*Working title 1: Large-scale GPS deployments reveal variation in migratory patterns for a short-distance migratory bird*

*Working title 2: Adapting hidden Markov models to data from small GPS transmitters*

*Working title 3: Adapting hidden Markov models to data from small GPS transmitters reveals extensive intra-species variation in migratory patterns*

**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 federal, state, provincial, non-profit, and university partners throughout the United States and Canada (www.woodcockmigration.org). We captured woodcock at 34 sites in Quebec, Ontario, Nova Scotia, Maine, Vermont, New York, Rhode Island, Pennsylvania, Maryland, West Virginia, Virginia, North Carolina, South Carolina, Georgia, Alabama, 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, and 6.3g PinPoint GPS Argos transmitters (Lotek Wireless Inc., Newmarket, Ontario, CA) to captured woodcock. Transmitters, bands, and attachment materials never exceeded 4% of a bird’s body weight, 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. Transmitters with a frequent schedule collected locations daily, and typically lasted throughout the duration of a single migration. Transmitters with an infrequent schedule collected locations every 3–5 days, with the aim of collecting data from several migrations. Hybrid schedules combined characteristics of frequent and infrequent schedules, collecting locations every 3–7 days outside of the migratory season, and collecting data every 1–2 days during the migratory season. Gap schedules used a similar timing to hybrid schedules, but additionally included a period of 1–3 months in which the transmitter did not collect locations to extend battery life over the course of multiple seasons. Each transmitter collected tk­–tk GPS locations, depending on transmitter size, 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, transmissions back to satellites are energetically demanding and transmitters occasionally fail to relay data as their battery life wanes, creating issues with sporadic missing data near the end of migration.

*2.2 Delineating spring and fall migration*

*2.2.1 Using HMMs to delineate woodcock migration*

For woodcock with a full migratory track (Fall: tk–tk, Spring: tk–tk), we define woodcock migration as beginning when woodcock make their first 30.2 km movement in a season and ending after woodcock make their final 30.2 km movement in a season. However, tagged woodcock in our study frequently had incomplete migratory tracks, either due to waning battery life or bird mortality before the end of the season. We therefore used hidden Markov Models (HMMs) trained on those birds with complete migratory tracks to estimate the final migratory state of birds with incomplete migratory tracks. We made several adjustments to these 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.

We accommodated for 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 tk (cite tk). This allowed the HMM to detect recursive movements more accurately during stationary periods using small numbers of infrequent locations. We only used the correlated random walk model to interpolate locations between points that were <30.2 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, single night migratory flights into a series of short movements over multiple days, making the HMM less likely to identify these movements as migratory.

While HMMs generally differentiate between 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 would allow the 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 tk). We measured recursive movements using the mean distance to the nearest 7 points, transformed using a natural logarithm. This measured whether bird locations over the period of a week reflected intensive use of the same area (presumably resource utilization) or spread-out movement throughout the area (reflecting exploration). We measured residence time using the time difference between the first and last day that the bird was within a 10km radius of the point. 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 tk 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).

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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 >tk km from its location at the beginning of the migratory season? |
| Step length threshold | Bernoulli | Is the current step length > 30.2km? Implemented with a fixed distribution so that all steps >30.2km are migratory. |
| Breeding range | Bernoulli | Does the step begin in the American Woodcock breeding range (Fink et al. 2022)? |
| 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. |

Table tk. Covariates for all spring/fall migratory models. 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.

*2.2.2 Model design*

We implemented HMMs in the R package momentuHMM (McClintock and Michelot 2018) due to its accommodation of multiple data streams and customized model structures. We designed separate models for the fall (tk–tk) and spring (tk–tk) migratory seasons. 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 distinguish between pre-migratory, migratory, and post-migratory movements (Fig. tk). Spring females and fall birds had 4 states in their model: pre-migration, migration, stopover, and post-migration. Pre-migration was the initial state that birds entered at the beginning of the season and continued as long as the bird made no movements >30.2km. When the bird made its first movement >30.2km it moved into a migration state, which was the only state in which movements >30.2km 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 lengthy period of recursive movements of <30.2 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 characterized when birds had completed movements >30.2km for the rest of the season.

The spring male model used one additional state, settling, to reflect an additional movement state that males entered in spring at the conclusion of migration. The settling state was likely due to male breeding behavior causing differential step lengths immediately after migration that faded as breeding displays concluded near the end of the spring. Birds were able to transition freely between the settling and post-migratory states, but birds were not able to reenter migration after entering either of these states.

In the frequent occasion that individual movement tracks were incomplete, and the HMM was uncertain whether a bird had concluded making >30.2km movements by the end of its movement track, the model HMM determined whether the bird’s track had ended in stopover, settling, or post-migration state based on covariates that correlated with each movement state, such as step lengths, turn angles, recursive movements, residence time, day of season, and location. For example, a spring migratory track that ended prematurely in late April, but whose final state was characterized by short step lengths, high turn angles, recursive movements, long residence time, and a northerly latitude in the breeding range would likely be designated as ending in the post-migration or settling state instead of stopover. However, a spring migratory track that ended prematurely on the same date but with larger step lengths, small turn angles, less recursive movements, short residence time, and a mid-latitude outside of the breeding range would likely be designated as a final state of stopover instead.

Remove birds with no individual step lengths >30.2km (20 miles). In practice this removes birds that never initiate a substantial migratory movement but doesn't penalize birds that DO migrate, as they always make at least one substantial movement.

Time periods: fall ends when spring begins

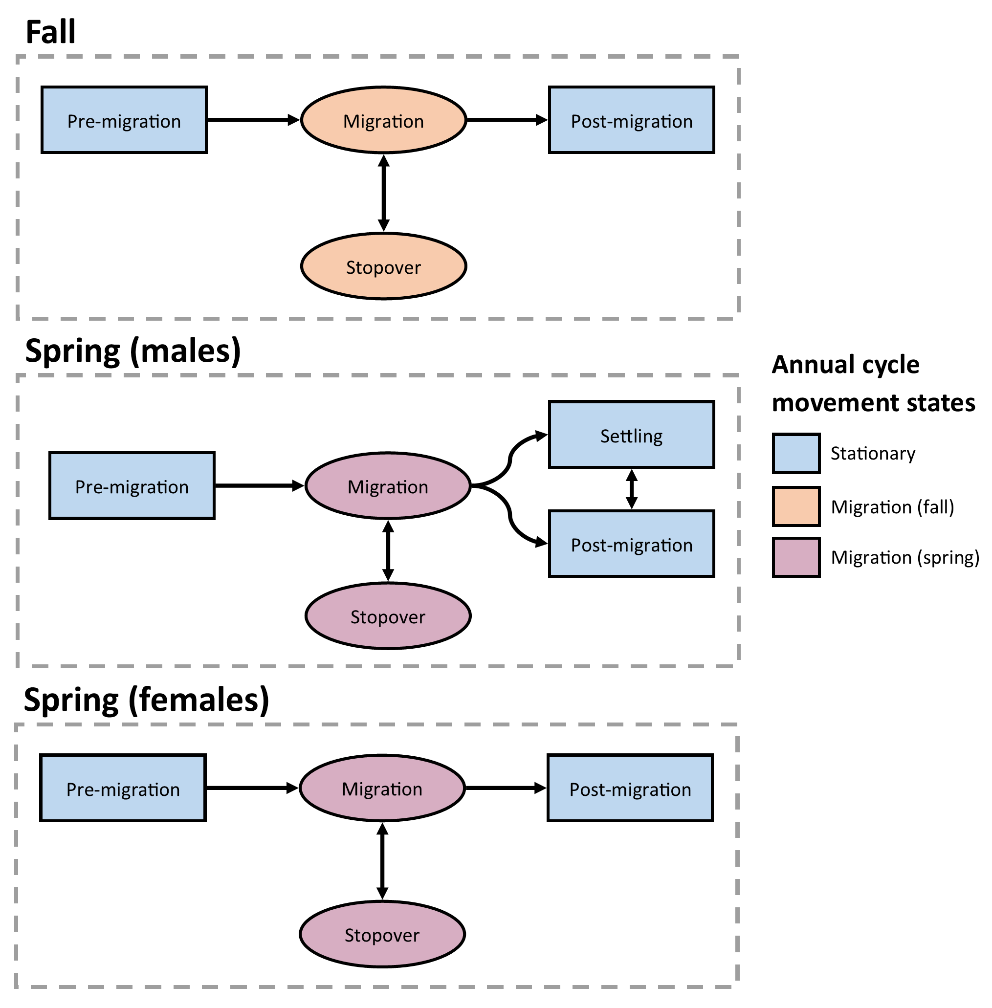


Figure tk.

*2.3 Classifying movements outside of spring and fall migration*

In addition to the timing of fall and spring migration, we were also interested in movements before or after migration had concluded. To examine these movements, we first matched the classifications from the fall and spring HMMs with the locations from each woodcocks’ full trajectory, which included locations in the summer which were not considered in either HMM. We simplified the classification states before we matched them to 3 classes, stationary, migration (fall), and migration (spring), as shown in Figure tk. We then manually classified movements from each bird which fell outside the migratory period. We added 3 additional movement states in this manual classification: summer migrations, foray loops, and dispersal events (Table tk). Summer migrations initiated after the conclusion of breeding activity but prior to the first date of consideration for fall migration (August 1). These movements resulted in southerly displacement which was considerable enough to preclude further migration in the fall. Foray loops were recursive movements which included step lengths >30.2 km but for which the resulting displacement was <30.2 km, reflecting exploratory movements which would eventually return to the original breeding or wintering site. Dispersal events were one-way movements which included step lengths >30.2 km and resulted in >30.2 km of displacement, reflecting one-way movements to a new breeding or wintering site. All 3 additional movement states were further constrained to begin and end in a stationary state. For example, a bird could make a dispersal movement after its migration had concluded, but it could not transition directly from a migration state into a dispersal event, as this would just be a continued migration.

Table tk. Definitions of all full annual cycle movement states delineated for American Woodcock.

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| **State** | **Definition** |
| Stationary | Recursive movements with steps < 30.2km that are associated with non-migratory behavior. |
| Migratory (fall/spring) | Directional movements along a latitudinal gradient that bring the bird from the breeding to the wintering range, or visa-versa. Steps can be >, =, or < 30.2 km. Fall migratory movements initiate between Aug 1 and Feb 1, while spring migratory movements initiate between Jan 1 and June 1. |
| Migratory (summer) | Post-breeding, southerly movements that initiate before Aug 1 and would preclude further migratory movements in the fall. |
| Foray loops | Movements that include step lengths > 30.2 km but result in < 30.2 km of net displacement between the first and last point. Can occur in any season, provided the starting and ending state is stationary. |
| Dispersal events | Movements that include step lengths > 30.2 km and result in > 30.2 km of net displacement between the first and last point, and do not preclude a fall or spring migration. Can occur in any season, provided the starting and ending state is stationary. |

*2.4 Exceptions to the rules*

Because of the incredible variation that we observed in the data, there were a number of exceptions to the methods outlined here that we needed to address. This included methods for birds captured during migration, bugs introduced by the correlated random walk, and treatments for birds which had transmitters that continued to transmit after the bird died. We have detailed these individual bug fixes and exceptions in Appendix tk.

**3 Results**

*Part 1: FAC phenology*

Incidence of each behavior (non-migratory, auxiliary)

Basic migration phenological stats

Approximate length (# days and km) of bird migration

Median and range of departure dates and termination dates

Dates of “peak migration”, where the most birds were in the air at once

With season-specific histograms

Basic auxiliary phenological stats

Verbal description of when these movements occurred

How long these movements lasted, distance they covered

*Part 2: Model evaluation*

Validation results (e.g. how accurately can we say that a bird has stopped migrating at any given point using the full model)?

How many birds did weird things that required me to make additional rules for them?

How much more accurately does the full model classify termination states than a model with just step lengths and turn angles?

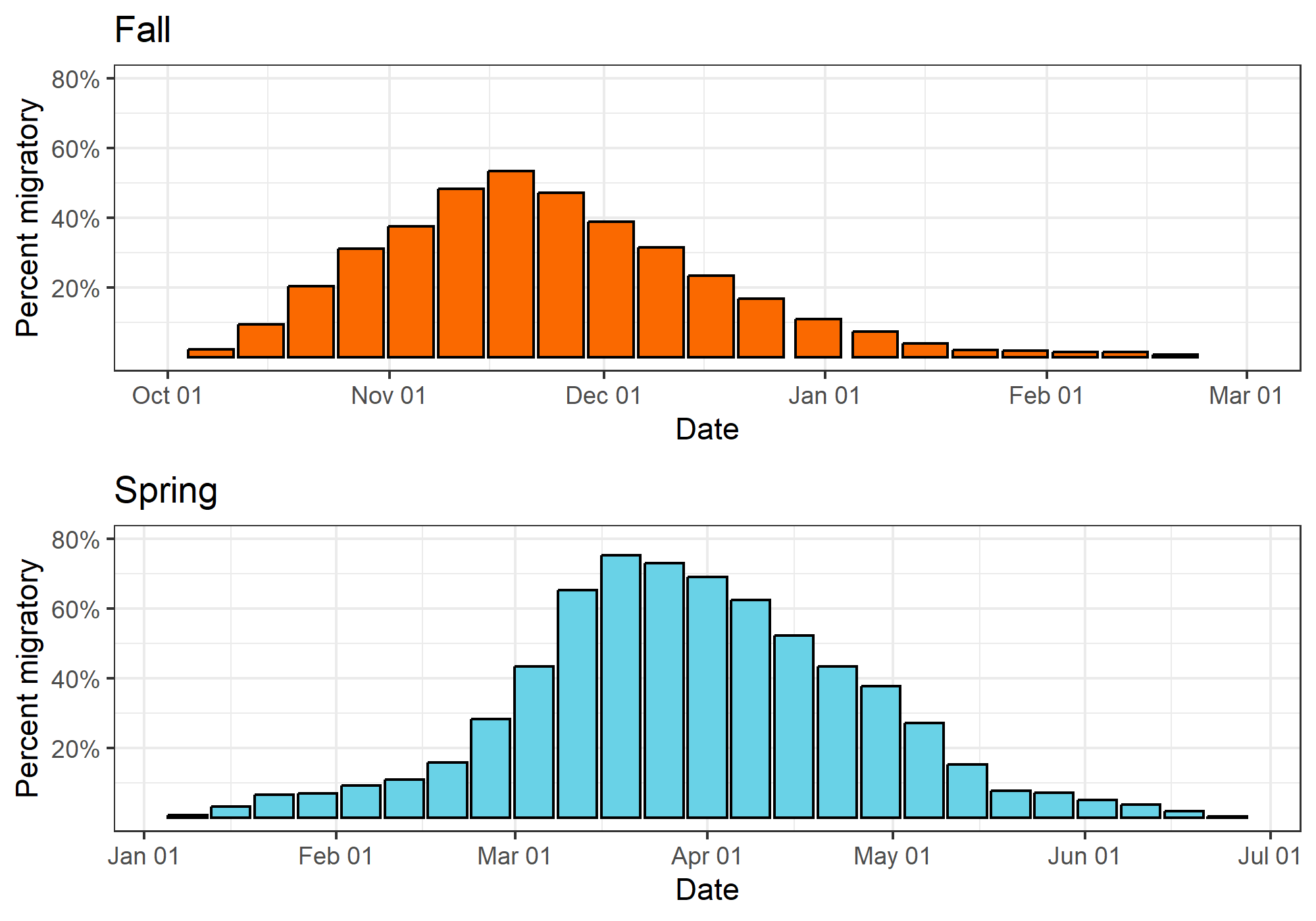


Figure tk. The Y axis is the percent of all locations in a week that belong to a give migratory state.

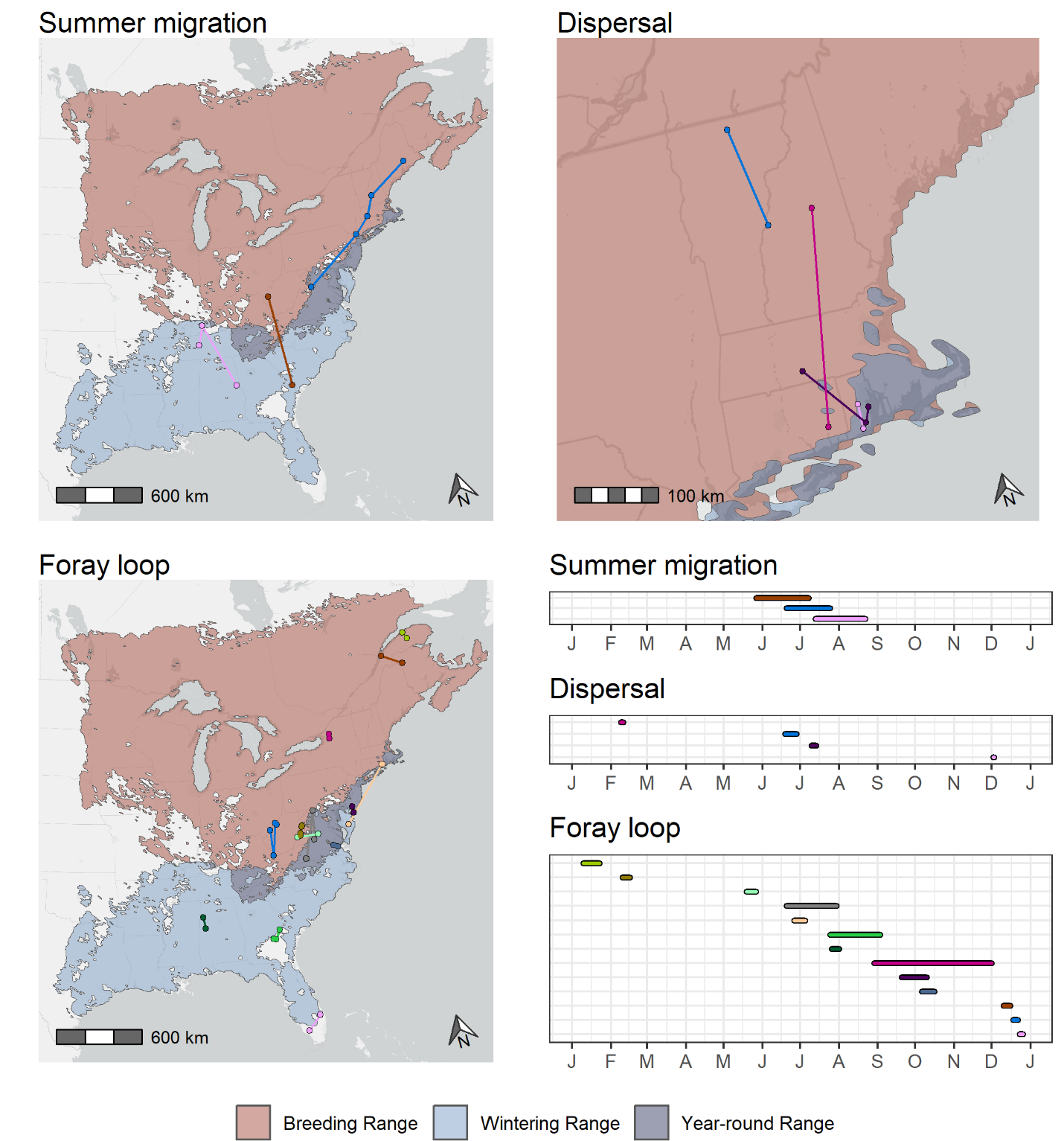


Figure tk

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