

A general discrete-time modeling framework for animal movement using multistate random walks

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Abstract. Recent developments in animal tracking technology have permitted the collection of detailed data on the movement paths of individuals from many species. However, analysis methods for these data have not developed at a similar pace, largely due to a lack of suitable candidate models, coupled with the technical difficulties of fitting such models to data. To facilitate a general modeling framework, we propose that complex movement paths can be conceived as a series of movement strategies among which animals transition as they are affected by changes in their internal and external environment. We synthesize previously existing and novel methodologies to develop a general suite of mechanistic models based on biased and correlated random walks that allow different behavioral states for directed (e.g., migration), exploratory (e.g., dispersal), area-restricted (e.g., foraging), and other types of movement. Using this “toolbox” of nested model components, multistate movement models may be custom-built for a wide variety of species and applications. As a unified state-space modeling framework, it allows the simultaneous investigation of numerous hypotheses about animal movement from imperfectly observed data, including time allocations to different movement behavior states, transitions between states, the use of memory or navigation, and strengths of attraction (or repulsion) to specific locations. The inclusion of covariate information permits further investigation of specific hypotheses related to factors driving different types of movement behavior. Using reversible-jump Markov chain Monte Carlo methods to facilitate Bayesian model selection and multi-model inference, we apply the proposed methodology to real data by adapting it to the natural history of the grey seal (*Halichoerus grypus*) in the North Sea. Although previous grey seal studies tended to focus on correlated movements, we found overwhelming evidence that bias toward haul-out or foraging locations better explained seal movement than did simple or correlated random walks. Posterior model probabilities also provided evidence that seals transition among directed, area-restricted, and exploratory movements associated with haul-out, foraging, and other behaviors. With this intuitive framework for modeling and interpreting animal movement, we believe that the development and application of custom-made movement models will become more accessible to ecologists and non-statisticians.

Key words: animal location data; Bayesian model selection; biased correlated random walk; grey seal; *Halichoerus grypus*; movement model; North Sea; reversible-jump Markov chain Monte Carlo; state-space model; switching behavior; telemetry.

INTRODUCTION

Our ability to track and monitor wildlife populations has greatly improved with recent technological advancements. These include animal-borne devices that allow the collection of accurate time series of individual location data (McConnell et al. 2010, Tomkiewicz et al. 2010), biotelemetry devices providing physiological information (Cooke et al. 2004, Payne et al. 2011), and

remote sensing and geographic information system (GIS) technologies for the acquisition of detailed landscape data at multiple spatial scales (Gao 2002). Along with these developments, new challenges have arisen in the collection, management, and analysis of georeferenced animal location data (Cagnacci et al. 2010, Urbano et al. 2010).

Although Global Positioning System (GPS) and other relocation technologies have enabled the collection of large amounts of animal location data from diverse terrestrial and aquatic taxa (Tomkiewicz et al. 2010), model development for the analysis of these data has lagged behind. This is beginning to change as new methods continue to appear in the ecological literature

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(Holoak et al. 2008, Schick et al. 2008), but unlike many other areas of ecology, no general estimation framework has been developed for the analysis of movement trajectories that is widely accepted by the practitioners collecting the majority of these data sets. For example, there are well-established inferential methods in population and community ecology for examining patterns of abundance (e.g., Otis et al. 1978, Buckland et al. 2001, Borchers et al. 2002), species occurrence (e.g., MacKenzie et al. 2006), and related vital rates that address uncertainties (e.g., imperfect detection) associated with the process by which the data were obtained (Williams et al. 2002, King et al. 2009). There also exists readily accessible software for the analysis of these data by wildlife professionals (e.g., White and Burnham 1999, Thomas et al. 2010). There remains a similar need (and desire) to develop accessible, inferential data analysis methods in movement ecology (Schwarz 2009, Morales et al. 2010).

As animals respond to physiological and environmental stimuli, they often exhibit different movement behavior states (or modes). Simple examples include “exploratory” and “encamped” states in elk (Morales et al. 2004) or, equivalently, “traveling” and “foraging” states in grey seals (Breed et al. 2009), where “exploratory” or “traveling” describe movement states associated with greater directional persistence and velocity relative to the “encamped” or “foraging” states. Inferring patterns and dynamics of movement from time series of animal location data often involves the estimation of movement parameters associated with different types of movement behavior states. However, because these states often cannot be observed directly, they must be inferred based on trajectories alone in the absence of ancillary information (but see *Discussion*). Estimation is complicated further by the fact that animal location data often contain considerable observation error in both time and space, as well as missing (or intermittent) observations. Sophisticated statistical models of the underlying movement and observation process are therefore required to facilitate reliable inference (Jonsen et al. 2005, Patterson et al. 2008, Schick et al. 2008).

A variety of approaches for analyzing animal location data have been proposed in recent years, and these primarily differ in the spatiotemporal conceptualization of the movement process. These include discrete-time and discrete-space (Brownie et al. 1993, Schwarz et al. 1993, Dupuis 1995, King and Brooks 2002), discrete-time and continuous-space (Morales et al. 2004, Jonsen et al. 2005), continuous-time and discrete-space (Ovaskainen et al. 2008), or continuous-time and continuous-space (Blackwell 2003, Johnson et al. 2008) movement process models. Similarly, latent behaviors associated with different types of movement can be treated as continuous (Forester et al. 2007) or discrete (Morales et al. 2004, Jonsen et al. 2005) states among which animals transition in response to changes in their internal and

external environment. The representation of movement also differs among these approaches, by specifying the movement process on the positions themselves (Blackwell 2003, Jonsen et al. 2006) or derived quantities, such as the differences between consecutive coordinates (Jonsen et al. 2005, Johnson et al. 2008), step lengths (Forester et al. 2007), or both step lengths and turning angles (Morales et al. 2004). Although earlier methods ignored error in the timing and location of observations (Blackwell 2003, Morales et al. 2004), most recent approaches simultaneously model both the movement process and observation process using state-space methods (Anderson-Sprecher and Ledolter 1991, Jonsen et al. 2005, Johnson et al. 2008, Patterson et al. 2008).

The myriad of proposed methodologies for analyzing movement data makes selection of any particular method (or model) a difficult task. The most sophisticated continuous-time approaches, although appealing from a theoretical perspective, are prohibitively technical for many non-statisticians. Further, continuous-time and continuous-behavior models are less appealing to practitioners because the parameters (e.g., instantaneous diffusion process parameters) can be difficult to interpret biologically. Discrete-space models often necessitate spatial resolutions requiring high-dimensional matrices or integrals that can lead to computational difficulties. Perhaps most inhibiting to general use by ecologists is the fact that the majority of movement models developed to date have focused on species-specific applications and relatively few behavioral states, with little scope for generalization. Given these challenges, it is certainly not surprising that even less attention has been given to strategies for model selection and multi-model inference (Hoeting et al. 1999, Burnham and Anderson 2002, King et al. 2009) in the analysis of movement data (but see King and Brooks 2002, 2004, Morales et al. 2004).

We synthesize many of the appealing elements of previous approaches (e.g., Dunn and Gipson 1977, Blackwell 1997, 2003, King and Brooks 2002, Morales et al. 2004, Jonsen et al. 2005, Johnson et al. 2008) in combination with novel methodologies to formulate a general modeling strategy for individual animal movement in discrete time and continuous space that can be readily adapted to accommodate many different types of movement and behavioral states. With an increased emphasis on ecological inference from animal location data, these states can be associated with directed (e.g., migratory or evasive), area-restricted (e.g., foraging or nesting), exploratory (e.g., dispersal or searching), and correlated movements as dictated by the species and application of interest. Using Bayesian analysis methods, we also propose a model selection and multi-model inference procedure based on weights of evidence for these different types of movement behaviors. We demonstrate the use of this mechanistic, inferential modeling framework by adapting it to the natural history of the grey seal (*Halichoerus grypus*) in the North

Sea. This apex marine predator often demonstrates characteristically complex movement patterns among haul-out colonies and foraging patches.

METHODS

A general model for individual movement in discrete time

We first formulate a general model for animal movement as a mixture of discrete-time random walks. An individual may switch among a set of discrete movement behavior states $z = 1, \dots, Z$, where each state is characterized by distributions for the step length and direction (or bearing) of movement between consecutive positions (X_{t-1}, Y_{t-1}) and (X_t, Y_t) for each time step $t = 1, \dots, T$. We assume the T time steps are of equal length (but see *State-space formulation*). The set of Z movement behavior states can include directed movements toward particular locations or “exploratory” movements that are not associated with any particular location. When these movement behavior states are not directly observable, this can be viewed as a hidden Markov model (Zucchini and MacDonald 2009, Langrock et al. 2012).

For flexibility and mathematical convenience, we follow Morales et al. (2004) by selecting a Weibull distribution for the step length (s_t) and a wrapped (w) Cauchy distribution for the direction (ϕ_t) of movement, but other distributions for step length (e.g., gamma) or direction (e.g., von Mises) could also be used (Codling et al. 2010). The movement process model is therefore a discrete-time, continuous-space, multistate random walk with step length $[s_t | z_t = i] \sim \text{Weibull}(a_i, b_i)$ and direction $[\phi_t | z_t = i] \sim \text{wCauchy}(\mu_i, \rho_i)$. Specifically, we have the following probability density functions:

$$f(s_t | z_t = i) = \frac{b_i}{a_i} \left(\frac{s_t}{a_i} \right)^{b_i-1} \exp[-(s_t/a_i)^{b_i}]$$

and

$$f(\phi_t | z_t = i) = \frac{1}{2\pi} \frac{1 - \rho_i^2}{1 + \rho_i^2 - 2\rho_i \cos(\phi_t - \mu_i)}$$

for $a_z > 0$, $b_z > 0$, $0 \leq \phi_t < 2\pi$, $0 \leq \mu_z < 2\pi$, $-1 < \rho_z < 1$, and $z = 1, \dots, Z$. Assuming independence between step length and direction within each movement behavior state (see *Discussion*), the joint likelihood for s_t and ϕ_t (conditional on the latent state variable z_t) is

$$f(\mathbf{s}, \boldsymbol{\phi} | \mathbf{z}) = \prod_{t=1}^T f(s_t | z_t) f(\phi_t | z_t).$$

For switches between movement behavior states, we assign a categorical distribution to the latent state variable z_t . The simplest approach assigns every time step to a movement behavior state independent of previous states or ancillary information:

$$z_t \sim \text{Categorical}(\psi_1, \dots, \psi_Z)$$

such that

$$\psi_i = \Pr(z_t = i)$$

where ψ_i is the (fixed) probability of being in state i at time t , and $\sum_{i=1}^Z \psi_i = 1$. This assumption is generally unrealistic for animal movements. Alternatively (and more realistically), one could incorporate memory into the state transition probabilities using a j th-order Markov process. Assuming that movement behavior states were known, Blackwell (1997, 2003) used a first-order Markov transition matrix to characterize switches between states in continuous time. For a first-order Markov process in discrete time,

$$[z_t | z_{t-1} = k] \sim \text{Categorical}(\psi_{k,1}, \dots, \psi_{k,Z})$$

and

$$\psi_{k,i} = \Pr(z_t = i | z_{t-1} = k)$$

for $k = 1, \dots, Z$ where $\psi_{k,i}$ is the probability of switching from state k at time $t-1$ to state i at time t , and $\sum_{i=1}^Z \psi_{k,i} = 1$. We note that this Markovian structure is analogous to the state transition probabilities for multistate capture–recapture models (e.g., Brownie et al. 1993, Schwarz et al. 1993).

The multistate movement model is specified according to the particular species and ecological conditions of interest. The various movement behavior states may be solely characterized by biased, correlated, or exploratory types of movement, but environmental covariates and alternative parameterizations may also be utilized to describe the movement process. Below we present a suite of models for different movement characteristics that can be combined to form complex movement behavior states. We emphasize that the proposed models fall under the same general modeling framework, with the more basic models remaining nested within the more complex models. These, and other extensions (see *Discussion*), may therefore be thought of as contributions to a “toolbox,” from which a wide range of custom-made multistate movement models in discrete time can be assembled. By adding or removing components from the toolbox, one may compare the different models nested within the most general model (see *Example: grey seal movement in the North Sea*). This allows simultaneous investigation of numerous hypotheses about animal movement, including those involving: (1) time allocations to different movement behavior states (i.e., “activity budgets”); (2) the use of navigation for directed movement toward specific locations; (3) the relative strength of bias toward (or away from) specific locations; (4) the existence of spatially unassociated (but potentially correlated) exploratory movement states; and (5) factors affecting transition probabilities between movement behavior states.

Biased movements.—Biased movement behavior states exhibiting attraction (or aversion) to particular locations can be incorporated within the proposed framework. Suppose the set of Z movement behavior states is composed entirely of attractions to one of c different

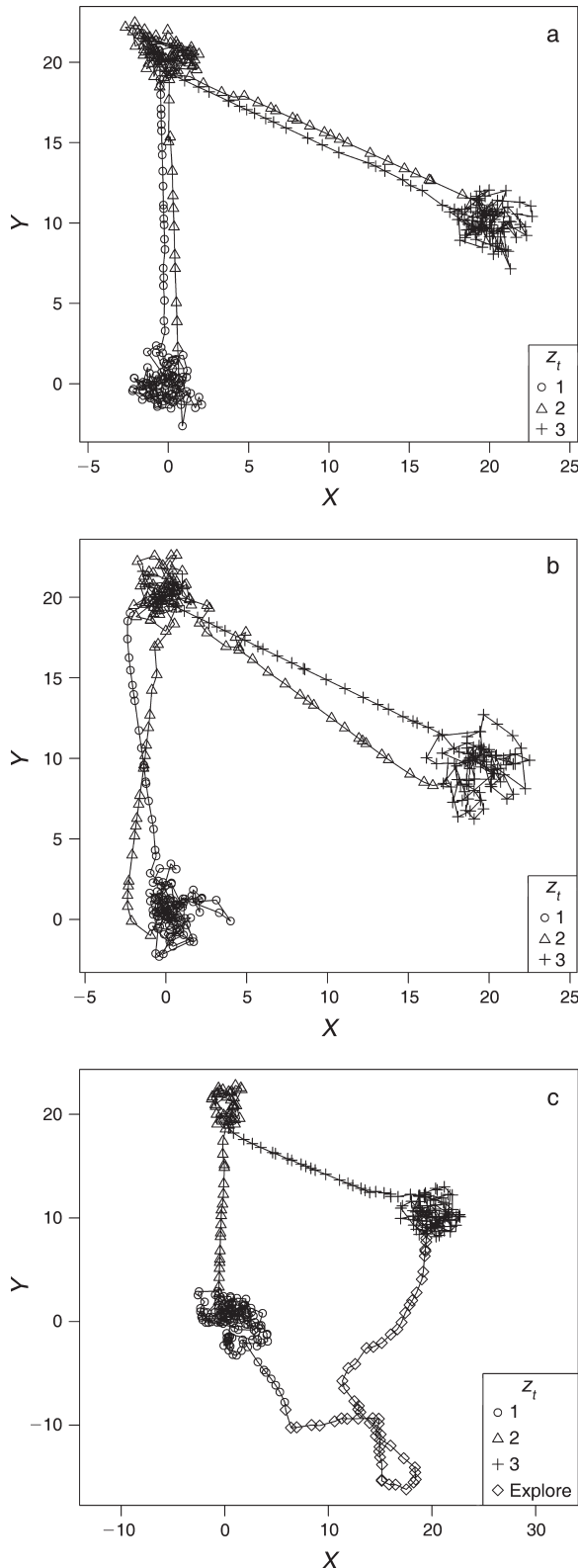


FIG. 1. Simulated time series of animal location data (position coordinates X and Y) using three centers of attraction from multistate (a) biased random walk, (b) biased correlated random walk, and (c) biased correlated random walk with an

“centers of attraction” (i.e., $Z = c$). Assuming movement at time t is biased toward center of attraction i (i.e., $z_t = i$), we calculate the expected movement direction ($\mu_{i,t}$) as the direction between the individual’s previous location (X_{t-1} , Y_{t-1}) and the location of the center of attraction (X_i^* , Y_i^*) at time t . We note that the coordinates of each center of attraction (X_z^* , Y_z^*), $z = 1, \dots, c$, are not necessarily assumed to be known (see *Example: grey seal movement in the North Sea*).

The strength of bias to each center of attraction is determined by the mean vector length of the wrapped Cauchy distribution ($0 \leq \rho_z < 1$). This strength of bias need not be constant. For example, in some instances one may expect less directed movement once an individual has reached the vicinity of the current center of attraction, so that we may specify:

$$\rho_{z,t} = \tanh(r_z \delta_t)$$

where δ_t is some metric of the distance (e.g., Euclidean) to the current center of attraction, $r_z \geq 0$ is a (state-dependent) scaling parameter, and \tanh is a hyperbolic tangent (see Appendix A). As an individual is located closer to the current center of attraction, $\rho_{z,t} \rightarrow 0$, and the movement direction is uniformly distributed on the unit circle. This allows for unbiased area-restricted searches (e.g., “encamped” or “foraging” types of movement; sensu Morales et al. 2004, Breed et al. 2009) once in the vicinity of the current center of attraction. As an individual is located farther from the current center of attraction, $\rho_{z,t} \rightarrow 1$, and ϕ_t is not allowed to deviate from $\mu_{z,t}$ (Fig. 1a). We note that this formulation also permits bias away from a “center of repulsion” when $-1 < \rho_z \leq 0$.

More complicated structural forms may be utilized for ρ_z . For example, when far away, an animal may have only a general sense of the location of a center of attraction, but the movement direction draws closer to $\mu_{z,t}$ as the distance to the center of attraction decreases (i.e., the individual “hones in” on its target). An additional quadratic term (q_z) allows this type of behavior to be included in the following model:

$$\rho_{z,t} = \tanh(r_z \delta_t + q_z \delta_t^2)$$

where r_z and q_z are constrained such that $\rho_{z,t} \geq 0$ for all reasonable δ_t within the study area. We note that alternative link functions, such as the logit link, may be utilized when specifying ρ_z as a function of covariates (see *Example: grey seal movement in the North Sea*).

Biased, correlated movements.—Additional structure can describe biased movement behavior states that exhibit correlations between successive movement direc-

←
exploratory state. The strength of bias toward the corresponding center of attraction at each time step t , $z_t = 1, 2, 3$, is a function of the Euclidean distance between the current location and the center of attraction.

tions (Fig. 1b):

$$[\phi_t | \phi_{t-1}, z_t = i] \sim \text{wCauchy}(\lambda_{i,t}, \rho_t)$$

with expected movement direction

$$\lambda_{z,t} = \eta_z \phi_{t-1} + (1 - \eta_z) \mu_{z,t}$$

where ϕ_0 is the (latent) movement direction prior to time step $t=1$. Now the expected movement direction ($\lambda_{z,t}$) is a weighted average of the strength of bias in the direction of the current center of attraction ($\mu_{z,t}$) and the previous movement direction (ϕ_{t-1}) for $0 \leq \eta_z \leq 1$. If $\eta_z = 0$, then movement reverts to a standard biased random walk. If $\eta_z = 1$, then movement becomes an unbiased correlated random walk. If $\rho_z = 0$, then movement is a simple (i.e., unbiased and uncorrelated) random walk. If $\rho_z = 1$, then movement is biased and deterministic (Barton et al. 2009). Because $\lambda_{z,t}$ is wrapped on the unit circle, we note that care must be taken in calculating $\lambda_{z,t}$ whenever $|\phi_{t-1} - \mu_{z,t}| > \pi$.

Exploratory movement states.—By specifying ρ_z as a function of distance, the model allows unbiased movements when an individual is in close proximity to a center of attraction. However, “exploratory” states may include unbiased movements that are not associated with any center of attraction. The set of Z movement behavior states can therefore be extended to include c center of attraction and h exploratory movement states, such that $Z = c + h$. Such exploratory states can be added easily within the framework previously described:

$$\rho_{z,t} = \begin{cases} 0 & \text{if } z \text{ is an exploratory state} \\ \tanh(r_z \delta_t) & \text{otherwise} \end{cases}$$

Exploratory movements may be unbiased, but they can often exhibit directional persistence (i.e., autocorrelation in movement direction). To include correlated exploratory states within the biased random walk model, set

$$[\phi_t | \phi_{t-1}, z_t = i] \sim \text{wCauchy}(\lambda_{i,t}, \rho_{i,t})$$

$$\lambda_{z,t} = \begin{cases} \phi_{t-1} & \text{if } z \text{ is an exploratory state} \\ \mu_{z,t} & \text{otherwise} \end{cases}$$

$$\rho_{z,t} = \begin{cases} v_z & \text{if } z \text{ is an exploratory state} \\ \tanh(r_z \delta_t) & \text{otherwise} \end{cases}$$

where $0 \leq v_z < 1$ is the strength of directional persistence. For a biased correlated random walk with correlated exploratory states (Fig. 1c):

$$[\phi_t | \phi_{t-1}, z_t = i] \sim \text{wCauchy}(\lambda_{i,t}, \rho_{i,t})$$

$$\lambda_{z,t} = \begin{cases} \phi_{t-1} & \text{if } z \text{ is an exploratory state} \\ \eta_z \phi_{t-1} + (1 - \eta_z) \mu_{z,t} & \text{otherwise} \end{cases}$$

and

$$\rho_{z,t} = \begin{cases} v_z & \text{if } z \text{ is an exploratory state} \\ \tanh(r_z \delta_t) & \text{otherwise} \end{cases}$$

Environmental covariates and alternative parameterizations.—Animal movement is often heavily influenced by environmental factors, such as landscape (e.g., slope or vegetation cover) or seascape (e.g., currents or temperature) conditions. These factors may be incorporated within the parameters using standard link functions. For example, if a set of k covariates was identified as potential predictors for step length, then one could assume:

$$[s_t | z_t = i] \sim \text{Weibull}(a_{i,t}, b_{i,t})$$

$$\log(a_{z,t}) = \alpha_{z,0} + \sum_{j=1}^k \alpha_{z,j} \omega_{t,j}$$

$$\log(b_{z,t}) = \beta_{z,0} + \sum_{j=1}^k \beta_{z,j} \omega_{t,j}$$

where $\omega_{t,j}$ is the value for linear predictor j at time step t . Similarly, covariates could also be incorporated into strengths of attraction (vectors \mathbf{r} and \mathbf{q}), state transition probabilities (matrix Ψ), or any other parameters in the model. This includes the use of habitat-level covariates on (X_t, Y_t) for predicting movements during missing or unobserved time steps (see *Example: grey seal movement in the North Sea*). Such predicted coordinates allow the overall movement path to reflect specific spatial features (e.g., lakes or mountains) of relevance to the species of interest.

Step length may also be a function of distance to the current center of attraction. One could envisage longer step lengths (e.g., due to increased velocity or strength of bias) when far away from the current center of attraction. Such effects could be incorporated by specifying

$$a_{z,t} = \gamma_z \tanh(\kappa_z \delta_t)$$

where the scale parameter of the Weibull distribution ($a_{z,t}$) is now a function of δ_t and a (state-dependent) scaling parameter (κ_z). When the animal is near the center of attraction, $a_{z,t}$ is closer to zero, and the step lengths are shorter. If the animal is far from the current center of attraction, $a_{z,t}$ will approach the (state-dependent) scale parameter asymptote γ_z . Alternative approaches could include change-points on the step length parameters:

$$a_{z,t} = \begin{cases} a_{z,1} & \text{if } \delta_t \in [0, d_{z,1}) \\ a_{z,2} & \text{if } \delta_t \in [d_{z,1}, d_{z,2}) \\ \vdots & \\ a_{z,k} & \text{if } \delta_t \in [d_{z,k-1}, d_{z,k}) \end{cases}$$

where $d_{z,l}$ is the threshold distance for change-point l of center of attraction state z , and l takes the values 1, 2, ..., k (see *Example: grey seal movement in the North Sea*).

Much of the biological interest in multistate movement models lies in the specification of behavioral state transition probabilities. Depending on the biological questions of interest, it may often be advantageous to reparameterize the state transition probability matrix. For example, with a migratory species it may be desirable to restrict state transitions until the individual is in the vicinity of the current center of attraction (i.e., so that “en route” switches are avoided). A simple reparameterization allows such behaviors to be more easily investigated:

$$\Psi = \begin{bmatrix} \alpha_1 & (1 - \alpha_1)\beta_{1,2} & \dots & (1 - \alpha_1)\beta_{1,c} \\ (1 - \alpha_2)\beta_{2,1} & \alpha_2 & & (1 - \alpha_2)\beta_{2,c} \\ \vdots & \vdots & \ddots & \vdots \\ (1 - \alpha_c)\beta_{c,1} & (1 - \alpha_c)\beta_{c,2} & \dots & \alpha_c \end{bmatrix}$$

where $\alpha_i = \Pr(z_t = i | z_{t-1} = i)$, $\beta_{k,i} = \Pr(z_t = i | z_{t-1} = k, k \neq i)$, and $\sum_{i \neq k}^c \beta_{k,i} = 1$ for $k = 1, 2, \dots, c$. Using logit-linear intercept (ζ_z) and slope (ξ_z) parameters, state transitions could incorporate the effects of distance: d

$$\text{logit}(\alpha_{z,t}) = \zeta_z + \xi_z \delta_t$$

whereby individuals could be more likely to remain in the current movement state until they are in close proximity to the associated center of attraction. More complicated covariate structures (e.g., the amount of time in the current state) or other reparameterizations could be incorporated in a similar fashion.

STATE-SPACE FORMULATION

Even in well-designed studies, there typically will be some degree of measurement error in spatiotemporal animal location data. Environmental conditions may affect the timing and location of fixes, as may animal behavior (e.g., diving or burrowing species). For reliable inference, these irregularities must be accounted for when applying the mechanistic movement models just described. To account for spatial error and temporal irregularity, we propose a continuous-time observation model to accompany our discrete-time movement process model in a state-space formulation.

In the movement process model, we assume that switches between behavioral states can occur at regular time intervals of equal length. The switching interval length must therefore be chosen at a temporal resolution of relevance to the species and conditions of interest. Similar to Jonsen et al. (2005), we assume that individuals travel in a straight line between times $t - 1$ and t . The observed locations are labeled according to the regular time interval into which they fall: we write $(x_{t,i}, y_{t,i})$ for the i th observation between time $t - 1$ and t , for $i = 1, \dots, n_t$. These are related to the regular locations (X_t, Y_t) via

$$x_{t,i} = (1 - j_{t,i})X_{t-1} + j_{t,i}X_t + \varepsilon_{x_{t,i}}$$

$$y_{t,i} = (1 - j_{t,i})Y_{t-1} + j_{t,i}Y_t + \varepsilon_{y_{t,i}}$$

with the following error terms:

$$\varepsilon_{x_{t,i}} \sim \mathcal{N}(0, \sigma_x^2)$$

$$\varepsilon_{y_{t,i}} \sim \mathcal{N}(0, \sigma_y^2)$$

where $j_{t,i} \in [0, 1)$ is the proportion of the time interval between locations (X_{t-1}, Y_{t-1}) and (X_t, Y_t) at which the i th observation between times $t - 1$ and t was obtained. Time intervals with no observations (i.e., $n_t = 0$) do not contribute to the observation model likelihood. In some applications (e.g., radiotelemetry triangulation or Argos satellite locations), the measurement errors are known to have more frequent large outliers than would occur under a normal distribution; in this case, a heavier-tailed error distribution could be employed (e.g., t distribution) that allows additional noncentral or scale parameters (e.g., Jonsen et al. 2005).

EXAMPLE: GREY SEAL MOVEMENT IN THE NORTH SEA

Background

We demonstrate the application of our model using hybrid-GPS transmitter data collected from grey seals (*Halichoerus grypus*) in the North Sea. Fastloc GPS transmitter (Wildtrack Telemetry Systems, Leeds, UK) tags were deployed in April 2008 and attempted to obtain a location every 30 minutes until battery failure in August or September 2008. Our multistate random walk model was initially deemed appropriate for grey seals because we suspected that they could display oriented movements among haul-out colonies and foraging patches. However, a combination of biological and technological issues necessitated use of the state-space model previously described: (1) positions are only attainable when an individual surfaces; hence, observations were obtained at irregular time intervals; and (2) following any “dry” period where a transmitter remained out of water for more than 10 minutes, no new fixes could be obtained until the transmitter returned to water continuously for 40 seconds. In other words, there were frequent missing data due to an inability to obtain locations while an individual was either hauled out or underwater.

We fitted a multistate random walk movement model to locations from a single grey seal (Fig. 2). The observed data consisted of 1045 locations irregularly spaced in time between 9 April and 13 August 2008. Based on the scale of movements of grey seals (McConnell et al. 1999) and the frequency of observations, we specified $T = 1515$ regular switching intervals of 120 min between times $t - 1$ and time t for $t = 1, \dots, T$. Our selection of 120-min intervals reflects a trade-off between computational efficiency, the temporal resolution of the data, and an acceptable temporal resolution for inference about grey seal movement behavior. The first of these 120-min intervals began at deployment on 9 April, and the last interval ended immediately after the final observed location on 13 August.

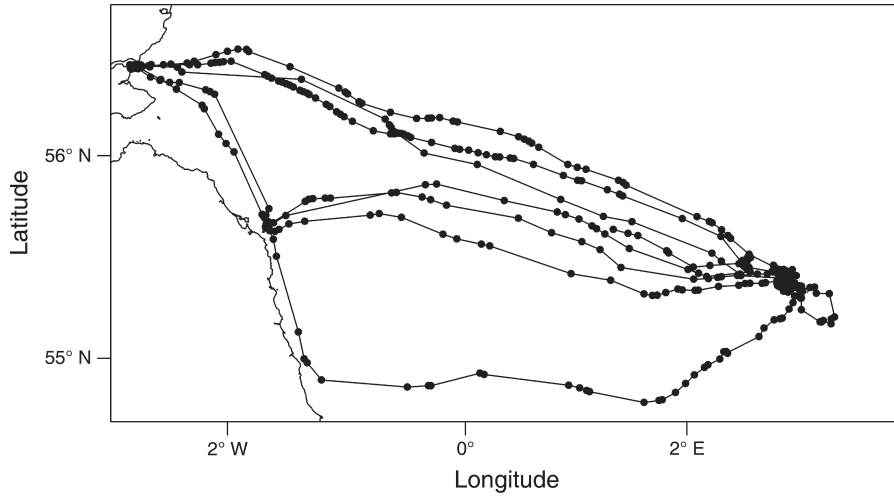


FIG. 2. Observed locations for a grey seal (*Halichoerus grypus*) as it traveled clockwise among a foraging area in the North Sea and haul-out sites on the eastern coast of Great Britain.

Movement model specification

For demonstrative purposes, we specify a simplified model of grey seal movement by limiting the number of centers of attraction ($c = 3$) and exploratory states ($h = 2$). Our most general first-order Markov movement process model therefore consisted of $Z = 5$ potential states, including state dependence on both movement direction and step length parameters:

$$[\phi_t | \phi_{t-1}, z_t = i] \sim \text{wCauchy}(\lambda_{i,t}, \rho_{i,t})$$

$$\lambda_{z,t} = \begin{cases} \eta_z \phi_{t-1} + (1 - \eta_z) \mu_{z,t} & \text{if } z \leq c \\ \phi_{t-1} & \text{if } z > c \end{cases}$$

$$\rho_{z,t} = \begin{cases} \text{logit}^{-1}(m_z + r_z \delta_t + q_z \delta_t^2) & \text{if } z \leq c \\ v_z & \text{if } z > c \end{cases}$$

$$[s_t | z_t = i] \sim \text{Weibull}(a_{i,t}, b_{i,t})$$

$$a_{z,t} = \begin{cases} a_{z,1}[1 - I_{[0,d_z]}(\delta_t)] + a_{z,2}I_{[0,d_z]}(\delta_t) & \text{if } z \leq c \\ a_z & \text{if } z > c \end{cases}$$

$$b_{z,t} = \begin{cases} b_{z,1}[1 - I_{[0,d_z]}(\delta_t)] + b_{z,2}I_{[0,d_z]}(\delta_t) & \text{if } z \leq c \\ b_z & \text{if } z > c \end{cases}$$

$$[z_t | z_{t-1} = k] \sim \text{Categorical}(\psi_{k,1}, \dots, \psi_{k,5})$$

where $k = 1, 2, 3, 4, 5$; m_z is an intercept term on the logit scale; $0 \leq \rho_{z,t} < 1$; δ_t is the (scaled) Euclidean distance between the predicted location (X_{t-1}, Y_{t-1}) and center of attraction (X_z^*, Y_z^*) at time t ; and $I_{[0,d_z]}(\delta_t)$ is an indicator function for $\delta_t \in [0, d_z]$. We chose to fit our state-space model using Bayesian analysis methods because of the general complexity of the model and the ease by which these methods can accommodate prior information, latent state variables, and missing data (Ellison 2004,

King et al. 2009). Posterior model probabilities also provide a straightforward means for addressing model selection uncertainty (see *Model selection and multi-model inference*).

For our Bayesian analysis, we specified uninformative prior distributions for most of the parameters (Table 1). Based on previous studies of grey seal movements (McConnell et al. 1999), we specified a (conservative) maximum sustainable speed of 2 m/s (such that $s_t \leq 14.4$ km). For the UTM coordinates of the centers of attraction (X_z^*, Y_z^*) , we specified joint discrete uniform priors over the coordinates of the predicted locations (X_t, Y_t) . This prior specification therefore assumes that the centers of attraction are located on the predicted movement path. We constrained state assignments for time steps corresponding to (X_z^*, Y_z^*) for each center of attraction, such that $z_t = k$ if $(X_k^*, Y_k^*) = (X_t, Y_t)$ for $k = 1, \dots, c$. For the coordinates of the initial location (X_0, Y_0) , we specified a joint uniform prior over the region (A) defined by the North Sea and coastline of Great Britain. We also constrained predicted locations (X_t, Y_t) to be within A for $t = 1, \dots, T$ (i.e., inland grey seal locations were prohibited a priori).

Model selection and multi-model inference

We used a reversible-jump Markov chain Monte Carlo (RJMCMC) algorithm (Green 1995) to fit the model and simultaneously investigate various (state-specific) parameterizations for the strength of bias toward any centers of attraction and the correlations between successive movements (see Appendix B). These parameterizations included models with linear bias [$\rho_{z,t} = \text{logit}^{-1}(m_z + r_z \delta_t)$] and quadratic bias [$\rho_{z,t} = \text{logit}^{-1}(m_z + r_z \delta_t + q_z \delta_t^2)$] toward centers of attraction for $z = 1, 2, 3$. We also investigated models with no correlation in movement direction between successive time steps when

TABLE 1. Parameter definitions and (uninformative) prior specifications for a Bayesian analysis of grey seal (*Halichoerus grypus*) location data using the multistate random walk movement model.

Parameter	Description	Prior distribution
m_z	Intercept term for the strength of bias as a function of distance to center of attraction, $z = 1, 2, 3$.	$N(0, \tau^2)$
r_z	Linear term for the strength of bias as a function of distance to center of attraction, $z = 1, 2, 3$.	$N(0, \tau^2)$
q_z	Quadratic term for the strength of bias as a function of distance to center of attraction, $z = 1, 2, 3$.	$N(0, \tau^2)$
τ^2	Prior variance for m_z , r_z , and q_z .	$\Gamma^{-1}(3, 2)$
η_z	Movement direction correlation term for center of attraction, $z = 1, 2, 3$.	$\text{Unif}(0, 1)$
v_z	Movement direction correlation term for exploratory state, $z = 4, 5$.	$\text{Unif}(0, 1)$
ϕ_0	Direction (or bearing) of movement for initial time step, $t = 0$.	$\text{Unif}(0, 2\pi)$
a_z	Scale parameter (meters) of the Weibull distribution for step length of states, $z = 1, 2, 3, 4, 5$.	$\text{Unif}(0, 14\,400)$
b_z	Shape parameter of the Weibull distribution for step length of states, $z = 1, 2, 3, 4, 5$.	$\text{Unif}(0, 30)$
d_z	Change-point distance (meters) for scale and shape parameters of the Weibull distribution for step length of center of attraction states, $z = 1, 2, 3$.	$\text{Unif}(0, 400\,000)$
σ_x^2	Measurement error variance for easting coordinates of observed locations ($x_{t,i}, y_{t,i}$).	$\Gamma^{-1}(10^{-3}, 10^{-3})$
σ_y^2	Measurement error variance for northing coordinates of observed locations ($x_{t,i}, y_{t,i}$).	$\Gamma^{-1}(10^{-3}, 10^{-3})$
$\Psi_{[k,\cdot]}$	The k th row vector of the state transition probability matrix, with each element ($\Psi_{k,i}$) corresponding to the switching probability from state k at time $t - 1$ to state $i = 1, 2, 3, 4, 5$ at time t .	$\text{Dirichlet}(1, 1, 1, 1, 1)$

in a center of attraction state ($\eta_z = 0$ for $z = 1, 2, 3$) or an exploratory state ($v_z = 0$ for $z = 4, 5$).

These different parameterizations yielded 256 potential models for evaluation via posterior model probabilities. For all models, we assumed equal prior model probabilities. For all parameters without standard full conditional posterior distributions, random walk Metropolis-Hastings updates were used (e.g., Brooks 1998, Givens and Hoeting 2005). After initial pilot tuning and burn-in, we produced a single MCMC chain of five million iterations for calculating posterior summaries and model probabilities. After thinning by 100 iterations to reduce memory requirements, Monte Carlo estimates (including model-averaged estimates) were obtained for each of the parameters from this single Markov chain. The RJMCMC algorithm was written in the C programming language (Kernighan and Ritchie 1988), with pre- and post-processing performed in R via the C Interface (R Development Core Team 2009).

Example results and discussion

Posterior model probabilities (Table 2) and model-averaged parameter summaries (Table 3) indicate biased movements toward all three centers of attraction. The estimated coordinates of the centers of attraction correspond to the Farne Islands haul-out site, the Abertay haul-out site, and the Dogger Bank foraging site (Fig. 3; Appendix C), and the strengths of bias to these three sites differed as a function of distance (Fig. 4). The Abertay haul-out site maintained a strong and consistent bias up to 350 km. Both the Farne Islands haul-out and Dogger Bank foraging sites exhibited a decreasing strength of bias curve, but we found little evidence of a quadratic effect of distance (Tables 2 and 3). Biased movements continued at greater distances (>350 km) and declined less rapidly from the Dogger

Bank foraging site than from the Farne Islands haul-out site. These patterns of directed movement as a function of distance could be indicative of the seal “honing in” on these targets, but ocean currents are also likely to be influencing the timing and direction of these movements (see Gaspar et al. 2006).

Model-averaged posterior summaries indicated a strong tendency for the seal to remain in its current movement state (Table 3), with switches between center of attraction states rarely occurring until the seal had reached the vicinity of the current center of attraction (Fig. 3). We found very little evidence of correlated

TABLE 2. Posterior model probabilities (PMP) for strength of attraction (q_z) and correlation (η_z and v_z) parameters for a grey seal in the North Sea.

PMP	Model parameter							
	q_1	q_2	q_3	η_1	η_2	η_3	v_4	v_5
0.17		1						
0.15		1	1					
0.13	1	1						
0.11	1	1	1					
0.07								
0.07			1					
0.06	1							
0.05	1		1					
0.03		1					1	
0.03		1	1				1	
0.02	1	1					1	
0.02	1	1	1				1	
MPP	0.43	0.68	0.48	0.01	0.00	0.00	0.16	0.01

Notes: For each parameter, “1” indicates presence in the model. The bottom row indicates the marginal posterior probabilities (MPP) for each parameter. Centers of attraction (denoted by variable subscript numbers) correspond to the Farne Islands haul-out site ($z = 1$), Abertay haul-out site ($z = 2$), and Dogger Bank foraging site ($z = 3$). Other states correspond to high-speed ($z = 4$) and low-speed ($z = 5$) exploratory states. Results are for models with a PMP of at least 0.02.

TABLE 3. Model-averaged posterior summaries for strength of attraction (r_z , q_z , m_z , and τ), correlation (η_z , v_z , and ϕ_0), step length (a_z , b_z , and d_z), observation error (σ_x and σ_y), and state transition probability ($\psi_{k,i}$) parameters.

Parameter	Estimate	95% HPDI	
		Lower	Upper
a) Strength of attraction			
m_1	3.08	2.31	3.91
m_2	4.54	3.85	5.37
m_3	3.49	2.86	4.21
r_1	-5.47	-8.35	-2.40
r_2	-0.70	-9.84	4.47
r_3	-3.41	-7.10	-1.77
q_1	-0.53	-4.90	4.13
q_2	3.40	-2.27	14.94
q_3	1.63	-1.39	5.01
τ	3.00	1.68	5.63
b) Correlation			
η_1	0.00	0.00	0.01
η_2	0.00	0.00	0.00
η_3	0.00	0.00	0.01
v_4	0.16	0.00	0.63
v_5	0.01	0.00	0.04
ϕ_0	0.06	3.47	3.13
c) Step length			
$a_{1,1}$	10 497.04	10 026.35	10 990.62
$a_{2,1}$	11 052.65	10 631.82	11 524.23
$a_{3,1}$	10 859.38	10 503.77	11 194.52
a_4	5 188.94	4 755.68	5 644.98
a_5	1 902.68	1 601.28	2 230.24
$b_{1,1}$	6.12	4.78	7.73
$b_{2,1}$	6.17	5.33	7.43
$b_{3,1}$	6.16	5.38	7.04
b_4	19.96	8.51	30.00
b_5	4.40	2.09	11.85
d_1	1 576.19	1 152.39	2 077.87
d_2	5 583.09	3 694.29	6 552.00
d_3	1 425.98	1 016.81	2 722.62
$a_{1,2}$	1 908.44	1 369.26	2 529.56
$a_{2,2}$	2 061.91	1 760.39	2 333.18
$a_{3,2}$	2 480.05	1 572.07	5 811.18
$b_{1,2}$	4.93	1.26	18.97
$b_{2,2}$	24.70	16.45	30.00
$b_{3,2}$	2.77	1.04	5.83
d) Observation error			
σ_x	562.32	510.92	619.68
σ_y	254.62	233.42	276.44
e) State transition probability			
ψ_{11}	0.95	0.92	0.98
ψ_{12}	0.00	0.00	0.01
ψ_{13}	0.00	0.00	0.02
ψ_{14}	0.03	0.00	0.06
ψ_{15}	0.01	0.00	0.03
ψ_{21}	0.00	0.00	0.01
ψ_{22}	0.81	0.76	0.85
ψ_{23}	0.13	0.09	0.18
ψ_{24}	0.02	0.00	0.05
ψ_{25}	0.03	0.01	0.06
ψ_{31}	0.00	0.00	0.01
ψ_{32}	0.09	0.06	0.13
ψ_{33}	0.84	0.80	0.88
ψ_{34}	0.02	0.00	0.04
ψ_{35}	0.04	0.02	0.06
ψ_{41}	0.10	0.02	0.23
ψ_{42}	0.16	0.01	0.33
ψ_{43}	0.09	0.01	0.21
ψ_{44}	0.41	0.20	0.62
ψ_{45}	0.19	0.04	0.36
ψ_{51}	0.01	0.00	0.03

TABLE 3. Continued.

Parameter	Estimate	95% HPDI	
		Lower	Upper
ψ_{52}	0.05	0.00	0.12
ψ_{53}	0.15	0.07	0.24
ψ_{54}	0.09	0.01	0.17
ψ_{55}	0.69	0.59	0.78

Notes: Summaries include posterior medians and 95% highest posterior density intervals (HPDI), conditional on the parameter being present in the model. Posterior means are reported for state transition probabilities. Center of attraction states correspond to the Farne Islands haul-out site ($z = 1$), Abertay haul-out site ($z = 2$), and Dogger Bank foraging site ($z = 3$). The high-speed ($z = 4$) and low-speed ($z = 5$) exploratory states are not associated with a center of attraction.

movements when in a center of attraction state, with marginal posterior parameter probabilities of 0.01, 0.00, and 0.00 for η_1 , η_2 , and η_3 , respectively. We found little evidence for directional persistence during the exploratory states not associated with any center of attraction (Table 3), with marginal posterior parameter probabilities of 0.16 for v_4 and 0.01 for v_5 . As expected, uncertainty in the coordinates of predicted locations (X_t , Y_t) was greatest during time steps with missing data, most notably during extended “dry” haul-out periods and foraging at Dogger Bank (Fig. 3b).

Based on posterior summaries for the step length and change-point parameters, we found strong evidence of shorter step lengths within 5 km of the three centers of attraction (Table 3). For the Farne Islands and Abertay sites, the predicted locations in close proximity to these centers of attraction suggest restricted movement in the vicinity of the haul-out colonies. For the Dogger Bank site, the predicted locations in the vicinity suggest area-restricted searches during foraging (Fig. 3). These findings are consistent with expected haul-out and foraging movement behaviors of grey seals (McConnell et al. 1999). Although neither of the exploratory states exhibited strong directional persistence, parameter estimates indicated relatively longer step lengths (i.e., higher speed) for one of these exploratory states (Table 3). This suggests transitory or searching movements during the “high-speed” exploratory state ($z = 4$), but the “low-speed” exploratory state ($z = 5$) could be indicative of foraging or resting at sea.

Based on posterior state assignments, the mean proportion of time (95% highest posterior density interval) between 9 April and 13 August 2008 that the seal spent in each state was 0.39 (0.37, 0.41) for the Dogger Bank foraging state, 0.27 (0.26, 0.29) for the Abertay haul-out state, 0.17 (0.16, 0.19) for the Farne Islands haul-out state, 0.12 (0.10, 0.13) for the low-speed exploratory state, and 0.05 (0.03, 0.06) for the high-speed exploratory state. Due to tortuosity in the movement path, there was some uncertainty in state assignments for transitory movements among centers of attraction. We suspect that these indirect paths are related to environmental cues or ocean currents. There

was also some state assignment uncertainty for movements in the vicinity of the Abertay and Dogger Bank centers of attraction. This could be attributable to a potential foraging area in the offshore sandbanks near the Abertay haul-out site, responses to prey movement in the Dogger Bank foraging area, and missing location data during “dry” or prolonged diving periods. Further model structure, including additional movement behavior states or environmental covariates, may be required to better explain these movements.

Given the reliability of locations using hybrid-GPS transmitters, we were not particularly concerned about spatiotemporal measurement error for these data. We were far more concerned about irregularly observed and missing data because we were unable to obtain locations while the seal was hauled out or underwater. Error terms (in meters) were relatively small, with posterior medians for $\hat{\sigma}_x = 562$ (95% HPDI: 511–620) and for $\hat{\sigma}_y = 255$ (95% HPDI: 233–276). Similar to Patterson et al. (2010), the larger value for σ_x reflects the prevalence of east–west movements between haul-out and foraging sites. There were several instances where small, but non-negligible, differences were found between observed and predicted locations (Fig. 3a), but we believe that these instances are more likely attributable to some deficiencies in the model than to location measurement error.

Previous studies on individual seal movement (Jonsen et al. 2005, Johnson et al. 2008, Breed et al. 2009, Patterson et al. 2010) limited models to simple and correlated random walks among haul-out and foraging areas. Based on posterior estimates and probabilities for simple (0% of posterior model probabilities), correlated (0%), biased (82%), and both biased and correlated (18%) random walk mixture models, we found overwhelming evidence that including bias (or drift) toward centers of attraction better explained seal movement than simple or correlated random walks. This result strongly supports the recognized ability of grey seals to rely on navigational capabilities for directed (and not simply correlated) movement among haul-out colonies and foraging patches.

Correlations among parameters and the large number of latent variables made the development of a model-fitting algorithm a computational challenge. To help diagnose convergence, we examined a series of additional chains with overdispersed initial values. With poor starting values for (X_z^*, Y_z^*) and (X_t, Y_t) , we found that the algorithm could diverge or get caught in local maxima. However, we achieved similar results for chains covering a range of reasonable starting values. Even with reasonable starting values, it required about five million iterations before chains appeared to converge. The centers of attraction do not necessarily need to be located on the predicted movement path, but we found that mixing and performance were greatly improved by this prior specification for the coordinates of the centers of attraction (X_z^*, Y_z^*) . We also believe it is reasonable to

assume that centers of attraction are visited (and hence located along the predicted path).

At the expense of some biological realism, we chose to keep this example relatively simple to demonstrate the application of this methodology to a general audience. If our intended audience were limited to marine mammalogists, we would have incorporated additional model complexity and prior information to better reflect the biology of grey seals. Similar to Johnson et al. (2008), we could have included an additional “dry” state for movement during periods when the seal was (presumably) out of water (e.g., smaller step lengths). Alternatively, landscape covariates could have been used for specifying “haul-out” movement states when the seal was located on land. We also could have constrained transition probabilities to make switches between states less likely until the seal reached the vicinity of the current center of attraction. Refinements such as these not only would add biological realism, but also would likely improve mixing and convergence of the RJMCMC algorithm.

DISCUSSION

With the development of an intuitive framework for modeling animal movement, ecologists may better appreciate the applicability of mechanistic, inferential movement models to a wide variety of species and conditions. We have proposed a discrete-time, continuous-space, and discrete-state conceptualization of the individual animal movement process to facilitate the biological interpretation of distinct movement behaviors and associated parameters. We believe that its mathematical simplicity and focus on ecology can make the application of custom-made movement models more straightforward for non-statisticians. This “toolbox” of model components allows researchers to construct custom-built mechanistic movement models for the species of interest, while providing a means to compare weights of evidence in support of specific hypotheses about different movement behaviors.

Perhaps most appealing is the ease with which new components can be added to the nested model-building toolbox. Although more components can lead to a large number of potential models to choose from, the framework can accommodate the additional model selection uncertainty in a straightforward quantitative manner. As demonstrated in our grey seal example, this approach enabled the simultaneous investigation of numerous hypotheses about seal movement, including the use of navigation and time allocations to different movement behavior states. To our knowledge, this is the first methodology utilizing model weights for selection and multi-model inference in the mechanistic movement model literature.

Although our main goal has been to present this suite of model-building tools, a serious study of animal movement should include some additional assessments of goodness of fit. Morales et al. (2004) and Dalziel et al.

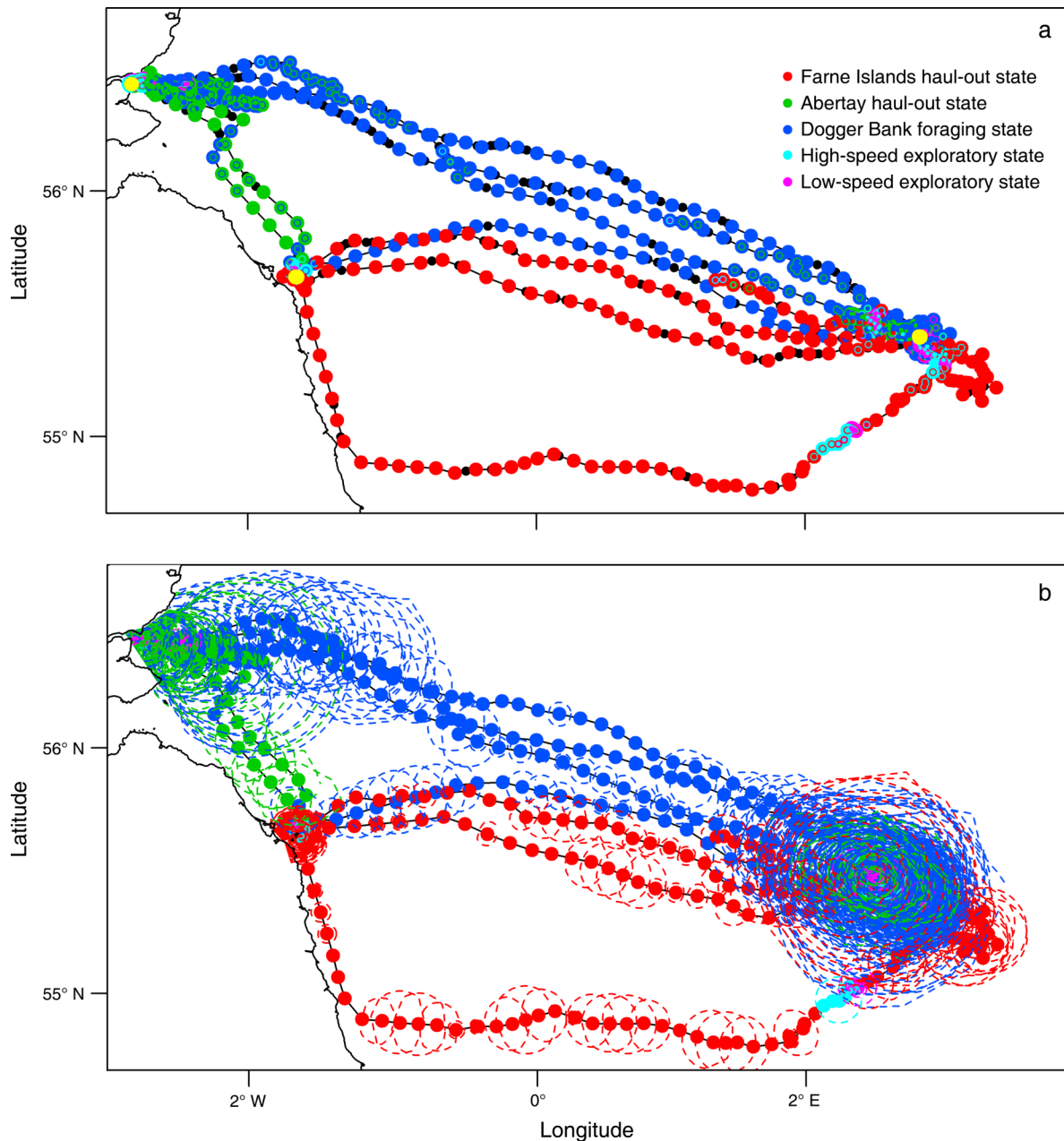


FIG. 3. Predicted locations, movement behavior states, and coordinates of three centers of attraction for a grey seal in the North Sea and eastern coast of Great Britain. Estimated movement states for the predicted locations (solid colored circles) correspond to the Farne Islands haul-out site (red), Abertay haul-out site (green), Dogger Bank foraging site (blue), or spatially unassociated high-speed (light blue) and low-speed (magenta) exploratory states. Solid yellow circles indicate the estimated coordinates of the three centers of attraction, and small solid black circles indicate observed locations in panel (a). Uncertainty in the estimated state (<95% posterior probability) is indicated by smaller hollow circles within predicted locations in panel (a). Uncertainty in estimated coordinates is indicated by symmetric 95% credible intervals (dashed circles) for predicted locations in panel (b). An animated version of this figure is available in Appendix C.

(2010) briefly explore this topic, including the use of posterior predictive checks and probes to test whether the fitted models are consistent with emergent properties of the movement process (e.g., autocorrelation patterns in displacements and habitat use). However, an assessment of absolute goodness of fit remains a daunting task

for mechanistic movement models. In the absence of classical tests of goodness of fit, it is particularly important that the model set be selected with care, utilizing the best biological information available for reliable inference. Conditional on this candidate model set, model comparisons (e.g., based on posterior model

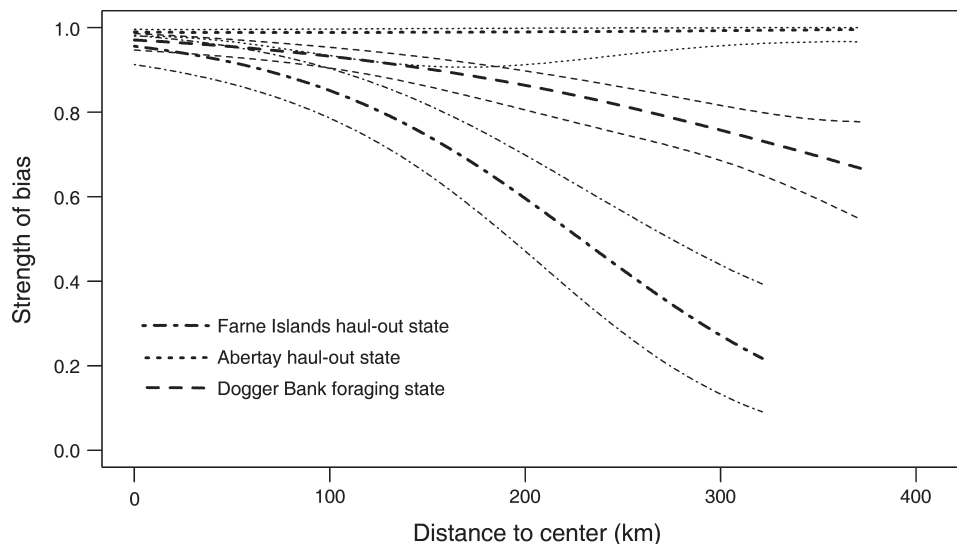


FIG. 4. Model-averaged strength of bias (p_z) to three centers of attraction as a function of distance from a grey seal in the North Sea. Center of attraction states correspond to the Farne Islands haul-out site, Abertay haul-out site, and Dogger Bank foraging site. Thinner lines indicate symmetric 95% credible intervals. Lines terminate at the maximum distance at which the seal was assigned to each respective center of attraction state.

probabilities or other model selection criteria) can provide some assessment of the relative goodness of fit.

There remain many potential extensions to the modeling framework beyond those already identified. In the grey seal example, we included two exploratory movement states not associated with any center of attraction, but additional spatially unassociated states that differ in their movement properties (and associated state parameters) may be incorporated (*sensu* Morales et al. 2004, Jonsen et al. 2005, Breed et al. 2009). These additional states could be used to further differentiate among exploratory movements (e.g., dispersal or search strategies) that have unique distributions for step length and the degree of correlation between successive movements.

We reiterate that centers of attraction do not necessarily refer to a single location in space. Rather, they can refer to any entity to which animals move in response. This includes immobile entities such as habitat patches, but also mobile entities such as conspecifics or prey. Any given entity (or group of entities) could therefore be used to define a different behavior state for movement toward, away from, or within each entity. Potential centers of attraction also can be dynamically incorporated within an individual's portfolio as its habitat is explored, thus allowing for explicit modeling of the effects of past experience on movement. Instead of centers of attraction, centers of repulsion (where $-1 < p_z \leq 0$) may be particularly useful for demonstrating avoidance behaviors related to encounters with conspecifics, predators, or undesirable habitats.

From a behavioral ecology perspective, perhaps most promising is the potential for modeling movement state

transition probabilities. By incorporating physiological or environmental covariate information into the framework, one can investigate hypotheses about the timing and motivations behind various movement behaviors as individuals respond to changes in the internal and external environment (Morales et al. 2010). Biotelemetry data (e.g., metabolic rate) or time of year (e.g., breeding season) are among many factors that may help to explain changes in movement behavior. Instead of relying solely on trajectories, ancillary data may also be helpful in the assignment of movement states. For example, additional landscape or seascape information may have better explained the indirect movements between the two haul-out colonies in our grey seal analysis. Recent advances, such as animal-borne accelerometers (Wilson et al. 2008, Holland et al. 2009, Payne et al. 2011), will probably provide additional ways to distinguish among different types of movement (e.g., predator hunting and feeding). There are also many ways by which memory can be incorporated into movements and state transitions. Here, we only explored two such mechanisms for memory, including Markov processes for state transitions and the existence of spatial locations that are committed to memory because they are (presumably) associated with specific goals.

The locations of centers of attraction are typically assumed to be known based on prior knowledge or qualitative assessments of the data. Indeed, one could relatively easily predict the coordinates of the three centers of attraction in our grey seal example using only the naked eye or previous studies. However, we envision more complicated movement paths where it is very difficult to identify or differentiate between potential

centers. We believe that a quantitative means for estimating the location of centers and their associated strengths of attraction (or repulsion), such as that proposed here, improves our ability to extract reliable information from novel or more complex movement paths.

For simplicity, we chose to specify three centers of attraction in our grey seal example. Although we found strong evidence of bias toward all three of these centers, if any center z receives little support for bias (e.g., $p_{z,t} \approx 0$ for all δ_t), alternative models removing such centers should be explored because state z essentially becomes an uncorrelated exploratory state. This may have undesirable consequences, including confounded exploratory states and poor MCMC mixing. Ideally, the model could be extended to accommodate an unknown number of centers and reduce any need for ad hoc assessments of the appropriate number of centers. This would require an additional parameter for the number of centers and (state-specific) movement parameters for each potential center. Similar to the multi-model inference procedure used here, a reversible-jump MCMC algorithm could be utilized to estimate the number of centers of attraction. This potential extension constitutes the focus of current research.

Additional information or structural complexity could also be specified in the observation process of the state-space model. For example, Jonsen et al. (2005) specified informative priors for measurement error parameters based on previously published records of location estimation error for Argos-tagged grey seals. State-dependent error or correlation terms (e.g., utilizing a multivariate normal error distribution) could also be incorporated. Although a great deal of previous effort in the analysis of animal location data has focused on the observation process, we expect greater emphasis on the movement process as the quality of location data continues to improve (e.g., with advances in GPS technology).

Although other approaches (e.g., Blackwell 2003, Jonsen et al. 2005, Johnson et al. 2008) potentially could be extended to include the various types of movement accommodated by our multistate model, we chose to extend the basic methodology of Morales et al. (2004) because of its intuitive appeal to ecologists and wildlife professionals. The discrete-time, continuous-space approach of Jonsen et al. (2005) can accommodate correlated and uncorrelated exploratory movements, but it does not include biased or area-restricted movements related to specific locations or habitats. An additional limitation of the correlated random walk approach of Jonsen et al. (2005) is a lack of independence between direction and step length, resulting in higher-order autocorrelations than found in standard correlated random walks. Our approach assumes independence between direction and step length for each movement behavior state, but a joint distribution including correlations could potentially be incorporated

if deemed appropriate (e.g., specifying shorter step lengths when movement is away from the current center of attraction).

The continuous-time, continuous-space approaches of Blackwell (2003) and Johnson et al. (2008) do allow correlated movements and “drift” that can (potentially) be related to specific locations (*sensu* Kendall 1974, Dunn and Gipson 1977). However, Blackwell (2003) assumes that movement behavior states are known and Johnson et al. (2008) only include a single state with known covariates; hence, neither approach includes an estimation framework for both movement state and switching behavior. Although satisfying from a mathematical and theoretical perspective, we believe the often difficult interpretation of continuous-time movement parameters (e.g., those related to Ornstein-Uhlenbeck and other diffusion processes) can, in practice, be discouraging to applied ecologists wishing to use or extend these methods. This may change as ecologists become more familiar with the principles of mechanistic movement models and computer software makes these approaches more accessible.

Unlike continuous-time movement process models, the primary disadvantage of a discrete-time approach is that the time scale between state transitions must be chosen based on the biology of the species and the frequency of observations. For any continuous- or discrete-time approach to be useful, the temporal resolution of the observed data must be relevant to the specific movement behaviors of interest. The timing and frequency of observations must therefore be carefully considered when designing telemetry devices and data collection schemes.

To encourage the broader application of movement models in ecology, user-friendly software for the analysis of animal location data is needed. Ovaskainen et al. (2008) and Johnson et al. (2008) provided important first steps in accessible software by creating *DISPERSE* and the R package *CRAWL* to perform the complicated computations that the models, respectively, require. Despite its relative mathematical simplicity, the large number of parameters and latent variables inherent to our modeling framework also make implementation a computational challenge. We therefore provide code for the full state-space formulation of our model (see Supplement) and are currently developing a software package for general use by practitioners (L. Milazzo, B. T. McClintock, R. King, L. Thomas, J. Matthiopoulos, and J. M. Morales, *unpublished software*).

By making individual movement models more accessible and readily interpretable to ecologists, we ultimately hope that progress can be made toward linking animal movement and population dynamics at the interface of behavioral, population, and landscape ecology (Morales et al. 2010). Although the mechanistic links between animal movement and population dynamics are theoretically understood, fitting population-level models to data from many individuals will pose

considerable mathematical and computational challenges. Scaling individual movement models up to population-level processes therefore remains a very promising avenue for future research.

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SUPPLEMENTAL MATERIAL

Appendix A

Strength of bias for the wrapped Cauchy distribution as a function of distance to a center of attraction (*Ecological Archives* M082-012-A1).

Appendix B

Reversible-jump Markov chain Monte Carlo algorithm for the multistate random walk model (*Ecological Archives* M082-012-A2).

Appendix C

Animation of Fig. 3 (*Ecological Archives* M082-012-A3).

Supplement

Computer code and data for implementing the reversible-jump Markov chain Monte Carlo algorithm for the multistate random walk model (*Ecological Archives* M082-012-S1).