82 (0.22)*			
temp + wind.assist	2	0.84	-0.28 (0.10)*	-1.07 (0.13)*				
temp + b.pres + temp×b.pres	3	1.49		-1.40 (0.15)*	-0.66 (0.24)*			0.41 (0.13)*[d]
temp + m.illum	2	1.51		-1.22 (0.12)*			-0.20 (0.11)	
temp + wind.spd	2	1.57		-1.13 (0.13)*		0.18 (0.09)*		
temp + b.pres + wind.assist	3	1.6	-0.27 (0.10)*	-1.29 (0.16)*	-0.77 (0.21)*			
temp + b.pres + wind.asssit + m.illum	4	1.83	0.34 (0.12)*	-1.53 (0.21)*	-1.15 (0.27)*		-0.43 (0.15)*	

Table 2.1 continued.

temp + wind.assist + wind.spd	3	1.91	-0.35 (0.10)*	-1.03 (0.13)*		0.27 (0.09)*

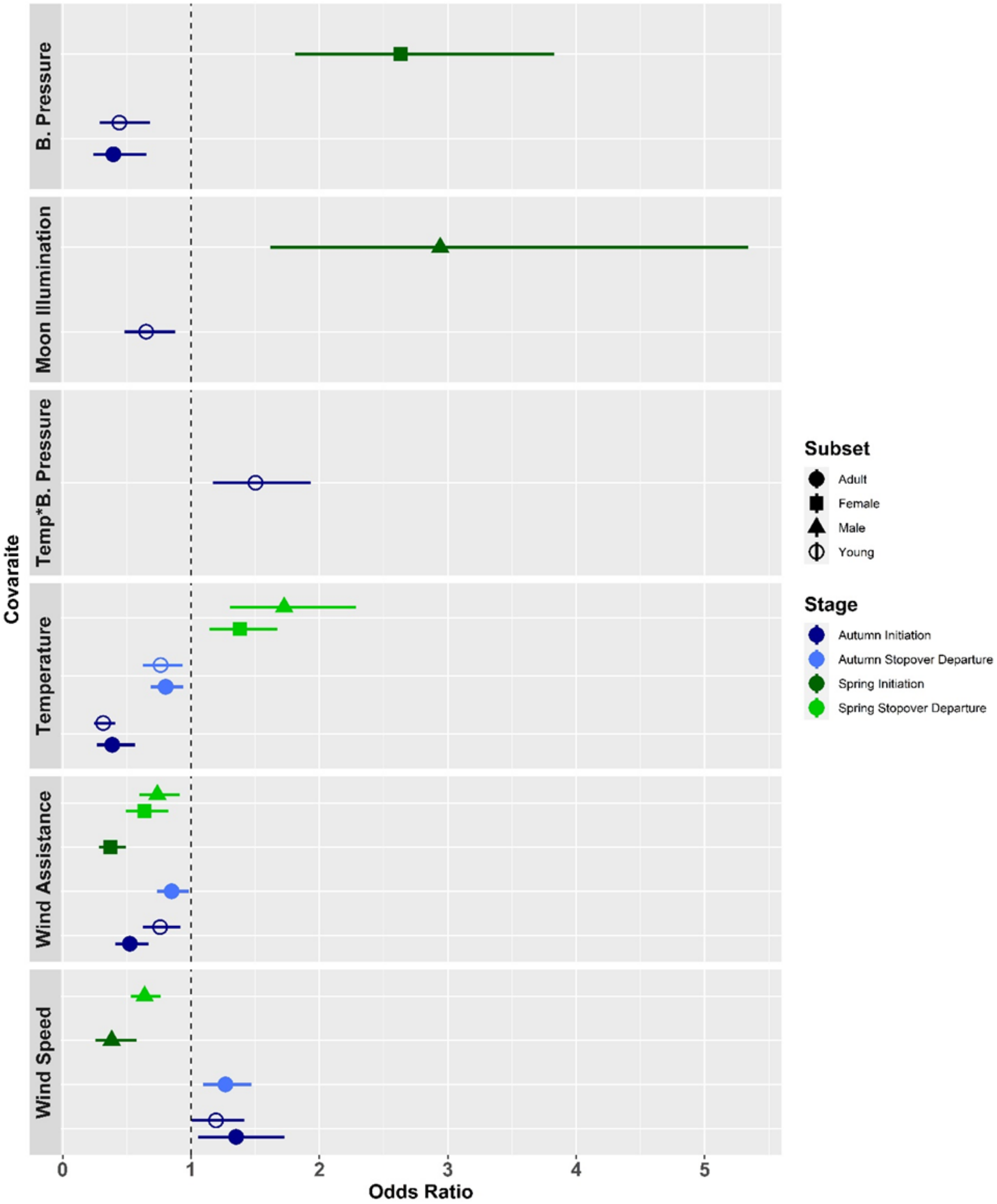

Figure 2.2. American Woodcock (*Scolopax minor*) relied on a variety of environmental cues when making migratory decisions, 2017-2020. Decisions varied by season, age, and sex of the individual. Only odds ratios with confidence intervals that did not overlap one from the competitive model sets were included in the plot. All covariates were z-standardized, so the magnitudes of the effects within and between covariates are directly comparable.

Departure from Autumn Stopover

Fifty-five individuals (27 adults and 28 young woodcock) provided 1,152 locations to evaluate the factors that influenced 127 departure events (66 adult and 61 young woodcock) from autumn stopover sites and 1,025 control days. Of the 19 a priori models, five were considered competitive for adults and six for young woodcock (Table 2.2; Table D.3). Similar to autumn migration initiation, temperature and wind were important predictors of departure events. Departures from stopover sites were associated with lower temperatures for both adult and young woodcock, but only adults showed significant selection for wind assistance and wind speed (Table 2.2). Similar to autumn migration initiation, adults selected for tailwinds and higher wind speeds when departing from stopover sites (Table 2.2). The competitive model set for both adults and young woodcock contained barometric pressure, but the confidence intervals overlapped zero in each case (Table 2.2). Compared to initiation of autumn migration, most autumn stopover departure models contained a single covariate, and the magnitude of the selected covariates were generally lower. These patterns indicated that the cues associated with departure from stopover sites may be less consistently selected, compared to initiation of autumn migration.

Table 2.2. Competing conditional logistic regression models and regression coefficients explaining which extrinsic factors are most important for autumn stopover departure in American Woodcock (*Scolopax minor*), 2017-2019. Models within 2 AIC_c units of the top model were considered competitive and. Five covariates were included in the competitive model set; barometric pressure (b.pres), temperature (temp), wind assistance (wind.assist), and wind speed (wind.spd). An asterisk indicates confidence intervals that do not overlap zero Regression coefficients were z-standardized with standard errors in parentheses. Based on 19 a priori models. 66 stopover departures from 27 adults and 61 stopover departures from 28 young birds were included. Samples sizes below indicate number of case and control points.

Model	**K**	**Delta AIC_c**	**wind.spd**	**temp**	**wind.assist**	**b.pres**
Adult (n = 682)						
wind.spd	1	0[a]	0.24 (0.08)*			
temp	1	0.54		-0.22 (0.08)*		
wind.assist	1	0.87			-0.16 (0.07)*	
temp + wind.spd	2	1.24	0.24 (0.08)*	-0.21 (0.07)*		
b.pres	1	1.31				0.08 (0.10)
Young (n = 470)						
temp	1	0[b]		-0.27 (0.10)*		
wind.spd	1	0.88	0.10 (0.08)			
wind.assist	1	1.02			-0.08 (0.07)	
b.pres	1	1.12				0.03 (0.14)
temp + wind.spd	2	1.86	0.08 (0.07)	-0.26 (0.10)*		
temp + b.pres	2	1.99		-0.28 (0.11)*		-0.06 (0.16)

[a]AICc score 38.05

[b]AICc score 39.77

Initiation of Spring Migration

Twenty-five individuals (8 male and 17 female) provided 466 locations to evaluate extrinsic factors influencing spring migration initiation, including 25 departure events and 441 control days. Of the 28 male and 34 female a priori models, five male and five female models were considered competitive (Table 2.3, Table D.2). Male and female woodcock selected for very different environmental conditions when initiating spring migration. Females generally selected for similar environmental conditions as autumn migration, although the directionality of some selections was opposite of autumn migration (Table 2.3). Females selected for tailwind, higher temperature, and higher barometric pressure, with the latter two being associated with warm fronts. In contrast, males initiated migration under low wind speed conditions with greater moon illumination (Table 2.3). Male selection of greater moon illumination contrasts with autumn migration, when young woodcock selected for less moon illumination. These general selection patterns suggest that females may be selecting for conditions that maximize energy efficiency (e.g., wind assistance), while males may be minimizing resistance (e.g., wind speed) during the initial stages of spring migration.

Table 2.3. Competing conditional logistic regression models and regression coefficients explaining which intrinsic factors are most important for spring migration initiation in American Woodcock (*Scolopax minor*), 2019-2020. Of the 28 (male) and 34 (female) a priori models were included in the analysis and only models ≤ 2 AICc units of the top model were considered competitive. Five covariates were included; optimal wind assistance (wind.assist), temperature (temp), barometric pressure (b.pres), wind speed (wind.spd), and moon illumination (m.illum). Regression coefficients were z-standardized with standard errors in parentheses. An asterisk indicates a covariates with confidence intervals that do no overlap zero. Initiation events for males (8) and for females (17) were included in the models. Samples sizes below indicate number of case and control points.

Model	**K**	**Delta AICc**	**m. illum**	**wind. spd**	**temp**	**wind. assist**	**b.pres**	**wind.assist *b.pres**
Male (n = 102)								
m.illum	1	0[a]	1.08 (0.30)*					
wind.sp	1	0.02		-0.96 (0.21)*				
wind.sp + m.illum	2	0.61	0.89 (0.27)*	-0.76 (0.19)*				
wind.sp + temp	2	1.65		-1.01 (0.21)*	0.44 (0.30)			
m.illum + temp	2	1.93	1.07 (0.34)*		0.24 (0.32)			
Female (n = 364)								
wind.assist + b.pres	2	0[b]				-0.98 (0.14)*	0.97 (0.19)*	
wind.assist + b.pres + temp	3	0.77			0.68 (0.14)*	-0.84 (0.14)*		
wind.assist	1	0.81				-0.79 (0.12)*		
wind.assist + b.pres + wind.assist * b.pres	3	1.93				-1.03 (0.16)*	1.10 (0.24)*	0.16 (0.20)
wind.assist + b.pres + wind.spd	3	1.95		-0.13 (0.11)		-0.95 (0.14)*	0.92 (0.20)*	

[a] AICc score 10.46

[b] AICc score 20.19

Departure from Spring Stopover

Forty individuals (18 male and 22 female) contributed 448 locations to evaluate which extrinsic factors influenced 75 departure events (35 male and 40 female woodcock) from spring stopovers sites compared with 373 control days. Of the 19 a priori models seven were considered competitive for males and four for females (Table 2.4, Table D.4). Similar to spring migration initiation, female woodcock showed strong selection for wind assistance and selected for warmer temperatures (Table 2.4). Males continued to select for lower wind speeds but also selected warmer temperatures (Table 2.4). Temperature was therefore an important cue woodcock used when departing from spring stopover sites, but males showed stronger selection for warmer temperatures than females (Table 2.2). Barometric pressure was included in the competitive model set for both sexes but was not significant for either. These patterns indicate that both sexes departed from spring stopover sites using similar cues, but that males and females responded more strongly to specific cues.

Table 2.4. Competing conditional logistic regression models and regression coefficients explaining which extrinsic factors are most important for spring stopover departure in American Woodcock (*Scolopax minor*), 2019-2020. Models within 2 AIC_c units of the top model were considered competitive. Five covariates were included in the competitive model set; barometric pressure (b.pres), temperature (temp), wind assistance (wind.assist), and wind speed (wind.spd). An asterisk indicates confidence intervals that do not overlap zero. Regression coefficients were z-standardized with standard errors in parentheses. Based on 19 a priori models. 35 stopover departures from 18 males and 40 stopover departures from 22 females were included. Samples sizes below indicate number of case and control points.

Model	**K**	**Delta AIC_c**	**wind.spd**	**temp**	**wind.assist**	**b.pres**
Male (n = 213)						
wind.spd + temp	2	0[a]	-0.45 (0.09)*	0.55 (0.14)*		
wind.spd	1	0.12	-0.30 (0.10)*			
wind.assist	1	0.38			-0.30 (0.11)*	
temp	1	0.67		0.29 (0.11)*		
wind.spd + temp + wind.assist	3	1.3	-0.47 (0.09)*	0.40 (0.15)*	-0.29 (0.13)*	
b.pres	1	1.52				0.01 (0.22)
wind.spd + temp + b.pres	3	1.68	-0.46 (0.10)*	0.67 (0.15)*		0.42 (0.28)
Female (n = 235)						
wind.assist	1	0[b]			-0.45 (0.13)*	
temp	1	1.21		0.32 (0.10)*		
wind.assist + temp	2	1.53		0.19 (0.10)	-0.38 (0.13)*	
wind.assist + b.pres	2	1.77			-0.48 (0.13)*	0.28 (0.20)

[a] AICc score 25.45

[b] AICc score 28.22

Migratory Efficiency

We used distances from 542 (360 autumn and 182 spring) single day migratory movements to evaluate flight distance. These movements represented 76 individuals in the autumn and 50 in the spring. In autumn the mean single-day flight distance was 254.16 km (min = 12.00 km, max = 1,015.23

km) and in spring the mean was 204.32 km (min = 11.74, max = 757.23). The top model in the autumn indicated that migration distance was conditionally affected by wind speed (β = 56.89 ± 11.18), wind assistance (β = -38.65 ± 11.21), and the interaction between wind speed and wind assistance (β = -32.73 ± 11.04; Table 2.5; Figure 2.3). Collectively, this model showed flight distance was greatest when departures occurred under high wind speed and tails winds (wind assistance = 0). The top model for spring migration indicated distance was negatively impacted by wind speed (β = -36.49 ± 11.05) and wind assistance (β = -44.11 ± 11.29), as well as affected by age (β = 64.23 ± 22.35; Table 2.5). Young woodcock on average migrated 64.23 km farther than adults when traveling between stopover locations in the spring (Figure 2.4). During both spring and autumn migration, woodcock that migrated with tailwinds traveled further than woodcock that migrated with crosswinds or headwinds. However, the relationship for wind speed depended on the season, with higher winds in the autumn contributing to larger migratory flight distances but resulting in shorter flight distances in the spring. There was no effect of sex or condition during either season. A complete list of ranked models for distance traveled during single day migratory steps are presented in Table D.5 and Table D.6.

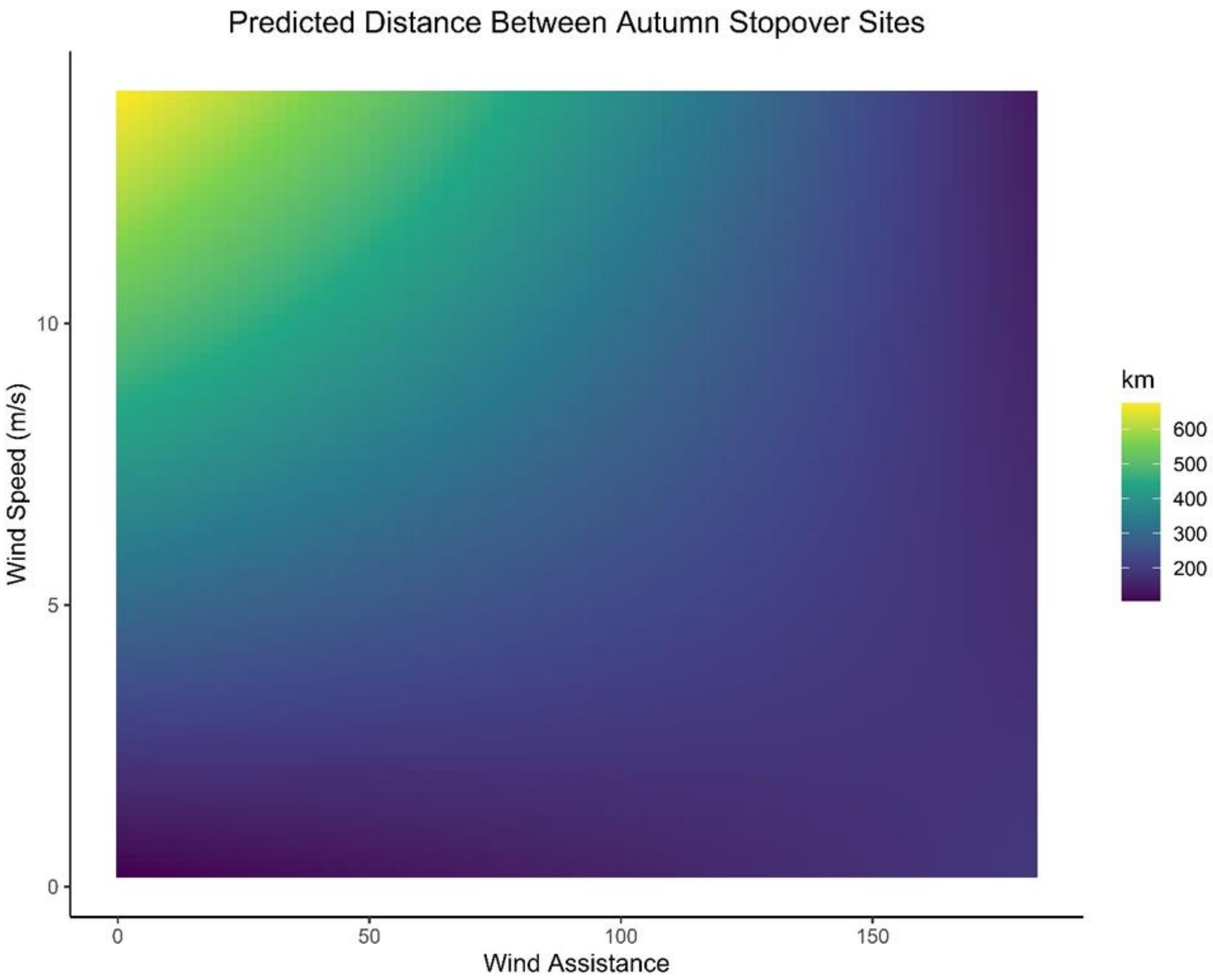

Figure 2.3. The distance between American Woodcock (*Scolopax minor*) autumn stopover sites was influenced by an interaction between wind speed and wind assistance, 2017-2019. The distance was greatest when wind assistance was maximized (e.g., 0) with strong wind speed.

Table 2.5. Regression coefficients for best supported models explaining distance between American Woodcock (*Scolopax minor*) stopover sites, 2017-2020. Linear mixed effect models were used for autumn, but the individual random effect would not converge for spring models, so general linear models were used. Adult were used as reference in the age covariate.

Season	n	Groups	Intercept	wind.spd	wind.assist	wind.spd*wind.assist	age
Autumn	360	76	253.56 (11.62)	56.89 (11.18)*	-38.65 (11.21)*	-32.73 (11.04)*	
Spring	182	NA	171.90 (16.00)	-36.49 (11.05)*	-44.11 (11.29)*		64.23 (22.35)*

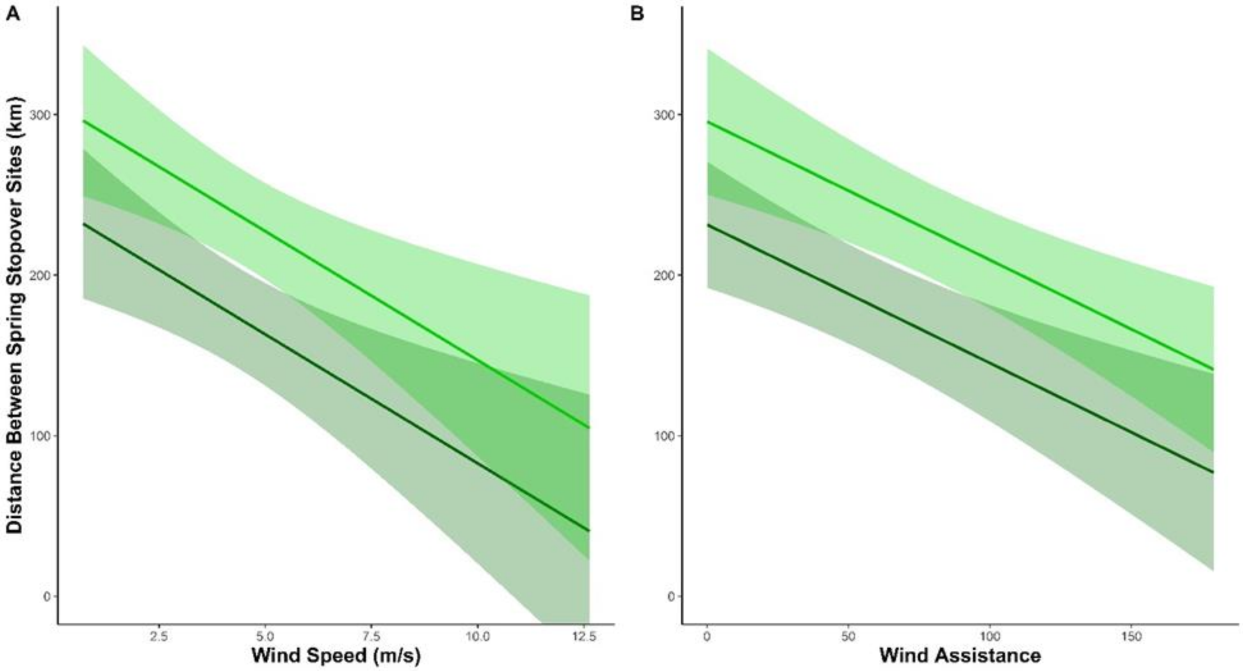

Figure 2.4. The distance between American Woodcock (*Scolopax minor*) spring stopover sites were influenced by wind speed and wind assistance, 2019-2020. Predictions from the top model show how young woodcock (light green) generally migrated further than adult woodcock (dark green) when making migratory steps. Wind speed had a stronger effect than wind assistance on distance between step lengths.

We calculated the pace of autumn migration for 90 individuals (30 adult female, 20 young female, 19 adult male, and 21 young male). A subset of the woodcock were missing weight or measurement data, and we therefore could only calculate condition for 75 individuals (26 adult female, 20 young female, 8 adult male, and 21 young female). The top supported model for the spatial, demographic and condition tiers all contained ending latitude (β = -123.41 ± 41.11), ending longitude (β = 51.57 ± 17.50), and an interaction between ending latitude and ending longitude (β = -1.53 ± 0.23; Table 2.6, Table D.7). This model indicated woodcock that terminated migration in the southeastern portion of the winter range had a faster pace of migration compared to woodcock that terminated migration on the southwestern and northeastern portions of the wintering range (Figure 2.5). Pace of migration was not influenced by starting latitude or longitude, nor was it affected by age, sex, or condition of the individual.

Table 2.6. Regression coefficients for top models explaining the pace of autumn migration for American Woodcock (*Scolopax minor*), 2017-2019. The pace of migration was described as kilometer per day. General linear models were used to generate the regression coefficients.

Season	**n**	**Intercept**	**end.latitude**	**end.longitude**	**end.latitude*end.longitude**
Spatial	90	4282.48	-123.41	51.57	-1.53
		(1396.84)	(41.11)*	(17.50)*	(0.23)*
Demographic	90	4282.48	-123.41	51.57	-1.53
		(1396.84)	(41.11)*	(17.50)*	(0.23)*
Condition	75	5489.23	-159.36	65.45	-1.94
		(2083.76)	(62.54)*	(25.50)*	(0.77)*

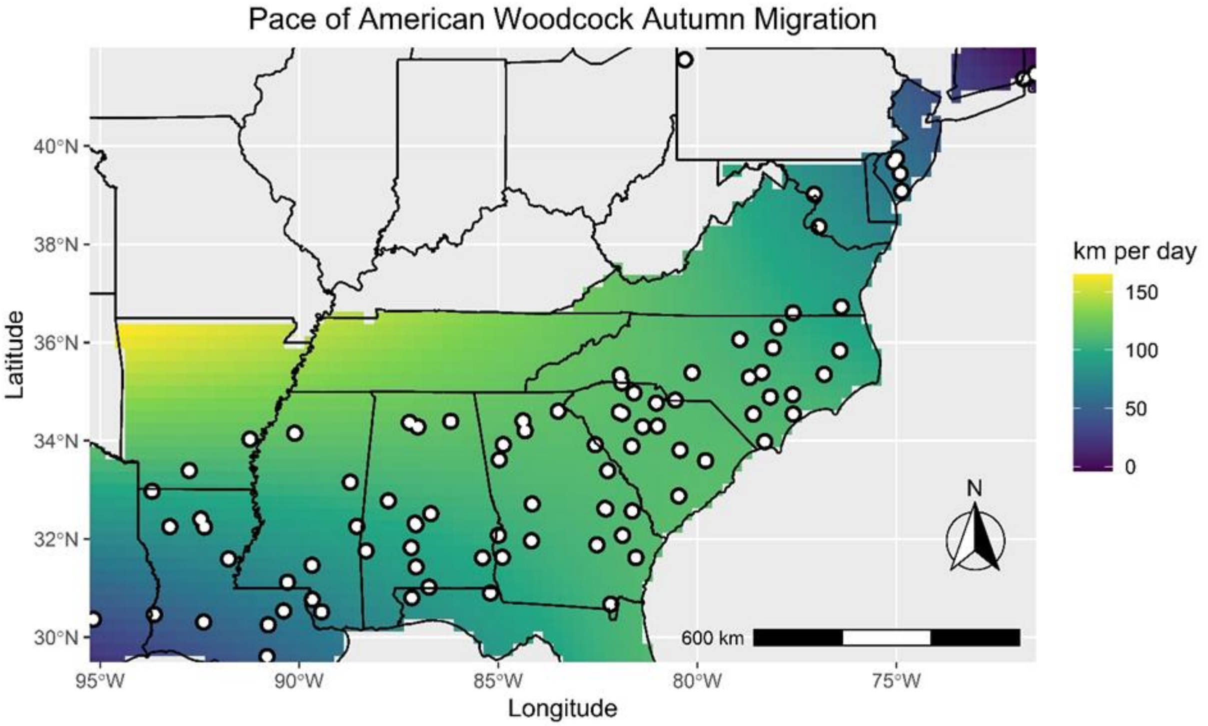

Figure 2.5. The predicted relationship between the pace of autumn migration and the locations where American Woodcock (*Scolopax minor*) terminated migration, 2017-2019. The shaded region represents the states where woodcock terminated migration and the circles represent locations where woodcock terminated (n = 91) migration. Termination locations ranged from coastal Rhode Island to eastern Texas and bounded the prediction area.

Discussion

Using GPS data collected from woodcock marked in eastern North America, we show that several environmental cues, including temperature, wind assistance, wind speed, barometric pressure and moon illumination, affected woodcock migratory departure decisions. Intraspecific variation in selection for many cues were dependent on season (barometric pressure, moon illumination, temperature, wind speed), sex (barometric pressure, moon illumination, wind assistance, wind speed), and the strength of selection often varied by age. Migration efficiency was influenced by wind speed and direction; woodcock that departed with strong tailwinds had longer single-flight distance, and young woodcock preformed longer flights than adults in the spring. The pace of migration was not influenced by demographic factors, but rather was only influenced by the location individuals terminated migration.

Wind speed and direction received consistent support for migratory initiation and departure decisions. The use of wind by individual woodcock varied considerably between spring and autumn migration, and among age and sex classes. In the autumn adult woodcock showed a stronger selection than young woodcock for tailwinds and wind speed, both of which have been attributed to migratory efficiency (Deppe et al. 2015, Sjöberg et al. 2015). Adult woodcock may use experience obtained during prior migrations to select conditions that minimize energy expenditure (Monti et al. 2018). Interestingly, when initiating both spring and autumn migration woodcock showed a stronger selection for wind assistance and speed compared to departure from stopover sites. The ability to leave a stopover site is likely constrained by a suite of variables beyond the constraints imposed by weather (e.g., foraging quality and refueling rates; Goymann et al. 2010, Morganti et al. 2011, Smith and McWilliams 2014, Dossman et al. 2016), and we were unable to explore those factors at the spatial scale of our study.

During spring migration, females selected for tailwinds and higher winds speeds, but males showed a contrasting selection for low wind speeds, and only used tailwinds when departing from stopover sites. This general pattern may be due in part to differing motivations of each sex between autumn and spring. In autumn, woodcock may be more driven to head south and less concerned with navigating to a precise destination, enabling them to select for the most efficient migration conditions.

Meanwhile, spring migrating male woodcock may be balancing the fitness advantages of arriving early on breeding areas (Lozano et al. 1996) with the need to make departure decisions that minimizing energy expenditure and maximizing navigation ability (Dierschke et al. 2005, Van Den Broeke and Gunkel 2021). Male selection of low wind speed suggests that they minimize resistance and energy expenditure, while enabling movements in any direction. Hence, male fitness may be less sensitive to efficiency of individual flights and more related to arrival and territory acquisition at a breeding site. In the spring, females migrated later than males (Chapter 1) and may delay departures until wind conditions are such that they maximize energetic conservation (e.g., tailwind and high wind speed), likely due to the energetic demands of nesting (Högstedt 1981, Chastel et al. 1995). The relationship between migration efficiency and reproductive fitness is complex and likely requires a concerted effort to comprehensively investigate.

Temperature was associated with migratory movements during both spring and autumn. The effect of temperature was opposite between seasons with lower temperatures associated with migratory movements during autumn and higher temperatures associated with spring movements. This general pattern of temperature influencing woodcocks' migratory decisions aligns with the Frost Wave hypothesis (Xu and Si 2019), which asserts that temperature changes impact resource availability and cause migratory movements. Woodcock primarily forage on earthworms (McAuley et al. 2020), and would have a limited ability to probe for earthworms when the soil freezes. In autumn, lower temperatures would result in frozen soil and restrict foraging opportunities, whereas warmer temperatures during the spring would result in the soil thawing and increase foraging opportunity; hence the opposing signs of temperature effects between autumn and spring seasons. While we were unable to explicitly determine whether the ground was in fact frozen at a particular site, we can assume that changing temperatures near a freezing threshold would likely lead to freezing and thawing of the soil. Young woodcock responded more strongly to temperature than adults, and it is possible that a change in resource availability was more important for naive individuals that had not previously migrated. Alternatively, young woodcock may have delayed departure to continue to gain weight and develop flight muscle strength for as long as possible prior to attempting their first migration (McCabe and Guglielmo 2019). In addition to foraging, cooler temperatures may also lead to direct mortality from freezing. It is important to note, however, that following most mass mortality events of woodcock associated with cold fronts, individuals found frozen were emaciated (Rice et al. 2000). Woodcock starvation and freezing are thus likely interdependent and will be difficult to explicitly disentangle.

Barometric pressure was primarily important for predicting initiation of spring and autumn migration; however not all demographic classes responded to changes in barometric pressure. Lower barometric pressure, which is commonly associated with cold fronts, influenced autumn migration while higher barometric pressure, commonly associated with warm fronts, influenced spring migration decisions. In the autumn, young woodcock relied on the interaction between barometric pressure and temperature when deciding to depart for migration. Initiation of autumn migration would be the first instance that a young woodcock has ever departed for migration, and after this first initiation, the young woodcock would then have experience on which to base future departure decisions. Perhaps barometric pressure-temperature interaction only received support for this age class because of the unique nature of young woodcock initiating their first migration. During spring migration, a change in barometric pressure was associated with migration initiation by females, but not departure from stopover sites. Spring barometric pressure was not associated with migration initiation or stopover departure by males. Intuitively, departure from stopovers is a more dynamic process, in which individuals must rest and rebuild energy reserves prior to departing from the stopover site (Goymann et al. 2010), which may require ignoring cues otherwise used to depart. Our findings support the observation described by Krementz et al. (1994), that spring migration initiation coincided with the passage of weather fronts (changing barometric pressure) in the southeastern US. However, we were able to build on their observations by describing the directionality of barometric change associated with autumn (low) and spring (high) woodcock migration initiation.

We did not find support for moon phase influencing migratory decisions but instead found support for moon illumination, the effect of which varied among age and sex classes in the autumn and spring. Previously woodcock have been described as departing near the full moon or leading up to the full moon during both spring and autumn (Coon et al. 1976, Krementz et al. 1994b, Meunier et al. 2008). In our dataset, male woodcock initiated spring migration with increased moon illumination, and in autumn young woodcock initiated migration under declining illumination levels. While our findings support those of Krementz et al. (1994) for the spring, we described the opposite relationship of Coon et al. (1976) and Meunier et al. (2008). This relationship may be due in part to the different migration initiation dates for woodcock across their breeding range (Meunier et al. 2008, Chapter 1). One complicating aspect of our dataset is that we were not able to investigate the specific time of night that woodcock made departure decisions, nor how those decisions related to moonrise or moonset times. If woodcock depart based on moonlight, then timing of moonrise and moonset, or cloud cover, may affect the availability of moonlight during different times of night, and would also be part of the departure decision making process. Conceptually, moon illumination near the full moon would aid in some aspects of navigation ability and influence selection (Moore 1987). This would be particularly important for males in the spring, as they display throughout spring migration and would need to locate suitable singing-grounds at each stopover site. In autumn when direction or destination is less important, low moon illumination and its effects on navigation may be less influential.

Woodcock consistently used environmental cues when making migration initiation and departure decisions. Packmor et al (2020) found that medium distance migrants were more likely to make migratory decisions based on environmental cues when compared to long-distance migrants, who often respond more strongly to intrinsic cues influenced by changes in photoperiod and may be less selective of environmental cues (Packmor et al. 2020). However, environmental cues, though less influential, are used by both medium- and long-distance migrants when making departure decisions (Klinner and Schmaljohann 2020), so their likely exists a hierarchy of cue inference that vary based on temporal and spatial scales, and are influenced by a species' natural history (McEvoy et al. 2015). This diversity in response to environmental cues can influence the wintering distribution of some species (Moreno-Contreras et al. 2021). In our analyses, comparisons among departure and non-departure days were conditioned on the season of migration for the local populations, and in doing so we explicitly controlled for the role of intrinsic drivers and focused instead on external cues.

What has been less clear is how departure decisions in response to environmental cues impact the efficiency of migration. Conceptually, individuals make decisions that minimize energy expenditure in order to travel as efficiently as possible (Alerstam 2011). We show individuals that departed under strong tailwinds traveled farther in single flights and may migrated more efficiently. When we investigated the efficiency of migration overall (e.g., pace of autumn migration), we only found support for spatial patterns that depended on where an individual terminated migration. Interestingly, the pace of autumn migration was not influenced by age or sex of the individual, and we ultimately do not yet understand the factors that contributed to individual woodcock selecting a wintering location. It is possible that migration efficiency is fundamentally an individual characteristic, or that it was independent of the relationships we explored. Complicating our efforts to investigate efficiency is that we were only able to collect frequent locations on individuals for a single migration. Therefore, we had minimal inference on site fidelity and repeated navigation between seasonally used areas. Understanding site fidelity and collecting data from individuals through repeated migrations would allow for a more comprehensive understanding of how woodcock used environment cues for their migration efficiency.

Our results highlight the variable nature of migratory departure decisions and reinforce the need to investigate the particular cues individual birds use when making decisions and the intraspecific variation present within a species. For woodcock, we were able to build on previously described migration phenology characteristics at regional scales to understand the cues used by woodcock across half of the species distribution. As satellite transmitter technologies continue to decrease in size and increase the frequency and volume of data collected, there will be an increased ability to evaluate the environmental cues other species use to make migratory decisions. Furthermore, satellite transmitters provide an opportunity to evaluate how migratory decisions can affect an individual’s survival during migration. Drawing parallels between migration decisions and individual fitness is central to understanding the evolutionary processes present within a species and predicting how species will respond to future climate conditions. These predictions can be incorporated in migratory bird conservation planning to help stabilize or reverse the declining abundance of many migratory bird species (Rosenberg et al. 2019).

CHAPTER 3

SURVIVAL of AMERICAN WOODCOCK (*SCOLOPAX MINOR*) THROUGHOUT EASTERN NORTH AMERICA DURING MIGRATORY PERIODS INFERRED FROM SATELLITE TELEMETRY

Abstract

Populations of migratory species are declining worldwide, and migratory birds in North America have declined sharply over the past fifty years. Management of migratory birds relies on an understanding of species' full-annual cycles, including demographic processes during all life stages. Migration is a particularly challenging life-stage to investigate given frequent long-distance movements of individuals, and this is especially true for small- or medium-bodied birds that can only carry small-tracking devices. Survival during migration may be lower than other life-stages with the potential to limit population growth for some species. We used data collected from PPT-enabled GPS-satellite transmitters to estimate survival during migratory periods for the American woodcock (Scolopax minor), a migratory North American gamebird that has persistently declined over the past fifty years. Woodcock were captured in three Canadian provinces and 14 US states between 2017 and 2020 during fall pre-migration (27 August to 30 October), fall migration (1 November to 14 December), and spring pre-migration (3 January to 29 February). After accounting for potential transmitter loss and failure, we used a live-encounter analysis framework and multi-state models in RMark, to estimate woodcock survival during three distinct migratory states (pre-migration, migration, and post-migration) for both fall and spring migrations. We used AIC_c to assess whether survival varied between age and sex classes, and depending on migration initiation latitude and longitude. A base model that allowed survival to vary among migratory states with a linear time trend received the most support during both spring (N = 107 individuals) and fall (N = 129 individuals) migration periods. Survival did not differ during any movement state among age/sex classes or based on location of origin. Weekly survival estimates generally declined through time in each migratory state, except for post-migration during the fall, in which case survival increased through time. Weekly survival was highest during migration (fall 0.95 ± 0.01 [Φ ± SE], spring 0.88 ± 0.04), lowest during post-migration (fall 0.80 ± 0.06, spring 0.52 ± 0.09), and at moderate levels during pre-migration (fall 0.91 ± 0.03, spring 0.81 ± 0.07). Cumulative survival estimates during each migratory period indicated lower survival during spring compared to the fall. Only 2.3 % of woodcock included in our analysis were harvested by hunters, all during fall pre-migration. High survival during migration indicates that conditions experienced during stationary periods (pre- and post-migration) likely reduce woodcock survival.

Introduction

The conservation of migratory species depends on a comprehensive understanding of the full annual cycle (Marra et al. 2015, Rushing et al. 2017), given these animals travel between spatially distinct seasonal use areas and are exposed to conditions that may differ, sometimes dramatically so (Kramer et al. 2018). As individuals migrate, they must continually locate suitable habitat, and the conditions experienced during migration may further limit population growth, or be the principle drivers of population declines (Rushing et al. 2017). Understanding survival dynamics during periods of migration, and relative to stationary periods, is critically needed to more effectively direct limited resources to conserve migratory species.

Despite its importance, survival during migration is poorly understood for many species of birds due to the inherent difficulty in relocating individuals as they migrate. Most investigations of migratory survival have relied on large-bodied birds that can carry transmitters of sufficient size to collect precise movement and survival data (Klaassen et al. 2014, Lok et al. 2015, Cheng et al. 2019, Buechley et al. 2021). However, for small- or medium-bodied birds that can only carry small-sized transmitters, there is a more limited ability to track individuals during migration to determine fate (Grüebler et al. 2014, Rockwell et al. 2017, Robinson et al. 2020). Even for birds with relatively high resighting rates (e.g., some shorebirds or wading birds), the limited encounter data collected during migration may be insufficient for estimating migratory survival (Roche et al. 2010, Swift et al. 2020). As a result, most estimates of migratory survival for small- and medium-bodied birds are derived from individual stopover sites (e.g. McAuley et al. 2019) or are inferred from multi-season banding during stationary periods and population trends (Sillett and Holmes 2002, Grüebler et al. 2014, Rockwell et al. 2017, Robinson et al. 2020, Swift et al. 2020). Despite two decades of research, interspecific survival for small- and medium-bodied migrant birds remains poorly understood, with even less known about differences in intraspecific survival among sex and age cohorts.

Survival during migratory periods is generally thought to be lower than during stationary periods (e.g., breeding, wintering), and is generally lower for young birds compared to adults (Sillett and Holmes 2002, Klaassen et al. 2014, Rockwell et al. 2017, Cheng et al. 2019, Buechley et al. 2021). Young birds do not have prior migratory experience during their first migration, and may be particularly susceptible to mortality when traversing inhospitable regions (e.g., deserts or oceans; Owen and Black 1989, Klaassen et al. 2014, Cheng et al. 2019). Additionally, young birds may still be developing flight muscles, or be in lower body condition, and suffer carry-over effects during migration as a result (Owen and Black 1989, Rotics et al. 2021). Even within periods of migration, birds may be exposed to different relative risks during distinct phases, such as coincident with departure or initial arrival at destination areas. For some species, survival may be lower during stationary periods with relatively greater survival during migration (Grüebler et al. 2014). Hence investigating species-specific survival during migration is necessary to better understand the factors contributing to mortality during migration, and thus facilitate effective approaches to conservation.

The American Woodcock (*Scolopax minor*; woodcock hereinafter) is a medium-bodied (140 – 230 g) bird that has experienced a prolonged population decline for the past five decades (Seamans and Rau 2019). Woodcock is a migratory gamebird native to eastern North America, breeding from states bordering the Gulf of Mexico north to southern Canada, and wintering primarily in states bordering the

Gulf of Mexico and the Atlantic Ocean from Florida to Rhode Island (McAuley et al. 2020). Most demographic research for woodcock has occurred during stationary periods (Longcore et al. 1996, 2000; Krementz and Berdeen 1997, Pace 2000, McAuley et al. 2005, Bruggink et al. 2013), with limited investigation during migratory periods (McAuley et al. 2019). Recent advances in satellite transmitters allow woodcock to be located at regular intervals throughout migration (Moore et al. 2019) by providing high-resolution spatial data on movement between seasonal use areas. While most previous work has focused on using these movement data to understand migration phenology, connectivity, and departure decision making (Chapter, 1, 2; Moore et al. 2019, 2021), it may also be applied to a live-encounter analysis (Klaassen et al. 2014, Cheng et al. 2019) framework to provide survival estimates during a critical component of the annual life cycle.

Woodcock exhibit phenological variation during migration with adults initiating migration prior to young birds, and adult females progressing through migration prior to other age or sex classes in the fall (Chapter 1). In fact, adult woodcock depart using tailwinds, likely to increase migratory efficiently, while young woodcock migrate later and in response to cooler temperatures (Chapter 2). Additionally, in the spring males initiate migration six days before females (Chapter 1), and are less likely than females to use tailwinds, potentially increasing energy expenditure (Chapter 2). We would expect these phenological differences to lead to differential mortality risk. Hence, our goal was to use data from GPS-marked woodcock to estimate their survival during migratory periods, and to investigate sources of variation in survival. Our specific objectives were to 1) quantify survival of woodcock engaged in pre-migration, migration, and post-migration movement states, 2), compare how survival varied between periods of fall and spring migration, 3) evaluate how survival differed among age and sex classes, and 4) understand how the latitude and longitude at the initiation location affected subsequent survival during migration.

Study Area

From 2017 to 2020, we captured woodcock throughout eastern North America, with particular emphasis on the Eastern Woodcock Management Region (Figure 1; Seamans and Rau 2019). The Eastern Management Region is one of two areas the United States Fish and Wildlife Service and Environment and Climate Change Canada use to manage woodcock populations, and generally corresponds to US states and Canadian provinces from Florida to the Canadian Maritimes, west to the lower Great Lakes and south along the Appalachian chain. We also included woodcock captured in Alabama and Ontario, which are part of the Central Management Region due to cooperator availability and proximity to the Eastern Management Region (Figure 3.1; Seamans and Rau 2019). During migration, woodcock commonly crossed management region boundaries, therefore our analysis included woodcock that traversed both the Central and Eastern Management Regions during their migrations.

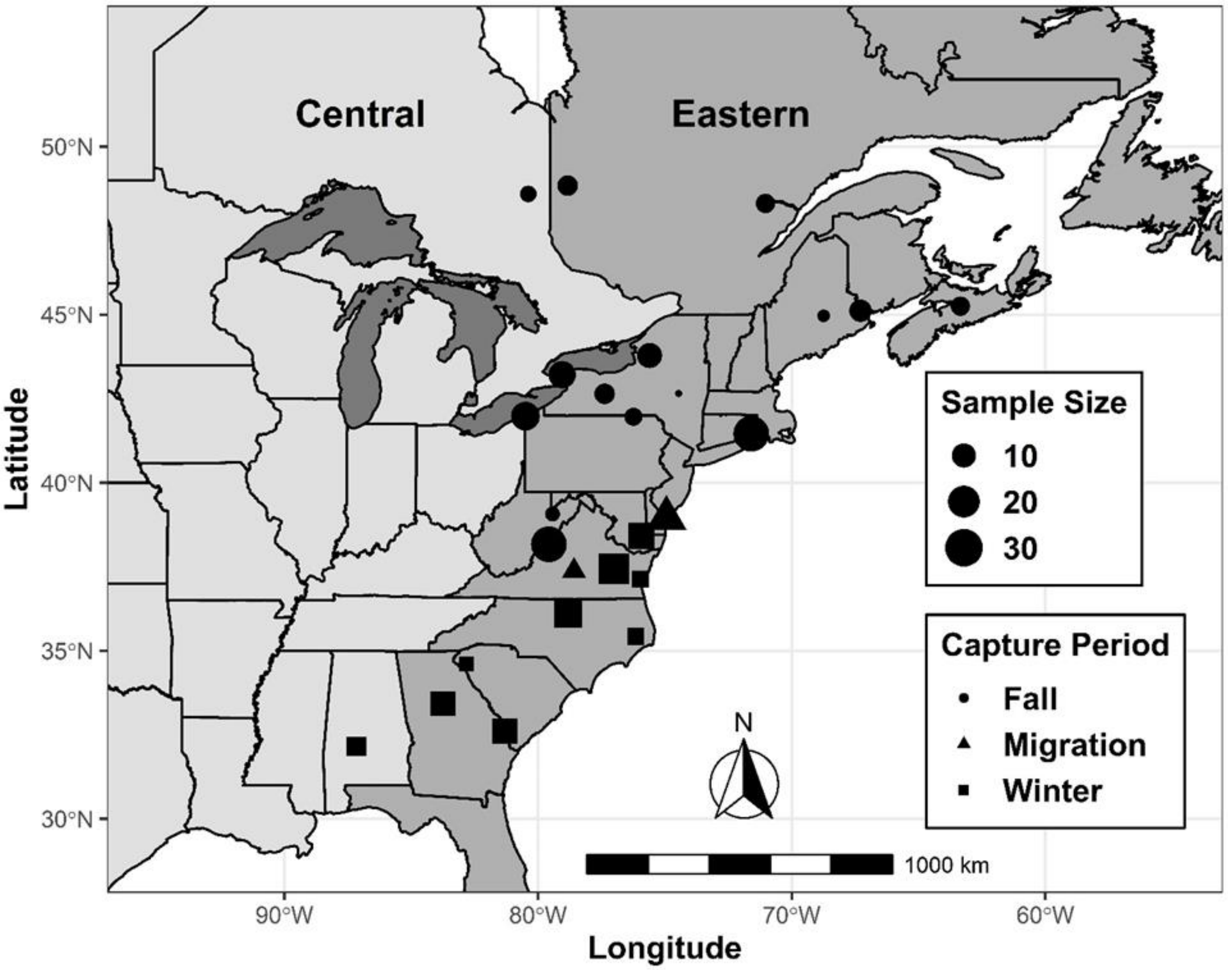

Figure 3.1 Distribution of American Woodcock (*Scolopax minor*) capture sites in the Eastern Management Region (dark gray) and the Central Management Region (light gray) in the United States and Canada. Woodcock were captured October 2017 – March 2020.

Methods

Capture and Marking

We captured the majority of woodcock prior to the onset of migration, between 27 August and 30 October during autumn 2017, 2018, and 2019, and between 3 January and 29 February during winters 2019 and 2020. A small number of individuals were captured during migration between 1 November and 14 December in the fall, and between 14 March and 16 April in the spring. We captured woodcock using mist nets (Sheldon 1960) or spotlights and hand nets (Rieffenberger and Kletzly 1966, McAuley et al. 1993, Moore et al. 2019). Once captured, woodcock were banded, and aged as either adult (after hatch year or after second year; > 1 year old) or young (hatch year or second year; < 1 year old) using a combination of wing plumage, bill length, and mass (Mendall and Aldous 1943, Martin 1964). Woodcock were fit with a rump-mounted Lotek Pinpoint GPS transmitter (model 75, or 120; Lotek Wireless INC., Newmarket, Ontario, CA) enabled with a Platform Transmitter Terminal (PTT). The PTT facilitated remote location uploads from the transmitter using the ARGOS satellite network. Transmitter with leg-loop harness weight did not exceed 4% of an individual's body mass, and in general comprised 3.06 ± 0.44% body mass (mean ± SD) for PinPoint 75, and 3.68 ± 0.25% for the PinPoint 120 models (Chapter 1). All capture and marking procedures were approved by the University of Maine Institutional Animal Care and Use Committee (protocol A2017-05-02).

Location Collection

PinPoint transmitters collected GPS locations at pre-programmed intervals and periodically uploaded locations to a central database using the ARGOS satellite system. Transmitters were programmed using LOTEK PinPoint Host Software (LOTEK Wireless Inc., Newmarket, Ontario, CA), and we stored all locations on Movebank (Kranstauber et al. 2011). Locations were collected an average of once every 1.74 days, with more frequent collection during peak migration (Chapter 1). The transmission process required the transmitter antenna to be elevated above the ground, therefore we stopped receiving locations due to either dropped transmitters or mortalities, resulting in signal attenuation, or if the transmitter otherwise failed. Thus, location data obtained from the GPS transmitters were equivalent to live encounter data, such as is typically obtained from studies of animal mark-recapture (Sandercock 2006).

Transmitter Lifespan and Retention

In order to apply the live encounter data from our GPS transmitters to a survival analysis, we had to first address two assumptions: that transmitters were retained throughout the study period and that the transmitter battery were functional and continually uploading data. Failure to address these assumptions could result in non-detections (i.e., locations stopped uploading to the database), thereby produce patterns in the encounter history that would be similar to permanent emigration in a standard mark-recapture dataset (e.g., Lindberg et al. 2001). We began assessing transmitter retention by reviewing all re-encounters of marked birds (recaptures and reported hunter harvest) between April 2018 to January 2021. Evaluating transmitter retention was important because live-encounter analysis assumed no tag loss and the transmitters could not indicate mortality. Both mortality events and dropped transmitters resulted in the termination of location transmission, leading to similar patterns in the encounter history. If rates of tag loss are high, failure to account for transmitter retention would thus biased survival estimates, because the probability of tag loss cannot be disentangled from that of mortality. We documented 22 re-encounters (e.g., recaptures, hunter harvest) of marked woodcock, with only two individuals dropping their transmitter prior to recovery. In both cases, woodcock retained their transmitters (based on data transmissions) for at least 114 days (6 October to 27 January; 102 locations collected) and 173 days (3 September to 22 February; 38 locations collected) following capture. For woodcock with retained transmitters (n = 20), birds were re-encountered on average 155 ± 168 days (mean ± SD; min = 2, max = 616) post-capture. We concluded that transmitter retention was high during migratory periods immediately following capture, and that tag retention during the period for which our survival analysis was constrained (described further below) was essentially 100%. This was consistent with other studies of tag retention in shorebirds using similar rump-mounted harnesses (Mong and Sandercock 2007), and thus we assumed inherently that our survival estimates were unbiased by tag loss.

We then assessed battery lifespan of the transmitters to ensure we did not under-estimate true survival. In particular we were concerned about biasing assessments of seasonality, given woodcock were generally captured pre-migration, and battery failure was more likely towards the end of the migratory periods. To assess the lifespan of transmitter batteries, we first fit our live encounter data using a Cormack-Jolly-Seber live-encounter analysis implemented in RMark (Laake, 2013) to assess apparent survival as a function of time since capture. We only included woodcock captured prior to migration initiation in the fall (e.g., Maine, New York, Ontario, Pennsylvania, Quebec, Rhode Island, Virginia, West Virginia) or spring (e.g., Alabama, Georgia, Maryland, North Carolina, South Carolina, Virginia), and woodcock captured during migration or in a previous season were removed from the Cormack-Jolly-Seber analysis.

We built a weekly encounter history for each woodcock, where the first interval was the initial week post-capture for every individual, and the history reflected time since capture, in weeks (Blomberg et al. 2018). We subset the data and ran separate analyses for each combination of season (fall or spring), transmitter model (PinPoint 75, PinPoint 120), and programming schedule (frequent, infrequent, hybrid; Chapter 1), as any of these factors potentially influenced battery lifespan. We constructed a single model for each data subset where both survival (Φ) and detection (p) components varied independently during each time interval. The small sample sizes for some transmitter-schedule combinations resulted in parameter estimates that failed to converge, so we combined all transmitters into either spring or fall categories for the evaluation. Additionally, we included all schedules and seasons in Appendix E for further reference. Based on a visual observation of the resulting parameter estimates, we observed a drop in apparent survival around week 14 for all data subsets, and we also began observing non-convergence in parameter estimates immediately following week 14 (Figure 3.2). Constancy of survival estimates prior to week 14 indicated that any transmitter failure was minimal, and likely occurred at random, whereas following week 14, post-capture battery failure was likely to confound survival estimation. The transmitter model, program schedule, and season did not appear to influence this cutoff point (Figure 2). We therefore censored all encounter histories in subsequent analysis such that only data during the first 14 weeks of transmitter deployment were included for each bird, effectively removing the confounding variation associated with battery failure from the analysis.

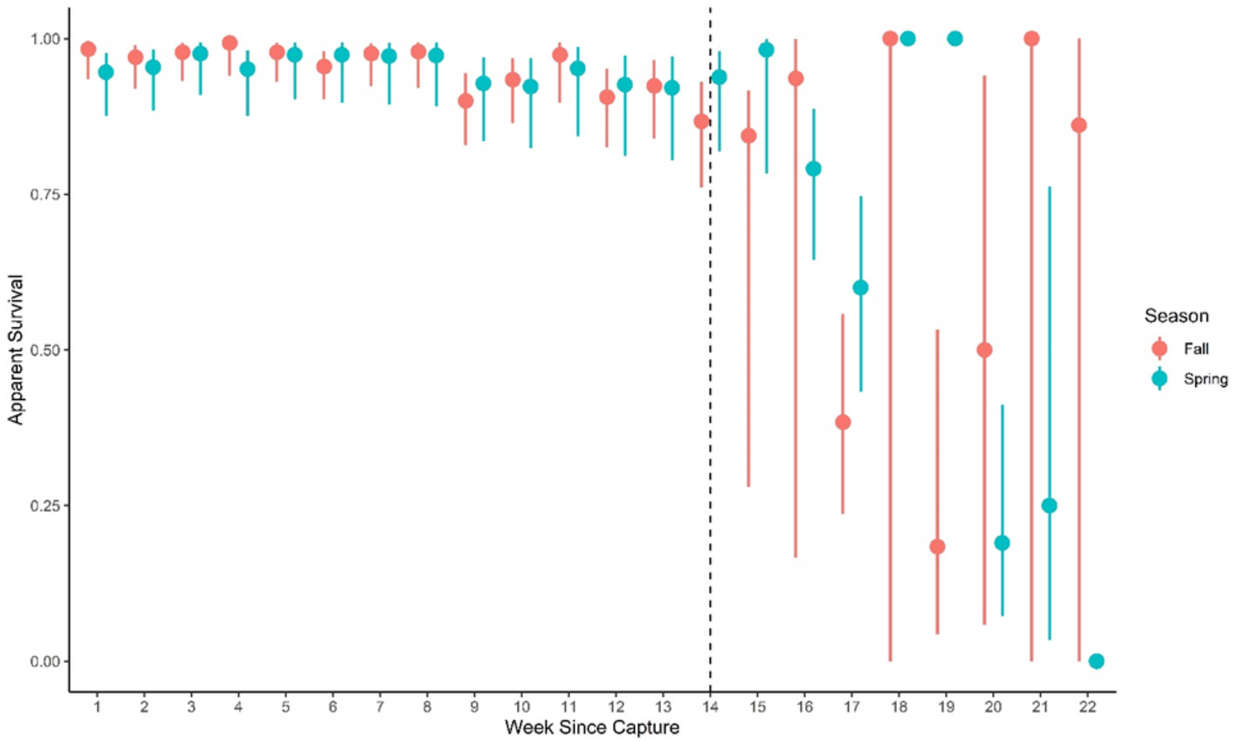

Figure 3.2 Weekly apparent survival of American Woodcock (*Scolopax minor*) during the fall and spring after marking. The parameter estimates and confidence intervals failed to converge after week 14.

Movement Modeling

We used Multivariate Hidden Markov Models (MHMM), implemented with the momentuHMM package (McClintock and Michelot 2018) in program R (R version 3.6.3, www.r-project.org, accessed 1 Dec 2020) to identify movement states related to migratory behaviors for each individual, as described in Chapter 1. We extracted woodcock locations from Movebank collected in spring (15 January to 18 June) and fall (1 October to 14 January) and assigned migratory movements following the model and procedures outlined in Chapter 1. During spring migration, there was uncertainty in the specific movement state assigned to locations after 1 April due to increased breeding activity. Females began initiating nests and often migrated between multiple nesting locations (Colby Slezak, University of Rhode Island, unpublished data). Therefore, all spring locations occurring after 1 April were aggregated within the post-migration movement state, and included both woodcock that had entered post-migration prior to 1 April, and all migratory states after 1 April. Hence, post-migration survival estimates prior to 1 April reflected only birds that had entered post-migration, whereas all estimates after 1 April included a combination of remnant migrants and early breeding birds.

For our analysis, we needed to condense movement state assignments to a weekly movement state for each individual. We used the lubridate package (Grolemund and Wickham 2011) to designate an ordinal week for each location, and combined all observations from each individual during each week to a single movement state. When a movement state transition occurred mid-week (i.e., pre-migration to migration or migration to post-migration), we used the migration movement state as the default assignment, since the individual had entering or exited migration during that week. Survival for the migratory movement state therefore reflected the probability of survival given that a woodcock was actively migrating during a given 1-week period. This also ensured that all woodcock which migrated spent at least one week in the migratory movement state prior to entering post-migration.

Survival Modeling

We estimated survival of woodcock during migratory periods, and evaluated how survival varied spatially and among age and sex classes, using multistate models implemented in RMARK (Laake, 2013). Multistate models estimate three parameters; survival (Φ), transition probability between pre-defined states (Ψ), and detection probability (p). We constructed a base model in which Φ was independent for each movement state with a state-specific linear time trend. Including the time trend enabled us to evaluate how weekly survival changed within each migratory state, and to compare how temporal variation in survival differed among states. If a specific movement state was not observed during a given time interval, we fixed the survival parameter to 1.0 for that interval, which assisted with estimation. For the Φ component, we initially built models that varied by movement state with independent estimates for each time interval; however, these parameter estimates often failed to converge, so we removed the time structure from the transition probabilities. Because our detection rates were high (typically $p > 0.95$) and Ψ were estimated independently as part of the HMM analysis, we assume there was relatively little unexplained variance in Ψ, such that an assumed mean value for Ψ would have little effect on estimates of Φ. We fixed any impossible Ψ (i.e., migration to pre-migration, post-migration to pre-migration, post-migration to migration) to zero, and we also fixed possible Ψ to zero during time intervals when we knew no transitions occurred (e.g., transition from pre-migration to migration following the last known initiation attempt). Finally, for the p component of the model, we explored models with p being dependent on the movement state and independent for each interval, but parameters in these models often failed to converge. Because detection probability was high and appeared relatively constant, we instead used a null structure on the p component of all models. We also fixed the detection parameters to 1.0 for any interval where the survival estimates were fixed to one.

After the base model was built, we evaluated how survival varied among age and sex classes, as well as based on breeding or wintering latitude or longitude. Woodcock at higher latitudes initiate and terminate migration before woodcock at lower latitudes (Chapter 1). Similarly, adult woodcock migrated prior to young birds, and adult females progress through migration earlier than all other age-sex classes (Chapter 1). These differences may be partially due to differences in how woodcock respond to environmental cues, with adults being more likely to migrate with tailwinds and young woodcock responding to lower temperatures (Chapter 2) and conceptually these differences may influence survival during migration. To compare survival between age and sex classes, we created a combined age and sex variable, so that survival was estimated independently for each age-sex class (i.e., adult females, young females, adult males, and young males). If a model’s coefficient for one age-sex class had 95% confidence intervals that did not overlap zero, we further explored age- or sex-specific models as a post hoc assessment. We further explored interactions between movement states and the four age-sex classes to test whether a given age or sex class had greater mortality risk during a particular stage of migration. Finally, we explored how pre-migration location (latitude and longitude), influenced survival.

We added additive effects of both starting latitude and starting longitude, their interaction, and interactions between latitude and movement state, to evaluate if survival varied spatially.

We used Akaike's Information Criterion corrected for small sample size (AIC_c) to rank models and select inference models. We constructed six a priori models based on the procedures outlined above, and selected the model with the lowest AIC_c score that contained no parameter(s) with 95% confidence intervals that overlapped zero as the most parsimonious model. We considered models within 2.0 AIC_c units, for every additional model parameter, of the top model competitive. Using the survival estimates from the best-supported spring and fall models, we calculated the cumulative period-specific survival for each migratory state. We ended spring migration on 31 May because most male woodcock had completed migration by this date (Erik Blomberg, The University of Maine, unpublished data). For each movement state, we determined which time intervals had > 50% of available individuals in the migratory state, and took the product of the interval-specific survival estimates within that date range to generate a cumulative survival probability for each state. This allowed us to generate a state-specific survival estimate that reflected both the relative weekly survival probability and the length of time on average woodcock spent in a particular movement state, which we could then compare between seasons and among movement states. We used the delta method in the emdbook package (Bolker et al. 2020) to calculate standard errors associated with each cumulative estimate, and we used the estimates and their error structure to compare survival within and between seasons.

Results

One-hundred twenty-nine woodcock (40 adult females, 28 young females, 30 adult males, and 31 young males) were included in the fall survival analysis. The model with an interaction between starting latitude and starting longitude failed to converge and was removed from the analysis. The base model (Φ(stratum*Time)Ψ(stratum)p(.)) received the most support, and all covariate parameters in lower ranked models had 95% confidence intervals that overlapped zero (Table 3.1). We did not find support for differences in survival among age-sex classes, or based on migration initiation latitude and longitude. The pre-migration and migration movement states had a negative survival trend through time, while post-migration had a positive survival trend (Figure 3.3). During pre-migration, weekly survival began at a maximum value of 0.99 ± 0.01 (Φ ± SE) in the first week of October, and decline to a value of 0.85 ± 0.11 by the first week of January. Migrating woodcock experienced a similar decline in weekly survival rates with a weekly survival rate of 1.00 ± 0.00 during the first week of October, and a decline to a value of 0.92 ± 0.05 by the first week of January. Woodcock in post-migration experienced an increase in survival with a minimum value of 0.90 ± 0.07 during the third week of November, and increasing to 0.95 ± 0.02 during the first week of January.

Table 3.1 Multistate models and model selection results used to describe survival patterns for American Woodcock during fall migratory period (1 October – 14 January, 2017 - 2020) in eastern North America.

Survival Model	**K^{a}**	**Delta AIC$_{c}$**	**Weight**
base^{b}	9	0.00^{c}	0.75
base + start.lat^{d} + start.lon^{e}	11	3.60	0.12
base + agesex	12	4.34	0.09
base + stratum×start.lat + start.lon	13	7.20	0.02
base + start.lat + start.lon + agesex	14	7.70	0.02
base + stratum×agesex	18	8.73	0.01

[a] number of parameters

[b] base model Φ(stratum×Time)p(~1)Ψ(~stratum)

[c] AIC$_{c}$ = 4368.12

[d] initiation of migration latitude

[e] initiation of migration longitude

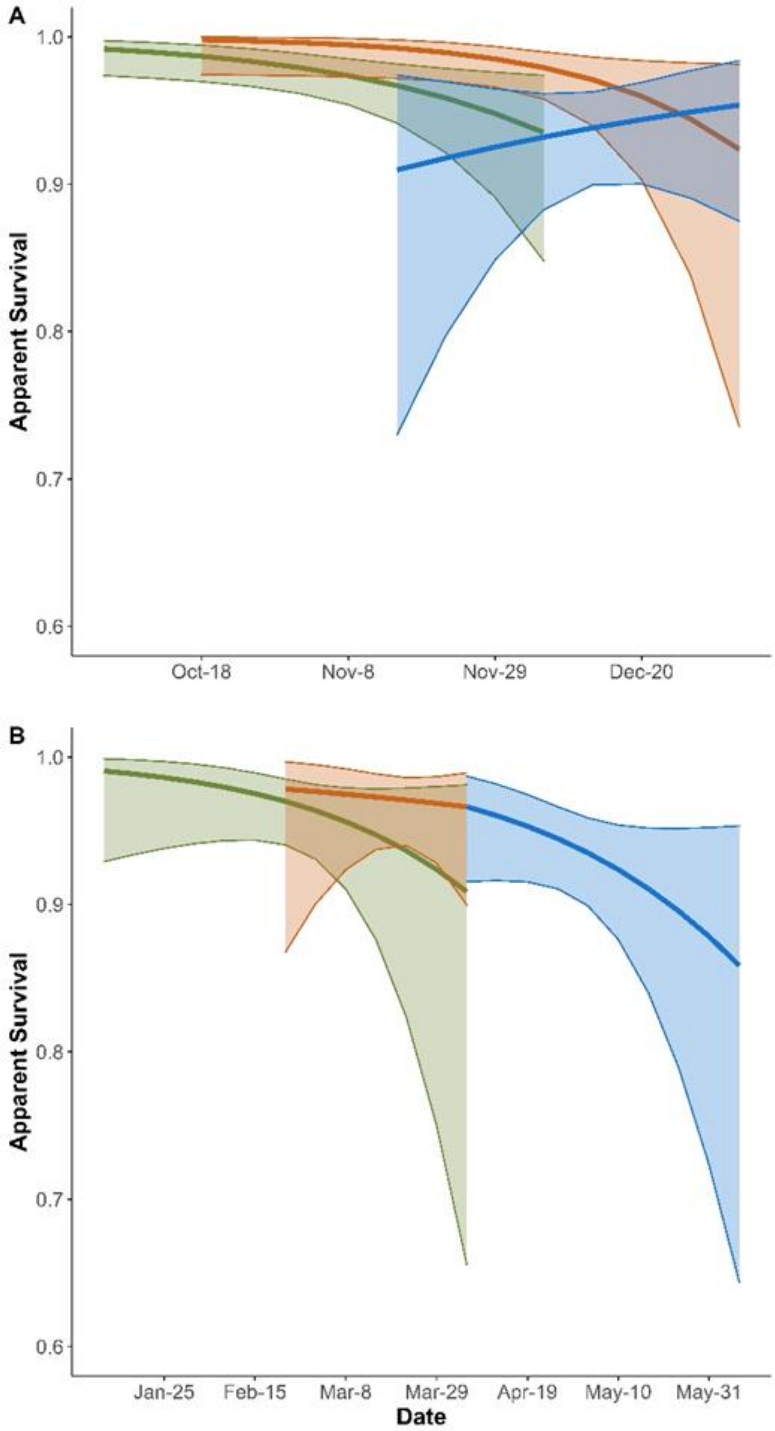

Figure 3.3 Weekly apparent survival estimates for American Woodcock (*Scolopax minor*) captured in eastern North America 2017-2020 during fall (A; 1 October to 14 January, 2017 - 2020) and spring (B; 15 January to 18 June, 2019 - 2020) migratory periods. Woodcock transitioned between pre-migration (green), migration (orange) and post-migration (blue) movement states. Only weekly intervals with at least 5 individuals recorded in each movement state are displayed.

One-hundred and seven woodcock (21 adult female, 33 young female, 20 adult male, and 33 young male) were included in the spring survival analysis. The model with an interaction between starting latitude and starting longitude failed to converge and was not included in the analysis. Additionally, the model with an interaction among movement state and age-sex classes failed to converge, so we ran two additional models with an interaction between the movement state and age or sex independently. Similar to the fall analysis, the base model (Φ(stratum*Time)Ψ(stratum)p(.)) received the most support, and all covariate model parameters had confidence intervals that overlapped zero (Table 3.2). We did not find any support for differences in survival among age or sex classes, or based on migration initiation latitude and longitude. All three movement states had a negative survival trend through time (Figure 3.3). During pre-migration, weekly survival was a maximum value of 0.99 ± 0.01 during the second week of January, and declined to a rate of 0.91 ± 0.07 by the last week of March. Woodcock in migration experienced a maximum survival rate of 0.98 ± 0.02 during the second week of February, and declined to a value of 0.97 ± 0.02 by the last week of March. During post-migration, weekly survival reached a maximum of 0.99 ± 0.01 during the fourth week of February, and declined to a minimum of 0.86 ± 0.07 by the second week of June.

Table 3.2 Multistate models and model selection results used to describe survival patterns for American Woodcock during spring migratory period (15 January – 18 June, 2019 - 2020) in eastern North America.

Survival Model	**K**[a]	**Delta AIC_c**	**Weight**
base[b]	9	0.00[c]	0.41
base + stratum$^{\times}$sex	12	1.87	0.16
base + stratum$^{\times}$start.lon[d] + start.lat[e]	13	2.56	0.12
base + stratum$^{\times}$start.lat + start.lon	13	3.12	0.09
base + agesex	12	3.41	0.08
base + stratum$^{\times}$age	12	3.42	0.07
base + start.lat + start.lon	11	3.84	0.06
base + start.lat + start.lon + agesex	13	7.38	0.01

[a] number of parameters

[b] base model S(stratum * Time)p(~1)Psi(~stratum)

[c] AIC_c = 15117.89

[d] initiation of migration latitude

[e] initiation of migration longitude

Period-specific apparent survival estimates for all three movement states in the spring were lower than for the fall (Figure 3.4). Within seasons, survival was generally greatest during migration (fall 0.95 ± 0.01, spring 0.88 ± 0.04), lowest post-migration (fall 0.80 ± 0.06, spring 0.52 ± 0.09), and at moderate levels pre-migration (fall 0.91 ± 0.03, spring 0.81 ± 0.07). For the fall estimates, pre-migration included six weeks, migration four, and post-migration four, as compared to spring when pre-migration included nine weeks, migration four, and post-migration seven, as these were when the majority of birds were in the movement state (Table 3.3).

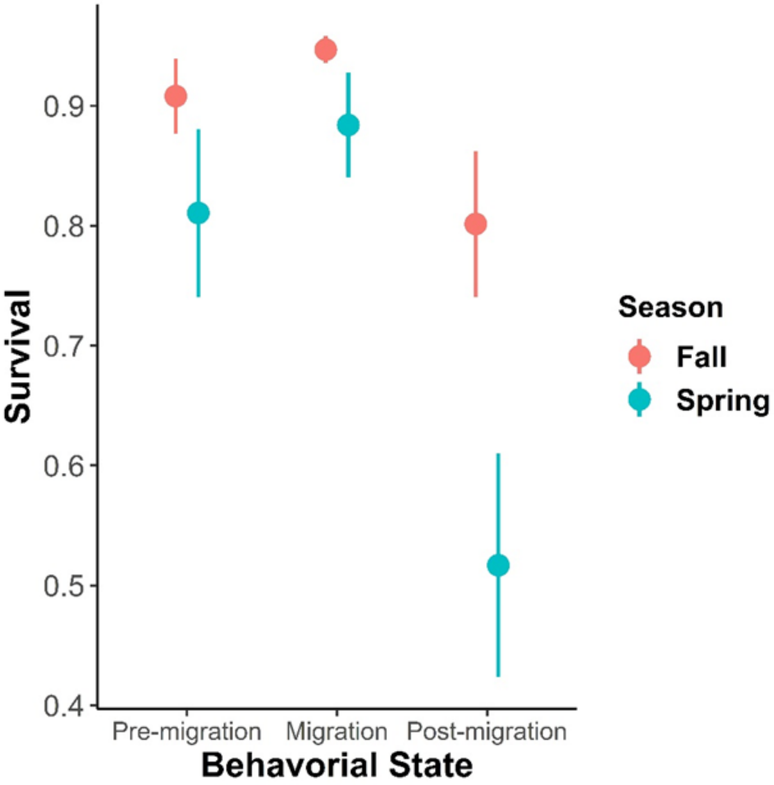

Figure 3.4 Movement-state-specific apparent survival estimates for American Woodcock (*Scolopax minor*) monitored during fall and spring migratory periods, 2017 - 2020. Estimates were cumulative across the weeks in which > 50% of available birds were in each movement state; six weeks for fall pre-migration, four for fall migration, four for fall post-migration, nine weeks for spring pre-migration, four for spring migration, and seven for spring post-migration.

Table 3.3 Number of American woodcock (*Scolopax minor*) included in the survival modeling for each time step. Weeks represents the first date associated with each time step. Woodcock were monitored between falls 2017-2019 and springs 2019-2020.

	Week	**Pre-migration**	**Migration**	**Post-migration**
Fall				
	1-Oct	58	2	0
	8-Oct	58	2	0
	15-Oct	75	6	0
	22-Oct	76	19	0
	29-Oct	73	33	0
	5-Nov	70	49	0
	12-Nov	45	72	1
	19-Nov	24	73	17
	26-Nov	19	63	31
	3-Dec	6	64	40
	10-Dec	5	49	49
	17-Dec	2	35	52
	24-Dec	2	20	54
	31-Dec	2	11	50
	7-Jan	2	6	31
Spring				
	13-Jan	8	0	0
	20-Jan	33	0	0
	27-Jan	32	0	0
	3-Feb	35	2	0
	10-Feb	37	6	0
	17-Feb	42	9	1
	24-Feb	46	17	1
	3-Mar	46	29	1
	10-Mar	34	46	2
	17-Mar	13	55	1
	24-Mar	9	54	5
	31-Mar	5	51	11
	7-Apr	-	-	64
	14-Apr	-	-	58
	21-Apr	-	-	56
	28-Apr	-	-	54
	5-May	-	-	42
	12-May	-	-	35
	19-May	-	-	30
	26-May	-	-	21

Table 3.3 continued.

2-Jun	-	-	7

Discussion

Our findings indicate that woodcock survival varied between spring and fall seasons, and among movement states within migratory periods. We also found support for previous research suggesting lower survival rates for woodcock on the wintering grounds (Longcore et al. 1996, 2000; Krementz and Berdeen 1997, Pace 2000, McAuley et al. 2005, Bruggink et al. 2013), although survival was lowest during the end of spring migration and coincident with the onset of breeding. We were able to fill gaps on previous survival research by including periods of migration. Generally, weekly survival rates declined the later an individual remained in a particular movement state, and individuals that transitioned between movement states experienced differing mortality risk depending on the timing of the transition.

We found that the timing of transition between movement states had consequences for individual woodcock by resulting in lower survival. For example, woodcock that transitioned from migration to post-migration early in the fall experienced lower survival, suggesting that early transitions may have been maladaptive. Similarly, birds that appeared to delay the onset of migration experienced decreasing weekly survival through time. This may be due, in part, to a tendency of migratory birds in poor body condition to delay migratory departures (Cooper et al. 2015) as they attempt to improve their condition. Our finding of low survival for individuals with relatively late migration departures may therefore reflect an increasing pool of remaining individuals with poorer body condition, that experience lower survival as a result (Owen and Black 1989, Guy Morrison et al. 2007, Cooper et al. 2015). Additionally, during fall migration later-departing, poor-condition individuals may be more likely exposed to cold fronts and the associated freezing of soil (Salewski et al. 2013, Acker et al. 2021), which is often associated with woodcock mortality (Rice et al. 2000), and may compound issues associated with poor body condition.

Woodcock generally experienced the highest weekly survival while in the migratory state during both spring and fall. However, woodcock that transitioned from migration to post-migration early in the fall had lower weekly survival compared to those that transitioned later in the migratory period. It is possible that individuals that transitioned into post-migration early did so by terminating migration outside of the core wintering range (Chapter 2) and may have died as a result of being exposed to more harsh northerly conditions (Rice et al. 2000). Our findings support the idea that the timing of transitions into and out of migration (e.g., initiation or termination), contributes to the survival experienced during migratory periods (Rotics et al. 2021). While some individuals certainly experienced mortality during migration (Klaassen et al. 2014, Buechley et al. 2021), the act of initiating or terminating migration may be of greater importance when attempting to understand where mortality occurs during migratory periods.

Survival during the fall migratory period was higher than during spring. While the spring migratory period was generally longer than the fall overall (22 weeks vs. 14 weeks, respectively), the cumulative survival estimates for migration during both seasons were based on four weeks, and indicated a 0.07 lower survival in the spring (Figure 4). While there is some support for spring migration being a period of lower survival in some species (e.g., wood thrush (*Hylocichla mustelina*); Rushing et al. 2017) there is also support for lower survival during fall in others (e.g., White stork (*Ciconia ciconia*); Cheng et al. 2019). Woodcock, like other medium-distance migrant species, tend to progress through spring migration and arrive on the wintering grounds earlier than long-distance migrants (Butler 2003). This tendency may expose earlier migrants to harsh environmental conditions and contribute to higher mortality during spring migration (Newton 2007). Furthermore, we had a limited ability to disentangle how breeding activities (e.g., displaying males, or nesting) may have affected survival in the spring post-migration, because of the inclusiveness of the movement state post 1 April. Additional investigation into the specific causes of spring mortality would assist in creating targeted conservation actions.

Our findings provide further support for a lack of age- or sex-specific survival differences for woodcock during the fall migratory period and while overwintering (Krementz and Berdeen 1997, Pace 2000, McAuley et al. 2005, Bruggink et al. 2013). For many species of migratory birds, young birds completing their first migration have lower survival than adults (Owen and Black 1989, Cheng et al. 2019), which has been partially attributed to the difficulty in navigating inhospitable regions (e.g., water bodies or deserts; Klassen et al. 2014, Buechley et al. 2021) or delaying migration to improve condition (Cooper et al. 2015, Rotics et al. 2021). While migrating woodcock in Eastern North America may attempt overwater crossings (e.g., Gulf of Maine, Delaware Bay, Chesapeake Bay), these crossings are likely only attempted by a subset of individuals. Hence, higher young bird mortality while crossing inhospitable regions may not be an important source of mortality for woodcock. Similar to woodcock, adult and young barn swallows exhibited comparable survival rates during the non-breeding season, so age-specific survival patterns during migration may vary depending on a species' natural history (Grüebler et al. 2014). During spring migration, we expected lower survival for male and young woodcock because males initiated spring migration six days prior to females (Chapter 1) and young woodcock migrated farther than adults (Chapter 2). Conceivably, early arriving birds, and individuals farther north, are more likely to encounter cold fronts and be subject to weather related mortality (Newton 2007, Salewski et al. 2013). However, our findings indicate that even with variation in migration timing and pace, woodcock age and sex classes experienced similar rates of mortality.

There was no effect of starting latitude and longitude on survival. We captured and monitored woodcock from across the breeding and wintering ranges in the Eastern Management Region, and considered our sample to be representative of the population at large. Conceptually, woodcock originating from higher latitudes spend more time migrating and potentially experience greater mortality risk compared to woodcock breeding near the southern range extent, which could conceivably complete migration in as short as a single flight. Our results indicating relatively high survival in the migratory movement state further support the idea that lower survival during stationary periods may influence woodcock populations (Krementz et al. 1994a, Krementz and Berdeen 1997). It is also possible that more complex spatial-mortality patterns are present in the data, with mortality hotspots operating at regional scales not reflected in starting latitude or longitude per se (McAuley et al. 2005, Bruggink et al. 2013). We suggest further investigation into the spatial-temporal survival relationship for woodcock throughout their annual cycle, across the species distribution.

One woodcock mortality factor could have been hunting, which occurs throughout the species' range, and differential harvest risk could result in time periods or regions with lower survival. Throughout the study area, the hunting season runs from September until the end of January, although the exact starting and ending dates vary between provinces and states (Chapter 1). Conceivably, an individual woodcock could be harvested during any fall migratory period, or just prior to spring migration, until 31 January throughout our study area. Only 2.3% of our marked woodcock (3 of 129 fall birds) were harvested with active transmitters, all during fall pre-migration (harvested October 2 to October 29), and no individuals with active transmitters were harvested during other movement states (e.g., migration or post-migration). These three individuals were harvested in Southern New England (New York, Pennsylvania, and Rhode Island), but with such a limited sample size we were unable to discern a spatial pattern related to harvest. Nevertheless these results indicate that hunter-harvest was not a substantial source of mortality for woodcock during the migratory period, suggesting most mortality occurs from sources other than hunting (McAuley et al. 2005, Bruggink et al. 2013).

The live-encounter approach we used lacked some precision in determining the timing and location of non-hunting related mortality, as our GPS tags only provided data on the last known live location. This may have produced some inherent uncertainty in state transitions; for example, if a woodcock transitioned between migratory states and died prior to uploading locations, the mortality was likely attributed to the previous migratory state. While the models inherently accounted for some of this uncertainty through the probabilistic nature of the state transitions, they may not have accounted for it fully. So, the decline in weekly survival for most migratory states may partially reflect the mortality of birds immediately following transitioning into the next movement state. For example, if woodcock experienced mortality upon their initial migratory departure but failed to upload a location from a stopover site, the mortality events would appear to have occurred at the end of pre-migration when in fact it occurred in the migratory movement state. Nonetheless, the change in survival associated with migration initiation indicates a certain level of risk and demonstrates how initiation decisions could still be an important source or mortality. Similarly, woodcock that terminated fall migration earlier in the season had lower survival than those that terminated later, possibly due to misclassification of the bird's last stopover as post-migration. However, on average, woodcock stopped uploading locations 37 ± 16 SD (min = 3, max = 66) days after transitioning into the post-migration state, and only 2 woodcock disappeared from the encounter history within 1 week of their transition to post-migration. Based on this evidence, we assume that relatively few stopovers were misclassified as post-migration locations.

None of the covariates we explored explained more of the variation than our base inference model, suggesting little variability in woodcock survival beyond that associated with the timing of migration and transitions among migratory states. It is possible that other unmeasured individual characteristics would better explain individual survival. For example, white storks that exhibited higher activity profiles or that selected particular stopover sites, had higher survival than conspecifics (Schaub et al. 2005, Rotics et al. 2021). Hence, individual variation or decisions making during migration can similarly impact an individual's survival. We were able to analyze satellite transmitter data in a live-encounter format, providing an analytical approach to estimating survival of GPS-marked birds during the migratory period. While there are inherent assumptions and limitations with this approach, it generates survival estimates based on data collected during migration, rather than relying on data collected during stationary periods (Sillett and Holmes 2002). Our approach further allowed us to generate survival estimates during discrete migratory movement stages, and to identify periods of survival (i.e., overwintering, and late spring) that can be targeted by management or conservation actions.

Management Implications

For woodcock, survival was lowest during pre- and post-migration states and highest while migrating, with some evidence of greater mortality at transition points both pre- and post-migration. Survival during spring migration was lower than the fall, especially during the post-migration state as woodcock began breeding activities. While the woodcock breeding range overlaps almost completely with the species' wintering range (McAuley et al. 2020), best management practices for woodcock may support both stationary and migrating individuals, however further investigation is necessary. Land managers should focus habitat management efforts on areas woodcock used during spring-post-migration (after 1 April), due to its low period-specific survival. The spring post-migration movement state included breeding individuals and we believe additional investigation into habitat relationships during the onset of breeding is necessary for targeted habitat management. Lastly, hunting related morality did not appear to be a significant source of mortality for woodcock during the migratory period, which is consistent with generally low harvest rate estimates for the species (McAuley et al. 2005, Bruggink et al. 2013). Even in the presence of harvest mortality, survival during the fall was much greater than the spring, reinforcing the need for management to target habitat used by woodcock during spring migration and their initial breeding period. Managers may consider changes to the current management framework to increase hunting opportunity and should expect only a nominal decrease in annual survival rates (McAuley et al. 2005, Bruggink et al. 2013).

CHAPTER 4

AN EXPERIMENTAL ASSESSMENT OF DORSALLY-MOUNTED TAG RETENTION USING MULTIPLE ATTACHMENT METHODS FOR SMALL TO MEDIUM-BODIED BIRDS

Abstract

Tracking devices are integral to understanding how free-ranging birds move and survive in space and time, and, as tags become smaller, they have become increasingly valuable for tracking the movements of small- and medium-bodied birds. Retention of these tracking devices (tags) is imperfect, with some amount of tag loss expected. Yet little comparison exists to evaluate how different attachment methods influence the rate of tag retention. Our goal was to experimentally evaluate how retention of dorsally-mounted tags varied with different attachment methods, primary using differing styles of leg-loop harnesses or glue, which varied by species and the type of tag. We identified three transmitter models used to track small- and medium-bodied birds, used a 3D printer to create replicate tags, and attached them to three model species, including 121 rock pigeons (*Columba livia*), 28 European starlings (*Sturnus vulgaris*), and 82 house sparrows (*Passer domesticus*). We attempted to resight birds twice per week, identified birds based on a unique set of colored leg bands, and recorded tag presence or absence. We used Multistate models in rMark to evaluate if attachment method influenced weekly retention rates, and calculated tag retention through time. Differences in leg-loop harness style did not influence tag retention in pigeons, whereas for sparrows a Rappole and Tipton figure-8 style harness had the lowest weekly tag loss (0.01) and a weak-link style harness the highest rate of loss (0.22). Glue-on tags, which are commonly assumed to have high loss rates, were lost at lower rates (0.12) than the weak-link harness, and we attribute this to deploying glue-on tags on sparrows soon after they completed their prebasic molt (October-December). Tag retention often varied by species, but attachment method influenced tag retention in house sparrows only. We recommend the Rappole and Tipton method when attaching tags that require long retention time, whereas the weak-link harness is more suitable for

shorter-term attachment periods where subsequent tag loss is desirable. We provide recommendations for selecting attachment method in relation to various data collection intervals, as well as insight into how molt cycles and species-specific effects may influence tag retention in small- and medium-bodied birds.

Introduction

Tracking individuals in space and time is fundamental to understanding the basic ecology for many species of birds (Egevang et al. 2010). Animal transmitter technology has vastly improved over the past few decades; for example, transmitters or location loggers have decreased substantially in size and weight, thereby enabling tracking of small- and medium-bodied animals, such as passerine birds (Schmaljohann et al. 2012). Individuals that undertake long-distance movements while foraging, ranging, or during seasonal migration (Pollet et al. 2014) are of particular interest, as there has been a limited ability to track birds across long distances. Tracking birds during these periods has facilitated novel understanding into avian life cycles, and has helped identify regions of high conservation concern (Kramer et al. 2018).

We expect there to be continued use of small tracking devices to support the conservation and management of passerine birds, however, tag retention is typically imperfect, and not all tags deployed on birds are expected to be retained for the lifespan of the tag (Schmaljohann et al. 2012, Pollet et al. 2014). Premature tag loss may reduce the amount of data collected or can result in complete data loss as in the case of archival tags (Pollet et al. 2014). Researchers may account for imperfect tag retention by marking additional individuals to ensure minimum samples sizes are obtained, but this may not be feasible due to logistic constraints or when working with small populations. Hence, minimizing tag loss to maximize data collection during focal periods is generally necessary, and maximizes the amount of data collected for the fewest number of individuals marked.

Attachment methods may be designed for tags to be dropped shortly after termination of data collection, in order to reduce long-term physical effects from extended tag retention (Mong and Sandercock 2007, Arlt et al. 2013). Optimizing tag retention to complement study objectives is only possible given a strong understanding of the factors influencing retention. Further complicating is that some tags must remain on an individual for an entire year or greater (Larkin et al. 2017, Witynski and Bonter 2018, Kramer et al. 2018), while others are expected to only remain attached for a few weeks or months (Hansbauer and Pimentel 2008, Kesler 2011, Diemer et al. 2014, Stanton et al. 2018). Physically recapturing birds to remove tags may not be feasible, especially when birds move over long distances, exhibit low site fidelity, or reside in inaccessible areas. Hence developing attachment methods that optimize tag retention for the data collection period requires developing recommendations for a variety of retention scenarios.

There are few resources available comparing retention rates among attachment methodss and species within a single study system, which makes it challenging to identify an attachment method that is most likely to maximize data collection while minimizing the amount of time individuals need to carry a tag post-data collection. Our goal was to understand patterns of tag retention and identify factors that influence tag loss for a variety of tag types and species. We identified harness or attachment styles commonly used to affix dorsal-mounted style tags to small- and medium-bodied birds, and evaluated their retention rates under an experimental design. Assuming that tag retention is imperfect, our objectives were to 1) quantify and understand weekly and cumulative tag loss, 2) compare retention rates among attachment methods and species, and 3) use these results to provide attachment recommendations for future work with small- and medium- bodied birds.

Methods

Study Site

We worked at the University of Maine's J. Franklin Witter Teaching and Research Center in Old Town, ME, USA (44.917351°, -68.664724°), a teaching laboratory that houses a small herd of dairy cows, horses, and sheep. The Witter Center's farm hosted both resident and transient populations of rock pigeons (*Columba livia*), European starlings (*Sturnus vulgaris*), and house sparrows (*Passer domesticus*). Transient individuals typically commuted between the farm and the neighboring communities of Old Town and Orono, ME, whereas resident birds rarely, if ever, left the farm and were available continually throughout the study period. Individuals were likely attracted to the farm to forage on animal feed. Generally, birds using the center increased in abundance throughout late summer and fall (August to October), reaching highest abundance during winter months (November to April). Bird abundance during the spring and summer (May to July) was generally low, presumably while birds were nesting and natural forage was more abundant.

Transmitter Construction

We based our experimental design on three different tag models previously used to study small- and medium-bodied birds, and were compatible with dorsal-mounted tags attached using either a leg-loop harness, or glue applied to the feathers. The first model was based on Lotek PinPoint 75 (Lotek Wireless INC., Newmarket, Ontario, CA; 5.1 g), which was used to track American Woodcock (*Scolopax minor*) during migratory periods (Table 4.1; Moore et al. 2019). The second model replicated a Very High Frequency (VHF hereafter; 0.55 g) transmitter constructed by Blackburn Custom Transmitters, which is typically used on passerine songbirds (e.g., Bachman's Sparrow [*Peucaea aestivalis*]; Table 4.1; Choi et al. 2021) during residency periods. For the VHF tag, we created one exact replicate tag and one tag that was twice the size of the original tag for use on larger small-bodied birds. The third model was based on Lotek PinPoint 10 archival GPS tags with a VHF tag beacon (Table 4.1; 1.5 g; Wilson 2020). This tag type was only attached using glue with an expected retention time of a few weeks (mean = 12.67; Wilson 2020) because these transmitters must be recovered to retrieve data. We created non-transmitting 3D surrogate models (Chan et al. 2016) of all tag designs using the TinkerCAD (Autodesk Incorporated, San Rafael, California, U.S.A) 3D modeling program, and printed them using a MakerBot 3D printer and MakerBot Polylactic Acid biodegradable thermoplastic (MakerBot Industries, Brooklyn, New York, U.S.A.). We used Loctite ethyl cyanoacrylate glue (Henkel Corporation, Rocky Hill, Connecticut, U.S.A.) to attach 1-2 lengths of plastic-coated braided steel wire (American Fishing Wire Fishing Brands, Coatesville, Pennsylvania, U.S.A.) to each tag to replicate transmitter antenna(s). For the PinPoint 75, we added copper spheres (Daisy Outdoor Products, Rogers, Arkansas, U.S.A.) to the transmitter to provide additional internal weight, so that tags approximated the mass of the original transmitter (5.1 g). The mass for the three remaining replicate tags was slightly less than the originals due to difficulty in adding additional weight. The VHF tags were 0.4 g and 0.9g, and the PinPoint 10 replicates were 0.9 g. All transmitters, except the PinPoint 10 tags, were coated with epoxy (Art 'N Glow, Plano, Texas, U.S.A.) to increase water resistance and prevent biodegradation of the Polylactic Acid biodegradable thermoplastic.

Table 4.1. Three tag retention scenarios used to monitor small- and medium-bodied birds using either GPS or VHF tags.

Tag Function	**Example Tag**	**Species**
Satellite-GPS Tag	Lotek PinPoint 75	Rock Pigeon
VHF Transmitter	Blackburn Custom Transmitters - VHF	House Sparrow and European Starling
Archival GPS	Lotek PinPoint 10	House Sparrow

We identified popular harness designs typically used for each transmitter type, and constructed harnesses accordingly. Leg-loop harnesses were commonly used for the PinPoint 75 and VHF tags, but a glue-on attachment style was used for the PinPoint 10 tags. For the PinPoint 75 replicate tags, we constructed an adjustable harness using a double strand of Stretch Magic Jewelry cord (Pepperell Braiding Company, Pepperell, Massachusetts, U.S.A.), two 10 cm sections of 1/16th inch inside diameter Tygon PVC tubing (Saint-Gobain, Akron, Ohio, U.S.A.) to prevent skin abrasion (Moore 2016), and two 2x2 mm metal crimps (The BeadSmith, Carteret, New Jersey, U.S.A.; Figure 4.1). We used three different methods for the harness knot, where the running end of the string was fed through either a single-loop, a double-loop, or was attached to a metal reinforced loop (Figure 4.2). For the VHF replicates, we used elastic thread (ZealorDirect, Shenzhen City, Guangdong Province, China) to construct one of four harness designs; a Rappole and Tipton figure-8 harness (Rappole and Tipton 1991), a weak-link harness (Kesler 2011), a modified weak-link design but without the break-away strand (Lislevand and Hahn 2013), and a transmitter with hollow tubes for the elastic thread to slide through (Figure 4.3; Doerr and Doerr 2002). The elastic thread was glued directly to the under-side of the tag for the figure-eight, weak-link, and modified weak-link harness designs. The PinPoint 10 replicated tags were attached to sparrows using either ethyl cyanoacrylate glue or eyelash adhesive (Revlon, New York, NY, U.S.A.), both of which have been reported as effective short-duration attachment methods (Mong and Sandercock 2007, Diemer et al. 2014, Zenzal et al. 2018). We originally considered eyelash adhesive as an alternative to ethyl cyanoacrylate glue, but stopped using it after the first 3 individuals dropped the tags during release. We varied the amount of glue on each tag to determine if the amount applied impacted retention time; glue covering the entire backside of the tag, with glue forming an ‘X’ shape, and with glue placed in small circles in each corner of the tag (Figure 4.4).

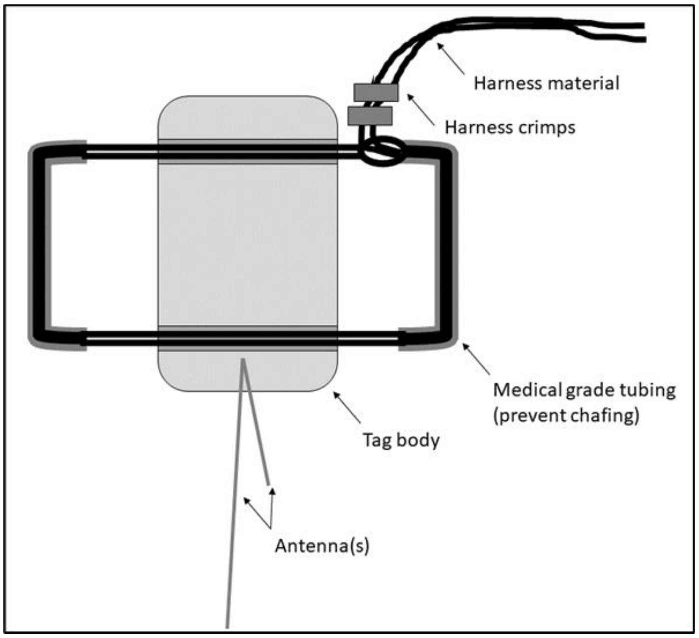

Figure 4.1. Example of the PinPoint 75 replicate tag and harness design used on rock pigeons.

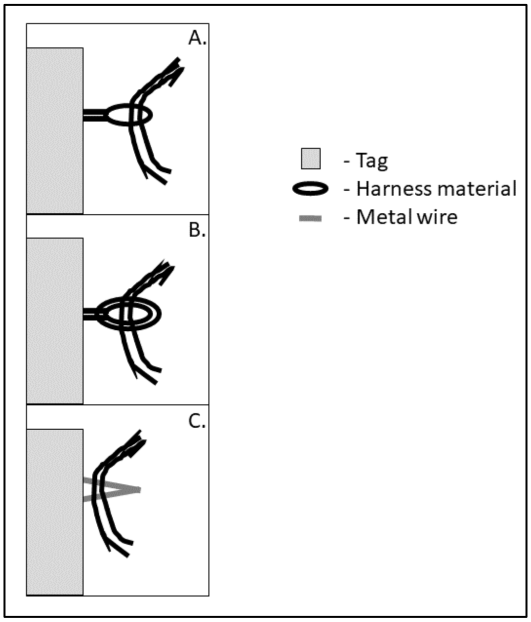

Figure 4.2. The PinPoint 75 replicate tags had three different material methods used to secure the harness when deployed. The single-loop (A), double-loop (B), and a metal reinforced loop were all expected to weather and be ‘dropped’ at different time intervals.

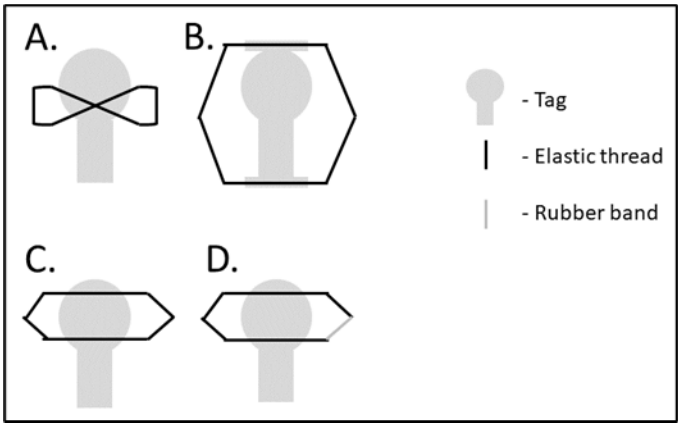

Figure 4.3. We used four popular harness methods to attach tags to house sparrows and European starlings. We used the Rappole and Tipton figure-8 (A), threaded harness material through pre-constructed 'tubes' in the harness (B), a modified version of the weak-link harness (C), and the weak-link harness (D). The tags were too small to use the tube method (B) on house sparrows.

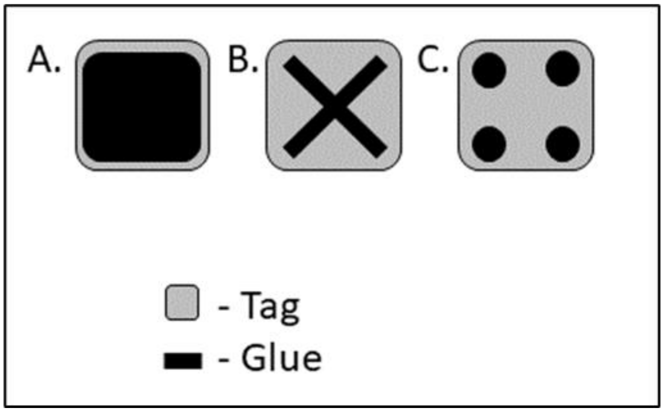

Figure 4.4. We placed varying amounts of ethyl cyanoacrylate glue on tags glued to house sparrow feather shafts. Generally, the pattern covered the entire surface of the tag (A), formed an 'X' shape pattern (B), or received a dot in each corner of the tag (C).

Field Methods

We captured sparrows, starlings, and pigeons using mist nets, and pigeons were also captured using walk-in traps and drop nets. Once captured, we attached a metal band with a unique identification number, a unique combination of colored leg bands, and randomly assigned a tag attachment method, or control (no tag), to each captured bird. Harnesses for the PinPoint 75 style tag attachment were custom-sized to each individual pigeon, and we used metal crimps to secure the fitted harness. VHF-style tags with leg-loop harnesses were attached to house sparrows and starlings, and were pre-sized. If an initial harness was too loose or tight, we selected another harness or harness design for that bird. Harnesses were fit so that the transmitter sat snuggly on the bird's back but not so tight as to alter normal leg position and movement. We repositioned feathers so that the harness and tag were close to the skin of the bird and generally covered by feathers. For house sparrows that received PinPoint 10-type glue-on tags, we trimmed feathers on the back to between 2 to 5 mm, and glued the tag to the cut feather shafts (Wilson 2020). All capture and marking procedures were approved by the University of Maine Institutional Animal Care and Use Committee (protocol A2018-05-05).

We attempted to resight previously marked birds twice per week using a combination of spotting scopes and binoculars with alternating observation periods between morning and evening to increase the likelihood of observing birds that commuted to the farm periodically to feed. Individuals were typically identified using their unique combination of color leg bands. We also visually searched for presence or absence of the tag, primarily based on evidence of the antenna extending past the bird's tail, as the tags themselves were rarely visible and were often covered by feathers. If neither the antenna nor the tag was observed, we recorded the tag as not observed. If we identified an individual but were unable to determine if the transmitter was present or absent, we did not include the observation in the analysis.

Statistical Analysis

We used a multistate modeling approach using the package rMark (Laake, 2013), which can be used to estimate transition between specified states, while accounting for imperfect detection and mortality of marked birds. We defined two states, tag 'present' or tag 'absent', during each encounter occasion. The model quantified the transition from tag presence to absence (tag loss), and absence to presence, which reflected misclassification due to observer error. We subset the resight data and conducted individual analyses by species, so that only similar attachment methods were compared within a species. Observations were converted into weekly encounter histories, and when individuals were observed both with and without a tag during a single week, we classified the individual as being in the 'tag present' state. Hence, transitions between tag absence and tag presence could only occur between, but not within, weeks. The encounter histories were designed so that occasion one represented each individual's week of capture, and 'time' reflected the number of weeks post-capture that elapsed for each individual.

We built a base multistate model and tested two different hypotheses to determine what factors influenced transition (Ψ) between states. Our first hypothesis was that transition between tag presence and tab absence was similar among all attachment methods, with no treatment effect, Ψ(stratum). The second was that tag loss varied depending on the attachment method Ψ(stratum + attachment method). Each model also generated rates of misclassification, when birds were observed without a tag, but a tag was actually attached. Because we had control birds in each analysis, we were able to generate positive misclassification rates for birds that never had tags, which was reflected in the probability of transition from tag absence to tag presence. We used this misclassification rate for both treatment and control birds to adjust transmitter retention estimates to reflect the true rate of tag loss that was corrected for the possibility of imperfect tag detection. We initially considered an interaction between stratum and harness design, which would allow for misclassification probability to be independent of harness design, but the model failed to converge for all species, so we used an additive relationship that assumed misclassification was independent of harness design. Models failed to converge to estimate tag retention among the harness designs used on starlings and for the varying amount of glue on sparrow tags, so, we combined all starling harness designs and all glue-on sparrow tags into single categories, and estimated tag retention independent of treatments. We set both the survival (Φ) and detection (p) parameters to constant (intercept-only) in all models, and in doing so assumed that both survival and detection probability could be described by a mean value that did not differ among harness styles. Since all attachment methods were deployed at random throughout the study under our experimental design, we believe this assumption is valid. We used Akaike's Information Criterion corrected for small sample size (AIC_c) to rank models, and selected inference models based on the lowest AIC_c. We did not consider models with parameter estimates that failed to converge.

We used the parameter estimates from the Ψ(stratum + attachment method) model, when the model converged, to generate tag retention estimates for each species and harness design as a function of time since marking, otherwise we used the Ψ(stratum) model. First, we defined the weekly probability of apparent tag loss within each attachment method as the transition between the tag presence and tag absence state (Ψ). However, some tagged individuals were certainly misclassified as untagged due to imperfect detection of the transmitters. So, we calculated the rate of misclassification for tag birds (λ) to correct our estimates of tag loss. We used control birds that never received a tag to approximate false misclassifications (τ), and subtracted τ from λ to estimate a true misclassification rate for each harness design as

$$Equation\ 1\colon \varUpsilon = \lambda - \tau$$

Where $\varUpsilon$ provides the probability that an apparently dropped tag was in fact retained. If $\varUpsilon < 0$, we rounded to zero to prevent inflation of Ψ. We then used $\varUpsilon$ from Equation 1 in Equation 2 to calculate the average rate of tag retention during some combined number of time intervals (t).

$$Equation\ 2\colon Tag\ Retention_t = (1 - [\varPsi(1 - \varUpsilon)])^t$$

We calculated mean retention rates using Ψ and λ specific to each attachment method. We repeated the tag retention calculation for each time interval to estimate how tag retention changed throughout the study period. We used the resulting retention estimates to compare attachment methods to determine how harness design influenced tag loss. We used the delta method in the emdbook package (Bolker et al. 2020) to calculate standard errors associated with each mean estimate.

Results

We captured 136 pigeons, 88 house sparrows, and 28 European starlings between 12 July 2018 and 7 June 2019 (Table 4.2). Fifteen pigeons and six house sparrows were released without tags due to escape during tag attachment or because of time processing constraints, but all individuals were banded. We resighted marked birds between 19 July 2018 and 26 July 2019, and collected 1,240 resightings of pigeons, 535 resightings of house sparrows, and 162 resightings of starlings.

Table 4.2. Number of birds marked with each attachment method to assess tag loss.

Species	Attachment method	n
Rock Pigeon		
	Control (No tag)	15
	Double-loop	41
	Metal reinforced loop	42
	One-loop	38
House Sparrow		
	Control (No tag)	6
	Weak-link	17
	Modified weak-link	15
	Glue-on	31
	Eyelash adhesive	3
	Rappole and Tipton figure-8	16
European Starling		
	Weak-link	5
	Modified weak-link	5
	Rappole and Tipton figure-8	13
	Tube	5

Model Selection

The top-supported model for pigeon tag retention was Ψ(stratum), receiving 88% of the model weight (Table 4.3), indicating that tag retention was similar among harness designs. Using the Ψ(stratum + attachment method) model, we estimated tag retention for 54 weeks, where retention for all harness designs decreased over time (Figure 4.5). The weekly rates of tag loss were 0.04 for the double loop, 0.03 for the one-loop, and 0.03 for the metal reinforced loop. At the end of the 54 weeks, the double-loop harness had the lowest retention rate (0.11 ± 0.06; μ ± SE), while the one-loop style harness had the highest retention (0.25 ± 0.12), and the metal reinforced loop harness was intermediate (0.17 ± 0.07; Figure 4.5).

Table 4.3. Model selection indicated that tag retention varied among species, with harness design being a stronger predictor of retention in sparrows. Tag loss was similar among harness designs for pigeons, and starlings. Glue-on tags for sparrows were similar to the control birds.

Species	Model	K	Δ AIC_c	wt	Deviance
Rock Pigeon					
	stratum	4	0.00^a	0.88	3149.17
	stratum + attachment method	7	4.02	0.12	3147.12
Sparrow (harness)					
	stratum + attachment method	7	0.00^b	1.00	1531.24
	stratum	4	24.59	0.00	1562.06
Sparrow (glue)					
	stratum	4	0.00^c	0.74	725.21
	stratum + attachment method	5	2.11	0.26	725.20
European Startling					
	stratum	4	0.00^d	1.00	579.51

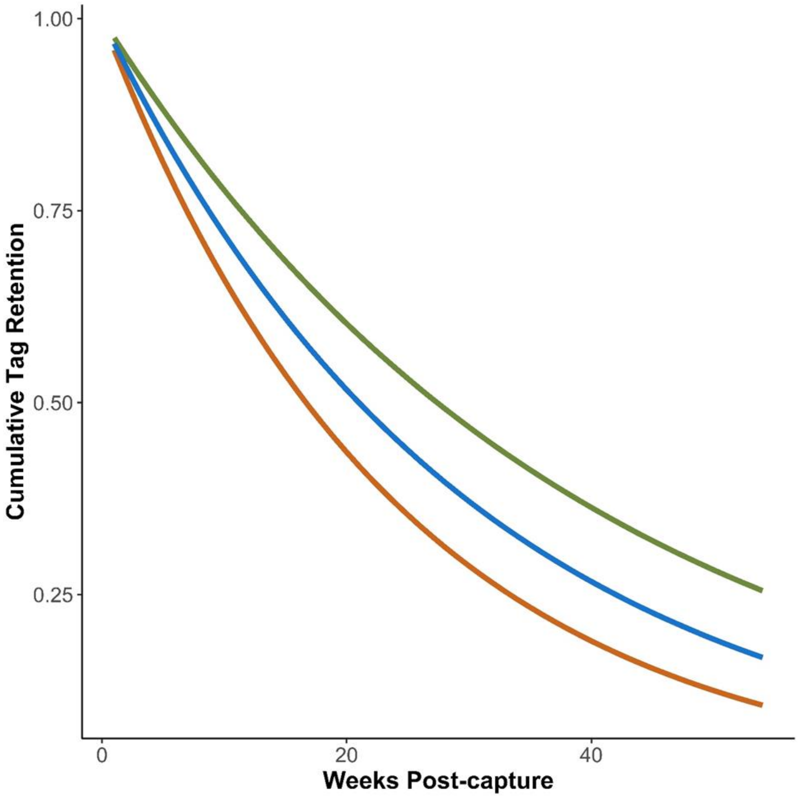

Figure 4.5. Predicted cumulative tag retention rates for pigeons using three attachment method; double-loop (brown), one-loop (green), and metal-reinforced loop (blue). The double-loop harness has the lowest retention rate, and the one-loop harness had the highest retention rate on rock pigeons.

The top-supported model for sparrow tags was the Ψ(stratum + attachment method) model receiving 100% of the cumulative weight, indicating a strong relationship between tag retention and harness design for sparrows. The weekly rates for sparrow tag loss were 0.01 for the Rappole and Tipton figure-8, 0.22 for the weak-link, and 0.10 for the modified weak-link. Tag retention declined through time and differed significantly by harness design (Figure 4.6). Using the Ψ(stratum + attachment method) model, we estimated retention for 51 intervals. At 20 weeks post-marking, the Rappole and Tipton figure-8 harness had the highest retention probability for sparrows (0.77 ± 0.10), the weak-link harness had the lowest (0.01 ± 0.01), and there was intermediate-low level of retention for the modified weak-link (0.12 ± 0.08). This general trend continued and by 40 weeks post-marking, retention was estimated to be 0.59 ± 0.16 for the Rappole and Tipton figure-8 harness, 0.00 ± 0.00 for the weak-link, and 0.01 ± 0.02 for the modified weak-link.

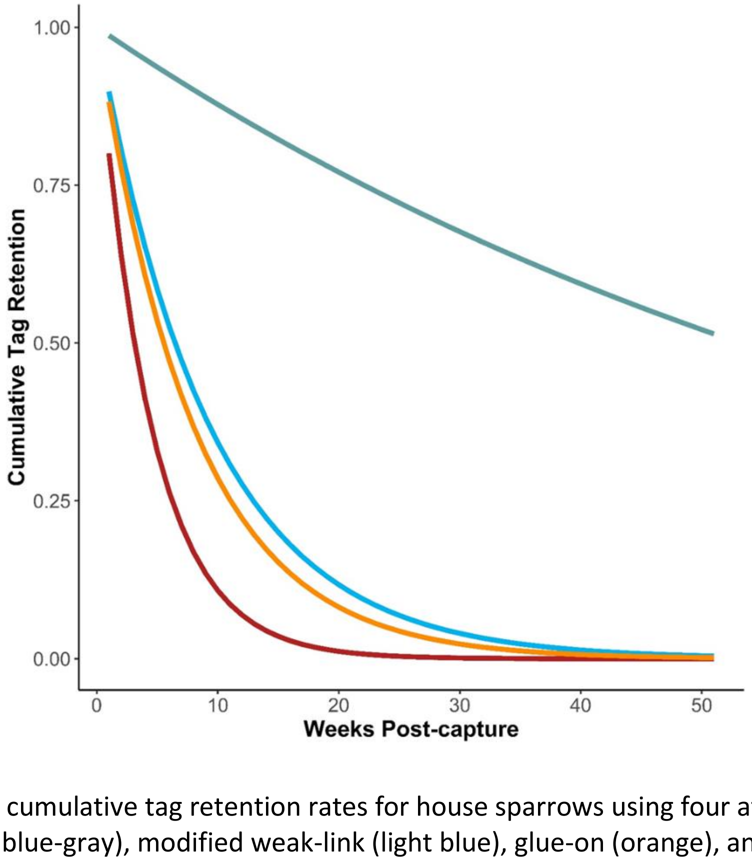

Figure 4.6. Predicted cumulative tag retention rates for house sparrows using four attachment methods, Rappole and Tipton (blue-gray), modified weak-link (light blue), glue-on (orange), and weak-link (red). The weak-link, glue-on, and modified weak-link attachment methods had the lowest retention rates, and the Rappole and Tipton harness had the highest retention rate on house sparrows.

We only ran one model to assess tag retention on starlings, therefore the Ψ(stratum) was the inference model, which indicated tag retention decreased through time with a mean tag loss rate of 0.05 per week. Using the Ψ(stratum) inference model, we estimated a retention rate of 0.40 ± 0.11 at week 20, 0.16 ± 0.09 at 40 weeks, and 0.09 ± 0.07 by the last interval (52 weeks; Figure 4.7). This retention trend indicated starlings generally dropped tags at a similar rate to sparrows, although we were unable to determine if the harness design influenced retention.

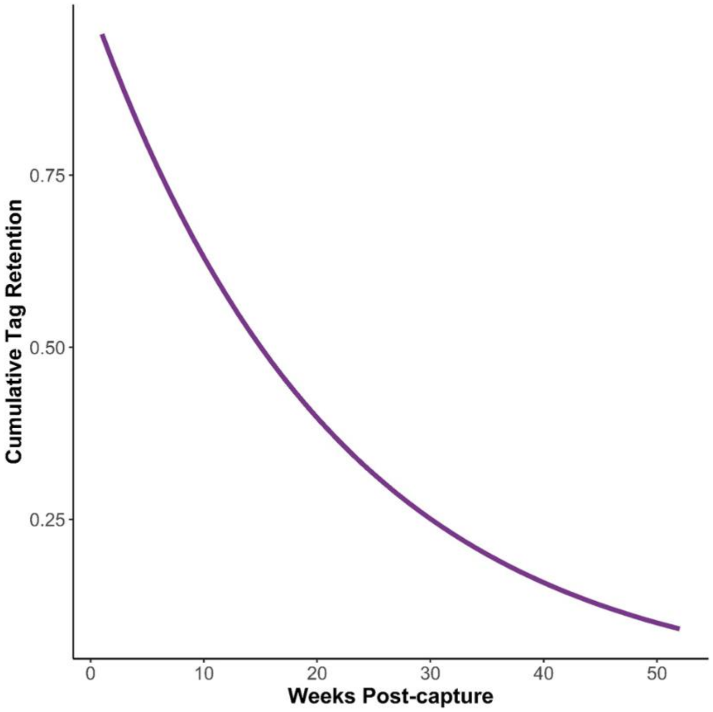

Figure 4.7. Predicted cumulative tag retention rate for leg-loop style harnesses on European Starlings. We were not able to estimate retention differences among the four harness designs used to affix tags to starlings, likely due to small sample sizes.

The top-supported model for sparrow glue-on tags was the Ψ(stratum) model, which received 74% of the cumulative weight. The weekly rate of loss for glue-on tags was 0.12 and tag retention decreased through time. Using Ψ(stratum + attachment method), we estimated tag retention to be 0.08 ± 0.05 at week 20, 0.01 ± 0.01 at week 40, and 0.00 ± 0.00 by week 43 of 51 weekly intervals (Figure 4.6). In practice, 71% of sparrows observed before week 4 had dropped their tags (22 of 31), 87% before week 8 (27 of 31), and 90% had dropped their tags before week 12 (28 of 31). The remaining three birds were last observed with their tags during intervals 15, 17, and 19.

Discussion

We found that tag retention for all three species was imperfect, and dependent on harness design for sparrows but not pigeons. Our results support previous findings that retention rates often varied by attachment method (Mong and Sandercock 2007, Hansbauer and Pimentel 2008) and species (Diemer et al. 2014). We evaluated tag retention on populations of free-living birds under an experimental design, whereas many prior investigations were restricted to captive individuals (Chan et al. 2016) whose behavior may not mimic wild birds. Our results provide a framework to make recommendations for attachment methods specific to the length of time the tag needs to be retained for data collection.

We did not find support for differences in retention rates for leg-loop harness designs attached to pigeons; the one-loop, double-loop, and metal reinforced loop harnesses did not appear to degrade at different rates, resulting in similar tag retention rates. If the knot was not the cause of failure, it is possible that the harness failed in another location, or that tag retention was more closely associated with species' morphology or behavior. Pigeons were frequently observed preening and picking at harnesses while loafing or roosting on the farm, and may have been able to move the leg-loop over the tibiotarsus-tarus joint and drop the tag independent of the harness degrading. We did not directly observe any tag removal events, and few harnesses were recovered so we were unable to assess the specific cause of harness failure. Similar harnesses attached to upland sandpiper (*Bartamia longicauda*; Mong and Sandercock 2007) failed to degrade and individuals were observed 1 to 2 years after tag deployment with tags still attached (Mong and Sandercock 2007). Similarly for American Woodcock, leg-loop harness retention was consistently high up to 14 weeks post-marking (Chapter 3). It is therefore likely that leg-loop harness designs are likely to result in long-term retention, with specific rates varying based on species' morphology or behavior.

Many birds require tag attachment methods that are specific to that species' morphology or natural history. For example, subcutaneous anchors are commonly used to attach tags to surf (*Melanitta perspicillata*) and white-winged scoters (*Melanitta perspicillat*; Lewis et al. 2017), Pacific black brant (*Branta bernicla nigricans*; Lewis and Flint 2008), and white-winged doves (*Zenaida asiatica*; Small et al. 2004). Pigeons are morphologically similar to doves and it is possible that leg-loop-style harnesses were not well-suited for pigeons. Hence, our failure to detect differences in retention rates for the three designs of leg-loop harnesses on pigeons may have been partially due to a mismatch between the harness and the species.

The Rappole and Tipton figure-8 harness had a higher retention rate than the other two attachment methods, which were retained similarly. The Rappole and Tipton figure-8 harness has been widely used to attach tags to small- and medium-bodied birds due to its relatively high rate of retention (Peterson et al. 2015, Larkin et al. 2017, Delancey et al. 2020). Conversely, the weak-link harness (Kesler 2011) had the lowest rate of tag retention, and generally tags dropped more quickly than all other sparrow attachment methods. We presume the weak-link degraded, as designed, and caused the harness to fail. Using the weak-link harness, Kesler (2011) observed Tuamotu kingfishers (*Todiramphus gambieri*) for between 23-66 days and 22 of 23 individuals were resighted without tags 6 to 15 months after the termination of their study, providing additional proof of low tag retention through time. We were surprised that the modified weak-link, lacking a 'weak-link' component, had a similar retention rate to the weak-link harness. The modified weak-link harness is commonly used to attach datalogging tags (e.g., geolocators) on migratory birds with the tags needing to be retained for approximately one year (Lislevand and Hahn 2013), although different harness material may be used and contribute to retention rate differences (Doerr and Doerr 2002, Lislevand and Hahn 2013). The primary difference between the modified weak-link and the Rappole and Tipton figure-8 harness is the location where the leg-loops attached to the tag. It is possible that a combination of the distance between the front and back of each leg loop and the harness material's ability to stretch could influence retention rates. Sparrows were frequently observed preening feathers adjacent to the leg-loop harness, and it is possible that preening birds could stretch the harness material in such a way that they dropped the tag. We used elastic thread because the material minimized skin irritation (Rappole and Tipton 1991), but other harness materials with less stretch may have reduced tag loss rates.

We documented low rates of tag retention for ethyl cyanoacrylic glue-on tags attached to house sparrows. Glue-on tags are commonly selected when tags only need to be attached to a bird for a few weeks to a month (Hansbauer and Pimentel 2008, Stanton et al. 2018), such as when recovery of the tag is needed for data retrieval (Wilson 2020). However, glue-on tags are commonly associated with premature detachment and may require marking an additional 15 to 38% of individuals to ensure the target sample size is reached (Stanton et al. 2018). We observed house sparrows with glue-on tags up to 19 weeks post marking, and this may in part be due to timing of the year relative to body molt. Glue-on tags were primarily attached during October - December after many individuals had completed a body molt, hence molting the feathers the tag was attached to may not have occurred until months to a year later during the next prebasic molt in August - December (Pyle 2001). For many North American bird species, molt occurs during the late summer, and glue-on tags attached during the breeding season would not be expected to be retained after molting (Stanton et al. 2018). Hence, glue-on tag retention time is likely related, in part, to the duration of attachment prior to the next body feather molt, making it important to understand the focal studies species' molt cycle, and select feathers that will allow retention for the focal period (e.g., tail; Stanton et al. 2018). The type of glue used can also impact tag retention. Eyelash adhesive was not an affective attachment method in our study, but has been used previously for transmitter attachment (Hansbauer and Pimentel 2008, Zenzal et al. 2018). Lastly, glue-on tags that are shed during molt cycles (e.g., end of breeding season) are unlikely to cause long-term negative fitness effects (Anich et al. 2009).

When researchers decide to use dorsally-mounted tags, the attachment method they choose will depend on the desired data collection period. If tags need to be retained for >30 days, researchers should consider using a leg-loop-style harness. Leg-loop-style harnesses, similar to what we used on the pigeons, can be retained for more than a year; however, researchers should nonetheless expect imperfect retention throughout time. If tags need to be retained for more than one year, researchers should mark additional birds to ensure they collect data sufficient to meet desired samples size while accounting for imperfect retention, or use alternative harness material (e.g., Teflon ribbon) with greater durability. Similarly, if tags need to be retained on small-bodied birds, we suggest using the Rappole and Tipton figure-8 design. The figure-8 harness had the highest retention rates in our study, and is commonly used to attach tags that must be retained for a year (Peterson et al. 2015). However, the Rappole and Tipton figure-8 harness may not be suitable for ground-dwelling passerine birds (e.g., Bachman's sparrow, savannah sparrow *[Passerculus sandichensis*]) due to entanglement in vegetation and subsequent mortalities (van Vliet and Stutchbury 2018, Choi et al. 2021). Thus, the Rappole and Tipton figure-8 harness should be considered only for birds that spend little time in dense grass (e.g., tree crowns, understory) to reduce transmitter-related mortality. If the research objectives require the tag to be shed >30 days post-marking for a small ground dwelling bird, we suggest using the weak-link or modified weak-link harnesses, which reduce or eliminate vegetation entanglements (Choi et al. 2021). While the weak-link had the lowest predicted retention rate (0.12 by 140 days) in our study, other researchers have found it effective over a 23-66 day study period, with most tags being shed within a year (Kesler 2011). If the tag needs to be retained for no greater than a month, we recommend glue-on tags, especially when tag retention is integral to the study design. Glue-on tags can be attached to the back (Mong and Sandercock 2007, Diemer et al. 2014), such as used in our study, or can be attached to tail feathers (Stanton et al. 2018). Researchers should select the feathers for the attachment site based on knowledge of molt cycles in relation to the desired retention period (Pyle 2001, Stanton et al. 2018). However, glue-on tags may not be effective for all species (Diemer et al. 2014).

We experimentally evaluated how tag retention varied using leg-loop style harness and glue-on tags and found that tag retention on free-ranging wild birds is imperfect and varies by attachment method. Once a researcher determines how long a tag needs to be retained for a desired data collection period, they should identify the attachment method and adjust their sample size to account for imperfect retention. In our experiment, we show that 3D-printed replicate tags can be deployed on abundant free-ranging wild birds to test tag retention prior to attaching and deploying expensive tags on study species. Pigeons, starlings, and house sparrows are abundant and ubiquitous, have high resightability, and provide an ideal system to assess tag retention. We recommend that researchers evaluate and quantify tag retention prior to deploying tags on wild birds, especially for those that are difficult to observe post-deployment.

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APPENDIX A: Multivariate Hidden Markov Models

Table A.1. Distribution of step length and turn angles associated with Maximum Likelihood Analysis of animal behavior using Multivariate Hidden Markov Models movement models designed to assign migratory behaviors to American Woodcock (*Scolopax minor*). Initial values were input into the models pre-analysis and the step length and turn angles provided. Values in parentheses are standard deviation for step length and concentration for turn angles. Locations span 01 October to 14 January (fall) and 15 January to June 18 (spring).

Data Stream	**Behavioral State**	**Initial Values**	**Fall**			**Spring**	
			2017	**2018**	**2019**	**2019**	**2020**
Step Length							
	Pre-migration	0.49 (0.73)	0.58 (0.82)	0.32 (0.46)	0.45 (0.68)	0.30 (0.43)	0.47 (0.69)
	Migration	211.93 (289.60)	338.00 (579.77)	61.82 (152.51)	77.83 (185.82)	47.27 (117.54)	61.61 (149.60)
	Post-migration	0.49 (0.73)	2.64 (6.05)	0.30 (0.43)	0.61 (0.95)	0.20 (0.30)	0.26 (0.38)
Turn Angle							
	Pre-migration	0 (0.5)	-3.08 (0.56)	3.14 (0.42)	3.10 (0.37)	-3.12 (0.44)	3.12 (0.42)
	Migration	0 (0.5)	-0.17 (0.22)	-3.09 (0.07)	-3.06 (0.12)	-3.05 (0.18)	-3.09 (0.12)
	Post-migration	0 (0.5)	-2.95 (0.45)	3.09 (0.35)	-3.08 (0.34)	3.12 (0.38)	3.11 (0.37)
Zero Mass							
	Pre-migration	0.03	0.00	0.02	0.05	0.04	0.02
	Migration	0.04	0.00	0.02	0.02	0.05	0.03
	Post-migration	0.03	0.06	0.03	0.03	0.11	0.09

Table A.2. Transition probability matrices for Maximum Likelihood Analysis of Animal Movement Behavior using Multivariate Hidden Markov Models for American Woodcock (*Scolopax minor*). Locations span 01 October to 14 January (fall) and 15 January to June 18 (spring).

	Pre-migration	**Migration**	**Post-migration**
Fall 2017			
Pre-migration	0.924	0.076	NA
Migration	NA	0.781	0.219
Post-migration	NA	NA	1.000
Fall 2018			
Pre-migration	0.931	0.069	NA
Migration	NA	0.960	0.040
Post-migration	NA	NA	1.000
Fall 2019			
Pre-migration	0.950	0.050	NA
Migration	NA	0.947	0.053
Post-migration	NA	NA	1.000
Spring 2019			
Pre-migration	0.939	0.061	NA
Migration	NA	0.973	0.027
Post-migration	NA	NA	1.000
Spring 2020			
Pre-migration	0.940	0.060	NA
Migration	NA	0.968	0.032
Post-migration	NA	NA	1.000

Appendix B Model Selection Results for Migration Phenology

Table B.1. Initiation of fall migration for American woodcock (*Scolopax minor*) marked with GPS transmitters in Eastern North America 2017-2019. Reference models in bold did not contain any non-significant parameters (beta coefficients 95% confidence intervals overlapping zero).

Analysis	**Model**	**K**[a]	**Delta AIC_c**[b]	**AIC_cWt**[c]	**Cum.Wt**[d]	**LogLik**[e]	**R^2**
Spatial (N = 117)							
	latitude×longitude	5	0.00[f]	0.66	0.66	-425.05	0.60
	latitude + longitude	**4**	**1.42**	**0.33**	**0.99**	**-426.85**	**0.59**
	state	13	8.10	0.01	1.00	-419.60	0.60
	latitude	3	19.39	0.00	1.00	-436.91	0.51
	null	2	102.65	0.00	1.00	-479.59	0.00
	longitude	3	104.54	0.00	1.00	-479.48	-0.01
Demographic (N = 117)							
	base[g] + age	**5**	**0.00[h]**	**0.47**	**0.47**	**-424.17**	0.60
	base[g] + age + sex	6	1.24	0.25	0.72	-423.68	0.60
	base[g]	4	3.18	0.10	0.82	-426.85	0.59
	base[g] + age×sex	7	3.36	0.09	0.91	-423.61	0.60
	base[g] + sex	5	3.38	0.09	1.00	-425.86	0.59
Body condition (N = 97)							
	base[i] + condition×age	7	0.00[j]	0.46	0.46	-343.60	0.63
	base[i] + condition	6	1.47	0.22	0.68	-345.50	0.62
	base[i]	**5**	**1.52**	**0.22**	**0.90**	**-346.66**	**0.61**
	base[i] + condition×latitude	7	3.68	0.07	0.97	-345.44	0.61
	base[i] + condition×sex	8	5.52	0.03	1.00	-345.17	0.61

[a] number of parameters

[b] difference between model and top AICc supported model

[c] model weight based on AICc model support

[d] cumulative model weight

[e] negative log likelihood

[f] AIC_c 860.64

glatitiude + longitude

[h] AIC_c 858.88

[i] latitude + longitude + age

[j] AIC_c 702.46

Table B.2. Termination of fall migration for American woodcock (*Scolopax minor*) marked with GPS transmitters in Eastern North America 2017-2019. Reference models in bold did not contain any non-significant parameters (beta coefficients 95% confidence intervals overlapping zero).

Analysis	Model	K[a]	Delta AIC_c[b]	AIC_cWt[c]	Cum.Wt[d]	LogLik[e]	R^2
Spatial (N = 93)							
	start.latitude×start.longitude	5	0.00[f]	0.44	0.44	-380.39	0.09
	start.latitude + start.longitude	**4**	**0.13**	**0.41**	**0.85**	**-381.57**	**0.08**
	start.latitude	3	3.95	0.06	0.91	-384.57	0.03
	start.longitude	3	4.69	0.04	0.95	-384.90	0.02
	null	2	5.57	0.03	0.98	-386.45	0.00
	end.latitude	3	7.63	0.01	0.99	-386.41	-0.01
	end.longitude	3	7.69	0.01	1.00	-386.44	-0.01
	end.latitude×end.longitude	5	9.65	0.00	1.00	-385.22	-0.01
	end.latitude + end.longitude	4	9.79	0.00	1.00	-386.40	-0.02
	start.state	12	10.36	0.00	1.00	-376.99	0.08
	end.state	15	22.09	0.00	1.00	-378.70	0.01
Demographic (N = 93)							
	base[g] + age	5	0.00[h]	0.41	0.41	-380.12	0.10
	base[g]	**4**	**0.67**	**0.30**	**0.71**	**-381.57**	**0.08**
	base[g] + age + sex	6	2.27	0.13	0.84	-380.11	0.09
	base[g] + sex	5	2.74	0.11	0.95	-381.49	0.07
	base[g] + age×sex	7	4.15	0.05	1.00	-379.88	0.08
Body condition (N = 78)							
	base[g]	**4**	**0.00[i]**	**0.27**	**0.27**	**-318.19**	**0.06**
	base[g] + condition×end.latitude	7	0.47	0.21	0.48	-314.90	0.10
	base[g] + condition	5	0.50	0.21	0.69	-317.29	0.07
	base[g] + condition×sex	7	1.37	0.14	0.83	-315.35	0.09
	base[g] + condition×age	7	2.24	0.09	0.92	-315.78	0.08
	base[g] + condition×start.latitude	6	2.24	0.09	1.01	-316.99	0.07

[a] number of parameters

[b] difference between model and top AIC_c supported model

[c] model weight based on AIC_c model support

[d] cumulative model weight

[e] negative log likelihood

[f] AIC_c 771.46

[g] start.latitude + start.longitude

[h] AIC_c 770.92

[i] AIC_c 644.92

Table B.3. Initiation of spring migration for American woodcock (*Scolopax minor*) marked with GPS transmitters in Eastern North America 2019-2020. Reference models in bold did not contain any non-significant parameters (beta coefficients 95% confidence intervals overlapping zero).

Analysis	**Model**	**K**[a]	**Delta AIC_c**[b]	**AIC_cWt**[c]	**Cum.Wt**[d]	**LogLik**[e]	**R^2**
Spatial (N = 108)							
	longitude	**3**	**0.00**[f]	**0.55**	**0.55**	**-438.06**	**0.09**
	latitude + longitude	4	1.75	0.23	0.78	-437.86	0.08
	latitude$^{\times}$longitude	5	2.88	0.13	0.91	-437.32	0.08
	latitude	3	4.82	0.05	0.96	-440.48	0.04
	state	12	6.18	0.03	0.99	-430.63	0.13
	null	2	8.52	0.01	1.00	-443.38	0.00
Demographic (N = 106)							
	base[g] **+ sex**	**4**	**0.00**[h]	**0.53**	**0.53**	**-428.55**	**0.12**
	base[g] + age + sex	5	2.15	0.18	0.71	-428.52	0.11
	base[g]	3	2.54	0.15	0.86	-430.90	0.08
	base[g] + age$^{\times}$sex	6	3.68	0.08	0.94	-428.16	0.10
	base[g] + age	4	4.70	0.05	0.99	-430.90	0.07
Body condition (N = 63)							
	base[i] **+ condition*sex**	**6**	**0.00**[j]	**0.90**	**0.90**	**-230.37**	**0.24**
	base[i]	4	5.51	0.06	0.96	-235.53	0.13
	base[i] + condition	5	7.85	0.02	0.98	-235.51	0.12
	base[i] + condition$^{\times}$latitude	7	8.88	0.01	0.99	-233.54	0.14
	base[i] + condtion$^{\times}$longitude	6	9.43	0.01	1.00	-235.08	0.12
	base[i] + conditon$^{\times}$age	7	10.18	0.01	1.01	-234.19	0.13

[a] number of parameters

[b] difference between model and top AIC_c supported model

[c] model weight based on AIC_c model support

[d] cumulative model weight

[e] negative log likelihood

[f] AIC_c 882.36

[g] longitude

[h] AIC_c 865.49

[i] longitude + sex

[j] AIC_c 474.23

Table B.4. Dates of fall stopover for American woodcock (*Scolopax minor*) marked with GPS transmitters in Eastern North America 2017-2019, were best described while accounting for state specific effects, age, and sex. Reference models in bold did not contain any non-significant parameters (beta coefficients 95% confidence intervals overlapping zero).

Analysis	Model	K[a]	Delta AIC$_c$[b]	AIC$_c$Wt[c]	Cum.Wt[d]	LogLik[e]	R^2
Spatial (N = 2068)							
	state	**34**	**0**[f]	**1.00**	**1.00**	**-7676.34**	**0.73**
	latitude + longitude	5	40.09	0.00	1.00	-7725.95	0.72
	latitude×longitude	6	41.62	0.00	1.00	-7725.72	0.72
	latitude	4	69.19	0.00	1.00	-7741.51	0.71
	longitude	4	292.52	0.00	1.00	-7853.18	0.69
	null	3	1284.73	0.00	1.00	-8350.28	0.48
Demographic (N = 2068)							
	base[g] + sex	35	0[h]	0.41	0.41	-7674.47	0.73
	base[g] + age×sex	**37**	**1.53**	**0.19**	**0.60**	**-7673.17**	**0.73**
	base[g]	34	1.66	0.18	0.78	-7676.34	0.73
	base[g] + age + sex	36	2.04	0.15	0.93	-7674.46	0.73
	base[g] + age	35	3.55	0.07	1.00	-7676.25	0.73

[a] number of parameters

[b] difference between model and top AICc supported model

[c] model weight based on AICc model support

[d] cumulative model weight

[e] negative log likelihood

[f] AIC$_c$ 15421.85

[g] state

[h] AIC$_c$ 15420.19

Appendix C Regression Coefficients Results

Table C.1. Covariates from top models determine how dates relates to fall migration phenology. All models only include significant parameters and fall initiation and termination use ordinal date beginning 1 October and spring initiation 1 January. Males and young birds were used as reference for sex and age categories respectively.

Analysis	Model covariate	Beta coefficient	Stand error	95% CI upper	95% CI lower
Fall initiation					
	(Intercept)	239.5618	22.5996		
	age	-6.5784	1.8290	-2.9936	-10.1632
	latitude	-3.6125	0.2987	-3.0270	-4.1980
	longitude	0.5740	0.1854	0.9374	0.2106
Spring initiation					
	(Intercept)	185.6254	31.1116		
	condition	-0.3348	0.1348	-0.0706	-0.5990
	sex	2.4690	2.6612	7.6850	-2.7470
	longitude	1.5274	0.3913	2.2943	0.7605
	condition×sex	0.5897	0.1838	0.9499	0.2295
Fall termination					
	(Intercept)	171.7378	42.1251		
	start.latitude	-1.2102	0.5307	-0.1700	-2.2504
	start.longitude	0.7853	0.3595	1.4899	0.0807

Table C.2. Top supported model describing when American Woodcock (*Scolopax minor*) were in a fall migratory behavior state 2017-2019. The model uses 1 October as the ordinal date start and males, young birds, and Alabama (N = 119) as references (coded zero) in the model. Confidence intervals were built using a 95% threshold.

Model covariate	**Beta coefficient**	**Stand error**	**CI upper**	**CI lower**	***n***
(Intercept)	71.2243	2.8302			
age	3.8833	3.7697	11.2719	-3.5053	
sex	-0.4236	3.9009	7.2222	-8.0694	
age*sex	-8.5644	5.3018	1.8271	-18.9559	
State[Arkansas]	-5.2553	4.1736	2.9250	-13.4356	6
State[Connecticut]	-36.1092	1.9356	-32.3154	-39.9030	71
State[District of Columbia]	-24.7818	4.2501	-16.4516	-33.1120	6
State[Delaware]	-25.2043	2.7854	-19.7449	-30.6637	21
State[Georgia]	-12.2939	1.6700	-9.0207	-15.5671	103
State[Indiana]	-27.5373	5.1133	-17.5152	-37.5594	5
State[Kentucky]	-14.5378	1.8269	-10.9571	-18.1185	104
State[Lousiana]	1.6537	2.0179	5.6088	-2.3014	57
State[Massachusetts]	-41.0310	3.0409	-35.0708	-46.9912	14
State[Maryland]	-19.2776	2.1922	-14.9809	-23.5743	62
State[Maine]	-41.9293	2.0066	-37.9964	-45.8622	51
State[Michigan]	-24.6329	2.7469	-19.2490	-30.0168	39
State[Mississippi]	5.1994	1.9451	9.0118	1.3870	71
State[North Carolina]	-14.7444	1.5096	-11.7856	-17.7032	247
State[New Hampshire]	-42.5029	3.9757	-34.7105	-50.2953	7
State[New Jersey]	-29.7675	2.0262	-25.7961	-33.7389	100
State[New York]	-31.9517	1.6488	-28.7201	-35.1833	101
State[Ohio]	-24.7383	1.8562	-21.1001	-28.3765	117
State[Ontario]	-32.8373	1.9180	-29.0780	-36.5966	71
State[Pennsylvania]	-30.3493	1.7073	-27.0030	-33.6956	73
State[Quebec]	-39.8826	2.0686	-35.8281	-43.9371	35
State[Rhode Island]	-32.1106	2.5710	-27.0714	-37.1498	24
State[South Carolina]	-1.4382	1.7304	1.9534	-4.8298	86
State[Tennessee]	-11.4680	1.7869	-7.9657	-14.9703	84
State[Virginia]	-19.2702	1.4574	-16.4137	-22.1267	257
State[West Virginia]	-21.7790	2.2163	-17.4351	-26.1229	32
State[Florida]	-1.5348	2.4928	3.3511	-6.4207	22
State[Illinois]	-7.0559	4.0761	0.9333	-15.0451	10
State[Nova Scotia]	-50.0783	2.5799	-45.0217	-55.1349	58
State[Texas]	15.9257	6.7469	29.1496	2.7018	2
State[Vermont]	-31.4345	6.5726	-18.5522	-44.3168	13

APPENDIX D: Model Selection Results for Migration Cue Use

Table D.1. Conditional logistic regression models explaining which extrinsic factors are most important for initiation of autumn migration for American Woodcock (*Scolopax minor*), 2017-2019. To test effects of age, the same models were run for both adults and young woodcock.

Model	K[a]	Delta AIC$_c$[b]	Cum. wt[c]	LogLik[d]
Adult (n = 454)				
wind.assist[e] + temp[f]	2	0.00[g]	0.18	-12.91
wind.assist + temp + b.pres[h]	3	0.32	0.32	-12.06
wind.assist + temp + wind.spd[i]	3	0.77	0.44	-12.29
wind.assist + temp + b.pres + m.illum[j]	4	1.64	0.52	-11.70
wind.assist + temp + wind.assist×temp	3	1.76	0.59	-12.78
wind.assist + temp + m.illum	3	1.89	0.66	-12.84
wind.assist + temp + b.pres + wind.spd	4	2.08	0.72	-11.92
wind.assist + temp + b.pres + wind.assist×b.pres	4	2.18	0.78	-11.97
wind.assist + temp + b.pres + wind.assist×temp	4	2.20	0.84	-11.98
wind.assist + temp + m.phase[k]	5	4.15	0.86	-11.94
temp	1	4.31	0.88	-16.07
temp + wind.spd	2	4.31	0.90	-15.07
temp + b.pres	2	4.32	0.92	-15.07
temp + b.pres + wind.spd	3	5.58	0.93	-14.69
wind.assist + temp + b.pres + wind.spd + m.phase	7	5.88	0.94	10.74
temp + m.illum	2	6.16	0.95	-15.99
temp + b.pres + temp×b.pres	3	6.21	0.96	-15.00
temp + wind.spd + m.illum	3	6.24	0.97	-15.02
temp + wind.spd + temp×wind.spd	3	6.34	0.98	-15.07
wind.assist	1	6.57	0.99	-17.20
temp + b.pres + wind.spd + m.illum	4	7.15	0.99	-14.46
wind.assist + b.pres + wind.spd	3	7.56	0.99	-15.68
wind.assist + temp + b.pres + wind.spd + m.illum + m.phase	8	7.73	0.99	-10.63
wind.assist + b.pres	2	8.35	1.00	-17.09
wind.assist + b.pres + wind.assist×b.pres	3	10.01	1.00	-16.90
wind.assist + b.pres + m.illum	3	10.34	1.00	-17.07
wind.assist + b.pres + m.phase	5	11.58	1.00	-15.65
wind.spd	1	14.78	1.00	-21.31
b.pres	1	16.01	1.00	-21.92
m.illum	1	16.79	1.00	-22.31
m.phase	3	17.56	1.00	-20.68
m.illum + m.phase + m.illum×m.phase	4	21.53	1.00	21.65
Young (n = 544)				
temp	1	0.00[l]	0.14	-14.13
temp + b.pres	2	0.63	0.24	-13.44

Table D.1 Continued.

temp + wind.assist	2	0.84	0.33	-13.54
temp + b.pres + temp×b.pres	3	1.49	0.39	-12.86
temp + m.illum	2	1.51	0.45	-13.88
temp + wind.spd	2	1.57	0.52	-13.91
temp + b.pres + wind.assist	3	1.60	0.58	-12.91
temp + b.pres + wind.asssit + m.illum	4	1.83	0.63	-12.01
temp + wind.assist + wind.spd	3	1.91	0.69	-13.07
temp + wind.assist + m.illum	3	2.11	0.73	-13.17
temp + wind.spd + b.pres	3	2.60	0.77	-13.41
temp + wind.assist + temp×wind.assist	3	2.68	0.81	-13.45
temp + m.illum + wind.spd	3	3.11	0.84	-13.67
temp + b.pres + m.illum + wind.spd	4	3.36	0.87	-12.78
temp + b.pres + wind.assist + wind.spd	4	3.38	0.90	-12.79
temp + b.pres + wind.assist + b.pres×wind.assist	4	3.40	0.92	-12.80
temp + wind.spd + temp*wind.spd	3	3.51	0.94	-13.87
temp + b.pres + wind.assist + b.pres× wind.assist	4	3.58	0.96	-12.89
temp + wind.assist + m.phase	5	3.80	0.98	-11.98
temp + b.pres + wind.assist + wind.spd + m.phase	7	4.67	0.99	-10.36
temp + b.pres + wind.assist + m.illum + wind.spd + m.phase	8	6.56	1.00	-10.28
wind.assist	1	8.70	1.00	18.48
b.pres + wind.assist + wind.spd	3	9.48	1.00	16.85
b.pres + wind.assist	2	10.70	1.00	-18.47
wind.spd	1	11.96	1.00	-20.11
b.pres + wind.assist + b.pres×wind.assist	3	12.23	1.00	-18.23
b.pres + wind.assist + m.illum	3	12.72	1.00	-18.47
m.illum	1	13.23	1.00	-20.75
b.pres	1	13.26	1.00	-20.76
b.pres + wind.assist + m.phase	5	14.05	1.00	-17.10
m.phase	3	15.64	1.00	-19.93
m.illum + m. phase + m.illum×m.phase	4	18.75	1.00	-20.47

[a] number of parameters

[b] AIC_c Akaike Information Criterion corrected for a small sample size difference from top supported model

[c] cumulative model weight

[d] Log Likelihood

[e] wind assistance

[f] temperature

[g] AIC_c 29.85

[h] barometric pressure

[i] wind speed

[j] moon illumination

[k] moon phase

[l] AIC_c 30.27

Table D.2. Conditional logistic regression models explaining which intrinsic factors are most important for initiation of spring migration for American Woodcock (*Scolopax minor*), 2019-2020. Models in the male tier that included the moon phase covariate, failed to converge and therefore were removed. To test effects of sex, the same models were run for both male and female woodcock.

Model	**K**[a]	**Delta AIC_c**[b]	**Cum wt**[c]	**LogLik**[d]
Male (n = 102)				
m.illum[e]	1	0.00[f]	0.14	-4.21
wind.spd[g]	1	0.02	0.28	-4.22
m.illum + wind.spd	2	0.61	0.39	-3.48
wind.spd + temp[h]	2	1.65	0.45	-3.99
m.illum + temp	2	1.93	0.50	-4.13
temp	1	2.40	0.54	-5.41
b.pres[i]	1	2.43	0.59	-5.42
m.illum + wind.spd + temp	3	2.43	0.63	-3.32
m.illum + wind.spd + m.illum×wind.spd	3	2.59	0.67	-3.40
wind.assist[j]	1	2.64	0.71	-5.53
wind.spd + b.pres + temp	3	3.32	0.74	-3.77
b.pres + temp	2	3.39	0.77	-4.87
wind.spd + temp + wind.spd×temp	3	3.75	0.79	-3.98
wind.spd + temp + wind.assist	3	3.77	0.81	-3.99
m.illum + temp + wind.assist	3	3.97	0.83	-4.09
m.illum + b.pres + wind.assist	3	4.01	0.85	-4.12
wind.spd + b.pres + wind.assist	3	4.18	0.87	-4.20
temp + wind.assist	2	4.31	0.89	-5.33
b.pres + wind assist	2	4.51	0.91	-5.42
m.illum + wind.spd + temp + b.pres	4	4.58	0.92	-3.32
temp + b.pres + temp×b.pres	3	5.37	0.93	-4.79
temp + b.pres + wind.assist	3	5.44	0.94	-4.83
b.pres + wind.assist + b.pres×wind.assist	3	5.45	0.95	-4.83
wind.spd + temp + b.pres + wind.assist	4	5.49	0.96	-3.77
temp + wind.assist + temp×wind.assist	3	5.81	0.97	-5.01
m.illum + temp + b.pres + wind.assist	4	6.10	0.98	-4.07
temp + b.pres + wind.assist + b.pres×wind.assist	4	6.58	0.99	-4.32
temp + b.pres + wind.assist + temp×wind.assist	4	7.14	1.00	-4.59
Female (n = 364)				
wind.assist + b.pres	2	0.00[k]	0.15	-8.08
wind.assist + b.pres + temp	3	0.77	0.26	-7.45
wind.assist	1	0.81	0.36	-9.49
wind.assist + b.pres + wind.assist×b.pres	3	1.93	0.42	-8.03
wind.assist + b.pres + wind.spd	3	1.95	0.48	-8.03

Table D.2 Continued.

wind.assist + b.pres + m.illum	3	2.01	0.53	-8.07
b.pres + temp	2	2.43	0.58	-9.30
wind.assist + b.pres + temp + wind.spd	4	2.50	0.62	-7.29
wind.assist + b.pres + temp + m.illum	4	2.66	0.66	-7.37
wind.assist + b.pres + temp + wind.assist×b.pres	4	2.76	0.70	-7.42
wind.assist + b.pres + temp + wind.assist×temp	4	2.78	0.74	-7.43
wind.assist + temp	2	2.83	0.78	-9.49
temp + m.illum	3	3.66	0.80	-8.89
wind.spd	1	4.13	0.82	-11.15
b.pres	1	4.16	0.84	-11.17
wind.assist + temp + wind.spd	3	4.17	0.86	-9.15
b.pres + temp + b.pres×temp	3	4.24	0.88	-9.18
temp	1	4.50	0.90	-11.34
wind.assist + temp + wind.assist×temp	3	4.66	0.91	-9.39
wind.assist + temp + m.illum	3	4.70	0.92	-9.41
temp + wind.spd	2	4.92	0.93	-10.54
b.pres + temp + wind.spd + m.illum	4	5.23	0.94	-8.65
m.illum	1	5.34	0.95	-11.76
wind.assist + b.pres + m.phase[l]	5	5.75	0.96	-7.89
wind.spd + m.illum	2	5.99	0.97	-11.07
temp + m.illum	2	6.52	0.98	-11.34
temp + wind.spd + temp×wind.spd	3	6.74	0.99	-10.43
temp + wind.spd + m.illum	3	6.93	1.00	-10.53
temp + wind.spd + m.phase	5	7.91	1.00	-8.96
wind.spd + m.illum + wind.spd×m.illum	3	8.01	1.00	-11.07
wind.assist + b.pres + temp + wind.spd + m.phase	7	8.53	1.00	-7.20
m.phase	3	8.75	1.00	-11.44
wind.assist + b.pres + temp + wind.spd + m.illum + m.phase	8	10.56	1.00	-7.17
m.illum + m.phase + m.illum×m.phase	4	11.29	1.00	-11.69

[a] number of parameters

[b] Akaike Information Criterion corrected for a small sample size difference from top supported model

[c] cumulative model weight

[d] Log Likelihood

[e] moon illumination

[f] AIC_c 10.46

[g] wind speed

[h] temperature

[i] barometric pressure

[j] wind assistance

[k] AIC_c 20.19

[l] moon phase

Table D.3. Conditional logistic regression models explaining which extrinsic factors are most important for initiation of autumn stopover departure in American Woodcock (*Scolopax minor*), 2017-2019. To test how the effect of age, the same models were run for adults and young woodcock.

Model	**K**[a]	**Delta AIC$_c$**[b]	**Cum wt**[c]	**LogLik**[d]
Adult (n = 682)				
wind.spd[e]	1	0.00[f]	0.17	-18.02
temp[g]	1	0.54	0.30	-18.29
wind.assist[h]	1	0.87	0.41	-18.46
temp + wind.spd	2	1.24	0.50	-17.64
b.pres[i]	1	1.31	0.59	-18.68
wind.assist + temp	2	2.40	0.64	-18.22
temp + b.pres	2	2.54	0.69	-18.29
wind.assist + b.pres	2	2.85	0.73	-18.44
wind.spd + temp + b.pres	3	3.01	0.77	-17.51
wind.spd + temp + wind.assist	3	3.13	0.81	-17.57
wind.spd + wind.assist + b.pres	3	3.24	0.84	-17.63
wind.spd + temp + wind.spd×temp	3	3.24	0.87	-17.63
wind.assist + b.pres + wind.assist×b.pres	3	3.71	0.90	-17.86
temp + wind.assist + temp×wind.assist	3	3.80	0.93	-17.91
temp + b.pres + temp×b.pres	3	3.94	0.95	-17.98
temp + wind.assist + b.pres	3	4.41	0.97	-18.21
wind.spd + temp + wind.assist + b.pres	4	4.94	0.98	-17.46
temp + wind.assist + b.pres + wind.assist×b.pres	4	5.46	0.99	-17.73
temp + wind.assist _ b.pres + temp×wind.assist	4	5.81	1.00	-17.90
Young (n = 470)				
temp	1	0.00[j]	0.19	-18.88
wind.spd	1	0.88	0.30	-19.32
wind.assist	1	1.02	0.41	-19.39
b.pres	1	1.12	0.52	-19.44
temp + wind.spd	2	1.86	0.59	-18.80
temp + b.pres	2	1.99	0.66	-18.87
wind.assist + temp	2	2.01	0.73	-18.88
wind.assist + b.pres	2	3.04	0.77	-19.39
temp + b.pres + temp×b.pres	3	3.21	0.81	-18.46
temp + wind.spd + temp×wind.spd	3	3.82	0.84	-18.77
temp + wind.spd + wind.assist	3	3.88	0.87	-18.80
temp + wind.spd + b.pres	3	3.89	0.90	-18.80
temp + wind.assist + b.pres	3	4.02	0.92	-18.87
temp + wind.assist + temp×wind.assist	3	4.03	0.94	-18.87
wind.assist + b.pres + wind.assist×b.pres	3	4.73	0.96	-19.23
wind.spd + wind.assist + b.pres	3	4.79	0.98	-19.25
temp + wind.assist + b.pres + wind.assist×b.pres	4	5.60	0.99	-18.64
temp + wind.spd + wind.assist + b.pres	4	5.92	1.00	-18.80

Table D.3 Continued.

temp + wind.assist + b.pres + temp×wind.assist	4	6.05	1.00	-18.86

[a] number of parameters

[b] Akaike Information Criterion corrected for a small sample size difference from top supported model

[c] cumulative model weight

[d] Log Likelihood

[e] wind speed

[f] AICc 38.05

[g] temperature

[h] wind assistance

[i] barometric pressure

[j] AIC_c 39.77

Table D.4. Appendix 4. Conditional logistic regression models explaining which extrinsic factors are most important for initiation of spring stopover departure in American Woodcock (*Scolopax minor*), 2019-2020. To test how the effect of sex, the same models were run for male and female woodcock.

Model	**K[a]**	**Delta AIC_c[b]**	**Cum wt[c]**	**LogLik[d]**
Male (n = 213)				
wind.spd[e] + temp[f]	2	0.00[g]	0.13	-10.70
wind.spd	1	0.12	0.26	-11.77
wind.assist[h]	1	0.38	0.37	-11.90
temp	1	0.67	0.47	-12.05
wind.spd + temp + wind.assist	3	1.30	0.54	-10.32
b.pres[i]	1	1.52	0.60	-12.48
wind.spd + temp + b.pres	3	1.68	0.66	-10.51
wind.spd + temp + wind.spd×temp	3	2.03	0.71	-10.68
temp + wind.assist	2	2.17	0.76	-11.78
wind.speed + wind.assist + b.pres	3	2.27	0.80	-10.80
temp + b.pres	2	2.36	0.84	-11.88
wind.assist + b.pres	2	2.39	0.88	-11.89
temp + wind.assist + temp×wind.assist	3	3.11	0.91	-11.22
wind.spd + temp + wind.assist + b.pres	4	3.14	0.94	-10.20
temp + wind.assist + b.pres	3	3.97	0.96	-11.65
temp + b.pres + temp×b.pres	3	4.40	0.97	-11.87
wind.assist + b.pres + wind.assist×b.pres	3	4.45	0.98	-11.89
temp + wind.assist + b.pres + temp×wind.assist	4	4.88	0.99	-11.07
temp + wind.assist + b.pres + wind.assist×b.pres	4	6.04	1.00	-11.65
Female (n = 235)				
wind.assist	1	0.00[j]	0.20	-13.10
temp	1	1.21	0.32	-13.70
wind.assist + temp	2	1.53	0.41	-12.85
wind.assist + b.pres	2	1.77	0.49	-12.97
temp + b.pres	2	2.66	0.55	-13.41
wind.spd	1	2.81	0.60	-14.50
b.pres	1	2.87	0.65	-14.54
wind.assist + temp + b.pres	3	2.89	0.70	-12.50
temp + wind.spd	2	2.96	0.75	-13.56
wind.assist + temp + wind.spd	3	3.33	0.79	-12.72
wind.assist + b.pres + wind.assist×b.pres	3	3.41	0.83	-12.76
wind.assist + temp + wind.assist×temp	3	3.56	0.86	-12.84
wind.assist + b.pres + wind.spd	3	3.72	0.89	-12.92
wind.assist + temp + b.pres + wind.assist×b.pres	4	4.52	0.91	-12.28
temp + b.pres + temp×b.pres	3	4.54	0.93	-13.33
temp + b.pres + wind.spd	3	4.57	0.95	-13.34
wind.assist + temp + b.pres + wind.spd	4	4.85	0.97	-12.45
wind.assist + temp + b.pres + wind.assist×temp	4	4.86	0.99	-12.45

Table D.4 Continued.

temp + wind.spd + temp×wind.spd	3	4.99	1.00	-13.56

[a] number of parameters

[b] Akaike Information Criterion corrected for a small sample size difference from top supported model

[c] cumulative model weight

[d] Log Likelihood

[e] wind speed

[f] temperature

[g] AICc 25.45

[h] wind assistance

[i] barometric pressure

[j] AICc 28.22

Table D.5. Linear mixed effect models evaluating what variables contribute to the distance American Woodcock (*Scolopax minor*) move between autumn stopover sites, 2017-2019. Only migratory movements known to occur over a one-day interval were included in the analysis. The analysis includes 360 migratory movements from 76 individuals.

Model	**K**[a]	**AIC_c**[b]	**Delta AIC_c**[c]	**AIC_c wt**	**Cum wt**[d]	**LogLik**[e]
w.speed[f]×wind[g]	6	4885.02	0.00	0.90	0.90	-2436.39
w.speed×wind + agesex[h]	9	4889.64	4.62	0.09	0.99	-2435.56
full	12	4895.38	10.36	0.01	1.00	-2435.24
w.speed + wind + agesex	8	4896.23	11.21	0.00	1.00	-2439.91
w.speed	4	4898.63	13.61	0.00	1.00	-2445.26
w.speed + wind×agesex	11	4901.65	16.63	0.00	1.00	-2439.45
wind	4	4911.42	26.40	0.00	1.00	-2451.65
wind + agesex	7	4914.90	29.88	0.00	1.00	-2450.29
wind×agesex	10	4919.35	34.33	0.00	1.00	-2449.36
null	3	4919.82	34.80	0.00	1.00	-2456.88
agesex	6	4923.27	38.25	0.00	1.00	-2455.51

[a] number of parameters

[b] Akaike Information Criterion corrected for a small sample size

[c] AICc difference from top supported model

[d] cumulative model weight

[e] Log Likelihood

[f] wind speed

[g] wind assistance

[h] adult female, young female, adult male, or young male

Table D.6. General linear models evaluating what variables contribute to the distance American Woodcock (*Scolopax minor*) move between spring stopover sites, 2019-2020. Only migratory movements known to occur over a one-day interval were included in the analysis. The analysis includes 184 migratory movements from 50 individuals.

Model	**K**[a]	**AIC_c**[b]	**Delta AIC_c**[c]	**AIC_c wt**	**Cum. wt**[d]	**LogLik**[e]
w.speed[f] + wind[g] + age[h]	5	2336.85	0.00	0.81	0.81	-1163.25
w.speed + wind + agesex[i]	7	2340.58	3.73	0.13	0.94	-1162.97
w.speed×wind + agesex	8	2342.71	5.86	0.04	0.98	-1162.94
w.speed×wind	5	2345.09	8.24	0.01	0.99	-1167.37
w.speed + wind×agesex	10	2346.82	9.97	0.01	1.00	-1162.77
wind + agesex	6	2349.03	12.18	0.00	1.00	-1168.27
full	11	2349.03	12.18	0.00	1.00	-1162.74
wind	3	2350.50	13.65	0.00	1.00	-1172.18
w.speed	3	2351.28	14.43	0.00	1.00	-1172.57
wind×agesex	9	2355.08	18.23	0.00	1.00	-1168.02
null	2	2355.74	18.89	0.00	1.00	-1175.83
agesex	5	2357.80	20.95	0.00	1.00	-1173.73

[a] number of parameters

[b] Akaike Information Criterion corrected for a small sample size

[c] AIC_c difference from top supported model

[d] cumulative model weight

[e] Log Likelihood

[f] wind speed

[g] wind assistance

[h] adult or young

[i] adult female, young female, adult male, or young male

Table D.7. General linear models evaluating the pace of American Woodcock (*Scolopax minor*) autumn migration, 2017-2019. Only individuals that successfully completed migration were included in this analysis.

Model	**K**[a]	**AIC$_c$**[b]	**Delta AIC$_c$**[c]	**AIC$_c$ wt**	**Cum. wt**[d]	**LogLik**[e]
Spatial tier (n = 90)						
end.latitude×end.longitude[f]	5	1048.17	0.00	0.52	0.52	-518.73
null	2	1050.73	2.56	0.15	0.67	-523.29
start.latitude	3	1051.93	3.76	0.08	0.75	-522.83
end.latitude	3	1052.46	4.29	0.06	0.81	-523.09
start.longitude	3	1052.84	4.67	0.05	0.86	-523.28
end.longitude	3	1052.85	4.68	0.05	0.91	-523.29
start.latitude×start.longitude	5	1053.71	5.54	0.03	0.94	-521.50
start.latitude + start.longitude	4	1054.11	5.94	0.03	0.97	-522.82
end.latitude + end.longitude	4	1054.25	6.08	0.03	1.00	-522.89
state[g]	10	1060.64	12.47	0.00	1.00	-518.93
Demographic tier (n = 90)						
base	5	1048.17	0.00	0.31	0.31	-518.73
age	6	1048.67	0.50	0.25	0.56	-517.83
sex	6	1049.24	1.07	0.18	0.74	-518.11
age + sex	7	1049.32	1.15	0.18	0.92	-516.98
age×sex	8	1050.94	2.77	0.08	1.00	-516.58
Condition tier (n = 75)						
base	5	877.60	0.00	0.58	0.58	-433.36
condition	6	879.69	2.09	0.20	0.78	-433.23
condition×age	8	880.18	2.58	0.16	0.94	-431.00
condition×latitude	8	883.64	6.04	0.03	0.97	-432.73
condition×sex	8	883.67	6.07	0.03	1.00	-432.74

[a] number of parameters

[b] Akaike Information Criterion corrected for a small sample size

[c] AIC$_c$ difference from top supported model

[d] cumulative model weight

[e] Log Likelihood

[f] end.latitude*end.longitude

[g] state or province of migration initiation

APPENDIX E: Cormack-Jolly-Seber Analysis with each Season and Tag Type Combination

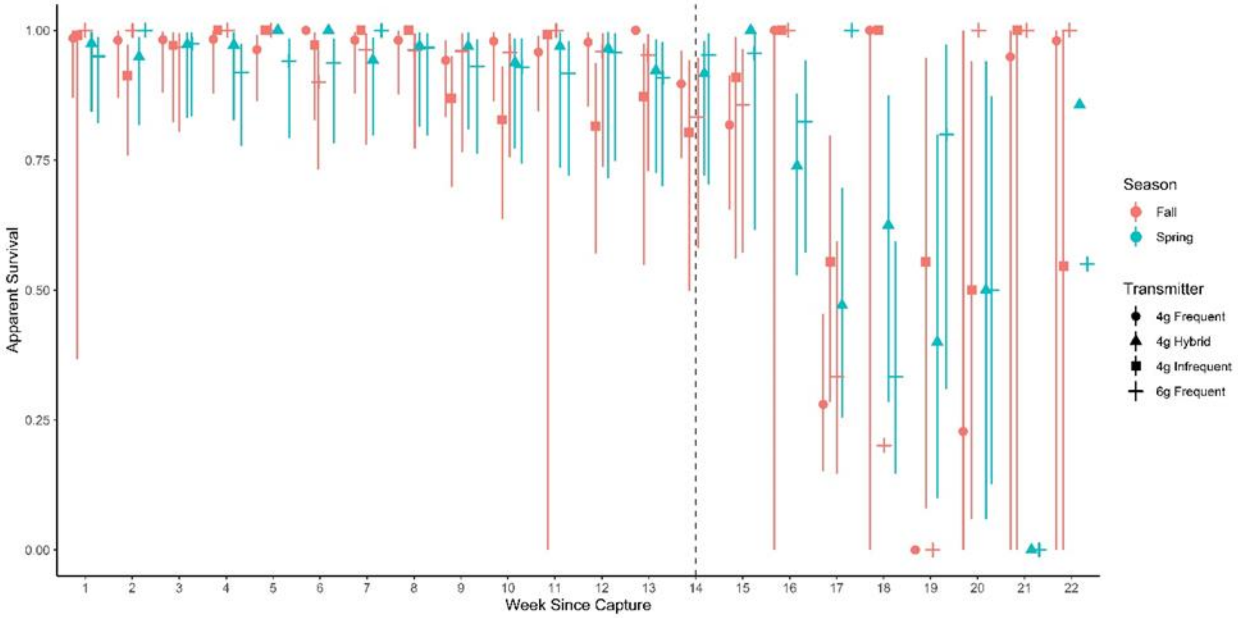

Figure E.1. Weekly apparent survival of American Woodcock (*Scolopax minor*) since capture during both the spring and fall. We subset each season by tag type and transmitter schedule to evaluate non-convergence patterns. Non-convergence was defined as unrealistic parameter estimates or confidence intervals. The dashed line at week 14 represents the last week transmitter batteries were expected to last.

BIOGRAPHY OF THE AUTHOR

Alexander Fish was born in Roseville, Minnesota on March 30, 1988. He was raised in Champlin, Minnesota and graduated from Champlin Park High School in 2006. He attended the University of Minnesota and graduated in 2009 with a Bachelor of Science degree in Fisheries, Wildlife, and Conservation Biology. After working as a temporary technician for a few years, he completed his Master of Science degree in Fisheries, Wildlife, and Conservation Biology at North Carolina State University in the spring of 2017. He then enrolled in the Wildlife Ecology program at the University of Maine in the fall of 2017. Prior to graduation, Alexander accepted a position as an Upland Game Bird Biologist with Rhode Island Division of Fish and Wildlife. Alexander is a candidate for the Doctor of Philosophy degree in Wildlife Ecology from the University of Maine in December 2021.