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The American Woodcock Singing Ground Survey largely conforms to the phenology of male woodcock migration

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Abstract

American woodcock (*Scolopax minor*; woodcock) are monitored, in part, by counts of displaying male woodcock collected via the American Woodcock Singing Ground Survey (SGS), which suggests long-term, range-wide declines in woodcock populations. Data from the SGS have been used extensively to develop conservation plans, direct management actions, and understand causes of decline. To avoid bias, the SGS should be timed to avoid spring migration, and the distribution of survey routes should coincide with woodcock breeding distribution. Our objectives for this research were to evaluate SGS timing with the phenology of male woodcock migration, relate the spatial coverage of the SGS to male woodcock breeding distributions, and explore other sources of variation in woodcock migration timing. We marked 133 male woodcock captured throughout eastern North America with global positioning system (GPS) transmitters during

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2019–2022, and compared the timing of their spring migration with the spatiotemporal stratification of the SGS. Most woodcock (74%) completed migration prior to the onset of the SGS. In the northernmost SGS zone, a greater percentage of males (34%) continued migration during the survey window; however, the influence of this mismatch is offset because SGS routes were run more frequently during the second half of the window. Young woodcock completing their first spring migration took 8.6 days longer to do so, on average, compared to adults, and so were more likely to migrate during the SGS window. We found little evidence that timing of migration varied among years. Existing SGS routes cover the majority of male woodcock post-migratory breeding distribution, with 90% of male woodcock establishing final breeding sites within the spatial coverage of the SGS. Our results confirm the SGS includes some migrating males, with the proportion relative to resident breeding males increasing in more northern survey strata. Our data suggests these errors are unlikely to bias trend estimates at large scales (e.g., within woodcock management regions), but there may be potential for bias at more local scales (e.g., state or provincial population indices).

KEYWORDS

American woodcock, GPS telemetry, hidden Markov movement models, migration, population survey, *Scolopax minor*, stopover

Count-based surveys are often used to efficiently estimate short- and long-term population trends and to express variation in density across large spatial scales (Pollock et al. 2002). In North America continental-scale monitoring of migratory birds is conducted via standardized surveys, which provide among the most expansive wildlife count data in existence (Anderson et al. 2018, Schummer et al. 2018, Sauer et al. 2021). These datasets are instrumental in conducting conservation status assessments (Rosenberg et al. 2016, 2019), developing management strategies (Nichols et al. 2007, Kelley et al. 2008), and understanding the consequences of global change to avian populations (Matthews et al. 2011, Stephens et al. 2016). But the degree to which survey design accommodates the timing of migration can affect data reliability (Finger et al. 2016, Schummer et al. 2018).

Longstanding concerns over range-wide population declines in American woodcock (*Scolopax minor*; woodcock) are based principally on data collected through the American Woodcock Singing Ground Survey (SGS; Sauer and Bortner 1991, Seamans and Rau 2022). Methods to survey woodcock using roadside counts were developed in the mid-twentieth century (Mendall and Aldous 1943, Owen 1977), and a standardized protocol and random sampling scheme formalized in 1968. The SGS is used to monitor woodcock population status at regional and state or provincial scales (Seamans and Rau 2022) and is used in various elements of woodcock management (e.g., woodcock harvest strategies; Rau et al. 2019). The SGS data have also been used to estimate regional abundance, set population and habitat goals (Kelley et al. 2008), and to support modeling efforts directed at woodcock conservation (Thogmartin et al. 2007, Loman et al. 2017, Roy et al. 2019, Saunders et al. 2019).

Male woodcock display throughout the spring migratory period, beginning on the wintering grounds and continuing as they migrate north (Whiting 2010, McAuley et al. 2020). If surveys coincide with periods of migration, counts of males may include migrating birds and not reflect true abundance of the local breeding population. To accommodate this, the timing of SGS is stratified by 5 latitudinal zones with zone-specific survey windows. Some female woodcock nest in southern areas more typically associated with wintering (Whiting et al. 2005, Whiting 2010), which are not included within the spatial coverage of the SGS. Furthermore, the extent of SGS routes at the northern edge of woodcock breeding distribution are constrained by access to roads in the more remote regions of Manitoba, Ontario, and Quebec, Canada (Sauer et al. 2008, Roy et al. 2019). Because some woodcock reproduction occurs both north and south of the SGS coverage area, some have questioned whether the current geographic scope of the survey is adequate (Whiting 2010, Sullins et al. 2016). Various attempts have been made to assess the survey accuracy considering these and other potential issues (Nelson and Andersen 2013, Tavernia et al. 2018, Bergh and Andersen 2019, Moore et al. 2019). Satellite tracking provides a new and potentially useful approach, which Moore et al. (2019) recently used to show a non-trivial number of woodcock continued migration during the SGS survey period. Transmitter mass available at the time of study prevented Moore et al. (2019) from marking a large sample of male woodcock, which are smaller-bodied than females (McAuley et al. 2020). More comprehensive studies based on larger sample sizes of males marked with satellite transmitters are needed (Moore et al. 2019).

Our goal was to classify the timing and spatial distribution of spring migration of male woodcock, and use that information to evaluate SGS design. Specifically, we sought to assess 1) the alignment of SGS timing with the phenology of male woodcock migration in each of the 5 SGS zones, 2) whether the spatial coverage of the SGS was consistent with male woodcock breeding distributions, and 3) assess annual variation in woodcock migration timing. To address these questions, we used data from global positioning system (GPS) transmitters deployed as part of the Eastern Woodcock Migration Research Cooperative, a consortium of dozens of state, federal, non-governmental, and university partners working across eastern North America to better understand woodcock migration at a continental scale (www.woodcockmigration.org).

STUDY AREA

We captured male woodcock at sites located throughout eastern North America (Figure 1) during autumn (September through October) in northern areas associated with breeding (Ontario, Quebec, Nova Scotia, Maine, New York, Vermont, Rhode Island, Pennsylvania, Virginia, and West Virginia) and during winter (December through February) in southern areas (Louisiana, Alabama, Florida, Georgia, South Carolina, North Carolina, Virginia, Maryland, and New Jersey). Forests occupied by woodcock in northern breeding areas were typically deciduous or mixed conifer-deciduous in early stages of succession, and climate in these regions was generally temperate, with annual precipitations (based on 30-year normal 1991–2020; PRISM Climate Group 2023) ranging from 90–150 cm and annual mean temperatures ranging from 3.9–12.2°C. Sites associated with woodcock wintering in the mid-Atlantic and southeastern United States comprised deciduous, mixed conifer-deciduous, or conifer-dominated forests. Climate at winter capture sites ranged from temperate to sub-tropical, with annual mean precipitation ranging from 100–175 cm, and annual mean temperatures ranging from 12.2–26.1°C. Specific patterns in land use and cover varied considerably among capture sites, although in most cases woodcock were associated with some interspersion of forested and open (e.g., agriculture, grassland) land cover types.

Woodcock are managed as 2 distinct populations affiliated with Central and Eastern management regions, approximately bisected by the crest of the Appalachian Mountains (Seaman and Rau 2022). We captured woodcock primarily within the Eastern Management Region; however, several capture sites were also located within the Central Management Region, and once marked with GPS transmitters, woodcock migrated throughout both regions. In total, 41% of the woodcock we marked entered the Central Management Region at some point, and we consider our scope of inference to include the geographic footprint of our marked birds.

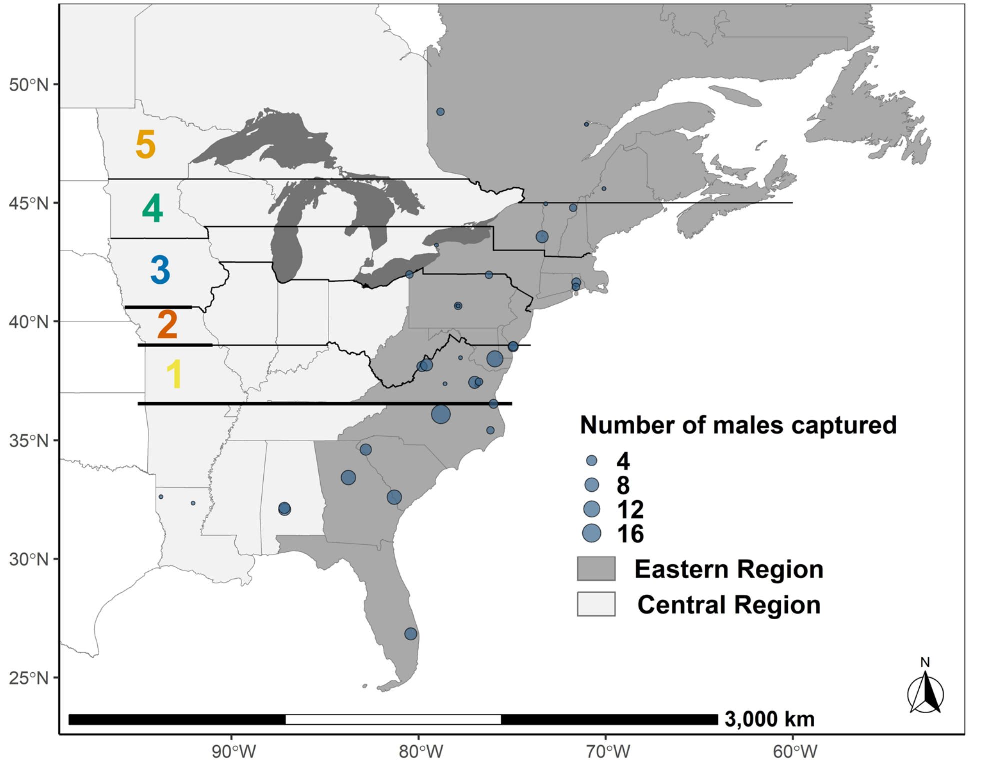

FIGURE 1 Locations where male American woodcock were captured and marked with global positioning system transmitters in eastern North America from 2018–2022. The size of each location symbol indicates male sample size. Latitudinal bands depict zones used to stratify timing of the American Woodcock Singing Ground Survey (SGS). Survey date windows are 10 April–30 April for zone 1, 15 April–5 May for zone 2, 20 April–10 May for zone 3, 25 April–15 May for zone 4, and 1 May–20 May for zone 5. Woodcock are managed in 2 regions: Eastern (dark gray) and Central (light gray).

METHODS

Field methods and GPS tagging

We captured woodcock using either mist nets during crepuscular flights, or by spotlighting in roosting areas at night (Fish 2021). We aged captured woodcock according to feather characteristics (Martin 1964), and we classified multiple age classes (hatch year, after hatch year, after second year, etc.) into 2 categories: young (<1 year of age) or adult (>1 year of age). Young woodcock were males undertaking their first spring migration, whereas adults were completing their second or later spring migration. We determined woodcock sex based on a combination of mass, bill length, and width of the outermost primary feathers (Martin 1964). Each woodcock received a United States Geological Survey aluminum leg band, and a rump-mounted GPS tracking device (GPS tag) equipped with an ARGOS-enable platform terminal transponder (PTT) transmitter (Lotek Pinpoint ARGOS 75p; Lotek, Newmarket, ON, Canada) affixed to the bird using a leg-loop harness (Moore et al. 2019, Fish 2021). For our purposes we used only GPS location data, and the PTT served to transmit GPS locations via the ARGOS satellite network. Transmitters weighed 4 g, and we did not mark birds if the total mass of marking materials (transmitter, harness, and band) would exceed 4% body mass. The GPS tags were programmed to collect GPS locations (±20 m accuracy) at pre-determined intervals that varied according to a number of project goals, not all of which were related to the objectives of this study. The GPS tags deployed on males during spring collected locations every 1–2 days between 15 February and 20 May, which approximately coincided with the period of spring migration. Prior to spring migration, and following a bird's initial migration post-capture, tags collected locations every 5–7 days; more frequent locations outside the primary migratory period were not possible because of constraints associated with transmitter battery life. Consequently, some males marked the previous fall contributed spring migration locations every 5–7 days; these males comprised 25% of the dataset (34 of 133 marked woodcock), and their transmitter batteries generally failed before completion of spring migration (described in greater detail below). Following every third GPS fix, locations were transmitted via a PTT link to the ARGOS satellite network (Woods Hole Group, Woods Hole, MA, USA), which we then transferred to the Movebank (www.movebank.org) online repository for long-term storage. The PTT uplink was disrupted >95% of the time when woodcock died and their transmitters came into contact with the ground (Fish 2021); therefore, we assumed all location data were from live woodcock.

Data management and the hidden Markov model

We used male woodcock locations collected between 5 January and 15 June, during 2019–2022. We subset observations to include only males with ≥3 locations and that made ≥1 movement >16.1 km from their location of capture. We identified this 16.1 km threshold by examining a histogram of log-transformed step distances from our marked birds, which clearly show a bimodal distribution of short- and long-distance movements with a separation between 7.0 and 16.0 km. We further used the criterion of 16.1 km to delineate unique sites used by each woodcock, including their pre-migratory (i.e., wintering) location, stopovers during migration, and their final destination (post-migration). We considered consecutive locations during migration that were <16.1 km apart to belong to unique stopover sites, and we classified time spent at each stopover as the number of days between movements >16.1 km. Because transmitter program schedules and failure to acquire GPS signals produced data gaps of >1 day between locations, we used the midpoint date between successive GPS locations to delineate approximate arrival and departure dates from each stopover, and departure and arrival dates for the initiation and termination of migration, respectively. On average the midpoint between 2 successive locations was 1.27 days ± 1.23 (SE), and 95% of midpoints occurred within 3 days of the next location; thus, we assumed a mean precision of about 1.5 days for delineating the timing of migratory events, and this is also the temporal grain over which we estimated stopover duration.

We fit male woodcock movement paths to a 3-state multivariate hidden Markov model (HMM; McClintock and Michelot 2018), using the momentuHMM package (McClintock and Michelot 2021) in program R (R Core Team 2022). We structured an idealized model of migration, with pre-migration, migration, and post-migration states that were distinguished by 2 data streams: step length and turn angle. We fixed transitions among states such that all woodcock began in the pre-migration state and then could either remain in pre-migration, or transition to the migration state, indicating the onset of migration (i.e., initiation). Once entering the migration state, birds either remained in the migration state or could transition to post-migration, which was a terminal state that could not be left once entered. The transition from migration to post-migration reflected the bird's arrival at its site of final residency (i.e., termination). In addition to fixing the state transitions as described, we also applied a covariate of the ordinal day of year to the state transition terms, which allowed the probability of transitioning into or out of a given state to change as migration progressed. We applied initial parameter values following Fish (2021), fit the model using the fitHMM() function, and assigned probabilistic state classifications (i.e., pre-migration, migration, final breeding residency) to each woodcock location using the viterbi() function.

We visually inspected each woodcock movement path and associated HMM migratory state assignments to ensure conformity and flagged individuals that demonstrated behaviors that were not consistent with typical migration. We removed 3 individuals from the analysis that made transient long-distance movements during pre-migration without also engaging in northward movements that would be consistent with migration; 2 of these birds stopped transmitting data before other birds in the sample had begun migration, whereas a third bird remained resident in southern Florida throughout the breeding season. We also reclassified the post-migration state assignment for 1 woodcock that ended migration in Maine during mid-March, and made a single recursive movement of approximately 53 km away from, and then back to, its final breeding site, which appeared to preclude correct HMM assignment to the post-migratory state. For this male, we reclassified all points following its arrival in Maine as post-migratory. Migratory behaviors of all other males appeared well-captured by our model.

When woodcock died or their transmitters stopped functioning, we inherently received no further data on continued migration. This could result in premature model assignment to the post-migration state despite not actually completing migration. To circumvent this issue, we restricted our assessment of termination dates to only woodcock with GPS tags that continued transmitting beyond the completion of all SGS windows (20 May). Birds that did not transmit beyond 20 May provided information on the timing of initiation and known stopovers but not termination. This also removed most woodcock marked during the fall from assessments of termination (both timing and location) because transmitter batteries for fall-caught woodcock generally failed prior to 20 May. Our sample size included 34 males marked during fall and 99 males marked during winter that contributed to timing of departure and stopover data; 69 males marked during winter and 5 males marked during fall contributed to timing and location of termination.

SGS timing and coverage assessment

The SGS routes are 5.4 km in length and are traveled along secondary roads placed in randomly selected 10-minute degree blocks (Seamans and Rau 2022). Observers drive among 10 listening points and record the number of males heard vocalizing during a 2-minute stop (Sauer and Bortner 1991, Seamans and Rau 2022). Males counted are summed for each survey route, and route-level abundance trends are estimated based on the difference in counts among years (Sauer et al. 2021). The timing of SGS is stratified by 5 latitudinal zones (Figure 1) each assigned a 20-day survey window, which begins in the southernmost zone (zone 1) on 10 April, begins 5 days later in each more northerly zone, and the northernmost survey window (zone 5) begins on 1 May. These survey strata were developed based on inferences from local observations of unmarked woodcock and are meant to avoid periods of migration (Goudy 1960, Duke 1966, Tautin et al. 1983).

To assess the correspondence between SGS windows and the migration state of woodcock, we intersected each GPS location with a shapefile of SGS zones using the sf package (Pebesma and Bivand 2023). We then calculated the number of days from the start date of the SGS window within that zone in comparison to the date of the location. A negative value represented locations occurring prior to the survey start for a given zone, a value between 1 and 20 coincided with the 20-day survey window within that zone, and a value >20 indicated a location following the completion of the survey window within the zone. Within each SGS zone, we summarized the number of male woodcock that recorded stopovers and terminated migration before, during, and after the 20-day SGS window for that zone. We further calculated the proportion of males in each of these categories based on the number of males that stopped over or terminated migration within each zone at any point in time.

To further understand alignment of SGS timing and completion of male woodcock migration, we calculated the proportion of migrations completed within a given SGS zone (*j*) during each day (*i*) of the 20-day survey window, as

$$Complete_{ij} = Early_j + Late_j \times (1 - Active_{ji}),$$

where *Early* provided the proportion of birds that stopped over in the SGS zone prior to the start of the survey, *Late* was the proportion that stopped over at some point during the SGS window (i.e., 1 − *Early*), and *Active* was the proportion of males still migrating in the zone on day *i*. On the first date of the SGS window *Active* = *Late* by definition, and *Active* declined progressively throughout the survey as additional males completed migrating within the zone (i.e., settled within the zone or migrated out of it). A value of *Complete* = 1.0 indicated that on day *i* all woodcock using zone *j* at any time had completed their migration within that zone.

We further considered that when SGS routes are run in practice would affect the degree to which migrating males were available to be counted. For example, if 20% of male woodcock were still migrating on day 1 of the SGS window, and all surveys were conducted on day 1, then as many as 20% of woodcock counted during surveys could be woodcock that are not part of the local breeding population. But if surveys were spread throughout the 20-day window, the number of birds actively migrating and available to be counted would be <20% because some would complete migration prior to when some surveys were run. We summarized the timing of the SGS using the most recent 5 years of survey data (2018–2022) and evaluated how realized survey timing related to migration phenology. For each zone, we calculated the proportion of surveys completed during each day of the survey window ($Surv_j$). On any given survey date, the proportion of migrating woodcock available to be counted and included in the SGS ($Available_{ij}$) is a product of the proportion of surveys conducted on that date and the proportion of woodcock still migrating:

$$Available_{ij} = Surv_{ij} \times (1 - Complete_{ij}).$$

When summed across the 20-day window, $\Sigma(Available)$ gives the cumulative proportion of birds available to be counted while they are still migrating, when considering the combined variability in migration phenology and SGS timing.

We further evaluated the extent to which the SGS captured the final breeding distribution of our GPS-marked birds. We used a GIS shapefile (Moore et al. 2019) that placed a 50-km buffer around 10-degree blocks containing SGS routes. This layer described the broad-scale distribution of the SGS (i.e., SGS coverage), rather than the precise geographic location of individual survey routes, but allowed us to make an assessment comparable to Moore et al. (2019). We intersected male termination points with this data layer, and tabulated the number of GPS-marked males that ended their migrations either within the SGS coverage or outside of it. For woodcock settling in Ontario and Quebec, we further evaluated the distance between woodcock settling locations and the northern edge of the 50-km buffer, which allowed us to assess whether spatial coverage of the SGS was adequate at the northern edge of the survey range (Sauer et al. 2008). Finally, for comparison with previous research, we compared termination points to 2 northern boundaries evaluated in Sullins et al. (2016), which included a northern cutoff occurring at approximately 47.5°N latitude, and the southern boundary of the Boreal Softwood Shield Bird Conservation Region, which Sauer et al. (2008) concluded was insufficiently covered by the SGS.

Sources of variation in male spring migration

We evaluated the duration of stopover (in days) and mean distance of stopovers from termination points for males that recorded stopovers during SGS windows. These 2 metrics provide ecological context for why some male woodcock exhibit late migration. For example, a relatively short distance between stopovers occurring during the SGS and termination points may suggest persistent environmental conditions (e.g., late spring snowpack) prevent males from establishing final breeding territories before the onset of the survey. Similarly, prolonged stopover duration towards the end of migration could suggest that males move among multiple final breeding sites (i.e., are transient). To assess this possibility, we visually compared the distribution of stopover duration (in days) recorded during SGS windows with that of all stopovers in the dataset. If timing was comparable among the full set of stopovers and the subset of stopovers during SGS windows, it would suggest stopovers during SGS windows were consistent with general stopover behavior. In contrast, timing that differed appreciably would suggest behavior consistent with an alternative hypothesis (e.g., breeding transience).

Finally, we sought to understand sources of variation in the timing of male spring migration. We first assessed the general distribution of migratory initiation, stopover, and termination points among our 4 study years. Second, we explored potential sources of variation in the timing of termination among males. We used linear models with the ordinal date of termination as a response variable, and assessed the importance of the following predictor variables: age, year (as a 4-level factor), starting latitude, starting longitude, ending latitude, ending longitude. We assumed *a priori* that age and year may affect the timing of migration independently from the starting (initiation) and ending (termination) points of migration, and we included age and year in all models. We ran 2 models with the form *date ~ age + year + latitude + longitude*, where *latitude* and *longitude* represented either initiation or termination locations, depending on the model. We interpreted β coefficients and their 95% confidence intervals for evidence of variable support and adjusted R^2 values as a measure of variable importance.

RESULTS

We collected migration data from 133 GPS-marked male woodcock, of which 19 were marked in wintering areas of the Central Management Region, while the remainder ($n = 112$) were marked in the Eastern Management Region. We marked 34 male woodcock during fall in northern areas and 99 woodcock on wintering areas prior to spring migration. These woodcock provided 5,287 locations during the spring migratory period. Seventy-three birds were young woodcock, 59 were adults, and 1 woodcock was of unknown age. We tracked 74 males past 20 May, providing comprehensive migration paths for 44 young and 30 adults. Most of these 74 males were marked during winter ($n = 69$), while 5 males were fall-captured.

Fifty one percent of males ($n = 38$) completed their migrations in SGS zone 5 (the northernmost zone), 23% completed migration in zone 4 ($n = 17$), 12.5% in zone 3 ($n = 9$), 9% in zone 2 ($n = 7$), and <3% ($n = 2$) in zone 1 (Figure 1). Most males terminated migration within the spatial coverage of the SGS (Figure 2); 91% ($n = 67$) of the 74

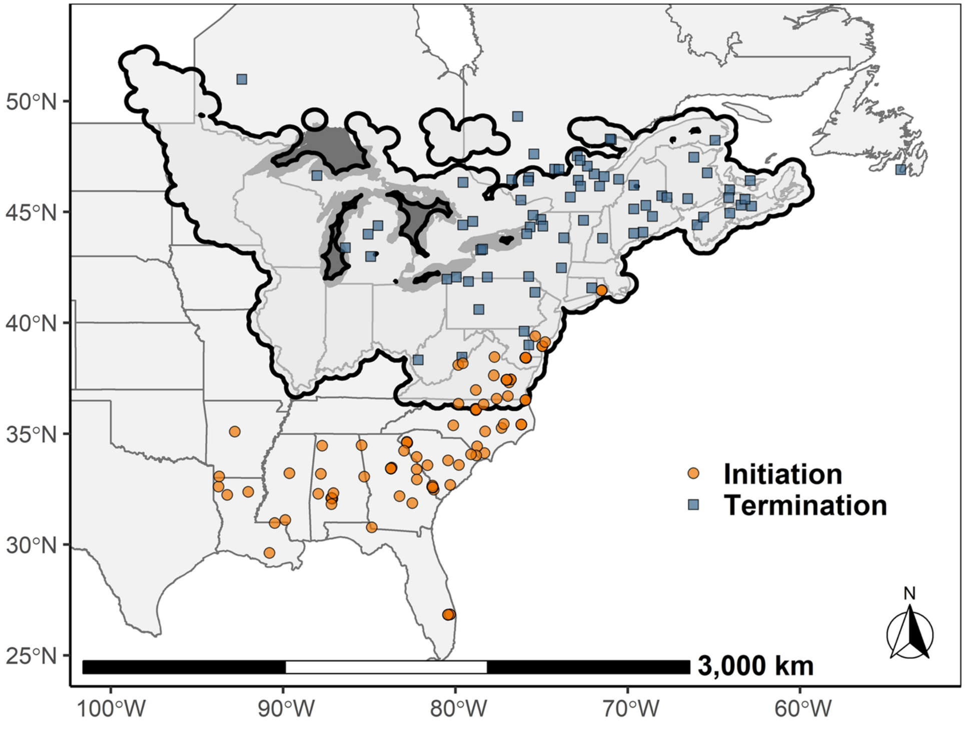

FIGURE 2 Starting (initiation) and ending (termination) points of migration tracks for global positioning system-marked male American woodcock during spring migration, 2019–2022, compared to the approximate spatial coverage of the American Woodcock Singing Ground Survey (SGS). We determined SGS spatial coverage from Moore et al. (2019) using 50-km buffers placed around 10-degree blocks containing SGS routes.

males with transmitters that functioned past 20 May settled within the SGS coverage area, including 62 of 69 males marked during winter (90%). Seven males migrated north of SGS coverage: 1 male migrated to Newfoundland, 5 males migrated to northern Quebec, and 1 male migrated to northwestern Ontario. Four additional males that settled in Ontario and Quebec did so <50 km from the northern edge of the SGS coverage layer (mean distance = 31.2 km). Five male woodcock migrated to termination points north of the SGS boundaries used by Sullins et al. (2016): 1 in Ontario, 3 in Quebec, and 1 in Newfoundland. An additional male, which we did not include in the analysis, remained in southern Florida throughout the period of spring migration; this was the only male that remained exclusively south of SGS coverage throughout the breeding season.

The degree to which woodcock migration overlapped with SGS timing varied depending on survey zone (Figure 3). Nearly all migration in the southernmost zone (zone 1; Figure 1) was completed before the SGS window; of the 66 males that recorded stopover locations in SGS zone 1, 3 (~4.5%) were present during the zone 1 SGS window. The proportion of birds that continued migrating during a survey window increased in more northern zones, with 7 birds (9% of 80 males) in zone 2, 6 birds (10% of 60 males) in zone 3, 9 birds (18% of 50 males) in zone 4, and 14 birds (36% of 39 males) in zone 5.

For zones 1 through 4, >80% of stopovers were completed before the start of the SGS; migration generally reached >90% completion by day 10 and reached 100% completion before the end of the window (Figure 4A). For zone 5 the degree that migration overlapped the SGS window was more extensive, with 64% of stopovers completed prior to the start of the survey, >85% completed by day 10, and about 3% of stopovers occurring after completion of the survey (Figure 4A). Between 2018 and 2022 (n = 3,698), SGS routes were generally surveyed more frequently during the second half of the 20-day window (Figure 4B). In zone 5 specifically, 34% of surveys were completed during the first 10 days of the window, while 66% of surveys were completed after day 10, and 35% after day 15. As a result, the proportion of woodcock still migrating but available to be counted during the SGS was lower than expected based strictly on migration timing because migration occurred more frequently during the first half of the window, but surveys were more frequently conducted later in the window. We estimate the proportions of males that are still migrating through each zone and are available to be counted during the SGS (incorrectly identified as settled into final breeding territories) based on the combination of migration timing and survey timing, were 0.003 in zone 1, 0.008 in zone 2, 0.036 in zone 3, 0.080 in zone 4, and 0.119 in zone 5.

Eighteen male woodcock with transmitters that functioned past 20 May recorded stopover locations during SGS windows, and these stopovers were an average of 253 km from the eventual termination point (range = 2.1–1,120 km; Figure 5). Half of all stopovers occurring during survey windows were <174 km from the final termination point, and 75% of stopovers were <230 km from termination (Figure 5A). Of stopovers made by males during survey windows (n = 70), 55% lasted only a single day, while 80% of stopovers lasted <10 days. One exception was a male that spent a month in southern Michigan, including more than half of the SGS window, before continuing migration northwest with stopovers during survey windows in Wisconsin, Minnesota, and Ontario, eventually moving into Manitoba. In general, stopover duration during SGS windows was similar to that of all male woodcock during spring migration (Figure 5B).

Across 4 years the phenology of migration was relatively consistent, particularly for initiation and stopovers (Figure 6). One potential exception was that our sample of male woodcock terminated migration earlier, on average, during 2021 (Figure 6C), although the range of dates was relatively equal among years. In a linear model that also included ending latitude, we did not find support for a statistical difference in mean termination date among years as evidenced by similar β coefficients with widely overlapping confidence intervals (Table 1). Among spatial predictors of termination timing, only ending latitude had a statistically supported effect, indicating males terminated migration 5.7 days later, on average, for every 1 degree of latitude farther north they traveled (Table 1; Figure 6B). Male age was also a significant predictor of termination timing, with young woodcock ending migration 8.6 days later, on average, than adults (Table 1). Together male age and ending latitude explained approximately 46% of the variance in the timing of the end of male migration (adjusted R^2 = 0.456). We found no evidence for effects of male age, year, or starting latitude or longitude on the timing of migration initiation (Table 1).

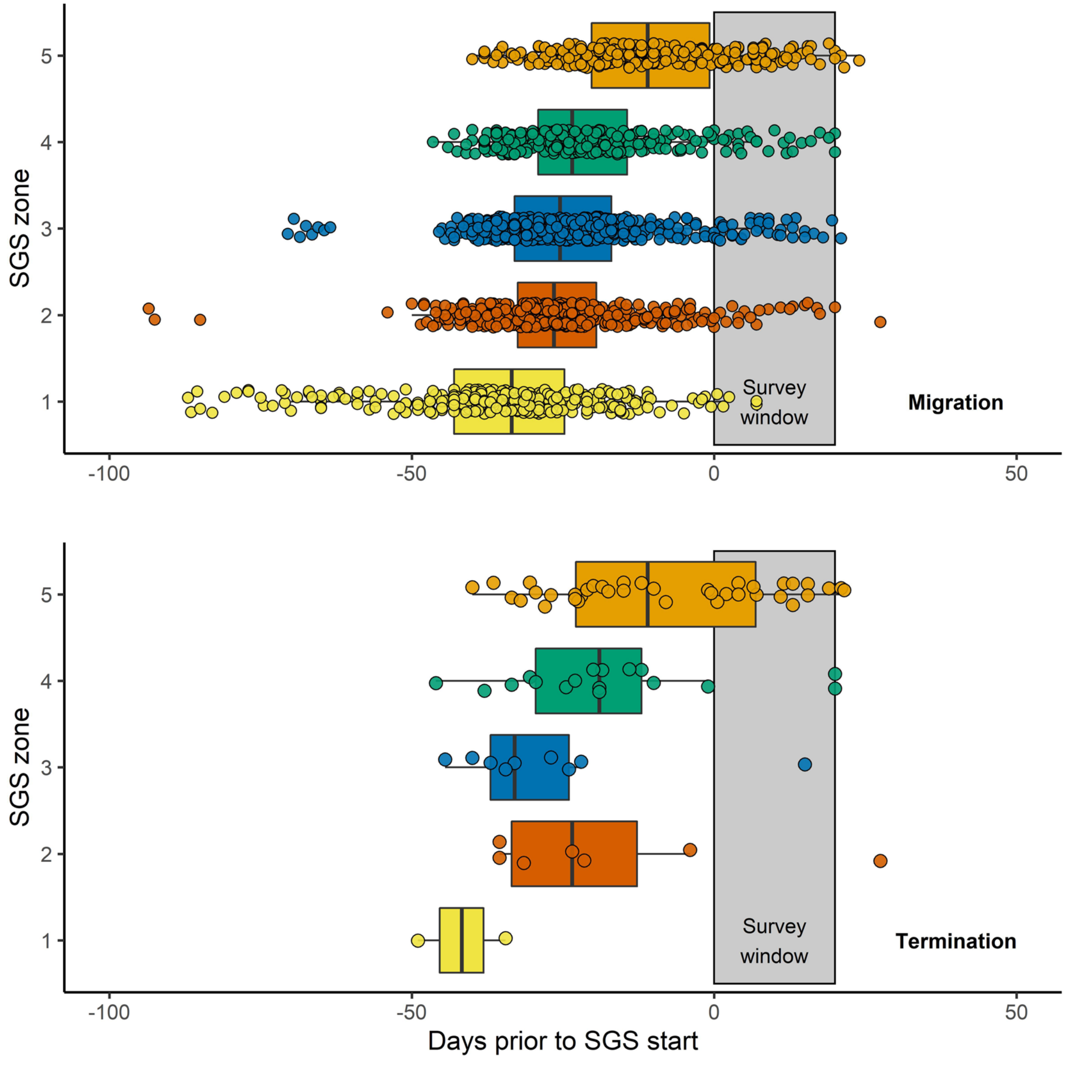

FIGURE 3 Distribution of migratory stopover and termination locations for global positioning system-marked male American woodcock in eastern North America with respect to timing of the American Woodcock Singing Ground Survey (SGS), 2019–2022. Boxes depict median (middle line) and 50th percentiles (box), while whiskers are 1.5 times the interquartile range. Points represent individual woodcock locations (i.e., the data depicted by the box and whisker plots) and have been jittered to avoid overlap. Points extending beyond whiskers are outliers. Data are stratified by SGS zones, and location dates have been standardized to the start of the survey window (period surveys are conducted; gray box), where day 0 reflects the starting date of the survey for each zone. Stopovers falling within the SGS window indicate migrant males that have not yet settled into a final breeding site but may be available for detection during the survey. Termination indicates the first date a male woodcock arrived at a permanent, post-migration territory.

DISCUSSION

Our results demonstrate that about 75% of woodcock in our sample completed migration prior to an SGS survey window and were not available to be counted during the SGS while still migrating. This is particularly the case in zones 1–4, where 80–90% of migration was completed prior to the SGS window. In the northernmost zone, 35% of

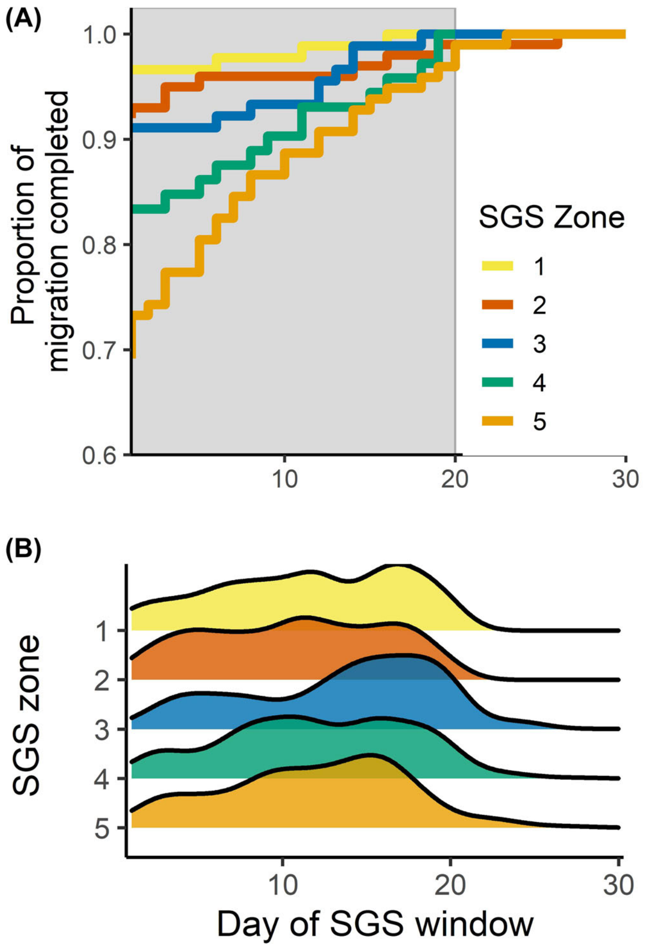

FIGURE 4 Progression of migration by male American woodcock marked with global positioning system transmitters in eastern North America during 2019–2022 (A) by American Woodcock Singing Ground Survey (SGS) zone, as a function of the survey window day within each zone. A value of 1.0 indicates that all migration by all woodcock was completed by that date of the survey. The *y*-intercept for each line indicates the proportion of marked woodcock that migrated through each zone before the start of the survey. Panel B provides the distribution of dates surveys were conducted in each zone, based on 3,698 surveys conducted between 2018 and 2022.

males that migrated in zone 5 at any time continued migration during a portion of SGS window; however, when considering the timing of surveys conducted during our study period, <12% of migrating woodcock in zone 5 were functionally available to be encountered during the SGS because most surveys were conducted during the latter half of the window while most migration occurred during the first half of the window. So, while some male woodcock migrate during active SGS windows, particularly in more northern survey zones, ≥90% of males counted during the SGS have likely established final breeding territories.

Double counting has been raised as a concern with SGS data (Moore et al. 2019) and could occur if migrating males are counted along one survey route and then the same male is counted again during a different survey farther along its migration. We suggest double counting is unlikely. Assuming a mean effective listening radius of 309 m (Bergh and Andersen 2019), each SGS stop has an effective area of about 30 ha. The roughly 15,000 survey stops in the entire SGS therefore have an approximate footprint of 4,500 km^2, while the full breeding distribution of woodcock spans >2,500,000 km^2. Although woodcock are clearly not present everywhere within this distribution,

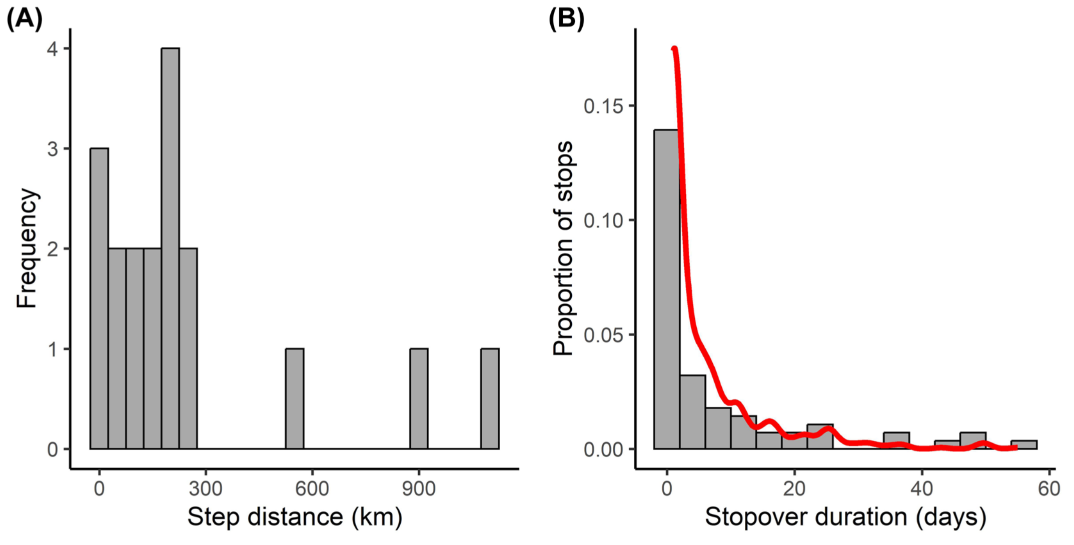

FIGURE 5 Distribution of A) the mean migratory step distance (km) between all the termination of migration and all stopover locations during American Woodcock Singing Ground Survey (SGS) windows recorded by male American woodcock marked with global positioning system transmitters in eastern North America during 2019–2022 and B) the length of stopovers (days) that overlapped with an SGS window in any survey zone (n = 70 unique stopovers). Histograms reflect data only for males with transmitters that functioned past 20 May, and that recorded stopovers during an active SGS window (n = 18 males). The solid line in panel B indicates the distribution of stopover duration for all marked male woodcock during spring migration (n = 609 unique stopovers) in eastern North America in 2019–2022.

the footprint of the SGS is nevertheless very small (<1%) in comparison to the broad span of areas where woodcock occur. Furthermore, each route is surveyed only once, and the probability of detecting a male woodcock during a single visit survey is <1.0 (Bergh and Andersen 2019). The probability a migrating woodcock is counted once, continues migration, settles along another SGS route, and is observed during the second route's survey, is clearly very small.

Of greater concern is the possibility that woodcock population indices derived from SGS data have spatial biases resulting from mischaracterization of migrating males as birds that have established their final breeding territories. For example, if migrating woodcock are counted more frequently in southern regions, SGS data would underestimate population indices farther north, potentially discounting the relative importance of northern areas. This bias could be compounded if a significant number of males settle outside SGS coverage. Males that migrated north of SGS coverage or were near the northern edge of the survey range, were primarily located in Ontario and Quebec. While SGS coverage appeared adequate to capture male breeding distribution at a continental scale, sub-regional population indices in Quebec and Ontario may fail to capture a non-trivial percent of males breeding in relatively inaccessible areas farther north. Woodcock stopovers that occurred during SGS windows averaged 250 km from the male's eventual destination, suggesting potential for non-trivial spatial bias in SGS counts. This would likely have the greatest consequence for sub-regional indices (e.g., state, provincial levels), and may be problematic in regions that are used disproportionally for stopovers, such as states along the Atlantic Coast.

Sullins et al. (2016) used feather stable isotopes to infer that between 14% and 43% of juvenile woodcock harvested by hunters during fall had natal origins north of SGS. This range was established using approximated boundaries for the northern limit of the SGS based on a latitudinal cutoff (14%) and the southern boundary of the Boreal Softwood Shield Bird Conservation Region (43%). Using a delineation based on known locations of SGS routes, we found that only 10% of males marked on the wintering grounds settled north of the current distribution

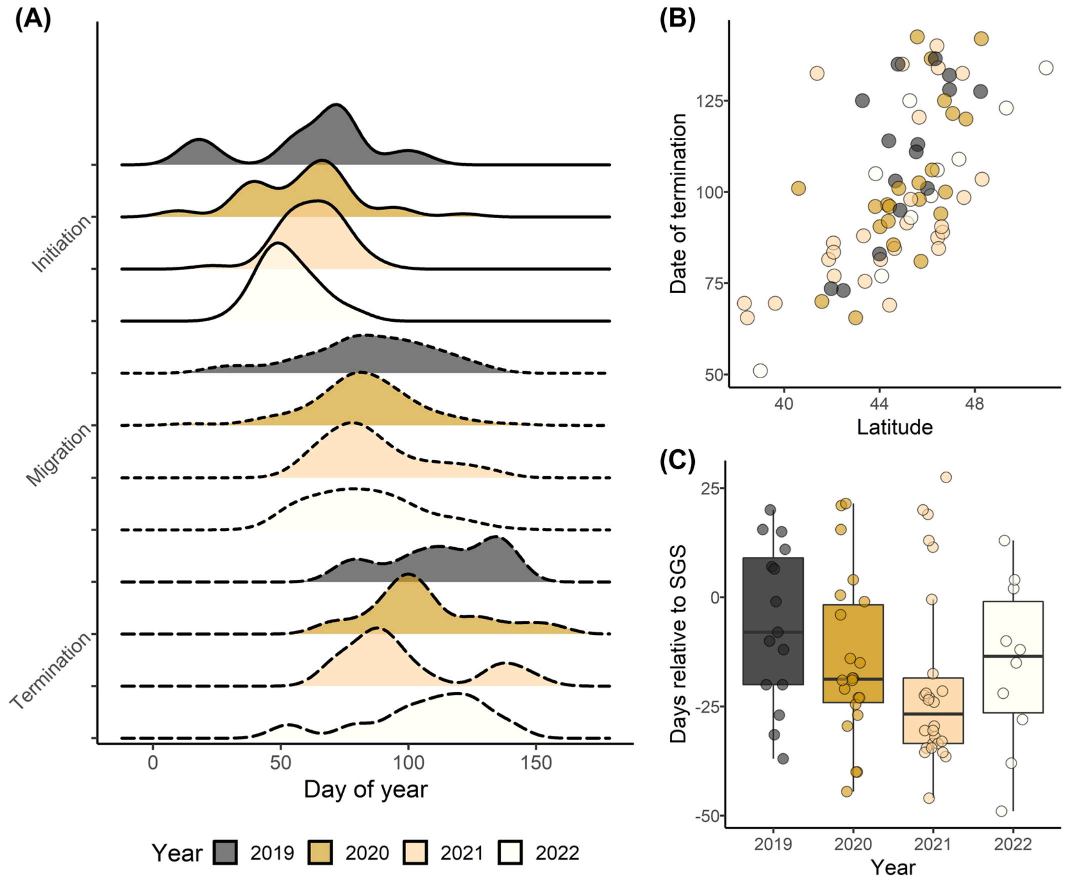

FIGURE 6 Phenology of male American woodcock spring migration in eastern North America during 2019–2022. A) Density plots showing general patterns in timing of initiation, migration, and termination dates among years, B) date of termination for males with complete migration paths based on ending latitude, and C) distribution of termination dates relative to the start of the American Woodcock Singing Ground Survey (SGS) zone in which males established residency (day 0 = SGS start date).

of SGS routes, and only 7% settled north of either boundary used by Sullins et al. (2016). Discrepancies between our findings and those of Sullins et al. (2016) could exist if male breeding distribution does not correlate with female reproductive success (i.e., if females breeding in more northern areas with lower densities of males are more likely to raise broods). Alternatively, differences could result from methodological discrepancies between the natal and breeding origin assignment based on feather stable isotopes, compared with satellite telemetry. We suggest that further work is needed to understand potential discrepancies between population indices derived from the SGS and woodcock recruitment patterns.

Only 1 male of 99 marked in wintering areas did not migrate north, suggesting that female woodcock nesting in southern areas not surveyed by the SGS (Whiting 2010) are not dependent on local resident males to fertilize eggs. Instead, these females likely mate with males prior to their departure for northward migration. This could explain why woodcock are often observed nesting in southern areas far earlier (e.g., January; Whiting et al. 2005) relative to northern nesting (March and April; McAuley et al. 2020), and corroborates results in Sullins et al. (2016) indicating greater southern recruitment (9% of hunter-shot juveniles) than would be expected based on our male migration data (1% of males remain in southern areas). Suggestions to expand the SGS to more southern areas (Whiting 2010)

TABLE 1 Parameter coefficients (β) and 95% confidence intervals (CI) from a linear model predicting variation in the timing (i.e., day of year) of migration by male American woodcock marked with global positioning system transmitters in eastern North America, 2019 through 2022. The termination model predicted termination date based on ending latitude and longitude, whereas the initiation model was based on beginning latitude and longitude.

	Termination		Initiation	
Model term[a]	β	95% CI	β	95% CI
Intercept	−122.23	−223.93–−20.54	87.17	−156.10–330.44
Age (young)	8.64	0.39–16.89	7.32	−3.84–18.49
Year (2020)	−8.00	−19.37–3.37	−7.04	−22.68–8.61
Year (2021)	−8.50	−19.58–2.57	−14.49	−29.95–0.97
Year (2022)	−12.02	−25.77–1.73	−10.23	−30.87–10.41
Latitude	5.71	4.03–7.38	−0.21	−2.14–1.71
Longitude	0.41	−0.25–1.08	0.04	−3.04–3.13
Adjusted R^2	0.456		0.01	

[a]Year 2019 lacks a coefficient term because these predictions are defined by the model intercept.

are unlikely to provide further insights into this phenomenon, as male woodcock only rarely remain south of SGS coverage throughout the breeding season. Alternative methods that do not depend on counts of male woodcock may be necessary to better understand the importance of southern nesting to woodcock populations.

The SGS data are used to estimate annual and long-term trends and evaluate woodcock populations status, within the 2 woodcock management regions and for individual states and provinces (Seamans and Rau 2022). Given a proportion of males counted during the SGS are migrating, significant annual variation in migration phenology could produce variability in short-term trends not necessarily associated with changing abundance. Within our 4-year dataset, there was no evidence of considerable deviations in the timing of each stage of migration among years. While there was an earlier mean termination apparent in our sample during 2021, this appeared to be an issue of sampling variance resulting from greater representation by more southerly breeding males during that year. Our distribution of sampling sites did not differ fundamentally in 2021, so we presume this occurred largely by chance.

On a longer timescale, shifting phenology could possibly introduce bias in long-term trend estimates. Climate-driven changes are regularly demonstrated for other species (Murphy-Klassen et al. 2005, Jonzén et al. 2006), and may be particularly pronounced for short-distance migrants (Butler 2003). Given that most male woodcock migrating during SGS windows also settled during the open window, it seems unlikely this would lead to fewer males counted overall, but rather males would be counted in different places, and a greater proportion would be counted during the correct stage of the life cycle. Future shifts in avian migration phenology coincident with global change is almost certain (Somveille et al. 2020), but the consequences to inference from SGS data remain unclear. Furthermore, if phenology has shifted since the inception of the survey, this could have implications for historical trends. Additional work using simulations and GPS-tracking data could provide insights in these areas.

We focused capture efforts principally (but not exclusively) in the Eastern Woodcock Management Region, and while our dataset spanned 70% of the species' longitudinal distribution, we acknowledge the migration and final breeding distributions of our marked birds skewed towards the eastern portion of the species' range as a result. If migration phenology of more westerly breeding male woodcock differed markedly from those in the east, it could have additional implications for SGS timing and coverage. Within our dataset, there was little evidence that wintering or final breeding longitude affected the timing of initiation or completion of migration, suggesting that timing is similar across the species' range; however, it is likely that a greater proportion of Central

Management Region woodcock end migration at more northern latitudes, particularly in northern Minnesota and western Ontario. This could result in later mean termination dates for the central region, and a greater potential for overlap between migration and the SGS window, especially in zone 5. Consistent with this prediction, Moore et al. (2019), who marked birds principally in the Central Management Region, reported the mean termination date for woodcock was 5 days later (18 April) than woodcock tracked during our study (13 April). Moore et al. (2019) also reported a greater proportion of marked woodcock ending migration outside SGS coverage (30% vs. 10%), and a greater total proportion of woodcock that continued migration during an SGS window (35% vs. 26%). One substantial difference between our study and this previous work is that we used data exclusively from male woodcock, whereas Moore et al. (2019) evaluated spring migration timing for males and females. Although the authors reported no difference in mean timing between sexes, Fish (2021) reported that males began spring migration roughly 6 days earlier than females. Additional data from GPS-marked males migrating in the Central Management Region would be useful to better understand the role of sex and longitude in shaping the range-wide phenology of woodcock spring migration.

In addition to latitude, age was an important predictor of when male woodcock completed migration. Young birds continued migration 9 days later, on average, than adults. This finding may have implications for the SGS if young males are more likely to be encountered while migrating during the survey. Among all male woodcock we followed to the end of migration, the age ratio was 1.43 young:adult, but for the sample of males that completed migration during or after an SGS window, the ratio increased to 2.17 young:adult. While we assume most male woodcock actively display throughout the period of migration, data are lacking on the frequency of display during stopovers, or whether this could vary between age classes. If young migrating birds are disproportionally counted during the SGS, it raises the possibility that annual variability or long-term trends in recruitment could change the degree to which migration influences SGS data.

RESEARCH IMPLICATIONS

The SGS has been used to monitor woodcock populations for more than a half century, and our research addressed long-standing questions about alignment between survey design and the phenology of woodcock migration. Our findings are relevant to practitioners of the survey and those who rely on SGS data for woodcock management. Mismatch between the SGS window and male woodcock migration was greatest in SGS zone 5, but the number of migrating woodcock available to be counted was reduced because SGS routes were typically run later in the 20-day window. Any broad changes to the survey design, such as delaying the survey window in zone 5, could have implications for long-term trend estimation and inference from the ≥50 year time series. We recommend that additional research should explore how overlap between migration and survey timing affects inferences from SGS data. Simulations that use our results should evaluate how survey overlap with migration affects trend estimation and indices at state and provincial and regional scales, how past and future phenological shifts associated with climate change may influence long-term trend estimation, and to test whether altering the survey structure produces a meaningful reduction in biases. We further recommend additional GPS marking of male woodcock in the Central Management Region to complement our data and provide a comprehensive, range-wide assessment of woodcock migration phenology.

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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 (protocols A2017_05_02 and A2020_07_01).

DATA AVAILABILITY STATEMENT

All data and R code required to conduct the analysis in this manuscript are archived at Blomberg, E., 2023. The American Woodcock Singing Ground Survey largely conforms to the phenology of male woodcock migration (1.0) [Data set]. Zenodo. https://doi.org/10.5281/zenodo.8187414.

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REFERENCES

Anderson, M. G., R. T. Alisauskas, B. D. J. Batt, R. J. Blohm, K. F. Higgins, M. C. Perry, J. K. Ringelman, J. S. Sedinger, J. R. Serie, D. E. Sharp, D. L. Trauger, and C. K. Williams. 2018. The migratory bird treaty and a century of waterfowl conservation. Journal of Wildlife Management 82:247–259.

Bergh, S. M., and D. E. Andersen. 2019. Detection probability and occupancy of American woodcock during singing-ground surveys. Proceedings of the Eleventh American Woodcock Symposium. University of Minnesota Libraries Publishing, Minneapolis, USA.

Butler, C. J. 2003. The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. Ibis 145:484–495.

Duke, G. E. 1966. Reliability of censuses of singing male woodcocks. Journal of Wildlife Management 30:697.

Finger, T. A., A. D. Afton, M. L. Schummer, S. A. Petrie, S. S. Badzinski, M. A. Johnson, M. L. Szymanski, K. J. Jacobs, G. H. Olsen, and M. A. Mitchell. 2016. Environmental factors influence lesser scaup migration chronology and population monitoring. Journal of Wildlife Management 80:1437–1449.

Fish, A. 2021. American woodcock (*Scolopax minor*) migration ecology in eastern North America. Dissertation, University of Maine, Orono, USA.

Goudy, W. H. 1960. Factors affecting woodcock spring population indexes in southern Michigan. Thesis, Michigan State University, East Lansing, USA.

Jonzén, N., A. Lindén, T. Ergon, E. Knudsen, J. O. Vik, D. Rubolini, D. Piacentini, C. Brinch, F. Spina, L. Karlsson, et al. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. Science 312:1959–1961.

Kelley, J., S. Williamson, and T. R. Cooper. 2008. American woodcock conservation plan: a summary of recommendations for woodcock conservation in North America. Wildlife Management Institute, Washington, D.C., USA.

Loman, Z. G., E. J. Blomberg, W. V. Deluca, D. J. Harrison, C. S. Loftin, and P. B. Wood. 2017. Landscape capability predicts upland game bird abundance and occurrence. Journal of Wildlife Management 81:1110–1116.

Martin, F. W. 1964. Woodcock age and sex determination from wings. Journal of Wildlife Management 28: 287–293.

Matthews, S. N., L. R. Iverson, A. M. Prasad, and M. P. Peters. 2011. Changes in potential habitat of 147 North American breeding bird species in response to redistribution of trees and climate following predicted climate change. Ecography 34:933–945.

McAuley, D. G., D. M. Keppie, and R. M. Whiting Jr. 2020. American woodcock (*Scolopax minor*). Version 1.0. *in* A. F. Poole, editor. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA.

McClintock, B. T., and T. Michelot. 2018. momentuHMM: R package for generalized hidden Markov models of animal movement. Methods in Ecology and Evolution 9:1518–1530.

McClintock, B., and T. Michelot. 2021. momentuHMM: maximum likelihood analysis of animal movement behavior using multivariate hidden Markov models. Version 1.5.4. https://CRAN.R-project.org/package=momentuHMM

Mendall, H. L., and C. M. Aldous. 1943. The ecology and management of the American woodcock. Maine Cooperative Wildlife Research Unit., Orono, USA.

Moore, J. D., T. R. Cooper, R. Rau, D. E. Andersen, J. P. Duguay, C. A. Stewart, and D. G. Krementz. 2019. Assessment of the American woodcock singing-ground survey zone timing and coverage. Proceedings of the Eleventh American Woodcock Symposium. University of Minnesota Libraries Publishing, Minneapolis, USA.

Murphy-Klassen, H. M., T. J. Underwood, S. G. Sealy, and A. A. Czrnyj. 2005. Long-term trends in spring arrival dates of migrant birds at Delta Marsh, Manitoba, in relation to climate change. Auk 122:1130–1148.

Nelson, M. R., and D. E. Andersen. 2013. Do singing-ground surveys reflect American woodcock abundance in the western Great Lakes region? Wildlife Society Bulletin 37:585–595.

Nichols, J. D., M. C. Runge, F. A. Johnson, and B. K. Williams. 2007. Adaptive harvest management of North American waterfowl populations: a brief history and future prospects. Journal of Ornithology 148:343–349.

Owen, R. B., Jr., chairman. 1977. American woodcock. Pages 149–186 *in* G. C. Sanderson, editor. Management of migratory shore and upland game birds in North America. University of Nebraska Press, Lincoln, USA.

Pebesma, E., and R. Bivand. 2023. Spatial data science: with applications in R. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Pollock, K. H., J. D. Nichols, T. R. Simons, G. L. Farnsworth, L. L. Bailey, and J. R. Sauer. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. Environmetrics 13:105–119.

R Core Team. 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rau, R. D., T. R. Cooper, and M. R. Nelson. 2019. American woodcock singing-ground survey: the logistical challenges associated with route consistency through time. Proceedings of the Eleventh American Woodcock Symposium. University of Minnesota Libraries Publishing, Minneapolis, USA.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra. 2019. Decline of the North American avifauna. Science 366:120–124.

Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Ford, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, G. S. Butcher, et al. 2016. Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States. Partners in Flight Science Committee.

Roy, C., M. Gendrom, S. W. Meyer, J. B. Pollard, J. Rodrigue, and J. R. Zimmerling. 2019. Retrospective analysis of American woodcock population and harvest trends in Canada. Proceedings of the Eleventh American Woodcock Symposium. University of Minnesota Libraries Publishing, Minneapolis, USA.

Roy, C., N. L. Michel, C. M. Handel, S. Van Wilgenburg, C. Burkhalter, K. A. B. Gurney, D. Messmer, K Prince, C. S. Rushing, J. E. Saracco, et al. 2019. Monitoring boreal avian populations: how can we estimate trends and trajectories from noisy data? Avian Conservation and Ecology 14:8.

Sauer, J. R., and J. B. Bortner. 1991. Population trends from the American woodcock singing-ground survey, 1970-88. Journal of Wildlife Management 55:300.

Sauer, J. R., W. A. Link, W. L. Kendall, J. R. Kelley, and D. K. Niven. 2008. A hierarchical model for estimating change in American woodcock populations. Journal of Wildlife Management 72:204–214.

Sauer, J. R., W. A. Link, M. E. Seamans, and R. D. Rau. 2021. American woodcock singing-ground survey: comparison of four models for trend in population size. Journal of Fish and Wildlife Management 12:83–97.

Saunders, S. P., M. T. Farr, A. D. Wright, C. A. Bahlai, J. W. Ribeiro, S. Rossman, A. L. Sussman, T. W. Arnold, and E. F. Zipkin. 2019. Disentangling data discrepancies with integrated population models. Ecology 100:e02714.

Schummer, M. L., A. D. Afton, S. S. Badzinski, S. A. Petrie, G. H. Olsen, and M. A. Mitchell. 2018. Evaluating the waterfowl breeding population and habitat survey for scaup. Journal of Wildlife Management 82:1252–1262.

Seamans, M. E., and R. D. Rau. 2022. American woodcock population status, 2022. U.S. Fish and Wildlife Service, Laurel, Maryland, USA.

Somveille, M., M. Wikelski, R. M. Beyer, A. S. L. Rodrigues, A. Manica, and W. Jetz. 2020. Simulation-based reconstruction of global bird migration over the past 50,000 years. Nature Communications 11:article 801. https://doi.org/10.1038/s41467-020-14589-2

Stephens, P. A., L. R. Mason, R. E. Green, R. D. Gregory, J. R. Sauer, J. Alison, A. Aunins, L. Brotons, S. H. M. Butchart, T. Campedelli, et al. 2016. Consistent response of bird populations to climate change on two continents. Science 352: 84–87.

Sullins, D. S., W. C. Conway, D. A. Haukos, K. A. Hobson, L. I. Wassenaar, C. E. Comer, and I.-K. Hung. 2016. American woodcock migratory connectivity as indicated by hydrogen isotopes. Journal of Wildlife Management 80:510–526.

Tautin, J., P. H. Geissler, R. E. Munro, and R. S. Pospahala. 1983. Monitoring the population status of American woodcock. Transactions of the North American Wildlife and Natural Resources Conference 48:376–388.

Tavernia, B. G., M. D. Nelson, R. Rau, J. D. Gardner, and C. H. Perry. 2018 American woodcock singing-ground survey sampling of forest type and age. Journal of Wildlife Management 82:1794–1802.

Thogmartin, W. E., J. R. Sauer, and M. G. Knutson. 2007. Modeling and mapping abundance of American woodcock across the Midwestern and Northeastern United States. Journal of Wildlife Management 71:376–382.

Whiting Jr., R. M. 2010. American woodcock singing ground surveys: should they be expanded? Proceedings of the American Woodcock Symposium 10:153–169.

Whiting Jr., R. M., D. A. Haukos, and L. M. Smith. 2005. Factors affecting January reproduction of American woodcock in Texas. Southeastern Naturalist 4:639–646.

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