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RESEARCH ARTICLE

American woodcock migration phenology in eastern North America: implications for hunting season timing

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Abstract

Understanding the phenology of migration is fundamental to management of migratory gamebirds, in part because of the

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role migratory timing plays in setting harvest regulations. Migratory timing is particularly important for determining appropriate dates for hunting seasons, which may be selected to coincide with major periods of migration, according to local management objectives. We used global positioning system (GPS)-transmitters to track American woodcock (*Scolopax minor*), characterize the timing of woodcock migration, and identify sources of variation in timing relative to current hunting season structures in eastern North America. We captured 304 woodcock in 3 Canadian provinces and 12 states from 2017 to 2020, primarily within the Eastern Woodcock Management Region. Using locations collected every 1.7 days on average, we assessed whether initiation, termination, or stopover timing of woodcock migration during fall and early spring varied geographically, differed among age and sex classes, or was influenced by individual body condition. During fall, woodcock migrating from summer use areas farther north and west (e.g., Ontario, Quebec, Canada) initiated and terminated migration earlier than woodcock migrating from areas farther south and east (e.g., Rhode Island, USA). Adult woodcock made multiday stopovers that were 3 days longer on average than juveniles and females made more stopovers on average (8.0 stopovers) compared to males (6.1 stopovers). During the onset of spring migration, woodcock that wintered farther west initiated migration before birds that spent the winter farther east, and males initiated migration on average 6 days earlier than females. Under the current 45-day harvest regulatory framework in the United States, hunting seasons in northern breeding and southern wintering areas are generally consistent with migration phenology. At more intermediate latitudes, however, periods of migration are generally longer than 45 days, resulting in many circumstances where migrating woodcock are present during periods when hunting seasons are closed. Managers in mid-latitude states could consider opening hunting seasons later, allowing hunters to harvest more migrant woodcock.

KEYWORDS
harvest, hidden Markov models, migration initiation, migration timing, momentuHMM, *Scolopax minor*

Harvest management for migratory gamebirds requires an understanding of migration phenology, given that hunting season structures often vary considerably across a species' range in response to spatially dynamic management objectives. Rules for harvest of migratory birds in North America are provided through federal regulatory processes (Anderson et al. 2017, Blomberg et al. 2022), where state and provincial managers establish the timing of hunting seasons within a framework prescribed via federal regulation. Managers generally seek to maximize hunter opportunity (Vrtiska 2021), but decisions may also be influenced by local population management goals. For example, southern breeding populations of American woodcock (*Scolopax minor*; woodcock) are generally less abundant than northern populations, and some managers of southern populations may hold hunting seasons later to encourage greater harvest of migrants from more northern areas. Misalignment of hunting seasons with migration timing may risk failure of management to meet harvest objectives, so understanding both the timing of migration, and factors affecting phenology more generally, are clearly important for decision-making.

The timing of bird migration often differs among age (Francis and Cooke 1986, Lozano et al. 1996, Shamoun-Baranes et al. 2017) or sex classes (Moore et al. 1990, Shamoun-Baranes et al. 2017), with many species exhibiting differential migration (Wobker et al. 2021). For example, males of many species may initiate and complete spring migration prior to females, but this is not universal (Rubolini et al. 2004, Pedersen et al. 2019, Krietsch et al. 2020). Some age classes may also migrate at different times because of prior migratory experience or navigation naivety (e.g., young birds are often recorded in greater densities than adult birds near geographic barriers that concentrate birds during migration, such as the Cape May Peninsula in New Jersey, USA; Krohn et al. 1977, Allen et al. 2020). This suggests that different segments of the population may be exposed to variable environmental conditions or anthropogenic hazards (Francis and Cooke 1986, Lerche-Jørgensen et al. 2018, Rousseau et al. 2020), which could include harvest (Sawyer et al. 2016). Understanding the potential for variation in risk among migratory cohorts therefore requires disentangling sources of variation in migration timing, which has traditionally been limited by available technology; however, modern advances in satellite transmitter technology have revolutionized tracking animals throughout migration (Bridge et al. 2011), allowing managers to better link the timing of migratory events with both population monitoring (Blomberg et al. 2023) and harvest management decisions (VonBank et al. 2023).

Global positioning system (GPS)-based satellite tags recently became small enough for use on woodcock (Moore et al. 2019), a migratory bird native to eastern North America that is both a popular game species and of conservation concern (Seamans and Rau 2019). Woodcock breed from southern Canada to the southeastern United States, with the highest breeding densities in the northern portions of the breeding range (Saunders et al. 2019, Seamans and Rau 2019). The highest overwintering densities occur in mid-Atlantic, southeastern, and Gulf Coast states, with some birds overwintering in coastal southern New England (McAuley et al. 2020). Because the woodcock range spans most of eastern North America, managers must be cognizant of migration timing as they set hunting seasons, where the relative abundance of local breeding residents compared to migrant birds may vary considerably among administrative divisions. Additionally, hunter harvest data for woodcock indicate a proportionally greater harvest of adult females, those aged >15 months, compared to other age and sex classes (Saunders et al. 2019, Seamans and Rau 2019). Adult females likely make the greatest contribution to population growth, so higher harvest of this cohort may be concerning in the context of prolonged woodcock population declines (Seamans and Rau 2019). The underlying factors contributing to greater harvest of adult females are poorly understood, particularly when paired with limited information on migratory phenology. A better understanding of the timing of woodcock migration, and how it varies among age and sex classes and spatially across the range, can assist managers with biologically sound harvest management.

Our goal was to use data from GPS-transmitters to describe American woodcock migration phenology throughout eastern North America in comparison with current woodcock hunting seasons. In pursuit of this goal, our objectives were to describe spatial variability in the timing of migration events (i.e., initiation, stopover, termination) among administrative boundaries, understand variation in migration timing among age and sex classes and evaluate the contribution of individual body condition to migration timing, and relate timing of migration to current hunting seasons.

STUDY AREA

Our research focused on the Eastern Woodcock Management Region, 1 of 2 spatial units by which the United States Fish and Wildlife Service and Environment and Climate Change Canada manage woodcock populations (Seamans and Rau 2019; Figure 1). The Eastern Woodcock Management Region includes states located east of the Appalachian Mountains and the Canadian provinces of New Brunswick, Newfoundland, Nova Scotia, Prince Edward Island, and Quebec. We included several sites from the Central Woodcock Management Region (eastern Ontario, Canada; Alabama, USA) because of their proximity to the Eastern Woodcock Management Region and the potential for woodcock to migrate across management region boundaries (Moore et al. 2019). The Eastern and Central Woodcock Management Region boundaries generally align with the Atlantic and Mississippi flyways (Seamans and Rau 2019). Woodcock occupy a range of deciduous and mixed conifer and deciduous forests, with early-seral forests favored in northern breeding areas (Dessecker and McAuley 2001), and greater use of mid- to late-seral forests during migration and wintering (Allen et al. 2020, McAuley et al. 2020). Land use, land cover, and topography varied considerably throughout the region, with woodcock generally associated with a mixture of forested and open areas, rather than contiguous closed canopy forest. Within the region, climate varied from temperate to sub-tropical, where more northern areas associated with woodcock breeding had shorter growing seasons and longer winters, while southern areas associated with woodcock wintering had longer growing seasons and hotter summers. Annual precipitation ranged from 90-175 cm, and annual mean temperatures ranged from 3.9 to 26.1°C, based on 30-year normals for 1991–2020 (PRISM Climate Group 2023). For the purpose of our study, we defined seasons based on major periods of migration for woodcock, where fall migration occurred between 1 October and 14 January, and spring migration occurred between 15 January and 18 June. Individual woodcock displayed considerable variability in the timing of their migration within these general migratory seasons (Blomberg et al. 2023).

METHODS

Capture and marking

We captured woodcock across 3 Canadian provinces and 12 states, generally prior to the onset of migration to maximize GPS tag life during migration and the number of individuals available to migrate. During September and October, our capture efforts targeted breeding populations in Maine, New York, Nova Scotia, Ontario, Pennsylvania, Quebec, Rhode Island, Virginia, and West Virginia (Figure 1). From December through March, our capture efforts shifted to overwintering areas including Alabama, Georgia, Maryland, New Jersey, North Carolina, South Carolina, and Virginia (Figure 1). Some individuals were captured during periods of fall migration (Nov-Dec) in Maryland, New Jersey, and Virginia (Figure 1). Fall captures spanned 27 August to 30 October during 2017, 2018, and 2019, and winter captures spanned 3 January to 29 February during 2019 and 2020. Some individuals were also captured during migratory periods (18 Nov–14 Dec 2018 and 2019). We located capture sites within cooperating states or provinces by relying on prior expert knowledge to identify areas near young forest management or other early successional vegetation where woodcock densities are highest (Dessecker and McAuley 2001). We captured woodcock during crepuscular flights (Sheldon 1960) by setting mist net arrays near known roosting fields, travel corridors, and forested wetlands to intercept birds as they left diurnal use areas and flew to night roosts. Additionally, we used spotlights and thermal imaging scopes to locate night-roosting woodcock and captured them with hand nets (Rieffenberger and Kletzly 1967, McAuley et al. 1993, Moore et al. 2019).

We aged captured woodcock as adult (after hatch year or after second year; >1 year old) or young (hatch year or second year; <1 year old) based on wing plumage characteristics, and determined sex using a combination of

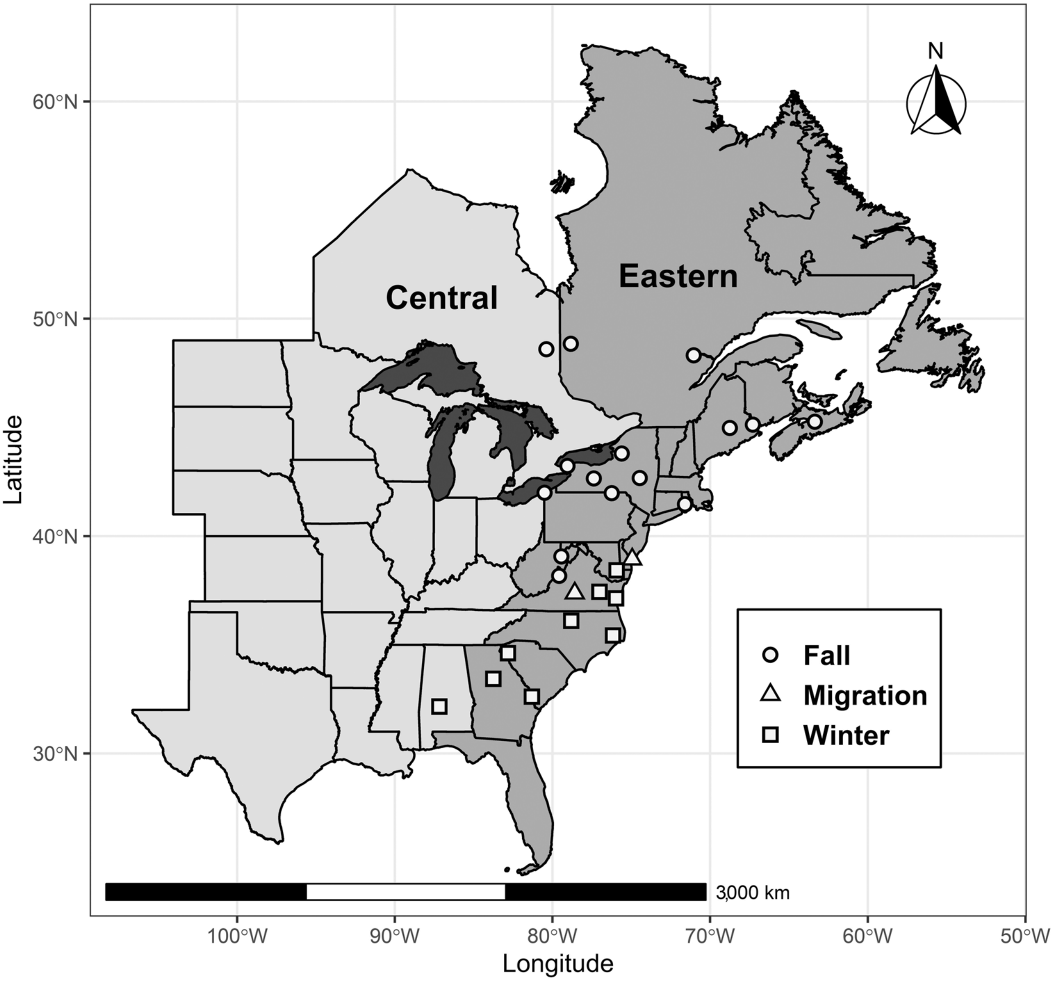

FIGURE 1 Distribution of capture locations in 2017–2020 and delineation of American woodcock Central and Eastern Management Regions, which generally covers the species' distribution in eastern North America. Capture sites were generally distributed within the Eastern Woodcock Management Region, with 2 sites in the Central Woodcock Management Region (Ontario and Alabama). Captures primarily occurred in fall and winter prior to migration initiation; however, some captures in the mid-Atlantic Region occurred during migration.

wing plumage and bill length (Mendall and Aldous 1943, Martin 1964). We also recorded the mass of each individual using a spring scale 300 ± 2 g (Pesola Präzisionswaagen AG, Schindellegi, Schwitzerland) and the lower leg length using a dial caliper (±0.1 mm) or metric ruler (±1 mm). The lower leg length comprised the intertarsal joint to the end of the foot excluding the toes (Blomberg et al. 2014). We fitted woodcock with a Lotek PinPoint GPS-transmitter (model 75 or model 120; Lotek Wireless, Newmarket, Ontario, Canada) enabled with a platform transmitter terminal (PTT) for transmitting locational data to the Argos satellite network; we only used positional data associated with the GPS locations. We attached satellite transmitters with a leg-loop style harness (Moore et al. 2019). Male body mass (mean ± SD) was 151.34 ± 13.78 g and female mass was 196.11 ± 17.09 g, with transmitters comprising between 3.06 ± 0.44% and 3.68 ± 0.25% of body mass, depending on sex and transmitter size. We did not fit transmitters on birds if the combined mass of all marking components (transmitter, harness, band) exceeded 4% body mass.

Woodcock location data collection

We programmed transmitters to collect GPS locations every 1-2 days during likely periods of migration using LOTEK PinPoint Host software (LOTEK Wireless). During likely non-migratory periods, transmitters collected locations less frequently (e.g., 1 location every 5-7 days) to extend battery life. In practice this approach allowed for collection of 1 fall or spring migratory track for all birds, with total transmitter battery life (generally <6 months), and hence potential to collect a second migration, dependent on the timing of capture, phenology of migration, and transmitter performance. Transmitters primarily collected locations during diurnal periods; however, some schedules contained nocturnal locations depending on objectives unrelated to this study, which represented about 2% of the locations collected during migration (39 of 2,068 locations). Transmitters used for this study did not provide ancillary data (e.g., altitude, accelerometry) that could be used to distinguish nocturnal migratory flights. The average number of stopovers we recorded per bird was 7, requiring 9 migratory flights, and the average woodcock took 23 days to complete migration. Therefore, we suspect that approximately a third of nocturnal locations, or 13 total migration locations, may have been in-flight locations. We stopped receiving locations when birds either died or dropped their transmitter, causing the transmitter to rest on the ground and attenuate the signal, or if the transmitter failed.

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

Movement modeling

We identified migratory behavioral states for each marked woodcock location using multivariate hidden Markov models, implemented with the momentuHMM package (McClintock and Michelot 2018) in program R (R Core Team 2020). The multivariate hidden Markov models identify latent behavioral states within animal movement trajectories, where probabilities of transitions among states are inferred from movement data streams and their underlying distributions (McClintock and Michelot 2018). We used 2 data streams (step length [Euclidean distance] and turning angle [bearing]) between each successive location in an individual's track, and specified a gamma distribution for step length and a wrapped Cauchy distribution for turn angle. We developed a model to identify 3 migratory behavioral states, which were constrained to a single migration of each individual: pre-migration, migration, and post-migration. We constrained transition among states such that individuals in the pre-migration state could only transition to migration, and once in the migration state, individuals could either remain in the migration state or transition into post-migration. Post-migration was specified as a terminal state, where once an individual entered it could not transition to another state. We specified state-specific initial values (Table A1, available in Supporting Information) for step length (mean, SD, zeromass) and turn angle (mean, concentration) following McClintock and Michelot (2018).

We subset woodcock location data into fall (1 Oct–14 Jan) and spring (15 Jan–18 Jun) migratory periods for each study year and conducted a separate multivariate hidden Markov model analysis for each of the 5 migratory periods (3 years for fall and 2 years for spring). We removed individuals with <3 locations during each seasonal period prior to analysis, as a minimum of 3 locations is required by momentuHMM. We used the resulting distribution of step lengths and turning angles to predict the behavioral state associated with each location using the viterbi function in momentuHMM. For each woodcock included in the multivariate hidden Markov model analysis, we manually validated the state assignments.

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

When we identified state transitions (i.e., initiation or termination events) with >1 day between successive locations, we used the mean date between locations to approximate the date of departure or arrival. We consider all locations associated with the migratory behavioral state to reflect migratory stopovers and refer to them as stopover locations. For every state or province with a stopover location, we reviewed 2023–2024 hunting regulations posted to each state or provincial wildlife agency web page, and summarized the dates associated with woodcock hunting seasons. We compared the timing of migration to hunting seasons by visually inspecting the overlap between hunting season dates and boxplots describing the distribution of migration events (e.g., departure, arrival at stopover) for each state or province.

Statistical analysis

Initiation and termination of migration

We developed a multi-tier modeling approach to explore the effects of spatial variation, demographic characteristics, and body condition on migration initiation and termination, using general linear or linear mixed effects models, where appropriate. First, we constructed *a priori* spatial models, evaluating how latitude, longitude, and administrative divisions (state or province) influenced date of migration initiation or termination. We considered additive effects of latitude, longitude, and their interaction to explore general spatial variation in migration timing, and we contrasted this with a competing model based on administrative divisions. While the administrative division models required more parameters, it provided a useful contrast to the more general model based on spatial coordinates and was also directly relevant to interests of woodcock managers within the region. Managers in each state and province manage woodcock populations within a woodcock harvest strategy framework regulated by federal wildlife agencies, which sets the allowable season lengths, bag and possession limits, and other rules governing woodcock harvest; state and provincial administrative divisions are the finest spatial unit within which specific management decisions (e.g., hunting season dates) are generally made under this framework.

Using the best-supported model from the first tier of analyses, we proceeded to evaluate demographic effects on migration phenology by adding age and sex covariates in the second analytical tier. We tested additive effects and interactions between age and sex. Woodcock are sexually dimorphic, with females being larger, and conceivably a larger body size may influence cold tolerance (Prescott 1994, Macdonald et al. 2016) and affect migration timing. We included an interaction effect between age and sex to investigate differences among the 4 age-sex cohorts, with a particular interest in adult females.

For the third analytical tier, we evaluated individual condition using the best-supported model from the first 2 tiers. We created *a priori* models including condition as an additive effect and as an interaction with age or sex and spatial predictors, as supported during earlier tiers of analysis. To characterize the condition of woodcock, we developed a general linear model using the STAT package (Bolar 2019) in Program R to relate body mass with body size (as indexed by leg length), sex, and age (Blomberg et al. 2014). This model confirmed a positive association between body mass and size ($\beta = 0.381 \pm 0.253$), greater body mass for females compared to males ($\beta = 42.730 \pm 1.851$), and lower body mass for adults compared to young ($\beta = -2.349 \pm 1.717$) and had a strong fit to the data ($R^2 = 0.74$, model intercept: $\beta_0 = 139 \pm 9.34$). Once the model was fit, we extracted individual residuals using the modelr package (Wickman 2020). A positive residual score indicated individuals that were heavier than expected (i.e., above-average condition) given their size, age, and sex, while individuals with a negative residual score were those lighter than expected (below-average condition; Blomberg et al. 2014). Woodcock in below-average condition would be expected to have lower energy reserves for migration, and this relationship may be more pronounced for certain age and sex classes, or individuals originating from specific locations. We were only able to include condition on a subset of individuals because of missing biometric data from some birds and others that were marked prior to a focal migratory period (e.g., marked in fall but still transmitting data during spring migration) where biometric data would not reflect pre-migration condition. Similarly, we did not include condition as a predictor in stopover timing, as an individual's condition continually changes during migration, and we were unable to monitor changes in condition.

We used Akaike's Information Criterion corrected for small sample size (AIC_c) to rank models for each step in the tiered modeling approach. We chose the model with the lowest AIC_c score that contained no parameters with 95% confidence intervals that overlapped zero as the most parsimonious model, and used this for further inference during the next tier of the analysis. For the categorical covariates age and sex, we coded young birds and males as 0 and adults and females as 1; slope coefficients produced from linear modeling must be interpreted with this understanding. We used the predict function in the car package (Fox and Weisberg 2019) to compare predictions of models based on latitude and longitude to those built using administrative divisions, which allowed us to further evaluate model fit and identify any outlier regions within the dataset.

Variation in stopover behavior

We explored sources of variation in the duration of stopover (number of days spent stopped) and the frequency of stopover (number of stopovers along the migration path) among migrant woodcock during fall migration. For stopover duration, we initially used linear mixed effect models implemented with the lme4 package (Bates et al. 2015) to incorporate an individual random intercept term to account for repeated sampling, and set the restricted maximum likelihood to false so we could perform model selection (Zurr et al. 2009). We found that the random effect variance was not sufficiently different from 0 for the random intercept term to converge, so we instead used simple linear models. To accommodate repeated sampling, we applied a weighting to each observation in the regression, where the weight was the inverse of the number of stopovers recorded for each individual. As with migration initiation and termination, we evaluated effects of latitude, longitude, age, and sex on stopover duration. We also included date as a term in the model set, as we predicted that woodcock might vary their stopover behaviors throughout the migratory season. We did not evaluate body condition effects on this metric, because in almost all cases we collected morphological measurements prior to the onset of migration. For this analysis, we also evaluated whether stopovers that occurred during hunting season had different durations than those occurring outside of a hunting season.

We conducted a separate analysis where we summed the number of stopovers for each woodcock, which we used as the response variable in a generalized linear model assuming a Poisson response distribution, with age, sex, and starting and ending latitude and longitude as potential predictor variables. We also summarized for each woodcock the proportion of stopover days that occurred during a hunting season and included this as a predictor variable. We calculated the McFadden R^2 for the Poisson regression, R^2_{MF}, as $1 - LL(\text{full})/LL(\text{null})$, based on the log-likelihoods (LL) of the best-supported (full) and intercept-only models (null). We restricted this analysis to only woodcock with full migration paths (i.e., those that terminated migration), and we further explored Pearson's correlations among the number of stopovers, total duration of migration (days), and mean stopover duration, which provided context for the relationship between latitudinal predictors and the overall duration of migration.

Finally, we used box and whisker plots, stratified by administrative divisions, to qualitatively assess the overlap of stopover timing with current hunting season structure. We did not conduct a formal analysis of stopover timing (e.g., date of stopover regressed on age or sex) because the timing of each individual stopover was sensitive to a number of preceding events, including the duration of prior stopovers and timing of onset of migration.

RESULTS

We captured and marked 304 woodcock including 6 in 2017, 75 in 2018, 163 in 2019, and 60 in 2020. Of these, 153 were males (69 adults, 84 young) and 151 were females (72 adults, 79 young; Table 1). We collected 18,074 GPS locations between 1 October 2017 and 18 June 2020, including 179 in 2017, 2,584 in 2018, 9,306 in 2019, and 5,909 in 2020. We removed 75 woodcock from the movement models because we did not obtain any locations post-capture ($n = 14$), data transmission terminated prior to initiating migration ($n = 44$), or we obtained ≤3 locations during a focal period ($n = 17$). Thirty-one woodcock marked in fall were included in spring initiation analysis (12 in 2019, 19 in 2020). The remaining 229 birds provided 260 migration attempts included in the movement models and subsequently had migratory states assigned to their respective locations (Table 2). A complete list of parameter outputs (e.g., step length and turning angle) from the movement models used to assign migratory behavioral states to locations and transition probability matrices can be viewed in Table A2 (available in Supporting Information).

Fall migration

The best-supported model for fall initiation of migration (Table B1, available in Supporting Information) was the demographic model, which explained 60% of the variation within the data ($R^2 = 0.60$) and included a combination of latitude ($\beta = -3.95 \pm 0.30$), longitude ($\beta = 0.85 \pm 0.18$), and age ($\beta = -4.07 \pm 1.77$). More specifically, woodcock marked farther north and west (e.g., Ontario, western Quebec) initiated migration before birds farther south and east (e.g., Rhode Island). For every 1° change in latitude or longitude, woodcock initiated migration 4.0 days (latitude) and 0.9 days (longitude) earlier, on average. Additionally, given a constant latitude and longitude, adults initiated migration an average of 4.1 days earlier than young birds (Table 3). Woodcock in better body condition also initiated fall migration earlier (Table 3); given a constant size, a woodcock with 20 g of additional body mass (~10–13% of total body mass) was predicted to initiate fall migration 1 day earlier. For fall migration initiation, we found no support for interactions between body condition and age or sex.

We recorded data on 839 unique stopovers during fall migration; 145 of these were multi-day stopovers, whereas the majority (694) were single-day stops. The best-supported model of duration for all stopovers (Table 4; Table B4, available in Supporting Information) included additive effects of latitude and date. For every 1° change in latitude as woodcock migrated south, the mean stopover duration increased by 0.2 days ($\beta = -0.22 \pm 0.05$). Woodcock also stopped for shorter durations on average earlier in the season. Although the effect size for this variable was relatively small ($\beta = -0.05 \pm 0.01$), it produced a 4-day change in mean stopover duration across the full range of dates we observed stopovers. This model explained <3% of the observed variance in the data (adjusted $R^2 = 0.026$), so the predictive capacity of both variables was small, and there was not support for effects of age, sex, longitude, or open hunting season on stopover duration.

When we repeated the analysis to only consider multi-day stopovers, we identified support for an effect of age and hunting season, on stopover duration. The best-supported model (Table 4; Table B4) indicated that adult woodcock made multi-day stopovers that were 3 days longer, on average, than young woodcock ($\beta = 3.16 \pm 1.63$), and that multiday stopovers occurring during a hunting season were 3.4 days shorter than those occurring when hunting was closed ($\beta = -3.39 \pm 1.64$). As with all stopovers, this model explained relatively little of the total

TABLE 1 The total number of American woodcock with transmitters attached between September 2017 and March 2020, prior to fall and spring migration, respectively. We aged woodcock either as adults (>1 year old) or young (<1 year old) and determined sex based on plumage characteristics.

	Male		Female		
State or province	Young	Adult	Young	Adult	Total
AL	1	2	2	2	7
GA	3	3	1	5	12
ME	5	1	3	4	13
MD	1	6	9	3	19
NJ	14	0	16	0	30
NY	8	7	12	12	39
NC	9	3	4	5	21
NS	3	0	4	0	7
ON	1	1	1	2	5
PA	5	5	3	11	24
QC	7	0	4	4	15
RI	0	24	0	6	30
SC	4	4	6	3	17
VA	21	12	13	15	61
WV	2	1	1	0	4
Total	84	69	79	72	304

TABLE 2 The number of American woodcock marked with transmitters in eastern North America that transitioned into a migratory behavior state (initiation) or out of a migratory state (termination), and the number of individual locations recorded in a migratory state (stopover locations) based on multivariate hidden Markov model classification of migration paths. Capture periods occurred during August to October for fall migration, and November to March for spring migration. Woodcock captured during November and December primarily occurred in the mid-Atlantic region during fall migration but were only considered for the spring analysis.

	Fall (Oct–Jan)				Spring (Jan–Apr)		
	2017	2018	2019	Total	2019	2020	Total
Individuals	6	40	80	126	52	82	134
Migration initiation	6	38	73	117	37	71	108
Migration termination	3	29	61	93			
Stopover locations	23	838	1,207	2,068			

variance in stopover duration (adjusted $R^2 = 0.04$). A second model was within 2.0 ΔAIC of the most supported model, and included effects of age and date (Table B4).

We collected complete full migration paths from 92 woodcock, which took between 1 and 87 days to complete fall migration and completed between 1 and 26 stopovers. The best supported model explaining the number of stopovers (Table B5, available in Supporting Information) included starting ($\beta = 0.06 \pm 0.01$) and

TABLE 3 Beta coefficients for the top supported general linear models describing American woodcock migratory phenology in eastern North America, 2017–2020. Coefficients with 95% confidence intervals that excluded 0.0 are denoted by an asterisk, and only these predictors were included in subsequent models. Models used males and young birds as reference (coded at intercept) for sex and age, respectively. Standard error is provided in parentheses.

			Spatial			Demographic		Body condition		
	n	Intercept	Latitude	Longitude	Latitude× longitude	Age	Sex	Condition	Condition× age	Condition× sex
Fall initiation										
Spatial	117	708.362 (237.028)	−13.762 (5.313)*	6.573 (3.059)*	−0.129 (0.069)					
Demographic	117	274.631 (21.258)	−3.948 (0.297)*	0.846 (0.177)*		−4.072 (1.769)*				
Body condition	97	239.909 (22.145)	−3.522 (0.299)*	0.639 (0.188)*		−5.845 (1.817)*		−0.245 (0.101)*	0.255 (0.134)	
Fall termination[a]										
Spatial	93	−425.729 (405.015)	12.196 (9.061)	−6.946 (5.216)	0.174 (0.117)					
Demographic	93	187.001 (36.766)	−1.457 (0.492)*	0.807 (0.319)*		−5.073 (3.063)				
Body condition	78	171.738 (42.125)	−1.210 (0.531)*	0.785 (0.360)*					(1)*	
Spring initiation										
Spatial	108	143.337 (24.674)		1.013 (0.306)*						
Demographic	106	146.164 (24.728)		1.085 (0.308)*			5.909 (2.734)*			
Body condition	63	185.625 (31.112)		1.527 (0.391)*			2.469 (2.661)	−0.335 (0.135)*		0.590 (0.184)*

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

TABLE 4 Beta coefficients for the top supported generalized linear models describing American woodcock migratory stopover in eastern North America, 2017–2019. We conducted analyses for all stopovers and for those lasting >1 day (multiday). Models used young birds as reference (coded at intercept) for age. Standard error is provided in parentheses.

Model	*n*	Intercept	Latitude	Date	Age	Hunting
All stopovers	839	12.462 (2.143)	−0.220 (0.047)	−0.047 (0.012)		
Multiday stopovers only	145	11.131 (1.471)			3.158 (1.631)	−3.390 (1.635)

ending latitude ($\beta = -0.11 \pm 0.02$), starting longitude ($\beta = -0.03 \pm 0.01$), and sex ($\beta = 0.18 \pm 0.08$). This model captured approximately 20% of the variance in the data ($R^2_{MF} = 0.21$). The spatial predictors in this model indicate that woodcock beginning migration farther north and west, and terminating migration farther south, make the greatest number of stopovers; however, we found no correlation between starting and ending latitude (Pearson's $r = -0.03$). Number of stops was strongly correlated with the number of days spent migrating (Pearson's $r = 0.78$), and moderately correlated with average stop duration (Pearson's $r = 0.47$), illustrating that woodcock migrating for a longer duration made a greater number of stopovers, and stayed at those stopovers for a greater length of time. Female woodcock made a greater number of stopovers than males ($\beta = 0.18 \pm 0.08$), averaging 8.0 stopovers compared with 6.1 stops for the average male. We found no support for effects of age, and nothing to indicate that the proportion of stopovers that occurred during hunting seasons affected the total number of individual stopovers.

The best-supported model of fall migration termination was the spatial model, which explained 8% of the variance ($R^2 = 0.08$) and included additive effects of starting latitude ($\beta = -1.25 \pm 0.48$) and starting longitude ($\beta = 0.79 \pm 0.32$; Table 3; Table B2, available in Supporting Information). Woodcock that initiated migration farther north and west in our sample (e.g., Ontario and western Quebec) terminated migration earlier than woodcock marked farther south and east (e.g., Rhode Island; Figure 2). On average, for every 1° change in starting latitude and starting longitude, woodcock terminated migration 1.3 days (latitude) and 0.8 days (longitude) earlier. Ending latitude and longitude did not have an influence on migration termination date and no age, sex, or condition covariates were supported.

Spring migration

The best-supported model for initiation of spring migration included a combination of longitude ($\beta = 1.53 \pm 0.39$), sex ($\beta = 2.47 \pm 2.66$), condition ($\beta = -0.34 \pm 0.16$), and an interaction between condition and sex ($\beta = 0.59 \pm 0.18$; Table 3; Table B3, available in Supporting Information). This model explained 24% of the observed variance in the data ($R^2 = 0.24$). Additive effects of sex from the demographic tier of analysis ($\beta = 5.91 \pm 2.73$) indicated that males initiated spring migration 5.9 days before females, and woodcock wintering farther west initiated spring migration an average of 1.5 days earlier for every 1° change in longitude. The interaction between sex and condition suggested that males in above-average condition initiated migration earlier, while females in above-average condition initiated migration later (Figure 3).

Model spatial predictions and intersection with hunting seasons

Model spatial predictions for the timing of fall migration initiation were generally well fit to the data (Figure 4), with most predicted mean initiation dates falling within the range of the observed values. The only

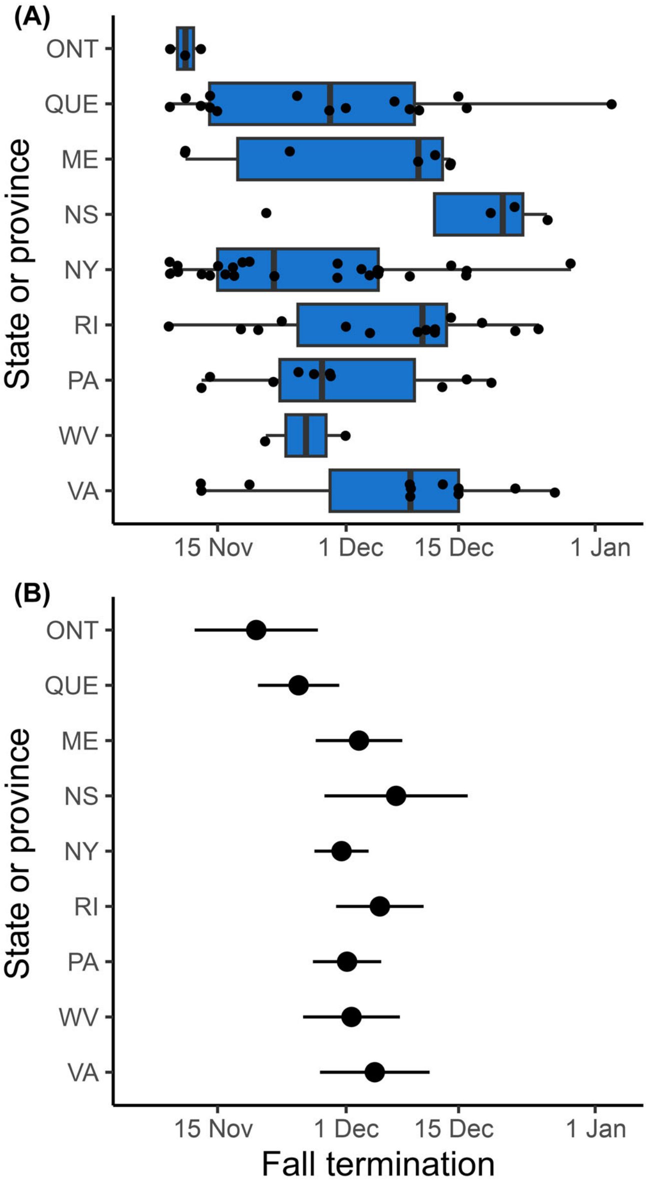

FIGURE 2 Termination of fall migration for American woodcock marked in eastern North America, 2017–2019, by administrative division of migration initiation. The distribution of termination dates by initiation administrative division (A), and the mean predicted termination date and 95% confidence interval of fall migration while accounting for initiation latitude and longitude (B). Black circles represent individual observations, and box-and-whisker plots display the median (solid line), 50th percentile (box), and 90th percentile (whiskers) distributions of the data for each administrative division.

exception for which the model predicted later initiation dates compared to the observations was for woodcock marked in Pennsylvania, but this may have resulted from our 2 captures sites being located on the northern border of that state. Predictions for fall migration termination also fit the data generally well (Figure 2); the 2 exceptions being woodcock from Ontario, which terminated migration earlier than model predictions, and woodcock from Nova Scotia, which terminated migration later. Lastly, predictions for spring

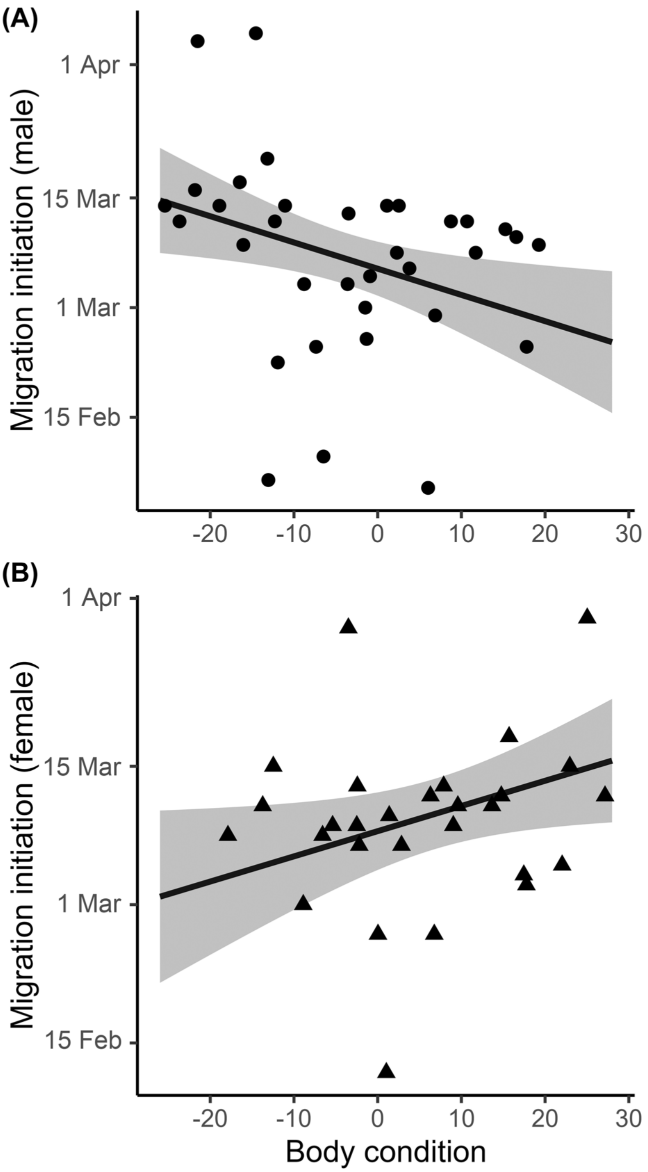

FIGURE 3 Mean predicted spring migration initiation date and 95% confidence interval for American woodcock in eastern North America, 2017–2019, captured on the wintering grounds prior to spring migration. Males (A) and females (B) showed inverse influences of condition on the timing of migration initiation. We removed 1 adult female with a condition score of 53 from the plot.

migration initiation performed relatively well, with the exception of Louisiana and Rhode Island (Figure 5). Woodcock wintering in Louisiana initiated spring migration later than model predictions, while woodcock wintering in Rhode Island initiated migration earlier than the model predicted.

The degree to which current woodcock hunting seasons coincided with migration timing varied among states and provinces, and generally followed a north to south pattern. In the Canadian provinces and most of the northern states where we marked woodcock prior to fall migration, most woodcock initiated fall migration during the hunting

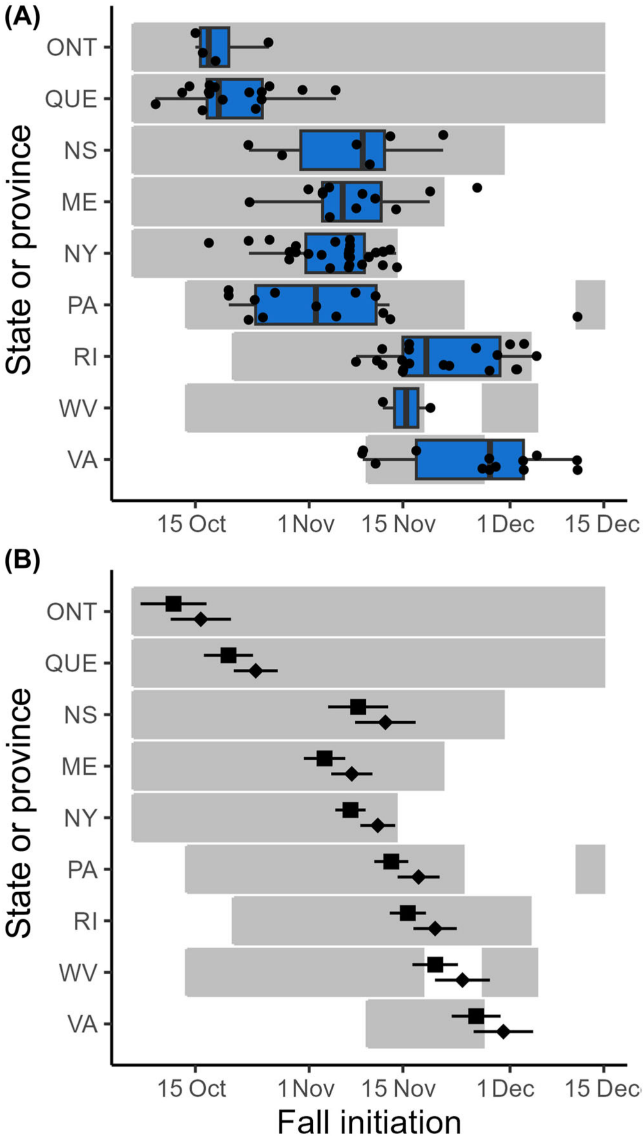

FIGURE 4 Initiation of fall migration for American woodcock marked in eastern North America, 2017–2019. The distribution of migration initiation dates by administrative division (A), and the mean predicted initiation date and 95% confidence interval of fall migration while accounting for spatial distribution and age (B). Black circles represent individual observations, and box-and-whisker plots display the median (solid line), 50th percentile (box), and 90th percentile (whiskers) distributions of the data for each administrative division. Squares represent adults >1 year of age and diamonds reflect young woodcock. Grey boxes represent woodcock hunting seasons for each state, and are cropped to dates within the extent of the graph (6 Oct–15 Dec).

season, with relatively few birds departing on migration after the close of the season (Figure 4). Hunting seasons in these areas generally also encompassed periods of stopover, although we observed at least some stopover after season closures in Nova Scotia, Maine, New Hampshire, Massachusetts, New York, and Michigan (Figure 6). Several states in the mid-Atlantic region held split hunting seasons, where woodcock stopovers generally coincided with the

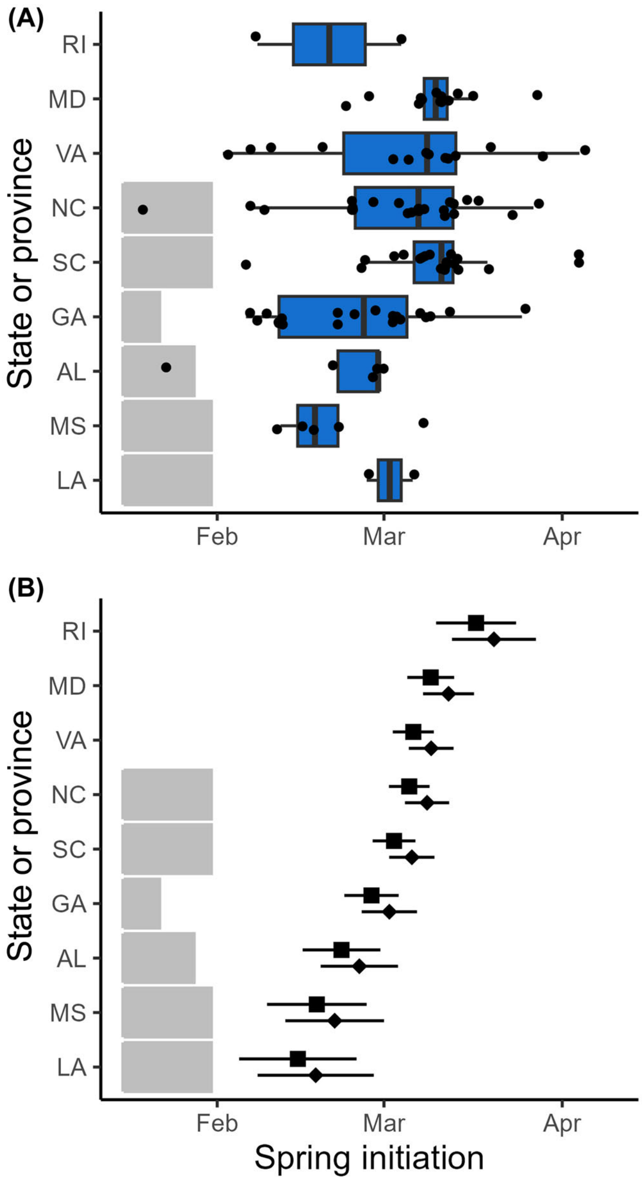

FIGURE 5 Initiation of spring migration for American woodcock marked in eastern North America, 2018–2020. The distribution of initiation dates by administrative division (A), and the mean predicted initiation date and 95% confidence interval of fall migration while accounting for longitude and sex (B). Boxes represent males and diamonds females. Black circles represent individual observations, and box-and-whisker plots display the median (solid line), 50th percentile (box), and 90th percentile (whiskers) distributions of the data for each administrative division. Grey boxes represent woodcock hunting seasons for each state, and are cropped to dates within the extent of the graph (16 Jan–10 Apr).

first of the 2 hunting periods, but also extended into the split period between seasons. The second periods of the split seasons in mid-Atlantic states, and the hunting seasons of southern states associated with woodcock wintering areas, generally opened after most woodcock had completed migration (Figure 7). Finally, most woodcock departed on spring migration ≥2–3 weeks after the close of hunting seasons in all wintering states (Figure 5).

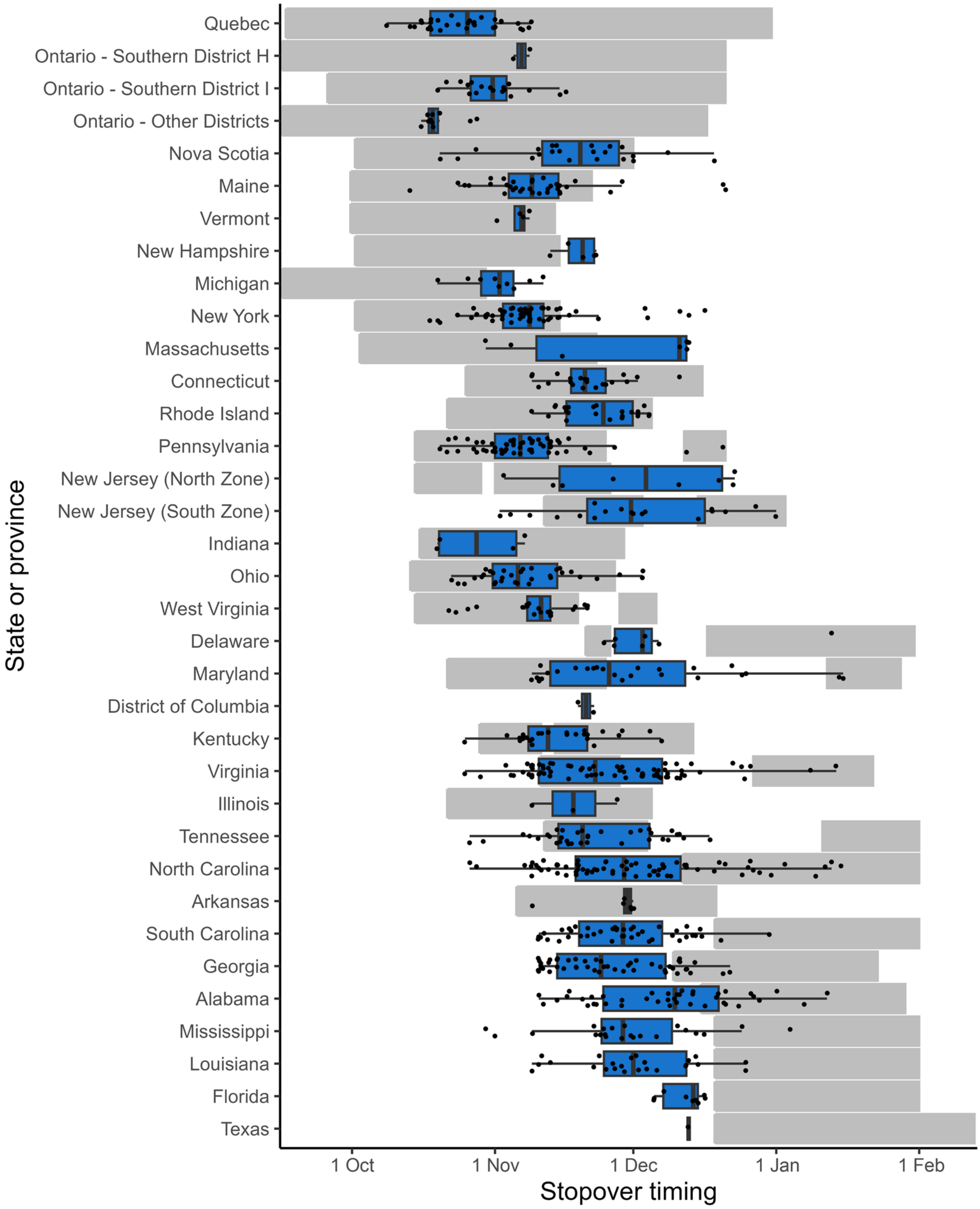

FIGURE 6 Timing of fall migration stopovers by state or province collected from American woodcock marked in in eastern North America, 2017–2019. Black circles represent the mid-point of individual stopover dates, and box-and-whisker plots display the median (solid line), 50th percentile (box), and 90th percentile (whiskers) distributions of the data for each administrative division. Grey boxes represent woodcock hunting seasons for each state or province, or within a subsection of state or province when hunting seasons were stratified by zones.

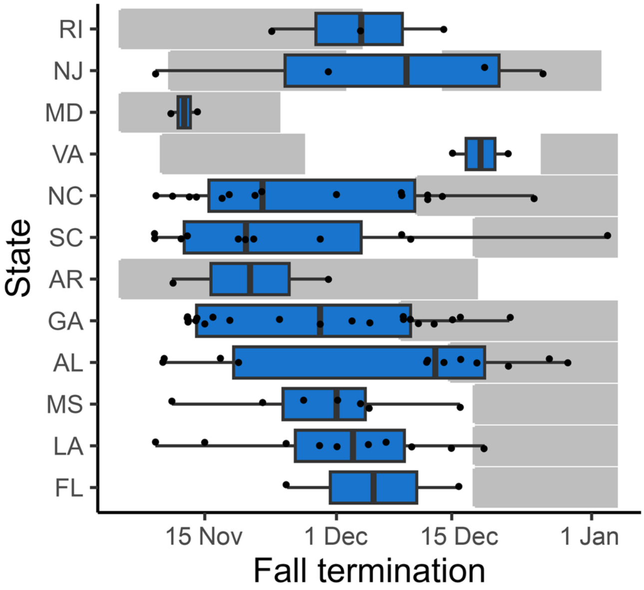

FIGURE 7 Termination of fall migrating American woodcock marked in eastern North America, 2017–2019, by administrative division of migration destination. Black circles represent individual observations, and box-and-whisker plots display the median (solid line), 50th percentile (box), and 90th percentile (whiskers) distributions of the data for each administrative division. Grey boxes represent woodcock hunting seasons for each state, and are cropped to dates within the extent of the graph (6 Oct–5 Jan).

DISCUSSION

Fall migration

Timing of fall migration of woodcock in eastern North America was influenced by a combination of spatial, demographic, and body-condition-based factors. There was a clear spatial pattern throughout our data that was generally well-captured by latitude and longitude, but the specific relationship varied across migratory events. Woodcock marked farther north initiated and terminated fall migration earlier than woodcock marked farther south, consistent with an earlier migration strategy for northern birds. That starting latitude and longitude affect fall migration initiation makes intuitive sense, as woodcock farther north and west experienced shortening day length, colder temperatures, and snowfall earlier in the fall than woodcock marked farther south and east. Conversely, more southern and coastal areas would experience more moderate temperatures and delayed freezing relative to northern locations and inland areas at the same latitude. These same processes likely explain why administrative divisions that bordered the Atlantic coast tended to have a greater range of dates associated with stopover timing; birds initiating fall migration later from coastal areas (e.g., Nova Scotia, Canada; Maine, Rhode Island, USA) typically migrated near the Atlantic coast, thus both departing later and experiencing more moderate conditions during migration.

The number of stopovers made by migrating woodcock was also affected by starting and ending latitude. As with initiation date, the association between latitude and number of stopovers is intuitive, as woodcock that travel the greatest distance require the most stops to accomplish migration. Starting and ending latitudes were essentially uncorrelated in our data, however, and the timing of termination was also independent of woodcock wintering latitude. Collectively these results suggest a system where summering location is the principal driver of fall migration timing via its effect on initiation date, and where the number of stopovers an individual makes, and the total migration duration, reflect a balance between starting and ending locations, which together define the net distance of migration. Working with satellite-marked woodcock in the Central Management Region, Moore et al. (2021) also reported that migration distance and number of stopovers were associated with the timing of initiation and termination.

During fall migration, age was an important predictor of initiation and thus timing of migration, with adults initiating fall migration earlier than young birds. This contrasts with earlier research that reported no effect of age on timing of departure (Sepik and Derleth 1993, Meunier et al. 2008). The differences between our results and these earlier studies may be explained by regional differences or smaller geographic scope, as both focused on regional analyses within 1–3 states (Sepik and Derleth 1993, Meunier et al. 2008). Adult woodcock may have used experience gained from previous migrations to select weather conditions that optimize migratory efficiency (e.g., tailwind; Mitchell et al. 2015). In contrast, young birds that have no prior migration experience and are presumably naïve to migratory weather cues may be less likely to initiate migration under optimal conditions (Mitchell et al. 2015). Age did not predict the number of stopovers, but young birds made shorter multi-day stopovers than adults, and there was no age effect on the timing of migration termination. Working with bluethroats (*Liscinia scecica*), Ellegren (1991) reported that adult birds exhibited shorter stopovers as a result of more efficient migration and better fat dynamics compared with juveniles. Our results suggest an opposite pattern for woodcock, where the earlier departure dates of adults afford them greater flexibility in stopover timing.

Our ability to predict fall migration phenology, as indicated by model R^2 values, varied widely among stages of migration. The greater R^2 values associated with initiation of fall migration indicated timing of these events were relatively predictable, likely because of shared cues (e.g., temperature or photoperiod) affecting all birds (Meunier et al. 2008). Stopover duration and the timing of migratory termination, in contrast, are likely more sensitive to the suite of dynamic environmental conditions encountered throughout migration (e.g., wind, temperature), how multiple decisions combine to affect the pace of migration, and the distance required to reach an individual's final destination point (Zehnder et al. 2001, Shamoun-Baranes et al. 2017, Haest et al. 2019, Bradarić et al. 2020). The variable nature of these events among individual woodcock likely results in lower predictability. Cues associated with woodcock migration decisions have received some attention, but most prior work focused on single sites (Coon et al. 1976, Krementz et al. 1994, Allen et al. 2020), with limited ability to follow individual birds throughout their migration cycle. Therefore, additional investigation is necessary to better understand the mechanisms influencing the timing of events beyond the onset of migration.

Spring migration

In contrast to fall migration, spring migration initiation was more influenced by longitude than by latitude. This relationship could have occurred because woodcock winter along a relatively narrow range of latitudes (~25 degrees), but a broader range of longitude (~40 degrees). While we observed some woodcock overwintering in southern New England and the mid-Atlantic, these cases were infrequent and likely reflect low over-wintering densities in these regions (McAuley et al. 2020).

The initiation of spring migration was the only aspect of migration phenology affected by individual body condition, with the effect of condition dependent on sex. Males in below-average condition likely spent more time building energy reserves and, therefore, delayed migration initiation relative to above-average males (Cooper et al. 2015). Owen and Krohn (1973) reported that male woodcock lost mass during fall migration and winter, and were at their lowest mass when they arrived on the breeding grounds in late spring. Therefore, securing energy reserves prior to initiating migration provides an important energetic buffer during migration. For females the slope of the relationship between body condition and spring initiation was positive, suggesting that females in better condition departed later; however, there was a lower effect size and weaker fit to the data compared to males, and it is possible that the true biological effect is a relatively neutral relationship between female condition and spring migration timing. We had a moderate ability to predict the timing of spring migration initiation, indicating some consistency between years, but additional intrinsic and environmental variables also likely influenced migration timing during spring (Hagan et al. 1991, Marra et al. 2005, Palm et al. 2009, Tøttrup et al. 2010).

Relation to harvest

Current federal harvest regulatory frameworks allow for a maximum of 45 days of harvest in the United States, while seasons are considerably longer in Canadian provinces (Table D1, available in Supporting Information). Conceptually, hunting opportunity is maximized when hunting seasons co-occur with the greatest abundance of woodcock, but overlap depends on the relative abundance of breeding, migrant, or wintering individuals within a given state or province. In most northern areas where woodcock regularly breed but do not overwinter, nearly all woodcock fall departures and stopovers overlapped with current hunting seasons. In Ontario and Quebec, there was also a substantial portion of the hunting season that extended into late November and December, during which we never observed stopovers in those provinces. For states that were farther south and received a greater proportion of migrant woodcock, such as New York and Ohio, a greater number of stopovers occurred after the close of current hunting seasons. This suggests that in these states it is more challenging to balance harvest of resident versus migratory woodcock under the current 45-day harvest regulatory framework. Many mid-latitude states used split hunting seasons, which is a strategy that can allow managers to target harvest at specific periods when migrant birds are most likely to be abundant (Vrtiska 2021). Split seasons successfully spanned multiple stages of migration in a number of states (e.g., in Virginia the early season coincided with the peak of stopover timing, while the late season occurred after the arrival of wintering woodcock. But in nearly all cases, holding split seasons resulted in a considerable number of stopovers occurring outside open hunting seasons, which suggests that some migrants will inevitably be missed when using split seasons. In southern states harvest is primarily targeted at overwintering woodcock, and in nearly all cases hunting seasons began after the majority of woodcock had arrived at wintering sites.

Variable timing of migration among age or sex classes could result in differential exposure to harvest or mortality (Newton 2006, 2007). Adult females are particularly important for population growth; therefore, if harvest management strategies could be implemented to reduce adult female harvest, there may be population benefits (Sæther and Bakke 2000). Adult woodcock initiated fall migration earlier and spent more time on multiday stopovers compared to young woodcock, and female woodcock of both age classes made more stopovers than males. Most of the stops we recorded (82%) lasted only a single day before woodcock continued migrating, and outside of fall initiation we found relatively few variables had a strong predictive relationship with the phenology of woodcock migration. Collectively these results suggest limited ability to affect harvest of specific age or sex classes of woodcock by changing hunting season dates. Multi-day stopovers by woodcock were shorter when they coincided with an open hunting season, which could result from local hunting pressure causing woodcock to continue migration more rapidly compared to when hunting seasons are closed. The effects of hunting disturbance on movement and migration has received considerable study in waterfowl. Pearse et al. (2023) reported that mallards (*Anas platyrhynchos*) were more likely to make migratory movements on weekend days, when hunting activity was greater, and spring hunting of light geese (*Anser* spp.) in North America changes the stopover dynamics of geese (Béchet et al. 2004) and other non-target waterfowl (Dinges et al. 2015). In our study we did not explicitly quantify hunting rates in the areas where our GPS-marked woodcock stopped, so we do not know when they were actually exposed to hunter activity, and this could be an area for future research.

Initiation of spring migration occurred from February through April, with mean initiation dates for most administrative divisions occurring in March (Figure 5). Most hunting seasons ended November to January, with seasons farther south generally terminating during January, and all terminated on or prior to 31 January as per federal regulation (Table D1, available in Supporting Information). Only 2 woodcock initiated spring migration during January, whereas the remainder initiated spring migration after the termination of hunting seasons, with approximately 10–15 days between the latest hunting seasons and onset of most migrations. Consequently, current harvest regulatory frameworks and their associated season dates are unlikely to interfere with timing of spring migration. Late-winter harvest has potential to overlap with southern-nesting woodcock, who may initiate nests as early as January (Roboski and Causey 1981, Wiley and Causey 1987), but the extent to which this affects reproduction is currently unknown. While our data were collected from a large sample of individuals marked across a wide geographic extent, only 2 years of migration data were included in this analysis. To the extent that there is significant annual variability in migration, or systemic changes in the future coincident with global change, managers may need to adapt harvest strategies in response.

MANAGEMENT IMPLICATIONS

Given that fall initiation and stopover timing for American woodcock were relatively predictable, our models provide tools to evaluate the timing of hunting seasons and assist with management decisions. For example, for the most northern populations, there may be a relatively short window in which migrants are available for harvest and residents are primarily harvested. Conversely, managers in more southern breeding areas may have small residential populations, with the greatest local woodcock abundance occurring during migratory or over-winter periods. In many mid-latitude states, split seasons are used to target migrant and wintering woodcock, and our results suggest that considerable stopover occurred after the closing of the first split in those states. If managers seek to buffer resident populations at mid-latitudes from harvest, they could open seasons later while maintaining hunter opportunities to harvest migrant woodcock that are missed under current season dates. Current harvest regulations in wintering areas are unlikely to interfere with the onset of spring migration, though some uncertainty remains regarding the potential for winter harvest pressure to affect breeding performance.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All capture and marking of woodcock was conducted under protocols approved by the University of Maine Institutional Animal Care and Use Committee (protocol A2017_05_02), and was approved under federal permits issued by the United States Geological Survey Bird Banding Lab or Canadian Bird Banding Office.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are available at https://github.com/EWMRC/amwo-phenology.

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