

RESEARCH ARTICLE

Functional Ecology



State-space modelling of the flight behaviour of a soaring bird provides new insights to migratory strategies

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Abstract

1. Characterising the spatiotemporal variation of animal behaviour can elucidate the way individuals interact with their environment and allocate energy. Increasing sophistication of tracking technologies paired with novel analytical approaches allows the characterisation of movement dynamics even when an individual is not directly observable.
2. In this study, high-resolution movement data collected via global positioning system (GPS) tracking in three dimensions were paired with topographical information and used in a Bayesian state-space model to describe the flight modes of migrating golden eagles (*Aquila chrysaetos*) in eastern North America.
3. Our model identified five functional behavioural states, two of which were previously undescribed variations on thermal soaring. The other states comprised gliding, perching and orographic soaring. States were discriminated by movement features in the horizontal (step length and turning angle) and vertical (change in altitude) planes and by the association with ridgelines promoting wind deflection. Tracked eagles spent 2%, 31%, 38%, 9% and 20% of their daytime in directed thermal soaring, gliding, convoluted thermal soaring, perching and orographic soaring, respectively. The analysis of the relative occurrence of these flight modes highlighted yearly, seasonal, age, individual and sex differences in flight strategy and performance. Particularly, less energy-efficient orographic soaring was more frequent in autumn, when thermals were less available. Adult birds were also better at optimising energy efficiency than subadults.
4. Our approach represents the first example of a state-space model for bird flight mode using altitude data in conjunction with horizontal locations and is applicable to other flying organisms where similar data are available. The ability to describe animal movements in a three-dimensional habitat is critical to advance our understanding of the functional processes driving animals' decisions.

KEYWORDS

3D states, GPS-GSM telemetry, hidden state model, Markov chain Monte Carlo, movement ecology, raptor, subsidised flight

1 | INTRODUCTION

The way in which animals move in space and over time has important implications on their vital rates and, ultimately, their fitness and demography (Nathan et al., 2008). Different movement modes often require varying levels of energy expenditure and may reflect different environmental constraints (Shepard et al., 2013). Understanding movement dynamics and characterising the way in which they combine into functional bouts of activity can therefore help formulate hypotheses regarding movement drivers, environmental influences and energetic and fitness implications of different behavioural strategies (Hays et al., 2016; Nathan et al., 2008).

Movement behaviour is difficult to observe directly for prolonged periods, especially for species that range over large distances and move through media that are mostly inaccessible to human observers (air or water). Recent advances in biologging technology allow tracking individuals over wide spatiotemporal ranges and in remote areas, opening windows on their life history at functionally relevant scales (Hays et al., 2016; Kays, Crofoot, Jetz, & Wikelski, 2015). Telemetry data collection was originally aimed at tracking an animal's geographical location. However, the proliferation of devices capable of collecting and storing information at fine temporal resolutions, combined with the refinement of statistical tools, means that these data can also be used to infer the behavioural patterns of tagged animals (Jonsen et al., 2013; Langrock et al., 2012; McClintock, Russell, Matthiopoulos, & King, 2013; Patterson, Thomas, Wilcox, Ovaskainen, & Matthiopoulos, 2008).

While various techniques have been proposed for the classification of behaviour, hidden state models offer several advantages, particularly because they explicitly account for the intrinsic autocorrelation of movement data (Jonsen et al., 2013; Langrock et al., 2012; McClintock et al., 2012). These approaches assume that observed movement metrics arise from distributions that depend on a latent sequence of discrete behavioural states or modes (known as emission distributions), and are thus consistent with the often unobservable nature of behaviour. State assignment is directly informed by the data, which can guide behavioural classification, reveal unexpected patterns and thus lead to a new understanding of behaviour. State-space models, which constitute a class of hidden state models, also allow accounting for any measurement error associated with observed metrics (Jonsen et al., 2013; Patterson et al., 2008). This occurs because they are composed of a process model, capturing the underlying transition between states, and an observation model, describing the way in which data are generated, with error.

Most classic developments and applications of movement models have focused on the marine realm (e.g., marine mammals, seabirds, elasmobranchs or large teleosts, see references in Jonsen et al., 2013) or on terrestrial non-volant mammals (e.g., Morales, Haydon, Frair, Holsinger, & Fryxell, 2004). The main objective of these studies has been distinguishing between two behavioural modes: periods where an individual rapidly moves through unprofitable areas or travel corridors (transit mode), and periods where it explores an area in search of patchy food resources (resident mode) (Jonsen et al.,

2013; Morales et al., 2004; Patterson et al., 2008). Recently, important progress has been made in finer discrimination of behaviour by providing additional data streams to inform the models, characterising, for example, attraction to specific locations (McClintock et al., 2012), central place foraging (Michelot et al., 2017; Pirotta, Edwards, New, & Thompson, 2018), diving (Bestley, Jonsen, Hindell, Harcourt, & Gales, 2015; Dean et al., 2013; Isojunno & Miller, 2015; Quick et al., 2017) and active foraging (Isojunno & Miller, 2015).

Few existing applications of hidden state models describe the behaviour of terrestrial birds (Leos-Barajas et al., 2017; Péron et al., 2017; Williams, Shepard, Duriez, & Lambertucci, 2015). For these species, characterising flight modes may be more relevant than distinguishing between transit and resident movement, because of the implications on their energy budget. Such characterisation requires either the use of additional sensors, such as accelerometers, or the introduction of a third movement dimension (altitude), which is conceptually comparable to the use of depth when modelling diving behaviour of marine animals (Isojunno & Miller, 2015; Quick et al., 2017). Birds adopt different strategies to move through air, depending on their size, body structure, reasons for moving and environmental and weather conditions (Duerr et al., 2015; Hedenstrom, 1993; Lanzone et al., 2012). Flapping flight is costly, and heavier species tend to soar (i.e., use air currents to support straight-winged flight) as a more efficient way to move over large distances (Hedenström & Ålerstam, 1995). Broadly speaking, there are two predominant soaring modes in terrestrial birds. Thermal soaring is defined as the use of thermals (i.e., layers of warm air that rise from the earth forming updrafts) to gain altitude, followed by periods of gliding towards other thermals to continue their progress. Conversely, orographic soaring relies on horizontal winds deflected upwards by ridges, trees, hills and other structures (Duerr et al., 2015; Kerlinger, 1989).

In this study, a large telemetry dataset from golden eagles (*Aquila chrysaetos*) in eastern North America was used to develop a Bayesian state-space model describing the flight behaviour of soaring birds. These birds are from a small population of approximately 5,000 individuals migrating between the breeding grounds in Canada and a wintering range in the northern and central Appalachian Mountains and surrounding regions (Dennhardt, Duerr, Brandes, & Katzner, 2015; Katzner, Smith et al., 2012). The population faces increasing pressure from wind power development in the southern part of its range and along its migratory route, which has sparked research on the factors influencing individuals' risk of colliding with turbines (Katzner, Brandes et al., 2012; Miller et al., 2014). The choice of different flight modes by these birds changes their altitude, speed and updraft use and, although it is likely to contribute to collision risk, is rarely accounted for when predicting fatality rates (Barrios & Rodríguez, 2004; Klaassen, Strandberg, Hake, & Ålerstam, 2008).

Golden eagles use both thermal and orographic soaring to maximise flight efficiency under different weather and environmental conditions (Duerr et al., 2012; Katzner et al., 2015; Lanzone et al., 2012). Therefore, they represent an ideal system for the development of a model to categorise flight modes, which could be easily applicable to other flying organisms. Below, the modelling framework

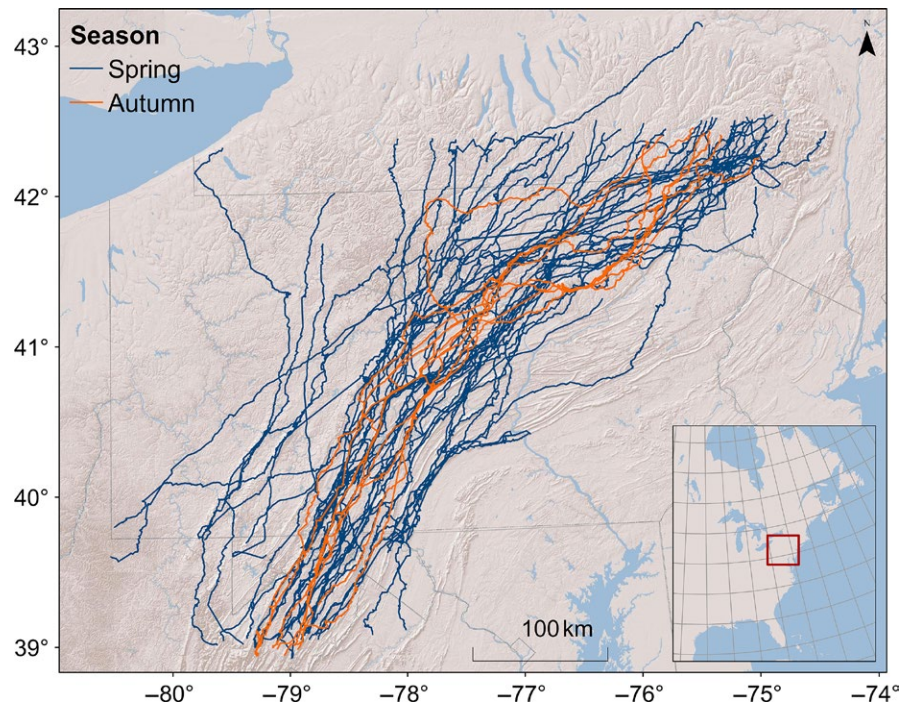


FIGURE 1 Map of study area and golden eagle tracks in autumn (48 tracks) and in spring (10 tracks)

is presented and utilised to characterise a high-resolution time series of golden eagle behaviour using location and altitude information collected via GPS, together with ancillary environmental data. The behavioural results are then analysed to investigate the activity budget of eagles belonging to different age and sex classes in different seasons, and to explore the functional mechanisms underpinning individual flight performance during migration.

2 | MATERIALS AND METHODS

2.1 | Data collection

We used existing golden eagle telemetry data collected between 2009 and 2016 (Duerr et al., 2012; Katzner et al., 2015; Miller et al., 2014). Eagles were captured and outfitted with CTT-1100 GPS-GSM telemetry systems (Cellular Tracking Technologies, LLC) attached as backpacks with Teflon™ ribbon (Bally Ribbon Mills in Bally, PA). Tags were programmed to record location and altitude above sea level (calculated as height above the geoid) every 30–60 s from sunrise to sunset. No locations were recorded at night. The GPS device measured instantaneous speed. If speed was less than 1 knot for 5 min, the unit switched to sampling data at 15-min intervals, thus conserving battery power and device memory when a bird was perching. Full details of the study area, deployment techniques, duty cycles, sampling regimes and permits are reported in Katzner et al. (2015) and Miller et al. (2014, 2016). For this study, a total of 58 tracks were used, 48 of which were collected during the spring migration and 10 in autumn (Figure 1). Tagged eagles included juveniles (first year of northbound migration, eight tracks), subadults (second–fourth year of migration, 22 tracks) and adults (>fourth year of migration, 28 tracks). Nineteen tracks were from female individuals and

39 from males. Some individuals were tracked over multiple years (Supporting Information Table S1).

2.2 | Data processing

Fixes with a horizontal dilution of precision (an indication of 2D location quality; HDOP) >10, and 2D fixes were removed to exclude any obvious error in GPS locations or altitudes. Vertical dilution of precision (VDOP) information was not available for the majority of the data. Due to the sampling regime, there were gaps in the recorded tracks. Gaps in flight data could also have occurred because of low battery voltage or gaps in the system's functionality. Furthermore, a unit could not collect and send data simultaneously so, if a bird was in flight and connected to the Global System for Mobile communications (GSM) network, GPS data were not collected. Therefore, to reduce extrapolation over long unobserved periods, tracks from individual eagles were split into separate segments whenever the interval between consecutive locations was greater than 5 min. Segments shorter than 10 min were excluded from further analysis to avoid biasing the probabilities regulating the temporal sequence of states (see below). Because hidden state models require a regular sampling unit, location and altitude data were linearly interpolated in R with custom code to a constant one-minute temporal resolution (R Development Core Team, 2016). As an alternative to using the interpolated values of the response variables over remaining short (<5 min) unobserved periods in the data, the model can be formulated to estimate the value of missing observations. Results of this reformulation are shown in Supporting Information Appendix S3.

At each minute, t , four variables were derived to characterise eagle behaviour (Supporting Information Table S2). The use of these variables for describing the behaviour of soaring birds was supported

by previous studies (Katzner et al., 2015). Three of the four were derived from the GPS data: step length x_t (the distance between location at t and location at $t + 1$, in metres), turning angle θ_t (the angle between the step from $t - 1$ to t and the step from t to $t + 1$, in radians) and altitude above sea level a_t (recorded by the GPS device, in metres). The fourth variable was hierarchical slope position (HSP, as defined by Murphy, Evans, & Storfer, 2010), a metric of topographic morphology used to quantify exposure and identify ridges. HSP was computed using package *spatialEco* in R (Evans, 2017) and based on ground elevation data obtained from the Global Multi-resolution Terrain Elevation Data 2010 at 30-arc-second spatial resolution (data available from the U.S. Geological Survey: <https://earthexplorer.usgs.gov/>). A value of HSP, h_t , was extracted from the surface below each eagle location at time t . These four variables constituted the vector of behavioural observations \mathbf{y}_t . Because the calculation of the turning angle θ_t requires three consecutive locations, the first and last locations of each segment were discarded.

We assumed that the error around GPS locations was negligible (Morales et al., 2004). This was supported by the low mean HDOP associated with retained GPS fixes (mean = 1.9; STD = 1.2), corresponding to location errors in the order of a few metres. In particular, the standard deviation of the position can be approximated by multiplying HDOP by the measurement standard deviation of the GPS device (Poessel, Duerr, Hall, Braham, & Katzner, 2018), which was 3 m for the devices used in this study (resulting in a standard deviation of 30 m when HDOP = 10). Considering the distribution of step lengths for tagged animals (mean = 540 m; STD = 398 m), this error was deemed irrelevant for our application. We used the published accuracy of the device in the third dimension to inform the error around altitude measurements in a state-space modelling framework (see details below; Lanzone et al., 2012).

We tested the use of altitude above-ground level for the vertical dimension, but found models with this variable to perform much worse than those with altitude above sea level. This was possibly due to error propagation (Péron et al., 2017) or due to the fact that altitude above-ground becomes difficult to interpret over steeply changing slopes, such as the ones used during orographic flight (Katzner et al., 2015).

2.3 | Model structure

We developed a Bayesian state-space model to estimate the time series of latent behavioural states, s_t , of tagged individuals, together with the state-specific parameters of the emission distributions for the observations \mathbf{y}_t . The process component of the model described the transition between the underlying states, regulated by a matrix of transition probabilities Γ . For M states, Γ had dimensions $M \times M$ and each element γ_{ij} indicated the probability of being in state j at time t , given that the animal was in state i at time $t - 1$. The Markov property was assumed for the time series of states; that is, state at time t only depended on state at time $t - 1$. The state process was informed by the four variables, step length, turning angle,

altitude and hierarchical slope position, at time t . Given state $s_t = i$ (with i in $1, \dots, M$), step lengths were modelled as emerging from a Weibull distribution (McClintock et al., 2012; Morales et al., 2004), with state-specific scale (α_i) and shape (β_i) parameters, determining the average step length per state and its variability, that is, $x_t \sim W(\beta_i, \alpha_i)$. Turning angles were assumed to have a wrapped Cauchy distribution (McClintock et al., 2012; Morales et al., 2004) with mean (μ) equal to 0 and state-specific concentration parameter (ρ_i), a measure of how angles are distributed around the mean, that is, $\theta_t \sim wC(0, \rho_i)$ (Breed, Costa, Jonsen, Robinson, & Mills-Flemming, 2012). The parameter ρ_i varies between 1 (angles concentrated around the mean 0, i.e., directed movement) and 0 (corresponding to directions uniformly distributed on the circle, i.e., a classic random walk allowing for convoluted movement). True, unobserved altitude at each minute t was modelled as a random walk Gaussian variable with state-dependent standard deviation σ_i (Isojunno & Miller, 2015; Langrock, Marques, Baird, & Thomas, 2014), $v_t \sim N(v_{t-1} + \pi_i, \sigma_i)$, where v_{t-1} is the true altitude in the previous minute and π_i denotes the state-specific mean vertical drift, that is, the change in altitude between minutes. A Gaussian observation model accounted for errors in altitude measurement, that is, $a_t \sim N(v_t, \epsilon)$. Finally, following data exploration, hierarchical slope position was assumed to emerge from a Gaussian distribution with state-specific mean κ_i and standard deviation ω_i , that is, $h_t \sim N(\kappa_i, \omega_i)$.

We tested several alternative structures for the model, including a range of potential latent states (three to six). A model with five states converged successfully and aligned with biological expectations, so only this parameterisation is presented here. It is important to note that, in an unsupervised inference setting such as this (i.e., one where the true states are unknown), the number of states is driven by the process generating observed data (Leos-Barajas et al., 2017). However, the use of appropriate movement and ancillary environmental variables, capturing relevant features of an animal's behaviour, can lead to the identification of biologically meaningful latent states (Leos-Barajas et al., 2017; McClintock et al., 2013). The five states used here were characterised by features of the response variables that broadly corresponded to directed thermal soaring (state 1), gliding (state 2), convoluted thermal soaring (state 3), perching (or on the ground; state 4) and orographic soaring (but potentially including periods of flapping flight; state 5).

2.4 | Priors

Following initial data exploration, a set of constraints was applied to the priors of state-specific parameters in order to facilitate model convergence and support the identification and assignment of functionally relevant latent states (Isojunno & Miller, 2015) (Supporting Information Appendix S1). This also prevented label switching, that is, the non-identifiability of state-dependent components due to the posterior distribution being invariant to permutation of state labels (Stephens, 2000). These constraints were broad and were only defining the overall tendency of the vertical movement (ascending,

descending or stable overall) and the relative degree of directedness, speed and topographic exposure among states (Supporting Information Appendix S1). The standard deviation of the observation model for altitude (ϵ) was set at a fixed value (25 m), but was large enough to conservatively account for the declared accuracy level (Lanzone et al., 2012).

2.5 | Model fitting

The model was fitted using JAGS run from R (package *runjags*; Supporting Information Appendix S2) (Denwood, 2016). Markov chain Monte Carlo (MCMC) algorithms were iterated until convergence of the latent states and model parameters. State convergence was assessed by monitoring the proportion $\delta_{1,...,5}$ of minutes classified under each latent state. We ran three parallel chains, starting at different initial values. Convergence was assessed by visually inspecting trace and density plots (Lunn, Jackson, Best, Thomas, & Spiegelhalter, 2013) and confirmed by checking that the Brooks–Gelman–Rubin (BGR) diagnostic fell below 1.1 and that Monte Carlo (MC) error was less than 5% of the sample standard deviation (Lunn et al., 2013). The R package *coda* was used to assess convergence, calculate effective sample size and extract posterior estimates (Plummer, Best, Cowles, & Vines, 2006).

2.6 | Model validation

To investigate the model's ability to characterise functional latent states, we compared the model's posterior state classifications with existing manual behavioural classifications for a subset of tagged eagles. In particular, data from 13 of the 48 spring tracks were previously evaluated manually as part of a prior study (Katzner et al., 2015). Flight modes were identified by an expert observer (T. A. Miller) based on the patterns of sequential GPS locations and on their overlap with topographical features. As a result, flight mode was classified into one of four states: thermal soaring, gliding, orographic soaring and unknown (Katzner et al., 2015). Model state classifications were obtained from the posterior median estimate of the categorical state. States 1 and 3 were combined and matched to manually classified thermal soaring, state 2 was matched to manually classified gliding, and state 5 to manually classified orographic soaring. Manual and model classifications were compared using confusion matrices. Because the model could not assign an "unknown" state and accuracy could not be evaluated for "unknown" segments, accuracy estimates from this matrix will be artificially low. In addition, we tested whether the occurrence of gaps in the tracking data and measurement error in the horizontal and vertical dimension could affect the results, using a simulation procedure based on the posterior estimates of model parameters (Supporting Information Appendix S4) and carried out posterior predictive checks to assess the goodness of fit of the model to the data (Supporting Information Appendix S5).

2.7 | Behavioural models

The results of the state-space model can be used to explore the ecology of the study species. To demonstrate this application, we carried out a descriptive investigation of the seasonal, age and sex differences in flight strategy and performance. Specifically, we fitted binomial mixed-effects models (package *lme4* in R; Bates, Maechler, & Bolker, 2012) to test whether the proportional occurrence of each behavioural state (directed thermal soaring, convoluted thermal soaring, gliding and orographic soaring) in a track varied as a function of the interaction between season (autumn and spring) and age category (adults and subadults). Because this analysis aimed to compare the occurrence of flight modes, steps classified as on the ground or perching were excluded. Moreover, due to the small sample size, tracks of juveniles were also excluded. In a separate model, we tested for the effect of sex on the flight performance of adult eagles in the two seasons (we excluded subadults as most of them were males). Because individuals were tracked over multiple years, we included a random effect of individual and year in all models. The random effects structure, as well as the inclusion of the fixed effects, was assessed using the Akaike's information criterion (Gurka, 2006), corrected for small sample sizes (AICc).

3 | RESULTS

The 58 filtered eagle tracks corresponded to 72,844 GPS fixes, which made up 599 segments longer than 10 min and separated from one another by more than 5 min. Regularisation of the 599 segments at a one-minute resolution reduced the sample analysed to 45,914 locations.

3.1 | State-space model

Visual inspection of trace plots suggested that the chains were randomly oscillating around a central value after 5,000 iterations, so these initial draws were discarded as burn-in. Diagnostics confirmed that the model converged adequately after 15,000 iterations (Supporting Information Table S3). We also verified that these iterations corresponded to an effective size of the posterior sample greater than 400 for all parameters (Lunn et al., 2013). Due to computing memory limitations, we only retained one in 10 iterations.

The results were consistent with our biological expectations of eagle behaviour, embedded in the priors, while describing the features of each state precisely. Under state 1 (directed thermal soaring), an individual gained substantial altitude and moved in large, directed steps. State 3 (convoluted thermal soaring) was similar to state 1, but steps were considerably shorter and turning angles had low concentration. Bouts of both states appeared to be followed by gliding periods (state 2). State 4 (on the ground or perching) was characterised by extremely small and convoluted horizontal steps, and visual investigation of the tracks confirmed it corresponded to periods when an eagle was not moving (e.g., Supporting Information

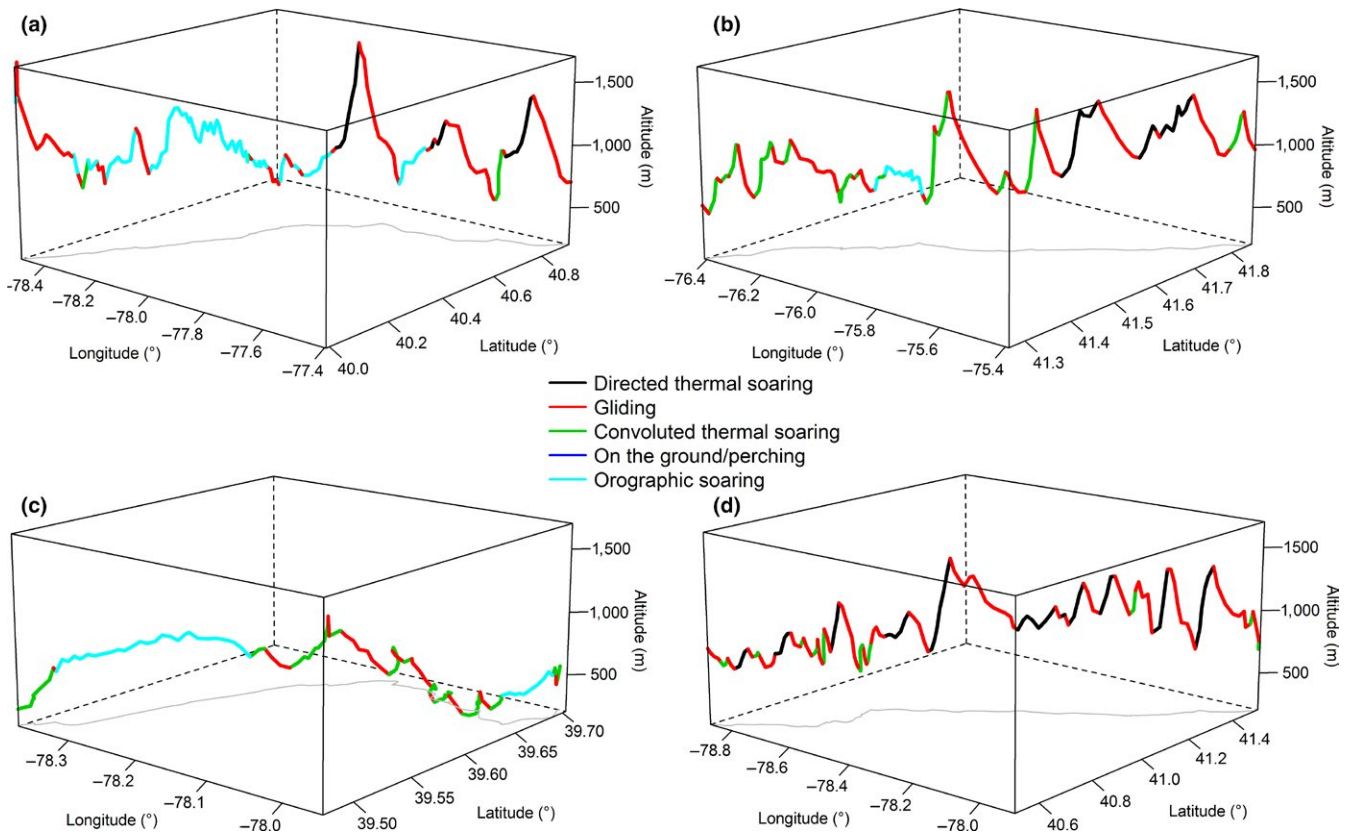


FIGURE 2 Four segments (a–d) of three-dimensional golden eagle tracks. Tracks are coloured based on model posterior medians of the behavioural state at each minute t . In grey, the shadow of the track projected onto the horizontal plane. The posterior median of true altitudes is used for the vertical dimension

TABLE 1 Estimated golden eagle activity budget, across both migration seasons and by migration season

	Directed thermal soaring (%)	Gliding (%)	Convoluted thermal soaring (%)	On the ground or perching (%)	Orographic soaring (%)
Overall	2	31	38	9	20
Spring	3	32	37	10	18
Autumn	0	24	43	8	25

Figure S2). Finally, state 5 (orographic soaring) showed large variation in the vertical drift, suggesting irregular gaining and losing of altitude. This flight mode was correctly classified to occur over topographies characterised by high exposure (such as ridgelines). The posterior distributions of the state-dependent parameters are summarised in Supporting Information Table S3, and the emission distributions of the four response variables (step length, turning angle, vertical drift and hierarchical slope position) are plotted in Supporting Information Figure S1.

The posterior median was used to classify the behavioural state at each time step. The comparison of model state classifications with manually classified flight modes returned a mean of 68% correct classifications across states (Supporting Information Table S4; 67% for thermal soaring, 70% for gliding and 65% for orographic soaring). As an example, we plotted four track segments coloured by state, where posterior true altitude values were used (Figure 2). On the

basis of posterior state classifications, we calculated eagles' activity budget, across both migration seasons and by migration season (Table 1). These data suggested that orographic soaring was less frequent in spring than in autumn.

The model also appeared to be robust to observed levels of sampling irregularity and measurement errors (Supporting Information Appendix S4). However, the posterior predictive checks highlighted potential issues with the validity of the Markov property given the small time interval between observations (Supporting Information Appendix S5, Figures S4 and S5).

3.2 | Behavioural models

Model selection highlighted differences among individuals and among years in the occurrence of most flight modes (Supporting Information Table S5, Figure S3). The use of orographic soaring

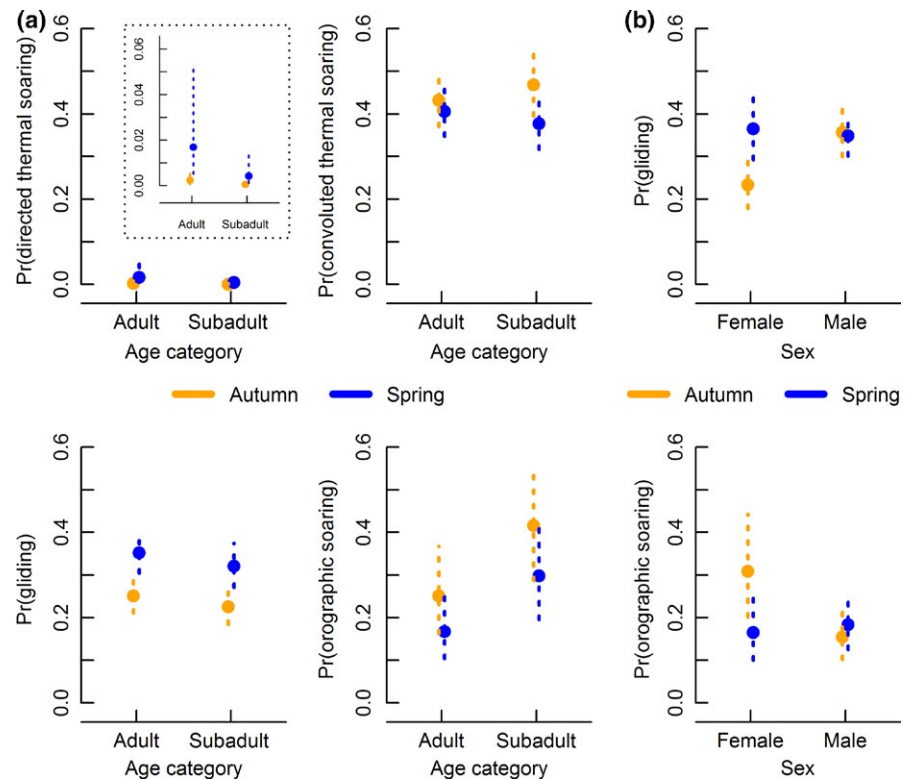


FIGURE 3 Results of the behavioural models by state (mean and 95% confidence intervals). The y-axis was standardised across plots, but the top left plot also includes a zoomed inset graph (dotted box) for clarity. (a) Effect of season and age category on the proportional occurrence of each state. (b) Effect of season and sex on the proportional occurrence of gliding and orographic soaring. Results for the two forms of thermal soaring are not reported because the effect of sex was not retained by model selection

varied by age category and season, suggesting that this flight mode occurred proportionally more in autumn and was used more by subadults (Figure 3a). In contrast, directed thermal soaring occurred more in spring and was used more by adults (Figure 3a). Convoluted thermal soaring appeared to be used more by subadults in autumn and by adults in spring, but the estimated effects had wide confidence intervals (Figure 3a). Gliding occurred more in spring and was used more by adults, although the latter effect showed large confidence intervals (Figure 3a). Model results also suggested that the proportional occurrence of orographic soaring and gliding varied between the sexes, but differently in the two seasons. Females used more orographic soaring and less gliding than males, but only in autumn (Figure 3b). No difference between the sexes was found for directed or convoluted thermal soaring (Supporting Information Table S5).

4 | DISCUSSION

To our knowledge, this study represents the first example of the use of altitude measurements in conjunction with horizontal information and ancillary environmental variables in hidden state models to characterise functional behavioural modes in three dimensions (McClintock, London, Cameron, & Boveng, 2017; McClintock et al., 2013). This is particularly useful for flying organisms, where studying the variation in flight mode might be more relevant than simply distinguishing resident and transit movement identified by models in two dimensions (Jonsen et al., 2013). In addition to identifying

expected behavioural states of golden eagles, our model was able to tease apart two types of thermal soaring with different directedness. Previous work has generally classified thermal soaring as a single category of behaviour (e.g., Katzner et al., 2015), while the combination of horizontal and vertical information in our study discriminated additional flight features. The degree of directedness while gaining altitude within a thermal is likely dependent upon the strength and distribution of thermals, the alignment of thermals with flight direction and wind conditions (Kerlinger, 1989). Whenever conditions cause thermals to drift, birds using this form of soaring will also drift, resulting in straighter movement in the horizontal dimension (Hedenström & Ålerstam, 1995). This can warrant faster forward progress with the same energy expenditure, but only if the thermals drift in the same direction as the primary axis of movement. However, most thermal soaring was convoluted, because stronger winds disrupt thermal lift (Kerlinger, 1989). Where the data exist, our approach could be used to test the effect of wind speed on thermal soaring explicitly.

The identification of behavioural states makes it possible to describe time allocation to different movement modes. This can shed light on an animal's decision-making process as it moves through space and adjusts to environmental conditions (Nathan et al., 2008) with flight modes of different efficiencies (Duerr et al., 2012). For example, eagles used different strategies to migrate depending on the season, as reflected in the higher occurrence of orographic flight in autumn and the higher occurrence of gliding and directed thermal soaring in spring. This is intuitive, as the availability of thermals is higher in spring (Duerr et al., 2015).

The behavioural models also highlighted differences in flight strategy and performance between age categories. Across both seasons, adults used gliding and directed thermal soaring more than subadults, which in turn used more orographic soaring, although these patterns were not reflected in the results for convoluted thermal soaring. Previous studies suggested that, in spring, adults need to move quickly towards the reproductive areas to secure nesting territories, while subadults can delay their migration and wait for energetically optimal weather conditions (Duerr et al., 2015; Miller et al., 2016). During spring migration, the relative use of different flight modes also changes as a result of these processes (Katzner et al., 2015). In contrast, our results highlight that, at a broader scale, adults' experience allows them to rely on more efficient flight modes compared to subadults despite the constraints of reproduction. This inconsistency with previous work may also be a by-product of the disproportionate classification of behavioural states manually identified as "unknown" into thermal soaring (Supporting Information Table S4).

We also found substantial individual and yearly variability in flight performance, as well as differences in the use of orographic soaring and directed thermal soaring between males and females in autumn (Supporting Information Table S5). The larger size of females and corresponding higher weight might explain some of these patterns, although further investigation is required to explore the underlying functional processes. Because flight modes are characterised by different energetic investment and movement efficiency (Duerr et al., 2012; Hedenstrom, 1993; Hedenström & Ålerstam, 1995), their variation among years, seasons, ages, sexes and individuals is relevant for an individual's energy budget, which will ultimately affect its ability to survive and reproduce successfully (Weimerskirch, Louzao, de Grissac, & Delord, 2012). Investigating any spatial or temporal patterns in flight mode distribution could therefore highlight the moments in time or areas that are critical in terms of energy requirements during migration (Shepard et al., 2013). The energetic insight our model can provide also suggests its relevance to the study of other organisms' flight modes and their variation in space and time (Alexander, 2015).

Beyond energetics, characterising behavioural states in flying animals is particularly important to evaluate their susceptibility to human activities, informing effective planning and management (Katzner, Brandes et al., 2012; Péron et al., 2017; Ross-Smith et al., 2016). For example, specific behavioural states, due to their horizontal and vertical characteristics, may put birds at higher risk of collision with turbines (Ross-Smith et al., 2016). For golden eagles in eastern North America, the spatiotemporal distribution of flight modes could be mapped to quantify their overlap with wind power developments within the population's range (Miller et al., 2014) and inform simulation models that estimate collision rates (New, Bjerre, Millsap, Otto, & Runge, 2015). In this sense, the mismatch between manual and model classifications may be irrelevant as long as movement features are described correctly, because vulnerability in a state may be more related to average altitude and speed, rather than the type of updraft birds are using.

Given that migration patterns are highly affected by weather conditions (Duerr et al., 2015; Lanzone et al., 2012; Miller et al., 2016), the viability of this, and other, populations of long-ranging migratory birds is also threatened by global climate changes (Møller, Rubolini, & Lehikoinen, 2008). The presence of two types of thermal soaring suggests sensitive responses by birds to variation in weather. Thus, major alterations of wind patterns and the increase in frequency of extreme weather events may affect flight decisions and energetic efficiency, potentially compromising birds' migratory abilities (Marra, Francis, Mulvihill, & Moore, 2005). Our model could be used to assess changes in activity budgets following altered weather conditions. In turn, a modified allocation of time to activities with different energetic efficiency could affect the energy balance of these species over the migration and, ultimately, have consequences on their survival and reproductive success (Weimerskirch et al., 2012).

From a methodological perspective, the state-space framework presented here advances previous work that modelled altitude data in isolation (Ross-Smith et al., 2016). In addition to altitude, it was the use of ancillary topographical information that supported the identification of orographic soaring, which is associated with ridges and other structures deflecting horizontal winds (Kerlinger, 1989; Mallon, Bildstein, & Katzner, 2016). Selecting appropriate ancillary metrics is critical for the successful discrimination of flight modes that are promoted by specific features of the environment (Murphy et al., 2010). Our analytical approach was unsupervised, in the sense that observed behavioural states were not used to tune the model (Leos-Barajas et al., 2017). However, as part of the preliminary exploration of the tracking dataset, five states were selected and suitable constraints were set to broadly match these states with potential flight modes. The fitting procedure returned posterior estimates of state-specific parameters that were consistent with initial observations and described these putative states in detail.

The approach we used aligns with recent analytical efforts to characterise diving and underwater foraging behaviour by marine mammals and seabirds, where depth is used as the third dimension instead of altitude (Bestley et al., 2015; Dean et al., 2013; Isojunno & Miller, 2015; Langrock et al., 2014; Quick et al., 2017). Together with these studies from the marine realm, it therefore represents a step towards developing a fully three-dimensional movement model as data from new sensors (e.g., accelerometry) become available (Leos-Barajas et al., 2017). To this purpose, a semi-Markov extension of the model might be considered (Isojunno & Miller, 2015; Langrock et al., 2014). The distribution of the durations of stays in the various flight modes is unlikely to be geometric, as implied by the Markov property (Langrock et al., 2014), particularly when using a short time step. The posterior predictive checks on our model confirmed that there was residual autocorrelation for some of the response variables under some states (Supporting Information Appendix S5). While this assumption may not affect appropriate behavioural classification, it becomes important when estimated probabilities are used to simulate new tracks.

5 | CONCLUSIONS

The proliferation of biologging devices offers the unique opportunity of detailing individuals' behavioural patterns at nested scales (Nathan et al., 2008). Identifying different behavioural modes that arise from animals' response to the underlying habitat and quantifying their spatiotemporal variation can provide valuable insights into the mechanisms driving behavioural, energetic and, in the long term, life-history decisions (Hays et al., 2016). However, new statistical tools are required to explore these large datasets and summarise the wide range of movement features into understandable states (Patterson et al., 2008). Here, we presented a model that describes a bird's latent behaviour as it switches among flight modes during migration. Model results highlighted two different patterns of thermal soaring flight. Moreover, the analysis of the relative occurrence of different flight modes showed yearly, seasonal, individual, age and sex differences in flight strategy and performance, shedding light on the functional processes underlying individual behavioural patterns in the context of a dynamic environment.

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AUTHORS' CONTRIBUTIONS

All authors contributed to discussions that led to the development of the research project; T.M., M.B., T.K. and A.D. collected and managed eagle telemetry data; E.P. and L.N. developed the modelling approach, E.P. led that exercise and the writing and all authors contributed to revisions.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.44v9r82> (Pirotta, Katzner et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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