A General Modeling Framework for Animal Movement in Discrete Time Using Multi-State Random Walks

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ABSTRACT

Recent developments in animal tracking technology have permitted the collection of detailed movement paths from individuals of many species. Despite this increasing wealth of information, model development for the analysis of movement data has not kept pace with these technological advancements. This is largely due to the inherent complexity of the movement process and the structure of animal location data, which often include considerable observation error in both time and space. Sophisticated statistical models of both the movement and observation process are therefore required to facilitate reliable inference. To better understand complicated animal movements in heterogeneous landscapes, we propose that movement paths can be dissected into a few general movement strategies among which animals transition as they are affected by changes in the internal and external environment. We develop a suite of state-space models of individual animal movement based on mixtures of biased and correlated random walks that include different behavioral states for oriented, exploratory, and area-restricted movements. Models may then be "custom-built" for a wide variety of species applications, thereby allowing the simultaneous estimation of time allocations to latent movement behavior states, state transition probabilities, locations of foraging or resident centers of attraction, and the strength of attraction (or repulsion) to specific locations. Using reversible jump Markov chain Monte Carlo methods to facilitate Bayesian model selection and multimodel inference, we apply the proposed methodology to grey seal movements among haul-out and foraging locations in the North Sea.

INTRODUCTION

- 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, model development for the analysis of these data has lagged behind
- We synthesize many of the appealing elements of previous approaches (e.g., Dunn and Gipson 1977, Blackwell 1997, 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

METHODS

- We first formulate a general model for animal movement as a mixture of discrete-time random walks, where an individual may switch among a set of discrete movement behavior states, $z = 1,\ldots,Z$, and each state is characterized by distributions for the step length (s_t) and bearing (ϕ_t) of movement between consecutive positions and for each time step $t = 1,\ldots,T$:

$$[s_t \mid z_t] \sim \text{Weibull}\,(a_{z_t}, b_{z_t})$$

$$[\phi_t \mid z_t] \sim \text{wCauchy}\,(\mu_{z_t}, \rho_{z_t})$$

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

- The multi-state 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 (e.g., towards a "center of attraction"), correlated, or spatially-unassociated "exploratory" types of movement, but environmental covariates and alternative parameterizations may also be utilized to describe the movement process (see *Example: grey seal movements in the North Sea*)

EXAMPLE: GREY SEAL MOVEMENTS IN THE NORTH SEA

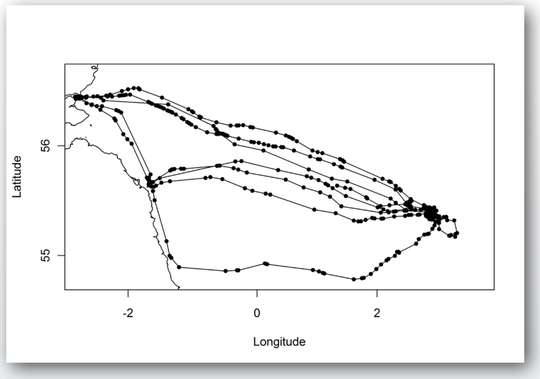

Figure 1. Observed locations for a grey seal as it traveled clockwise among a foraging area in the North Sea and haul-out sites on the eastern coast of Great Britain.

North Sea grey seal (*Halichoerus grypus*)

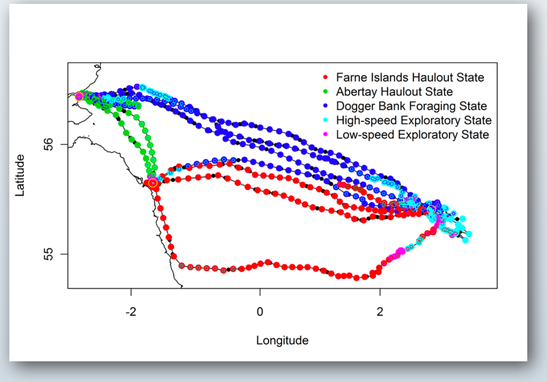

Figure 2. Predicted locations, movement behavior states, and coordinates of three centers of attraction for a grey seal in the North Sea and eastern coast of Great Britain. Estimated movement states for the predicted locations (solid colored circles) correspond to the Farne Islands haul-out site (red), Abertay haul-out site (green), Dogger Bank foraging site (blue), or spatially-unassociated high-speed (light blue) and low-speed (magenta) exploratory states. Hollow yellow circles indicate the estimated coordinates of the three centers of attraction, and solid black circles indicate observed locations. Uncertainty in the estimated state (< 95% posterior probability) is indicated by smaller hollow circles within predicted locations.

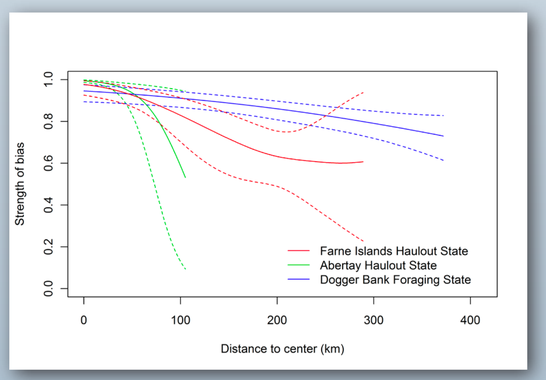

Figure 3. Model-averaged strength of bias to c = 3 centers of attraction as a function of distance from a grey seal in the North Sea. Center of attraction states correspond to the Farne Islands haul-out site (red), Abertay haul-out site (green), and Dogger Bank foraging site (blue). Dashed lines indicate symmetric 95% credible intervals. Lines terminate at the maximum distance at which the seal was assigned to each respective center of attraction state.

Model Specification and Analysis Methods

- We demonstrate the application of our model using hybrid-GPS transmitter data collected from grey seals (*Halichoerus grypus*) in the North Sea between 9 April and 13 August 2008 (Figure 1)
- Missing data resulting from an inability to obtain locations while an individual was either hauled out or underwater necessitated use of a state-space model
- We specify a simplified model of grey seal movement by limiting the number of center of attraction ($c = 3$) and exploratory ($h = 2$) states:

$$[\phi_t \mid z_t] \sim \text{wCauchy}\left(\lambda_{z_t}, \rho_{z_t}\right)$$

$$\lambda_{z_t} = \begin{cases} \eta_{z_t}\phi_{t-1} + \left(1-\eta_{z_t}\right)\mu_{z_t} & \text{if } z_t \le c \\ \phi_{t-1} & \text{if } z_t > c \end{cases}$$

$$\rho_{z_t} = \begin{cases} \text{logit}^{-1}\left(m_{z_t} + r_{z_t}\delta_t + q_{z_t}\delta_t^2\right) & \text{if } z_t \le c \\ \upsilon_{z_t} & \text{if } z_t > c \end{cases}$$

$$[s_t \mid z_t] \sim \text{Weibull}(a_{z_t}, b_{z_t})$$

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

where m_{z_t} is an intercept term on the logit scale, and δ_t is the (scaled) Euclidean distance between the predicted location and center of attraction at time t. We also included a change-point on the Weibull shape and scale parameters based on δ_t

- 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. Posterior model probabilities also provide a straightforward means for addressing model selection uncertainty

Example Results

- 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 (Figure 2), and the strengths of bias to these three sites differed as a function of distance (Figure 3)
- Posterior model probabilities (Table 1) strongly suggest an effect of distance on the strength of bias towards all three centers of attraction, but we found very little evidence for correlated movements when in a center of attraction state. We also found little evidence for directional persistence during the exploratory states not associated with any center of attraction

Table 1. Posterior model probabilities (PMP) for strength of attraction (q_z) and correlation parameters for a grey seal in the North Sea. For each parameter, a '1' indicates presence in the model. The bottom row indicates the marginal posterior probabilities (MPP) for each parameter. Centers of attraction correspond to the Farne Islands haul-out site, Abertay haul-out site, and Dogger Bank foraging site . Results are for models with a PMP of at least 0.003.

PMP	Model							
	q_1	q_2	q_3	η_1	η_2	η_3	υ_4	υ_5
0.44	1	1						
0.18	1	1	1					
0.15	1							
0.07		1						
0.05								
0.04	1		1					
0.03		1	1					
0.01			1					
0.01	1	1						1
0.00	1	1					1	
	0.83	0.74	0.28	0.00	0.00	0.00	0.01	0.01

Table 2. Estimated proportion of study period (9 April to 13 August 2008) spent in each movement behavior state.

	Proportion of Study Period	LCI	UCI
Farne Islands Haulout	0.15	0.13	0.18
Abertay Haulout	0.22	0.20	0.26
Dogger Bank Foraging	0.28	0.24	0.32
High-speed Exploratory	0.20	0.13	0.24
Low-speed Exploratory	0.15	0.13	0.17

- We found strong evidence of shorter step lengths within 5km of the three centers of attraction. 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
- Although neither of the exploratory states exhibited strong directional persistence, one of the exploratory states was found to have considerably longer step lengths than the other. This suggests transitory or searching movements during the high-speed exploratory state, but the low-speed exploratory state could be indicative of foraging or resting at sea
- These findings are consistent with expected haul-out and foraging movement behaviors of grey seals (McConnell et al. 1999)

DISCUSSION

- 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
- This "tool-box" 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. It therefore enables the simultaneous investigation of numerous hypotheses about movement, including the use of navigation and time allocations (i.e., "activity budgets") to different movement behavior states
- There remain many potential extensions to the modeling framework beyond those already identified
- 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. The timing and frequency of observations must therefore be carefully considered when designing telemetry devices and data collection schemes.
- By making individual movement models more accessible and readily interpretable to ecologists, we ultimately hope progress can be made towards linking animal movement and population dynamics at the interface of behavioral, population, and landscape ecology

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