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

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Target: Ornithological Applications

**Abstract**

Recent advances that allow 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 -7.3% (range -45.8%–4.7%). Migratory characteristics measured using the full model were similar to the base model in fall and for spring males, although the full model was 2.12 times more likely to identify a migratory endpoint than the base model for spring females. The duration and distance of migration was similarly underestimated by 7 days and 278 kilometers for the base model as opposed to the full model for spring females. Long distance movements outside of fall and spring migration, such as dispersals and foray loops, were less frequently observed with the base model (3 dispersals, 15 foray loops) as opposed to the full model (4 dispersals, 18 foray loops). This technique may be broadly applicable to avian species with widespread distributions and extended stopover behaviors and provides an example of 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 over the last decade (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 rely on satellite networks, such as Argos and GPS satellite platform transmitting terminals (SAT-PTT), can provide data at a high temporal resolution with near global coverage. GPS SAT-PTT transmitters can additionally provide data at high geographic resolution which can be used in studies of bird habitat during migration. Satellite transmission has traditionally required large batteries or solar panels which limit SAT-PTT transmitters 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 usually classified into movement states such as pre-migration, migration, and post-migration. Assignment into movement states can be done using one of several simple frameworks. The range delineation method (Fig. 1; Linscott et al. 2022) is based on the known breeding and wintering ranges of a bird, 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 dictates that migration begins with the first step longer than the distance threshold and ends with the last step longer than the distance threshold. The step-threshold method relaxes the assumption that breeding and wintering ranges do not overlap with the migratory range, which allows this method to be applicable to a much wider range of 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 transmitter failure occurs during the temporal period of migration, it is impossible to determine whether the bird has made its final migratory step of the season and therefore the bird’s final state is unknown (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 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 been applied to a variety of bird taxa, delineating foraging, dispersal, and migratory behaviors for 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, regularized location data over long periods of time, which assists with fitting hidden Markov models. However, small size and forest dwelling habits (i.e. no direct sunlight for solar panels) may preclude high frequency data collection for GPS transmitters attached to smaller birds and impede fitting that data using traditional hidden Markov model approaches.

To demonstrate a situation of a small-bodied bird with a paucity of GPS data, we’ve selected the American Woodcock (*Scolopax minor*; hereafter woodcock). Woodcock are an early successional forest habitat specialist which primarily eats earthworms and are associated more closely with upland habitats than most other North American shorebirds (McAuley et al. 2020). Woodcock are widely distributed throughout eastern North America, typically breeding throughout the northern United States and southern Canada and wintering throughout 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 occasionally nest in the migratory and wintering ranges and have been observed undergoing migratory movements between nesting attempts (Slezak et al. in press). Woodcock can be tracked using GPS SAT-PTT transmitters of 4–6 g (woodcock mass: 116–279 g; McAuley et al. 2020), although extending the data collection period throughout a full migratory season produces infrequent and irregular GPS locations, which provide obstacles for fitting hidden Markov models.

Here we present a modified approach that allows 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 a given GPS point. We demonstrate this approach on data collected from American Woodcock during a range-wide study of their migratory phenology, habitat use, and survival. Our objectives were to determine whether the use of additional data streams would improve estimation of terminal movement states from incomplete GPS tracks and improve our characterization of woodcock migratory distance, duration, phenology, and long-distance movements outside of fall and spring migration. These objectives demonstrate the potential of a hidden Markov model approach for dealing with sparse and irregular GPS data and the ecological insights that can be gained from the application of those models to data from migratory birds.

**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 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 in 2017–2022. 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. The most frequent schedules recorded locations daily, while infrequent schedules recorded locations every 3–7 days outside of migratory time periods. 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. 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 missing programmed locations near the end of battery life.

*2.2 Delineating spring and fall migration*

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

We delineated woodcock movements during fall and spring, 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; 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 a day before the subsequent spring migration began for that individual.

We elected to interpolate daily locations within each track prior to fitting HMMs, as infrequent and missing locations can 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 stopovers and post-migratory settlement. We filled in data gaps using a correlated random walk model implemented in the R package crawl (Johnson and London 2018, R Core Team 2024). Correlated random walk models interpolate locations at a more frequent or regular interval based on its prior and subsequent location, speed, and direction. The addition of interpolated locations allows the HMM to detect recursive movements more accurately during stationary periods using a limited number of infrequent locations. However, during migratory movements, the correlated random walk model can break long migratory steps into a series of short daily movements, making the HMM less likely to identify these movements as migratory. To combat 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 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 far exceeded the distance between observed points and replaced the loops with sets of predicted locations spaced evenly along a line between the observed points.

We first applied the threshold method (Burnside et al. 2017) to define migration for each individual GPS track. We classified woodcock migration within each season on an individual basis, with migration 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*

To assess how the addition of more data streams affected our ability to delineate migratory states using an HMM, we measured a subset of variables which we believed would allow models to better differentiate between stopovers and post-migratory locations (Table 1). The first additional data stream, log mean distance to the nearest 7 points, 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. The second data stream, residence time, measured 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. The third data stream was an ordinal day variable, reflecting woodcocks’ tendency to migrate at similar times each year. The fourth data stream was latitude, reflecting latitudinal differences in the breeding, migratory, and wintering ranges of woodcock. The fifth data stream 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. The sixth additional data stream 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 the model. The base model included just the step length, turn angle, and step length threshold data streams, while the full model included all 6 additional data streams (Table 1). We derived error rates, migratory characteristics, and long-distance movements separately for each base and full model 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 fall and spring HMMs in the R package momentuHMM (McClintock and Michelot 2018). 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 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 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 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 can 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 which 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. Because birds captured in Virginia, New Jersey, and Maryland were sometimes captured after many birds had initiated fall or spring migration, we allowed the HMM to estimate the initial state of the model for birds captured in these locations. 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 (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

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

*2.3 Model assessment*

*2.3.1 HMM error rates*

We assessed the accuracy of final HMM state assignments for the full and base models using a leave-one-out simulation, in which we truncated the tracks of individuals with transmitters that functioned past the end of each migration period, reran the HMM, and evaluated whether the model correctly assigned the final movement state. We iteratively assessed 50 individuals for each seasonal simulation, testing the accuracy of final state assignment when tracks were truncated 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 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.

*2.3.2 Variable importance*

To determine which additional data streams had the highest impact on model error rates, we additionally ran the leave-one-out simulation described in section 2.3.1 on a series of HMMs which followed a similar structure to the full model but omitted one of the additional data streams (included in the full but not the base model) specified in Table 1. We then measured how Type I and Type II error from the model with the omitted data stream changed compared to the full and base models to infer the importance of that data stream for HMM fitting.

*2.3.3 Migratory characteristics*

We calculated several metrics using the base and full models to describe the duration, distance, and timing of each movement state. We calculated durations by summing 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). We calculated distances by summing the total distance of all steps in each movement state 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 the timing of migratory initiation and termination, as medians are well suited to accommodating outliers that were common in the initiation and termination dates.

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

To determine if the full and base models affected our ability to detect extra-seasonal long-distance movements, we manually classified 3 potential movement states outside of spring and fall migration periods: foray loops, dispersals, and summer migrations (Table 2). Foraging loops and dispersals were both presumably exploratory movements, although dispersals resulted in displacement from the original site while foray loops did not. 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. Summer migrations were movements analogous to fall migration, with southerly displacement into the wintering range, but which occurred prior to the nominal onset of the fall migratory season (Aug. 1). 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. All long-distance movement states were constrained to begin and end in a non-migratory state (pre-migration or post-migration), ensuring that long-distance movements were separate from early or continued migration. Small sample sizes prevented reporting standard deviations for the duration and distance traveled of foray loops (full model: n = 18, base model: n = 15), dispersals (full model: n = 4, base model: n = 3), and summer migrations (n = 3), so we reported ranges for these metrics.

To determine if the use of the full and base models impacted our detection of non-migratory individuals, 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.

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

|  |  |
| --- | --- |
| **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 Distribution of methods and results*

To make this data available for use in future research, we have 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 -0.1%, range -1.20–0.19%) on the 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 (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 greatest 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. In comparison, the base model caused a 0.04–2.98% reduction in Type II error rates for those 3 models.

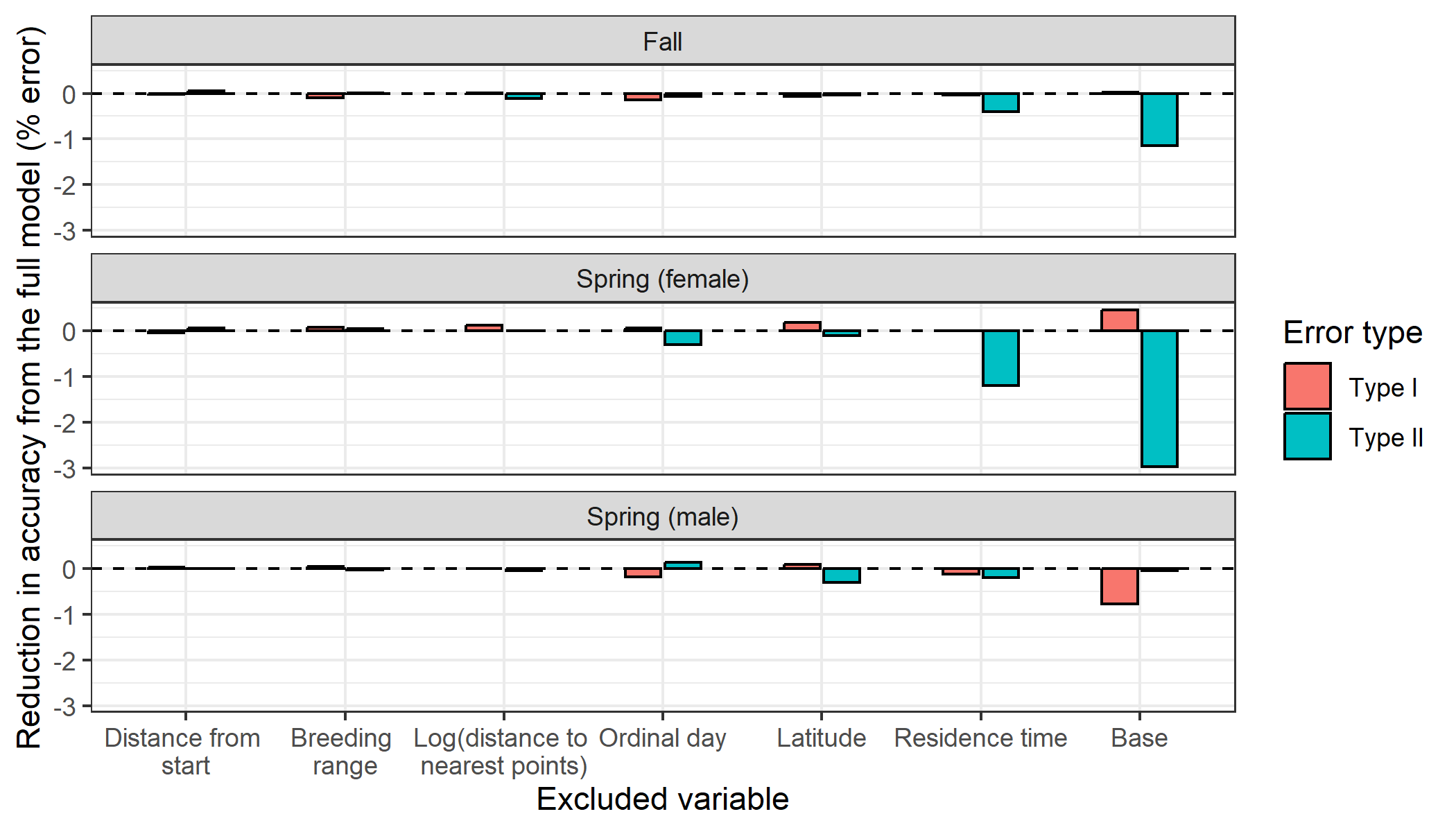


Figure 5. Reduction in accuracy from the full model due to removal of individual data streams, as well as the base model which included none of these 6 data streams. Type I errors occurred when the ending state was falsely classified as migratory, and Type II errors occurred when the ending state was 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*

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). For the spring male model, the full model was 1.15 times more likely to identify a migratory endpoint than the base model. There was no difference in median migratory duration between the two models, although the base model underestimated median 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 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 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. 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**

We found that the use of additional data streams allowed hidden Markov models to fit the migratory movements of American Woodcock with lower error rates for several seasonal models. The most substantial improvement was among Type II error rates 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 migratory characteristics of certain seasonal models seems to be due to several added data streams working in aggregate, although each individual variable has a reduced impact 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 which has considerable overlap in seasonal ranges and migratory/non-migratory periods (Chapter 1 of this dissertation, Fish et al. 2024).

These results demonstrate that certain seasons, in particular spring female migration, are more difficult to fit with the base model than others, and there is a greater benefit to using additional data streams to delineate migration in those seasons. The difficulties encountered with spring females are likely due to female woodcocks’ tendency to make nesting attempts during spring migration, frequently with continued migration after the presumed failure of a nesting attempt (Slezak et al. in press). This reproductive system may produce similar step lengths and turn angles between the stopover and post-migratory states for spring females, which causes the base model to encounter difficulties in differentiating between the two. The addition of data streams, especially residence time, ordinal day, and latitude, increased the accuracy of the spring female model (Fig. 5), likely by helping the model to differentiate between early, southerly nesting attempts that are prone to failure and resumption of migration and later nesting attempts in the breeding range 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 this one could be used to estimate the likelihood that a GPS-tagged Sora in the Chesapeake was in a breeding or staging state based on its 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), and 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, including dispersals, foray loops, and summer migrations. The motivations for these movements, which were observed rarely in our dataset (dispersals: 0.7% of individuals in the full model; foray loops: 4%; summer migrations: 5%), 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, and are most frequently observed after the breeding season (Earl et al. 2016, Cooper and Marra 2020, Hoepfner 2023). Dispersal movements and foray loops observed during our study occurred throughout the year in contrast to post-breeding periods in most other bird species, 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. We similarly posit that the prevalence of dispersals and foray loops throughout the full year is likely underestimated due to the prevalence of single-season movement studies (Marra et al. 2015) and lack of robust frameworks for differentiating those movements from fall and spring migratory behaviors.

While the use of additional data streams to inform animal movement HMMs has traditionally focused on data collected by the transmitter, such as acceleration, altitude, or depth (Dean et al. 2013), such data streams are frequently not available for small transmitters. Our results demonstrate that substituting external data streams, such as spatial and temporal variables, can have a similar benefit for predicting migratory states. Habitat use may also be an informative predictor of migratory state, based on observed differences in migratory habitat from that used during other times of the year (Stanley et al. 2021). 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 largely distinguish migratory stopover behavior from post-migratory resource utilization (Zucchini et al. 2008).

Modeling migratory bird movements, using either HMMs or other movement modeling tools, can present several challenges that differ from other data types. As demonstrated here, the small transmitters that are 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 that impede the fitting of models which 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 eBird citizen science 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.

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