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The `movetrack` Git repository: https://codeberg.org/g-rppl/movetrack

movetrack: An R package to model flight paths from radio-telemetry networks

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ABSTRACT Tracking small- to large-scale movements of animals is important for studying their interactions with the environment, including how they adjust and adapt their migration in response to environmental and human-induced changes. Despite the technical progress in tracking devices, a major challenge remains for small animals—such as songbirds, bats, and insects—because GPS transmitters are still too heavy to be carried by these lightweight species. Automated radio-telemetry offers a lightweight, scalable alternative. However, unlike GPS, radio-telemetry does not yield precise location data—only information about receiving antennas and the strength of detected signals. Existing localisation methods either rely solely on receiver locations or offer only small-scale, site-specific estimates, limiting their ability to reconstruct full flight paths. We fill this gap by presenting `movetrack`, an R package that reconstructs animal trajectories from automated radio-telemetry data—such as that collected by the Motus Wildlife Tracking System—using a hidden Markov model (HMM) framework. Our approach combines coarse geometric position estimates—based on antenna bearing and signal strength—with an HMM that accounts for measurement error, temporal gaps, and movement dynamics. The model distinguishes behavioural states such as migratory flight, local movement, and stopovers by analysing directional persistence and speed of the animal. We validate `movetrack` using controlled low-altitude aircraft flights, simultaneously recorded with GPS and radiotelemetry, to simulate migratory flights of aerial species. Our results convincingly demonstrate that

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`movetrack` produces biologically realistic flight path estimates with quantifiable uncertainty, enhancing localisation in telemetry-based movement research. `movetrack` provides a straightforward and practical approach, without requiring enhanced mathematical knowledge, to precisely reconstruct flight movements in a high spatiotemporal resolution. The R package enables researchers and conservationists to better study the response of aerial animals to environmental change and, ultimately, to formulate more effective conservation measures, for instance in relation to potential conflicts with anthropogenic stressors, such as artificial light at night, pesticides, and human-made structures.

KEYWORDS animal movement; hidden Markov model; random walk; R package; radio-telemetry; animal-tracking

1 Introduction

Tracking the intricate movements of individual animals is essential for understanding their behaviour and interactions with the environment, such as habitat use and foraging strategies (Kays et al. 2015). Collecting movement data across many individuals enables us to uncover their roles in broader ecological processes, such as biomass flow or pollination (Bauer and Hoye 2014; Schick et al. 2008; Nathan et al. 2008), as well as how migratory species adjust and adapt to environmental change (Both et al. 2006; Kubelka et al. 2022). While the technical progress and miniaturisation of GPS tracking devices has revolutionised our ability to track larger species with remarkable spatial and temporal precision (e.g., Williams et al. 2020), the same level of detail remains elusive for smaller animals such as most songbirds, bats, and insects. This is because the 'high' weight of currently 2 g even in the lightest GPS transmitters (Microwave Solar PTT, Lotek Sunbird) is not feasible for tagging animals lighter than 40 g, given the commonly accepted guideline that tags should weigh less than 5% of the animal's body weight (Bridge et al. 2011; L. Mitchell et al. 2025). Radio-telemetry, which utilises lightweight transmitters (currently down to 0.06 g, CTT BlūMorpho) suitable for animals of > 1.2 g, offers a commonly used alternative to GPS transmitters (Taylor et al. 2017; L. Mitchell et al. 2025). Unlike the latter, which transmit recorded locations via satellite or cellular networks, radio transmitters emit frequent radio signals in a unique manner—either on a specific frequency or in an individually distinct signal pattern. These signals must then be recorded by specialised receiving devices. Traditionally, this was done manually using handheld radio antennas and receivers operated by researchers. Today the process is often largely automated by arranging multiple digital receiving stations—each commonly equipped with several antennas—in a network, and by continuously listening to the selected frequency of the transmitters' signals. This approach has improved data collection efficiency significantly in terms of manpower, the spatial and temporal coverage, as well as the corresponding resolution of location estimates (e.g. Taylor et al. 2017; Griffin et al. 2020).

Unlike GPS, radio-telemetry does not yield precise location data—only information about receiving antennas and the strength of detected signals. As a result, most previous studies relied on coarse, station-level location estimates, typically by connecting the positions of the receiving stations (G. W. Mitchell et al. 2012; Smetzer, King, and Taylor 2017; Lagerveld et al. 2024; Brust and Hüppop 2021, Figure 1), while other methods are constrained to fine-scale movements derived from triangulation (Gottwald et al. 2019; Fisher et al. 2020), signal arrival time of difference (Beardsworth et al. 2022), or signal strength measurements alone (Rueda-Uribe et al. 2024). The latter two typically require site-specific calibrations, limiting scalability and reducing reproducibility across study areas.

To overcome these limitations, integrating hidden Markov models (HMMs) into movement analysis offers a powerful solution (Baldwin et al. 2018; Jonsen, Flemming, and Myers 2005). HMMs are uniquely suited to handle temporally irregular data with varying spatial errors, making them ideal for reconstructing positions as well as behavioural states from telemetry data (Jonsen, Flemming, and Myers 2005; Jonsen et al. 2013; Baldwin et al. 2018). By applying this method to radio-tracking data of aerial movements, researchers can generate more detailed flight tracks with higher spatial and temporal resolution (Figure 1, 2). Based on such tracks, we would gain deeper insights into the spatiotemporal behaviour of small species, for instance how individual animals may adjust their paths to human-made structures, e.g. in terms of avoidance behaviour to wind turbines or bridges (Barré et al. 2020; Schwemmer et al. 2023), or artificial light at night, e.g. in terms of attraction and reaction (McLaren et al. 2018; Desouhant et al. 2019). With the R package `movetrack`, we aim at making this approach more accessible to a broad audience, bridging the gap between technological capability and ecological understanding.

2 Methodology

2.1 Calculate coarse raw positions

Unlike with data from GPS devices, exact geographic positions cannot directly be inferred from radio-telemetry data. Instead, it is necessary to estimate the geographic positions of an animal from available information about the location of the radio-receiving station(s), the antenna bearing, its spatial probability of detection and the strength of the detected radio signal. For this purpose, `movetrack` uses a geometric approach described in Baldwin et al. (2018). This is a three-step process that utilises basic principles of antenna geometry (Figure 3): (i) For each detection, a coarse raw position is calculated along the directional beam of the receiving antenna. The distance to the station is assumed to be half of the theoretical antenna detection range, which can be specified for each antenna type (Birds Canada 2025). Detections from omnidirectional antennas are omitted. (ii) All raw positions are provided with oscillating longitudinal and latitudinal standard deviations, i.e. measurement errors, that arise from antenna geometry and orientation (Baldwin et al. 2018, see Supplement S1). Longitudinal error reaches up to half the theoretical antenna detection range when the antenna is oriented east or west and is minimal when oriented north or south; the opposite is true for latitudinal error (see Supplement S1). (iii) Finally, the raw positions and measurement errors from all antennas are aggregated over user-defined time intervals. For each interval, weighted means—based on signal strength (e.g., measured in dB)—are calculated for both the raw positions and measurement

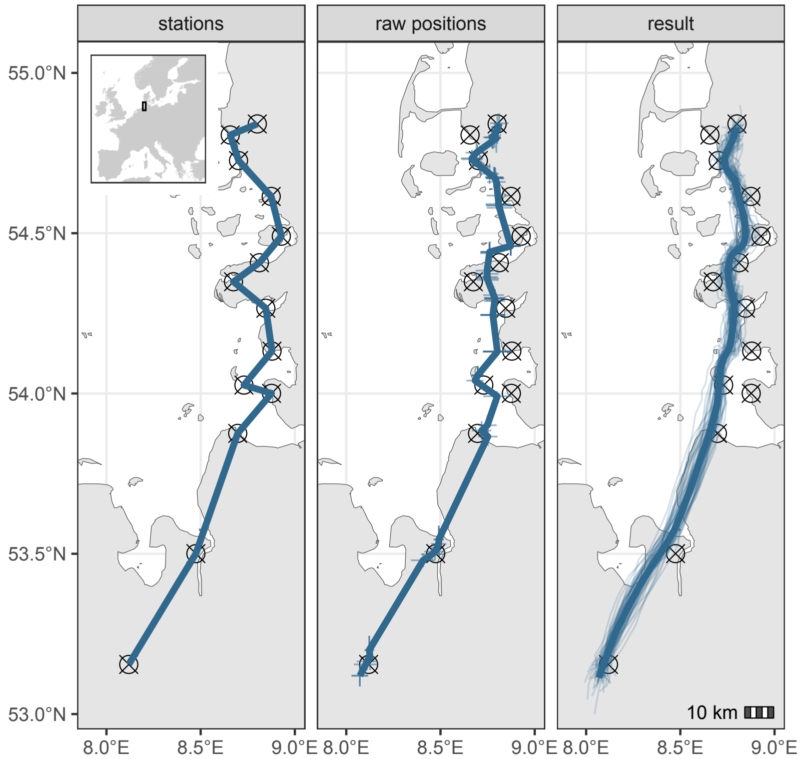

Figure 1: Example track of a nocturnal flight bout by a Eurasian reed warbler *Acrocephalus scirpaceus* (6.1 s burst interval) during autumn migration along the German North Sea coast reconstructed using different methods. This track is part of the data included with the package. Left: Receiving radio-telemetry stations (⊗) connected to form a track based on the last signal received at each station. Middle: Coarse raw positions calculated internally with default settings for each time interval. Segments indicate longitudinal and latitudinal standard deviations, i.e. estimated measurement errors. Right: Final posterior median positions with 100 sampled tracks from the posterior distribution obtained using default `movetrack` arguments.

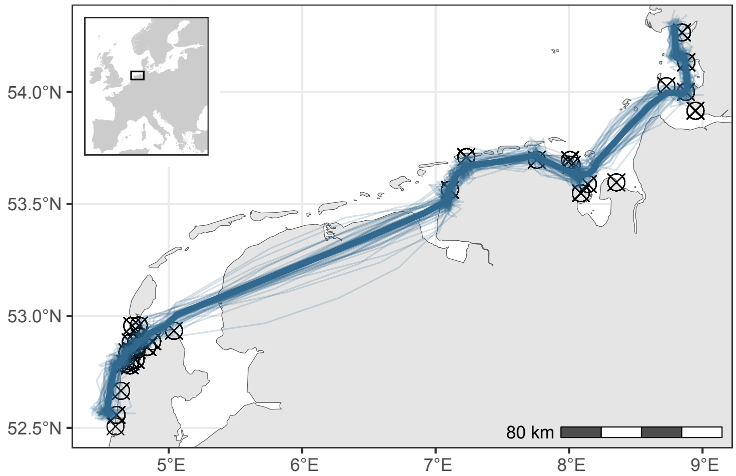

Figure 2: Example track of a nocturnal flight bout by a song thrush *Turdus philomelos* (7.3 s burst interval) during autumn migration along the German North Sea coast reconstructed using default `movetrack` arguments. Shown are posterior median positions and 100 sampled tracks from the posterior distribution together with receiving radiotelemetry stations (⊗). This track is part of the data included with the package.

errors (Figure 1). This data forms the basis of the observational part in the HMM.

2.2 Hidden Markov model

HMMs describe the evolution of a hidden state process, $\{S_t\}$ (i.e. behavioural states), which is not directly observable through telemetry data but can be inferred from an associated sequence of observable random variables, $\{Y_t\}$, such as locations derived from telemetry (Auger-Méthé et al. 2021). In the case of `movetrack`, the user specifies the number of hidden states, N, which determines the range of behavioural patterns the model can represent. These states might correspond to behaviours such as 'migratory flight', 'local movement', or 'stopover', but these are merely examples—the actual interpretation of states depends on the number chosen by the user (default: 2) and the data at hand.

In the process model, each true location z—that is, the actual, unobserved two-dimensional location of the animal at time t, governed by the hidden state process and distinct from the potentially noisy telemetry observations—is assumed to be generated by one of N distributions, where N is the number of states. The hidden state process that determines which of the distributions is chosen at time t is modelled as a Markov chain: the probability of being in a particular state at time t depends only on the state at $t-1$ (Auger-Méthé et al. 2021, Figure 4). An observation model then links these latent true locations to the coarse raw positions, incorporating their measurement errors obtained in the previous step. The HMM therefore consists of three components described below.

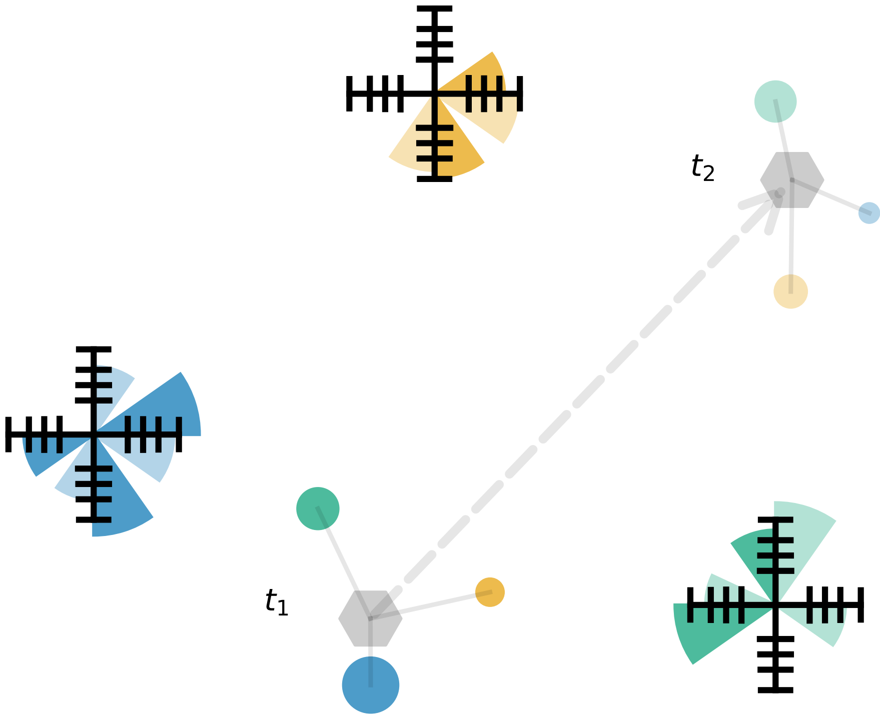

Figure 3: Illustration of how raw positions are estimated by integrating data from station locations, antenna bearings, and signal strength (represented by wedge length). Detections from all stations and antennas are aggregated over fixed time intervals, producing a single coarse raw position per interval—illustrated here for two consecutive intervals t_1 and t_2. For simplicity, only the combined contributions from each station (shown as coloured dots) to the resulting coarse raw positions (diamonds) are displayed. Each position is computed as a signal-strength-weighted mean, with point size indicating the strength of contribution. Estimation accuracy improves with the number of contributing stations and antennas.

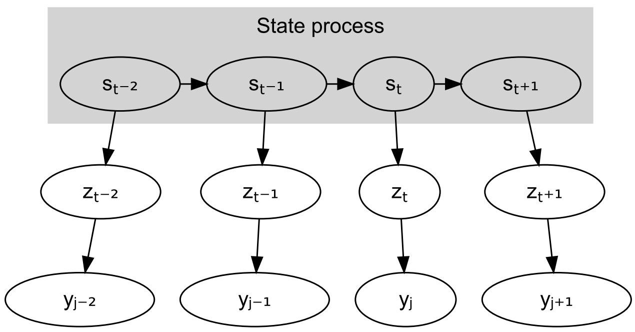

Figure 4: Basic model structure showing the hidden state process $\{S_t\}$ governing the real locations z and the observed locations y at time t.

2.2.1 State process

The state process $\{S_t\}$ of a N-state HMM for T time steps is characterised by its state transition probability matrix $\Gamma^{(t)} = (\gamma_{i,j}^{(t)})$, where $i, j = 1, \dots, N$ and $\gamma_{i,j}^{(t)} = \Pr(s_{t+1} = j | s_t = i)$. The probability of transitioning to state s_t from state s_{t-1} is

$$s_t \sim \text{Categorical}(\Gamma^{(t-1)}), \quad 1 \leq t \leq T.$$

2.2.2 Process model

The process equation for the true locations of the animal at regular time intervals t, $z_t = \begin{bmatrix} z_{t,\text{lon}} \\ z_{t,\text{lat}} \end{bmatrix}$, assumes that the animal's location at time t does not only depend on the previous location, z_{t-1}, but also on the animal's previous movement in each coordinate, $z_{t-1} - z_{t-2}$:

$$z_t = z_{t-1} + \lambda_n (z_{t-1} - z_{t-2}) + \epsilon_t, \quad \epsilon_t \sim \text{N}(0, \Omega), \quad 1 \leq n \leq N,$$

where the covariance matrix for the process variation, Ω, is

$$\Omega = \begin{bmatrix} \tau^2_{\epsilon,\text{lon}} & 0 \\ 0 & \tau^2_{\epsilon,\text{lat}} \end{bmatrix}.$$

The state-dependent parameter λ_n ranges between 0 and 1 (i.e. $0 \leq \lambda \leq 1$) and controls how strongly the animal's current movement is influenced by its previous direction and speed. Higher values of λ_n, approaching 1, indicate strong directional persistence—suggesting that the animal continues to move in a similar direction and at a consistent speed—typical of migratory flights. In contrast, lower values of λ_n reflect more random or diffusive movement patterns, where current direction and speed are less dependent on past movement—characteristic of local movements. During stopovers, λ_n is expected to be close to 0, reflecting that the animal did not move or remained within a certain local patch.

By default, `movetrack` estimates track-specific λ_n values. While it is also possible to use a common λ_n across all tracks, this is not typically recommended. A shared value for λ_n may be advantageous in specific scenarios—such as (i) when all tracks are expected to exhibit similar movement patterns, or (ii) when individual tracks have relatively few observations, in which case pooling information across tracks can enhance model stability. In most applications, however, allowing individual λ_n values better captures the track-specific movement patterns of each individual.

2.2.3 Observation model

The observed locations of an animal, $y_j = \begin{bmatrix} y_{j,\text{lon}} \\ y_{j,\text{lat}} \end{bmatrix}$ (i.e. the calculated coarse raw positions), often have irregular time intervals j, with J representing the total number of observed locations. Therefore, the true location of the animal is linearly interpolated to the time of the observation, with w_j representing the proportion of the regular time interval between $t-1$ and t when the observation y_j was made:

$$y_j = w_j z_t + (1 - w_j) z_{t-1} + \theta_j, \quad \theta_j \sim \text{T}(0, \sigma_j), \quad 1 \leq j \leq J,$$

where $\mathrm{T}(0, \sigma_j)$ denotes a bivariate Student's t-distribution with measurement error $\sigma_j = \begin{bmatrix} \sigma_{j,\mathrm{lon}} \\ \sigma_{j,\mathrm{lat}} \end{bmatrix}$. The HMM is implemented using Hamilton Monte Carlo in Stan (Carpenter et al. 2017).

3 Application

3.1 Workflow

The methods provided in this package are applicable to various types of automated radio-telemetry data, including—but not limited to—the Motus Wildlife Tracking System (Taylor et al. 2017). Below, we present a brief walkthrough of the `movetrack` package for data of the latter system and demonstrate how to inspect and visualise the results. For the latest quickstart example, refer to the package documentation (https://g-rppl.codeberg.page/movetrack).

Data preprocessing: Start by 'cleaning' and refining the raw detection data—which consists of signal strengths recorded for each antenna at every receiving station over time—to eliminate false positives, for instance by following the principles explained in Birds Canada (2024). Also address any other data quality issues specific to your telemetry setup, such as time synchronisation errors or inconsistent metadata. Identify and extract periods of interest from the detection data—such as continuous migratory flights during a single night (e.g., 10 hours in nocturnal migrants (Liechti et al. 2018)) or localised movement during foraging bouts (e.g., 5 hours in short-ranging seabirds (Davoren and Montevecchi 2003)). The maximum duration of each track is influenced by both the number and quality of detections. Animals that are continuously recorded with high detection frequency can support longer segments, whereas sparse or irregular detections should be divided into shorter intervals to minimise the impact of data gaps. As a general guideline, each track segment should be limited to a maximum duration of 24 hours. Exceptions may apply to long, uninterrupted migratory flights, such as those in waders (Anderson et al. 2019), especially across continental networks of receiving stations (Taylor et al. 2017). This recommendation supports computational efficiency and generally helps avoid introducing large gaps or inconsistencies that often emerge over longer timeframes. That said, this timespan can be extended by adjusting the `dTime` argument in the next step, which defines the duration over which detections are aggregated to estimate a position. A lager `dTime` value—i.e. lower temporal resolution—permits aggregation over longer periods, provided data continuity remains sufficient. Finally, organise the processed data into a table of distinct tracks, each representing an individual movement bout and assigned a unique identifier. By default, the Motus `tagDeployID` will be used. Example Motus data is included in the package.

Modelling: Parse your preprocessed raw data to `track()` and adjust additional arguments summarised in Table 1 as needed. Input arguments are unique track IDs, timestamps, station locations, antenna bearings, and signal strength for each detection. By default, these input variable names align with standard Motus variable conventions. Use `aRange` to specify theoretical antenna detection ranges in kilometres. This can be a single integer value or a named list of values for different antenna types defined in the `aType` column.

Table 1: Summary table of input arguments and output variables contained in the `movetrack` object returned by `track()`.

Input	Output
• Track IDs[a] • Timestamp[a] • Receiver location[a] • Antenna bearing[a] • Signal strength[a] • `aRange` • `dTime` • `states` • `i_lambda`	Posterior distributions[b] for: • longitudes and latitudes, • distances between points in m, • and speed in ms^{-1} per Track ID and `dTime`.

[a]By default, these variables use standard Motus variable names.
[b]These can be summarised using highest density intervals or quantiles of any desired width.

Table 2: Default antenna types and their corresponding theoretical detection ranges used by `track()`.

Antenna type	Theoretical range
3-element Yagi	~5 km
4-element Yagi	~6 km
5-element Yagi	~8 km
6-element Yagi	~10 km
9-element Yagi	~15 km

By default, approximations for different Yagi-antennas, as summarised in Table 2, are used (Birds Canada 2025; Mills et al. 2011). With `dTime`, specify the time interval in minutes for which positions are estimated. The default is 2 min, but this should be adjusted according to the tag's burst interval and the expected flight speed—longer burst intervals, e.g. 29 s, or faster movements, e.g. 30 ms^{-1} due to tailwind, typically require longer intervals, e.g. 5 min. Specify the number of states in the model using the `states` argument, where each state represents a distinct movement behaviour such as migratory flight, local movement, or stopover (default: 2). Optionally, the argument `i_lambda` can be used to fix the lag-correlation parameter λ_n across all tracks (see Section 2.2.2). `track()` returns a `movetrack` object containing complete posterior distributions for positions at each time step, along with corresponding distances and speeds between positions. Set `model = FALSE` to extract the internally calculated coarse raw positions and measurement errors for each time interval without modelling.

Inspect results: The `movetrack` object, i.e., the fitted model object, can be summarised in different ways. Median results can be converted to a `data.frame` using `as.data.frame()`, and posterior distributions for specific output variables can be summarised using highest density intervals or quantiles via `summarise()`. For visual representation, `plot()` provides graphical summaries of individual variables, while `mapTrack()` creates geographic visualisations of the estimated tracks.

3.2 Limitations

The accuracy of the model is highly dependent on sufficient detection data. Specifically, (i) adequate receiver coverage is essential to avoid large spatial gaps, as such gaps can lead to inaccurate estimates, particularly for flight speed. (ii) The burst intervals of the tags should be matched to the expected airspeed of the animal. Faster-moving individuals require shorter intervals to accurately capture their movements, whereas longer intervals may lead to coarser and less reliable movement estimates. For migrating animals, suitable burst intervals are likely in the range of 10 to 30 seconds, although this may vary depending on the species and ecological context. (iii) Data should be pre-filtered to focus on continuous tracks, rather than isolated detections spread over extended time periods, as large temporal gaps between detections likely distort movement patterns and reduce model accuracy.

Due to the inherent limitations of radio-telemetry data, flight altitude is intentionally not estimated in this package. As always, results should be interpreted with caution, considering the geographical characteristics of the area, the migration ecology of the species and the overall ecological context of the movement behaviour.

4 Validation study

Validation is a crucial step in assessing the reliability and applicability of movement models, especially when working with radio-telemetry data that lacks direct positional information. By comparing model outputs to known or controlled conditions, validation studies help evaluate how accurately the model reconstructs true flight tracks and accounts for observational limitations such as signal noise and antenna array geometry. This process is essential to ensure that the resulting inferences are biologically meaningful, robust, and suitable for ecological interpretation.

4.1 Procedure

On July 9 and 11, 2024, we conducted test flights using a Robin DR 400 aircraft to simulate bird movement along a predefined flight path over a total distance of 1,554 km. The aircraft was flown at low altitudes, predominantly below 250 m above sea level, and at minimal possible ground speed ranging between 30–65 ms^{-1} (see Supplement S2), reflecting the low-altitude flight patterns as closely as possible while being two to six times faster than typical ground speed of flying birds (Bruderer and Boldt 2001; Bruderer, Peter, and Korner-Nievergelt 2018; Alerstam et al. 2007). We attached five uniquely coded NTQB2-2 radio tags (Lotek Wireless Inc.) with different burst intervals `tagBI`—7.1, 7.3, 19.1, and 29.3 s (two tags)—to the aircraft's non-metallic wings and undercarriage covers using duct tape. The signals from the tags were recorded through a regional automated radio-telemetry receiver network positioned along the German North Sea coast (see Supplement S3). This network forms part of the Motus Wildlife Tracking System, a global collaborative network for tracking wildlife movements (Taylor et al. 2017; L. Mitchell et al. 2025, https://motus.org).

Most radio-receiving stations were equipped with three or four 6-element Yagi antennas (Vårgårda, Sweden) pointing in different directions (see Supplement S3). The antennas of the onshore stations on the mainland were predominantely directed towards the North Sea and along the coastline, often lacking an antenna pointing inland (see Supplement S3). Radio-telemetry data collected via Motus was then compared with GPS-accurate location data of the aircraft obtained from FlightRadar24 (https://flightradar24.com), by matching each Motus detection to the temporally closest GPS data point. The datasets were closely synchronised, with a maximum time difference of 6.3 seconds between a Motus detection and its nearest corresponding GPS fix. All input parameters (see Table 1) were systematically varied to evaluate their influence on the location estimates. The theoretical antenna detection range (`aRange`) was held constant across antenna types within each model run but varied between runs. Specifically, we used `aRange` values of 10, 15, 20, and 25 km, `dTime` values of 0.5, 1, 2, and 3 min, and models with one and two states.

4.2 Results and discussion

Due to the limited coverage of the radio-telemetry network, particularly inland, telemetry data was obtained for only a subset of the entire GPS track (Figure 5, 6). The number of detections by Motus stations ranged from 3,062 (`tagBI = 7.3` s) to 96 (`tagBI = 29.3` s) per tag, highlighting the critical role of the tag's burst interval configuration in optimising radio-telemetry performance. For the relatively fast-moving aircraft, burst intervals of 19.1 s or longer were insufficient for meaningful position estimates (see Supplement S4, S5). Consequently, the analysis focuses on data from the tag with a burst interval of 7.3 s.

An analysis of the input arguments `aRange` and `dTime` showed a moderate effect on positional accuracy (Figure 7). The optimal combination (`aRange = 10` km, `dTime = 0.5` min, `states = 2`) achieved a median horizontal error of 2,757 m (90% highest density interval: 255–10,382 m), reflecting substantial variability in accuracy across scenarios (Figure 5, 6, see Supplement S6). Given the aircraft's ground speed of 30–65 ms^{-1}, the optimal `dTime` values were considerably shorter than those suitable for birds, whose ground speed is approximately 10–20 ms^{-1} (Bruderer and Boldt 2001; Alerstam et al. 2007). For such speeds, the default time interval of 2 min would likely be a reasonable starting point.

Overall, 68% of true locations fell within the 90% highest posterior density interval (HPDI) of the estimated positions for the corresponding time step, and 85% were within the 99% HPDI. Positional accuracy varied with both, the distance between the aircraft and radio-telemetry stations, as well as the number of antennas receiving the signal simultaneously (Figure 8). Greater distances and fewer receiving antennas correlated with reduced accuracy, underscoring the importance of station configuration and network density for effective tracking.

5 Conclusion

Here, we introduce `movetrack`, an R package designed to reconstruct animal movement tracks from automated radio-telemetry data using a HMM. By integrating information on antenna geometry, signal strength, and spatiotemporal uncertainty, `movetrack` overcomes key limitations of traditional approaches that rely solely on receiver locations. The package is broadly

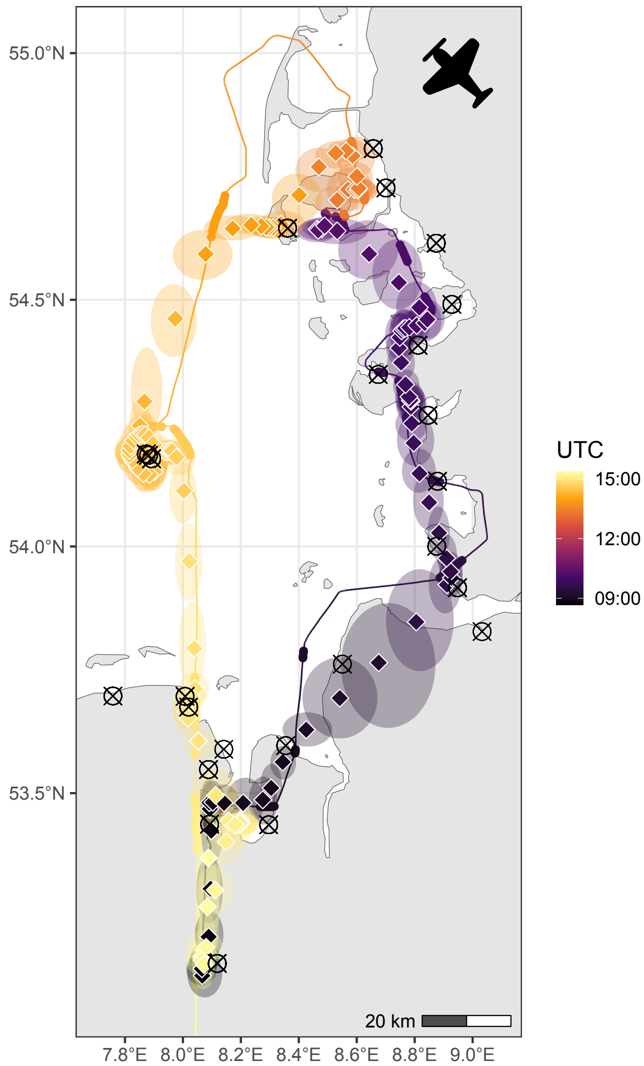

Figure 5: Estimated positions (diamonds) together with the GPS track of the test flight (line), colour-coded by coordinated universal time (UTC). GPS locations with detections of the corresponding tag (`tagBI = 7.3 s`) by radio-telemetry stations (⊗) are represented by dots, longitudinal and latitudinal model uncertainties (90% HPDI) are indicated by ellipses.

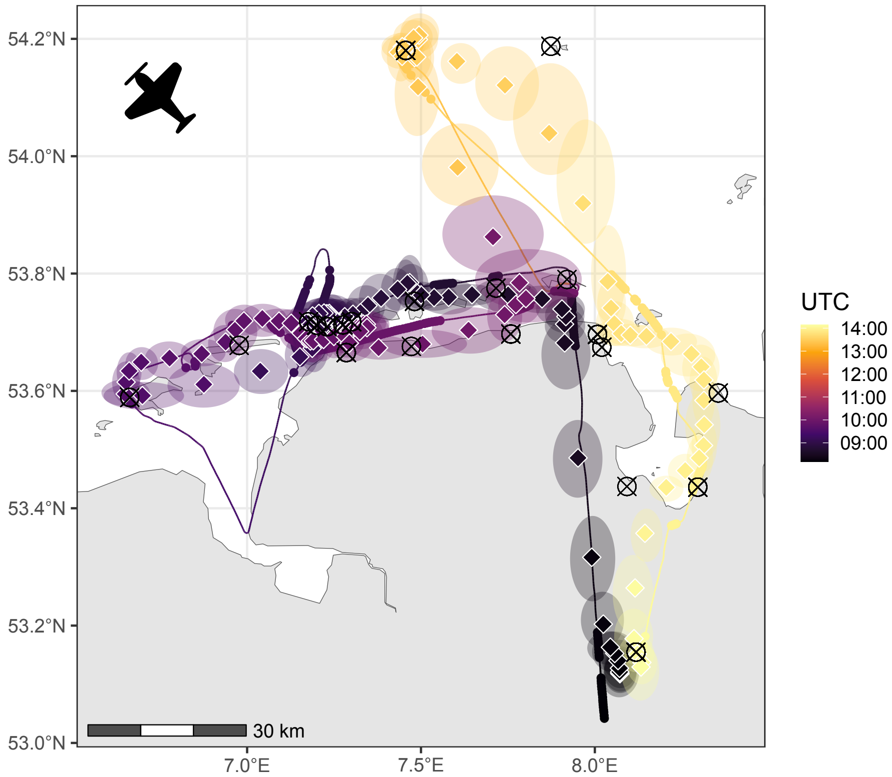

Figure 6: Estimated positions (diamonds) together with the GPS track of the test flight (line), colour-coded by coordinated universal time (UTC). GPS locations with detections of the corresponding tag (`tagBI = 7.3 s`) by radio-telemetry stations (⊗) are represented by dots, longitudinal and latitudinal model uncertainties (90% highest posterior density interval) are indicated by ellipses.

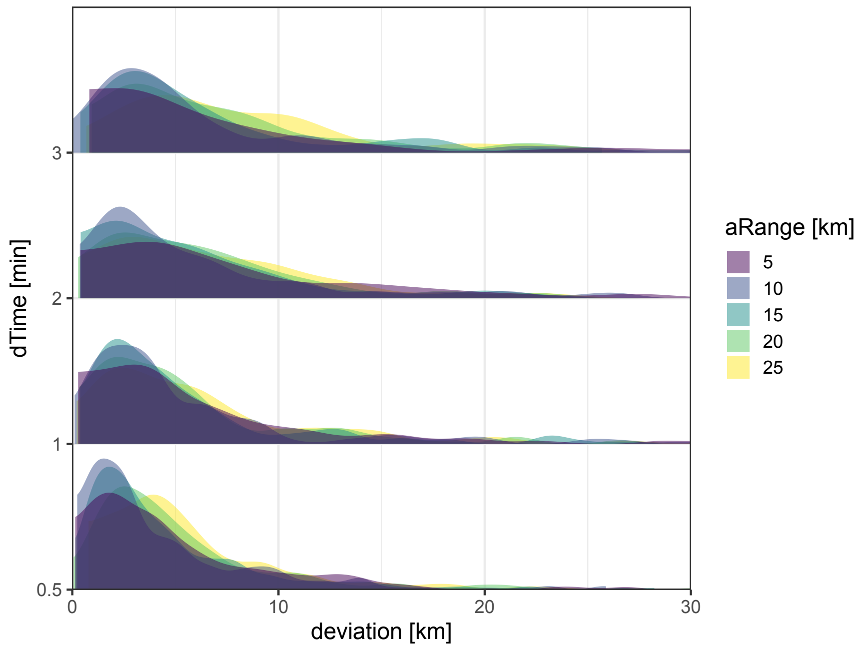

Figure 7: The influence of the input arguments `aRange` (the theoretical antenna detection ranges) and `dTime` (the time interval for which positions are estimated) on the deviation between the estimated positions and the GPS locations was moderate (`tagBI = 7.3 s`).

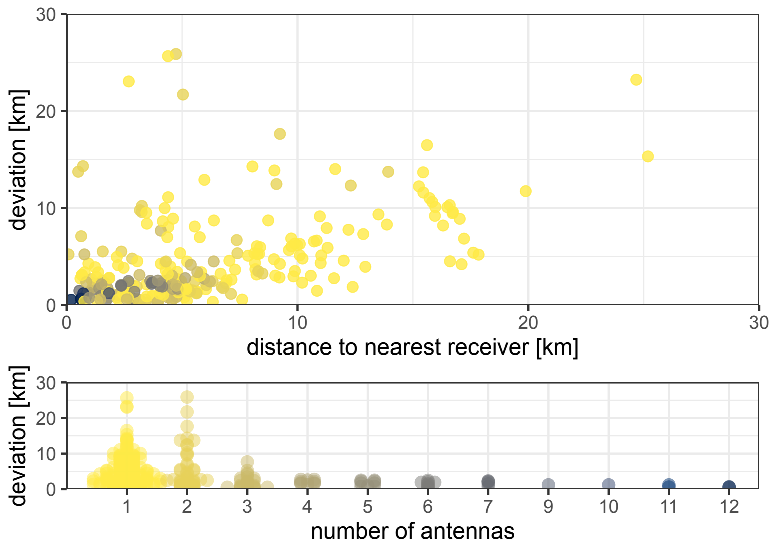

Figure 8: Model uncertainty, i.e. the deviation between the estimated positions from the radio-telemetry data and the GPS locations, increased based on the aircraft's distance to the nearest receiver station (upper panel) and decreased with the number of antennas simultaneously receiving the signal (`tagBI = 7.3 s`), represented by different colours (lower panel).

applicable across species and telemetry systems. Our validation study highlights the package's potential to reconstruct large-scale movement patterns, while also underscoring the challenges of achieving high spatial precision with sparse telemetry data. Performance depends on factors such as the alignment between tag burst intervals and animal ground speed, as well as the spatial layout of the telemetry network—particularly receiver density and antenna orientation. Although accuracy is constrained by data quality, `movetrack` provides a robust framework for studying movements of small animals. Future developments, such as incorporating barometric pressure into radio tags for altitude estimation, could further expand the package's capabilities. Potential applications include investigating individual flight decisions, describing for instance migratory routes and comparing behavioural patterns across populations, species and animal classes (L. Mitchell et al. 2025). This will provide the basis for a more detailed study of how flying animals react and adapt to anthropogenic changes on a large spatial and temporal scale.

6 Code availability

`movetrack` is licensed under the MIT License and available on Codeberg at https://codeberg.org/g-rppl/movetrack. Contributions of all kinds, including pull requests and bug reports, are highly encouraged and warmly welcomed! Data and code to reproduce the validation study are available from the Codeberg Git repository https://codeberg.org/migecol/motus_localisation or through the accompanying Dataverse at https://doi.org/10.57782/WGHWTT.

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References

Alerstam, Thomas, Mikael Rosén, Johan Bäckman, Per G. P Ericson, and Olof Hellgren. 2007. "Flight Speeds Among Bird Species: Allometric and

Phylogenetic Effects." Edited by Ben Sheldon. *PLoS Biology* 5 (8): e197. https://doi.org/10.1371/journal.pbio.0050197.

Anderson, Alexandra M., Sjoerd Duijns, Paul A. Smith, Christian Friis, and Erica Nol. 2019. "Migration Distance and Body Condition Influence Shorebird Migration Strategies and Stopover Decisions During Southbound Migration." *Frontiers in Ecology and Evolution* 7 (July): 251. https://doi.org/10.3389/fevo.2019.00251.

Auger-Méthé, Marie, Ken Newman, Diana Cole, Fanny Empacher, Rowenna Gryba, Aaron A. King, Vianey Leos-Barajas, et al. 2021. "A Guide to State-Space Modeling of Ecological Time Series." *Ecological Monographs* 91 (4): e01470. https://doi.org/10.1002/ecm.1470.

Baldwin, Justin W., Katie Leap, John T. Finn, and Jennifer R. Smetzer. 2018. "Bayesian State-Space Models Reveal Unobserved Off-Shore Nocturnal Migration from Motus Data." *Ecological Modelling* 386 (October): 38–46. https://doi.org/10.1016/j.ecolmodel.2018.08.006.

Barré, K., K. Spoelstra, Y. Bas, S. Challéat, R. Kiri Ing, C. Azam, G. Zissis, D. Lapostolle, C. Kerbiriou, and I. Le Viol. 2020. "Artificial Light May Change Flight Patterns of Bats Near Bridges Along Urban Waterways." *Animal Conservation* 24 (2): 259–67. https://doi.org/10.1111/acv.12635.

Bauer, S., and B. J. Hoye. 2014. "Migratory Animals Couple Biodiversity and Ecosystem Functioning Worldwide." *Science* 344 (6179): 1242552. https://doi.org/10.1126/science.1242552.

Beardsworth, Christine E., Evy Gobbens, Frank van Maarseveen, Bas Denissen, Anne Dekinga, Ran Nathan, Sivan Toledo, and Allert I. Bijleveld. 2022. "Validating ATLAS: A Regional-Scale High-Throughput Tracking System." *Methods in Ecology and Evolution* 13 (9): 1990–2004. https://doi.org/10.1111/2041-210x.13913.

Birds Canada. 2024. *motus: Fetch and Use Data from the Motus Wildlife Tracking System*. https://motusWTS.github.io/motus.

———. 2025. *Motus Docs - Antenna Types*. https://docs.motus.org/stations/station-equipment/antennas#antenna-types.

Both, Christiaan, Sandra Bouwhuis, C. M. Lessells, and Marcel E. Visser. 2006. "Climate Change and Population Declines in a Long-Distance Migratory Bird." *Nature* 441 (7089): 81–83. https://doi.org/10.1038/nature04539.

Bridge, Eli S., Kasper Thorup, Melissa S. Bowlin, Phillip B. Chilson, Robert H. Diehl, René W. Fléron, Phillip Hartl, et al. 2011. "Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds." *BioScience* 61 (9): 689–98. https://doi.org/10.1525/bio.2011.61.9.7.

Bruderer, Bruno, and Andreas Boldt. 2001. "Flight Characteristics of Birds: I. Radar Measurements of Speeds." *Ibis* 143 (2): 178–204. https://doi.org/10.1111/j.1474-919x.2001.tb04475.x.

Bruderer, Bruno, Dieter Peter, and Fränzi Korner-Nievergelt. 2018. "Vertical Distribution of Bird Migration Between the Baltic Sea and the Sahara." *Journal of Ornithology* 159 (2): 315–36. https://doi.org/10.1007/s10336-017-1506-z.

Brust, Vera, and Ommo Hüppop. 2021. "Underestimated Scale of Songbird Offshore Migration Across the South-Eastern North Sea During Autumn." *Journal of Ornithology* 163 (1): 51–60. https://doi.org/10.1007/s10336-021-01934-5.

Carpenter, Bob, Andrew Gelman, Matthew D. Hoffman, Daniel Lee, Ben Goodrich, Michael Betancourt, Marcus Brubaker, Jiqiang Guo, Peter Li, and Allen Riddell. 2017. "Stan: A Probabilistic Programming Language." *Journal of Statistical Software* 76 (1): 1–32. https://doi.org/10.18637/jss.v076.i01.

Davoren, Gail K., and William A. Montevecchi. 2003. "Consequences of Foraging Trip Duration on Provisioning Behaviour and Fledging Condition of Common Murres *Uria Aalgae*." *Journal of Avian Biology* 34 (1): 44–53. https://doi.org/10.1034/j.1600-048x.2003.03008.x.

Desouhant, Emmanuel, Elisa Gomes, Nathalie Mondy, and Isabelle Amat. 2019. "Mechanistic, Ecological, and Evolutionary Consequences of Artificial Light at Night for Insects: Review and Prospective." *Entomologia Experimentalis Et Applicata* 167 (1): 37–58. https://doi.org/10.1111/eea.12754.

Fisher, Kelsey Elizabeth, Phil M. Dixon, Gang Han, James Stephen Adelman, and Steven P. Bradbury. 2020. "Locating Large Insects Using Automated VHF Radio Telemetry with a Multi-Antennae Array." Edited by Edward Codling. *Methods in Ecology and Evolution* 12 (3): 494–506. https://doi.org/10.1111/2041-210x.13529.

Gottwald, Jannis, Ralf Zeidler, Nicolas Friess, Marvin Ludwig, Christoph Reudenbach, and Thomas Nauss. 2019. "Introduction of an Automatic and Open-Source Radio-Tracking System for Small Animals." Edited by Chris Sutherland. *Methods in Ecology and Evolution* 10 (12): 2163–72. https://doi.org/10.1111/2041-210x.13294.

Griffin, Andrea S., Culum Brown, Bradley K. Woodworth, Guy-Anthony Ballard, Stuart Blanch, Hamish A. Campbell, Tara L. Crewe, et al. 2020. "A Large-Scale Automated Radio Telemetry Network for Monitoring Movements of Terrestrial Wildlife in Australia." *Australian Zoologist* 40 (3): 379–91. https://doi.org/10.7882/az.2019.026.

Jonsen, Ian D., M. Basson, S. Bestley, M. V. Bravington, T. A. Patterson, M. W. Pedersen, R. Thomson, U. H. Thygesen, and S. J. Wotherspoon. 2013. "State-Space Models for Bio-Loggers: A Methodological Road Map." *Deep Sea Research Part II: Topical Studies in Oceanography* 88–89 (April): 34–46. https://doi.org/10.1016/j.dsr2.2012.07.008.

Jonsen, Ian D., Joanna Mills Flemming, and Ransom A. Myers. 2005. "Robust State-Space Modeling of Animal Movement Data." *Ecology* 86 (11): 2874–80. https://doi.org/10.1890/04-1852.

Kays, Roland, Margaret C. Crofoot, Walter Jetz, and Martin Wikelski. 2015. "Terrestrial Animal Tracking as an Eye on Life and Planet." *Science* 348 (6240): aaa2478. https://doi.org/10.1126/science.aaa2478.

Kubelka, Vojtěch, Brett K. Sandercock, Tamás Székely, and Robert P. Freckleton. 2022. "Animal Migration to Northern Latitudes: Environmental Changes and Increasing Threats." *Trends in Ecology &Amp; Evolution* 37 (1): 30–41. https://doi.org/10.1016/j.tree.2021.08.010.

Lagerveld, Sander, Pepijn de Vries, Jane Harris, Sue Parsons, Elisabeth Debusschere, Ommo Hüppop, Vera Brust, and Heiko Schmaljohann. 2024. "Migratory Movements of Bats Are Shaped by Barrier Effects, Sex-Biased Timing and the Adaptive Use of Winds." *Movement Ecology* 12 (1): 81. https://doi.org/10.1186/s40462-024-00520-7.

Liechti, Felix, Silke Bauer, Kiran L. Dhanjal-Adams, Tamara Emmenegger, Pavel Zehtindjiev, and Steffen Hahn. 2018. "Miniaturized Multi-Sensor

Loggers Provide New Insight into Year-Round Flight Behaviour of Small trans-Sahara Avian Migrants." *Movement Ecology* 6 (1): 19. https://doi.org/10.1186/s40462-018-0137-1.

McLaren, James D., Jeffrey J. Buler, Tim Schreckengost, Jaclyn A. Smolinsky, Matthew Boone, E. Emiel van Loon, Deanna K. Dawson, and Eric L. Walters. 2018. "Artificial Light at Night Confounds Broad-scale Habitat Use by Migrating Birds." Edited by Ryan Norris. *Ecology Letters* 21 (3): 356–64. https://doi.org/10.1111/ele.12902.

Mills, Alexander M., Bethany G. Thurber, Stuart A. Mackenzie, and Philip D. Taylor. 2011. "Passerines Use Nocturnal Flights for Landscape-Scale Movements During Migration Stopover." *The Condor* 113 (3): 597–607. https://doi.org/10.1525/cond.2011.100186.

Mitchell, Greg W., Amy E. M. Newman, Martin Wikelski, and D. Ryan Norris. 2012. "Timing of Breeding Carries over to Influence Migratory Departure in a Songbird: An Automated Radiotracking Study." *Journal of Animal Ecology* 81 (5): 1024–33. https://doi.org/10.1111/j.1365-2656.2012.01978.x.

Mitchell, Lucy, Vera Brust, Thiemo Karwinkel, Susanne Åkesson, Dmitry Kishkinev, Gabriel Norevik, Tibor Szep, et al. 2025. "Conservation-Focused Mapping of Avian Migratory Routes Using a Pan-European Automated Telemetry Network." *Conservation Biology*, March. https://doi.org/10.1111/cobi.70017.

Nathan, Ran, Wayne M. Getz, Eloy Revilla, Marcel Holyoak, Ronen Kadmon, David Saltz, and Peter E. Smouse. 2008. "A Movement Ecology Paradigm for Unifying Organismal Movement Research." *Proceedings of the National Academy of Sciences* 105 (49): 19052–59. https://doi.org/10.1073/pnas.0800375105.

Rueda-Uribe, Cristina, Alyssa J. Sargent, María Ángela Echeverry-Galvis, Pedro A. Camargo-Martínez, Isabella Capellini, Lesley T. Lancaster, Alejandro Rico-Guevara, and Justin M. J. Travis. 2024. "Tracking Small Animals in Complex Landscapes: A Comparison of Localisation Workflows for Automated Radio Telemetry Systems." *Ecology and Evolution* 14 (10): e70405. https://doi.org/10.1002/ece3.70405.

Schick, Robert S., Scott R. Loarie, Fernando Colchero, Benjamin D. Best, Andre Boustany, Dalia A. Conde, Patrick N. Halpin, Lucas N. Joppa, Catherine M. McClellan, and James S. Clark. 2008. "Understanding Movement Data and Movement Processes: Current and Emerging Directions." *Ecology Letters* 11 (12): 1338–50. https://doi.org/10.1111/j.1461-0248.2008.01249.x.

Schwemmer, Philipp, Moritz Mercker, Karena Haecker, Helmut Kruckenberg, Steffen Kämpfer, Pierrick Bocher, Jérôme Fort, et al. 2023. "Behavioral Responses to Offshore Windfarms During Migration of a Declining Shorebird Species Revealed by GPS-Telemetry." *Journal of Environmental Management* 342 (September): 118131. https://doi.org/10.1016/j.jenvman.2023.118131.

Smetzer, Jennifer R., David I. King, and Philip D. Taylor. 2017. "Fall Migratory Departure Decisions and Routes of Blackpoll Warblers *Setophaga Striata* and Red-Eyed Vireos *Vireo Olivaceus* at a Coastal Barrier in the Gulf of Maine." *Journal of Avian Biology* 48 (11): 1451–61. https://doi.org/10.1111/jav.01450.

Taylor, Philip D., Tara L. Crewe, Stuart A. Mackenzie, Denis Lepage, Yves Aubry, Zoe Crysler, George Finney, et al. 2017. "The Motus Wildlife Tracking System: A Collaborative Research Network to Enhance the Understanding of Wildlife Movement." *Avian Conservation and Ecology* 12 (1): 8. https://doi.org/10.5751/ace-00953-120108.

Williams, H. J., E. L. C. Shepard, Mark D. Holton, P. A. E. Alarcón, R. P. Wilson, and S. A. Lambertucci. 2020. "Physical Limits of Flight Performance in the Heaviest Soaring Bird." *Proceedings of the National Academy of Sciences* 117 (30): 17884–90. https://doi.org/10.1073/pnas.1907360117.