Ornithological Applications
AmericanOrnithology.org

Volume 124, 2022, pp. 1–16
https://doi.org/10.1093/ornithapp/duac011

RESEARCH ARTICLE

Cross-seasonal effects in the American Woodcock: Conditions prior to fall migration relate to migration strategy and implications for conservation

Clayton L. Graham,[1,*] Tanner Steeves,[2] and Scott R. McWilliams[1]

[1] Department of Natural Resources Science, University of Rhode Island, Kingston, Rhode Island, USA
[2] Rhode Island Department of Environmental Management, Division of Fish and Wildlife, West Kington, Rhode Island, USA
*Corresponding author: clayton.l.graham@gmail.com

Submission Date: November 2, 2021; Editorial Acceptance Date: February 17, 2022; Published March 7, 2022

ABSTRACT

How postbreeding habitat quality and body composition of migratory birds carry over to influence fall migration strategies and residency merits consideration when creating cross-seasonal conservation plans, especially in breeding populations that are partial migrants. We assessed the influence of postbreeding habitat quality on departure body composition and fall migration patterns in a southern New England breeding population of American Woodcock (*Scolopax minor*). Woodcock that overwintered near breeding areas ($n = 5$) had less fat upon capture in fall and used lower quality habitat during the fall than birds that eventually 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 or similar fat stores, stopped over for shorter periods on migration, 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 similar or more fat upon departure, stopped over for longer periods on migration, and arrived relatively late to their more northerly wintering areas. These differences in migration strategies were evident under the same fall environmental conditions and did not appear related to individuals responding to their own condition as would be expected if they were classic condition-based carry-over effects. As such, the southern New England breeding population of woodcock is best categorized as nonfacultative 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 states deserve conservation and management attention in order to preserve critical habitat throughout their wintering range.

Keywords: American Woodcock, body composition, fall migration, partial migrant, postbreeding movements, upland gamebird

LAY SUMMARY

- Effective conservation of migratory birds requires knowing how conditions prior to migration relate to the timing, routes, and destinations of birds during migration.
- We used VHF radiotelemetry to track American Woodcock (*Scolopax minor*) in southern New England throughout the summer and fall, recaught them prior to fall migration and used the deuterium-dilution method to nondestructively estimate their departure body composition, and then used GPS radiotelemetry to track them every few days throughout fall migration until they reached their wintering areas.
- At the time of fall migration, resident woodcocks were less fat than individuals that eventually migrated. Migratory woodcock that inhabited higher quality landscapes in the fall departed earlier and, with less or similar fat stores, stopped over for shorter periods on migration, and arrived earlier on their more southerly wintering areas than birds that inhabited lower quality landscapes. However, if we assume fattening rates were maximal for woodcock inhabiting higher quality landscapes, then departure fat of woodcock was similar in different quality landscapes.
- Given that this southern New England breeding population of woodcock included residents that overwintered as well as short- and long-distance migrants, these woodcock are best categorized as nonfacultative partial migrants.
- To preserve such variation in migratory strategies requires conserving key stopover and overwintering areas in the coastal mid-Atlantic and southeastern United States.

Efectos estacionales cruzados en *Scolopax minor*: las condiciones previas a la migración de otoño se relacionan con la estrategia migratoria y las implicaciones para la conservación

RESUMEN

La forma en que la calidad del hábitat luego de la reproducción y la composición corporal de las aves migratorias condicionan las estrategias migratorias de otoño y la residencia debe ser considerada al momento de crear planes de conservación pluri-estacionales, especialmente en poblaciones reproductoras que son migrantes parciales. Evaluamos la influencia de la calidad del hábitat luego de la reproducción en la composición corporal al momento de la partida y los patrones migratorios de otoño en una población reproductora de *Scolopax minor* del sur de Nueva Inglaterra. Los individuos de *S. minor* que pasaron el invierno cerca de las áreas de reproducción (n = 5) tuvieron menos grasa al ser capturadas en el otoño y usaron un hábitat de menor calidad durante el otoño que las aves que finalmente partieron en migración (n = 17). Los individuos de *S. minor* que partieron antes fueron migrantes de larga distancia que habían habitado paisajes de mayor calidad antes de la migración, partieron con reservas de grasa menores o similares, se detuvieron por períodos más cortos durante la migración y llegaron antes a sus áreas de invernada más al sur. Por el contrario, los individuos de *S. minor* que partieron más tarde fueron migrantes de corta distancia que habían habitado paisajes de menor calidad antes de la migración, pero que almacenaron una cantidad similar o mayor de grasa al partir, se detuvieron durante períodos más largos durante la migración y llegaron relativamente tarde a sus áreas de invernada más al norte. Estas diferencias en las estrategias de migración fueron evidentes bajo las mismas condiciones ambientales de otoño y no parecieron estar relacionadas con individuos que respondieran a su propia condición como se esperaría si fueran efectos de arrastre clásicos basados en la condición. Como tal, la población reproductora de *S. minor* del sur de Nueva Inglaterra se clasifica mejor como migrantes parciales no facultativos (i.e., incluye residentes, migrantes de corta distancia y migrantes de larga distancia) que demuestran una conectividad débil entre las etapas de vida; tales poblaciones son excelentes para el estudio de los costos y beneficios de la migración. Las áreas de escala e invernada utilizadas por *S. minor* en los estados costeros medios del Atlántico merecen atención en términos de conservación y gestión para preservar hábitat crítico en toda su área de invernada.

Palabras clave: ave de caza de tierras altas, composición corporal, migración de otoño, migrante parcial, movimientos post reproductivos, *Scolopax minor*

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 (*Setophaga ruticilla*) and Black-tailed Godwits (*Limosa limosa*) 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 territorial birds where late arrival to breeding areas may limit available areas to forage and the availability of mates (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 premigratory 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 Savannah Sparrows (*Passerculus sandwichensis*), which caused delays in fall departure and arrival to the wintering ground (Stutchbury et al. 2011, Mitchell et al. 2012). Most migratory birds must use stopover sites to rest and refuel to continue migrating (Hedenström and Alerstam 1997, Wikelski et al. 2003, Newton 2008), and birds with larger premigratory 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 conditions can also affect access to resources on the wintering ground (Newton 2006), and survival during fall migration (Fayet et al. 2016); however, the nonbreeding season rather than the transition from breeding to nonbreeding may more likely influence fitness (Senner et al 2014, Saino et al. 2017, van Wijk et al 2017, Briedis et al. 2018). Although such carry-over effects may be important, few studies have directly addressed how the quality of breeding and postbreeding habitats relates to the body composition of individuals as they prepare for fall migration, and its subsequent effects on the phenology and routes used during fall migration to winter destinations.

The study of carry-over effects from summer breeding to fall migration and winter is particularly intriguing to study in bird populations that include residents as well as seasonal migrants (Alerstam 1990, Hegemann et al. 2015). Partial migration may be a more ubiquitous migratory strategy than currently documented compared to the more well-studied obligate long-distance and short-distance forms 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 trade-offs 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, in a review of partial migration in birds, Pulido (2011) found that 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 versus migration. 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 carry-over effects.

Our objectives for this study were to examine the influence of body condition and quality of breeding and premigratory 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. American Woodcock have nonmigratory and migratory populations in the southern U.S., and may make large movements in response to extreme winter weather (Krementz et al 1994). Woodcock may also overwinter in coastal areas annually in Rhode Island; however, the breeding-ground origin of these birds is largely unknown (Sullivan et al. 2009, C. Graham personal observation). This suggests potential variation in the migratory strategies of woodcock among individuals and the possibility that woodcock may be partial migrants. We tested the hypotheses, derived from studies of carry-over effects between nonbreeding to breeding areas (Studds and Marra 2005, Paxton and Moore 2015) that (1) birds from higher quality summer and fall-staging sites depart on migration earlier and with more fat, and (2) 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 American Woodcock (42 = hatch year [HY], 25 = after hatch year [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). Woodcock were caught within fields in Department of Environmental Management Areas and a Nature Conservancy preserve in Rhode Island, USA, (see Supplementary Material Figure S1 for location information). Sex and age of captured woodcock were 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). Woodcock were located 3 times each week during the morning (0700–1200), afternoon (1200–1600), and the late afternoon (1600–1900) in a randomized order. Locations were marked with a handheld GPS unit, on average, ≤ 17.7 ± 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, Ontario, CN). We used a 48-hr duty cycle for males and a hybrid schedule for females consisting of a 24-hr duty cycle between November 10 and January 1 and a 48-hr duty cycle after January 1. Captured and retagged woodcock were released at the capture site. Ten additional woodcocks (*n* = 6 AHY males, 4 AHY females) were opportunistically caught before November 10th and also affixed with a Pinpoint GPS tag scheduled with a 24-hr or 48-hr schedule for males, or hybrid schedule as above for females. We assume that woodcock opportunistically caught in Rhode Island before mid-November are likely local breeders based on preliminary data from the Eastern Woodcock Migration Research Cooperative that suggests more northerly breeding woodcock do not initiate fall migration earlier than mid-November (A. Fish, E. Blomberg, personal communication). Male and female tags were designed to record and transmit 75 and 120 locations, respectively, until failure. 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 Premigration

We used Masse et al. (2014) resource selection function (RSF) developed during the postbreeding period to estimate the quality of summer home ranges (during May to August) and premigratory sites (September to November) and used these estimates to assess whether summer and fall habitat quality influenced fall departure decisions and body condition. In general, for woodcock in our study system, the best-performing RSF assigns a relative likelihood-of-use to each 10 × 10 m pixel based on the following parameters: forest cover type, slope, elevation, distance to existing young forest, distance to agricultural openings, distance to hydric soil, and distance to streams (Masse et al. 2014). More specifically, higher likelihood-of-use habitat for woodcock in our region is characterized by higher elevations and lower slopes, and higher densities of streams, hydric soils, young forest, agricultural openings, and deciduous forest (Masse et al. 2014). Recently, Brenner et al. (2019) used a reciprocal transplant experiment during the breeding period to confirm that habitat selection of woodcock in our study system was consistent with that predicted from this RSF. They found that woodcock moved from high to low likelihood-of-use areas returned over many miles to the higher quality sites, whereas birds moved from low to high likelihood-of-use areas stayed in their new-found higher quality sites. Thus, woodcock seem to assess habitat quality in a manner consistent with that predicted by the RSF at least in our study system. During the summer (May 24 to August 16), we obtained, on average, 34.81 ± 4.92 VHF locations for each bird (range: 26–47 locations). Summer locations for recaptured woodcock were used 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, R Development Core Team 2018). The probability of use raster map developed by Masse et al (2014) was scaled between 0 and 100 to serve as a probability of use score for each 10 × 10 m pixel in Rhode Island. We calculated the size of each bird's 95% kernel home range and 50% kernel 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 individual's summer home range quality.

For the fall premigratory 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 2 different "habitat quality" indices. Given that during the premigration period we had fewer locations to estimate home range size, we estimated the size of the fall premigratory 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 bird's premigratory 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 premigratory period for each individual were within a 4-km^2 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-km^2 landscapes (after Brenner et al. 2019) and, thus, provide an estimate of the "Landscape likelihood of use" for each individual. We used the same RSF values to extract the summer RSF score and the fall RSF score, as woodcock mostly stayed within their summer home ranges, the RSF covariates did not change between seasons, and the fall RSF score was an explanatory variable in only one of our top models. 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) using the same RSF thresholds as Brenner et al. (2019) in their validation of Masse et al. (2014) RSF. We felt justified in using a 4-km^2 area to define the landscape quality in fall because previous work in Rhode Island found that woodcock differentiate between the quality of a landscape at this 4-km^2 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 nonmigratory (e.g., summer) 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 migratory or nonmigratory. In order to identify the fall departure and winter arrival locations, we used the final location prior to the first location in a migratory state as the fall departure location, and the location immediately after the final location in a migratory state as the location of winter arrival. We calculated the first migratory flight length as the first step length after the location of fall departure. We used a *k*-means cluster analysis to identify 2 groups of departing birds; an early-departing group that departed before November 16 and a late-departing group that departed after November 21. We defined a "stopover site" during fall migration as any place with 2 or more consecutive locations within a <20-ha area (i.e., stays that lasted >2 days) and "stops" as any place with only 1 location (i.e., stays that lasted ≤2 consecutive days). This differentiation between stopover sites and stops presumably relates to the relative importance of the site for refueling and resting. The length of total migration for each bird was calculated by summing the straight-line distances between the fall departure location, each consecutive stopover location(s), and the wintering location. The rate of migration (km day^{-1}) was calculated by dividing the total length of migration by total days spent migrating (i.e., from fall departure to winter arrival, so not including the initial fueling time).

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 as described in detail in Graham and McWilliams (2021). In brief, within 30 min of capture, we used a prefilled 1-mL insulin syringe (22004270, Fisher Scientific, Pittsburgh, Pennsylvania, USA) to inject each woodcock in the pectoral muscle with 297 ± 0.99 mg (mean ± SE) of 99.9% deuterium oxide (Sigma-Aldrich, St. Louis, Missouri, 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 uL of blood into heparinized capillary tubes that were immediately flame sealed. We used predictive models developed by Graham and McWilliams (2021) 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 and McWilliams (2021): the date at which this population of woodcock, on average, initiated fattening in fall (September 22), and the estimated fattening rate of woodcock from this population (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. We recognize that our population-level estimate of a consistent fattening rate may be an oversimplification, as individuals may fatten at different rates (Le Tourneux et al 2021, Prop et al. 2003, Pot et al. 2019). However, given the difficulty of recapturing woodcock after GPS transmitters had been deployed, and tag sizes are currently too small to provide accelerometer data for individuals to infer feeding rates, a population-level estimate is currently our best option to estimate the rate of fattening in woodcock for the present study. We assessed the implications of this assumption of constant fattening rate by also estimating a maximum fattening rate for woodcock and applying this to birds that inhabited high-quality landscapes where fattening may have been more rapid. We used the upper standard error of the fattening rate (reported in Graham and McWilliams 2021) to estimate a maximal fattening rate for our population of woodcock (0.51 g fat day^{-1}). We also used a maximal rate of fattening (0.58 g fat day^{-1}) reported in Owen and Krohn (1973) for females that were recaptured during fall in Maine, this being the only study that reported higher fattening rates for woodcock than those we report here. We used these two estimates of maximal fattening rate to calculate the maximum fat mass for birds that inhabited high-quality landscapes during fall prior to departure on migration.

Statistical Analysis

We used a mixed effect generalized linear model with a gaussian distribution to determine the effect of site, distance from home range, home range size, landscape quality in fall, and summer RSF score and fall RSF score on departure fat mass and departure body mass of birds recaught in the fall ($n = 12$). A mixed effect generalized linear model with a gaussian distribution and was also used to assess the influence of site, home range, home range size, landscape quality in fall, summer RSF score and fall RSF, departure fat mass, and departure body mass on the date of departure. In all cases, we used single parameter models given the sample sizes available, and all reported analyses conformed to the assumptions of normality and homogeneity of variance.

A combined dataset consisting of birds that were recaught or randomly captured in the fall ($n = 17$) was used to assess the influence of fall body condition on migratory phenology. Specifically, we used a generalized linear model with a gaussian distribution to assess the influence of wing chord, departure fat, departure mass, sex, and the date of departure on the first flight distance, and stopover duration. We used a generalized linear model with a Poisson distribution to assess the influence of wing chord, departure fat, departure mass, sex, and the date of departure on the number of stopovers used. We also used a generalized linear model with a gaussian distribution 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 was used to assess whether landscape quality in the fall and fall RSF scores influenced whether woodcock migrated or overwintered in Rhode Island. An analysis of covariance (ANCOVA) was used to assess whether residents had lower fat mass at capture than birds that migrated. We used the dredge function in the *MumIn* package to create single parameter candidate models from global models and used the Akaike Information Criteria adjusted for small sample size (AIC_c) and model weights (w_i) to select the top models among candidate models (Barton 2020, Burnham and

Anderson 2002). 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 for analysis. 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 16.80 ± 4.60 GPS locations during the fall premigratory period (range: 10–28; Table 1) for the 14 birds that we recaptured in fall. Probability of use scores for premigratory locations used during fall were, on average, 21.35 ± 1.59 (range: 7.80–33.92; 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 (t = –0.4, P = 0.68; Table 1).

Five birds remained in Rhode Island throughout the winter (2 of 14 birds recaptured in fall (Table 1), 3 of 9 new fall-captures; 1 female, 4 males); 1 remained all winter within its summer home range (i.e., year-round residency) whereas 4 relocated a short distance, on average, 17.75 ± 8.07 km from fall capture locations and 23.64 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).

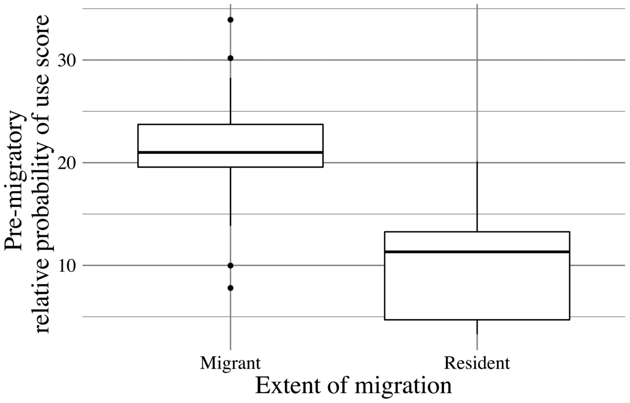

FIGURE 1. Woodcock that remained in Rhode Island, USA (n = 5) during winter resided in low-quality sites during the fall premigration period compared to woodcock that eventually migrated in fall from Rhode Island to wintering areas in the mid-Atlantic and southern USA region (n = 17). Site quality is indexed as relative probability of use scores from a Resource Selection Function derived from tracking woodcock (Masse et al. 2014; see text).

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 g 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 = 0.001; Figure 2). Given that woodcock from this population in the same 2 years began to deposit body fat, on average, on September 22 with a fat deposition rate of 0.42 ± 0.09 g fat day^{-1} (from Graham and McWilliams 2021), 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). We estimated that migrating male woodcock (n = 12) departed with, on average, 36.42 ± 1.64 g of fat (Figure 2) and weighed 169.10 ± 2.57 g upon departure. Likewise, we estimated that migrating female Woodcock (n = 5) departed with 38.36 ± 2.5 g of fat (Figure 2) and weighed 203.12 ± 4.04 g. Although females were heavier than males upon departure (t = –7.1, P = <0.001), we detected no significant difference in fat mass (g) between females and males upon departure (t = –0.7, P = 0.53). If we assume that woodcock inhabiting high-quality landscapes fatten at higher rates (0.58 g fat day^{-1}) than the average fattening rate for this population (0.42 ± 0.09 g fat day^{-1}), then we estimated that male woodcock departed with, on average, 39.06 ± 1.25 g of fat while females departed with, on average, 38.02 ± 0.41 g of fat (Table 1).

Our best supported model for estimating departure fat included landscape quality in fall as a covariate (F = 8.9, R^2 = 0.50, df = 1 and 9, P = 0.015; Table 2, Supplementary Material Table S2). Our best-supported model predicting departure date from Rhode Island included only departure fat as a covariate (F = 22.37, R^2 = 0.71, df = 1 and 9, P = 0.001; Table 2, Supplementary Material Table S3). We excluded site as a random effect in our models estimating departure fat and date of departure, since the top model with site as a random effect had a ΔAIC > 4 compared to the top model that excluded the random effect. In general, woodcock that inhabited higher quality landscapes in fall tended to depart earlier and with less or similar fat stores compared to woodcock that inhabited lower quality landscapes in fall (Figure 3). However, these differences in departure fat for woodcock inhabiting high- and low-quality landscapes depended on the assumption that fattening rates did not differ with landscape quality. If we instead assume that woodcock inhabiting high-quality landscapes fatten at higher rates (0.51 or 0.58 g fat day^{-1}) than the average fattening rate for this population (0.42 ± 0.09 g fat

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 American Woodcocks 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). Rhode Island's maximal rate of fattening was estimated using the upper threshold of the fattening rate standard error added to the mean fattening rate. A maximal rate of fattening for birds in Maine was estimated using data from females in Owen and Krohn (1973).

Departure group [a]	Sex	95% core use area (ha)	50% core use area (ha)	RSF Summer score [b]	RSF Fall score [b]	Fall MCP (ha) [c]	Number of premigratory GPS locations	Fall recapture date	Site[d]
Early	f	12.7	3.4	16.42	10.0	428.1	20	11/1/19	FC
Early	f	22.4	10.6	19.22	20.6	3.6	15	10/08/19	GS
Early	m	50.6	2.1	19.33	23.0	42.5	10	10/16/19	FC
Early	m	8.7	0.5	19.66	21.0	91.1	15	9/20/19	GS
Early	m	11.7	7.0	20.66	19.6	69.9	14	9/27/19	GS
Early	m	8.5	0.6	26.55	23.7	41.7	18	9/3/19	Till
Early	m	1.5	0.4	27.22	25.1	22.4	12	9/3/18	GS
Late	m	2.1	1.3	4.21	7.8	7.8	25	9/9/18	BR
Late	m	8.9	0.2	10.33	30.2	190.1	22	9/25/18	FC
Late	m	33.8	5.1	21.46	19.3	271.6	23	9/12/18	FC
Late	m	1.9	0.6	30.11	28.3	556.2	19	9/23/19	FC
Late	m	NA[h]	NA[h]	NA[h]	23.4	158.3	18	10/16/19	GS
Resident	m	5.0	2.3	5.11	4.7	196.6	11	10/2/19	BR
Resident	m	17.9	0.8	21.35	11.3	289.5	14	10/31/19	BR

Departure group [a]	Fall landscape quality [e]	Recapture body mass (g)	Wing chord (mm)	Departure date	Estimated departure fat (g)	(A) Estimated maximal departure fat (g) [f]	(B) Estimated maximal departure fat (g) [g]	Estimated departure mass (g)
Early	Low	190	129	11/15/19	37.6	–	–	196.3
Early	High	184	133	11/15/19	32.3	35.6	38.4	199.1
Early	Low	160	124	11/12/19	31.8	–	–	171.8
Early	High	138	123	11/10/19	30.6	37.1	39.7	156.9
Early	High	142	121	11/12/19	30.4	34.6	38.2	161.7
Early	High	158	122	11/12/19	36.5	40.7	44.5	177.7
Early	High	143	121	11/5/18	32.4	36.0	39.2	159.3
Late	Low	146	120	11/30/19	44.6	–	–	173.3
Late	Low	151	125	11/30/18	38.2	–	–	178.3
Late	Low	144	126	11/28/18	41.1	–	–	170.5
Late	Low	138	120	11/24/19	40.1	–	–	162.8
Late	High	141	120	11/24/19	27.7	31.3	34.5	157.8
Resident	Low	135	123	NA	NA	NA	NA	NA
Resident	Low	135	121	NA	NA	NA	NA	NA

[a] Birds that departed early (before November 16), late (after November 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 premigratory 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 Supplementary Material Figure S1).

[e] Landscape quality during the fall premigratory period was categorized by site as high or low based on the average probability of use values in each 4-km^2 area surrounding a capture site (see text for details).

[f] For birds that used high-quality landscapes during fall, maximal departure fat mass (A) was estimated using our reported maximal fattening rate (0.51 g fat day^{-1}).

[g] For birds that used high-quality landscapes during fall, maximal departure fat mass (B) was also estimated using Owen and Krohn (1973)'s reported maximal fattening rate for birds breeding in Maine (0.58 g fat day^{-1}).

[h] This 1 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 recaught.

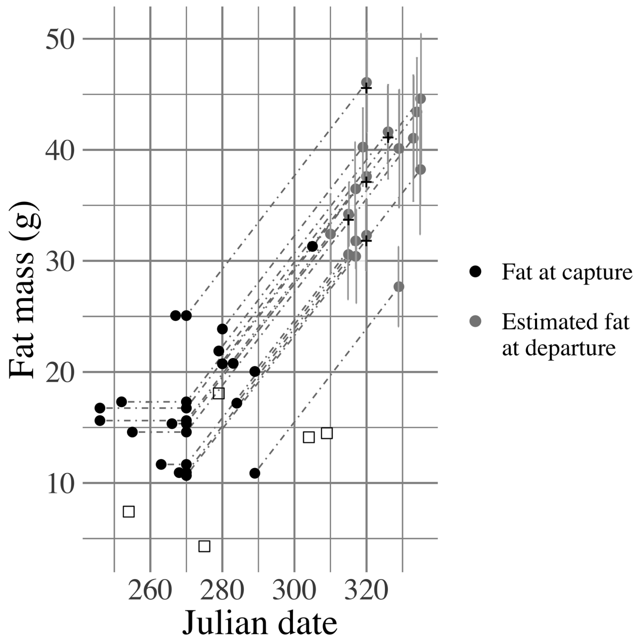

FIGURE 2. Estimated departure fat load (gray circles ± SE) of woodcock given their whole-body fat at capture (black circles) and known date of departure in fall (November 6 to December 2, Julian dates 310 to 335) from Rhode Island, USA. The longest gap of days without departures was between November 16–22 (Julian dates 321–326). Five birds were caught during the premigration 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 day^{-1} (sloped dashed line; based on Graham and McWilliams 2021) until their known departure date (gray circles). Females (black cross under gray circles) were heavier and larger than males (see text) although males and females had similar fat mass upon departure. Range of estimated fat departure for each bird (gray vertical lines) was calculated using the upper and lower standard error of the fattening rate (reported in Graham and McWilliams 2021) and the number of days spent fattening prior to departure.

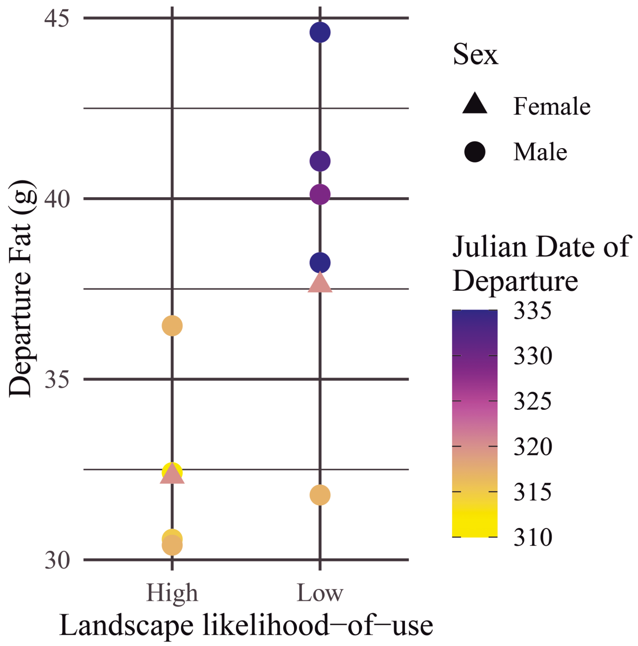

FIGURE 3. Woodcock tracked throughout the summer and fall in Rhode Island (n = 11) and that resided in high-quality landscapes (4-km^2 areas with average likelihood of use scores > 45) prior to fall migration departed on migration with less fat and earlier than woodcock that resided in low-quality landscapes (4-km^2 areas with average scores < 35) prior to fall migration. The depicted differences in departure fat of woodcock inhabiting high- and low-quality landscapes were based on the assumption that fattening rates did not depend on landscape quality (see text for details).

per day^{-1}), then woodcock inhabiting high-quality landscapes which departed earlier had similar departure fat mass as those from low-quality landscapes which departed later (t = 1.59 for 0.51 g fat day^{-1}; p = 0.14; t = 0.01, p = 0.98 for 0.58 g fat day^{-1}; Table 1).

Postbreeding Conditions in Relation to Fall Migratory Phenology

We were able to track 22 of the 29 birds with GPS tags over the fall migratory period, with 17 birds migrating from Rhode Island and 5 birds overwintering within Rhode Island (Supplementary Material Table S1). Six transmitters provided <5 locations and then failed (n = 5 in 2018, 1 in 2019) with 1 of these 6 birds shot prior to departure in 2018, and 1 transmitter in 2018 never recording any locations. These 7 transmitters were censored from subsequent analysis. Of the 17 birds that migrated, 12 were birds that were recaptured after tracking them throughout the summer and fall (2018, n = 4 and 2019, n = 8). In general, for the 17 individuals for which we present fall migration information, the transmitters provided >85% of the expected locations given their duty cycle (Supplementary Material Table S1). One female was captured 3 times (first fall, next spring, second fall) yielding 1.5 years of location data including 2 fall migrations to wintering areas in 2018 and 2019 (Figure 4D).

American 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 to 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 (range: 0–4 stopovers; Figure 5) along their migratory

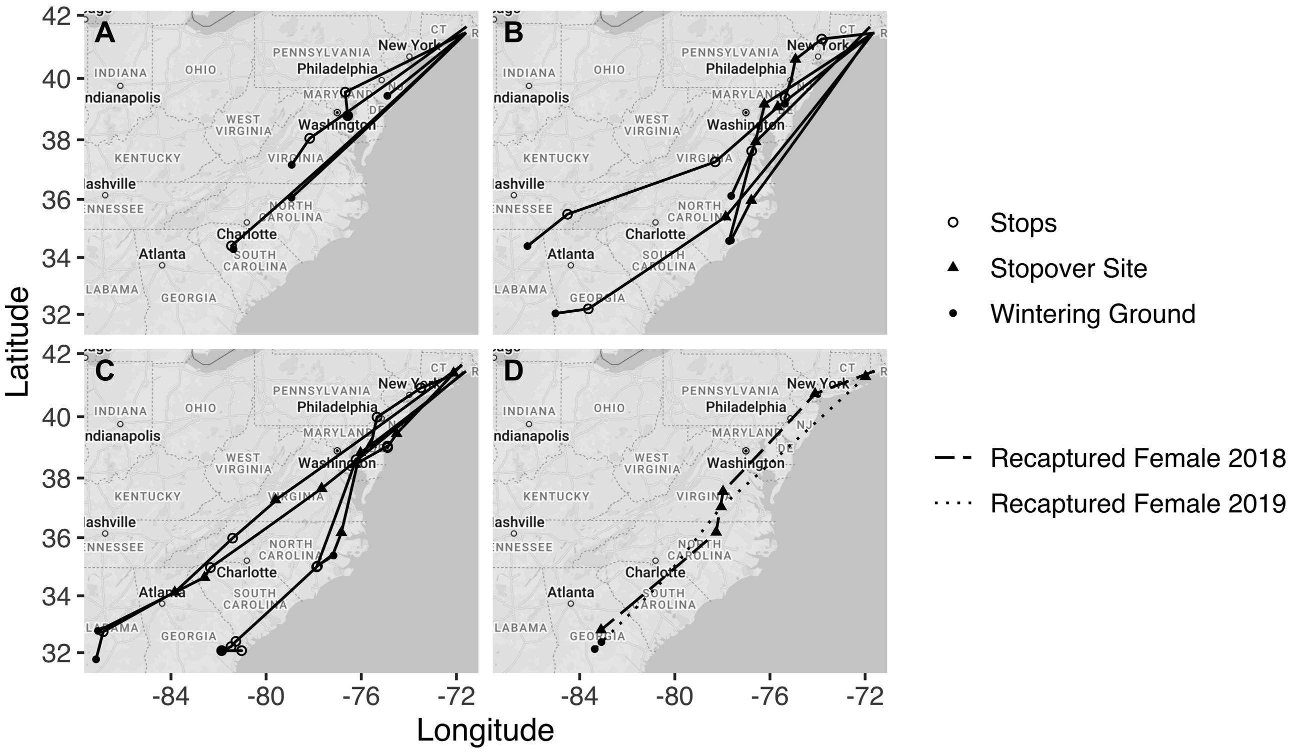

FIGURE 4. Migratory tracks, stopover sites (>2 consecutive locations within a site; triangles), nonstopover sites (≤2 consecutive locations within a site; open circles) and wintering locations (filled circles) for 16 American Woodcock from their departure location in Rhode Island to their wintering area. (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 1 recaptured female (D) tracked in 2 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 4 stopover sites in Virginia; whereas in 2019 (dotted line), the female migrated more directly and faster (24 days) and used 2 stopover sites that were not used the previous year.

TABLE 2. Top model coefficients and covariates used to estimate departure fat (g), date of departure, number of stopovers, duration of stopover, 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). Supplementary Material tables report the top 10 models for each model response variable. k = number of variables, w_i = Akaike weight.

Model response	Top models	k	logLik	w_i
Departure fat	(–0.005) L_Quality	3	–28.18	0.73
Date of departure	(1.56) Depart_fat	3	–32.18	0.92
Number of stopovers	(–0.86) Sex	2	–21.54	0.30
Duration of stopover	(0.40) Depart_mass	3	–59.04	0.53
Rate of migration	(–2.47) Stopdur	3	–82.61	0.67
Migratory length	(195.15) Stopovers	3	–124.63	0.45
Total days migrated	(0.92) Stopdur	3	–57.31	0.99
Date of arrival	(1.29) Datedep	3	–38.71	0.76
Wintering latitude	(–1.26) Stopovers	3	–38.25	0.38

route. Early- and late-departure groups did not differ in the amount of time spent at stopovers ($t = 0.7$, $P = 0.48$) or the number of stopovers used ($t = 0.1$, $P = 0.91$) and spent, on average, 10.06 ± 2.64 days (0–38 days) at a given stopover site. Stopover duration was predicted by departure mass, where birds that were heavier spent more time stopping over ($F = 12.52$, df = 1 and 15, $P = 0.003$; Supplementary Material Table S5). The top model predicting number of stopovers included sex as a covariate ($F = 3.72$, df = 12 and 154, $P = 0.05$; Table 2, Supplementary Material Table S4); however, this model was also competitive with the null model. Although the top model was competitive with the null model, in general females used twice as many stopovers than males, and birds with more stopovers migrated further ($F = 4.45$, df = 1 and 15, $P = 0.05$; Table 2, Figure 4, Supplementary Material Table S7).

Total distance traveled during migration was, on average, 1,149.18 ± 105.57 km (range: 359–1,731 km). Departing woodcock took, on average, 19.41 ± 3.00 days to reach their wintering grounds. Duration of migration was predicted

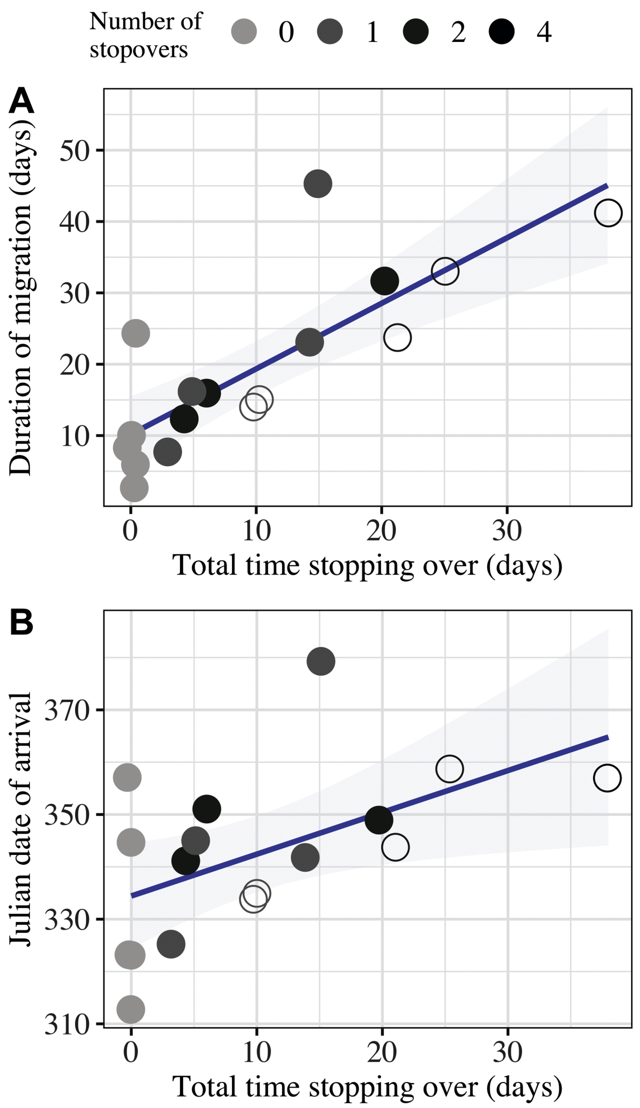

FIGURE 5. Number of days spent at stopover sites during fall migration increased with the (A) duration of migration (total number of days) for each individual, and (B) the Julian date of arrival on the wintering area. Males are depicted as filled circles (shading denotes number of stopover days) whereas 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).

by stopover duration where birds with longer stopover durations required more time to migrate ($F = 28.47$, df = 1 and 15, $P = < 0.001$; Table 2, Supplementary Material Table S8). The top model with date of arrival at the wintering area was predicted by the date of departure ($F = 11.71$, df = 1 and 15, $P = 0.004$; Table 2). In general, woodcock that took longer to migrate and arrived later to the wintering areas used more stopovers and departed later (Figure 5). Birds that spent 0–15 days stopping over spent twice as many days migrating as birds that stopped over for 15–30 days ($F = 10.5$, df = 1 and 15, $P = 0.005$; Supplementary Material Figure S2 and Supplementary Material Table S6). Woodcock traveled, on average, 81.03 ± 10.17 km per day (range: 14.8–167.6 km).

Location of Wintering Areas in Relation to Postbreeding Conditions

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 ($t = -3.0$, $P = 0.01$) with early-departing woodcock arriving at wintering areas on December 1 ± 4.32 days (November 9 to December 23) and late-departing woodcock arriving on December 19 ± 4.88 days (December 7 to January 14). For winter locations with more than one woodcock ($n > 1$), woodcock arrived, on average, on December 1 ± 15.1 days to North Carolina (latitude: 34.57–36.1), December 10 ± 9.0 days to Georgia (latitude: 32.03–32.32), December 12 ± 12.7 days to New Jersey (latitude: 39.18–39.43), December 13 ± 2.3 days to Alabama (latitude: 31.76–34.39), and December 22 ± 2.1 days to Maryland (latitude: 38.46–38.79). Although the null model was competitive with the top model, 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, Supplementary Material Table S10). Birds that used more stopovers 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 (Supplementary Material Table S10). No models were predictive of the wintering area longitude, as the top model was the null model.

DISCUSSION

Premigratory Habitat Quality in relation to Fall Departure Body Composition and Timing of Departure

We found support for the hypothesis that the quality of areas inhabited prior to migration was associated with differences in body composition at departure and timing of departure, but not always in the expected way. We predicted that birds from higher quality summer and fall staging sites would depart earlier and with more fat. We found that woodcock that inhabited higher quality landscapes in fall departed on migration earlier, as predicted, although they had less estimated fat mass (Figure 3). In contrast, woodcock that departed later in fall had, on average, more estimated fat mass and had inhabited lower quality landscapes prior to migration (Figure 3). However, these differences in departure fat for woodcock inhabiting high- and low-quality landscapes depended on our assumption that fattening rates of woodcock (i.e., 0.42 ± 0.09 g fat day^{-1}) were consistent across landscapes. When we instead assumed that woodcock inhabiting high-quality landscapes fattened at observed maximal fattening rates (i.e., 0.51–0.58 g fat day^{-1}) compared to the slower fattening rate of 0.42 g fat day^{-1} for woodcock that inhabited low-quality landscapes, then the estimated amount of fat at departure was similar for woodcock in both landscapes. Determining whether fattening rates and fat mass of woodcock at departure depends on landscape quality or migration strategy requires tracking many more individuals that are caught throughout the fall staging period including just prior to departure. Given that the timing of molt seems related to the timing of fat deposition in fall-migrating woodcock (Owen and Krohn 1973), determining the extent to which molt schedules in fall vary across individuals could provide insights into the timing of fat deposition. These results suggest that the woodcock population we studied includes individuals with quite different migration strategies: long-distance migrants that depart early with less or similar fat stores, and short-distance migrants that depart later in fall with similar or more fat stores. 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 of estimated fat (or 21% of departure body mass). As noted earlier, these estimates of fat load at departure somewhat depend on the assumed fattening rate (see Table 1 for examples). Like other migratory birds, woodcock may depart on migration only after reaching some minimum fat threshold (e.g., 27–34 g for woodcock in this study depending on assumed fattening rate). Red Knots (*Calidris canutus*) 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, Swainson's Thrushes (*Catharus ustulatus*) departed from stopover sites when reaching a minimum threshold of fat, but also when daily maximum temperatures exceeded 21°C and wind strength was <10 km hr^{-1} (Bowlin et al. 2005). Woodcock began to accumulate fat mass, on average, on September 22 (Graham and McWilliams 2021), 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 prebasic 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 only after the peak of molt and began departing from Maine in Mid-October (Owen Jr and Krohn 1973). Timing of fall departure did not differ between sexes in our study, which is also consistent with the results of previous studies (Coon et al. 1976, Derleth and Sepik 1990, Meunier et al. 2008). In sum, photoperiod and the timing of molt and subsequent fat deposition seem to primarily influence timing of fall departure for woodcock in southern New England.

Conditions at Fall Departure and the Timing, Pace, and Distance of Fall Migration

We found support for the hypothesis that conditions at fall departure (e.g., fat stores, body mass, phenology) were positively associated with the subsequent timing, pace, and distance of migration. Woodcock that departed earlier used more stopovers, stayed less long at stopovers, migrated further, and arrived earlier on their wintering areas. In contrast, woodcock that departed later stayed longer at stopovers, migrated less far, and took longer to get to their wintering areas. We recognize that these conclusions are derived from single-variable statistical models that do not adequately consider possible interactions between variables. Future studies that track individuals across multiple years and migrations are needed to determine the extent to which individuals modify their migration strategies, if at all, and the causes and consequences of such variation in migration strategies.

Quality of the landscape used by woodcock prior to fall migration was associated with differences in estimated body fat at departure, although these body fat estimates were sensitive to assumed fattening rates, 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 premigratory period also departed earlier, although these individuals had less or similar fat mass than later departing individuals depending on the assumed fattening rates. Woodcock that departed earlier may have reached the 27–34 g threshold of fat before birds that departed later, or possibly were higher quality individuals than birds which departed later. If our population-level estimates of fattening rates of woodcock are oversimplifications and instead fattening rates vary with habitat quality (e.g., birds in high-quality areas have higher fattening rates), then birds from higher quality habitats may have more energetic capital to leave earlier and migrate further distances compared to birds inhabiting lower quality sites in fall. Female woodcock also used more stopovers during migration and heavier females 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 and lower reward agricultural habitats compared to males that used more profitable marine habitats for foraging (Baert et al. 2018). These differences in migration strategies of woodcock were evident under the same fall environmental conditions and did not appear related to individuals responding to their own condition as would be expected if they were classic condition-based carry-over 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 premigratory locations that were of lower quality than that of birds that departed. In general, long-distance migrating woodcock departed earlier, stopped over for longer periods, migrated faster, and wintered further south. However, short-distance migrating woodcock departed, on average, later, spent less time stopping over, were slower, took longer to migrate, arrived later to wintering areas, and wintered further north. 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), and stayed at stopover sites anywhere from 1 to 28 days with a median use of 3 days. 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, shorter-, and longer-distance) within this population.

Given that these differences in migration strategies (i.e., resident as well as short- and long-distance migrants) occurred under the same fall environmental conditions and did not appear related to individual body condition, our population of woodcock are best classified as nonfacultative partial migrants (sensu Newton 2008). Blackcap Warblers (*Sylvia atricapilla*) and European Robins (*Erithacus rubecula*) also include migratory and resident populations that have been shown through carefully controlled breeding experiments to have a heritable basis (Berthold and Querner 1981, Biebach 1983, respectively). Partial migration in birds is more commonly observed at intermediate latitudes where winter conditions are variable, neither always very harsh or benign (Lundberg 1988). This led Lack (1954) and many others (reviewed in Newton 2008, 2012) to suggest that partial migration, in general, evolved in response to varying winter conditions and winter food limitation that created different mortality and breeding costs/benefits for residents compared to migrants.

Previous work has suggested that woodcock may be 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 temperature 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 shorter-distance migration may be a risky strategy in some years (Mendall and Aldous 1943, Docherty et al. 1994). Of the 5 woodcock (4 males, 1 females) that we documented over-wintering in Rhode Island, 4 birds made short distance (<25 km) 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 5 birds that overwintered were males that had been previously tracked during the summer: 1 bird remained within its summer home range through the following fall, winter and spring, while the other bird overwintered in coastal Rhode Island and made a 30-day migration to Western Pennsylvania the following spring. This bird then flew to Eastern Pennsylvania to breed 352 km away from his fall capture location. 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 migratory as well as resident individuals that differ in behavior and fat deposition, and so are best classified as nonfacultative 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 premigratory period (0.92; Derleth and Sepik 1990). 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 south 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. Our conclusions regarding migratory strategies are correlative as we did not manipulate the condition of individuals. However, male woodcocks are more philopatric than female woodcocks (Sepik et al. 1993) and female woodcocks stay within the same fall foraging habitats unless conditions become unfavorable (Doherty et al. 2010). We also saw this trend within our data, as 89% of birds remained within the summer home ranges during the fall. 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 Rhode Island-breeding woodcock include individuals with distinct migration strategies that spend the winter throughout the mid-Atlantic and southeastern U.S., measures focused on conserving such individual variation within a population would require managing habitat at many key stopover and wintering locations throughout their nonbreeding range. For example, key stopover sites used by migrants along the southern New England coast, the Delmarva Peninsula, Eastern Virginia, Eastern North Carolina, and Southern New Jersey would be especially important to conserve because they are close to migratory barriers such as the Long Island Sound and Delaware Bay and the majority of woodcock migrating from Rhode Island passed through this migratory bottleneck. In addition, our study of southern New England breeding woodcock has demonstrated that this population is best classified as nonfacultative 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.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

ACKNOWLEDGMENTS

We thank the following for their assistance in the field: S. Thielacker, J. Kaelbein, G.Emery, A. Jones, C. Slezak, P. Woodward, C. Cooper-Mullin, K. DeMoranville, W. Carter, A Frawley, L Corcoran, S. Clode, M. Muller, 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 work was supported by the USDA National Institute of Food and Agriculture, McIntire-Stennis project 1019907.

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: S.R.M. and C.L.G. developed and designed the research with input from T.S. C.L.G. conducted the research. C.L.G. wrote the paper with substantial input from S.R.M. C.L.G. analyzed the data. S.R.M. and T.S. contributed substantial resources.

Data depository: Analyses reported in this article can be reproduced using the data provided by Graham et al. (2022).

LITERATURE CITED

Alerstam, T. (1990). Bird Migration. Cambridge University Press, Cambridge, UK.

Anderson, A. M., S. Duijns, P. A. Smith, C. Friis, and E. Nol (2019). Migration distance and body condition influence shorebird migration strategies and stopover decisions during southbound migration. Frontiers in Ecology and Evolution 7:251.

Atkinson, P. W., A. J. Baker, K. A. Bennett, N. A. Clark, J. A. Clark, K. B. Cole, A. Dekinga, A. Dey, S. Gillings, P. M. González, K. Kalasz, et al. (2007). Rates of mass gain and energy deposition in red knot on their final spring staging site is both time- and condition-dependent. Journal of Applied Ecology 44:885–895.

Baert, J. M., E. W. M. Stienen, B. C. Heylen, M. M. Kavelaars, R. J. Buijs, J. Shamoun-Baranes, L. Lens, and W. Müller (2018). High-resolution GPS tracking reveals sex differences in migratory behaviour and stopover habitat use in the Lesser Black-backed Gull *Larus fuscus*. Scientific Reports 8:1–11.

Baker, A. J., P. M. González, T. Piersma, L. J. Niles, I. De Lima Serra no Do Nascimento, P. W. Atkinson, N. A. Clark, C. D. T. Minton, M. K. Peck, and G. Aarts (2004). Rapid population decline in red knots: Fitness consequences of decreased refueling rates and late arrival in Delaware Bay. Proceedings of the Royal Society B: Biological Sciences 271:875–882.

Barton, K. (2020) MuMIn: Multi-model inference. R Package version 1.40.4. https://CRAN.R-project.org/package=MuMIn

Berthold, P. (1996). Control of Bird Migration. Chapman & Hall, London, UK.

Berthold, P. (1999). A comprehensive theory for the evolution, control and adaptability of avian migration. Ostrich 70:1–11.

Berthold, P. and U. Querner. (1981). Genetic basis of migratory behavior in European warblers. Science 212:77–9.

Biebach, H. (1983). Genetic determination of partial migration in the European robin (*Erithacus rubecula*). The Auk 100:601–606.

Bowlin, M. S., W. W. Cochran, and M. C. Wikelski (2005). Biotelemetry of New World thrushes during migration: Physiology, energetics and orientation in the wild. Integrative & Comparative Biology 45:295–304.

Boyle, W. A. (2011). Short-distance partial migration of Neotropical birds: A community-level test of the foraging limitation hypothesis. Oikos 120:1803–1816.

Bregnballe, T., M. Frederiksen, and J. Gregersen (2006). Effects of distance to wintering area on arrival date and breeding performance in Great Cormorants *Phalacrocorax carbo*. Ardea 94:619–630.

Brenner, S. J., B. Buffum, B. C. Tefft, and S. R. McWilliams (2019). Landscape context matters when American Woodcock select singing grounds: Results from a reciprocal transplant experiment. The Condor: Ornithological Applications 121:duy005.

Briedis, M., M. Krist, M. Král, C. C. Voigt, and P. Adamík (2018). Linking events throughout the annual cycle in a migratory bird—nonbreeding period buffers accumulation of carry-over effects. Behavioral Ecology and Sociobiology 72:1–12.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second edition. Springer, New York, NY, USA.

Calenge, C. (2006). The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Cohen, E. B., F. R. Moore, and R. A. Fischer (2012). Experimental evidence for the interplay of exogenous and endogenous factors on the movement ecology of a migrating songbird. PLoS One 7:e41818.

Coon, R. A., P. D. Caldwell, and G. L. Storm (1976). Some characteristics of fall migration of female woodcock. The Journal of Wildlife Management 40:91–95.

Dawson, A. (2012). The effect of latitude on photoperiodic control of gonadal maturation, regression and molt in birds. General and Comparative Endocrinology 190:129–133.

Derleth, E. L., and G. F. Sepik (1990). Summer–fall survival of American Woodcock in Maine. The Journal of Wildlife Management 54:97–106.

Diefenbach, D. R., E. L. Derleth, W. Matthew, V. Haegen, J. D. Nichols, and J. E. Hines (1990). American Woodcock winter distribution and fidelity to wintering areas. The Auk 107:745–749.

Docherty, D. E., K. A. Converse, W. R. Hansen, and G. W. Norman (1994). American Woodcock (*Scolopax minor*) mortality associated with a reovirus. Avian Diseases 38:899–904.

Doherty, K. E., D. E. Andersen, J. Meunier, E. Oppelt, R. S. Lutz, and J. G. Bruggink (2010). Foraging location quality as a predictor of fidelity to a diurnal site for adult female American woodcock Scolopax minor. Wildlife Biology 16:379–388.

Fayet, A. L., R. Freeman, A. Shoji, H. L. Kirk, O. Padget, C. M. Perrins, and T. Guilford (2016). Carry-over effects on the annual cycle of a migratory seabird: An experimental study. Journal of Animal Ecology 85:1516–1527.

Graham, C. G., and S. R. McWilliams (2021). Body composition of American Woodcock during fall staging: A validation of the non-invasive deuterium dilution method. Journal of Ornithology 163:213–222.

Graham, C. L., T. Steeves, and S. R. McWilliams (2022). Data from: Cross-seasonal effects in the American Woodcock: Conditions prior to fall migration relate to migration strategy and implications for conservation. Ornithological Applications 124:duac011. doi:10.5061/dryad.pc866t1qv

Gunnarsson, T. G., J. A. Gill, P. M. Potts, P. W. Atkinson, R. E. Croger, G. Gélinaud, A. Gardarsson, and W. J. Sutherland (2005). Estimating population size in Black-tailed Godwits *Limosa limosa islandica* by colour-marking. Bird Study 52:153–158.

Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop (2011). Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology 80:4–18.

Hedenström, A., and T. Alerstam (1997). Optimum fuel loads in migratory birds: Distinguishing between time and energy minimization. Journal of Theoretical Biology 189:227–234.

Hegemann, A., A. M. Fudickar, and J. Å. Nilsson (2019). A physiological perspective on the ecology and evolution of partial migration. Journal of Ornithology 160:893–905.

Hegemann, A., P. P. Marra, and B. I. Tieleman (2015). Causes and consequences of partial migration in a passerine bird. The American Naturalist 186:531–546.

Hijmans, R. J. (2019). Geosphere: spherical trigonometry. R package version 1.5–10. https://CRAN.R-project.org/package=geosphere

Kokko, H. (1999). Competition for early arrival in migratory birds. Journal of Animal Ecology 68:940–950.

Krementz, D. G., J. T. Seginak, and G. W. Pendleton (1994). Winter movements and spring migration of American woodcock along the Atlantic coast. The Wilson Bulletin 106:482–493.

Lack, D. (1954). The Natural Regulation of Animal Numbers. Oxford University Press, Oxford, UK.

Le Tourneux, F., T. Grandmont, F. Dulude-de Broin, M.C. Martin, J. Lefebvre, A. Kato, J. Bêty, G. Gauthier, and P. Legagneux (2021). COVID19-induced reduction in human disturbance enhances fattening of an overabundant goose species. Biological Conservation 255:108968.

Lundberg, P. (1988). The evolution of partial migration in Birds. Trends in Ecology & Evolution 3:172–5.

Marra, P. P., K. A. Hobson, and R. T. Holmes (1998). Linking winter and summer events in a migratory bird by using stable- carbon isotopes. Science 282:1884–1886.

Masse, R. J., B. C. Tefft, J. A. Amador, and S. R. McWilliams (2013). Why woodcock commute: Testing the foraging-benefit and predation-risk hypotheses. Behavioral Ecology 24:1348–1355.

Masse, R. J., B. C. Tefft, and S. R. McWilliams (2014). Multiscale habitat selection by a forest-dwelling shorebird, the American woodcock: Implications for forest management in southern New England, USA. Forest Ecology and Management 325:37–48.

McAuley, D. G., J. R. Longcore, and G. F. Sepik (1993). Techniques for research into woodcocks: Experiences and recommendations. In Proceedings of the Eighth American Woodcock Symposium (J. R. Longcore and G. F. Sepik, Editors). U.S. Fish and Wildlife Service biological Report 16, Washington, D.C., USA. pp. 5–11.

McAuley, D. G., G. Zimmerman, B. Allen, C. Dwyer, and T. R. Cooper (2019). Survival rates and stopover persistence of American Woodcock using Cape May, New Jersey, during fall migration. Proceedings of the Eleventh Woodcock Symposium (D. G. Krementz, D. E. Anderson and T. R. Cooper, Editors). University of Minnesota, Minneapolis, MN, USA. pp. 146–153.

Mendall, H. L., and C. M. Aldous (1943). The Ecology and Management of the American Woodcock. Maine Cooperative Wildlife Research Unit, Orono, ME, USA.

Meunier, J., R. Song, R. S. Lutz, D. E. Andersen, K. E. Doherty, J. G. Bruggink, and E. Oppelt (2008). Proximate cues for a short-distance migratory species: An application of survival analysis. The Journal of Wildlife Management 72:440–448.

Michelot, T., R. Langrock, and T. A. Patterson (2016). moveHMM: An R package for the statistical modelling of animal movement data using hidden Markov models. Methods in Ecology and Evolution 7:1308–1315.

Mitchell, G. W., N. T. Wheelwright, C. G. Guglielmo, and D. R. Norris (2012). Short- and long-term costs of reproduction in a migratory songbird. Ibis 154:325–337.

Moore, J. D., D. E. Andersen, T. R. Cooper, J. P. Duguay, S. L. Oldenburger, C. Al Stewart, and D. G. Krementz (2019). Migratory connectivity of American Woodcock derived using satellite telemetry. The Journal of Wildlife Management 83:1617–1627.

Newton, I. (2006). Can conditions experienced during migration limit the population levels of birds? Journal of Ornithology 147:146–166.

Newton, I. (2008). The Migration Ecology of Birds. Academic Press, London, UK.

Newton, I. (2012). Obligate and facultative migration in birds: Ecological aspects. Journal of Ornithology 153 (Supplement):S171–S180.

Norris, D. R. (2005). Carry-over effects and habitat quality in migratory populations. Oikos 109:178–186.

Owen, R. B. Jr., and W. B. Krohn (1973). Molt patterns and weight changes of the American Woodcock. The Wilson Bulletin 85:31–41.

Owen, R. B. J., J. M. Anderson, J. W. Artmann, E. R. Clark, T. G. Dilworth, L. E. Gregg, F. W. Martin, J. D. Newsom, and S. R. Pursglove (1977). American Woodcock. In Management of Migratory Shore and Upland Game Birds in North America (G. C. Sanderson, Editor). International Association of Fish and Wildlife Agencies, Washington D.C., USA. pp. 149–186.

Paxton, K. L., and F. R. Moore (2015). Carry-over effects of winter habitat quality on en route timing and condition of a migratory passerine during spring migration. Journal of Avian Biology 46:495–506.

Piersma, T. (1987). Hop, skip, or jump? Constraints on migration of Arctic waders by feeding, fattening, and flight speed. Limosa 60:185–194.

Pot, M.T., S. de Koning, C. Westerduin, W.F. de Boer, M. Shariatti, and T.K. Lameris (2019). Wintering geese trade-off energetic gains and costs when switching from agricultural to natural habitats. Ardea 107:183–196.

Prop, J., J. M. Black, and P. Shimmings (2003). Travel schedules to the high arctic: Barnacle Geese trade-off the timing of migration with accumulation of fat deposits. Oikos 103:403–414.

Pulido, F. (2007). The genetics and evolution of avian migration. BioScience 57:165–174.

Pulido, F. (2011). Evolutionary genetics of partial migration—The threshold model of migration revis(it)ed. Oikos 120:1776–1783.

R Core Team (2018). R: A Language and Environment for Statistical Computing. The R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rieffenberger, J. C., and R. C. Kletzly (1967). Woodcock night-lighting techniques and equipment. U.S. Sport Fisheries Bureau and Wildlife, Special Report. Wildlife 101:33–35.

Saino, N., Ambrosini, R., Caprioli, M., Romano, A., Romano, M., Rubolini, D., Scandolara, C. and F. Liechti (2017). Sex-dependent carry-over effects on timing of reproduction and fecundity of a migratory bird. Journal of Animal Ecology 86:239–249.

Sedinger, J., J. S. Sedinger, and R. T. Alisauskas (2014). Cross-seasonal effects and the dynamics of waterfowl populations. Wildfowl Special Issue 4:277–304.

Senner, N. R., W. M. Hochachka, J. W. Fox, and V. Afanasyev (2014). An exception to the rule: Carry-over effects do not accumulate in a long-distance migratory bird. PLoS One 9:86588.

Sepik, G. F., and E. L. Derleth (1993). Premigratory disperal and fall migration of American Woodcocks in Maine. Proceedings of the Eighth Woodcock Symposium (J. R. Longcore and G. F. Sepik, Editors). U.S. Fish and Wildlife Service Biological Report 16, Washington D.C., USA. pp. 36–40.

Sheldon, W. G. (1967). The Book of the American Woodcock. University of Massachusetts Press, Amherst, MA, USA.

Studds, C. E., and P. P. Marra (2005). Nonbreeding habitat occupancy and population processes: An upgrade experiment with a migratory bird. Ecology 86:2380–2385.

Stutchbury, B. J. M., E. A. Gow, T. Done, M. MacPherson, J. W. Fox, and V. Afanasyev (2011). Effects of postbreeding moult and energetic condition on timing of songbird migration into the tropics. Proceedings of the Royal Society B: Biological Sciences 278:131–137.

Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling (2009). eBird: A citizen-based bird observation network in the biological sciences. Biological Conservation 142:2282–2292.

Tonra, C. M., P. P. Marra, and R. L. Holberton (2011). Migration phenology and winter habitat quality are related to circulating androgen in a long-distance migratory bird. Journal of Avian Biology 42:397–404.

Vander Haegen, M. W., R. B. J. Owen, and W. B. Krohn (1994). Metabolic rate of American Woodcock. The Wilson Bulletin 106:338–343.

van Wijk, R. E., M. Schaub, and S. Bauer (2017). Dependencies in the timing of activities weaken over the annual cycle in a long-distance migratory bird. Behavioral Ecology and Sociobiology 71:73.

Wikelski, M., E. M. Tarlow, A. Raim, R. H. Diehl, R. P. Larkin, and G. H. Visser (2003). Costs of migration in free-flying songbirds. Nature 423:704.

Yong, W., and F. R. Moore (1994). Flight morphology, energetic condition, and the stopover biology of migrating thrushes. The Auk 111:683–692.

Zúñiga, D., Y. Gager, H. Kokko, A. M. Fudickar, A. Schmidt, B. Naef-Daenzer, M. Wikelski, and J. Partecke (2017). Migration confers winter survival benefits in a partially migratory songbird. eLife 6:e28123.