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THE INFLUENCE OF PRE-MIGRATORY BODY COMPOSITION AND HABITAT QUALITY ON FALL MIGRATION IN THE AMERICAN WOODCOCK (*SCOLOPAX MINOR*)

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THE INFLUENCE OF PRE-MIGRATORY BODY
COMPOSITION AND HABITAT QUALITY ON FALL
MIGRATION IN THE AMERICAN WOODCOCK
(*SCOLOPAX MINOR*)

BY
CLAYTON L. GRAHAM

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
IN
BIOLOGICAL AND ENVIRONMENTAL SCIENCES

UNIVERSITY OF RHODE ISLAND

2020

MASTER OF SCIENCE THESIS

OF

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UNIVERSITY OF RHODE ISLAND
2020

ABSTRACT

Young forests and the wildlife that are dependent upon them are uncommon and declining within the Northeastern U.S. As such, forest management plans have been implemented to create and maintain young forest for wildlife, including migratory birds such as the American Woodcock (*Scolopax minor*) that use young forest to meet their life history needs. Given that most Northeastern woodcock migrate between more northerly breeding areas and southern wintering areas, information about how post-breeding habitat quality and body composition carry over to influence fall migration strategies and residency is important for their management but currently unknown. I investigated how habitat quality prior to fall migration influenced the timing of departure, departure body composition and subsequent migratory phenology of the American Woodcock. First, I validated the non-destructive deuterium dilution method for estimating body composition of woodcock prior to departure in fall and used these models to estimate the rate of fattening for free-living fall-staging woodcock in Rhode Island (Chapter 1). Second, I assessed the influence of post-breeding habitat quality on departure body composition and fall migration patterns in a southern New England breeding population of American Woodcock (Chapter 2).

In Chapter 1, I report the first validation of the deuterium-dilution method for estimating the body composition of a fall staging shorebird. I captured male ($n=35$) and female ($n=13$) woodcock in the fall of 2018 and 2019 (September – November), directly measured the body composition of 20 woodcock and used predictive models to estimate the body composition of fall-staging 28 woodcock which were released to continue on fall migration. I directly measured for each wild-caught woodcock ($n =$

20) their total body water, age, body mass, and fat score, and then used multiple regression and measured whole-body water and body composition to estimate the whole-body lean mass and fat mass of woodcock with relative errors of 1.37% and 11.26 % for the wet lean mass and fat mass, respectively. Estimates of body composition using only morphometrics such as fat score were poor predictors of body composition. I used the estimated fat at capture to assess the rate of fattening in free-living fall staging woodcock ($n = 28$) in southern New England. On average, woodcock initiated fat deposition on September 22, and deposited fat at a rate of 0.42 ± 0.09 g fat per day⁻¹. Our results suggest that the deuterium dilution method offers a reliable, accurate and non-destructive method to estimate the body composition of woodcock during the fall. This information can be used by managers as an effective tool to assess how habitat management affects body composition dynamics at staging and stopover sites used by woodcock.

In a complimentary study (Chapter 2), I used VHF and satellite telemetry to track woodcock prior to and during fall migration and quantified the pre-migratory habitat quality and departure body composition for fall migrating woodcock. Woodcock that overwintered within Rhode Island had lower fat upon capture, as well as used lower quality habitat during the fall than woodcock that migrated. Woodcock migrated after reaching a threshold of 27 g of fat. Woodcock that departed earlier were long-distance migrants that had inhabited higher quality landscapes prior to migration, stored less fat upon departure, migrated faster, used more stopovers during migration, and migrated to more southern wintering areas. In contrast, woodcock that departed later were short-distance migrants that had inhabited lower quality landscapes prior to

migration yet stored more fat upon departure, used fewer stopovers during migration, and migrated to more northerly wintering areas. During migration, woodcock used on average 1.07 ± 0.26 stopovers in Virginia, North Carolina, Maryland, Delaware, New Jersey, Connecticut, New York, South Carolina and Georgia, and migrated 1149.18 ± 105.57 km along the Atlantic Coastal Plain to wintering grounds distributed from Maryland to Alabama. I found that woodcock that breed in southern New England are obligate partial migrants that include residents, and shorter- and longer-distance migrants. Given the anticipated effects of climate change and urbanization on partial migration strategies, the proportion of residents overwintering in Rhode Island or using short-distance migratory strategies may increase, and as such these overwintering areas deserve conservation and management attention.

ACKNOWLEDGMENTS

The research presented in this thesis would not have been possible without the mentorship, advice and guidance of my advisor, Scott McWilliams. Scott, I couldn't have met you at a better time in my life and will always feel indebted to the care, mentorship and support I received as your graduate student. Thank you for your time invested in me, patience, encouragement of pie-in the sky ideas, and facilitation of an amazing environment to explore and discuss science. Without a doubt, these last three years will influence the rest of my career and many aspects of my life. I would also like to thank Tanner Steeves, the state coordinator, for help with logistics related to field work and research. Tanner, thanks for your help with all aspects of field work from catching woodcock, to coordinating additional help, access to field sites and your research input.

I would also like to thank my committee members, Bill Buffum, Gavino Puggioni, and Howard Ginsberg. Bill, the discussions we had related to spatial analysis, GIS, and catching up about the progress of my research and experiences in the field, were a true joy. Thank you for your helpfulness with GIS, advice on my research questions and methods, and always making the time to catch up and chat. Thank you, Gavino, for your help with statistical advice, for serving on my committee and in providing an excellent course on ecological statistics. Thank you to Howard Ginsberg for chairing my defense.

I appreciated the opportunity to mentor Coastal Fellows including Sophia Theilacker, Jess Kaelbein, Gwen Emery, and Alicia Jones and could not have asked for a better crew of passionate, hardy and curious undergraduate students to work

with. Sophia, thank you for your hard-work, organization, cheerful disposition and interest in birds. It's been awesome getting to know you and to watch your interest in birdwatching blossom. Jess, I appreciated your passion for conservation and how committed you were to the project, from driving all the way from Attleboro each day to lugging around the cover board through the swamp for your coastal fellow project. Thank you both for your patience, hard-work, the lively discussions we had about woodcock ecology, and for making the 2018 field season so successful. To the 2019 field crew, Gwen and Alicia, I'm incredibly grateful for the skill and time you both invested in the 2019 field season. Gwen, it's clear how eager and dedicated you are to wildlife and conservation; thank you for your field work aplomb, and excitement towards learning telemetry skills and working with birds. Alicia, I so appreciated your devotion and field skills you brought to the project given your other commitments, and your enthusiasm for science and spatial ecology is absolutely infectious. I am massively indebted to the help offered by Patrick Woodward and Liam Corcoran, from scouting to telemetry and catching woodcock in the middle of night, it was an absolute joy to work with and get to know you both. Each of your collective efforts contributed substantially to my research and the success of this project. I would also like to thank the countless volunteers who helped scout and band woodcock in the spring of 2018 and 2019.

I owe a deep amount of gratitude to members and past graduates of the McWilliams Lab, and couldn't have asked for a more kind and welcoming group of colleagues to work with. Roger Masse, thank you for your availability and willingness to help with all questions woodcock, and for your past work which contributed

substantially to this thesis. Erin Harrington, Colby Slezak and Steve Brenner, thank you for being part of the woodcock branch of the lab and enriching my knowledge of the ecology and peculiarities associated with woodcock. Colby, thanks for all of your help with catching and tracking woodcock, and I wish you the best of luck as you continue your woodcock research. Steve, I especially am indebted to your knowledge of field sites in Rhode Island and field work with woodcock, and absolutely relished our morning chats about woodcock and all things ornithology. Martina Müller, Abby Frawley and Wales Carter, thank you both for being excellent officemates and friends, helping scout and catch woodcock, and always being there to enjoy an early morning or afternoon cup of coffee together. Dustin Meattey and Juliet Lamb, thank you for your help with all sorts of spatial ecology and GIS questions, and for your advice on my research and statistical analysis. I especially need to thank Kristen DeMoranville and Clara Cooper-Mullin, both of whom helped with all aspects of this project from statistical advice to editing drafts and helping with field work, and contributed substantially to how I approach ecology and science. One of the things I missed most before starting graduate school was having discussions on current science in ornithology, and conversations on hypotheses and how to potentially address them: thank you all for cultivating a space to learn, be curious, and address the unanswered questions.

I would be remiss without mentioning others who have helped me throughout the course of this thesis. Deb Bourassa, much of my work couldn't have been done without your supreme organization skills and knowledge of the administrative inner workings. A massive thank you for all your help with processing paper work,

managing the ins and outs of working with coastal fellows, navigating payment for field supplies and the ARGOS account each month, and being exceedingly reliable. Thank you to Scott Comings and The Nature Conservancy for granting access for the usage of the Francis Carter Nature Preserve and Tillinghast Management Area. I am indebted to the support and advice given by Erik Blomberg and Alex Fish. Erik and Alex, I couldn't have asked for better collaborators; thank you for your time, effort and intention you placed into the collaboration. I would also like to thank Sarah Mabey and Denny Taylor who helped provide foundational knowledge and field experiences which informed many aspects of this thesis and my development as a field biologist.

Funding for my research was provided by the Rhode Island Department of Environmental Management via USFWS Wildlife and Sport Fisheries Restoration to RI project W23R (Job 1-12), the Rhode Island Agricultural Experiment Station and the Department of Natural Resources Science at University of Rhode Island. Thank you to the Ruffed Grouse Society for donating nearly half of our GPS tags. Thank you to those who helped secure funding for this project.

Finally, I especially have to thank my family and friends who have supported me throughout graduate school. Thank you, Roberto and Ellen Vargas, Haley Hardwick-Witman, Tillie Leonard-Fritzmeier, Jack Hartman, and Brady Shambaugh for making April and I feel so welcome in Providence, and providing much needed levity. Mom, from our morning bird-watching/ sketching adventures as a kid and in middle school, to always making time for birding on family vacations, thank you for fostering and encouraging my dreams. To my brother Nate and sister-in law Lindsay,

it's hard to convey how thankful I am to have you both in my life; I couldn't ask for a better family. Thank you both for always providing familial support when I was working on my graduate work, exceptional advice, phone check ins at odd times not limited to being within a swamp, and much needed comic relief. Lastly, I absolutely have to thank my fiancé April. April, thank you for your constant trust, steady love and encouragement over the last three years. Even when coming home in the early morning from catching woodcock, I still can't get over that you always managed to meet me with a smile! Small, yet significant, moments like this, going for a quick walk, birding in between writing and tracking or sharing meals and morning coffees with you were true wings that supported this thesis. I hope to help you pursue your dreams as you have encouraged me to pursue mine, and I love you with all of my heart.

DEDICATION

This thesis is dedicated to the memory of:

Jeff Graham; an uncommon man and father, fiercely loving, kind and beyond
generous.

PREFACE

This thesis was prepared according to the Manuscript Format guidelines established by the Graduate School at University of Rhode Island. Manuscript 1, “Body composition of American Woodcock during fall staging: a validation of the non-invasive deuterium dilution method”, is formatted for publication in the *Journal of Ornithology*.

Manuscript 2, “Cross-seasonal effects in the American Woodcock: how conditions prior to fall migration relate to variation in migratory strategy and its implications for conservation”, is formatted for publication in the journal *The Condor*.

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CHAPTER 1

“Body composition of American Woodcock during fall staging: a validation of the non-invasive deuterium dilution method”

by

Clayton L. Graham^{1,2}, and Scott R. McWilliams¹

Is submitted to *Journal of Ornithology*

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Abstract

We conducted the first validation of the deuterium dilution method as a nonlethal technique for estimating the body composition of a shorebird during fall staging as birds fatten in preparation for their migration. For this validation, we captured male ($n = 12$) and female ($n = 8$) American Woodcock (*Scolopax minor*) in the fall of 2018 and 2019 in southern New England, USA. We developed predictive models for estimating body composition of woodcock given each bird's body mass and deuterium space, a proxy for total body water space, estimated using the deuterium dilution method. Accuracy and precision of these predictive models was assessed by comparing the model predictions with directly measured body composition. The top models predicted whole-body lean and fat mass with a relative error of 1.37% and 11.26%, respectively. In comparison, conventionally used morphology-based condition indices were poor predictors of fat mass in fall-staging woodcock. We applied this method to accurately estimate body composition dynamics of free-living woodcock ($n = 28$) during fall staging, a period of fattening in the annual cycle that is pertinent to subsequent migratory movements, phenology and survival, and habitat management for woodcock. On average, woodcock initiated fat deposition on September 22, and deposited fat at a rate of 0.42 ± 0.09 g fat per day⁻¹. This nonlethal technique also has broad applicability to other migratory birds that show substantial changes in body composition as they prepare for key life history events such as migration.

Introduction

Many birds alter their body composition in preparation for seasonal changes, and the extent of these seasonal changes in body composition often has important implications for their ecology and management (Karasov and Pinshow 1998; Williams et al. 1999; Battley et al. 2001; Servello et al. 2005). For instance, the body condition of birds just prior to migration affects the timing of their departure, rate of migration, and distance traveled prior to resting at a stopover site (Deppe et al. 2015; Buler et al. 2017). For northern-breeding waterfowl and shorebirds, body condition of females at staging areas during spring migration affects the timing of arrival at the breeding grounds and subsequent reproductive success (Alisauskas and Ankney 1992; Tulp et al. 2009; Eichhorn et al. 2010). Body condition also may indicate the quality of a given environment because, for example, anthropogenic disturbance and development, and exposure to disease and parasites, can restrict access to higher quality resources and thus reduce the rate of fat deposition at stopover sites used during migration (Klaassen et al. 2012). Therefore, understanding the dynamics of body composition of birds across seasons provides important insights into how birds prepare for key life history events such as migration and how this is influenced by the environment.

A variety of methods have been developed to assess body composition of animals (Blem 1990; Speakman et al. 2001). Directly measuring body composition (e.g, fat-free or lean mass, fat mass) is most accurate but requires killing the animal (Ellis and Jehl 1991). Indirect methods use nonlethal techniques to estimate body composition although all such methods must be validated (Speakman et al 2001; McWilliams and Whitman 2013). The deuterium dilution method is an indirect method that uses the dilution of injected heavy water within an animal to estimate total body

water (Speakman et al. 2001). Given that an individual's total body water is stored almost entirely within their lean (fat-free) mass, and fat is relatively water free (<3% water), both lean and fat mass of an animal can be predicted given an estimate of total body water and measurement of body mass (Speakman et al. 2001; Eichhorn and Visser 2008). To date, the deuterium dilution method has been validated and successfully used to estimate body composition of four species of passerines (McWilliams and Whitman 2013), Barnacle Geese (Eichhorn and Visser 2008), and Common Eider (Beuth et al. 2016). Our goal was to validate the deuterium dilution method for estimating body composition of fall pre-migratory American Woodcock (*Scolopax minor*) that inhabit southern New England as they fatten in preparation for their fall migration. To our knowledge this is the first validation of the deuterium dilution method for estimating body composition of a shorebird, and the first estimates of fattening rates of woodcock during fall staging.

Methods

Field Methods

During September 1 to November 20, 2018 and 2019, 110 American Woodcock were captured using handnets or mistnets at roosting sites within fields in Rhode Island Department of Environmental Management Areas and a Nature Conservancy preserve (see Table A.1 for location information). Each bird was sexed in the field using their wing chord, culmen length, and width of outer 3 primaries, and aged using molt limits and secondary feather patterns as hatch-year (HY) or after-hatch-year (AHY) (Mendall and Aldous 1943, Sheldon 1967). We also visually estimated the fat score (0-5; Helms and Drury, 1960) and measured the weight of each bird to include these

covariates within our predictive models. We selected the 20 Woodcock used for the validation study from the larger group of captured birds ($n = 110$), so that individuals represented the weight range of males (130–180 g) and females (170–230 g) encountered during fall in southern New England. We similarly selected an additional 28 woodcock to which we applied the deuterium dilution method (details below) and then immediately released these individuals. We used the predictive models developed from the 20 validation birds to estimate the body composition of these additional 28 released bird and then estimated the timing and rate of fattening of woodcock ($n = 48$) during fall staging.

We directly measured total body water and body composition (lean and fat mass) of each of the 20 validation birds, and estimated deuterium space (a proxy for total body water space) of each of the 20 validation birds plus the additional 28 released birds following the methods described in Beuth et al. (2016). In brief, while still in the field and within 30 minutes of capture, we used a prefilled 1 mL insulin syringe (22004270, Fisher Scientific, Pittsburgh, PA, USA) to inject each woodcock in the pectoral muscle with 297 ± 0.99 mg (mean $\pm$ SE) of 99.9% deuterium oxide (Sigma-Aldrich, St. Louis, MO, USA). Each syringe was weighed before and after injection to determine the exact amount of deuterium injected. After injection, birds were placed in cloth bags for 60 ± 3 min to allow the deuterium to equilibrate in their body pool of water. We then collected ca. 100 μ L of blood into heparinized capillary tubes (22-362566, Fisher Scientific, Pittsburgh, PA, USA) after brachial venipuncture. The bird was placed back in the bird bag while we flame-sealed the glass heparinized capillary tubes. All blood samples in the sealed glass tubes were stored at 4.4°C until

laboratory analyses. We then released the 28 woodcock used only to estimate the timing and rate of fall fattening, and euthanized via cervical dislocation each of the 20 woodcock selected for the validation study. We placed carcasses within two Ziploc freezer bags and stored frozen specimens (-17°C) until we completed total carcass analysis in the laboratory. In sum, we were able to estimate body composition of 48 woodcock throughout the fall staging period. All methods were approved by the University of Rhode Island Institutional Animal Care and Use Committee (Protocol No. AN 10-02-017).

Laboratory Methods

A deuterium validation study involves developing a predictive relationship between body composition measured directly from carcass analyses and deuterium space (a proxy for total body water space) estimated by deuterium dilution, as described in Eichhorn and Visser (2008) and McWilliams and Whitman (2013). Below we first describe the direct measurement of each body component from the carcass analysis, then the methods used to estimate deuterium space from the deuterium dilution, and finally the statistical analyses used to develop the predictive relationship.

Measuring Total Body Water

Thawed validation birds were weighed, shaved and plucked free of their feathers, and then the shaved carcass was reweighed to determine by difference each bird's feather mass. We homogenized each shaved carcass four times (Floor Mixer, Hobart, Troy, OH, USA) and then dried 4 10°C g samples of homogenized carcass in aluminum trays at 90°C until the homogenate reached a constant mass. Water content (%) of each bird

was determined as the difference in weight between the 10-g fresh sample and dried homogenate divided by the fresh homogenate multiplied by 100. Total body water (TBW) was the percent water content multiplied by the shaved carcass mass.

Measuring Fat Mass, Lean Mass, and Ash Content of Validation Birds

We dried an additional 4 10-g samples of each homogenized carcass in aluminum trays at 60°C until constant mass (Dobush et al. 1985). Each dried sample was then further homogenized using a mortar and pestle. Ten grams of dried homogenate was placed in two previously dried (60°C) ceramic thimbles and refluxed in a Soxhlet extractor with petroleum ether for a minimum of 8 hours (Dobush et al. 1985). The thimbles were removed, dried for four hours at 60°C, and then reweighed. Fat content (%) of each thimble was determined by taking the difference between the weight of dry sample prior to extraction and the fat-free dry sample divided by the dry sample mass multiplied by 100. We used the mean % fat content of the replicates multiplied by the shaved carcass mass to determine the total whole-body fat mass. Two 5.0 g samples of lean-dry sample were placed within a dry ash oven at 550°C to determine mineral (ash) content. Total whole-body lean dry mass was estimated as the difference between shaved carcass dry mass and the combined total fat mass and mineral content.

Measuring Protein

Each pair of replicate fat-extracted samples from each carcass were combined and we used a mortar and pestle to further homogenize each lean-dry sample. We measured 3 1-mg replicates of lean, dry homogenate into 4 × 6-mm aluminum capsules

(Costech, Valencia, CA, USA) and then directly measured nitrogen content using a continuous-flow isotope ratio mass spectrometer (Elementar Americas, Mount Laurel, NJ, USA). Protein content was determined by multiplying the nitrogen content by 6.25 (Parker and Holm 1990). As expected, total protein estimated from nitrogen content was closely related to total lean dry mass across individuals ($r^2 = 0.91$, $P < 0.001$), so we report below only the results for total lean dry mass.

Measuring Deuterium Concentration

Each blood sample was micro distilled following methods outlined in Nagy (1983) to separate the blood water from the whole blood sample. Using an FT-IR spectrophotometer (L160000A Perkin-Elmer, Norwalk, CT, USA), we measured deuterium concentration in five 1 μ L subsamples of blood water, with the last three samples retained and the first two samples discarded to reduce carryover from previous samples. We converted deuterium enrichment in parts per million (ppm) to atom percent concentration using the following equation:

$$\text{Atom \%} = (100 + 0.0001557 \times (X/1,000 + 1)) / (1 + 0.0001557 \times (X/1,000 + 1)) \quad (1)$$

where 0.0001557 was the mole fraction of deuterium in Vienna Standard Mean Ocean Water (Coplen et al. 2002) and X was the measured deuterium enrichment (ppm) of the sample.

Estimating Total Body Water

We used the following equation from Karasov and Pinshow (1998), McWilliams and Whitman (2013) and Beuth et al. (2016) to estimate deuterium space (S , a proxy for total body water space) of the 20 American Woodcock used for the validation study plus the 28 birds that were injected with deuterium, bled approximately 60 min after injection, and then released.

$$E = 100 \times \{0.999 \times (B/20) / [0.999 \times (B/20) + 0.001 \times (B/18) + (S/18)]\} \quad (2)$$

where E was the measured enrichment (atom %) of deuterium in the blood water, 0.999 was the proportion of injected solution that was deuterated water, 0.001 was the proportion of injected solution that was unlabeled water, B was the measured injection mass in grams, 20 was the molar mass of deuterated water, 18 was the molar mass of unlabeled water, and S was deuterium space in grams. We multiplied the measured deuterium enrichment by 1.16 to correct for FT-IR spectrophotometer drift that produced a consistent underprediction of the deuterium space (50–80% is biologically reasonable; McWilliams and Whitman 2013). This equation can be rearranged given we know the actual amount of deuterium injected (B) and measured enrichment (E) to estimate the deuterium space (S):

$$S(g) = 18 \times \{ \{ 100 \times [0.999 \times (B/20)] \} / E - [0.999 \times (B/20)] - [0.001 \times (B/18)] \} \quad (3)$$

Statistical Analysis

For the validation study, we used multiple regression analysis to create predictive models to estimate wet lean (fat-free) and fat mass of woodcock given their deuterium

space (S), and body mass, structural size, age, and sex. Structural size (wing chord, culmen length, width of outer 3 primaries) was condensed into orthogonal estimates using a principal component analysis (PCA), which were then used in the multiple regression analysis. A Levene's test was used to check for normality and homoscedasticity for both the regression and PCA. We used the R 3.3.2 statistical open-source software (www.r-project.org), and the *segmented* and *caret* packages to perform all statistical analyses with an alpha level of 0.05 for all statistical tests (Kuhn 2008, Muggeo 2008).

Models were selected using Akaike's Information Criterion corrected for small sample sizes (AIC_c), with a Leave-One-Out Cross Validation for model selection. Accuracy and precision of all predictive models was assessed in part by r^2 values and the root mean square error (RMSE). We calculated RMSE using the following equation: $\sqrt{(\sum(\sqrt{p} - \sqrt{m})^2/n)}$, where ($\sqrt{p}$) is the predicted value, ($\sqrt{m}$) was the measured value, and n was the number of birds over which the squared difference between predicted and measured was summed (Olden and Jackson 2000). Since coefficients of determination such as RMSE are not always indicative of error when evaluating the usefulness of regression equations (e.g., Skagen et al. 1993), we also present absolute and relative errors of the predictive models (McWilliams and Whitman 2013). Each individual bird's absolute error (g) was calculated as $|\text{predicted} - \text{measured}|$ and the relative error (%) as $(\text{absolute error}/\text{measured}) \times 100$.

We used the top predictive models generated from the validation birds to estimate the body composition of the 28 released birds. We then pooled estimates of body composition for released and validation birds ($n = 48$) and fit a nonlinear curve

to describe the overall change in body composition during the fall (Sept – Nov). We used piecewise linear regression to estimate the date of fat deposition initiation and then used linear regression to estimate the rate of fattening of woodcock during the fall staging period (~ Mid Sept – Nov).

Results

Capture of Woodcock

Validation females ($n = 8$) included two HY and six AHY birds and body mass averaged 200.4 ± 6.71 g (range 170–230 g; Table 1). Validation males ($n = 12$) included eight HY and four AHY birds and body mass averaged 149.5 ± 4.22 g (range 134–180 g; Table 1).

Body Composition and Size of Woodcock

Female woodcock were on average 51 g heavier, had 32 g more wet lean mass, had 22 g more total body water, and were structurally larger than males (Table 1). Male and female woodcock had similar dry lean mass and fat mass (Table 1). The first principal component (PC1) accounted for 81% of the variance with $PC1 = \text{culmen} (0.552) + \text{primary width} (0.581) + \text{wing chord} (0.597)$. Principal component two (PC2) accounted for 12% of the variance with $PC2 = \text{culmen} (0.813) + \text{primary width} (-0.533) + \text{wing chord} (-0.233)$. Principal component three (PC3) accounted for 7% of the variance with $PC3 = \text{culmen} (-0.183) + \text{primary width} (-0.615) + \text{wing chord} (0.766)$. Given that PC1 explained >80% of the variance in structural size, we used only PC1 as a measure of structural size in our validation models.

Predictive Models for Estimating Body Composition of Woodcock

Deuterium space (S) estimated using the deuterium dilution method was strongly correlated with TBW where $S = (26.973/(E*1.16)) - 0.269429$, $r^2 = 0.98$. As expected, the deuterium space overpredicted TBW by $9.82 \pm 0.9851\%$, which is within the overprediction range of previous studies (8.63–20.86%; Karasov and Pinshow 1998, Speakman et al. 2001, Eichhorn and Visser 2008, McWilliams and Whitman 2013, Beuth et al. 2016).

The best supported model for predicting wet lean mass (Table 2) included age, body mass, fat score, and deuterium space (Model 1). The most parsimonious model (fewest covariates) to predict wet lean mass included body mass, fat score and deuterium space (Model 2) although this model was not as well supported given the lower delta AIC (>2.0).

The best supported and most parsimonious model for predicting fat mass (Table 3) included body mass, fat score, and deuterium space (Model 1). Final predictive models using the deuterium dilution method predicted wet lean mass with an absolute error of 2.07 g and relative error of 1.37%, and fat mass with an absolute error of 3.44 grams and 11.26% relative error (Table 4). Models with fat score alone were not as accurate at predicting fat mass (absolute error of 6.74 g, relative error of 27.38%) (Table 3, Model 6). Predictive models using fat score to estimate fat mass explained only 51% of the variation in fat mass (Table 3, Model 6), whereas final predictive models using the deuterium dilution method to estimate fat mass (Table 4) explained 92% of the variation in fat mass (Fig. 1).

Rates and Timing of Fattening During Fall Staging for Woodcock

The 28 released birds were captured between September 3 and November 5, 2018 ($n = 13$) and 2019 ($n = 15$). In early September, woodcock are completing their pre-basic molt (Owen and Krohn 1973) and the subset of individuals captured during that time were apparently losing weight. Woodcock started to build fat stores after September 22 at a rate of on average 0.42 ± 0.09 g fat per day⁻¹ ($r^2 = 0.38$, $p = <0.001$; Fig. 2). Estimated protein content was not correlated with date ($r^2 = 0.05$, $p = 0.10$) indicating that woodcock did not build lean mass prior to fall migration. In 2018 and 2019 woodcock departed Rhode Island in fall during mid to late November (i.e. after Julian date 320; Graham and McWilliams, unpublished).

Discussion

We present the first validation of the deuterium dilution method to estimate the body composition of a shorebird, the American Woodcock, during their fall pre-migration fattening period. The resulting predictive models for nonlethally estimating whole-body fat and wet lean mass of woodcock require the visual estimation of both fat score and age, and the measurement of body mass and deuterium space, a proxy for total body water space. The predictive power of our model (relative error of $1.37 \pm 0.31\%$ for lean mass and $11.26 \pm 2.52\%$ for fat mass) is similar to previous studies that have used the deuterium dilution method to estimate body composition of birds other than shorebirds. Beuth et al. (2016) predicted the wet lean and fat mass of Common Eider with a relative error of $2.0 \pm 0.4\%$ and $20.2 \pm 3.9\%$, respectively. Eichhorn and Visser (2008) predicted the wet lean and fat mass of barnacle geese with a relative error of

$1.2 \pm 1.4\%$ and $10.1 \pm 10.1\%$, respectively. McWilliams and Whitman (2013) predicted the wet lean and fat mass for three passerines with a relative error of $0.96 \pm 0.70\%$ to $5.31 \pm 1.55\%$ and $26.36 \pm 18.6\%$ to $34.13 \pm 10.25\%$, respectively. The deuterium dilution method provides reasonably accurate estimates of body composition for a variety of birds - within 1–3% for fat-free lean mass and 10–34% for fat mass - and this accuracy is adequate enough to detect seasonal changes in body composition, given that the whole-body wet lean and fat mass of migratory birds can change seasonally by as much as 25-50% (Blem 1990; Piersma and Van Brederode 1990; Seewagen and Guglielmo 2011).

The estimates of fat mass for woodcock during their fall pre-migration fattening period that we obtained using the deuterium dilution method were more accurate than those obtained using other nonlethal techniques. For example, fat score predicted whole-body fat mass with a relative error of $27.38 \pm 6.12\%$ (Table 3, Model 6) and was much less accurate than our best fit model using body mass, fat score, and deuterium space (Table 3, Model 1 and Figure 1). In contrast, McWilliams and Whitman (2013) found that fat mass of songbirds with fat scores greater than 1 could be more accurately predicted given only fat score compared to using total body electrical conductivity (TOBEC) or the deuterium dilution method. However, most of these songbirds had fat scores of <1.0 and the fat mass of these leaner birds was more accurately predicted using the deuterium dilution method. In comparison, body mass, fat score, and the first principal component predicted whole-body fat mass for fall woodcock with a relative error of $25.36 \pm 5.67\%$ (Table 3, Model 5), which is more than double the error of our best fit model that included deuterium space (Table 3,

Model 1). Fat score may be a poor predictor of actual fat mass within woodcock because like other birds they may deposit fat subcutaneously or in areas not visible when assessing fat score (Seewagen and Slayton 2008; Labocha and Hayes 2012). TOBEC has been used to estimate body composition of several species of shorebirds although relative error for predicted fat mass was, for example, 30–40% for intraspecific models and 46 – 73% for interspecific models (Lyons and Haig 1995). In general, TOBEC is not accurate for estimating fat mass for birds lighter than 215 g, making TOBEC unsuitable for the analysis of body composition of woodcock (Morton et al. 1991; McWilliams and Whitman 2013). We conclude that the deuterium dilution method provides the most accurate tundra-tested (McWilliams and Whitman 2013) field method to predict fat mass of woodcock and likely most other shorebirds.

Understanding the dynamics of body composition of woodcock as well as other migratory birds is important to managers and biologists because fat and protein stores affect migratory movement, phenology, and success (Stutchbury et al. 2011; Bruggink et al. 2013). For instance, woodcock initiate migration only after acquiring enough fat stores and completing their pre-basic molt (Owen Jr and Krohn 1973). Fall staging woodcock that inhabited poorer-quality landscapes (e.g., lower densities of earthworms) moved greater distances in search of food and this may delay the accumulation of fat and affect the tempo and pace of their subsequent migration (Doherty et al. 2010). Many migratory birds shift their diets and thus habitats in late-summer to track shifts in resource availability, and this may affect their ability to acquire sufficient fuel stores to use during fall migration (Connors 1984; Leinaas and Ambrose 1999; Churchwell et al. 2018)). For example, fall-staging semipalmated

sandpipers in the Bay of Fundy selected foraging sites based on the availability of lipid-rich *Corophium volutator* and biofilms to be able to deposit enough fat to fuel their non-stop flight to South America (Maillet and Weber 2006; Quinn and Hamilton 2012). Many species of post-breeding songbirds also substantially switch their habitat use during fall, in this case from mature forest to early successional habitat where high fruit densities advance the molt and body condition of birds (Vitz and Rodewald 2006; Stoleson 2013). Thus, providing adequate resources and appropriately managing habitat for birds as they prepare for migration requires knowing where and when birds initiate their preparations for migration (i.e., the dynamics of body composition) and how best to manage habitat to provide the resources they need.

Although survival rates are relatively high for woodcock in the fall in comparison to the spring, a reduction in fat stores and body mass is associated with increased mortality and may in turn reduce recruitment rates (McAuley et al. 2005). For example, a reo-virus outbreak in Virginia and New Jersey substantially reduced the body condition of woodcock resulting in a die-off of these local populations (Docherty et al. 1994). Survival rates may also be reduced during summer droughts, and drought conditions which continue into fall staging may slow or delay molting strategies and subsequently inhibit the accumulation of fat stores for fall migration (Sepik et al. 1993). Thus, information on the dynamics of woodcock body composition can provide managers information on population susceptibility to periodic disturbances (e.g., drought, disease), and how these events affect population dynamics.

We estimated that woodcock in southern New England fattened at a rate of 0.42 ± 0.09 g fat per day⁻¹, a 0.24% increase in body mass per day, during the fall pre-

migration period. Sharp-tailed Sandpipers (*Calidris acuminata*) had similar fattening rates during the early pre-migratory fattening period (males: 0.4 ± 0.2 g day⁻¹, females: 0.3 ± 0.2 g day⁻¹) but then accelerated their fattening rate starting in mid-September as they prepared to migrate on average 7100 km (Lindström et al. 2011); males: 4.2 ± 0.3 g day⁻¹ or 6.3% increase relative to lean body mass (LBM) per day; females: 3.2 ± 0.3 g day⁻¹ or 5.7% of LBM per day). Red Knots (*Calidris canutus*) staging in fall at Ottenby, Sweden deposited fat on average by 2.8% of LBM per day⁻¹ (Helseth et al. 2005). Fall-staging Red-Necked Phalaropes (*Phalaropus lobatus*) deposited fat at a rate of 1.0 g per day in preparation for their long distance flight from New Brunswick to South America (Mercier 1985). In general, our estimates of fattening rates of fall-staging woodcock in southern New England conform to the trend observed by others that shorebirds departing higher latitudes and covering larger migratory distances deposit fat at a greater rate than shorebirds migrating from lower latitudes (Aharon-Rotman et al. 2016).

The deuterium dilution method and the predictive models presented here provide biologists an accurate and repeatable method to nonlethally estimate lean and fat mass of woodcock at fall staging and stopover locations. This method also provides managers and ecologists an effective tool to address how habitat management practices affect the body composition dynamics of woodcock and their preparation for fall migration (Moore and Yong 1991; Petit 2000). Future validation studies are needed to estimate the body composition of male and female woodcock during the spring, as their physiology and body composition dynamics during spring may differ from that in fall because it includes preparation for migration as well as breeding.

Acknowledgements

We thank the following for their knowledgeable advice and assistance in the field and lab: C. Slezak, P. Woodward, C. Cooper-Mullin, K. Demoranville, W. Carter, A. Frawley, L. Corcoran, S. Clode, R. McKinney, M. Müller and A. Huth. We thank Dr. C. Lee for the use of his Food Science and Nutrition Laboratory at URI in which we conducted some of the carcass analyses. A. Huth provided additional forms of indispensable logistical support, advice and assistance. This is contribution number XXXX of the Rhode Island Agricultural Experiment Station.

Funding statement: This study was funded by the Rhode Island Department of Environmental Management via the USFWS Wildlife and Sport Fisheries Restoration to RI project W23R (Job 1-12), the Rhode Island Agricultural Experiment Station, and the College of Environment and Life Sciences at the University of Rhode Island (URI) to SRM.

Conflicts of interest: The authors declare that they have no conflict of interest.

Ethics approval: All birds were captured under a master bander permit from the U.S. Geological Survey Bird Banding Laboratory, and all research activities were approved by the University of Rhode Island Institutional Animal Care and Use Committee (#AN10-02-017). This research was conducted in compliance with the Guidelines to the Use of Wild Birds in Research.

Data availability: Data is available in dryad.

<https://datadryad.org/stash/share/T46JIJrrCeX9T8poGIJtFF8knjQ2QFzDmhc5ocGyH>
Kg

Code availability: Code will be made available upon acceptance

Author contributions: SRM and CLG developed and designed the research. CLG conducted the research. CLG wrote the paper with substantial input from SRM. CLG analyzed the data. SRM contributed substantial resources.

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Fig 1. Relationship between predicted lean mass and actual lean mass (**A**) and predicted fat mass and actual fat mass (**B and C**) measured by chemical extraction for American woodcock caught in southern New England. Regression line and confidence intervals are for (**A**) predicted wet lean mass (g) given age, body mass, fat score, and deuterium space (see Table 4) in relation to actual wet lean mass; (**B**) predicted fat mass (g) given body mass, fat score, and deuterium space (see Table 4) in relation to actual fat mass; (**C**) predicted fat mass (g) given only fat score (Table 3, Model 4) in relation to actual fat mass. 95% confidence intervals are shown by the gray bands.

Fig 2. Estimated whole-body fat (black circles) of 48 American woodcock during fall in southern New England based on the deuterium dilution method. Changes in whole-body fat starting in early-September (blue line: nonlinear best-fit regression) and after Day 265 (September 22) when birds initiated fattening (red line: linear regression). The slope of the red line estimates the rate of fat accumulation during fall staging (0.42 ± 0.09 g fat day⁻¹). 95% confidence intervals are shown by the gray bands.

Table 1. Body mass, body composition, and structural size measures (mean $\pm$ SE) of male and female woodcock caught from September to November, 2018 and 2019, in Rhode Island, USA, and used for the validation of the deuterium dilution method. Statistical results (t-test and *p*-values) compare males and females for each trait.

	Male <i>n</i> = 12 Mean $\pm$ SE	Female <i>n</i> = 8 Mean $\pm$ SE	t-test	<i>p</i> -value
Body mass (g)	149.5 $\pm$ 4.22	200.4 $\pm$ 6.71	6.1	<0.001
Wet lean mass (g)	118.7 $\pm$ 2.14	150.6 $\pm$ 3.59	7.62	<0.001
Dry lean mass (g)	72.6 $\pm$ 2.83	82.74 $\pm$ 5.16	1.73	0.11
Fat mass (g)	20.19 $\pm$ 2.81	31.31 $\pm$ 4.63	2.05	0.06
Water mass (g)	46.12 $\pm$ 2.72	67.81 $\pm$ 6.12	3.23	0.01
Feather mass (g)	9.99 $\pm$ 0.53	11.75 $\pm$ 0.33	2.81	0.01
Culmen (mm)	6.55 $\pm$ 0.05	7.17 $\pm$ 0.07	6.84	<0.001
Wing chord (mm)	122.4 $\pm$ 0.57	130.8 $\pm$ 0.45	11.44	<0.001
Primary width (mm)	10.08 $\pm$ 0.29	12.62 $\pm$ 0.32	5.87	<0.001

Table 2. Top four *a priori* candidate models used to estimate wet lean mass of American woodcock captured in Rhode Island USA, during the fall of 2018 and 2019, given measured age, body mass (mb), fat score (fat), estimated deuterium space (*S*), a proxy for total body water space, structural size (first principal component, PC1) and sex. Root mean square error (RMSE g), and absolute (Abs g) and relative (Rel %) errors $\pm$ standard errors (SE) are provided as indicators of model accuracy and precision.

Model No.	Wet Lean Mass Models	AIC _c ^a	Δ AIC ^a	RMSE(g)	Abs $\pm$ SE (g)	Rel $\pm$ SE (%)
1	age + mb + fat + <i>S</i>	104.3	0	3.21	2.58 $\pm$ 0.57	1.96 $\pm$ 0.44
2	mb + fat + <i>S</i>	108.1	3.87	3.15	2.81 $\pm$ 0.72	2.14 $\pm$ 0.48
3	age + mb + fat + <i>S</i> + PC1	108.8	4.48	3.28	2.68 $\pm$ 0.75	2.04 $\pm$ 0.47
4	age + mb + fat + <i>S</i> + sex	108.9	4.64	3.39	2.74 $\pm$ 0.77	2.09 $\pm$ 0.46

^aAIC_c = Akaike Information Criterion corrected for small sample size;
 Δ AIC_c = differences in AIC_c from top model.

Table 3. Top four *a priori* candidate models used to estimate fat mass of American woodcock captured in Rhode Island USA, during the fall of 2018 and 2019, given measured age, body mass (mb), fat score (fat), estimated deuterium space (*S*), a proxy for total body water space, structural size (first principal component, PC1) and sex. Root mean square error (RMSE g), absolute (Abs g), and relative (Rel %) errors $\pm$ standard errors (SE) are provided as indicators of model accuracy.

Model No.	Total Fat Models	AIC _c ^a	Δ AIC ^a	RMSE(g)	Abs $\pm$ SE (g)	Rel $\pm$ SE (%)
1	mb + fat + <i>S</i>	119.5	0	4.33	3.52 $\pm$ 0.78	14.3 $\pm$ 3.2
2	age + mb + fat + <i>S</i>	122.2	2.67	4.57	3.72 $\pm$ 0.83	15.12 $\pm$ 3.38
3	mb + fat + <i>S</i> + PC1	123.5	4.03	4.53	3.69 $\pm$ 0.82	14.96 $\pm$ 3.34
4	mb + fat + <i>S</i> + sex	123.6	4.06	4.84	3.86 $\pm$ 0.86	15.67 $\pm$ 3.5
5	mb + fat + PC1	148.3	28.76	8.41	6.25 $\pm$ 1.4	25.36 $\pm$ 5.67
6	fat	149	29.47	9.08	6.74 $\pm$ 1.51	27.38 $\pm$ 6.12

^a AIC_c = Akaike Information Criterion corrected for small sample size, Δ AIC_c = differences in AIC_c from top model.

Table 4. Final predictive models for estimating wet lean and fat mass of American woodcock given age, body mass (mb), fat score and estimated deuterium space (*S*), a proxy for total body water space, based on measurements from all validation woodcock (*n* = 20) collected during fall 2018 and 2019 in Rhode Island, USA. Root mean square error (RMSE g), and absolute (Abs g), and relative (Rel %) errors $\pm$ standard errors (SE) are provided as indicators of model accuracy and precision.

Final Predictive Models	RMSE(g)	Abs $\pm$ SE (g)	Rel $\pm$ SE (%)
Fat Mass = $-5.3599 + 0.5358$ (mb) + 7.6506 (fat) + -0.5765 (<i>S</i>)	3.44	$2.77 \pm$ 0.62	11.26 ± 2.52
Wet Lean Mass = $3.676 +$ 3.2529 (age) + 0.478 (mb) + -8.5239 (fat) + 0.4221 (<i>S</i>)	2.07	$1.80 \pm$ 0.47	$1.37 \pm$ 0.31

Fig 1.

Fig 2.

Appendix A. Supplemental Material

Table A.1 Capture locations (RI DEM Management Area, coordinates) and date, age, gender, body mass, and morphometric measures for the 20 American Woodcock used for the deuterium validation study conducted in southern New England. Individuals are organized by gender and then in order of increasing body mass.

Management Area Name	Latitude	Longitude	Date	Age	Sex	Mass (g)	Wing Chord (cm)	Bill Length (mm)	Primary Width (mm)	Fat ^a
Francis										
Carter	41.434	-71.676	10/11/19	AHY	F	170	132	7.2	13	0
Great Swamp										
	41.453	-71.592	10/10/18	HY	F	184	131	6.9	14	0
Tillinghast	41.653	-71.76	10/4/18	AHY	F	194	129	7.1	13	0
Tillinghast	41.653	-71.76	10/4/18	HY	F	198	130	7.4	13	0
Tillinghast	41.653	-71.76	10/4/18	AHY	F	199	132	7.1	11	1
Great Swamp										
	41.453	-71.592	10/8/18	AHY	F	210	132	6.9	13	1
Big River	41.644	-71.578	10/28/19	AHY	F	218	131	7.4	12	1
Big River	41.644	-71.578	10/28/19	AHY	F	230	129	7.4	12	1
Tillinghast	41.653	-71.76	10/6/18	HY	M	134	120	6.6	9	0
Francis										
Carter	41.434	-71.6763	9/30/19	AHY	M	137	122	6.4	9	0
Big River	41.644	-71.578	10/1/19	HY	M	137	125	6.2	10	0
Francis										
Carter	41.434	-71.676	9/28/18	HY	M	144	122	6.6	11	0
Nicholas Farms	41.683	71.773	9/21/19	AHY	M	147	122	6.6	12	0
Francis										
Carter	41.434	-71.676	10/1/18	HY	M	148	125	6.4	10	0
Francis										
Carter	41.434	-71.676	10/20/19	AHY	M	151	120	6.6	10	0
Francis										
Carter	41.434	-71.676	10/1/18	HY	M	152	120	6.6	9	0
Tillinghast	41.653	-71.76	10/7/18	HY	M	156	121	6.9	9	0
Francis	41.434	-71.676	10/1/18	HY	M	162	123	6.5	10	1

Carter										
Francis										
Carter	41.434	-71.6763	11/12/18	HY	M	176	125	6.6	11	1
Francis										
Carter	41.434	-71.6763	11/26/18	AHY	M	180	124	6.7	11	1

^a Fat score was estimated using a 0-5 scale visually with whole and half units (Helms and Drury 1960).

CHAPTER 2

“Cross-seasonal effects in the American Woodcock: how conditions prior to fall migration relate to variation in migratory strategy and its implications for conservation”

by

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Is formatted for submission to *The Condor*

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ABSTRACT

How post-breeding habitat quality and body composition of migratory birds carry over to influence fall migration strategies and residency is relatively understudied especially in breeding populations that are partial migrants. We assessed the influence of post-breeding habitat quality on departure body composition and fall migration patterns in a southern New England breeding population of American Woodcock. Woodcock were captured ($n = 67$) at singing grounds in Rhode Island Management areas during the spring of 2018 and 2019, tracked over the summer using radio-telemetry, recaptured ($n = 20$) or randomly captured ($n = 10$) in the fall and affixed with a satellite transmitter after removal of their radio transmitter. To assess the influence of habitat quality and body composition on fall migratory phenology, we used a resource selection function and predictive models derived from the deuterium dilution method to estimate the quality of summer home ranges and pre-migratory sites and to estimate each woodcock's departure body composition. Woodcock that overwintered ($n = 5$) had less fat upon capture and used lower quality habitat during the fall than birds that departed on migration ($n = 17$). Woodcock that departed earlier were long-distance migrants that had inhabited higher-quality landscapes prior to migration, departed with less fat stores, used more stopovers and stopped over longer on migration, migrated faster, and arrived earlier on their more southerly wintering areas. In contrast, woodcock that departed later were short-distance migrants that had inhabited lower quality landscapes prior to migration yet stored more fat upon departure, used fewer stopovers during migration, and arrived relatively late to their more northerly wintering areas. We found no evidence that these differences in

migration strategies were the product of individuals assessing their condition and the environment and thus were contingency-based as would be expected if they were classic condition-based carryover effects. As such, the southern New England breeding population of woodcock are best categorized as obligate partial migrants (i.e., includes residents, short-distance migrants, and long-distance migrants) that demonstrate weak connectivity between life stages; such populations are excellent for the study of the costs and benefits of migration. The stopover and wintering areas used by woodcock in the coastal mid-Atlantic deserve conservation and management attention because of the anticipated loss of long-distance migration due to climate change and urbanization.

INTRODUCTION

For many migratory birds, conditions experienced during one phase of the life cycle can carry over into subsequent periods, ultimately affecting survival and population dynamics. For example, poor habitat quality on the wintering ground of American Redstarts and Black-tailed Godwits delayed their spring departure and arrival to breeding grounds, causing reduced breeding success (Gunnarsson et al. 2005, Norris 2005). This can create a “domino effect” for birds where late arrival to breeding areas may limit available areas to forage due to early intraspecific arrival and territoriality (Piersma 1987). Most of the previous work related to migratory carry-over effects has focused on how conditions during winter influenced subsequent breeding success (Harrison et al. 2011, Sedinger et al. 2014); however, conditions experienced during the summer breeding season can influence pre-migratory body composition and in turn affect the timing of departure and migratory behavior. For example, delayed

breeding affected the timing of the prebasic molt and fat deposition in fall in Wood Thrush (*Hylocichla mustelina*) and Savanna Sparrows (*Passerculus sandwichensis*) which caused delays in fall departure and arrival to the wintering ground (Stutchbury et al. 2011, Mitchell et al. 2012). As few birds are able to make a single nonstop flight to and from their breeding and wintering areas, migrants must use stopover sites to rest and refuel to continue migrating (Hedenström and Ålerstam 1997, Wikelski et al. 2003, Newton 2008). Birds with larger pre-migratory fat stores may be able to take advantage of favorable weather patterns for departure, stop less frequently at stopover sites, have more fat throughout migration and spend less time at stopover sites (Yong and Moore 1994, Cohen et al. 2012). Summer breeding season conditions can also affect access to resources on the wintering ground (Newton 2006), and survival during fall migration (Fayet et al. 2016). Although such carry-over effects may be important, few studies have directly addressed how the quality of breeding and post-breeding habitats affect the body composition of individuals as they prepare for fall migration, and its subsequent effects on the phenology and routes used during fall migration and on winter destinations.

The study of carryover effects from summer breeding to fall migration and winter is particularly important to study in bird populations that include residents as well as seasonal migrants (Ålerstam 1990, Hegemann et al. 2015). Such so-called ‘partial migration’ may be a more ubiquitous migratory strategy than currently documented compared to the more well-studied obligate long-distance form of migration (Berthold 1999, Hegemann et al. 2019). Partial migration is considered to be an evolutionary precursor to obligate long-distance migration (Berthold 1996) and

may occur because of shifting tradeoffs between the costs and benefits of residency (e.g., the benefits of early establishment of breeding territories (Boyle 2011) and the costs of migration (e.g., avoiding the cold during winter (Berthold 1996, Pulido 2007)). In addition, conditions experienced during fall staging may influence an individual's ability to migrate or overwinter as a resident (Newton 2012). For example, body condition, density of individuals, risk of predation, and response to inclement weather during fall staging differed for migratory versus resident individuals and helped to elucidate the costs and benefits of residency vs. migration (Pulido 2011, Hegemann et al. 2019). Attributes of resident and migratory individuals (e.g., habitat quality used during summer, body composition in fall) can be compared to reveal some of the associated costs and benefits that maintain partial migration in the population, as well as the potential strength of carryover effects.

Our objectives for this study were to examine the influence of body condition and quality of breeding and pre-migratory staging areas on whether American Woodcock (*Scolopax minor*) migrated or remained resident, and for those that departed, the influence of these factors on fall migratory movements. We tested the hypotheses, derived from studies of carry-over between non-breeding to breeding area (Studds and Marra 2005, Paxton and Moore 2015) that (1) conditions during post-breeding positively affect conditions at departure on fall migration (i.e., birds from higher quality summer and fall-staging sites depart earlier and with more fat), and (2) conditions at fall departure positively affect conditions during fall migration (i.e., woodcock in better departure condition use fewer stopovers and spend less total time migrating and travel further south).

METHODS

Initial Capture, Tracking, and Recapture of Woodcock

We used mist-nets to capture 67 woodcock (42 = HY, 25 = AHY) at singing grounds from April 5 to May 27, 2018 ($n = 37$ males and 3 females) and 2019 ($n = 24$ males and 3 females) within fields in Rhode Island Department of Environmental Management Areas and a Nature Conservancy preserve (see Table A.1 for location information). Sex and age of captured woodcock was determined using plumage characteristics of the wings (Mendall and Aldous 1943, Sheldon 1967). We weighed and banded each bird and then used cattle tag cement (Nasco, Fort Atkinson, Wisconsin, USA) and a crimped wire belly band to affix a VHF transmitter (4.5 g, < 3% body mass; Advanced Telemetry Systems A5400 VHF, Isanti, Michigan, USA) to the back of each bird (detailed methods in McAuley et al. 1993, Masse et al. 2014). We gathered daytime locations for each tagged woodcock 3-4 times per week between May 24 and August 16 of 2018 and 2019 during all representative daytime hours (0700 – 1900). Locations were marked with a handheld GPS unit on average $\leq 17.7 \pm 8.3$ m from the bird to avoid flushing it and so influence its location (Masse et al. 2013, 2014).

Between September 1 and November 20, 2018 ($n = 9$) and 2019 ($n = 11$) we used handnets and spotlights to recapture summer-tracked woodcock at fall roosting locations (Rieffenberger and Kletzly 1967, McAuley et al. 1993). Recaptured woodcock had their VHF tag carefully removed and replaced with a Pinpoint GPS tag (4.0 g for males, 6.3 g for females; < 3% of body mass; Lotek Wireless, Newmarket, ON, CN). We used a 48-hour duty cycle for males and a hybrid schedule for females

consisting of a 24-hour duty cycle between November 10 and January 1 and a 48-hour duty cycle after January 1. Captured and retagged woodcock were released at the capture site. Ten additional woodcock ($n = 6$ AHY males, 4 AHY females) were opportunistically caught and also affixed with a Pinpoint GPS tag scheduled with a 24-hour or 48-hour schedule for males, or hybrid schedule as above for females. Male and female tags were designed to record and transmit 75 and 120 locations, respectively. All capture methods and transmitter attachment protocols were approved by Univ of Rhode Island IACUC (#AN10-02-017) and were authorized by USFWS Banding Lab (permit number 22923).

Quality of Sites Used by Woodcock During Summer and Pre-migration

We used Masse et al's (2014) resource selection function to estimate the quality of summer home ranges (during May – August) and pre-migratory sites (September to November) and used these estimates to assess whether summer and fall habitat quality influenced fall departure decisions and body condition. During the summer (May 24 - Aug 16), we obtained on average 34.81 ± 4.92 VHF locations for each bird (range: 26 - 47 locations). We used summer locations for recaptured woodcock to create 95% and 50% core use areas using a Gaussian kernel with likelihood cross validation bandwidth estimator in the *adehabitat* package in R (Calenge 2006). The probability of use raster map developed by Masse et al (2014) was scaled between 0 – 100 to serve as a probability of use score for each 10 x10 m pixel in Rhode Island. We calculated the size of each bird's home range and core use areas, as well as the average probability of use score in the core-use areas. We randomly sampled 100 points from

each core-use area and averaged the probability of use score (summer RSF score) of each core use area to estimate each individuals summer home range quality.

For the fall pre-migratory period (September 1 to December 1 or date of departure), we obtained on average 21.73 ± 8.44 GPS locations for each bird (range: 10 – 35) and used these locations to estimate two different ‘habitat quality’ indices. Given that during the pre-migration period we had fewer locations to estimate home range size, we estimated the size of the fall pre-migratory area for each bird using the minimum convex polygon (mcp) function in the *adehabitat* package. First, a comparable index for the summer home range quality was created for the fall, as birds may have left or used different areas in their summer home ranges and this may have influenced each birds pre-migratory fat deposition. To estimate fall home range quality we extracted and averaged the probability of use scores for the recorded GPS locations in the mcp to estimate the “fall RSF score”. Second, given that 89+% of locations in the fall pre-migratory period for each individual were within 4 km² area of their fall recapture locations, we used the focal statistics tool in ArcMap 10.6 to calculate the average probability of use score within each of these 4 km² landscapes (after Brenner et al. 2019) and thus provide an estimate of the “Landscape likelihood of use” for each individual. For some of the statistical analyses (see below), we categorized each landscape as either high-likelihood of use (> 45 average score) or low-likelihood of use (< 35 average score). We felt justified in using a 4km² area to define the landscape quality in fall as previous work in Rhode Island found that woodcock differentiate between the quality of a landscape at this 4km² scale (Brenner

et al. 2019). We used the *geosphere* package in R (Hijmans 2019) to calculate the average distance from each bird's summer home range to their GPS locations.

Phenology of Woodcock Migration

To assess when a bird transitioned from a non-migratory (e.g., summer and winter) to a migratory state (e.g., fall migration), we fit a two-state Hidden Markov Model to each bird's migratory track using the *moveHMM* package (Michelot et al. 2016).

Hidden Markov models use the distribution of step lengths and turning angles from an observed series of locations to characterize unobservable movement states. We generated random parameters for each state using a gamma distribution for step lengths and a von Mises distribution for turning angles. The best-fit Markov model was used to characterize each location's state as being in a migratory or non-migratory. In order to identify the departure and arrival locations, we identified the location prior to the first location in a migratory state as being the departure location, and the location following the last location in a migratory state as the location of arrival. We calculated the first migratory flight length as the first step length following the location of departure. We defined a stopover as consisting of more than two consecutive locations within a < 20 ha area. The length of total migration for each bird was calculated by using the straight-line distance between the departure location, the consecutive stopover locations and the wintering location. Each bird's average angle of migration and the initial angle of migration were calculated using the *fossil* package in R (Vavrek 2011). We considered the 'initial angle of migration' as the angle of departure from Rhode Island to each individual's next recorded location, and the 'average angle of migration' as the average of all angles between the departure

location and each subsequent migratory location or a stopover site until final arrival on the wintering ground. The rate of migration (km/day) was calculated by dividing the length of migration divided by total days spent migrating.

Body Composition of Woodcock at Capture and Upon Departure

We used the deuterium dilution method to estimate the whole-body fat of woodcock at capture. In brief, within 30 minutes of capture we used a prefilled 1 mL insulin syringe (22004270, Fisher Scientific, Pittsburgh, PA, USA) to inject each woodcock in the pectoral muscle with 297 ± 0.99 mg (mean $\pm$ SE) of 99.9% deuterium oxide (Sigma-Aldrich, St. Louis, MO, USA). Birds were placed in cloth bags for 60 ± 3 mins to allow for the deuterium to equilibrate in the body pool of water, and then we collected 100 μ L of blood into heparinized capillary tubes which were immediately flame sealed. We used predictive models developed by Graham and McWilliams (2020) to estimate the body composition of each woodcock at capture. We estimated the whole-body fat of each woodcock at their departure for fall migration using two pieces of information presented in Graham & McWilliams (2020): the date at which this population of woodcock on average initiated fattening in fall (September 22), and the estimated fattening rate of woodcock (0.42 ± 0.09 g fat day⁻¹). For each individual we used the fat at capture as the body composition when fattening was initiated on September 22 and then multiplied the rate of fattening by the number of days until departure to estimate the fat mass (g) at departure. The estimated departure fat was added to the body mass at capture to estimate the body mass (g) at departure.

Statistical Analysis:

We used generalized linear models with data from birds that were recaptured in the fall ($n = 12$) to determine the effect of distance from home range, home range size, landscape quality in fall, summer RSF score and fall RSF score on departure fat mass, and departure body mass. Atmospheric conditions including the average pressure, average temperature and percent lunar illumination on each bird's date of departure was collected using the National Oceanic and Atmospheric Administration (NOAA) weather station at T.F. Greene Airport (41° 43' 12" N, -71° 25' 48" W) and the *lunar* package in R (Lazaridis 2014). A generalized linear model with data from birds that were recaptured was used to assess the influence of home range, home range size, landscape quality in fall, summer RSF score and fall RSF score, departure fat mass, departure body mass, air pressure, average temperature, and percent lunar illumination on the date of departure.

A combined dataset consisting of birds that were recaptured or randomly captured in the fall ($n = 17$) was used to assess the influence of fall body condition on migratory phenology. Specifically, we used generalized linear models with data from the combined dataset to assess the influence of wing chord, departure fat, departure mass, sex, and the date of departure on the first flight distance, number of stopovers, stopover duration, and the average and initial angle of migration. We also used generalized linear models with data from the combined dataset to assess the influence of wing chord, departure fat, departure mass, sex, the date of departure, number of stopovers used, and stopover duration on the rate of migration, duration of migration, migratory length, date of arrival, and the latitude and longitude of wintering grounds. A generalized linear model with binomial error distribution with the combined dataset

was used to assess whether landscape quality in the fall and fall RSF scores influenced whether woodcock migrated or overwintered in Rhode Island. An ANCOVA was used to assess whether residents had lower fat mass at capture than birds which migrated. We used the Akaike Information Criteria adjusted for small sample size (AICc), and model weights to select the top models among candidate models (Anderson et al. 2000). All statistical testing was completed using R opensource software (version 3.3.2; www.r-project.org).

RESULTS

Quality of Summer and Fall Habitats in Relation to Partial Migration

We obtained 35.53 ± 4.75 VHF locations during the summer for 13 of the 14 birds that we eventually recaptured in fall; one bird left the study area mid-way through the summer and so provided too few locations. The 95% and 50% core use areas were on average 14.77 ± 4.61 ha and 2.87 ± 1.02 ha, respectively (Table 1). Probability of use scores for 50% core use areas during summer averaged 19.52 ± 2.24 (range 4.21 – 30.06; Table 1).

We obtained 16.8 ± 4.60 GPS locations during the fall pre-migratory period (range: 10 – 28; Table 1) for the 14 birds that we recaptured in fall. Probability of use scores for pre-migratory locations used during fall were on average 21.35 ± 1.59 (range 7.8 – 33.92; Table 1). Most (68%) of the fall GPS locations were within the summer 95% core use areas. Given that birds used similar areas during summer and fall, it is not surprising that the probability of use scores for the two periods were closely related (Table 1; $t = -0.412$, $p = 0.68$).

Five woodcock remained in Rhode Island throughout the winter (2 of 14 birds recaptured in fall, 3 of 9 new fall-captures; 1 female, 4 males); one remained all winter within its summer home range (i.e., year-round residency) whereas four relocated a short distance, on average 17.75 ± 8.07 km from fall capture locations and 23.64 ± 0.08 km distance from their previous summer home range. Resident woodcock used fall sites with lower probability of use scores than woodcock that migrated ($p = 0.02$; Figure 1).

Quality of Summer and Fall Habitats in relation to Fall Body Composition for Migrants and Residents

Resident woodcock ($n = 5$) had on average 11.68 ± 2.52 grams of fat at capture (range 4.30 – 18.07 g) and consistently carried less fat than individuals that eventually migrated ($n = 17$) and that were caught at the same time in fall ($F = 5.99$, $df = 2$ and 19, $p = 0.009$; Figure 2). Given that woodcock from this population in the same two years began to deposit body fat on average on September 22 with a fat deposition rate of 0.42 ± 0.09 g fat per day⁻¹ (from Graham and McWilliams 2020), we estimated that woodcock departed Rhode Island on average 53 ± 1.95 days after initiating fat deposition and that they accumulated substantial fat prior to their departure (Figure 2). Migrating male woodcock ($n = 12$) departed with on average 36.42 ± 1.64 grams of fat (Figure 2) and weighed 169.1 ± 2.57 grams upon departure. Migrating female Woodcock ($n = 5$) departed with 38.36 ± 2.5 grams of fat (Figure 2) and weighed 203.12 ± 4.04 grams. Although females were heavier than males upon departure ($t = -7.10$, $p = 0.0001$), we detected no significant difference in fat mass (g) between females and males upon departure ($t = -0.65$, $p = 0.53$).

Our best supported model for estimating departure fat included only landscape quality in fall as a covariate ($F = 8.9$, $df = 1$ and 9 , $p = 0.01$; Table 2) although the size of home range (95% core use area) used during summer was also important (Table A.2). Our best supported model predicting departure date from Rhode Island included only departure fat as a covariate ($F = 22.37$, $df = 1$ and 9 , $p = 0.0001$; Table 2). In general, woodcock that departed with less fat stores had inhabited higher quality landscapes in fall and tended to depart earlier (Figure 3), and those that departed later in fall had on average more fat mass and inhabited lower quality landscapes in fall (Figure 3). Ambient temperature, moon phase and barometric pressure were not included in the top 10 models for predicting date of departure (Table A.3).

Post-breeding Conditions Influence Fall Migratory Direction and Phenology

We were able to track 17 of the 30 birds that migrated with GPS tags over the fall migratory period, 12 of which were birds that were recaptured after tracking them throughout the summer and fall (2018, $n = 4$ and 2019, $n = 8$, Table A.1). The remaining 13 tags included five residents and eight GPS tags which failed or never recorded any locations. Six transmitters provided less than fifteen locations and then failed ($n = 5$ in 2018, 1 in 2019) with one of these six birds shot prior to departure in 2018, and two transmitters in 2018 never recorded any locations. These eight transmitters were censored from subsequent analysis. In general, for the 17 individuals for which we present fall migration information, the transmitters provided more than 85% of the expected locations given their duty cycle (Table A.1). One female was captured three times (first fall, next spring, second fall) yielding 1.5 years of location data including two fall migrations to wintering areas in 2018 and 2019 (Figure 4D).

Woodcock departed Rhode Island throughout the last 3 weeks of November and early December with 10 birds departing early to mid-November (November 6 – November 16) and 7 birds departing after November 21 (Figure 2) with the average date of departure on November 19 ± 1.95 days (range: November 6 - December 1: Figure 2). During fall migration, woodcock ($n = 17$) followed the Atlantic coastal plain (Figure 4) and used stopovers in Virginia ($n = 5$), North Carolina ($n = 4$), Maryland ($n = 2$), Delaware ($n = 2$), New Jersey ($n = 2$), Connecticut ($n = 1$), New York ($n = 1$), South Carolina ($n = 1$) and Georgia ($n = 1$). Woodcock used on average 1.07 ± 0.26 stopovers (0 – 4 stopovers; Fig. 4) along their migratory route. Early - and late - departure groups did not differ in the amount of time spent at stopovers ($t = 0.72$, $p = 0.48$) or the number of stopovers used ($t = 0.11$, $p = 0.91$) and spent on average 10.06 ± 2.64 days (0 – 38 days) at a given stopover site. Stopover duration was predicted by departure mass and sex, where birds that were heavier and female spent more time stopping over ($F = 6.72$, $df = 2$ and 14 , $p = 0.01$, Table A.5). The top model predicting number of stopovers included departure fat, body mass and sex as covariates ($F = 3.35$, $df = 2$ and 14 , $p = 0.05$, Table 2). In general, birds with less fat mass at departure used 25% more stopovers. In addition, heavier birds at departure and females used twice as many stopovers as lighter individuals and males, respectively, and birds with more stopovers migrated further ($F = 4.45$, $df = 1$ and 15 , $p = 0.05$; Table 2; Figure 4).

Total distance traveled during migration was on average 1149.18 ± 105.57 km (range: 359 km to 1731 km). Departing woodcock took on average 19.41 ± 3.00 days to reach their wintering grounds. Duration of migration and date of arrival at the

wintering area were predicted by the date of departure, number of stopovers, sex, and stopover duration ($F = 11.74$, $df = 4$ and 12 , $p = 0.0004$) and ($F = 53.79$, $df = 4$ and 12 , $p = < 0.0001$), respectively; Table 2). In general, woodcock that took longer to migrate and arrived later on the wintering areas used more stopovers, stopped over longer, departed later, and were female (Figure 5). However, birds that departed earlier and spent less time stopping over travelled twice as fast as birds that departed later ($F = 12.39$, $df = 4$ and 12 , $p = 0.0007$; Figure 6). Woodcock travelled on average 81.03 ± 10.17 km per day (range 14.8 – 167.6 km).

Initial angle of departure from Rhode Island was not strongly influenced by any of the covariates (i.e., null model was the most supported). The average angle of migration across the entire trip from breeding to wintering area was in an overland west-southwest direction (i.e., 226.98 ± 3.58 degrees, range: 209.46 – 271.81) from Rhode Island (Figure 4) and was also not strongly influenced by any of the covariates (i.e., null model included in the top four models; Table A.6) although wing chord length ($F = 3.95$, $df = 1$ and 15 , $p = 0.06$; Table 2) and body mass at departure were weakly predictive (Table A.6). In general, birds with longer wing chords (125 – 137 mm) tended to migrate in a more west by south west direction (270 – 230 degrees), whereas birds with shorter wing lengths (120 – 124 mm) tended to migrate in a more south by southwest direction (229 – 209 degrees); however, the female outlier with a wing chord of 137 mm which took the most western route (271 degrees) influenced this model.

Location of Wintering Areas in Relation to Post-breeding Condition

Rhode Island-breeding woodcock spent the winter in North Carolina ($n = 5$), Virginia ($n = 1$), Georgia ($n = 3$), Alabama ($n = 3$), Maryland ($n = 2$), South Carolina ($n = 1$) and New Jersey ($n = 2$) (Figure 4). Departure groups differed in their arrival time ($t = -2.97$, $p = 0.01$) with early-departing woodcock arriving at wintering areas on December 1 ± 4.32 days (November 9 – December 23) and late-departing woodcock arriving on December 19 ± 4.88 days (December 7 – January 14). Woodcock arrived on average on November 19 to South Carolina (latitude: 34.28), December 1 ± 15.05 days to North Carolina (latitude: 34.57-36.11), December 9 to Virginia (latitude: 37.16), December 10 ± 9 days to Georgia (longitude: 32.03 – 32.32), December 12 ± 12.72 days to New Jersey (latitude: 39.18 – 39.43), December 13 ± 2.3 days to Alabama (latitude: 31.76 – 34.39), and December 22 ± 2.12 days to Maryland (latitude: 38.46 – 38.79). The latitude of wintering locations was predicted by the number of stopovers used ($F = 4.87$, $df = 1$ and 15 , $p = 0.04$; Table 2) although date of departure was also important (Table A.11). Birds that used more stopovers and departed earlier wintered further south, whereas the days spent on migration and date of arrival were not associated with wintering latitude. Wing chord length was not included in any of the top models for predicting the wintering site location (Table A.11) even though they differed in their average angle of migration. No models were predictive of the wintering area longitude, as the top model was the null model.

DISCUSSION

Pre-migratory Habitat Quality Affects Fall Departure Body Composition and Timing of Departure

We found support for the hypothesis (H1) that the quality of areas inhabited prior to migration affects body composition at departure and timing of departure, but not in the expected way. We predicted that birds from higher quality summer and fall-staging sites would depart earlier and with more fat. Instead, we found that woodcock that inhabited higher quality landscapes in fall departed on migration earlier and had less fat mass, whereas those that departed later in fall had on average more fat mass and had inhabited lower quality landscapes prior to migration (Figure 3). These somewhat counterintuitive results suggest that the woodcock population we studied includes individuals with quite different migration strategies: longer-distance migrants that depart early with less fat stores, and shorter-distance migrants that depart with more fat stores and on average later in the fall. We discuss in the next section the migration and wintering aspects of these different migration strategies.

All woodcock that migrated from Rhode Island in the fall departed with at least 27 g of estimated fat (or 17.5% of departure body mass), and as much as 46 g fat (or 21% of departure body mass). Like other migratory birds, woodcock may depart on migration only after reaching some minimum fat threshold (e.g., 27 g for woodcock in this study). Red Knots use a threshold of 50 g fat before departing from the Delaware Bay to their Arctic breeding grounds (Baker et al. 2004, Atkinson et al. 2007). Similarly, thrushes departed from stopover sites when reaching a minimum threshold of fat, but also when daily maximum temperatures exceeded 21°C and wind strength was less than 10 km/hr. (Bowlin et al. 2005). Woodcock began to accumulate fat mass on September 22 (Graham and McWilliams 2020), and delays in molting may have constrained fat accumulation in late-departing birds. For many birds, photoperiod

and gonadal development or regression is the primary cue to initiate molt (Dawson et al. 2012). In Maine, woodcock initiated their pre-basic molt in early June, molting heavily in August and completing their molt by mid-October (Owen Jr and Krohn 1973). Due to the energy intensive nature of molt, Maine woodcock began to deposit fat in early September after the peak of molt and began departing from Maine in Mid-October (Owen Jr and Krohn 1973). Previous work on woodcock has also assessed the influence of exogenous cues (e.g. moon phase, barometric pressure, wind direction, temperature) on fall departure decisions. Meunier et al. (2008) suggested that the timing of departure was influenced by photoperiod rather than direct environmental cues, as woodcock departed Wisconsin, Minnesota, and Michigan around the same time each year, despite variation in pressure, moon phase and temperature. We also did not find evidence that temperature, moon phase or barometric pressure were significant predictors of the timing of departure in Rhode Island. Timing of fall departure did not differ between sexes in our study, which is also consistent with the results of previous studies (Sepik and Derleth n.d., Coon et al. 1976, Meunier et al. 2008). In sum, photoperiod and the timing of molt and subsequent fat deposition seem to primarily influence timing of fall departure in woodcock.

Conditions at Fall Departure Affect Fall Migration Behavior

We found support for the hypothesis (H2) that conditions at fall departure (e.g., fat stores, body mass, phenology) positively affect subsequent timing and pace of migration, although these affects seemed associated with different migration strategies rather than classic carryover effects. Woodcock that departed with less fat mass and that were heavier used more stopovers, stopped over longer, and migrated further and

arrived earlier on their wintering areas. In contrast, woodcock that departed with more fat mass departed later, used fewer stopovers, migrated less far and took longer to get to their wintering areas. Quality of the landscape used prior to fall migration was associated with differences in departure body fat and this in turn influenced the date of departure and subsequent pace of migration. American Redstarts that departed earlier from their wintering areas had used higher quality overwintering habitat and were in better condition than birds that departed later (Marra et al. 1998, Tonra et al. 2011). Woodcock that inhabited higher quality landscapes during the fall pre-migratory period also departed earlier although these individuals had less fat mass than later departing individuals. Woodcock may depart earlier with less fat mass in order to increase maneuverability and speed while migrating, especially given the rounded wings of woodcock are more suitable for navigating within dense vegetation and so cause them to fly much more slowly than other migratory birds (Coon et al 1976, Newton 2008). Woodcock that had less departure fat, higher departure body mass, and were female also used more stopovers during migration; heavier birds that were female spent more time stopping over. In comparison, fall migrating shorebirds that stopped over longer in James Bay had more fat mass upon departure and were less likely to use another stopover site on the way to their wintering grounds (Anderson et al. 2019). Female Lesser Black-backed Gulls (*Larus fuscus*) also spent more days at stopover sites in the fall as they completed their molt during migration and used lower risk - lower reward agricultural habitats compared to males which used more profitable marine habitats for foraging (Baert et al. 2018). We found no evidence that these differences in migration strategies were the product of individuals assessing their

condition and the environment and thus were contingency-based as would be expected if they were classic condition-based carryover effects.

American Woodcock as Partial Migrants

The Rhode Island woodcock population included birds that remained resident overwinter as well as individuals that migrated shorter or longer distances to southern wintering areas. Birds that remained year-round residents ($n=5$) used fall pre-migratory locations that were of lower quality than that of birds that departed. In general, longer-distance migrating woodcock departed earlier and with less fat mass, stopped over for longer periods, migrated faster and wintered further south. Shorter-distance migrating woodcock departed later with more fat, spent less time stopping over, were slower, took longer to migrate, arrived later to wintering areas, and wintered further north on average. Although stopover duration was variable (0 - 38 days) woodcock spent on average 10 days at stopover sites and used on average one stopover per migration. In comparison, woodcock migrating in the central flyway used more stopover sites with a median of 2 stopover sites used during autumn migration (Moore et al. 2019), as well as used stopover sites anywhere from 1- 28 days with a median use of 3 days. Woodcock that migrated from Rhode Island travelled at a faster rate (81.03 ± 10.17 km/day) than central management region birds that travelled at a rate of 69.1 ± 2.9 km/day (Moore et al. 2016). This difference between woodcock in the two flyways is likely due to the longer distances travelled from the upper Midwest to wintering locations in the Central flyway (Myatt and Krementz 2007, Moore et al. 2019). Although females used more stopovers than males, we found no evidence for sex differences in wintering latitude, a result similar to Diefenbach et al (1990) based

on band recoveries. In sum, the Rhode Island woodcock population are partial migrants in the sense that there is clear between-individual variation in migratory behavior (i.e., residents, short- and long-distance) within this population.

Given that we found no evidence that individuals changed their migratory behavior between years or in response to environmental conditions, our population of woodcock are best classified as obligate partial migrants (*sensu* Newton 2008). Previous work has suggested the possibility of woodcock being facultative partial migrants in the sense that migration distance flown by individuals depends on variation in annual winter condition and declining temperatures (Sheldon 1967, Owen et al. 1977). Specifically, woodcock were hypothesized to overwinter as far north as possible in a given year so they could return early to breeding areas (Sheldon 1967, Owen 1977). Woodcock have lower critical thresholds than most shorebirds and can withstand ambient temperatures as low as 22°C before needing to increase heat production to maintain their body temperature (Vander Haegen et al. 1994). However, mass mortality events of individuals that winter too far north have been reported during periods of extended harsh weather; thus, residency or short-distance migration may be a risky strategy in some years (Mendall and Aldous 1943, Docherty et al. 1994). Woodcock overwinter in coastal areas annually in Rhode Island; however, the breeding-ground origin of these birds is unknown (Sullivan et al. 2009, Graham Pers. Comm.). Of the five woodcock (4 males, 1 females) that over-wintered in Rhode Island, four birds made short distance movements to winter in coastal Rhode Island, which tends to receive less snow and be warmer than inland areas in Rhode Island. Two of the five birds that overwintered had been previously tracked during the

summer: one bird remained within its summer home range through the following fall, winter and spring, while the other bird overwintered in coastal Rhode Island and migrated to Western Pennsylvania the following spring. All resident woodcock in our study used poorer quality habitat and did not accumulate appreciable fat compared to those individuals that migrated which provides further evidence that this population is composed of individuals with more fixed migratory (or resident) behavior and so are obligate partial migrants.

Newton (2008) proposed that elucidating the costs and benefits of migration is best done in breeding populations that are partially migratory, such as the Rhode Island-breeding woodcock population. Although our sample size precludes us from conducting a formal costs-benefit analysis of migration that compares survival over winter, survival during the migratory periods, and breeding success between residents and migrants, we can provide a brief summary of the evidence from other studies that pertains to such costs and benefits of migration. In the fall, survival for woodcock is relatively high during the pre-migratory period (0.92; Derleth and Sepik 1990); no comparable information for survival over the migration period is available although a current Atlantic Flyway-wide telemetry study of woodcock should provide such information (Fish et al. 2020). In general, resident birds have higher rates of survival during the migratory period than those that migrate due to the energetic costs and risks associated with long-distance flight (Silllett and Holmes 2002, Newton 2006). The wintering period for woodcock has lower rates of survival than any other period of the annual cycle, and birds that overwinter further north may have lower rates of survival than birds that migrate further south (Derleth and Sepik 1990, Zúñiga et al. 2017,

McAuley et al. 2019). For instance, Krementz et al. (1994) estimated a survival rate of 0.647 for the months of December through March in Georgia, South Carolina and Virginia, whereas woodcock overwintering in the months of November to January at Cape May, New Jersey, had survival rates of 0.365 - 0.706, with increased mortality attributed to avian predation and exposure to snowstorms (McAuley et al. 2019).

Woodcock that overwinter further south may slowly migrate in the spring, possibly breeding at stopover sites as they wait for conditions to improve (Moore et al. 2019), while woodcock that overwinter less far or that remain resident may be able to arrive earlier to their breeding sites and outcompete individuals that migrate from further south (Bregnballe et al. 2006, Kokko 1999). Due to the poor performance of our 2-day duty cycle tags that were programmed to continue working through the spring (range: 23-74 locations collected), as well as the lack of a mortality signal, we were unable to assess the influence of partial migration on spring breeding opportunities and annual cycle survival. As tracking technology develops, woodcock such as those that breed in Rhode Island appear to be an excellent system to address the causes and consequences of partial migration, and this information would be helpful in guiding conservation efforts for woodcock.

Conservation Implications:

Given that coastal urbanization and climate change may reduce the propensity to migrate long-distances, the stopover sites and wintering areas used by resident and short-distance migrating woodcock should be a high priority for conservation and management. In general, the proportion of residents and short-distance migratory birds is predicted to increase with climate change as winters become more moderate or

entirely snow-free (Meller et al. 2016). Thus, key stopover and wintering areas used by resident and short-distance migrants such as the southern New England coast, the Delmarva Peninsula, Eastern Virginia, Eastern North Carolina and Southern New Jersey are especially important to conserve because they are close to migratory barriers such as the Long Island Sound and Delaware Bay and will likely have to support increasing numbers of woodcock. In addition, highly urbanized areas, including much of coastal Rhode Island, may provide especially favorable microclimates and access to food in winter (Butler et al. 2012, Møller et al. 2014) that benefit overwintering woodcock. The portion of the population that remains resident in the partial-migrant European Blackbird has increased with urbanization presumably for these reasons (Møller et al 2014). Our study of southern New England breeding woodcock has demonstrated that these populations are obligate partial migrants that include individuals that winter in a wide variety of areas and so are less vulnerable to catastrophic events at one or a few of these wintering areas. The current Atlantic Flyway-wide telemetry study of woodcock (www.woodcockmigration.org) will provide important additional information about the connectivity between various breeding populations and wintering areas that will further inform conservation of the American Woodcock at large.

ACKNOWLEDGEMENTS

We thank the following for their assistance in the field: S. Theilacker, J. Kaelbein, G. Emery, A. Jones, C. Slezak, P. Woodward, C. Cooper-Mullin, K. DeMoranville, W. Carter, A. Frawley, L. Corcoran, S. Clode, M. Müller, and A. Huth. We thank J. Lamb,

C. Cooper-Mullin, and K. DeMoranville for their statistical advice. E. Blomberg and A. Fish provided invaluable help with satellite tag logistics. We thank the Ruffed Grouse Society for the contribution of about half the GPS tags used for this project. This is contribution number XXXX of the Rhode Island Agricultural Experiment Station.

Funding statement: This study was funded by the Rhode Island Department of Environmental Management via the USFWS Wildlife and Sport Fisheries Restoration to RI project W23R (Job 1-12), the Rhode Island Agricultural Experiment Station, and the College of Environment and Life Sciences at the University of Rhode Island (URI) to SRM.

Ethics statement: All birds were captured under a master bander permit from the U.S. Geological Survey Bird Banding Laboratory (SRM Master Bander#22923), and all research activities were approved by the University of Rhode Island Institutional Animal Care and Use Committee (#AN10-02-017). This research was conducted in compliance with the Guidelines for the Use of Wild Birds in Research.

Author contributions: SRM and CLG developed and designed the research with input from TS. CLG conducted the research. CLG wrote the paper with substantial input from SRM. CLG analyzed the data. SRM and TS contributed substantial resources.

Data Availability: Data will be made available in Dryad upon acceptance

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FIGURE 1. Relative probability of use (derived from Resource Selection Function, see text) of sites used in fall during the pre-migration period in relation to whether woodcock migrated in fall to wintering areas in the mid-Atlantic and southern region ($n = 17$) or remained resident in Rhode Island, USA ($n = 5$). Woodcock that remained in Rhode Island during winter resided in lower-quality sites during the previous fall compared to woodcock that eventually migrated from Rhode Island, USA.

FIGURE 2. Estimated departure fat load (gray circles) of woodcock given their whole-body fat at capture (black circles) and known date of departure in fall (November 6 to December 2, julian dates 310 to 335) from Rhode Island, USA. The longest gap of days without departures was between 16 - 22 Nov (julian dates 321 - 326). Five woodcock were caught during the pre-migration period (unfilled squares) and then remained year-round residents and did not migrate. Whole-body fat at capture was estimated using the deuterium dilution method (see text). We assume that birds caught before September 22 maintained their capture fat mass until this date (horizontal dashed line) and then accumulated fat at a rate of 0.42 ± 0.09 g fat per day¹ (sloped dashed line; based on Graham et al. 2020) until their known departure date (gray circles). Females (cross under gray circles) were heavier and larger than males (see text) although males and females had similar fat mass upon departure.

FIGURE 3. Landscape likelihood-of-use (an index of quality) for the 4 km² area around the fall recapture site for woodcock (n=11) in relation to their estimated fat mass upon departure from Rhode Island, USA. Woodcock that resided in high-quality landscapes (4 km² areas with average likelihood of use scores > 45) in the fall departed with less fat and earlier than woodcock that resided in low-quality landscapes (4 km² areas with average scores < 35).

FIGURE 4. Migratory tracks, stopover sites (> 2 consecutive locations within a site; triangles), non-stopover sites (≤ 2 consecutive locations within a site; open circles) and wintering locations (filled circles) for 16 American Woodcock from their departure location in Rhode Island to their wintering area. (A) Woodcock that used no stopover sites (n = 5), (B) birds that used 1 stopover site (n = 5), and (C) birds that

used 2 stopovers sites ($n = 5$) during fall migration. Movements during migration for one recaptured female (D) tracked in two subsequent falls (2018 and 2019). This female wintered in the same area in Georgia. In 2018 (dashed line), this female migrated much less directly and slower (41 days) and used four stopover sites in Virginia, whereas in 2019 (dotted line) she migrated more directly and faster (24 days) and used two stopover sites that were not used the previous year.

FIGURE 5. Number of days spent at stopover sites during fall migration increased with the (A) duration of migration (total number of days) for each individual, and (B) the julian date of arrival on the wintering area. Males are depicted as filled circles (shading denotes number of stopover days) whereas females are depicted with the ♀ symbol. Woodcock that spent more time stopping over (least squares regression line with shaded 95% confidence interval) were more often female (♀) and individuals that tended to migrate later in the season and also stopped more often (darker colors).

FIGURE 6. Rate of migration (kilometers per day) generally decreased with the date of departure and total days spent stopping over. Woodcock that departed earlier (least squares regression line with shaded 95% confidence interval) and spent less days stopping over (smaller circles) migrated faster than birds that departed later and spent more time stopping over (larger circles).

TABLE 1: Migrant group, sex, summer 95% and 50% core use area, summer and fall probability of use scores, fall minimum convex polygon, fall recapture date and site, and fall landscape quality, body mass and size (wing chord) at recapture, departure date, and estimated body composition upon departure for 14 woodcock tracked throughout the summer and fall in Rhode Island, USA in 2018 and 2019. Departure body fat, body mass and date were not estimated for birds that were year-round residents in Rhode Island. An additional 3 of 10 woodcock not tracked during summer but caught in fall and tracked throughout fall and winter also remained resident in Rhode Island (see text).

Departure Group ^a	Sex	95% core use area (hectare)	50% core use area (hectare)	RSF Summer Score ^b	RSF Fall Score ^b	Fall MCP (hectare) ^c	# of Pre-migratory GPS Locations	Fall Recapture Date	Site ^d	Fall Landscape Quality ^e	Recapture Bodymass (g)	Wing Chord (mm)	Departure Date	Estimated Departure fat (g)	Estimated Departure mass (g)
early	f	12.7	3.4	16.42	10.0	428.1	20	11/1/19	FC	Low	190	129	11/15/19	37.6	196.3
early	f	22.4	10.6	19.22	20.6	3.6	15	10/08/19	GS	High	184	133	11/15/19	32.3	199.1
early	m	50.6	2.1	19.33	23.0	42.5	10	10/16/19	FC	Low	160	124	11/12/19	31.8	171.8
early	m	8.7	0.5	19.66	21.0	91.1	15	9/20/19	GS	High	138	123	11/10/19	30.6	156.9
early	m	11.7	7.0	20.66	19.6	69.9	14	9/27/19	GS	High	142	121	11/12/19	30.4	161.7
early	m	8.5	0.6	26.55	23.7	41.7	18	9/3/19	Till	High	158	122	11/12/19	36.5	177.7
early	m	1.5	0.4	27.22	25.1	22.4	12	9/3/18	GS	High	143	121	11/5/18	32.4	159.3
late	m	2.1	1.3	4.21	7.8	7.8	25	9/9/18	BR	Low	146	120	11/30/19	44.6	173.3
late	m	8.9	0.2	10.33	30.2	190.1	22	9/25/18	FC	Low	151	125	11/30/18	38.2	178.3
late	m	33.8	5.1	21.46	19.3	271.6	23	9/12/18	FC	Low	144	126	11/28/18	41.1	170.5
late	m	1.9	0.6	30.11	28.3	556.2	19	9/23/19	FC	Low	138	120	11/24/19	40.1	162.8

late	m	NA ^f	NA ^f	NA ^f	23.4	158.3	18	10/16/19	GS	High	141	120	11/24/19	27.7	157.8
resident	m	5.0	2.3	5.11	4.7	196.6	11	10/2/19	BR	Low	135	123	NA	NA	NA
resident	m	17.9	0.8	21.35	11.3	289.5	14	10/31/19	BR	Low	135	121	NA	NA	NA

- a. Birds that departed early (before November 16), late (after Nov 21), or overwintered within Rhode Island (resident).
- b. Summer and fall probability of use (RSF) scores were derived from Masse et al. 2014, see text for details. Higher scores indicate higher suitability for woodcock.
- c. Fall minimum convex polygon (MCP) derived from each individual's pre-migratory locations
- d. Capture Site locations were as follows: Francis Carter Nature Preserve (FC), Great Swamp Management Area (GS), Tillinghast Management Area (Till), and Big River Management Area (BR). See Supplemental Materials Figure S1.
- e. Landscape quality during the fall pre-migratory period was categorized by site as high or low based on the average probability of use values in each 4km² area surrounding a capture site. See text for details.
- f. This one male moved outside the study area after initial capture during spring and so was not tracked during summer prior to returning to the study area in the fall and being recaptured.

TABLE 2: Top model coefficients and covariates used to predict departure fat (g), date of departure, number of stopovers, duration of stopover, average angle of migration, rate of migration, migratory length (km), total days migrated, date of arrival and wintering latitude for woodcock that migrated from Rhode Island, USA. Top model covariates included landscape quality in the fall (L_Quality), departure fat (Depart_fat), departure mass (Depart_mass) date of departure (Datedep), wing chord (wing), total days migrated (migtime), sex, total stopover duration in days (Stopdur), and number of stopover sites used (Stopovers). Supplemental tables report the top 10 models for each model response variable.

Model Response	Top Models	df	logLik	weight
Departure fat	(6.46) L_Quality	3	-28.52	0.32
Date of departure	(1.55) Depart_fat	3	-32.18	0.40
Number of stopovers	(-0.09) Depart_fat + (0.04) Depart_mass	4	-20.23	0.18
Duration of stopover	(0.40) Depart_mass	3	-59.04	0.27
Average angle of migration	(1.37) wing	3	-67.38	0.20
Rate of migration	(-2.52) Datedep + (-2.81) Stopdur	4	-78.46	0.32
Migratory length	(195.15) Stopovers	3	-124.63	0.20
Total days migrated	(0.26) Datedep + (18.28) sex + (1.42) Stopdur + (-3.41) Stopovers	6	-45.95	0.47
Date of arrival	(1.60) Datedep + (8.78) sex + (1.77) Stopdur + (-5.57) Stopovers	6	-46.00	0.50
Wintering latitude	(-1.26) Stopovers	3	-38.25	0.16

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Figure 6.

APPENDIX A. SUPPLEMENTARY MATERIAL

Figure A.1. Fall capture sites (4 km² circles) and management areas (hatched areas) where woodcock were tracked over the summer, and sites where they were recaptured or randomly captured in the fall in southern Rhode Island, USA of 2018 and 2019. The darker or lighter shading of the 4 km² areas (circles) around the fall capture sites denote higher or lower landscape quality sites, respectively.

Table A.1 Band number, migrant status, sex, capture site, and (re)capture date during fall when satellite tags were deployed, as well as last date of GPS transmission, GPS tag weight, GPS duty cycle, expected number of locations given tag type, number of locations uploaded and recorded, actual duration of tag transmissions (date of deployment to date of last record transmitted), number of locations that were not recorded, and possible mortality for 23 woodcock that migrated from or overwintered in Rhode Island, USA in 2018 and 2019. The Lotek Pinpoint satellite tags transmitted locations after deployment every day after deployment (1-day duty cycle), every other day (2-day duty cycle), or a 1-day duty cycle before January 1, switching to a 2-day duty cycle after January 1 (hybrid duty cycle).

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Band #	Migrant	Sex	Site ^a	Fall (re)capture Date	Date of Last Record	Tag Weight (g)	Duty Cycle	Expected Locations	Actual Locations	Duration (days)	Locations not recorded ^b	Mortality ^c
1713-83175	Resident	f	GS	9/11/18	4/7/19	6.3	hybrid	120	52	208	65	
1713-83180	Migrant	f	Till	10/6/18	5/9/19	6.3	hybrid	120	107	215	23	
1713-83182	Migrant	f	GS	10/10/18	4/24/19	6.3	hybrid	120	122	196	6	
1873-09009	Migrant	f	GS	9/24/19	12/24/20	6.3	hybrid	120	41	91	21	
1713-83182	Migrant	f	GS	10/11/19	1/25/20	6.3	hybrid	120	69	105	3	Y
1873-09002	Migrant	f	FC	11/1/19	5/13/20	6.3	hybrid	120	120	193	12	
1713-83163	Migrant	m	GS	9/3/18	11/30/19	4.0	1-day	75	30	88	10	Y
1713-83181	Migrant	m	Till	10/7/18	2/10/19	4.0	1-day	75	93	126	17	

1873-09010	Resident	m	BR	10/6/19	2/16/20	4.0	1-day	75	105	133	10	
1713-83179	Migrant	m	Till	10/6/19	2/4/20	4.0	1-day	75	77	121	19	
1873-09011	Migrant	m	GS	10/7/19	2/25/20	4.0	1-day	75	115	141	10	
1873-09012	Resident	m	GS	11/5/19	2/26/20	4.0	1-day	75	96	113	16	
1713-83148	Migrant	m	BR	9/9/18	4/17/19	4.0	2-day	75	74	220	4	
1713-83168	Migrant	m	FC	9/12/18	12/23/19	4.0	2-day	75	32	72	2	Y
1713-83172	Migrant	m	FC	9/25/18	5/1/19	4.0	2-day	75	68	218	3	
1713-83195	Migrant	m	Till	9/3/19	2/17/20	4.0	2-day	75	57	167	8	
1713-83193	Migrant	m	GS	9/20/19	12/9/20	4.0	2-day	75	27	80	1	Y
1713-83199	Migrant	m	FC	9/23/19	1/22/20	4.0	2-day	75	45	121	4	Y
1873-09003	Migrant	m	GS	9/27/19	12/9/20	4.0	2-day	75	23	73	3	Y
1873-09006	Resident	m	BR	10/2/19	4/3/20	4.0	2-day	75	47	152	21	
1713-83198	Migrant	m	GS	10/16/19	2/25/20	4.0	2-day	75	59	132	5	Y
1713-83200	Migrant	m	FC	10/16/19	5/1/20	4.0	2-day	75	61	197	5	
1873-09005	Resident	m	BR	10/31/19	2/15/20	4.0	2-day	75	32	107	22	

^aWoodcock were captured at Great Swamp Management Area (GS), Tillinghast Management Area (Till), Francis Carter Nature Preserve (FC), and Big River Management Area (BR) in southern Rhode Island, USA (see Fig. S1)

^b Number of locations that were not recorded by a GPS tag (i.e., the number of skipped transmissions up until GPS tag failure)

^c Possible mortality given the tag had been regularly recording and uploading locations to satellites just before going offline

Table A.2 Top 10 a priori models used to predict departure fat (g) in woodcock ranked by number of parameters (k), log likelihood estimates (logLik), difference in Akaike Information Criteria (Δ AICc), and Akaike weights (w_i). Model covariates included sex, landscape quality in the fall (L_Quality), 95% core use area size (HR_95), 50% core use area size (HR_50), summer core use area probability of use score (RSF_Summer), fall pre-migratory probability of use score (RSF_Fall), distance to home range (Dist_2_HR) and fall minimum convex polygon (Fall_HR).

Models: Departure fat (g)	df	logLik	Δ AICc	w_i
L_Quality	3	-28.52	0	0.32
HR_95 + L_Quality	4	-25.99	0.42	0.26
Null	2	-32.30	4.00	0.04
L_Quality + RSF_Fall	4	-28.09	4.46	0.03
Dist_2_HR + L_Quality	4	-28.26	4.72	0.03
HR_50 + RSF_Summer	4	-28.41	5.02	0.02
L_Quality+RSF_Summer	4	-28.43	5.03	0.02
L_Quality + sex	4	-28.46	5.23	0.02
L_Quality+Fall_HR	4	-31.49	5.84	0.02
Fall_HR	3	-31.74	6.30	0.02

Table A.3 Top 10 a priori models used to estimate the date of departure in woodcock ranked by number of parameters (k), log likelihood estimates (logLik), difference in Akaike Information Criteria (Δ AICc), and Akaike weights (w_i). Model covariates included departure fat mass (Depart_fat), departure bodymass (Depart_mass), landscape quality in the fall (L_Quality), sex, 95% core use area size (HR_95), 50% core use area size (HR_50), summer core use area probability of use score (RSF_Summer), fall pre-migratory probability of use score (RSF_Fall), distance to homerange (Dist_2_HR) and fall minimum convex polygon (Fall_HR).

Models: Date of departure	df	logLik	Δ AICc	w_i
Depart_fat	3	-32.18	0	0.40
Depart_fat + RSF_Summer	4	-31.02	2.92	0.09
Depart_fat + Dist_2_HR	4	-31.37	3.61	0.06
Depart_fat + L_Quality	4	-31.43	3.74	0.06
Depart_fat + RSF_Fall + RSF_Summer	5	-27.81	3.83	0.05
Depart_fat + RSF_Fall	4	-31.59	4.07	0.05
Depart_fat + HR_50	4	-31.63	4.15	0.05
Depart_fat + HR_95	4	-31.73	4.34	0.04
Depart_fat + Depart_Mass	4	-32.17	5.23	0.02
L_Quality	3	-34.84	5.33	0.02

Table A.4 Top 10 a priori models used to estimate the number of stopover sites used by woodcock that departed Rhode Island, USA. Models are ranked by number of parameters (k), log likelihood estimates ($\log\text{Lik}$), difference in Akaike Information Criteria (ΔAICc), and Akaike weights (w_i). Model covariates included date of departure (Datedep), departure fat mass (Depart_fat), departure body mass (Depart_Mass), wing chord (wing) and sex.

Models: Number of stopover sites used	df	logLik	ΔAICc	w_i
Depart_fat + Depart_mass	4	-20.23	0	0.18
sex	3	-22.26	0.56	0.13
Depart_mass	3	-22.39	0.81	0.12
Datedep + Depart_fat + Depart_mass	5	-18.85	1.35	0.09
Depart_fat + Depart_mass + wing	5	-19.44	2.53	0.05
Null	2	-24.82	2.69	0.04
Depart_fat + sex	4	-21.77	3.07	0.03
sex + wing	4	-21.89	3.30	0.03
Datedep + Depart_fat + Depart_mass + wing	6	-17.46	3.51	0.03
Depart_fat + Depart_mass + sex	5	-19.95	3.55	0.03

Table A.5 Top 10 a priori models used to estimate the number of days spent stopping over used for woodcock that departed Rhode Island, USA. Models are ranked by number of parameters (k), log likelihood estimates ($\log\text{Lik}$), difference in Akaike Information Criteria (ΔAICc), and Akaike weights (w_i). Model covariates included date of departure (Datedep), departure fat mass (Depart_fat) and departure body mass (Depart_Mass), sex, and wing chord (wing).

Models: Stopover duration	df	logLik	ΔAICc	w_i
Depart_mass	3	-59.04	0	0.27
sex	3	-59.40	0.73	0.18
Depart_fat + Depart_mass	4	-58.06	1.54	0.12
Datedep + Depart_mass	4	-58.69	2.78	0.06
Depart_mass + sex	4	-58.75	2.92	0.06
Depart_mass + wing	4	-59.00	3.40	0.04
sex + wing	4	-59.39	4.18	0.03
Datedep + sex	4	-59.39	4.19	0.03
Depart_fat + sex	4	-59.40	4.22	0.03
wing	3	-61.63	5.18	0.02

Table A.6 Top 10 a priori models used to estimate the average angle of migration for woodcock that departed Rhode Island, USA. Models are ranked by number of parameters (k), log likelihood estimates ($\log\text{Lik}$), difference in Akaike Information Criteria (ΔAICc), and Akaike weights (w_i). Model covariates included date of departure (Datedep), departure fat mass (Depart_fat) and departure body mass (Depart_Mass), sex, and wing chord (wing).

Models: Average angle of migration	df	logLik	ΔAICc	w_i
wing	3	-67.38	0	0.20
Depart_mass + wing	4	-66.02	0.77	0.14
Null	2	-69.37	0.98	0.12
sex	3	-68.37	1.99	0.07
sex + wing	4	-67.28	3.27	0.04
Depart_mass	3	-69.07	3.37	0.03
Depart_fat	3	-69.09	3.42	0.03
Depart_fat + wing	4	-67.35	3.43	0.03
Depart_fat + Depart_mass+ wing	5	-65.30	3.45	0.03
Datedep + wing	4	-67.38	3.48	0.03

Table A.7 Top 10 a priori models used to estimate the rate of migration (km/day) for woodcock that departed Rhode Island, USA. Models are ranked by number of parameters (k), log likelihood estimates (logLik), difference in Akaike Information Criteria ($\Delta AICc$), and Akaike weights (w_i). Model covariates included the date of departure (Datedep), departure fat mass (Depart_fat), and departure body mass (Depart_Mass), sex, duration of stopover (Stopdur), number of stopovers used (Stopovers), and wing chord (wing).

Models: Rate of migration	df	logLik	delta	w_i
Datedep + Stopdur	4	-78.45	0	0.32
Datedep + Stopdur + Stopovers	5	-77.37	1.94	0.12
Datedep + Depart_fat+ Stopdur	5	-77.93	3.07	0.06
Depart_fat + Stopdur	4	-80.11	3.31	0.06
Datedep + Stopdur + wing	5	-78.28	3.77	0.04
Datedep + sex + Stopdur	5	-78.36	3.94	0.04
Datedep + Depart_mass + Stopdur	5	-78.44	4.08	0.04
Stopdur	3	-82.61	4.81	0.02
Depart_fat + Stopovers	4	-81.03	5.14	0.02
Depart_fat + sex + Stopdur	5	-79.45	6.12	0.014

Table A.8 Top 10 a priori models used to estimate the length of migration (km) for woodcock that departed Rhode Island, USA. Models are ranked by number of parameters (k), log likelihood estimates (logLik), difference in Akaike Information Criteria (Δ AICc), and Akaike weights (w_i). Model covariates included the date of departure (Datedep), departure fat mass (Depart_fat), and departure body mass (Depart_Mass), sex, duration of stopover (Stopdur), number of stopovers used (Stopovers), and wing chord (wing).

Models: Length of migration (km)	df	logLik	Δ AICc	w_i
Stopovers	3	-124.63	0	0.20
Null	2	-126.88	1.50	0.09
Stopdur	3	-125.48	1.69	0.08
Stopovers + wing	4	-124.53	3.28	0.03
Depart_fat + Stopovers	4	-124.55	3.33	0.03
Depart_mass	3	-126.30	3.35	0.03
sex + Stopovers	4	-124.59	3.40	0.03
Stopdur + Stopovers	4	-124.61	3.44	0.03
Datedep + Stopovers	4	-124.62	3.47	0.03
Depart_mass + Stopovers	4	-124.63	3.48	0.03

Table A.9 Top 10 a priori models used to estimate the duration of migration for all woodcock that migrated from Rhode Island, USA. Models are ranked by number of parameters (k), log likelihood estimates ($\log\text{Lik}$), difference in Akaike Information Criteria (ΔAICc), and Akaike weights (w_i). Model covariates included the date of departure (Datedep), departure fat mass (Depart_fat), and departure body mass (Depart_Mass), sex, duration of stopover (Stopdur), number of stopovers used (Stopovers), and wing chord (wing).

Models: Total days migrated	df	logLik	ΔAICc	w_i
Datedep + sex + Stopdur + Stopovers	6	-45.95	0	0.47
Datedep + Stopdur + Stopovers	5	-50.31	3.77	0.07
Datedep + sex + Stopdur	5	-50.42	4.00	0.06
Datedep + Depart_mass + Stopdur + Stopovers	6	-48.16	4.42	0.05
Datedep + Stopdur	4	-52.79	4.62	0.04
Datedep + Stopdur + Stopovers + wing	6	-48.61	5.31	0.03
Depart_fat + sex + Stopdur	5	-51.29	5.74	0.02
Datedep + sex + Stopdur + Stopovers + wing	7	-45.84	5.84	0.02
Datedep + Depart_mass + sex + Stopdur + Stopovers	7	-45.87	5.88	0.02
Datedep + Depart_fat + sex + Stopdur + Stopovers	7	-45.88	5.91	0.02

Table A.10 Top 10 a priori models used to estimate the date of arrival for woodcock that departed Rhode Island, USA. Models are ranked by number of parameters (k), log likelihood estimates ($\log\text{Lik}$), difference in Akaike Information Criteria (ΔAICc), and Akaike weights (w_i). Model covariates included the date of departure (Datedep), departure fat mass (Depart_fat), and departure body mass (Depart_Mass), sex, duration of stopover (Stopdur), number of stopovers used (Stopovers), and wing chord (wing).

Models: Date of arrival	df	logLik	ΔAICc	w_i
Datedep + sex + Stopdur + Stopovers	6	-46.00	0	0.50
Datedep + sex + Stopdur	5	-50.32	3.69	0.07
Datedep + Stopdur + Stopovers	5	-50.37	3.79	0.07
Datedep + Depart_mass + Stopdur + Stopovers	6	-48.17	4.35	0.05
Datedep + Stopdur	4	-52.75	4.43	0.05
Datedep + Stopdur + Stopovers + wing	6	-48.53	5.07	0.03
Datedep + Depart_mass + Stopdur + Stopovers	7	-45.93	5.91	0.02
Datedep + Depart_fat + sex + Stopdur + Stopovers	7	-45.93	5.91	0.02
Datedep + sex + Stopdur + Stopovers + wing	7	-45.94	5.93	0.02

Table A.11 Top 10 a priori models used to estimate the wintering site latitude for all woodcock that departed Rhode Island, USA. Models are ranked by number of parameters (k), log likelihood estimates ($\log\text{Lik}$), difference in Akaike Information Criteria (ΔAICc), and Akaike weights (w_i). Model covariates included the date of departure (Datedep), departure fat mass (Depart_fat), and departure body mass (Depart_Mass), sex, duration of stopover (Stopdur), number of stopovers used (Stopovers), and wing chord (wing).

Models: Wintering site longitude	df	logLik	ΔAICc	w_i
Stopovers	3	-38.25	0	0.16
Datedep + Stopovers	4	-37.31	1.60	0.07
Null	2	-40.64	1.79	0.06
Stopdur	3	-39.46	2.40	0.04
Depart_fat + Stopovers	4	-37.95	2.87	0.03
Datedep	3	-39.81	3.11	0.03
Stopdur + Stopovers	4	-38.09	3.16	0.03
Stopovers + wing	4	-38.18	3.34	0.03
Depart_mass	3	-39.94	3.37	0.03
Depart_mass + Stopovers	4	-38.23	3.45	0.02

Fig A.1.