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

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Target: Ornithological Applications

**Abstract**

Recent technological advances resulting in the widespread collection of tracking data from migratory birds necessitates tools for the effective processing and classification of that data. Tools such as hidden Markov models provide opportunities to classify movement states from high-resolution Global Positioning System (GPS) data collected at frequent, regular intervals. However, small-bodied migratory birds frequently cannot carry large enough tags to collect GPS data frequently. Use of additional data streams may assist with assigning cryptic movement states to sparse and irregular GPS data. Here we apply a correlated random walk model and additional data streams to fit hidden Markov models to GPS data from American Woodcock (*Scolopax minor*; hereinafter woodcock). Our objectives were to determine if the use of additional data streams resulted in an improved capacity to predict migratory states and characterize woodcock migratory distance, duration, phenology, and the presence of long-distance movements outside of fall and spring migration. We found that individual data streams only marginally improved model performance, but collectively data streams decreased model error rates by a median value of 5.93%. Migratory characteristics measured using the full model (all additional data streams) were similar to the base model (only step length and turn angle) for all birds during fall and for males during spring, although the full model was 2.12 times more likely to identify a migratory endpoint than the base model for females during spring. The mean duration and distance of migration was also underestimated by 7 days and 278 kilometers for the base model as opposed to the full model for females during spring. Long-distance movements outside of fall and spring migration, such as dispersals and foray loops, were less frequently identified with the base model (3 dispersals, 15 foray loops) as opposed to the full model (4 dispersals, 18 foray loops). Using additional data streams may be beneficial for birds with overlapping seasonal distributions and prolonged stopovers, demonstrating the benefits that new or repurposed movement models may have for understanding avian migratory ecology.

**Introduction**

The amount of tracking data collected from small birds has exploded in the 21st century (Iverson et al. 2023b), providing opportunities to address facets of bird migration that have long eluded ornithologists, such as migration phenology (Wright et al. 2021), habitat use (Moskát et al. 2019, Iverson et al. 2023a), survival (Klaassen et al. 2014), and connectivity (Combreau et al. 2011). In particular, tracking devices that record GPS locations can provide data at a high temporal resolution with near global coverage. GPS transmitters have traditionally required large batteries or solar panels which limit their use to larger birds. However, recent innovations in these technologies have allowed GPS technology to become available for a much larger group of bird species than has historically been the case (Flack et al. 2022, Bridge et al. 2011).

In order to answer questions about bird migration, GPS data are often classified into movement states that delineate periods of pre-migration, migration, and post-migration, under one of several simple frameworks. The range delineation method (Fig. 1A; Linscott et al. 2022) is based on the known breeding and wintering ranges, where a bird is considered to have begun migration when it leaves the breeding range, and completed migration when it enters the wintering range, and vice versa. The range delineation method has the advantage of being robust to incomplete tracks; if a bird dies or transmitter failure occurs during the bird’s migration, the bird’s final state is still apparent. However, the range delineation method requires constrained breeding and wintering ranges that have little overlap with the migratory range (ex. Bar-tailed Godwit, *Limosa lapponica*; Battley et al. 2012). The step-length or distance threshold (Burnside et al. 2017) method defines the start of migration by the first step longer than a defined distance threshold, and migration ends with the last step longer than the distance threshold (Fig. 1B). The step-threshold method relaxes the assumption that breeding and wintering ranges do not overlap with the migratory range, making this method applicable to birds with widespread breeding and wintering ranges (ex. Pine Siskin, *Spinus pinus*; Dawson 2020). However, the step-threshold method does not handle incomplete tracks well; if a bird dies or its transmitter fails during migration, it is impossible to determine whether the bird has made its final migratory step (Fig. 2). Quantifying the terminal migration state is particularly important for survival and connectivity analyses, but also has relevance for phenology and habitat analyses for which accurate migratory delineation is important.

A diagram of a method and steps

Description automatically generated

Figure 1. Range delineation (Linscott et al. 2022) and step-threshold (Burnside et al. 2017) methods of delineating migratory tracks. Using the range delineation method (Panel A), migratory locations can be defined as all locations outside both the breeding and the wintering range. Using the step-threshold method (Panel B), migratory locations can be categorized as all locations occurring after the first migratory step (determined using a threshold step length) and prior to the final migratory step.

A diagram of migration

Description automatically generated

Figure 2. Complete and incomplete tracks of a theoretical migratory bird. For birds with complete tracks (Panel A; encompassing the entire temporal period of migration), the pre-migratory, migratory, and post-migratory stages of the track are apparent, and can be identified using the range delineation or step-length threshold methods. For birds with incomplete tracks (Panels B and C) the final state of the bird cannot be determined using a step-length threshold. If points cannot otherwise be delineated using breeding and wintering ranges, incomplete tracks end in an uncertain state that could be either migratory or post-migratory.

Hidden Markov models use observed distributions of outcome variables to assign movement states to animal tracking data and could potentially overcome limitations of rule-based assignments, particularly for the final movement state of incomplete movement tracks (Langrock et al. 2012, Zucchini et al. 2017). Step length and turn angle are the two most common data streams used by hidden Markov models in movement analyses, although additional data streams (such as acceleration, depth/altitude, and immersion in water) can be used to improve the model’s predictive capabilities (Dean et al. 2013). Hidden Markov models have delineated foraging, dispersal, and migratory behaviors for a variety of bird taxa including shorebirds, sage-grouse, prairie grouse, and seabirds (Blomberg et al. 2023, Berigan et al. 2024, Dean et al. 2013, Picardi et al. 2022, Mander et al. 2022, Zhang et al. 2019). These taxa can carry large transmitters (often with solar panels) that provide high frequency, regular location data over long periods of time, which assists with fitting hidden Markov models. However, the small size and forest dwelling habits (i.e., no direct sunlight for solar panels) of smaller birds may preclude high frequency data collection for GPS transmitters attached to them and complicate fitting those data using traditional hidden Markov model approaches.

We illustrate the fitting of HMMs to low-frequency GPS data using American woodcock (*Scolopax minor*; hereinafter woodcock). Woodcock are widely distributed throughout eastern North America, typically breeding in the northern United States and southern Canada and wintering in the southern United States. They are frequently among the latest migrants to leave the breeding range as frost encroaches in the fall and the earliest to arrive as snow melts in the spring (Moore et al. 2021). Woodcock are particularly flexible in their migratory and reproductive timing; females regularly nest in the migratory and wintering ranges and have been observed migrating among nesting attempts (Slezak et al. in press). Woodcock are of appropriate size to carry small GPS transmitters, which are often constrained by limited battery life (woodcock mass: 116–279 g, transmitter mass: 4–6 g; McAuley et al. 2020).

Here we present a modified approach combining step-threshold and hidden Markov models to classify large-scale movement behaviors, such as migration, using sparse and irregular GPS data. We suggest a three-stage process: 1) interpolation of data at a regular interval using a correlated random walk model (Kareiva and Shigesada 1983), 2) delineating known movement states using the step-threshold method, and 3) estimating unknown movement states using a hidden Markov model with additional data streams that describe the time, location, and movement characteristics of each GPS point. We demonstrate this approach on data collected from American Woodcock during a range-wide study of migratory phenology, habitat use, and survival. Our objectives were to determine whether use of additional data streams facilitated estimation of terminal movement states from incomplete GPS tracks and improved our ability to quantify of woodcock migratory distance, duration, phenology, and long-distance movements outside of fall and spring migration.

**2 Methods**

*2.1 Collecting data via GPS transmitters*

We used GPS-tracking data from 2017–2022 collected by the Eastern Woodcock Migration Research Cooperative, a collaboration of 42 agency, non-profit, and academic organizations in eastern North America (Blomberg et al. 2023, Clements et al. 2024, Fish et al. 2024). We captured woodcock at 78 sites throughout 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. We used mist nets to capture woodcock during morning and evening flights (Sheldon 1960) and using spotlights and dip nets on night roosts (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 # A2017-05-02 and 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 according to specific project objectives. The most frequent schedules recorded locations daily, while infrequent schedules recorded locations every 2–3 days during migratory time periods and every 3–7 days outside of migration. Certain schedules were programmed to switch between frequent and infrequent modes, and transmitters were occasionally set to go dormant for periods of 1–3 months during summer and fall to preserve battery life for separate study objectives. Transmitters were predicted to collect a maximum of 75–150 GPS locations, depending on transmitter size and schedule, at 12–60m accuracy. Transmitters relayed GPS locations to the ARGOS satellite network after every 3rd location; however, transmitters occasionally failed to relay data, sometimes resulting in missing programmed locations.

*2.2 Delineating spring and fall migration*

*2.2.1 Track interpolation and application of the step-threshold method*

We delineated woodcock movements during periods of fall (Aug. 1st–Feb. 25th) and spring (Jan. 5th–Jun. 30th) migration. However, for a small subset of birds (n = 14; 3%) we extended these date ranges due to migratory movements that occurred outside these periods (Supplementary Information A). To ensure that fall and spring migratory movements were delineated separately, we modeled spring migrations first for each woodcock, and shortened the end of the default fall migration timeframe (Aug. 1–Feb. 25) to 1 day before the subsequent spring migration began for that individual.

We interpolated daily locations within each track prior to fitting HMMs, as infrequent and missing locations can impede the ability of the HMMs to detect recursive movements (defined as repeated visitations to the same locations in a systematic manner, sensu Berger-Tal and Bar-David 2015) which could be indicative of stopovers and post-migratory settlement. We used a correlated random walk model implemented in the R package crawl (Johnson and London 2018, R Core Team 2024), which interpolated locations based on prior and subsequent location, speed, and direction. We predicted that interpolated locations would improve the capacity of the HMM to detect recursive movements more accurately during stationary periods, however, during initial model fitting, we observed that they did not accurately reflect the distribution of known migratory movements. To address this tendency, 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). Due to the directional consistency inherent in correlated random walks, models occasionally produced erroneous loops of interpolated points 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 did not incorrectly assign these loops as migratory movements, we removed all loops of interpolated points for which the total length of the loop exceeded 10 times the distance between observed points and replaced the loops with predicted locations spaced evenly between the observed points.

Following point interpolation, we applied the threshold method (Burnside et al. 2017) to define migration for each season on an individual basis, beginning after the first movement ≥16.1 km and ending after the final ≥16.1 km movement. We chose a 16.1 km threshold as it roughly bisects the bimodal distribution of log-transformed step lengths in the dataset (Blomberg et al. 2023). We then used HMMs to refine movement state classifications and assign ending states to incomplete migration tracks.

*2.2.2 Use of additional data streams to inform HMMs*

We measured a subset of variables as additional data streams, which we believed would allow models to better differentiate between stopovers and post-migratory locations (Table 1). Log mean distance to the nearest 7 points measured whether the nearest 7 bird locations (meant to approximate space use over the period of 1 week) reflected intensive use of the same area, and presumably resource utilization, or spread-out movement throughout the area, possibly reflecting exploration. Residence time measured the time difference between the first and last day that the bird was located within a 10 km radius of a focal location. This reflected the difference between the amount of time that woodcock spent occupying stopover sites as opposed to their post-migratory sites. Ordinal day captured woodcocks’ annual phenology of migration. Latitude reflected latitudinal differences in the breeding, migratory, and wintering ranges of woodcock. Distance from start measured whether a bird had moved ≥16.1 km from its position at the beginning of the season, indicating it had departed its initial site to begin migration. Breeding range 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).

We created two versions of each seasonal HMM, described as base and full models, with different suites of data streams used to inform each. The base model included only step length, turn angle, and step length threshold data streams, while the full model included all 6 additional data streams (Table 1). We estimated error rates, migratory characteristics, and long-distance movements separately for each base and full model (described further below) to allow us to infer how additional data streams changed the model’s predictive capacity and ability to make inferences into migratory ecology.

Table 1. Covariates used to delineate movement states in hidden Markov Models (HMMs), and the type of distribution fit to each covariate in the HMMs. Data streams are categorized by their appearance in the base and full models, with the base model using only the 3 core data streams and the full model using all 9 data streams. 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** |
| *Base & Full Model* |  |  |
| Step length | Gamma | Length of the current step |
| Turn angle | Wrapped Cauchy | Angle between the current and previous step |
| Step length threshold | Bernoulli | Binomial indicating if the current step length is ≥16.1 km. Implemented with a fixed distribution so that all steps ≥16.1 km are migratory. |
| *Full model* |  |  |
| 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. |
| Ordinal day | Normal | Days since the beginning of the migratory season |
| Latitude | Normal | Latitude at the beginning of the step |
| Distance from start threshold | Bernoulli | Binomial indicating if the bird moved >16.1 km from its location at the beginning of the migratory season |
| Breeding range | Bernoulli | Binomial indicating if the step begins in the American Woodcock breeding range (Fink et al. 2022). |

*2.2.3 Seasonal HMM design*

We implemented HMMs in the R package momentuHMM (McClintock and Michelot 2018). We conducted separate HMMs for fall and spring migration, and further subset spring migration by sex due to different breeding motivations during spring migration (Blomberg et al. 2023, Slezak et al. in press) which we assumed a priori would result in fundamentally different movement characteristics. We constructed a multi-state model for each HMM to identify transitions occurring between movement states (Fig. 3). 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 transitioned to migration following the first movement ≥16.1 km, which was the only state in which movements ≥16.1 km were permitted. From the migration state, birds could remain in migration or enter either a stopover state or a post-migration state. Once entering the stopover state, birds could remain in stopover or transition back to the migration state. The post-migration state could only be reached from the migration state and did not allow for any further state transitions. These state assignments were generally enforced 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 differed by inclusion of two post-migration 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 switching to less-frequent transmission late in the spring migratory season. Infrequent locations 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 could transition between freely, allowed the model to better account for this source of variation in turn angles when delineating post-migratory movements.

We excluded any birds that did not have at least 1 step ≥16.1 km, or which collected fewer than 3 points, from migratory delineation in the respective season. We assigned a fixed pre-migration state for the initial step of most birds captured during breeding or wintering, and a fixed migration state if the first step was ≥16.1 km. Because birds captured in Virginia, New Jersey, and Maryland were sometimes captured during migration, we allowed the HMM to estimate the initial state of the model for birds captured in these locations. We fixed final steps to the post-migratory state for any fall woodcock that were also known to initiate a subsequent 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 (6% of tracks), early initiation or late termination of migration (3%) or transmitter error (1%). There were also additional issues with initial state designations that were encountered only by the base model (3% of tracks). In these cases, we manually reclassified state assignments (Supplementary Information A). Woodcock that 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.

A diagram of a spring migration

Description automatically generated

Figure 3. Movement state transition diagram for each hidden Markov Model (HMM).

*2.3 Model assessment*

*2.3.1 HMM error rates and variable importance*

We assessed the accuracy of HMM state assignments using a leave-one-out validation based on individuals with known terminal states. For individuals with transmitters that functioned past the end of each migration period, we truncated the movement track by removing one week of points, simulating a scenario where data transmission was lost prior to the end of migration. We then refitted the HMM to the truncated data, and evaluated whether the model correctly assigned the known final movement state. We repeated this process by truncating an additional week of data from each track to evaluate the capacity of models to correctly assign latent states throughout the period of migration (fall: Oct. 1st–Jan 15th, spring: Mar. 15th–Jun. 15th). We repeated the validation process for 50 individuals, with replacement, for each model set. We measured the accuracy of final state assignment based on Type I and Type II errors, where a Type I error occurred when a known post-migratory state was falsely classified as migratory, and a Type II error occurred when a known migratory state was falsely classified as post-migratory.

To determine which additional data streams had the greatest impact on model error rates, we repeated the leave-one-out validation but omitted one of the additional data streams from the full model (Table 1) and measured how Type I and Type II error changed compared to the full and base models. We inferred variable importance based on the relative change in Type I and II errors following removal.

*2.3.2 Migratory characteristics*

We calculated several migration metrics that described the duration, distance, and timing of each movement state. Duration was the sum of the number of days between the first movement in each state and the initial location of the subsequent movement state (e.g. the start and end of migration). Distance was the sum of the total step distance in each movement state. For birds undergoing fall or spring migration, total distance excluded movements designated as stopovers, i.e. steps <16.1 km, and only reflected the summed distance of migratory steps. Timing was the ordinal date of the transition point between movement states. We used medians and ranges to report the population-level timing of migratory initiation and termination, as medians are well suited to accommodating outliers that were common in the initiation and termination dates. We compared all migration metrics between full and base models to evaluate improvements in inference resulting from the more complex full model.

*2.3.3 Long-distance movements and non-migratory individuals*

Woodcock occasionally underwent long-distance movements outside of the spring and fall migratory periods. To determine if the full and base models affected our ability to detect these long-distance movements, we manually classified 3 potential movement states: foray loops, dispersals, and summer migrations (Table 2). Foray loops and dispersals were both presumably exploratory movements, where dispersals resulted in displacement from the original site while foray loops did not. We counted the frequency of dispersals and foray loops based for all birds with locations spanning at least 1 month, which was long enough to correctly classify movement classes. Summer migrations were movements of similar distance and direction to fall migration, but occurred prior to August 1, well before the normal onset of fall migration. We counted the frequency of summer migrations based on all birds tracked between May 1st–Sep. 1st.

To determine if the use of the full and base models impacted our detection of non-migratory individuals, we calculated the percentage of individuals that 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 that 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 the same time periods to determine whether a bird migrated during the season before or after its non-migratory season.

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

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| --- | --- |
| **Class** | **Definition** |
| Summer Migratory | 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. |

*2.4 Data and code availability*

To make data available for use in future research, we uploaded all woodcock GPS locations and their movement state assignments to a Movebank repository (reference ID 351564596). The process of refining 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 HMM error rates*

We analyzed 522 seasonal movement tracks from 401 tagged woodcock, of which 45 tracks (9%) in the full model and 56 tracks (11%) in the base model required modifications to the methods described above to correctly fit the seasonal HMMs (detailed in Supplementary Information A). The full model improved classification accuracy for all three seasonal HMMs compared to the base model (Fig. 4). Type I error rates were similar for full (median 6.0%, range 0–24.2%) and base models (median 6.0%, range 0–24.2%) during fall migration, but Type II error rates were lower for the full model (median 0%, range 0–4.3%) compared to the base model (median 10.6%, range 0–28.3%). The spring male full model exhibited lower rates of Type I (median 8.3%, range 0–15.6%) error than the base model (median 15.6%, range 0–61.1%), and comparable rates of Type II error (full: median 4.3%, range 0–11.4%; base: median 4.3%, range 0–13.6%). The spring female full model exhibited greater Type I errors (median 6.8%, range 0–18.8%) during some time periods than the base model (median 2.1%, range 0–4.2%), but also exhibited reduced Type II error rates (median 6.3%, range 2.0%–11.4%) compared with the base model (median 52.1%, range 10.0–77.6%).

A graph of different seasons

Description automatically generated with medium confidence

Figure 4. Error rates for movement state assignments by hidden Markov models (HMMs) 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.

*3.2 Variable importance*

Individual removal of variables from the full model had low overall impact (median -0.31%, range -17.17–2.70%) on Type I and Type II error rates of the seasonal models (Fig. 5). The importance of a withheld variable often differed by season, with the removal of some variables (e.g., ordinal day) leading to reduced error in one season and increased error in another. Residence time produced the greatest reduction in error rates, with a 2.81–17.17% drop in Type II error rates for all 3 seasonal models. The full model caused a 0.71–42.55% reduction in Type II error rates for those 3 models, suggesting that these variables have a more appreciable impact on error rates when used in aggregate.

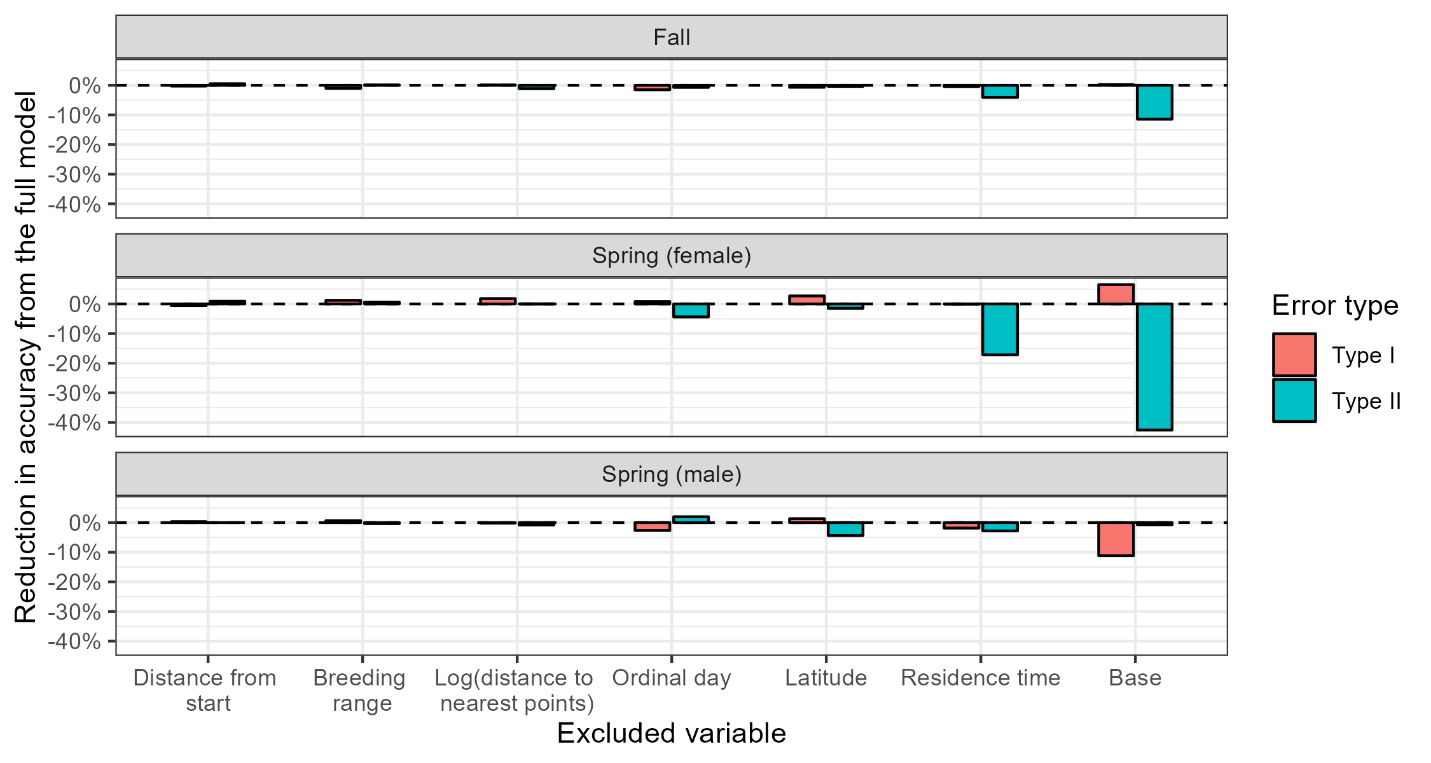


Figure 5. Reduction in accuracy from the full model due to removal of individual data streams, as well as the base model which included none of these 6 data streams. Type I errors occurred when the ending state was falsely classified as migratory, and Type II errors occurred when the ending state was falsely classified as post-migratory. Negative values indicate reductions in accuracy, while positive values indicate that accuracy improved when the variable was excluded from the model.

*3.3 Migratory characteristics*

Among all seasons, the measured characteristics of woodcock migratory movements, such as distance, duration, phenology, and the percentage of individuals completing migration, changed least between the fall full and base models (Table 3). The full spring male model was 1.15 times more likely to identify a migratory endpoint than the base model. There was no difference in mean migratory duration between the two models, although the base model underestimated mean migratory distance by 45 km compared to the full. The spring male base model estimated that the median migratory initiation and termination dates were two days earlier than the full model. The spring female model exhibited more drastic differences between the base and full models, with the full model 2.12 times more likely to identify a migratory endpoint than the base model. The mean duration and distance of spring female migration was underestimated by 7 days and 278 km for the base model as compared to the full model, while the median initiation date of the base model was 4 days earlier and the median termination date was 12 days earlier than that of the full model.

Table 3. Migratory characteristics of full and base models for each seasonal hidden Markov model, in addition to detection rates for long-distance movements outside of spring and fall migration.

|  |  |  |  |
| --- | --- | --- | --- |
| **Season** | **Metric** | **Full model** | **Base model** |
| Fall migration | Percent completed migration1 | 56% | 55% |
|  | Duration2 | 32 days (± 26, 1–134 days) | 32 days (± 26, 1–134 days) |
|  | Distance3 | 1353 km (± 647, 20–3210 km) | 1344 km (± 645, 20–3210 km) |
|  | Initiation date4 | Nov. 7th (Aug. 29th–Jan. 11th) | Nov. 7th (Aug. 29th–Jan. 11th) |
|  | Termination date5 | Dec. 6th (Oct. 28th–Feb. 4th) | Dec. 5th (Oct. 28th–Feb. 4th) |
| Spring migration (male) | Percent completed migration1 | 75% | 86% |
|  | Duration2 | 39 days (± 24, 4–95 days) | 39 days (± 25, 4–95 days) |
|  | Distance3 | 1554 km (± 644, 296–3337 km) | 1509 km (± 649, 262–3337 km) |
|  | Initiation date4 | Feb. 29th (Jan. 6th–Apr. 14th) | Feb. 27th (Jan. 6th–Apr. 17th) |
|  | Termination date5 | Apr. 6th (Jan. 20th–Jun. 7th) | Apr. 4th (Jan. 20th–Jun. 7th) |
| Spring migration (female) | Percent completed migration1 | 55% | 26% |
|  | Duration2 | 49 days (± 29, 2–128 days) | 42 days (± 28, 2–101 days) |
|  | Distance3 | 1671 km (± 626, 455–3424 km) | 1393 km (± 698, 248–3424 km) |
|  | Initiation date4 | Mar. 5th (Jan 14th–Apr. 26th) | Mar. 1st (Jan 14th–Apr. 23rd) |
|  | Termination date5 | Apr. 25th (Mar. 10th–Jun. 28th) | Apr. 13th (Mar. 2nd–May. 25th) |
| Long-distance movements | Dispersals6 | 3 detected (0.7%; 2 M, 1 F) | 2 detected (0.4%; 2 M, 1 F) |
|  | Foray loops7 | 18 detected (4%; 8 M, 10 F) | 15 detected (3%; 7 M, 8 F) |
|  | Summer migrations8 | 3 detected (5%; 2 M, 1 F) | 3 detected (5%; 2 M, 1 F) |

1 Percent of birds which completed their migration prior to the end of their track.

2 Mean duration of migration, with standard deviation and range.

3 Mean distance of migration, with standard deviation and range.

4 Median and range of migratory initiation dates.

5 Median and range of migratory termination dates.

6 Number of individuals which underwent a dispersal among all birds tracked for at least one month (n = 456), including the percentage of birds which underwent a dispersal and the number of dispersals associated with males and females. Note that one bird underwent two dispersals, bringing the total number of dispersal movements detected to 4 for the full model and 3 for the base model.

7 Number of individuals which underwent a foray loop among all birds tracked for at least one month (n = 456), including the percentage of birds which underwent a foray loop and the number of foray loops associated with males and females.

8 Number of individuals which underwent a summer migration among all birds tracked throughout May 1st–Sep. 1st (n = 65), including the percentage of birds which underwent a summer migration and the number of summer migrations associated with males and females.

*3.3 Long-distance movements and non-migratory individuals*

Long distance movements outside of spring and fall migration were less frequently detected using the base model than the full model, with the full model detecting 3 more foray loops and 1 more dispersal than the base model (Table 3). Using the long-distance movements detected by the full model, we found that dispersal movements had a mean duration of 6 days (1–10 days) and the mean distance traveled was 129 km (30–263 km). Foray loops had a mean duration of 20 days (2–95 days) and a mean total distance traveled of 221 km (34–951 km). The number of summer migrations detected was not impacted by use of the full or base model, with 3 of 65 birds (5%; 2 males, 1 female) tracked throughout May 1st–Sep. 1st migrating south during the summer. These summer migratory movements initiated around May 27th, Jun. 20th, and Jul. 13th and terminated around Jul. 8th, Jul. 25th, and Aug. 22nd (Fig. 6). Summer migrations had a mean duration of 39 days (35–42 days) and a mean distance traveled of 756 km (523–1106 km).

Non-migrants were detected by both the full and base models, with some differences in detection rates. The full model detected 6 non-migrants in the fall (3% of individuals tracked between Oct. 15th–Dec. 5th; 3 males, 3 females) and spring (3% of individuals tracked between Feb. 15th–Mar. 29th; 1 male, 5 females). The base model detected one fewer non-migrant in fall (3% of individuals tracked between Oct. 15th–Dec. 8th; 2 males, 3 females) and the same number of non-migrants in spring (3% of individuals tracked between Feb. 15th–Mar. 28th; 1 male, 5 females). The fall non-migrants detected using the full model overwintered in Rhode Island (3), Pennsylvania (1), Connecticut (1), and Virginia (1), while the spring non-migrants summered in Virginia (2), Maryland (1), Florida (1), Georgia (1), and Alabama (1). Individuals that abstained from migration during one season were observed migrating in prior or subsequent seasons when data were available (5 of 5 birds detected in the full model).

A screenshot of a map

Description automatically generated

Figure 6. 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 (Fink et al. 2022). Timelines depict the duration of each movement by month, and each movement is matched from the map to the timeline by color. These long-distance movements are derived from the full model, which includes all possible data streams for informing delineations of woodcock migratory movements.

**Discussion**

Combining the step-threshold method with a set of hidden Markov models resulted in a technique that could be used to estimate the migratory state of American Woodcock with a quantifiable level of accuracy. We found that the use of additional data streams allowed HMMs to fit the migratory movements of woodcock with lower error rates for several seasonal models. The most substantial improvement was among Type II errors for spring females (full: median 6.3%, range 2.0%–11.4%; base: median 52.1%, range 10.0–77.6%), although spring males also had some improvements in Type I error rates early in the season (full: median 8.3%, range 0–15.6%; base: median 15.6%, range 0–61.1%). These differences were mirrored by our migratory characteristics results, which found that spring females had the most substantial differences between the full and base models, with less pronounced differences for spring males and few differences for fall birds (Table 3). Individual variable results suggest that the improved error rates and classification of migratory characteristics seems to be due to several added data streams working in aggregate, with each individual variable having a reduced influence when used in isolation (Fig. 5). The three most important of these variables, ordinal day, latitude, and residence time, demonstrate how spatial and temporal variables can assist in delineating migratory and post-migratory states even for a species that has considerable overlap in seasonal ranges and migratory/non-migratory periods (Chapter 1 of this dissertation, Fish et al. 2024).

Our results demonstrate that certain seasons, in particular spring female migration, are more difficult to accurately characterize using only step length and turn angle. The difficulties encountered with spring females are likely due to female woodcocks’ tendency to nest during spring migration, with continued migration following nest failure (Slezak et al. in press). Under this reproductive system, movement patterns of female woodcock during stopover may be very similar to those post-migration, which may lead to difficulties in discriminating among movement states based only on step length and turn angle. The addition of data streams, especially residence time, ordinal day, and latitude, increased the accuracy of the spring female model (Fig. 5), likely distinguishing among early, southerly nesting attempts that are prone to failure and resumption of migration and later nesting attempts which are less likely to have a subsequent migratory movement. While woodcock have an uncommon breeding system (Slezak et al. in press), this technique for refining HMMs may be useful for any migratory bird with lengthy stopovers and spatial overlap in their seasonal ranges. For example, Sora (*Porzana carolina*) use the Chesapeake Bay in Virginia, Maryland, and Delaware, USA, as both a breeding and a staging area during spring migration, and an HMM technique like ours could be used to differentiate between breeding and staging states based on movement characteristics (Duerr and Watts 2012). This technique may be widely applicable to shorebirds and waterbirds, for which extended stopover and staging behaviors are common (Colwell 2010, Stafford et al. 2014), as well as facultative migrants (e.g. American Robin, *Turdus migratorius*) which encounter substantial overlap in their migratory, breeding, and wintering ranges (Vanderhoff et al. 2020).

We found that the increased classification accuracy of the full model allowed us to identify more long-distance movements outside of fall and spring migration. These movements were relatively uncommon (dispersals: 0.7% of individuals in the full model; foray loops: 4%; summer migrations: 5%), and motivations may range from avoiding negative environmental conditions in the winter (e.g., movements from Rhode Island to Maryland and back) to foraging and exploratory behaviors. Dispersal movements and foray loops have been observed among a variety of songbird, grouse, and shorebirds, most frequently occurring after the breeding season (Earl et al. 2016, Cooper and Marra 2020, Hoepfner 2023). During our study we observed dispersal movements and foray loops throughout the year, including dispersal movements during summer and winter and foray loops during every season except for the peak of spring migration. Cooper and Marra (2020) suggest that the prevalence of dispersals and foray loops is underestimated due to the difficulty of tracking small birds at fine spatial scales, and this may be exacerbated due to the prevalence of single-season movement studies (Marra et al. 2015). Dispersals can in some cases allow population exchange and gene flow among subpopulations, and identifying these movements is important for understanding avian life history and population dynamics (Bohonak 1999, Morales et al. 2010). Robust frameworks for differentiating these movements from fall and spring migrations, such as we present here, could improve our ability to document these movements in future studies.

Onboard data collected by the transmitter, such as acceleration, altitude, or depth, have traditionally been used as data streams to inform animal movement HMMs (Dean et al. 2013), but these data are frequently unavailable for small transmitters. Our results demonstrate that external data streams, such as spatial and temporal variables derived from the movement track, can have a similar benefit for predicting migratory states. Extensions of HMMs which incorporate feedback when calculating transition probabilities, such as an increased likelihood of switching from a foraging state to a transit state after spending time feeding, may also be well suited to explaining the temporal patterns that distinguish migratory stopover behavior from post-migratory resource utilization (Zucchini et al. 2008).

Modeling migratory bird movements presents several challenges that differ from other classes of animal movement. As we demonstrate, small transmitters carried by migratory birds collect sparse and irregular data that can cause difficulty in fitting movement models. Migratory birds also undergo rapid shifts between slow, recursive movements at stopover sites and fast, direct movements during migratory flights, which may impede models that assume consistency in movement modes (e.g., correlated random walk models, Kareiva and Shigesada 1983; see section 2.2.1 of this manuscript for issues encountered). Other studies have demonstrated these issues can be overcome by incorporating new or repurposed statistical models or supplementing GPS data with seasonal abundance data (Rieber 2023, Nicol et al. 2023, Fuentes et al. 2022). Further research on these techniques may allow us to extend movement modeling techniques to a much greater array of avian species and give us greater insight into the ecology and habits of migratory birds.

**References**

Battley, P. F., N. Warnock, T. L. Tibbitts, R. E. Gill, T. Piersma, C. J. Hassell, D. C. Douglas, D. M. Mulcahy, B. D. Gartrell, R. Schuckard, D. S. Melville, and A. C. Riegen (2012). Contrasting extreme long-distance migration patterns in bar-tailed godwits Limosa lapponica. Journal of Avian Biology 43:21–32.

Berger-Tal, O., and S. Bar-David (2015). Recursive movement patterns: review and synthesis across species. Ecosphere 6:art149.

Berigan, L. A., C. S. H. Aulicky, E. C. Teige, D. S. Sullins, K. A. Fricke, J. H. Reitz, L. G. Rossi, K. A. Schultz, M. B. Rice, E. Tanner, S. D. Fuhlendorf, and D. A. Haukos. 2024. Lesser prairie-chicken dispersal after translocation: Implications for restoration and population connectivity. Ecology and Evolution 14:e10871.

Blomberg, E. J., A. C. Fish, L. A. Berigan, A. M. Roth, R. Rau, S. J. Clements, G. Balkcom, B. Carpenter, G. Costanzo, J. Duguay, C. L. Graham, et al. (2023). The American Woodcock Singing Ground Survey largely conforms to the phenology of male woodcock migration. The Journal of Wildlife Management 87:e22488.

Bohonak, A. J. (1999). Dispersal, Gene Flow, and Population Structure. The Quarterly Review of Biology 74:21–45.

Bridge, E. S., K. Thorup, M. S. Bowlin, P. B. Chilson, R. H. Diehl, R. W. Fléron, P. Hartl, R. Kays, J. F. Kelly, and W. D. Robinson (2011). Technology on the move: recent and forthcoming innovations for tracking migratory birds. BioScience 61:689–698.

Burnside, R. J., N. J. Collar, and P. M. Dolman (2017). Comparative migration strategies of wild and captive‐bred Asian Houbara *Chlamydotis macqueenii*. Ibis 159:374–389.

Clements, S. J., L. A. Berigan, A. C. Fish, R. L. Darling, A. M. Roth, G. Balkcom, B. Carpenter, G. Costanzo, J. Duguay, and K. Filkins (2024). Satellite tracking of American Woodcock reveals a gradient of migration strategies. Ornithology:ukae008.

Colwell, M. A. (2010). Shorebird ecology, conservation, and management. Univ of California Press.

Combreau, O., S. Riou, J. Judas, M. Lawrence, and F. Launay (2011). Migratory pathways and connectivity in Asian houbara bustards: evidence from 15 years of satellite tracking. PloS one 6:e20570.

Cooper, N. W., and P. P. Marra (2020). Hidden long-distance movements by a migratory bird. Current Biology 30:4056-4062.e3.

Dawson, W. R. (2020). Pine Siskin (Spinus pinus), version 1.0. In Birds of the World (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA.

Dean, B., R. Freeman, H. Kirk, K. Leonard, R. A. Phillips, C. M. Perrins, and T. Guilford (2013). Behavioural mapping of a pelagic seabird: combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. Journal of The Royal Society Interface 10:20120570.

Duerr, A. E., and B. D. Watts. 2012. Waterbirds of the Chesapeake Bay: Status, ecological requirements, and threats. Center for Conservation Biology, College of William and Mary/Virginia Commonwealth University, Williamsburg, VA.

Earl, J. E., S. D. Fuhlendorf, D. Haukos, A. M. Tanner, D. Elmore, and S. A. Carleton (2016). Characteristics of lesser prairie-chicken (Tympanuchus pallidicinctus) long-distance movements across their distribution. Ecosphere 7:e01441.

Fink, D., T. Auer, A. Johnston, M. Strimas-Mackey, S. Ligocki, O. Robinson, W. Hochachka, L. Jaromczyk, A. Rodewald, C. Wood, I. Davies, and A. Spencer (2022). eBird Status and Trends.

Fish, A. C., A. M. Roth, G. Balkcom, L. Berigan, K. Brunette, S. Clements, G. Costanzo, C. L. Graham, W. F. Harvey, M. Hook, D. L. Howell, S. Maddox, S. McWilliams, S. W. Meyer, T. C. Nichols, J. Bruce Pollard, C. Roy, J. Stiller, D. Washington, L. Williams, and E. J. Blomberg. 2024. American woodcock migration phenology in eastern North America: implications for hunting season timing. The Journal of Wildlife Management n/a:e22565.

Flack, A., E. O. Aikens, A. Kölzsch, E. Nourani, K. R. S. Snell, W. Fiedler, N. Linek, H.-G. Bauer, K. Thorup, J. Partecke, M. Wikelski, and H. J. Williams. 2022. New frontiers in bird migration research. Current Biology 32:R1187–R1199.

Fuentes, M., B. M. Van Doren, D. Fink, and D. Sheldon. 2023. BirdFlow: Learning seasonal bird movements from eBird data. Methods in Ecology and Evolution 14:923–938.

Hoepfner, S. A. (2023). High-Frequency GPS Transmitters Allow Understanding of Breeding Shorebird Movements and Nest Survival Without Human Disturbance. [Online.] Available at https://www.proquest.com/docview/2858557102/abstract/F71320D7248F4BB4PQ/1.

Iverson, A. R., D. L. Humple, R. L. Cormier, and J. Hull (2023a). Land cover and NDVI are important predictors in habitat selection along migration for the Golden-crowned Sparrow, a temperate-zone migrating songbird. Movement Ecology 11:2.

Iverson, A. R., J. L. Schaefer, S. M. Skalos, and C. E. Hawkins (2023b). Global positioning system (GPS) and platform transmitter terminal (PTT) tags reveal fine-scale migratory movements of small birds: A review highlights further opportunities for hypothesis-driven research. Ornithological Applications 125:duad014.

Johnson, D. S., and J. M. London (2018). crawl: an R package for fitting continuous-time correlated random walk models to animal movement data. [Online.] Available at https://doi.org/10.5281/zenodo.596464.

Kareiva, P. M., and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. Oecologia 56:234–238.

Klaassen, R. H. G., M. Hake, R. Strandberg, B. J. Koks, C. Trierweiler, K. Exo, F. Bairlein, and T. Alerstam (2014). When and where does mortality occur in migratory birds? Direct evidence from long‐term satellite tracking of raptors. Journal of Animal Ecology 83:176–184.

Langrock, R., R. King, J. Matthiopoulos, L. Thomas, D. Fortin, and J. M. Morales (2012). Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. Ecology 93:2336–2342.

Linscott, J. A., J. G. Navedo, S. J. Clements, J. P. Loghry, J. Ruiz, B. M. Ballard, M. D. Weegman, and N. R. Senner (2022). Compensation for wind drift prevails for a shorebird on a long-distance, transoceanic flight. Movement Ecology 10:11.

Mander, L., I. Nicholson, R. M. W. Green, S. G. Dodd, R. M. Forster, and N. H. K. Burton (2022). Individual, sexual and temporal variation in the winter home range sizes of GPS-tagged Eurasian Curlews *Numenius arquata*. Bird Study 69:39–52.

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra (2015). A call for full annual cycle research in animal ecology. Biology letters 11:20150552.

McAuley, D. G., D. M. Keppie, and R. M. Whiting Jr. (2020). American Woodcock (Scolopax minor), version 1.0. In Birds of the World (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA.

McAuley, D. G., J. R. Longcore, and G. F. Sepik (1993). Techniques for Research into Woodcocks: Experiences and Recommendations. Proceedings of the eighth American woodcock symposium. U.S. Fish and Wildlife Service, p. 5.

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.

Mills, K. J., B. R. Patterson, and D. L. Murray (2006). Effects of variable sampling frequencies on GPS transmitter efficiency and estimated wolf home range size and movement distance. Wildlife Society Bulletin 34:1463–1469.

Moore, J. D., D. E. Andersen, T. Cooper, J. P. Duguay, S. L. Oldenburger, C. A. Stewart, and D. G. Krementz (2021). Migration phenology and patterns of American woodcock in central North America derived using satellite telemetry. Wildlife Biology 2021.

Morales, J. M., P. R. Moorcroft, J. Matthiopoulos, J. L. Frair, J. G. Kie, R. A. Powell, E. H. Merrill, and D. T. Haydon (2010). Building the bridge between animal movement and population dynamics. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2289–2301.

Moskát, C., M. Bán, A. Fülöp, J. Bereczki, and M. E. Hauber (2019). Bimodal habitat use in brood parasitic Common Cuckoos (Cuculus canorus) revealed by GPS telemetry. The Auk: Ornithological Advances 136:uky019.

Nicol, S., M. Cros, N. Peyrard, R. Sabbadin, R. Trépos, R. A. Fuller, and B. K. Woodworth. 2023. FlywayNet: A hidden semi‐Markov model for inferring the structure of migratory bird networks from count data. Methods in Ecology and Evolution 14:265–279.

Picardi, S., P. Coates, J. Kolar, S. O’Neil, S. Mathews, and D. Dahlgren (2022). Behavioural state‐dependent habitat selection and implications for animal translocations. Journal of Applied Ecology 59:624–635.

R Core Team (2024). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rieber, C. (2023). Treed Gaussian processes for animal movement modeling. Thesis. Kansas State University, Manhattan, Kansas.

Rieffenberger, J. C., and R. C. Kletzly (1966). Woodcock night-lighting techniques and equipment. WH Goudy, compiler. Woodcock research and management:33–35.

Sheldon, W. G. (1960). A method of mist netting woodcocks in summer. Bird-banding 31:130–135.

Slezak, C. R., E. J. Blomberg, L. A. Berigan, R. Darling, A. C. Fish, S. J. Clements, A. M. Roth, R. D. Rau, G. Balkcom, B. Carpenter, G. Costanzo, et al. (In press). Unconventional life-history in a migratory shorebird: desegregating reproduction and migration. Proceedings of the Royal Society B.

Stafford, J. D., A. K. Janke, M. J. Anteau, A. T. Pearse, A. D. Fox, J. Elmberg, J. N. Straub, M. W. Eichholz, and C. Arzel. 2014. Spring migration of waterfowl in the northern hemisphere: a conservation perspective. Wildfowl:70–85.

Vanderhoff, N., P. Pyle, M. A. Patten, R. Sallabanks, and F. C. James. 2020. American Robin (Turdus migratorius), version 1.0. P. G. Rodewald, editor. Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA.

Wright, J. R., J. A. Johnson, E. Bayne, L. L. Powell, C. R. Foss, J. C. Kennedy, and P. P. Marra (2021). Migratory connectivity and annual cycle phenology of Rusty Blackbirds (Euphagus carolinus) revealed through archival GPS tags. Avian Conservation & Ecology 16.

Zhang, J., M. Rayner, S. Vickers, T. Landers, R. Sagar, J. Stewart, and B. Dunphy (2019). GPS telemetry for small seabirds: using hidden Markov models to infer foraging behaviour of Common Diving Petrels (Pelecanoides urinatrix urinatrix). Emu - Austral Ornithology 119:126–137.

Zucchini, W., I. L. MacDonald, and R. Langrock (2017). Hidden Markov models for time series: an introduction using R. CRC press.

Zucchini, W., D. Raubenheimer, and I. L. MacDonald (2008). Modeling time series of animal behavior by means of a latent‐state model with feedback. Biometrics 64:807–815.