*Adapting hidden Markov models to data from small GPS transmitters for tracking migratory birds*

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Target: Ornithological Applications

Overview of the paper

1. Tracking devices are getting smaller, and data is getting coarser, but movement models are still designed to require lots of data.
2. We demonstrate how the creative application of additional data streams and correlated random walk models can allow movement models to fit coarse and irregular data gathered by small GPS transmitters.
3. We demonstrate these methods through the delineation of American Woodcock migratory movements. By adding additional data streams and a correlated random walk model to interpolate missing locations, we can fit hidden Markov Models to woodcock migratory tracks and estimate woodcock movement states to a reasonable degree of accuracy, even when tracks are incomplete.

**Background**

The analysis of animal behavior is critical to

HMMs allow for the incorporation of covariates (cite tk)

HMMs require regularly timed locations (cite tk)

Movement models provide a tool that can be used to determine behavioral states from GPS tracking data. Modeling tools such as hidden Markov models (cite tk) were initially applied to data from large mammal species (cite tk), which can carry transmitters as heavy as tk kg and collect locations at an interval as frequent as tk min (cite tk). By measuring the step lengths and turn angles between successive points, hidden Markov models can approximate changes in behavioral states throughout an animal’s GPS track. Behavioral states can include directed, exploratory, or area-restricted movement (cite tk).

dispersal (cite tk, maybe me), foraging (cite tk), nomadism (cite tk), or encamped (cite tk). Hidden Markov models have been widely used to identify behavioral patterns such as tk.

In recent years, hidden Markov models have seen more utility in application outside of large-bodied mammals, including taxa such as birds and tk (cite tk). SAT-PTT transmitters have allowed researchers to use hidden Markov Models to explore topics related to the movement ecology of these taxa, such as their foraging ecology (cite tk), dispersal frequency (cite me tk), and migratory phenology (cite tk). Hidden Markov Models have been most frequently applied to these taxa using transmitters weighing >10 g with solar panels, which allows transmitters to collect data at high frequency (i.e. multiple locations per day) over an extended period of time. However, there are many species of small-bodied animals which are too light to carry large transmitters or live in habitats that do not receive enough direct sunlight for a solar panel to function. In these cases, smaller SAT-PTT transmitters are available for use, but small transmitters without solar panels provide GPS data at a lower frequency and are more likely to provide incomplete tracks or missing data than their larger counterparts. New applications of HMMs are necessary to fit models to data from small GPS transmitters and facilitate the use of HMMs to study the ecology of small-bodied animals.

We demonstrate the use of HMMs on data from small GPS transmitters during the delineation of American woodcock (*Scolopax minor*, hereafter woodcock) migration. Woodcock are short distance migrants that winter in the southern United States, breed in the northern United States and southern Canada, and persist year-round between tk and tk degrees latitude (Fig tk range map). Woodcock weigh tk–tk g and favor dense, understory vegetation away from direct sunlight (cite tk). These factors make woodcock well suited to small, non-solar SAT-PTT transmitters with limited battery life. Woodcock also have outstanding questions regarding their migratory phenology, such as their migratory length and duration and the frequency of migratory abstention and extra-seasonal movements. Here we illustrate how the use of correlated random walk models and additional data streams can allow HMMs to fit with sparse and incomplete GPS data and produce valuable insights into the migratory ecology of a small-bodied animal.

**2 Methods**

*2.1 Collecting data via GPS transmitters*

We delineated American Woodcock movements throughout the full annual cycle using GPS-tracking data from the Eastern Woodcock Migration Research Cooperative, a collaboration of 42 agency, non-profit, and academic organizations in eastern North America (www.woodcockmigration.org). We captured woodcock at 78 sites in Quebec, Ontario, Nova Scotia, Maine, Vermont, New Jersey, New York, Rhode Island, Pennsylvania, Maryland, West Virginia, Virginia, North Carolina, South Carolina, Georgia, Alabama, Louisiana, and Florida using mist nets during morning and evening flights (Sheldon, 1960), and on night roosts using spotlights and dip nets (Rieffenberger and Kletzly, 1966; McAuley et al., 1993). We attached 4g, 5g, or 6.3g PinPoint GPS Argos transmitters (Lotek Wireless Inc., Newmarket, Ontario, CA) to captured woodcock. Transmitters, bands, and harness materials never exceeded 4% of a bird’s body mass, and all capture and handling were conducted with methods approved by the University of Maine Institutional Animal Care and Use Committee (Protocol # A2020-07-01).

GPS transmitters were programmed with one of several schedules, each of which collected data at a slightly different pace to optimize battery life. The most frequent schedules would record locations daily, while infrequent schedules would record locations every 3–7 days. Certain schedules were programmed to switch between frequent and infrequent modes outside of migratory time periods, and transmitters were occasionally set to go dormant for periods of 1–3 months during summer and fall to preserve battery life for a separate study objective. Each transmitter was predicted to collect a maximum of 75–150 GPS locations, depending on transmitter size and schedule, at 12–60m accuracy. Transmitters relayed GPS locations back to the ARGOS satellite network after every 3rd location, allowing recovery of data without recapture of the bird. However, transmitters occasionally failed to relay data, sometimes resulting in sporadic missing data near the end of battery life.

*2.2 Delineating spring and fall migration*

*2.2.1 Using HMMs to delineate woodcock migration*

We delineated woodcock movements within fall and spring migratory seasons, where fall generally encompassed Aug. 1st–Feb. 25th and spring encompassed Jan. 5th–Jun. 30th based on the periods of time when most birds were migrating. However, for a small subset of birds (n = 14) we had to define custom date ranges due to prolonged migratory movements (Supplementary Information A). To ensure that fall and spring migratory movements were not conflated by our models, we delineated spring migrations first, and shortened the end of the default fall migration timeframe (Aug. 1–Feb. 25) to a day before the subsequent spring migration began for that individual.

We defined woodcock migration as beginning when woodcock make their first ≥16.1 km movement in a season and ending after woodcock make their final ≥16.1 km movement in a season. We chose a 16.1 km threshold as it roughly bisects the bimodal distribution of log-transformed step lengths collected by our migratory birds (Blomberg et al., n.d.). However, tagged woodcock in our study frequently had incomplete migratory tracks, either due to waning battery life or bird mortality before the end of migration, making it unclear when their final ≥16.1 km movement occurred. We therefore used hidden Markov Models (HMMs; Ephraim and Merhav, 2002; Zucchini et al., 2017) to delineate woodcock migrations, which allowed birds with complete migratory tracks to inform the final migratory state designation of birds with incomplete migratory tracks. We made several adjustments to the HMMs to allow them to better function with infrequent locations and missing data and provided additional data streams to allow the models to better differentiate between stopovers and post-migratory locations.

Infrequent locations and missing data can complicate the process of fitting an HMM to bird movement data, as they impede the ability of the model to detect recursive movements (defined as “repeated visitations to the same particular locations in a systematic manner”; Berger-Tal and Bar-David, 2015) which could be indicative of short-distance movements during stopovers and post-migratory settlement. We accommodated infrequent locations and missing data using a correlated random walk model to interpolate daily locations at stopover, pre-migratory, and post-migratory sites using the R package crawl (Johnson and London, 2018; R Core Team, 2022). This allowed the HMM to detect recursive movements more accurately during stationary periods using a limited number of infrequent locations. We only used the correlated random walk model to interpolate locations between points that were <16.1 km apart (i.e., when the bird was either at a stopover or not migrating), as the correlated random walk model tended to break long migratory steps into a series of short daily movements, making the HMM less likely to identify these movements as migratory. Due to the directional consistency inherent in correlated random walks, correlated random walk models occasionally produced erroneous loops of interpolated points to explain directional changes when birds made recursive movements during non-migratory periods. These interpolated loops were often lengthy and could artificially create step lengths ≥16.1 km. To ensure that HMMs didn’t incorrectly interpret these loops as migratory movements, we removed all loops of interpolated points for which the total length of the loop was more than 10 times the distance between observed points and replaced the loops with sets of predicted locations spaced evenly along a line between the observed points.

While HMMs generally differentiate among different movement states using step lengths and turn angles, we encountered difficulties inferring the final movement state of incomplete tracks using these data streams alone. To overcome this issue, we added additional data streams that allowed models to better differentiate between stopovers and post-migratory locations. Additional data streams measured recursiveness, residence time, day of season, and location of a given point (Table 1). We measured recursive movements using the mean distance to the nearest 7 points, transformed using a natural logarithm. This measured whether the nearest 7 bird locations (meant to approximate space use over the period of a week) reflected intensive use of the same area, and presumably resource utilization, or spread-out movement throughout the area, possibly reflecting exploration. We measured residence time using the time difference between the first and last day that the bird was within a 10 km radius of a location. This reflected the difference between the amount of time that woodcock spent occupying stopover sites as opposed to their post-migratory sites. We measured day of season using an ordinal day variable, reflecting woodcocks’ tendency to migrate at similar times each year. We measured location using latitude and two binomial variables. The first binomial location variable determined whether a bird had or had not moved >16.1 km from its position at the beginning of the season and had thus departed its initial site to begin migration. The second binomial location variable reflected whether the bird was currently within the woodcock breeding range, as delineated using the eBird 2021 Status and Trends abundance maps (Fink et al., 2022).

Table 1. Covariates used to delineate movement states in hidden Markov Models (HMMs), and the type of distribution used to fit to each covariate in the HMMs. Point-specific attributes (latitude, ordinal day, distance from start, breeding range, log(distance to nearest points), residence time) are based on the woodcock’s location at the beginning of the step.

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| **Covariate** | **Distribution** | **Description** |
| Step length | Gamma | Length of the current step |
| Turn angle | Wrapped Cauchy | Angle between the current and previous step |
| Latitude | Normal | Latitude at the beginning of the step |
| Ordinal day | Normal | Days since the beginning of the migratory season |
| Distance from start threshold | Bernoulli | Has the bird moved >16.1 km from its location at the beginning of the migratory season? |
| Step length threshold | Bernoulli | Is the current step length ≥16.1 km? Implemented with a fixed distribution so that all steps ≥16.1 km are migratory. |
| Breeding range | Bernoulli | Does the step begin in the American Woodcock breeding range [8]? |
| Log(distance to nearest points) | Normal | Natural logarithm of the mean distance to the nearest 7 points. |
| Residence time | Normal | Number of days that the bird has spent/will spend within a 10km radius. |

*2.2.2 Model design*

We implemented fall and spring HMMs in the R package momentuHMM (McClintock and Michelot, 2018) due to its accommodation of multiple data streams and customized model structures. We used separate HMMs for males and females in spring due to differential breeding movements, and together during the fall as movements were similar between sexes. We constructed a multi-state model for each HMM to delineate distinct stages of migration and identify transitions occurring between stages (Fig. 1). Models for spring migration by females and all woodcock during fall featured 4 states: pre-migration, migration, stopover, and post-migration. Birds began the season in a pre-migration state and remained as long as the bird made no movements ≥16.1 km. When the bird made its first movement ≥16.1 km it moved into a migration state, which was the only state in which movements ≥16.1 km were permitted. From the migration state, birds could enter either a stopover state or a post-migration state. The stopover state was characterized by a period of recursive movements <16.1 km, where the only possible state transition was back into the migration state. The post-migration state could only be reached from the migration state and did not allow for any further state transitions. This state indicated that the bird had completed movements ≥16.1 km for the remainder of the season. These state assignments were generally enforceable using the fixed transition framework in the momentuHMM package, but occasional errors occurred when improbable state assignments caused the framework to fail to enforce state transition rules. These errors and their fixes are detailed in Supplementary Information B.

The spring male model splits post-migration into two states, post-migration (frequent) and post-migration (infrequent), which males could enter in spring at the conclusion of migration. The inclusion of these two states fixed an artifact in the dataset caused by male-specific transmission schedules, which switched to a less-frequent transmission schedule late in the spring migratory season. Infrequent transmissions caused the correlated random walk model to infer a greater proportion of steps during the late migratory period, producing a much narrower turn angle distribution than observed earlier in the season. The inclusion of two post-migratory states with separate turn angle distributions, which birds can transition between freely, allows the model to better account for this source of variation in turn angles when delineating post-migratory movements.

To remove birds from consideration which did not make migratory movements or did not collect enough data to fit an HMM, we excluded any birds which did not have at least 1 step ≥16.1 km, or which collected fewer than 3 points in a given season. We assigned a fixed pre-migration state for the initial step of most birds captured during breeding or wintering. However, birds captured in Virginia, New Jersey, and Maryland were sometimes captured after widespread migratory initiation in the fall or spring, creating uncertainty whether a bird caught during one of these periods entered the HMM in a pre-migration or a migration state. To counteract uncertainty in the initial state for Virginia, New Jersey, and Maryland caught birds in the season of their capture, we allowed the HMM to estimate the initial state of the model instead of using a fixed pre-migration state for the initial step. The only other circumstance in which we allowed the initial state for a bird to vary from pre-migration was when the first step length was ≥16.1 km, in which case we set the first step to a known migration state. We fixed final steps to the post-migratory state for fall woodcock that were also known to initiate spring migration.

We visually inspected all HMM state assignments, which sometimes identified circumstances where birds did not fit model predictions due to extra-seasonal movements, early initiation or late termination of migration, or transmitter error. In those cases, we manually reclassified state assignments (Supplementary Information A). We also encountered issues with mortality locations, as birds which died during migration occasionally continued to transmit and caused the HMM to falsely classify dead birds as post-migratory. We have included methods used in delineating GPS mortalities and removing them from the dataset in Supplementary Information C.

*2.3 Assessment of HMM accuracy*

In all models, transition to post-migratory states was incumbent on no further steps ≥16.1 km after the transition. Because we rarely observed migratory movements beyond Jan. 15th for fall migration and Jun. 15th for spring migration, we considered the date of post-migratory transition (the date of the bird’s final ≥16.1 km movement) to be known for birds that survived and continued to transmit past the cutoff date. For birds that stopped sending data before the cutoff date, we relied on HMMs to determine whether each bird had reached its final ≥16.1 km movement of the season or was still migrating. We assessed the accuracy of our final state assignments of incomplete tracks using a leave-one-out simulation, in which we artificially removed locations from the ends of tracks for individual birds with known post-migratory transition dates, reran the HMM, and evaluated whether the model correctly determined the final movement state. We iteratively assessed 50 individuals for each seasonal simulation, testing the accuracy of final state assignment when tracks were cut off to dates from Oct. 1st–Jan 15th in fall and Mar. 15th–Jun. 15th in spring. We measured the accuracy of final state assignment based on Type I and Type II errors, where a Type I error occurred when the ending state was falsely classified as migratory, and a Type II error occurred when the ending state was falsely classified as settling or post-migratory. We conducted this assessment on the full model for each HMM and a reduced model for each season that used only step length and angle to train the HMM. Running both full and reduced models allowed us to examine how both Type I and Type II errors changed with the inclusion of additional variables in the HMM and to evaluate whether the inclusion of these variables improved the predictive capacity of the HMM.

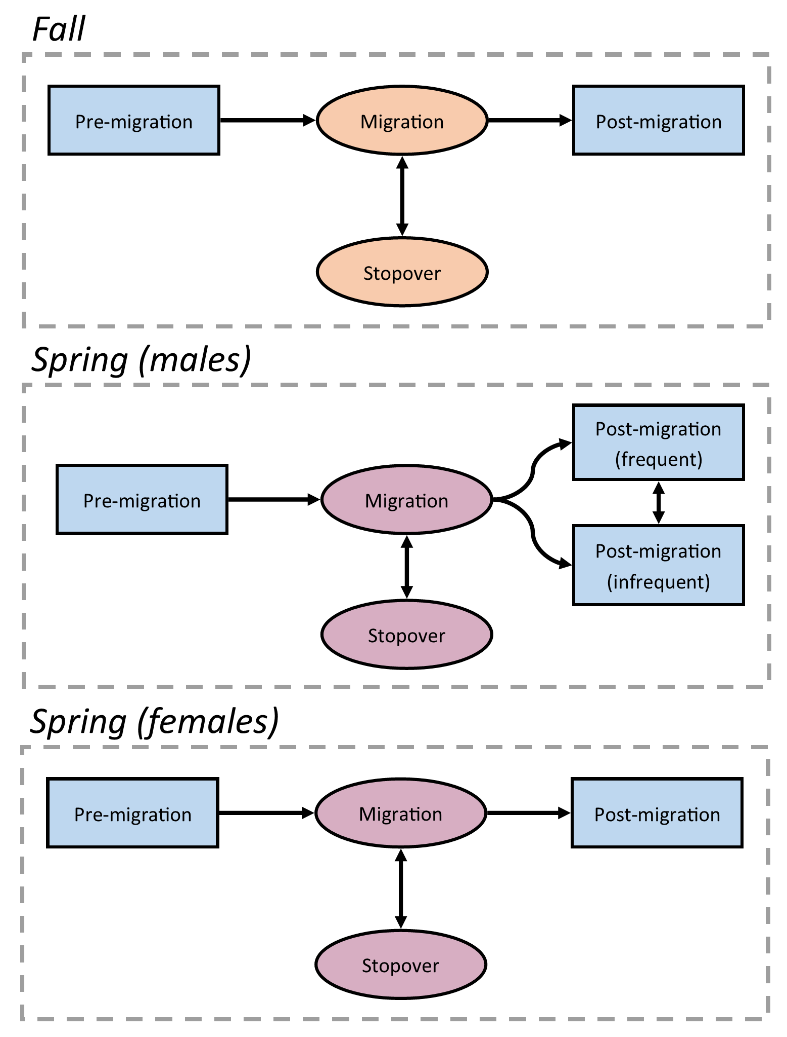


Figure 1. Movement state transition diagram for each hidden Markov Model (HMM).

*2.4 Classifying movements outside of spring and fall migration*

In addition to the timing of fall and spring migration, we were also interested in long-distance movements that occurred outside the period of migration. To examine these movements, we manually classified 3 potential long-distance movement states: summer migrations, foray loops, and dispersals (Table 2). Summer migrations were southerly movements >16.1 km that were initiated after the conclusion of spring migration but prior to the period of fall migration (Aug. 1). These movements resulted in southerly displacement considerable enough to preclude further migration during the fall. Foray loops were circular or out-and-back movements that included steps ≥16.1 km, but for which the bird’s eventual displacement was <16.1 km. Dispersals were one-way movements including steps ≥ supl16.1 km that resulted in ≥16.1 km of displacement, reflecting one-way movements to a new summering or wintering site. Birds could only transition between a long-distance movement state and a non-migratory state (pre-migration, settling, or post-migration), ensuring that long-distance movements were separate from early or continued migration.

Table 2. Definitions of long-distance movement states manually delineated for American Woodcock.

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| **Class** | **Definition** |
| Migratory (summer) | Post-breeding, southerly movements initiated before Aug 1 that preclude fall migratory movements. |
| Foray loops | Circular or out-and-back movements with steps ≥16.1 km that result in <16.1 km of net displacement between the first and last point. Foray loops can occur during any season, provided they are temporally distinct from a bird’s migratory movements. |
| Dispersals | Movements that include step lengths ≥16.1 km and result in ≥16.1 km of net displacement between the first and last point. Dispersal movements follow directions which are not typical of co-occurring seasonal migrations. |

*2.5 Calculation of full annual cycle phenology metrics*

We calculated several metrics to describe the prevalence, length, distance, and timing of each movement class. We summed the number of days between the first movement in each class and the initial location of the subsequent movement class (e.g. the start and end of migration). We also summed the total distance of all steps in each movement class for each bird. For birds undergoing fall or spring migrations, total distance excluded movements designated as stopovers, i.e. steps <16.1 km that occurred while the individual was migrating. We used medians and ranges to report dates of migratory initiation and termination, as medians are well suited to accommodating outliers that were common in the initiation and termination dates. We delineated migratory peaks by calculating the proportion of locations which fell into a migratory class during any given week, and reporting the week in which the proportion of migratory locations was greatest.

We calculated the percentage of individuals which did not migrate using the pool of all individuals tracked between the nominal start of the migratory season (Fall: Oct. 15, Spring: Feb. 15) and the date by which most birds had initiated migration (95th quantile of the departure dates for that season). Any individuals which had at least one location before, during, and after this period, but did not enter a corresponding migratory state, were designated as non-migratory for that season. We used similar time periods to determine whether a bird migrated during the season before or after its non-migratory season. We counted the frequency of summer migrations based on all birds tracked between May 1st–Sep. 1st, with dates chosen based on the first initiation date and last termination date observed in the dataset. We counted the frequency of dispersals and foray loops based on all birds with locations spanning at least 1 month, which was long enough to correctly classify movement classes. Sample sizes prevented reporting standard deviations for the duration and distance traveled of summer migrations, foray loops, and dispersal movements, so we reported ranges for these metrics.

*2.6 Distribution of methods and results*

For use in other studies, we simplified the movement state assignments to only include migratory, non-migratory, and long-distance movement designations and uploaded these designations to a Movebank repository (reference ID 351564596). The process of simplifying these designations for use in Movebank is detailed in Supplementary Information D. All code used in this study is publicly available at https://github.com/EWMRC/fac-classification.

**3 Results**

*3.1 Model evaluation*

We analyzed 522 seasonal movement tracks from 401 tagged woodcock, of which 43 (10.7%) required exceptions to the methods described above to correctly fit the seasonal HMMs. These misclassification errors, and the individual modifications to the seasonal HMMs needed to correct them, are detailed in full in Supplementary Information A. All three seasonal HMMs exhibited improved validation accuracy with the full model (included additional data streams) compared to the base model (only step length and turn angle) (Fig. 2). The full fall model had a comparable Type I error rate (0–24.2%) to the base model (0–24.2%), but the full model had a Type II error rate (0–4.3%) which was generally lower than that of the reduced model (0–28.3%). The spring male full model exhibited lower rates of Type I (0–15.6%) error than the base model (0–61.1%), and comparable rates of Type II error (Full: 0–11.4%, Base: 0–13.6%). The spring female full model exhibited greater Type I errors (0–18.8%) during some time periods than the base model (0–4.2%), but also exhibited reduced Type II error rates (2.0%–11.4%) compared with the base model (10.0–77.6%).

Individual removal of variables from the full model had low overall impact (range: -1.20–0.19%) on the Type I and Type II error rates of the seasonal models, suggesting redundancy between included variables (Fig tk.). The impact of a withheld variable often differed by season, with the removal of some variables (ex., ordinal day) leading to positive impacts on error rates in one season and negative impacts in another season. The withheld variable which led to the highest reduction in error rates was residence time, which caused a 0.20–1.20% drop in Type II error rates for all 3 seasonal models.

*3.2 Full annual cycle phenology*

Duration of fall migrations averaged 23.8 days (SD 19.9, range 2–83 days) with a mean distance (excluding stopovers) of 1393 km (SD 571, range 23–3010 km) for males, and 33.0 days (SD 29.4, range 1–142 days) with a distance of 1353 km (SD 683, range 158–2980 km) for females. Spring migrations lasted 39.2 days (SD 24.3, range 4–95 days) with a distance of 1554 km (SD 644, range 296–3337 km) for males and 49.6 days (SD 29.3, range 2–128 days) with a distance of 1672 km (SD 626, range 455–3424 km) for females. The median date of departure for fall migration was Nov. 8th (range: Sep. 24th–Dec. 11th) for males and Nov. 7th (Aug. 29th–Jan. 11th) for females. The median date of migratory termination was Dec. 1st (Nov. 1st–Jan. 28th) for males and Dec. 6th (Oct. 25th–Feb. 4th) for females. The median date of departure for males during spring migration was Mar. 1st (Jan. 6th–Apr. 14th), and the median date of migratory termination was Apr. 4th (Jan. 11th–Jun. 7th). The median date of departure for females during spring migration was Mar. 5th (Jan 19th–Apr. 26th), and the median date of migratory termination was Apr. 26th (Feb. 20th–Jul. 28th). Fall migration peaked during the week of Nov. 18th–Nov. 25th for both males and females, with 54% and 59% of male and female locations in that week being migratory, respectively. Spring migration peaked on the week of Mar. 18th–Mar. 25th for males and Mar. 25th–Apr. 1st for females, with 78% and 83% of locations in those weeks being migratory, respectively (Fig. 3).

Six of 176 birds (3%) tracked between Oct. 15th–Dec. 5th did not migrate during fall, and 6 of 193 birds (3%) tracked Feb. 15th–Mar. 29th did not migrate during spring. Of those birds that did not migrate during fall, 3 overwintered in Rhode Island, 1 in Pennsylvania, 1 in Connecticut, and 1 in Virginia. Of birds that did not migrate during spring, 2 oversummered in Virginia, and 1 each oversummered in Maryland, Florida, Georgia, and Alabama. Individuals that abstained from migration during one season did not necessarily repeat that behavior in other seasons, as non-migratory birds were observed migrating in prior or subsequent seasons when data were available (5 of 5 birds). Three of 65 birds (5%) tracked from May 1st–Sep. 1st migrated south during the summer. Summer migratory movements initiated on a mean date of Jun. 19th (May 27th–Jul. 13th) and terminated on a mean date of Jul. 28th (Jul. 8th–Aug. 22nd; Fig. 4), had a mean duration of 39 days (35–42 days) and a mean distance traveled of 756 km (523–1106 km). Three of 456 birds (0.7%) tracked for at least 1 month underwent non-migratory dispersal, with one bird making 2 dispersal movements approximately 2 months apart. Dispersals were observed during December, February, June, and July, and were restricted to the northeastern United States. Dispersal movements had a mean duration of 6 days (1–10 days) and the mean distance traveled was 129 km (30–263 km). Sixteen of 456 birds (4%) tracked for at least 1 month underwent a foray loop, which were observed in all months except for March and April (the peak of spring migration) with a mean duration of 20 days (3–95 days) and a mean distance traveled of 247 km (38–951 km).

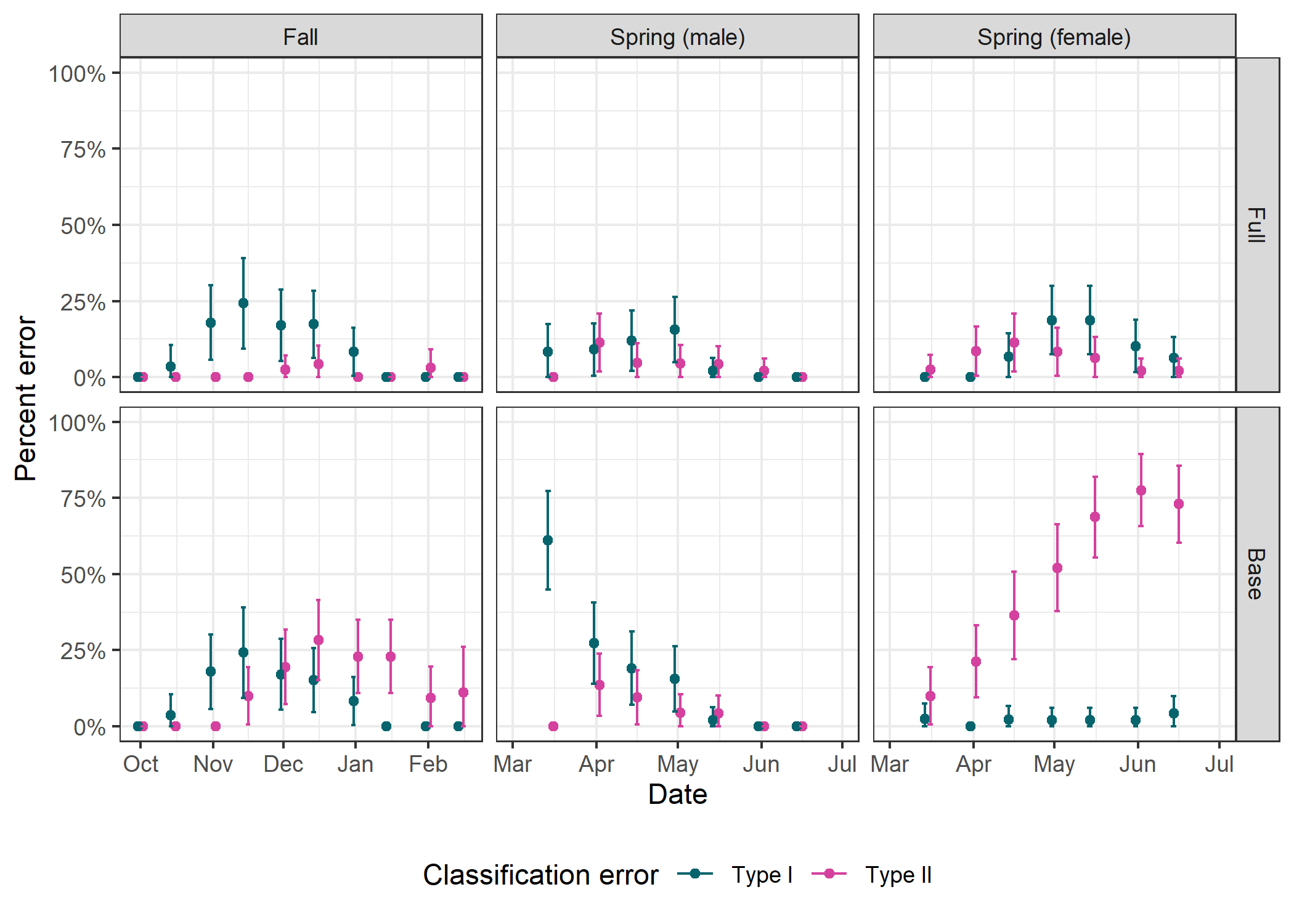


Figure 2. Error rates for movement state assignments by hidden Markov Models (HMM) for fall, spring (male), and spring (female) migrations, as measured through the model validation process. The horizontal axis reflects the cutoff date for each model that was used to simulate an incomplete track ending on that date. HMMs were grouped into full and base models, where full models included all possible data streams and base models including only step length and turn angle. Type 1 errors reflected false classification as post-migratory while the true state was migratory, whereas Type 2 errors reflected false classification as migratory while the true state was post-migratory. Bars show the 95% confidence interval of the mean.

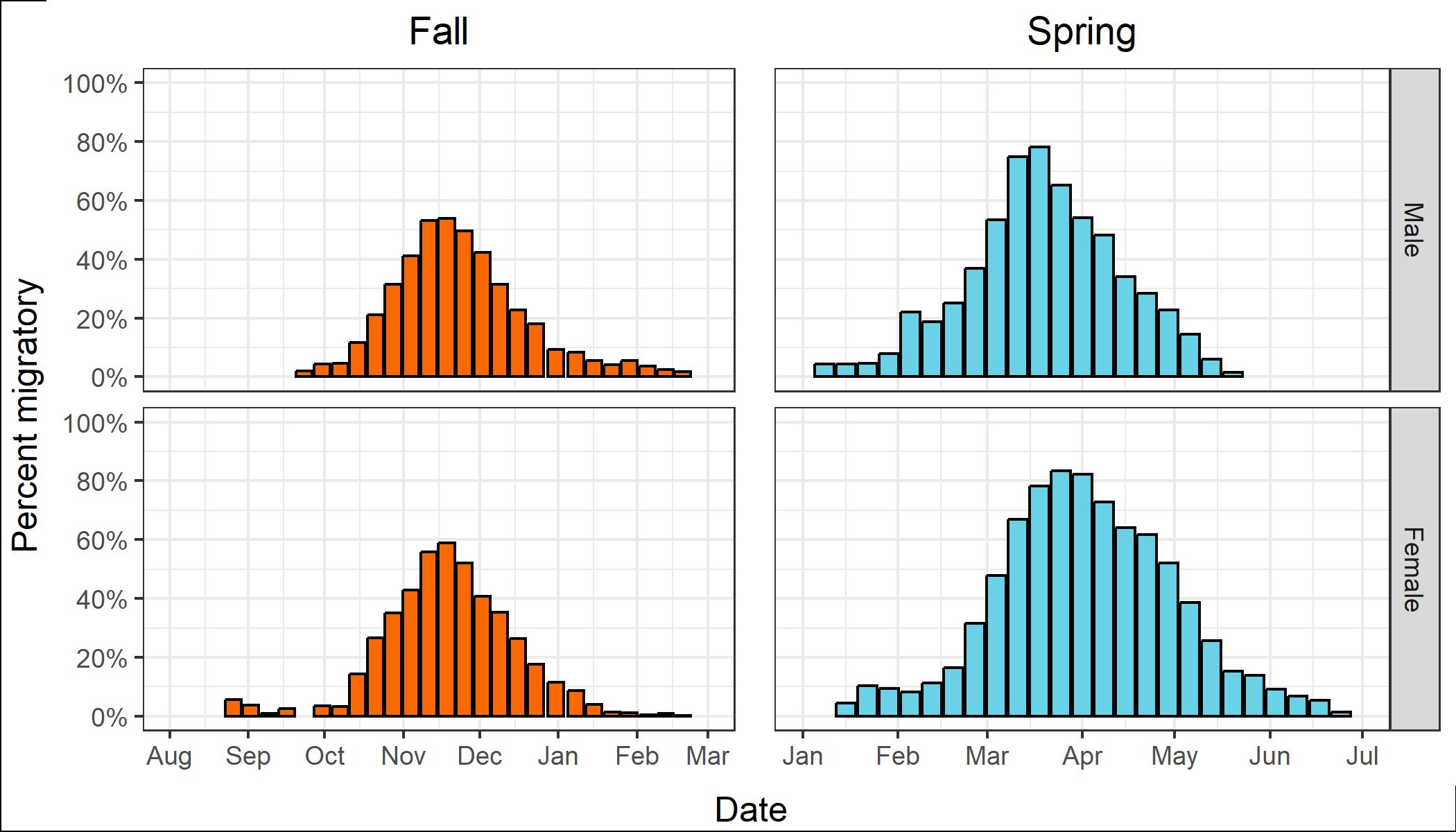


Figure 3. Peak migration dates of male and female American Woodcock throughout the fall and spring migratory seasons. Color indicates season, and the vertical axis reflects the percentage of all locations in each week that fell into fall or spring migratory movement classes.

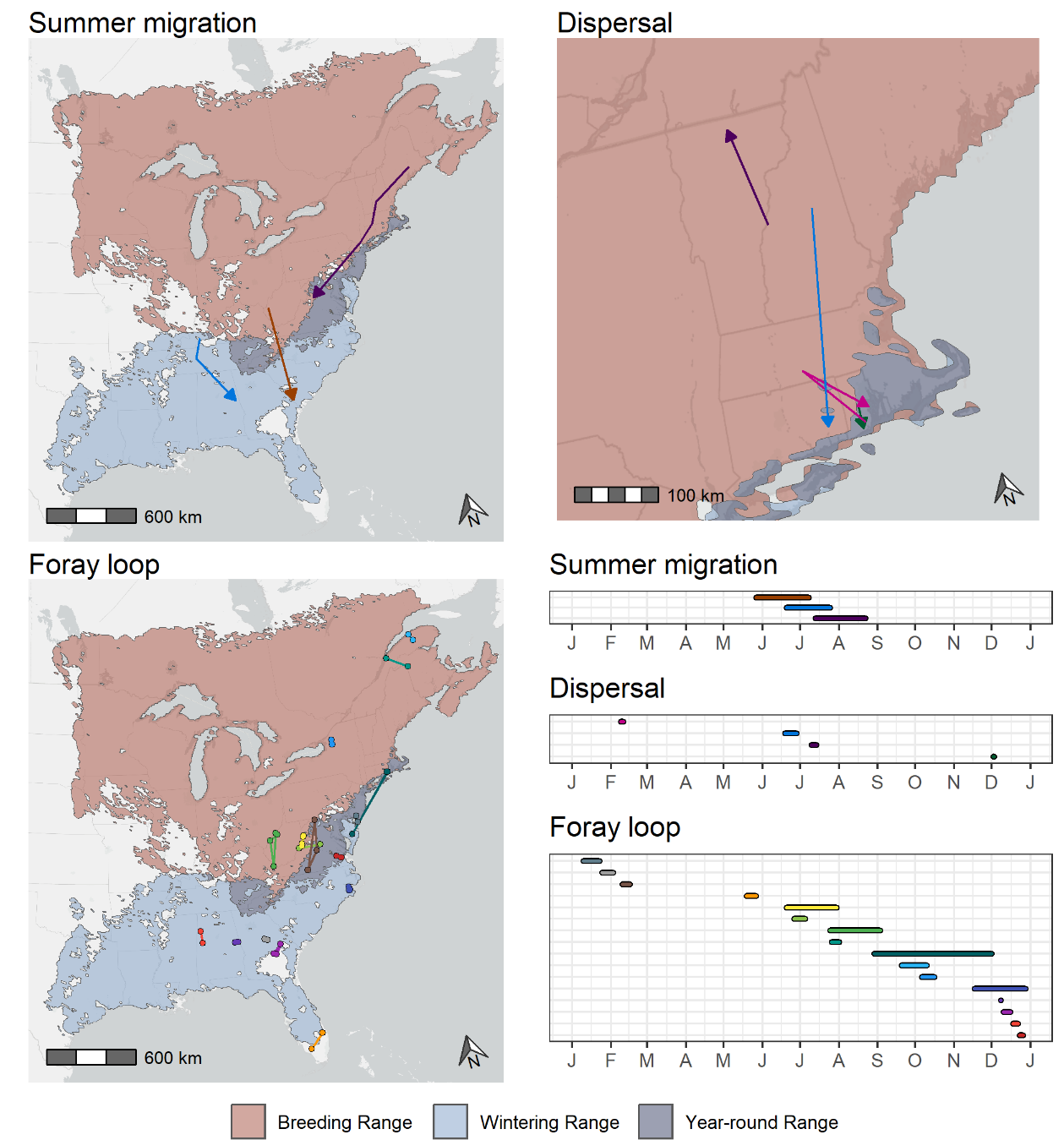


Figure 4. Spatial and temporal distribution of summer migrations, dispersals, and foray loops of American Woodcock marked with GPS transmitters in eastern North America. Maps are superimposed over the breeding, wintering, and year-round range of the American Woodcock as delineated by the eBird Status and Trends dataset [8]. Timelines depict the duration of each movement by month. Each movement is matched from the map to the timeline by color.

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