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Satellite tracking of American Woodcock reveals a gradient of migration strategies

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ABSTRACT

Diversity in behavior is important for migratory birds in adapting to dynamic environmental and habitat conditions and responding to global change. Migratory behavior can be described by a variety of factors that comprise migration strategies. We characterized variation in migration strategies in American Woodcock (*Scolopax minor*), a migratory gamebird experiencing long-term population decline, using GPS data from ~300 individuals tracked throughout eastern North America. We classified woodcock migratory movements using a step-length threshold, and calculated characteristics of migration related to distance, path, and stopping events. We then used principal components analysis (PCA) to ordinate variation in migration characteristics along axes that explained different fundamental aspects of migration, and tested effects of body condition, age-sex class, and starting and ending location on PCA results. The PCA did not show evidence for clustering, suggesting a lack of discrete strategies among groups of individuals; rather, woodcock migration strategies existed along continuous gradients driven most heavily by metrics associated with migration distance and duration, departure timing, and stopping behavior. Body condition did not explain variation in migration strategy during the fall or spring, but during spring adult males and young females differed in some characteristics related to migration distance and duration. Starting and ending latitude and longitude, particularly the northernmost point of migration, explained up to 61% of the variation in any one axis of migration strategy. Our results reveal gradients in migration behavior of woodcock, and this variability should increase the resilience of woodcock to future anthropogenic landscape and climate change.

Keywords: animal tracking, migratory behavior, migratory strategies, movement, *Scolopax minor*

How to Cite

LAY SUMMARY

- We used movement data from GPS-tracked American Woodcock to characterize migration strategies within the species.
- We found that migration strategy in woodcock occurs along a gradient rather than in discrete groups, and that much of the variation in strategies is associated with the northernmost point of spring and fall migrations.
- We found limited evidence for effects of body condition or age-sex class on migration strategies.
- Overall, the diverse migration strategies used by American Woodcock suggests that the species should be adaptable to landscape and climate change.

El seguimiento satelital de *Scolopax minor* revela un gradiente de estrategias migratorias

RESUMEN

La diversidad en el comportamiento es importante para las aves migratorias en su adaptación a las condiciones dinámicas ambientales y de hábitat, y en respuesta al cambio global. El comportamiento migratorio puede ser descrito por una variedad de factores que comprenden estrategias de migración. Caracterizamos la variación en las estrategias de migración en *Scolopax minor*, un ave migratoria de caza que está experimentando una disminución poblacional a largo plazo, utilizando datos de GPS de ~300 individuos rastreados a lo largo del este de América del Norte. Clasificamos los movimientos migratorios de *S. minor* utilizando un umbral de longitud de vuelo, y calculamos las características de la migración relacionadas con la distancia, el recorrido y los eventos de parada. Luego usamos un análisis de componentes principales (PCA por sus siglas en inglés) para ordenar la variación en las características de la migración a lo largo de ejes que explicaban diferentes aspectos fundamentales de la migración, y probamos los efectos de la condición corporal, la clase de edad-sexo, y la ubicación de inicio y finalización en los resultados del PCA. El PCA no mostró evidencia de agrupamiento, lo que sugiere una falta de estrategias discretas entre grupos de individuos; más bien, las estrategias migratorias de *S. minor* existieron a lo largo de gradientes continuos impulsados principalmente por métricas asociadas con la distancia y la duración de la migración, el momento de salida y el comportamiento de parada. La condición corporal no explicó la variación en la estrategia migratoria durante el otoño o la primavera, pero durante la primavera los machos adultos y las hembras jóvenes difirieron en algunas características relacionadas con la distancia y la duración de la migración. La latitud y longitud de inicio y finalización, particularmente el punto más septentrional de la migración, explicaron hasta el 61 % de la variación en cualquiera de los ejes de la estrategia migratoria. Nuestros resultados revelan gradientes en el comportamiento migratorio de *S. minor*, y esta variabilidad debería aumentar la resiliencia de la especie ante futuros cambios en el paisaje antropogénico y en el clima.

Palabras clave: comportamiento migratorio, estrategias migratorias, movimiento, rastreo animal, *Scolopax minor*

INTRODUCTION

Diversity is critical to the resilience of ecosystems, species, and populations (Evans and Sheldon 2008, Mori et al. 2013, Weeks et al. 2022), and characterizing diversity is therefore important for guiding and evaluating conservation, monitoring, and management action (Merrick and Koprowski 2017, Gunn et al. 2022, Wojtusik et al. 2022). Many migratory birds have experienced significant, long-term population declines, in part resulting from landcover and climatic change (Bairlien 2016, Howard et al. 2020). Migratory animals depend on multiple regions and landscapes as they move throughout their annual cycle, so they may be more vulnerable to global change than non-migratory animals (Wilcove and Wikelski 2008). However, behavioral variation during migration can also help individuals and species respond to dynamic environmental pressures (Pulido and Berthold 2010, Senner et al. 2019).

Migration strategy refers to the suite of behaviors, such as use of migratory pathways, choices in stopover sites, and timing of movements that individuals use to balance energy acquisition against expenditure given the circumstances of their migration (Colwell 2010). In birds, diversity in migration strategy within species is associated with increased resilience to population decline (Gilroy et al. 2016), and migration strategy may explain inter- and intra-specific variation in bird population trends. For example, among 30 species breeding in Europe, Sanderson et al. (2006) found that longer-distance migrants showed more negative population trends than short-distance migrant and resident birds. Within-species, Common Cuckoo (*Cuculus canorus*) from a declining population in the United Kingdom used 2 distinct migration routes, where survival was lower in birds using the shorter route (Hewson et al. 2016). Landscape and climate change have influenced the decline of migratory birds and are

expected to continue doing so into the future (Galbraith et al. 2014). Migratory birds are vulnerable to loss of habitat, changes in the phenology of prey emergence, altered hydrological regimes, and other environmental stressors (Galbraith et al. 2014, Bairlein 2016).

The migratory connectivity literature has highlighted the importance of diversity in migratory routes, for example, in persistence through stopover habitat loss (Iwamura et al. 2013) and the potential for environmental change to differentially affect demographic subgroups (Briedis and Bauer 2018). Migratory connectivity refers to the extent to which individuals within a species that begin at a given breeding area migrate to the same nonbreeding area, or vice versa, so lower migratory connectivity in a species indicates higher variability in where individuals migrate (Webster et al. 2002), and, likely, how they migrate. However, migratory connectivity shows a limited picture of migration behavior, and other behavioral characteristics of migration strategy remain difficult to study without relatively high-resolution location data. Although some species show limited variability in migration strategy, others exhibit substantial variation among individuals or groups (Piersma 2007). A number of studies have focused on measuring individual characteristics of migration (Exo et al. 2019, Moore et al. 2021, Herbert et al. 2022), but few have addressed how entire suites of characteristics, in aggregate and through their interactions, define the complex strategies exhibited by migrants. Understanding how migratory behaviors aggregate into strategies, and how strategies vary among and within populations, is important for understanding how species will respond to change (Skagen et al. 2005, Shuert et al. 2023).

The American Woodcock (*Scolopax minor*; hereinafter woodcock) is a migratory bird experiencing long-term population decline (Seamans and Rau 2022). The species

is distributed across much of eastern and central North America, with a range extending from the southern United States to Canada and encompassing most of the forested environments of eastern North America (McAuley et al. 2020). This large geographic range coincides with overlapping breeding and nonbreeding ranges, indicating that there is potential for a diversity of migratory behaviors (McAuley et al. 2020), and recent advances in methods for tracking migration have provided insights into migration phenology and migratory connectivity (Moore et al. 2019, 2021, Fish 2021). For woodcock captured in the western portion of the species' range, there is considerable variability in migration routes, even among woodcock wintering in common areas (Moore et al. 2019). Further, Fish (2021) found differences in woodcock migration phenology according to age-sex classes; adults initiated migration before young birds in the fall, males initiated earlier than females in the spring, and young birds tended to move farther between stopover sites than adults. Moore et al. (2021) calculated several migration metrics and found relationships between migration characteristics such as number of stopovers, migration duration, and individual decisions such as departure time and migration rate. Stable isotopes from the wings of woodcock also suggest variation in fall migration distance with latitude (i.e., leapfrog migration), where more northern individuals are thought to initiate migration earlier and migrate farther than more southern individuals (Sullins et al. 2016). Determining migration strategies in woodcock, and the behavioral and individual mechanisms that affect them, could be useful for monitoring the species, and provide a framework adaptable to other species where there is a lack of information on how individual characteristics synthesize into migration strategies.

Our goal was to characterize diversity in woodcock migration strategy and identify potential drivers of such variation. The woodcock is an interesting focal species for this work, given its broad geographic range, diversity of migration paths, and differences in phenology and responses to environmental conditions among demographic groups (Moore et al. 2019, 2021, Fish 2021, Graham et al. 2022). We aimed to answer 3 main questions: (1) which migration metrics or characteristics contribute to variation in strategies among individuals, (2) which individual characteristics (e.g., location, body condition, age) explain variation in migration strategy, and (3) do woodcock throughout the species' range exhibit either discrete migration strategies or show variation along a gradient? We expected that migration distance and duration would be the strongest contributors to variation in migration strategy because of the broad breeding range of woodcock, and that starting latitude and longitude would explain variation in strategy in the fall and spring. We further predicted that body condition and age-sex class would explain variation in migration strategy during fall and spring. We predicted that fall migration strategies would show a clustered distribution best explained by age, as hatch-year birds are less experienced, possibly resulting in a different strategy than experienced birds. In contrast, during spring, we predicted clustering of migration strategy primarily associated with sex, as Fish (2021) observed differences in migration phenology between male and female woodcock, and because we expected differences in reproductive strategies between the sexes would result in differing motivations during migration (McAuley et al. 2020).

METHODS

Bird Capture and Location Data Collection

We captured woodcock between 2017 and 2022 in 14 US states and 3 Canadian provinces (Figure 1, Supplementary Material Figure 1). All captures were permitted by the U.S. Geological Survey Bird Banding Laboratory or the Canadian Bird Banding Office. We captured birds using mist nets and spotlighting, collected morphometric measurements, and aged and sexed each bird based on remiges and bill length (Martin 1964). We used leg-loop harnesses (Sanzenbacher et al. 2000) to attach fixed-battery (i.e., not solar-rechargeable) Pinpoint GPS Argos devices (Lotek; Newmarket, ON) of 3 sizes (4-g PinPoint 75, 5-g Pinpoint 120, 6.3-g Pinpoint 150). The combination of tag, harness, and band did not exceed 4% body mass at the time of capture, and generally larger devices were deployed on females, which are larger than males (McAuley et al. 2020). These devices collected GPS locations, at an approximate accuracy of 20 m, and ARGOS/PTT locations, which had variable accuracy depending on signal quality. To ensure consistency of location accuracy, we only used GPS locations in this study. We programmed devices to collect locations on several duty cycles to meet various project objectives and preserve battery life. Generally, tags collected locations every 1–2 days during the first migration after deployment, and every 5–7 days thereafter. For the data set used in the analysis of fall migration, there was an average of one location every 1.79 days, and 95% of locations were collected within 5.25 days of the preceding location (n = 193 birds) For data used to characterize spring migration, there was an average of one location every 1.97 days and 95% of locations were collected within 4.75 days of the preceding location (n = 132 birds). Prior to 2020, all locations were collected during the day, while starting in 2020 locations were collected during the day and at night for a subset of birds.

Data Preparation

We used only individuals with a complete migration path sufficient to identify pre-migration, post-migration, and stopping sites. For fall migration, we used data collected from 1 August to 31 December, and for spring migration we used data from 5 January to 15 June; in each case these date ranges encompassed expected periods of migration. To subset the data to complete migrations, we first eliminated birds with tracking devices that stopped collecting data before December 1 for fall, and before May 1 for spring, based on expected arrival dates of woodcock to post-migration locations (Fish 2021). The resulting dataset consisted of birds monitored for a sufficiently long period to provide a complete migration path for fall or spring migration, which was necessary so that all migration metrics (described further below) could be calculated for all individuals in the analysis.

Frequency of location collection influences calculations of migration metrics from GPS data (Clements 2022). Therefore, to increase consistency among individuals regardless of device duty cycles or transmission success, we used the *crawl* package (Johnson et al. 2008) in R (R Core Team 2022) to predict locations along the movement path of each woodcock. We used the package to fit a continuous-time correlated random walk model (Johnson et al. 2008, Derville et al. 2020), which we used to predict locations at a rate of one location every 24 hours based on the realized movement path. We then combined predicted and raw data, such that
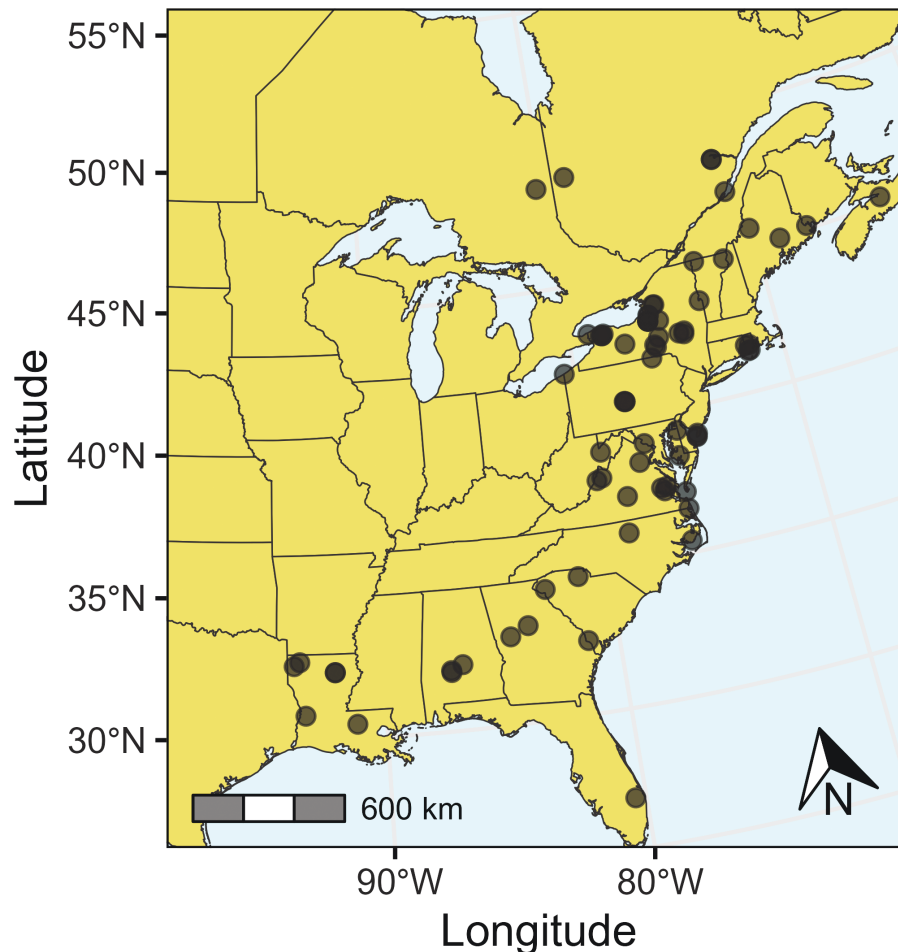
FIGURE 1. American Woodcock capture locations in the eastern United States and Canada; each circle represents an Eastern Woodcock Migration Research Cooperative capture site.

predicted locations were excluded if they were collected on the same ordinal date as a true location. Inference from movement models can be influenced by the frequency of locations collected (Knight et al. 2021), and we found that when GPS locations were collected > 3 days apart, they often produced unreliable predicted points relative to the known migration paths. Therefore, we eliminated predicted locations between true GPS locations that were collected > 3 days (72 hr) apart. For fall migration across all birds, the resulting tracks were comprised of 63% true locations and 37% predicted locations. For spring migration, tracks were comprised of 61% true locations and 39% predicted locations. While we do not expect predicted locations to be spatially accurate (i.e., a predicted location does not reflect an exact stopover location), for our questions the spatial location of the bird was not as important as understanding the timing of migratory events. Using the correlated random walk approach provided a defensible means of assigning probabilistic timing based on the information otherwise contained within the movement path, and is consistent with approaches used previously (Knight et al. 2021, Watts et al. 2022).

Quantifying Migration Behavior

To identify pre-migration areas, post-migration areas, and stopovers, we used a 16-km distance threshold based on the distribution of step lengths in our original data set (i.e., not including predicted locations; Supplementary Material Figure 2), which shows a clear bimodal distribution between short- (<16 km) and long-distance (>16 km) movements, following Blomberg et al. (2023). Pre-migration areas were defined as all locations that occurred prior to the first movement > 16 km, while post-migration areas were defined as the last cluster of locations < 16 km apart. This approach is consistent with the absolute displacement method described by Soriano-Redondo et al. (2020). We visually inspected all tracks, and if a bird made one long movement during the pre- or post-migration periods, and returned to its point of origin (i.e., a recursive movement), we assumed those movements were part of normal pre- or post-migration ranging and manually adjusted the pre- or post-migration area to reflect this. In general, these long-distance movements were rare; 10% of fall migration birds and 3% of spring migration birds used in the analysis had movements that were manually reclassified. We separated stopping events into stops, which were migratory locations that did not occur within 16 km of another location (i.e., a single day stop), and stopovers, which were migratory locations that occurred within 16 km of at least one additional GPS point (i.e., more than 1 day was spent at the site; Graham et al. 2022). In cases where a bird moved more than 16 km from its previous location, and subsequently made a recursive movement back to within 16 km of the prior location, the outlier location as well as the stopover

locations before and after it were classified as a single stop-over. We identified stops and stopovers within the broader category of stopping events due to the presumed differences in resting and refueling behavior when a bird remains at a site for multiple days (Graham et al. 2022). Because woodcock migrate at night and stop during the day (Coon et al. 1976), we assumed that each day of migration contained either a stop or part of a stopover. Note that for a small number of points that were nocturnal, the bird may have been in flight, introducing some uncertainty about whether a stop or a stopover occurred that day. However, we did not expect this to substantially influence our results.

We calculated 7 metrics to characterize migration strategy: number of stopping events, proportion of time in stopover, migration duration, mean stopping event duration, mean distance from coast, total migration distance, deviation from straight line distance, and departure index (Table 1A; Supplementary Material Figures 3–4). We considered these metrics inclusive of the characteristics of individual migrations that were reasonable to calculate given the nature of our GPS tracking data and were similar to those used in other studies (Anderson et al. 2019, Clements et al. 2022, Wong et al. 2022). They were chosen to encompass multiple facets of migration, including timing (departure index), stopping behavior (mean stopping event duration), and migration length and path (number of stopping events, migration duration, mean distance from coast, and deviation from straight line distance). To calculate departure index, we used linear regressions to correct for latitude and age for fall migration and longitude and sex for spring migration (Fish 2021) and used the residuals as a relative departure timing index. An additional 5 metrics were calculated as intermediate steps in the development of our 7 focal metrics (Table 1B), but we did not include them in our full analyses because using them for subsequent calculations meant they were inherently confounded with our 7 focal metrics.

Characterizing Migration Strategies
We used principal components analysis (PCA; Smith 2002, James et al. 2014) implemented with the *factoextra* package (Kassambara and Mundt 2017) in R (R Core Team 2022) to explore variation in migration strategy based on our focal migration metrics (Table 1). PCA is a dimension-reduction technique (Smith 2002) that is typically used for analyses in which a larger set of variables need to be summarized for principal components (PC) regression, or as an unsupervised learning technique for data exploration (James et al. 2014). In the context of our analysis, PC loading vectors provided the aggregations of migration metrics that explained the greatest variability in the data (i.e., axes of migration strategy), and PC scores for individual birds provided their position along that axis of migration strategy (James et al. 2014). PCA loadings represent the effect sizes for the linear combination of all migration metrics within each PC and ranged from −1 to 1. We interpreted any variable loading with an absolute value > 0.4 as important for explaining a PC (Guadagnoli and Velicer 1988) and limited our interpretations to axes explaining at least 10% of the variation in the data.

We chose to use PCA to address our objectives because it did not explicitly divide observations into clusters, whereas alternative clustering techniques assume that clusters exist, and in doing so force their identification (James et al. 2014).

Rather than assuming the existence of discrete clusters, we visually examined ordination plots for all combinations of PCs that explained > 10% of the variance in the data. We searched for evidence of deviations in patterns (i.e., clusters of points) that would indicate discrete combinations of migratory characteristics reflecting unique strategies for migration, and we interpreted lack of such discrete patterns as evidence that migratory strategies followed a continuous gradient. We also evaluated two-dimensional patterns in component scores between each pair of PCs (e.g., PC1 compared to PC2) by sub-dividing ordination plots into quarters centered at zero for each axis, and visually inspecting the distribution of points within each quarter. This allowed us to better understand the relationships among the different axes of migration characteristics and how they combined to influence an overall strategy.

Most focal metrics were only weakly correlated, but the number of stopping events was positively correlated ($r > 0.5$) with migration duration ($r = 0.54$ fall, $r = 0.52$ spring), migration distance ($r = 0.73$ fall, $r = 0.75$ spring), and deviation from straight line distance ($r = 0.57$ fall, $r = 0.65$ spring) in the fall and spring (Supplementary Material Tables 1–2). These correlations were expected, because we assumed that at least one stopping event occurred on each day of migration. However, because PCA reduces sets of variables that may be correlated with others in the set to a smaller set of uncorrelated variables (Lafi and Kaneene 1992), these correlations were unlikely to influence the ecological interpretations of our results. For this analysis, we only used individual birds for which all focal metrics could be estimated (a pre-requisite of PCA) and ran separate analyses for fall and spring migration.

Investigating Variables Associated with Variation in Migration Strategy
We conducted a secondary analysis using linear models to test relationships between PC scores, starting and ending location, and individual characteristics (age-sex class and body condition). For fall migration, age classes were defined as "young" for hatch-year birds, and "adult" for after-hatch-year, second-year, and after-second-year birds (Fish 2021). For spring migration, age classes were defined as "young" for second-year birds caught during winter and "adult" for all other after-hatch-year birds. A young woodcock signified a bird undertaking its first fall or spring migration. For birds with sufficient information available, we calculated a body condition index that provided the relative mass corrected for age class, sex, and date of capture, following Fish (2021). To calculate this index, we used a general linear model in R (R Core Team 2022) with body mass related to leg length (a proxy for body size), sex, and age (Fish 2021). We then obtained residuals from the model for each individual using the *modelr* package (Wickham 2023) and used these residual values as our body condition index (Blomberg et al. 2014, Fish 2021). Positive scores indicated an individual was heavier than an average individual of its size, age, and sex, while negative scores indicated an individual was lighter than average (Blomberg et al. 2014, Fish 2021). We only evaluated effects of body condition for birds at time of capture within 2 months of the season where the focal migration was initiated, because body condition is very dynamic, and we would expect substantial changes in body condition between capture and a subsequent season or year (Brown 1996, Graham et al.

TABLE 1. Definitions of metrics calculated for fall and spring migration of GPS-marked woodcock in eastern North America. The first column is the term we use to refer to the metric and the second is a brief definition. Section (**A**) shows for metrics used in our PCA analysis and section (**B**) shows metrics that were used as an intermediate step to calculate the metrics we used.

Migration metric	Definition
(A) Metrics used in PCA	
Number of stopping events	Combined number of stops and stopovers
Migration duration	Difference in time (days) between departure and arrival times
Mean stopping event duration	Mean duration of all stopping events, including stops and stopovers, in hours (assuming that stops are 12 hours)
Mean distance from coast	Mean distance of all migration GPS points from the nearest point on the Atlantic coastline
Migration distance	Total distance of GPS track from the last point of pre-migration to the first point of post-migration in kilometres
Deviation from straight line distance	Difference between straight migration distance and total migration distance in kilometres (km)
Departure index	Departure time relative to birds with similar characteristics using residuals from linear regressions predicting departure time (Fish 2021). For fall migration, we accounted for latitude, longitude, and age, and for spring migration, we accounted for latitude and sex.
(B) Intermediate metrics (not used in PCA)	
Number of stops	Number of stopping events during migration that lasted ≤ 1 day
Number of stopovers	Number of stopping events during migration that last > 1 day
Departure time	Date/timestamp halfway between last point of pre-migration and first of fall migration
Arrival time	Date/timestamp halfway between last point of fall migration and first of post-migration
Straight migration distance	Straight-line distance between the last point of pre-migration and the first point of post-migration

2022). The distribution of capture dates for all birds is shown in Supplementary Material Figure 1.

We used general linear regression to evaluate if starting and ending latitude and longitude of migration, body condition, or age-sex class explained variation in each PC. We ran 3 separate models to evaluate these effects because we lacked morphometric data for all birds, producing different sample sizes among model sets. First, we evaluated the effects of starting and ending location ($n = 183$ for fall, $n = 122$ for spring). The starting and ending location model can be written as

$$Y_i = \beta_0 + \beta_1 start\_lat_i + \beta_2 start\_lon_i + \beta_3 end\_lat_i + \beta_4 end\_lon_i$$

where Y represents a PC score, $start\_lat$ is starting latitude, $start\_lon$ is starting longitude, end_lat is ending latitude, and end_lon is ending longitude for each individual i and β_0 is the intercept. To examine the influence of individual bird characteristics on PC scores, we added age-sex class ($n = 183$ for fall, $n = 122$ for spring) and body condition ($n = 159$ for fall, $n = 112$ for spring) to the stating/ending location models. The formula for the age-sex models was

$$Y_{i,j} = \beta_0 + \beta_1 start\_lat_i + \beta_2 start\_lon_i + \beta_3 end\_lat_i + \beta_4 end\_lon_i + \beta_j age\_sex_i$$

where age_sex is age-sex class (a factor with j levels, adult female, young female, adult male, or young male, with adult female as the reference condition) for each individual i. The formula for the body condition models was

$$Y_i = \beta_0 + \beta_1 start\_lat_i + \beta_2 start\_lon_i + \beta_3 end\_lat_i + \beta_4 end\_lon_i + \beta_5 BCI_i$$

where starting and ending location effects are represented the same as above, BCI is body condition index. We did not include a year effect in any models because preliminary analysis revealed a significant effect only for 2022, which was also a

year where capture locations were not consistent with other years woodcock (Supplementary Material Figure 1), so we were unable to separate true effects of year from sampling variance. We considered an effect to be significant if $P \leq 0.05$ and interpreted effect sizes and r^2 values for each model. We further calculated partial (part.) r^2 for each predictor variable in all models to determine the proportion of variation in the response explained by each predictor term, using the *rsq* package (Zhang 2022) in R (v. 4.2.2; R Core Team 2022). In the case of r^2 and partial r^2, we considered values > 0.1 to reflect a meaningful amount of variation explained, and we generally restricted our interpretations to variables that met our criteria for both significant and meaningful effect sizes. We ran all models using the *glm* function in the *stats* package in R (R Core Team 2022).

RESULTS

Of 220 birds with data collected during the fall migration period, 193 individuals met our criteria for inclusion in the analysis (i.e., displayed migratory behavior and had frequent enough locations). Of 147 birds with data collected during the spring migration period, 132 met our criteria for inclusion. During fall, the age distribution was approximately 54% young and 46% adult, and the sex distribution was approximately 53% female and 47% male. In the spring, age distribution was approximately 58% young and 42% adult, and age was 44% female and 56% male. Woodcock exhibited considerable variability in each of the migration metrics we measured, overall and within age-sex classes (Supplementary Material Figures 3–4).

For fall migration, 86% of variation among individuals was explained by the first 4 principal components: 44% by PC1, 17% by PC2, 14% by PC3, and 11% by PC4 (Table 2). PCs 5, 6, and 7 each explained < 10% of variation and only 14% overall. PC1 can be interpreted as a gradient from spatially

TABLE 2. PCA loadings for each variable describing the fall migration of American Woodcock in eastern North America. Terms with a loading of above the absolute value of 0.4 in a principal component explaining at least 10% of variability in the data set are bold.

	PC1 (44%)	PC2 (17%)	PC3 (14%)	PC4 (12%)	PC5 (6%)	PC6 (4%)	PC7 (3%)
Number of stopping events	**−0.46**	0.22	−0.16	0.29	−0.50	0.51	0.35
Migration duration	**−0.46**	**−0.40**	0.01	0.01	−0.17	−0.68	0.38
Mean stop duration	−0.17	**−0.44**	**0.81**	0.05	0.00	0.33	−0.11
Total migration distance	**−0.51**	0.19	−0.04	0.06	−0.15	−0.19	−0.80
Mean distance from coast	−0.26	0.29	0.14	**−0.89**	−0.02	0.07	0.15
Deviation from straight line	**−0.44**	0.23	0.02	0.23	0.82	0.07	0.18
Departure index	−0.18	**0.65**	**0.54**	0.25	−0.17	−0.36	0.16

TABLE 3. PCA loadings for each variable describing the spring migration of American Woodcock in eastern North America. Terms with a loading of above the absolute value of 0.4 in a principal component explaining at least 10% of variability in the data set are bold.

	PC1 (43%)	PC2 (18%)	PC3 (14%)	PC4 (10%)	PC5 (5%)	PC6 (4%)	PC7 (3%)
Number of stopping events	**−0.48**	0.19	−0.21	0.30	−0.11	0.32	−0.69
Migration duration	**−0.44**	−0.35	0.06	0.10	−0.31	−0.75	0.06
Mean stop duration	−0.06	**−0.72**	**0.40**	0.37	0.16	0.39	0.03
Migration distance	**−0.50**	0.18	−0.04	0.09	−0.41	0.33	0.66
Distance from coast	−0.30	0.05	**0.59**	**−0.71**	−0.04	0.13	−0.20
Deviation from straight line	**−0.47**	0.12	−0.08	0.01	0.84	−0.14	0.19
Departure index	0.10	**0.52**	**0.66**	**0.50**	0.00	−0.18	0.01

and temporally short migrations, with direct routes and few stopping events (more positive PC scores), to spatially and temporally longer migrations with less direct routes and more stopping events (more negative PC scores). PC2 can be interpreted as a gradient between early departure with longer stops (more negative PC scores) and later departure but with shorter stops (more positive PC scores). PC3 can be interpreted as a gradient between leaving early and making more stops and fewer stopovers (positive PC scores) or leaving later and making relatively more stopovers with fewer stops (negative PC scores). PC4 can be interpreted as a gradient from inland migration routes (positive PC scores) to coastal migration routes (negative PC scores). For all PCs, woodcock showed high variability in PC score for fall migration, and there were no substantial differences in PC score among age-sex classes (Supplementary Material Figure 5).

For spring migration, the first 4 PCs explained 85% of the variation among individuals: 43% by PC1, 18% by PC2, 14% by PC3, and 10% by PC4 (Table 3). The remaining PCs each explained < 10% of variation, and only 15% combined. The interpretation of loadings on each PC was generally similar to fall migration. PC1 can be interpreted as a gradient from shorter, more direct migrations (more positive PC scores) to longer and less direct migrations (more negative PC scores). PC2 can be interpreted as a gradient of shorter stopping events with later departures (more positive PC scores) to longer stops with earlier departures (more negative PC scores). PC3 can be interpreted as a gradient from birds that departed later, migrated farther from the coast and took longer stopping events (more positive PC scores) to those departing earlier, migrating closer to the coast, and making shorter stopping events (more negative PC scores). PC4 can

be interpreted as a gradient from birds that departed later but migrated closer to the coast (more positive PC scores) to those departing earlier and migrating farther from the coast (more negative PC scores). The difference in loading of the mean distance from coast variable between PCs 3 and 4 allowed more coastal migrants to differ in their relative departure time. For all PCs, woodcock showed high variability in PC score for spring migration and there were no substantial differences in PC score among age-sex classes (Supplementary Material Figure 6).

PCs showed no evidence of distinctive clusters of points reflecting discrete migration strategies during either spring or fall (Figures 2 and 3; Supplementary Material Figures 7 and 8), suggesting instead that woodcock migratory characteristics, and therefore migration strategies, existed along a continuous gradient. A notable pattern observed during fall (Figure 2) and to a lesser extent spring (Figure 3) was that values for PCs 2, 3, and 4 were most conserved (showed the least variability) when PC1 scores were positive. As PC1 was associated with the distance and duration of migration, this suggests that birds making relatively short, direct migrations (i.e., those with positive PC1 scores) were inherently more consistent in other migratory traits. In contrast, those birds migrating greater distances with longer duration were afforded greater flexibility in other characteristics of migration such as departure timing or stopover duration.

Starting and ending location explained substantial variation in many principal components during spring and fall (Figure 4, Supplementary Material Table 5). Most prominent of these during fall were a negative relationship between PC1 and starting latitude (part. r^2 = 0.29), and a positive relationship between PC1 and ending longitude (part. r^2 = 0.13).
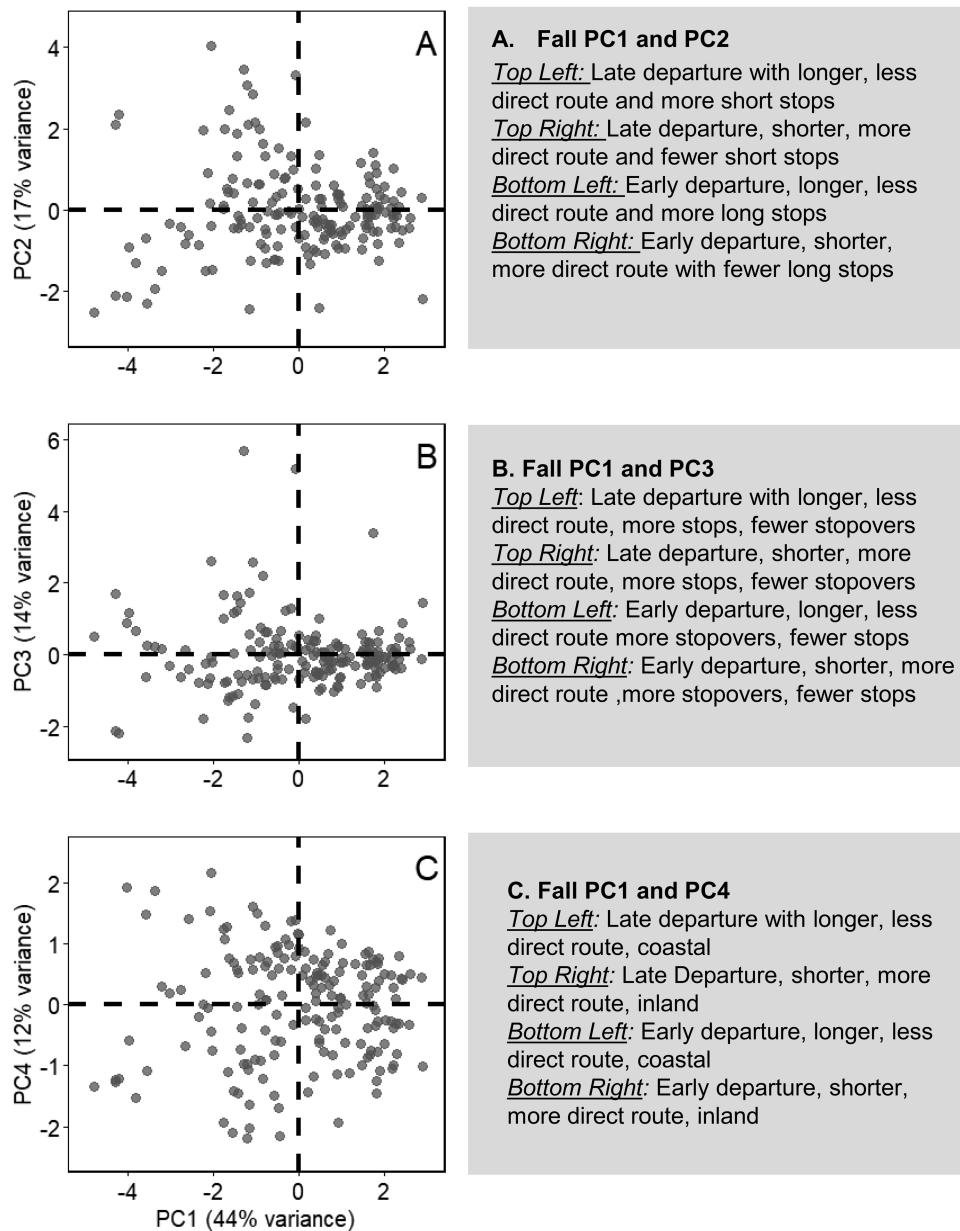
A. Fall PC1 and PC2
Top Left: Late departure with longer, less direct route and more short stops
Top Right: Late departure, shorter, more direct route and fewer short stops
Bottom Left: Early departure, longer, less direct route and more long stops
Bottom Right: Early departure, shorter, more direct route with fewer long stops

B. Fall PC1 and PC3
Top Left: Late departure with longer, less direct route, more stops, fewer stopovers
Top Right: Late departure, shorter, more direct route, more stops, fewer stopovers
Bottom Left: Early departure, longer, less direct route more stopovers, fewer stops
Bottom Right: Early departure, shorter, more direct route ,more stopovers, fewer stops

C. Fall PC1 and PC4
Top Left: Late departure with longer, less direct route, coastal
Top Right: Late Departure, shorter, more direct route, inland
Bottom Left: Early departure, longer, less direct route, coastal
Bottom Right: Early departure, shorter, more direct route, inland

FIGURE 2. Ordination plots with one point per individual showing PC1 scores for fall migration on the *x*-axis and (**A**) PC2, (**B**) PC3, and (**C**) PC4 scores on the *y*-axis. Dashed lines indicate a score of 0 for each PC (i.e., an "average" bird). In the shaded boxes associated with each plot, the characteristics of individual American Woodcock that fall in each quadrant based on the combination of PC loadings are listed. No clusters are visible that would indicate discrete migration strategies but points more clustered around 0 may indicate more constrained migratory traits, and points spread more widely around 0 would indicate less constrained migratory traits.

Collectively starting and ending locations explained 61% of the variance in fall PC1 scores ($r^2 = 0.61$). PC4 was also strongly influenced by starting (part. $r^2 = 0.18$) and ending longitude (part. $r^2 = 0.15$), with 46% of the overall variance in PC4 associated with the starting and ending points ($r^2 = 0.46$). While starting and ending locations had significant effects on PC2 and PC3, they explained considerably less of the variation in these axes (Supplementary Material Table 5). During the spring, PC1 was affected by a negative association with ending latitude (part. $r^2 = 0.36$), while PC3 and PC4 were most affected by ending longitude, with negative (part. $r^2 = 0.32$) and positive (part. $r^2 = 0.38$) associations, respectively. Adding age-sex classes to the models with starting and ending location resulted in several signifi-

cant effects (Table 4); however, the only case where an effect explained > 10% of the variation was for spring, where compared to adult females, young female birds had significantly lower PC1 scores and adult males had significantly greater PC1 scores, while young males did not differ significantly from adult females (Table 4). In aggregate, age-sex class explained an additional 14% of variance in PC1 (part. $r^2 = 0.14$) beyond starting and ending location. No other age-sex classes differed significantly with respect to any PC scores in either season (Table 4). The addition of body condition to starting and ending location models also revealed no significant effects and explained no additional variance in PC scores during either fall or spring migration (Supplementary Material Table 6).
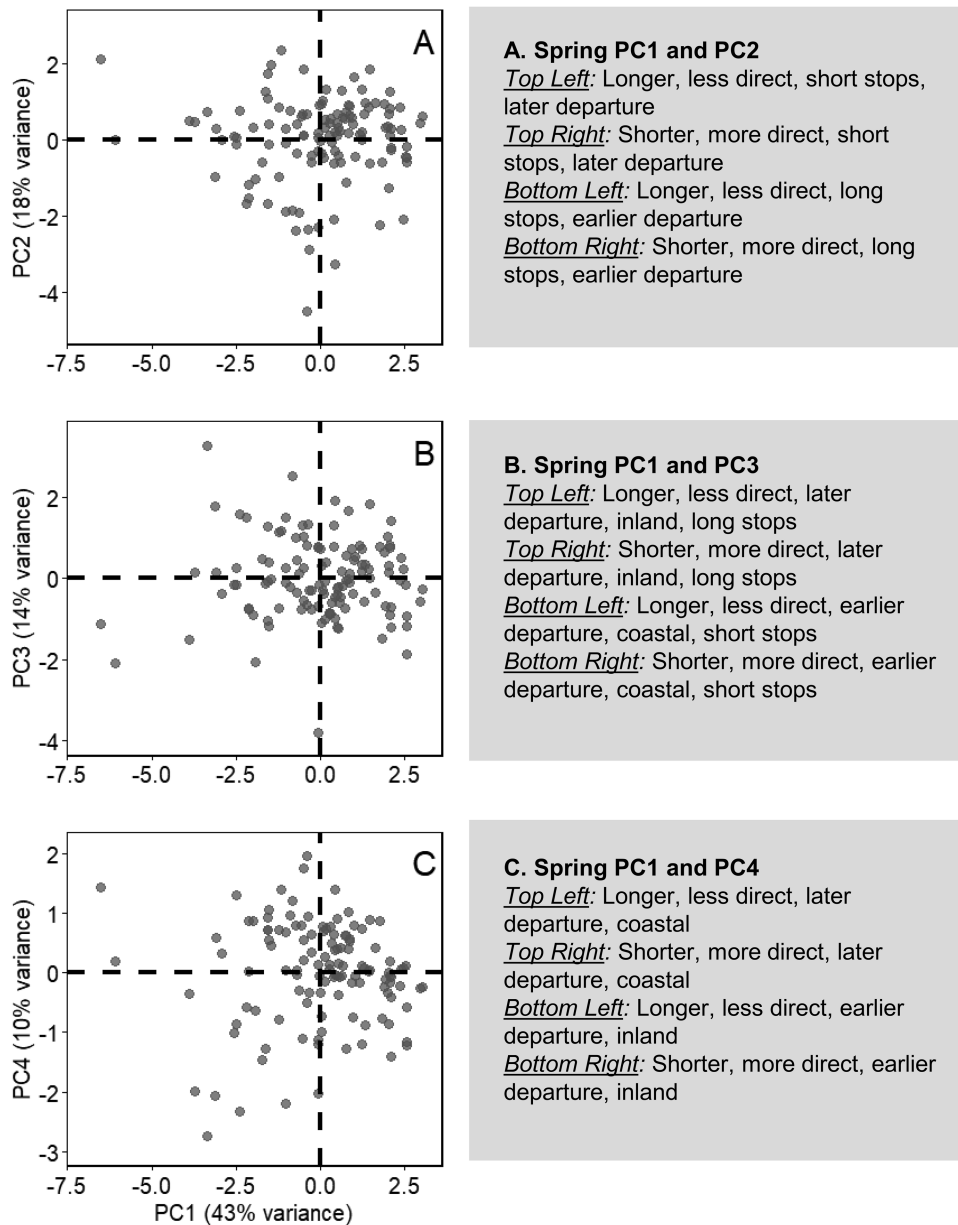
A. Spring PC1 and PC2
Top Left: Longer, less direct, short stops, later departure
Top Right: Shorter, more direct, short stops, later departure
Bottom Left: Longer, less direct, long stops, earlier departure
Bottom Right: Shorter, more direct, long stops, earlier departure

B. Spring PC1 and PC3
Top Left: Longer, less direct, later departure, inland, long stops
Top Right: Shorter, more direct, later departure, inland, long stops
Bottom Left: Longer, less direct, earlier departure, coastal, short stops
Bottom Right: Shorter, more direct, earlier departure, coastal, short stops

C. Spring PC1 and PC4
Top Left: Longer, less direct, later departure, coastal
Top Right: Shorter, more direct, later departure, coastal
Bottom Left: Longer, less direct, earlier departure, inland
Bottom Right: Shorter, more direct, earlier departure, inland

FIGURE 3. Ordination plots with one point per individual showing PC1 scores for spring migration on the *x*-axis and (**A**) PC2, (**B**) PC3, and (**C**) PC4 scores on the *y*-axis. Dashed lines indicate a score of 0 for each PC (i.e., an "average" bird). In the shaded boxes associated with each plot, the characteristics of individual American Woodcock that fall in each quadrant based on the combination of PC loadings are listed. No clusters are visible that would indicate discrete migration strategies but points more clustered around 0 may indicate more constrained migratory traits, and points spread more widely around 0 would indicate less constrained migratory traits.

DISCUSSION

We found that woodcock tracked throughout the fall and spring migration seasons exhibited considerable variation in migration metrics but no evidence for discrete migration strategies. There was minimal evidence that individual characteristics such as age, sex, or body condition were consistently associated with migration strategy, contrary to our predictions. Instead, woodcock exhibited gradients in migratory characteristics along a continuum that was best explained by the starting and ending points of migration. Woodcock that started fall migration, or ended spring migration, at more northern latitudes during summer, or that traveled farther from east to west, necessarily covered a greater distance during migration, and took longer to do

so. Greater time and distance in migration was also associated with greater flexibility in other migration characteristics in our analysis. Woodcock residing in more northern breeding areas (e.g., portions of eastern Canada) had the greatest degree of variability in migration strategies, whereas more southern breeding woodcock were considerably more similar. However, the starting and ending points of migration explained at most 60% of the variance in any one axis of the migration behaviors we measured, which suggests considerable additional variability even among individuals originating from the same location. In general, these results demonstrate that woodcock exhibit considerable within-species variation and a continuum of migration strategy characteristics across spatial gradients.
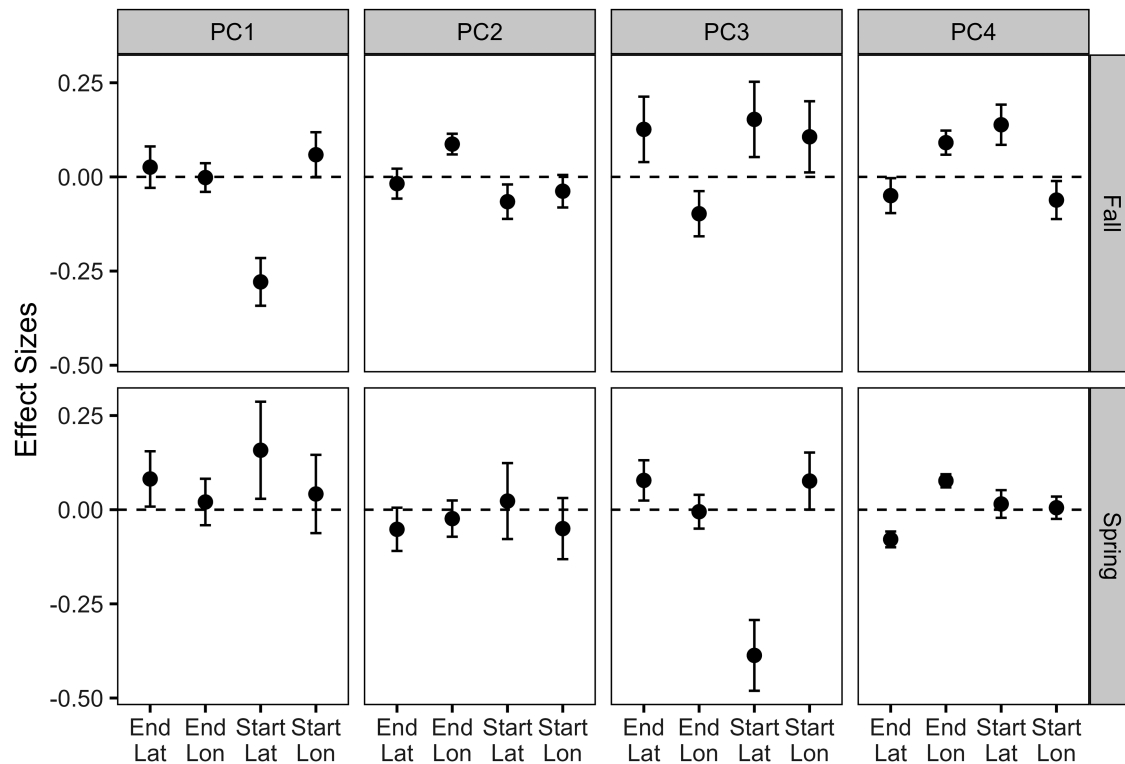
FIGURE 4. Effect sizes for each location predictor and principal component. Each panel represents a different model. Points represent the mean effect size (β) for each covariate and bars represent the 95% confidence intervals. Dashed line indicates 0 (i.e., no effect).

Spatial gradients in movement characteristics are common in birds across a range of scales among and within taxa; for example, species vary along worldwide spatial gradients in dispersal ability (Sheard et al. 2020). Wong et al. (2022) observed that more northern breeding Arctic Terns (*Sterna paradisea*) took longer to complete southward migration. We found that starting latitude and longitude were among the most important drivers of gradients in woodcock migration strategy, suggesting decisions made toward the end of spring migration, or preceding departure in fall, are substantially associated with within-species variation in strategy. The greatest variation in woodcock migration strategy was associated with migration distance, the overall length and duration of migration, and the number of stopping events, the combination of which explained almost half of variation observed in our data. It is not surprising that the length in space and duration of time in migration is driving variability in woodcock migration strategies because migration distance, duration, and number of stopping events can be influenced by a variety of physiological, behavioral, and environmental characteristics (Graham et al. 2022).

The length of migration can drive variability in migration strategy within and among species. For example, Anderson et al. (2019) found that longer-distance and shorter-distance migrant shorebirds exhibited different southward migration strategies. However, this is not always the case; for example, Brown et al. (2021) found that in Lesser Black-backed Gulls (*Larus fuscus*) in Europe, shorter-distance migrants showed a similar level of variation in strategy to longer-distance migrants, indicating that migration distance did not constrain migratory behavior in that system. We saw that woodcock with shorter fall migrations had considerably less variability in characteristics associated with PC 2, 3, and 4 scores, such as mean stopping event duration, number of stopovers, and

distance from coast (Figure 3), consistent with shorter migrations requiring less flexibility in other aspects of migration strategy. Interestingly, the pattern showing more consistency among individuals with shorter migrations was less pronounced in the spring. Because breeding occurs during spring, reproductive behavior likely has an influence on migration that is not present in the fall. Woodcock can breed as early as January in the southern portion of their range (McAuley et al. 2020), so early failed breeding attempts and subsequent migratory movements may result in added variability in migration duration, distance, or stopover characteristics in the spring. In addition, woodcocks are some of the earliest migrants in eastern North America (McAuley et al. 2020). In the spring, storms (Marra et al. 2005, Loss et al. 2020) or snow cover (Schummer et al. 2010) may delay their progress to more northern latitudes. In our study, occasionally individuals that appeared to arrive at unsuitable sites would make additional movements within the region, presumably seeking more favorable conditions (e.g., lack of snow cover). This increased their migration distance, duration, and number of stopping events.

We anticipated that body condition would explain variation in migration strategy, but it did not explain substantial variation in migration strategy in the spring or fall. We expected body condition to be related to migration strategy because it is influential on the migration behavior of many migratory shorebird species (Anderson et al. 2019, Herbert et al. 2022). However, Graham et al. (2022) found that for woodcock in southern New England, body condition was consistent across birds that differed in departure timing and migration strategy. Our findings that body condition did not explain variation in migration strategy suggests that this pattern may apply range-wide for woodcock. Although it is likely that body condition influences some aspects of migratory behavior, such as

TABLE 4. Relationships between each principal component (PC) score and age-sex class, while still including starting and ending latitude and longitude for American Woodcock in eastern North America. A separate model was run for each PC in each season (fall and spring), and r^2 associated with each model is shown in the first row, followed by the mean effect size, and upper and lower value of the 95% confidence interval, and partial r^2 for each predictor variable. Significant effects ($p \leq 0.05$) are indicated with an asterisk (*) next to the mean effect size.

PC (response)		Fall					Spring			
		PC1	PC2	PC3	PC4		PC1	PC2	PC3	PC4
	r^2	0.61	0.11	0.06	0.48	r^2	0.48	0.11	0.38	0.43
Starting latitude	β	–0.28*	-0.49	0.03	0.00	β	0.17*	0.04	0.08*	0.02
	2.5%	–0.34	0.11	–0.03	–0.04	2.5%	0.05	–0.06	0.00	–0.42
	97.5%	0.21	0.01	0.08	0.03	97.5%	0.29	0.14	0.16	0.08
	Part. r^2	0.29	0.01	0.01	0.00	Part. r^2	0.06	0.01	0.04	0.04
Starting longitude	β	–0.06*	0.03	–0.02	0.09*	β	0.06	–0.04	–0.06	–0.03
	2.5%	–0.11	–0.01	–0.06	–0.06	2.5%	–0.03	–0.12	–0.12	–0.75
	97.5%	0.02	0.08	0.02	0.11	97.5%	0.15	0.05	–0.12	–0.75
	Part. r^2	0.04	0.01	0.00	0.18	Part. r^2	0.01	0.01	0.03	0.03
Ending latitude	β	0.15*	–0.11*	0.12*	–0.09*	β	–0.39*	0.07*	0.08*	–0.01
	2.5%	0.05	–0.21	0.04	–0.15	2.5%	–0.48	0.00	0.08	–0.01
	97.5%	0.25	–0.02	0.21	–0.03	97.5%	–0.30	0.15	0.13	0.04
	Part. r^2	0.05	0.02	0.03	0.07	Part. r^2	0.33	0.02	0.11	0.00
Ending longitude	β	0.14*	0.06*	–0.05*	0.09*	β	0.01	0.01	–0.08*	0.08*
	2.5%	0.09	0.01	–0.09	0.06	2.5%	–0.02	–0.02	–0.10	0.06
	97.5%	0.19	0.11	0.00	0.12	97.5%	0.05	0.03	–0.58	0.09
	Part. r^2	0.13	0.03	0.02	0.14	Part. r^2	0.00	0.00	0.32	0.32
Age-sex class	Part. r^2	0.00	0.02	0.01	0.03	Part. r^2	0.14	0.05	0.01	0.01
Young female	β	–0.24	–0.03	–0.19	0.32*	β	–0.78*	0.02	0.10	0.00
	2.5%	–0.71	–0.46	0.60	0.04	2.5%	–1.49	–0.58	–0.33	–0.37
	97.5%	0.26	0.41	0.21	0.60	97.5%	–0.08	0.62	0.53	0.36
Adult male	β	–0.17	–0.28	–0.11	0.13	β	0.71*	0.23	–0.01	–0.09
	2.5%	–0.65	–0.28	–0.11	–0.15	2.5%	0.00	–0.38	–0.45	–0.46
	97.5%	0.30	0.73	0.30	0.41	97.5%	1.42	0.83	0.43	0.28
Young Male	β	–0.14	–0.14	–0.13	0.08	β	–0.05	–0.45	0.19	–0.01
	2.5%	–0.58	–0.53	–0.51	–0.17	2.5%	–1.07	–1.01	–0.21	–0.35
	97.5%	0.28	0.29	0.25	0.34	97.5%	0.26	0.12	0.60	0.34

departure timing (Fish 2021), it is unlikely to influence overall migration strategy for this species. Additionally, our assessment of body condition was necessarily based on mass and size variables measured prior to migration. Assuming that individual body condition is highly dynamic during migration and affected by both energy expenditure and the capacity of birds to refuel (Brown 1996), there may be a more nuanced relationship between body condition and migration strategies that we could not explore further.

We found limited evidence for the importance of age-sex class on most aspects of migration strategy. The only case in which age-sex class explained variation in migration strategy was for PC1 (associated with migration distance and duration) in the spring but not the fall. Young females had relatively shorter migrations and fewer stopping events, while adult males had relatively longer migrations and more stopping events. Age-sex class was expected to be important (Briedis et al. 2019) particularly for PCs with heavy loadings for migration distance and duration-related metrics. Fish (2021) and Moore et al. (2021) found that young woodcock initiate migration earlier than adult woodcock, and Fish (2021) found that adult female woodcock migrate earlier than young males and females and adult males. These potential differences were accounted for in the departure index, but nevertheless, the

limited effects of age-sex class on most PCs suggest that there is enough variability in woodcock migration that influences of age-sex class on individual decision-making form few distinct patterns explaining variation in migration strategy.

There are other aspects of migration strategy that we did not consider in detail in this analysis. We could not include birds that did not migrate in our migration strategy analysis, but foregoing migration is part of the migration ecology of woodcock (McAuley et al. 2020, Graham et al. 2022). In our dataset, apparent non-migrant individuals were uncommon; we observed only 9 woodcock during fall migration (4%) and 10 during spring migration (7%) that were excluded because they appeared resident throughout the period of migration. We do not know whether this behavior is fixed within individuals or if it varies annually, but this is an ongoing question that would be relevant in situations where migration strategy is being considered. In the context of our findings more broadly, our findings suggest that < 10% of woodcock exhibit a non-migrant strategy in any given year. Previous work has also suggested woodcock exhibit leapfrog migration (Sullins et al. 2016), where individuals recruited at more northern latitudes will migrate greater distances and overwinter farther south than individuals recruited at more southern latitudes. While we did not explicitly test for leapfrog migration,

we did not see a strong negative relationship between starting and ending latitude in the fall or vice-versa in the spring (Supplementary Material Tables 3–4). Our observations may have differed from Sullins et al. (2016) due to our inclusion of both adult and young birds in our analysis. While some degree of leapfrog migration may occur in young woodcock that does not persist into adulthood, we do not expect leapfrog migration itself to influence our focal migration metrics. Additionally, we acknowledge that limitations of our tracking devices prevented us from fully characterizing all aspects of woodcock migration behavior, and it is possible migratory characteristics we could not measure might affect migration strategies. Specifically, our GPS tags collected locations at relatively course (≥1 day) intervals, and we could not consider finer-scale movements and behaviors associated with them. As tracking technology improves and devices collect more frequent data, it is possible more subtle aspects of migration strategy may emerge.

We expected to see discrete clustering of migratory strategies, but instead found that variation in strategy occurred along gradients, with considerable overlap in migration strategy among age-sex classes and spatial areas. While such differences do exist in the overall timing of migration (Fish 2021), the wide range in space and time over which woodcock are known to breed and migrate provides a broad space over which variation in migration strategies can occur (McAuley et al. 2020, Moore et al. 2021). Relatively recent northward range expansion may further contribute to the variability of migration strategy in woodcock, given that the species likely underwent rapid range expansion after the glacial retreat during the late Pleistocene (Rhymer et al. 2005). More recently, the species may have expanded northward as availability of their preferred early-successional forest habitat increased following expansive timber harvest in the boreal forest (Keppie et al. 1984, Sauer et al. 2008), widespread agricultural abandonment in the northern United States and southern Canada during the 19th century (Foster et al. 2002), and changes to biotic communities (Galbraith et al. 2014, Nuzzo et al. 2009). Range expansion is facilitated by diversity in dispersal ability, which is governed by physical and behavioral traits (Chuang and Peterson 2016). In addition, woodcock require thawed ground to feed (McAuley et al. 2020), and bird movement patterns often occur in response to food availability (van Wijk et al. 2016). Therefore, in the northern part of the range less predictable timing of freezing and thawing likely introduces variation in movement patterns. In general, species ranges are shifting northward as the climate changes (Hitch and Leberg 2007), so if woodcocks' variable migration strategy is in part due to ongoing northward range expansion, the species should be resilient to future landscape and climate change. Despite the behavioral diversity we see in woodcock and their potential to adapt to future conditions, the species is still declining and should be monitored to help identify other potential drivers of population decline.

Our findings demonstrate a gradient of migration strategies which, coupled with a wide geographic range, may support resiliency in woodcock populations. Species with flexible life history traits should have greater adaptive capacity and greater resilience to change over evolutionary time scales (Nicotra et al. 2015), and this extends to variable migration behaviors within species, which should contribute to increased resilience of migratory populations to anthropogenic change (Gilroy et al. 2016). Additionally, a lack of overall within-species behavioral diversity can make a species more vulnerable; for example, strong migratory connectivity (similar migration routes among many individuals) in shorebirds can exacerbate the effects of habitat degradation due to many individuals using the same stopover sites (Iwamura et al. 2013). Similar ordination techniques as we have used here can be used to aggregate characteristics of migration into strategies for other species and thus predict the extent to which they are expected to respond well to environmental change. The relationship between behavioral diversity and resilience could be critical to understand species' vulnerability to anthropogenic landscape and climate change.

Supplementary material

Supplementary material is available at *Ornithology* online.

Ethics statement

All capture and marking of woodcock were conducted under protocols approved by the University of Maine Institutional Animal Care and Use Committee (Protocols A2017_05_02 and A2020_07_01) and permits issued by the USGS Bird Banding Laboratory or Canadian Bird Banding Office.

Conflict of interest statement

There are no conflicts of interest in this work.

Author contributions

S.J.C. and E.J.B. developed the idea for the study; S.J.C. analyzed the data and wrote the manuscript with substantial input from E.J.B., L.A.B., and S.R.M.; R.L.D., L.A.B., A.C.F., E.J.B., S.R.M., and A.M.R. oversaw project management and data curation, and all authors contributed to data collection and management and have approved of submission of the manuscript.

Data availability

Woodcock movement data are archived on Movebank ("American Woodcock Migration Ecology in Eastern North America"; Study ID 3515664596) and also available from Clements et al. (2024).

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