2   **A general discrete-time modeling framework for animal movement**

3   **using multi-state random walks**

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25   *Abstract*. Recent developments in animal tracking technology have permitted the

26   collection of detailed data on the movement paths of individuals from many species.

27   However, analysis methods for these data have not developed at a similar pace, largely

28   due to a lack of suitable candidate models, coupled with the technical difficulties of

29   fitting such models to data. To facilitate a general modeling framework, we propose

30   that complex movement paths can be conceived as a series of movement strategies

31   among which animals transition as they are affected by changes in their internal and

32   external environment. We synthesize previously existing and novel methodologies to

33   develop a general suite of mechanistic models based on biased and correlated random

34   walks that allow different behavioral states for directed (e.g., migration), exploratory

35   (e.g., dispersal), area-restricted (e.g., foraging), and other types of movement. Using

36   this "tool-box" of nested model components, multi-state movement models may be

37   custom-built for a wide variety of species and applications. As a unified state-space

38   modeling framework, it allows the simultaneous investigation of numerous hypotheses

39   about animal movement from imperfectly observed data, including time allocations to

40   different movement behavior states, transitions between states, the use of memory or

41   navigation, and strengths of attraction (or repulsion) to specific locations. The inclusion

42   of covariate information permits further investigation of specific hypotheses related to

43   factors driving different types of movement behavior. Using reversible jump Markov

44   chain Monte Carlo methods to facilitate Bayesian model selection and multi-model

45   inference, we apply the proposed methodology to real data by adapting it to the natural

46   history of the grey seal (*Halichoerus grypus*) in the North Sea. Although previous grey

47   seal studies tended to focus on correlated movements, we found overwhelming evidence

48   that bias towards haul-out or foraging locations better explained seal movement than

49   simple or correlated random walks. Posterior model probabilities also provided

50   evidence that seals transition among directed, area-restricted, and exploratory

51   movements associated with haul-out, foraging, and other behaviors. With this intuitive

52   framework for modeling and interpreting animal movement, we believe the

53   development and application of bespoke movement models will become more

54   accessible to ecologists and non-statisticians.

55   *Key words: animal location data, biased correlated random walk, movement*

56   *model, state-space model, switching behavior, telemetry.*

57   INTRODUCTION

58   Our ability to track and monitor wildlife populations has greatly improved with recent

59   technological advancements. These include animal-borne devices that allow the

60   collection of accurate time-series of individual location data (McConnell et al. 2010,

61   Tomkiewicz et al. 2010), biotelemetry devices providing physiological information

62   (Cooke et al. 2004, Payne et al. 2010), and remote sensing and geographic information

63   system (GIS) technologies for the acquisition of detailed landscape data at multiple

64   spatial scales (Gao 2002). Along with these developments, new challenges have arisen

65   in the collection, management, and analysis of geo-referenced animal location data

66   (Cagnacci et al. 2010, Urbano et al. 2010).

67   Although Global Positioning System (GPS) and other relocation technologies

68   have enabled the collection of large amounts of animal location data from diverse

69   terrestrial and aquatic taxa (Tomkiewicz et al. 2010), model development for the

70   analysis of these data has lagged behind. This is beginning to change as new methods

71   continue to appear in the ecological literature (Holyoak et al. 2008, Schick et al. 2008),

72   but unlike many other areas of ecology, no general estimation framework has been

73   developed for the analysis of movement trajectories that is widely accepted by the

74   practitioners collecting the majority of these data sets. For example, there are well-

75   established inferential methods in population and community ecology for examining

76   patterns of abundance (e.g., Otis et al. 1978, Buckland et al. 2001, Borchers et al. 2002),

77   species occurrence (e.g., MacKenzie et al. 2006), and related vital rates that address

78   uncertainties (e.g., imperfect detection) associated with the process by which the data

79   were obtained (Williams et al. 2002, King et al. 2009). There also exists readily

80   accessible software for the analysis of these data by wildlife professionals (e.g., White

81   and Burnham 1999, Thomas et al. 2010). There remains a similar need (and desire) to

82   develop accessible, inferential data analysis methods in movement ecology (Schwarz

83   2009, Morales et al. 2010).

84   As animals respond to physiological and environmental stimuli, they often

85   exhibit different movement behavior states (or modes). Simple examples include

86   "exploratory" and "encamped" states in elk (Morales et al. 2004) or, equivalently,

87   "traveling" and "foraging" states in grey seals (Breed et al. 2009), where "exploratory"

88   or "traveling" describe movement states associated with greater directional persistence

89   and velocity relative to the "encamped" or "foraging" states. Inferring patterns and

90   dynamics of movement from time-series of animal location data often involves the

91   estimation of movement parameters associated with different types of movement

92   behavior states. However, because these states often cannot be observed directly, they

93   must be inferred based on trajectories alone in the absence of ancillary information (but

94   see *Discussion*). Estimation is complicated further by the fact that animal location data

95   often contain considerable observation error in both time and space, as well as missing

96   (or intermittent) observations. Sophisticated statistical models of the underlying

97   movement and observation process are therefore required to facilitate reliable inference

98   (Jonsen et al. 2005, Patterson et al. 2008, Schick et al. 2008).

99   A variety of approaches for analyzing animal location data have been proposed

100   in recent years, and these primarily differ in the spatio-temporal conceptualization of the

101   movement process. These include discrete-time and discrete-space (Schwarz et al.

102   1993, Brownie et al 1993, Dupuis 1995, King and Brooks 2002), discrete-time and

103   continuous-space (Morales et al. 2004, Jonsen et al. 2005), continuous-time and

104   discrete-space (Ovaskainen et al. 2008), or continuous-time and continuous-space

105   (Blackwell 2003, Johnson et al. 2008) movement process models. Similarly, latent

106   behaviors associated with different types of movement can be treated as continuous

107   (Forester et al. 2007) or discrete (Morales et al. 2004, Jonsen et al. 2005) states among

108   which animals transition in response to changes in their internal and external

109   environment. The representation of movement also differs among these approaches, by

110   specifying the movement process on the positions themselves (Blackwell 2003, Jonsen

111   et al. 2006) or derived quantities, such as the differences between consecutive

112   coordinates (Jonsen et al. 2005, Johnson et al. 2008), step lengths (Forester et al. 2007),

113   or both step lengths and turning angles (Morales et al. 2004). Although earlier methods

114   ignored error in the timing and location of observations (Blackwell 2003, Morales et al.

115   2004), most recent approaches simultaneously model both the movement process and

116   observation process using state-space methods (Anderson-Sprecher and Ledolter 1991,

117   Jonsen et al. 2005, Johnson et al. 2008, Patterson et al. 2008).

118   The myriad of proposed methodologies for analyzing movement data makes

119   selection of any particular method (or model) a difficult task. The most sophisticated

120   continuous-time approaches, although appealing from a theoretical perspective, are

121   prohibitively technical for many non-statisticians. Further, continuous-time and

122   continuous-behavior models are less appealing to practitioners because the parameters

123   (e.g., instantaneous diffusion process parameters) can be difficult to interpret

124 biologically. Discrete-space models often necessitate spatial resolutions requiring high-

125 dimensional matrices or integrals that can lead to computational difficulties. Perhaps

126 most inhibiting to general use by ecologists is the fact that the majority of movement

127 models developed to date have focused on species-specific applications and relatively

128 few behavioral states, with little scope for generalization. Given these challenges, it is

129 certainly not surprising that even less attention has been given to strategies for model

130 selection and multi-model inference (Hoeting et al. 1999, Burnham and Anderson 2002,

131 King et al. 2009) in the analysis of movement data (but see Morales et al. 2004, King

132 and Brooks 2002; 2004).

133   We synthesize many of the appealing elements of previous approaches (e.g.,

134 Dunn and Gipson 1977, Blackwell 1997, King and Brooks 2002, Blackwell et al. 2003,

135 Morales et al. 2004, Jonsen et al. 2005, Johnson et al. 2008) in combination with novel

136 methodologies to formulate a general modeling strategy for individual animal

137 movement in discrete-time and continuous-space that can be readily adapted to

138 accommodate many different types of movement and behavioral states. With an

139 increased emphasis on ecological inference from animal location data, these states can

140 be associated with directed (e.g., migratory or evasive), area-restricted (e.g., foraging or

141 nesting), exploratory (e.g., dispersal or searching), and correlated movements as

142 dictated by the species and application of interest. Using Bayesian analysis methods,

143 we also propose a model selection and multi-model inference procedure based on

144 weights of evidence for these different types of movement behaviors. We demonstrate

145 the use of this mechanistic, inferential modeling framework by adapting it to the natural

146 history of the grey seal (*Halichoerus grypus*) in the North Sea, an apex marine predator

147 often demonstrating characteristically complex movement patterns among haul-out

148 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 $z = 1, \ldots, Z$, where each state is characterized by distributions for the step length and direction (or bearing) of movement between consecutive positions $\left(X_{t-1}, Y_{t-1} \right)$ and $\left(X_t, Y_t \right)$ for each time step $t = 1, \ldots, T$. 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 towards 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 $\left(s_t \right)$ and a wrapped Cauchy distribution for the direction $\left(\phi_t \right)$ 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, multi-state random walk with step length $\left[s_t \mid z_t = i \right] \sim \mathrm{Weibull}(a_i, b_i)$ and direction $\left[\phi_t \mid z_t = i \right] \sim \mathrm{wCauchy}(\mu_i, \rho_i)$. Specifically, we have the probability density functions

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

and

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

171   for $a_z > 0$, $b_z > 0$, $0 \le \phi_t < 2\pi$, $0 \le \mu_z < 2\pi$, $-1 < \rho_z < 1$, and $z = 1,\ldots,Z$. Assuming

172   independence between step length and direction within each movement behavior state

173   (see *Discussion*), the joint likelihood for s_t and ϕ_t (conditional on the latent state

174   variable z_t) is:

175
$$f\left(s,\phi \mid z\right) = \prod_{t=1}^{T} f\left(s_t \mid z_t\right) f\left(\phi_t \mid z_t\right).$$

176   For switches between movement behavior states, we assign a categorical

177   distribution to the latent state variable z_t. The simplest approach assigns every time

178   step to a movement behavior state independent of previous states or ancillary

179   information:

180
$$z_t \sim \text{Categorical}(\psi_1,\ldots,\psi_Z),$$

181   such that

182
$$\psi_i = \Pr(z_t = i),$$

183   where ψ_i is the (fixed) probability of being in state i at time t, and $\sum_{i=1}^{Z} \psi_i = 1$. This

184   assumption is generally unrealistic for animal movements. Alternatively (and more

185   realistically), one could incorporate memory into the state transition probabilities using

186   a jth-order Markov process. Assuming movement behavior states were known,

187   Blackwell (1997; 2003) used a first-order Markov transition matrix to characterize

188   switches between states in continuous time. For a first-order Markov process in discrete

189   time,

190
$$\left[z_t \mid z_{t-1} = k\right] \sim \text{Categorical}(\psi_{k,1},\ldots,\psi_{k,Z})$$

191   and

192
$$\psi_{k,i} = \Pr(z_t = i \mid z_{t-1} = k),$$

193   for $k = 1, \ldots, Z$ where $\psi_{k,i}$ is the probability of switching from state k at time $t - 1$ to

194   state i at time t, and $\sum_{i=1}^{Z} \psi_{k,i} = 1$. We note that this Markovian structure is analogous

195   to the state transition probabilities for multi-state capture-recapture models (e.g.,

196   Brownie et al. 1993, Schwarz et al. 1993).

197   The multi-state movement model is specified according to the particular species

198   and ecological conditions of interest. The various movement behavior states may be

199   solely characterized by biased, correlated, or exploratory types of movement, but

200   environmental covariates and alternative parameterizations may also be utilized to

201   describe the movement process. Below we present a suite of models for different

202   movement characteristics that can be combined to form complex movement behavior

203   states. We emphasize that the proposed models fall under the same general modeling

204   framework, with the more basic models remaining nested within the more complex

205   models. These, and other extensions (see *Discussion*), may therefore be thought of as

206   contributions to a "tool-box", from which a wide range of bespoke multi-state

207   movement models in discrete time can be assembled. By adding or removing

208   components from the tool-box, one may compare the different models nested within the

209   most general model (see *Example: grey seal movement in the North Sea*). This allows

210   simultaneous investigation of numerous hypotheses about animal movement, including

211   those involving: 1) time allocations to different movement behavior states (i.e., "activity

212   budgets"); 2) the use of navigation for directed movement towards specific locations; 3)

213   the relative strength of bias towards (or away from) specific locations; 4) the existence

214   of spatially-unassociated (but potentially correlated) exploratory movement states; and

215   5) factors affecting transition probabilities between movement behavior states.

216   <u>Biased movements</u>

217   Biased movement behavior states exhibiting attraction (or aversion) to particular

218   locations can be incorporated within the proposed framework. Suppose the set of Z

219   movement behavior states is composed entirely of attractions to one of c different

220   "centers of attraction" (i.e., $Z = c$). Assuming movement at time t is biased towards

221   center of attraction i $\left(\text{i.e.,} \ z_t = i \right)$, we calculate the expected movement direction

222     $\left(\mu_{i,t} \right)$ as the direction between the individual's previous location $\left(X_{t-1}, Y_{t-1} \right)$ and the

223   location of the center of attraction $\left(X_i^*, Y_i^* \right)$ at time t. We note that the coordinates of

224   each center of attraction $\left(X_z^*, Y_z^* \right)$, $z = 1, \ldots, c$, are not necessarily assumed to be known

225   (see *Example: grey seal movement in the North Sea*).

226   The strength of bias to each center of attraction is determined by the mean vector

227   length of the wrapped Cauchy distribution $\left(0 \le \rho_z < 1 \right)$. This strength of bias need not

228   be constant. For example, in some instances one may expect less directed movement

229   once an individual has reached the vicinity of the current center of attraction, so that we

230   may specify:

231 $$\rho_{z,t} = \tanh \left(r_z \delta_t \right)$$

232   where δ_t is some metric of the distance (e.g., Euclidean) to the current center of

233   attraction, and $r_z \ge 0$ is a (state-dependent) scaling parameter (see *Appendix A*). As an

234   individual is located closer to the current center of attraction, $\rho_{z,t} \to 0,$ and the

235   movement direction is uniformly distributed on the unit circle. This allows for unbiased

236   area-restricted searches (e.g., "encamped" or "foraging" types of movement, *sensu*

237   Morales et al. 2004 and Breed et al. 2009) once in the vicinity of the current center of

238   attraction. As an individual is located further from the current center of attraction,

239    $\rho_{z,t} \rightarrow 1$, and ϕ_t is not allowed to deviate from $\mu_{z,t}$ (Figure 1a). We note that this

240   formulation also permits bias away from a "center of repulsion" when $-1 < \rho_z \leq 0$.

241   More complicated structural forms may be utilized for ρ_z. For example, when

242   far away, an animal may have only a general sense of the location of a center of

243   attraction, but the movement direction draws closer to $\mu_{z,t}$ as the distance to the center

244   of attraction decreases (i.e., the individual "hones in" on its target). An additional

245   quadratic term $\left(q_z \right)$ allows this type of behavior to be included in the model:

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

247   where r_z and q_z are constrained such that $\rho_{z,t} \geq 0$ for all reasonable δ_t within the study

248   area. We note that alternative link functions, such as the logit link, may be utilized

249   when specifying ρ_z as a function of covariates (see *Example: grey seal movement in the*

250   *North Sea*).

251   <u>Biased, correlated movements</u>

252   Additional structure can describe biased movement behavior states that exhibit

253   correlations between successive movement directions (Figure 1b):

254    $$\left[\phi_t \mid \phi_{t-1}, z_t = i \right] \sim \text{wCauchy}\left(\lambda_{i,t}, \rho_i \right)$$

255   with expected movement direction

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

257   where ϕ_0 is the (latent) movement direction prior to time step $t = 1$. Now the expected

258   movement direction $\left(\lambda_{z,t} \right)$ is a weighted average of the strength of bias in the direction

259   of the current center of attraction $\left(\mu_{z,t} \right)$ and the previous movement direction $\left(\phi_{t-1} \right)$ for

260    $0 \leq \eta_z \leq 1$. If $\eta_z = 0$, then movement reverts to a standard biased random walk. If

11

261     $\eta_z = 1$, then movement becomes an unbiased correlated random walk. If $\rho_z = 0$, then

262   movement is a simple (i.e., unbiased and uncorrelated) random walk. If $\rho_z = 1$, then

263   movement is biased and deterministic (Barton et al. 2009). Because $\lambda_{z,t}$ is wrapped on

264   the unit circle, we note that care must be taken in calculating $\lambda_{z,t}$ whenever

265     $\left| \phi_{t-1} - \mu_{z,t} \right| > \pi$.

266   <u>Exploratory movement states</u>

267   By specifying ρ_z as a function of distance, the model allows unbiased movements when

268   an individual is in close proximity to a center of attraction. However, "exploratory"

269   states may include unbiased movements that are not associated with any center of

270   attraction. The set of Z movement behavior states can therefore be extended to include

271   c center of attraction and h exploratory movement states, such that $Z = c + h$. Such

272   exploratory states can be easily added within the above framework:

273
$$\rho_{z,t} = \begin{cases} 0 & \text{if } z \text{ is an exploratory state} \\ \tanh\left(r_z \delta_t \right) & \text{otherwise} \end{cases}$$

274   Exploratory movements may be unbiased, but they can often exhibit directional

275   persistence (i.e., autocorrelation in movement direction). To include correlated

276   exploratory states within the biased random walk model,

277
$$\left[\phi_t \mid \phi_{t-1}, z_t = i \right] \sim \text{wCauchy}\left(\lambda_{i,t}, \rho_{i,t} \right)$$

278
$$\lambda_{z,t} = \begin{cases} \phi_{t-1} & \text{if } z \text{ is an exploratory state} \\ \mu_{z,t} & \text{otherwise} \end{cases}$$

279
$$\rho_{z,t} = \begin{cases} \upsilon_z & \text{if } z \text{ is an exploratory state} \\ \tanh\left(r_z \delta_t \right) & \text{otherwise} \end{cases}$$

280   where $0 \le \upsilon_z < 1$ is the strength of directional persistence. For a biased correlated

281   random walk with correlated exploratory states (Figure 1c):

282
$$[\phi_t \mid \phi_{t-1}, z_t = i] \sim \text{wCauchy}\left(\lambda_{i,t}, \rho_{i,t}\right)$$

283
$$\lambda_{z,t} = \begin{cases} \phi_{t-1} & \text{if } z \text{ is an exploratory state} \\ \eta_z \phi_{t-1} + (1 - \eta_z) \mu_{z,t} & \text{otherwise} \end{cases}$$

284   and

285
$$\rho_{z,t} = \begin{cases} \upsilon_z & \text{if } z \text{ is an exploratory state} \\ \tanh(r_z \delta_t) & \text{otherwise} \end{cases}$$

286   Environmental covariates and alternative parameterizations

287   Animal movement is often heavily influenced by environmental factors, such as

288   landscape (e.g., slope or vegetation cover) or seascape (e.g., currents or temperature)

289   conditions. These factors may be incorporated within the parameters above using

290   standard link functions. For example, if a set of k covariates was identified as potential

291   predictors for step length, then one could assume:

292
$$[s_t \mid z_t = i] \sim \text{Weibull}\left(a_{i,t}, b_{i,t}\right)$$

293
$$\log(a_{z,t}) = \alpha_{z,0} + \sum_{j=1}^{k} \alpha_{z,j} \omega_{t,j}$$

294
$$\log(b_{z,t}) = \beta_{z,0} + \sum_{j=1}^{k} \beta_{z,j} \omega_{t,j}$$

295   where $\omega_{t,j}$ is the value for linear predictor j at time step t. Similarly, covariates could

296   also be incorporated into strengths of attraction $(r \text{ and } q)$, state transition probabilities

297   (ψ), or any other parameters in the model. This includes the use of habitat-level

298   covariates on (X_t, Y_t) for predicting movements during missing or unobserved time

299   steps (see *Example: grey seal movement in the North Sea*). Such predicted coordinates

300   allow the overall movement path to reflect specific spatial features (e.g., lakes or

301   mountains) of relevance to the species of interest.

13

302   Step length may also be a function of distance to the current center of attraction.

303   One could envisage longer step lengths (e.g., due to increased velocity or strength of

304   bias) when far away from the current center of attraction. Such effects could be

305   incorporated by specifying

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

307   where the scale parameter of the Weibull distribution $\left(a_{z,t}\right)$ is now a function of δ_t and

308   a (state-dependent) scaling parameter $\left(\kappa_z\right)$. When the animal is near the center of

309   attraction, $a_{z,t}$ is closer to zero, and the step lengths are shorter. If the animal is far

310   from the current center of attraction, $a_{z,t}$ will approach the (state-dependent) scale

311   parameter asymptote γ_z. Alternative approaches could include change-points on the

312   step length parameters:

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

314   where $d_{z,l}$ is the threshold distance for change-point l of center of attraction state z (see

315   *Example: grey seal movement in the North Sea*) .

316   Much of the biological interest in multi-state movement models lies in the

317   specification of behavioral state transition probabilities. Depending on the biological

318   questions of interest, it may often be advantageous to reparameterize the state transition

319   probability matrix. For example, with a migratory species it may be desirable to restrict

320   state transitions until the individual is in the vicinity of the current center of attraction

321   (i.e., so that "en-route" switches are avoided). A simple reparameterization allows such

322   behaviors to be more easily investigated:

323
$$\psi = \begin{bmatrix} \alpha_1 & (1-\alpha_1)\beta_{1,2} & \cdots & (1-\alpha_1)\beta_{1,c} \\ (1-\alpha_2)\beta_{2,1} & \alpha_2 & & (1-\alpha_2)\beta_{2,c} \\ \vdots & \vdots & \ddots & \vdots \\ (1-\alpha_c)\beta_{c,1} & (1-\alpha_c)\beta_{c,2} & \cdots & \alpha_c \end{bmatrix}$$

324   where $\alpha_i = \Pr(z_t = i \mid z_{t-1} = i)$, $\beta_{k,i} = \Pr(z_t = i \mid z_{t-1} = k, k \neq i)$, and $\sum_{i \neq k}^{c} \beta_{k,i} = 1$ for $k =$

325   1,2,…,c. Using logit-linear intercept (ζ_z) and slope (ξ_z) parameters, state transitions

326   could incorporate the effects of distance:

327
$$\text{logit}(\alpha_{z,t}) = \zeta_z + \xi_z \delta_t$$

328   whereby individuals could be more likely to remain in the current movement state until

329   they are in close proximity to the associated center of attraction. More complicated

330   covariate structures (e.g., the amount of time in the current state) or other

331   reparameterizations could be incorporated in a similar fashion.

332   *State-space formulation*

333   Even in well-designed studies, there will typically be some degree of measurement error

334   in spatio-temporal animal location data. Environmental conditions may affect the

335   timing and location of fixes, as may animal behavior (e.g., diving or burrowing species).

336   For reliable inference, these irregularities must be accounted for when applying the

337   mechanistic movement models described above. To account for spatial error and

338   temporal irregularity, we propose a continuous-time observation model to accompany

339   our discrete-time movement process model in a state-space formulation.

340   In the movement process model, we assume switches between behavioral states

341   can occur at regular time intervals of equal length. The switching interval length must

342   therefore be chosen at a temporal resolution of relevance to the species and conditions

343   of interest. Similar to Jonsen et al. (2005), we assume that individuals travel in a

344   straight line between times $t-1$ and t. The observed locations are labeled according to

15

345   the regular time interval into which they fall: we write $\left(x_{t,i}, y_{t,i} \right)$ for the ith observation

346   between time $t-1$ and t, for $i = 1,\ldots,n_t$. These are related to the regular locations

347     $\left(X_t, Y_t \right)$ via:

348
$$x_{t,i} = \left(1 - j_{t,i} \right) X_{t-1} + j_{t,i} X_t + \varepsilon_{x_{t,i}}$$

349
$$y_{t,i} = \left(1 - j_{t,i} \right) Y_{t-1} + j_{t,i} Y_t + \varepsilon_{y_{t,i}}$$

350   with error terms

351
$$\varepsilon_{x,i} \sim N(0, \sigma_x^2)$$

352
$$\varepsilon_{y,i} \sim N(0, \sigma_y^2)$$

353   where $j_{t,i} \in [0,1)$ is the proportion of the time interval between locations $\left(X_{t-1}, Y_{t-1} \right)$ and

354     $\left(X_t, Y_t \right)$ at which the ith observation between times $t-1$ and t was obtained. Time

355   intervals with no observations (i.e., $n_t = 0$) do not contribute to the observation model

356   likelihood. In some applications (e.g., radio-telemetry triangulation or Argos satellite

357   locations), the measurement errors are known to have more frequent large outliers than

358   would occur under a normal distribution; in this case, a heavier-tailed error distribution

359   could be employed (e.g., t-distribution) that allows additional non-central or scale

360   parameters (e.g., Jonsen et al. 2005).

361   EXAMPLE: GREY SEAL MOVEMENT IN THE NORTH SEA

362   *Background*

363   We demonstrate the application of our model using hybrid-GPS transmitter data

364   collected from grey seals (*Halichoerus grypus*) in the North Sea. Fastloc[TM] GPS

365   transmitter (Wildtrack Telemetry Systems, Leeds, UK) tags were deployed in April

366   2008 and attempted to obtain a location every 30 minutes until battery failure in August

367   or September 2008.   Our multi-state random walk model was initially deemed

368   appropriate for grey seals because we suspected they could display oriented movements

369   among haul-out colonies and foraging patches. However, a combination of biological

370   and technological issues necessitated use of the state-space model described above: 1)

371   positions are only attainable when an individual surfaces, hence observations were

372   obtained at irregular time intervals; and 2) following any "dry" period where a

373   transmitter remained out of water for more than 10 minutes, no new fixes could be

374   obtained until the transmitter returned to water continuously for 40 seconds. In other

375   words, there were frequent missing data due to an inability to obtain locations while an

376   individual was either hauled out or underwater.

377   We fitted a multi-state random walk movement model to locations from a single

378   grey seal (Figure 2). The observed data consisted of 1045 locations irregularly spaced

379   in time between 9 April and 13 August 2008. Based on the scale of movements of grey

380   seals (McConnell et al. 1999) and the frequency of observations, we specified

381     $T = 1515$ regular switching intervals of 120min between times $t-1$ and time t for

382     $t = 1,\ldots,T$. Our selection of 120min intervals reflects a trade-off between

383   computational efficiency, the temporal resolution of the data, and an acceptable

384   temporal resolution for inference about grey seal movement behavior. The first of these

385   120min intervals began at deployment on 9 April, and the last interval ended

386   immediately after the final observed location on 13 August.

387   *Movement model specification*

388   For demonstrative purposes, we specify a simplified model of grey seal movement by

389   limiting the number of center of attraction ($c = 3$) and exploratory ($h = 2$) states . Our

390   most general first-order Markov movement process model therefore consisted of $Z = 5$

391   potential states, including state-dependence on both movement direction and step length

392   parameters:

393
$$[\phi_t \mid \phi_{t-1}, z_t = i] \sim \text{wCauchy}(\lambda_{i,t}, \rho_{i,t})$$

394
$$\lambda_{z,t} = \begin{cases} \eta_z \phi_{t-1} + (1 - \eta_z)\mu_{z,t} & \text{if } z \leq c \\ \phi_{t-1} & \text{if } z > c \end{cases}$$

395
$$\rho_{z,t} = \begin{cases} \text{logit}^{-1}\left(m_z + r_z\delta_t + q_z\delta_t^2\right) & \text{if } z \leq c \\ \upsilon_z & \text{if } z > c \end{cases}$$

396
$$[s_t \mid z_t = i] \sim \text{Weibull}(a_{i,t}, b_{i,t})$$

397
$$a_{z,t} = \begin{cases} a_{z,1}\left[1 - \mathbf{I}_{[0,d_z)}(\delta_t)\right] + a_{z,2}\mathbf{I}_{[0,d_z)}(\delta_t) & \text{if } z \leq c \\ a_z & \text{if } z > c \end{cases}$$

398
$$b_{z,t} = \begin{cases} b_{z,1}\left[1 - \mathbf{I}_{[0,d_z)}(\delta_t)\right] + b_{z,2}\mathbf{I}_{[0,d_z)}(\delta_t) & \text{if } z \leq c \\ b_z & \text{if } z > c \end{cases}$$

399
$$[z_t \mid z_{t-1} = k] \sim \text{Categorical}(\psi_{k,1}, \ldots, \psi_{k,5})$$

400   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

401   (scaled) Euclidean distance between the predicted location (X_{t-1}, Y_{t-1}) and center of

402   attraction (X_z^*, X_z^*) at time t, and $\mathbf{I}_{[0,d_z)}(\delta_t)$ is an indicator function for $\delta_t \in [0, d_z)$. We

403   chose to fit our state-space model using Bayesian analysis methods because of the

404   general complexity of the model and the ease by which these methods can

405   accommodate prior information, latent state variables, and missing data (Ellison 2004,

406   King et al. 2009). Posterior model probabilities also provide a straightforward means

407   for addressing model selection uncertainty (see *Model selection and multi-model*

408   *inference*).

409   For our Bayesian analysis, we specified uninformative prior distributions for

410   most of the parameters (Table 1). Based on previous studies of grey seal movements

411   (McConnell et al.1999), we specified a (conservative) maximum sustainable speed of 2

412   meters per second (such that $s_t \leq 14.4\,\mathrm{km}$). For the UTM coordinates of the centers of

413   attraction $\left(X_z^*, Y_z^*\right)$, we specified joint discrete uniform priors over the coordinates of

414   the predicted locations $\left(X_t, Y_t\right)$. This prior specification therefore assumes the centers

415   of attraction are located on the predicted movement path. We constrained state

416   assignments for time steps corresponding to $\left(X_z^*, Y_z^*\right)$ for each center of attraction, such

417   that $z_t = k$ if $\left(X_k^*, Y_k^*\right) = \left(X_t, Y_t\right)$ for $k = 1, \ldots, c$. For the coordinates of the initial

418   location $\left(X_0, Y_0\right)$, we specified a joint uniform prior over the region (A) defined by the

419   North Sea and coastline of Great Britain. We also constrained predicted locations

420    $\left(X_t, Y_t\right)$ to be within A for $t = 1, \ldots, T$ (i.e., inland grey seal locations were prohibited *a*

421   *priori*).

422   *Model selection and multi-model inference*

423   We used a reversible jump Markov chain Monte Carlo (RJMCMC) algorithm (Green

424   1995) to fit the model and simultaneously investigate various (state-specific)

425   parameterizations for the strength of bias towards any centers of attraction and the

426   correlations between successive movements (see *Appendix B*). These parameterizations

427   included models with linear bias $\left[\rho_{z,t} = \mathrm{logit}^{-1}\left(m_z + r_z\delta_t\right)\right]$ and quadratic bias

428    $\left[\rho_{z,t} = \mathrm{logit}^{-1}\left(m_z + r_z\delta_t + q_z\delta_t^2\right)\right]$ towards centers of attraction for $z = 1,2,3$. We also

429   investigated models with no correlation in movement direction between successive time

430   steps when in a center of attraction state ($\eta_z = 0$ for $z = 1, 2, 3$) or an exploratory state

431   ($\upsilon_z = 0$ for $z = 4,5$).

432   These different parameterizations yielded 256 potential models for evaluation

433   via posterior model probabilities. For all models, we assumed equal prior model

434   probabilities. For all parameters without standard full conditional posterior

19

435   distributions, random walk Metropolis-Hastings updates were used (e.g., Brooks 1998,

436   Givens and Hoeting 2005). After initial pilot tuning and burn-in, we produced a single

437   MCMC chain of five million iterations for calculating posterior summaries and model

438   probabilities. After thinning by 100 iterations to reduce memory requirements, Monte

439   Carlo estimates (including model-averaged estimates) were obtained for each of the

440   parameters from this single Markov chain. The RJMCMC algorithm was written in the

441   C programming language (Kernighan and Ritchie 1988), with pre- and post-processing

442   performed in R via the .C Interface (R Development Core Team 2009).

443   *Example results and discussion*

444   Posterior model probabilities (Table 2) and model-averaged parameter summaries

445   (Table 3) indicate biased movements towards all three centers of attraction. The

446   estimated coordinates of the centers of attraction correspond to the Farne Islands haul-

447   out site, the Abertay haul-out site, and the Dogger Bank foraging site (Figure 3,

448   *Appendix C*), and the strengths of bias to these three sites differed as a function of

449   distance (Figure 4). The Abertay haul-out site maintained a strong and consistent bias

450   up to 350km. Both the Farne Islands haul-out and Dogger Bank foraging sites exhibited

451   a decreasing strength of bias curve, but we found little evidence of a quadratic effect of

452   distance (Tables 2, 3). Biased movements continued at greater distances (> 350km) and

453   declined less rapidly from the Dogger Bank foraging site than from the Farne Islands

454   haul-out site. These patterns of directed movement as a function of distance could be

455   indicative of the seal "honing in" on these targets, but ocean currents are also likely to

456   be influencing the timing and direction of these movements (see Gaspar et al. 2006).

457   Model-averaged posterior summaries indicated a strong tendency for the seal to

458   remain in its current movement state (Table 3), with switches between center of

459   attraction states rarely occurring until the seal had reached the vicinity of the current

460   center of attraction (Figure 3). We found very little evidence of correlated movements

461   when in a center of attraction state, with marginal posterior parameter probabilities of

462   0.01, 0.00, and 0.00 for η_1, η_2, and η_3, respectively. We found little evidence for

463   directional persistence during the exploratory states not associated with any center of

464   attraction (Table 3), with marginal posterior parameter probabilities of 0.16 for υ_4 and

465   0.01 for υ_5. As expected, uncertainty in the coordinates of predicted locations

466   (X_t, Y_t) was greatest during time steps with missing data, most notably during extended

467   "dry" haul-out periods and foraging at Dogger Bank (Figure 3b).

468   Based on posterior summaries for the step length and change-point parameters,

469   we found strong evidence of shorter step lengths within 5km of the three centers of

470   attraction (Table 3). For the Farne Islands and Abertay sites, the predicted locations in

471   close proximity to these centers of attraction suggest restricted movement in the vicinity

472   of the haul-out colonies. For the Dogger Bank site, the predicted locations in the

473   vicinity suggest area-restricted searches during foraging (Figure 3). These findings are

474   consistent with expected haul-out and foraging movement behaviors of grey seals

475   (McConnell et al. 1999). Although neither of the exploratory states exhibited strong

476   directional persistence, parameter estimates indicated relatively longer step lengths (i.e.,

477   higher speed) for one of these exploratory states (Table 3). This suggests transitory or

478   searching movements during the "high-speed" exploratory state ($z = 4$), but the "low-

479   speed" exploratory state ($z = 5$) could be indicative of foraging or resting at sea.

480   Based on posterior state assignments, the mean proportion of time (95% highest

481   posterior density interval) between 9 April and 13 August 2008 that the seal spent in

482   each state was 0.39 (0.37, 0.41) for the Dogger Bank foraging state, 0.27 (0.26, 0.29)

483   for the Abertay haul-out state, 0.17 (0.16, 0.19) for the Farne Islands haul-out state, 0.12

484   (0.10, 0.13) for the low-speed exploratory state, and 0.05 (0.03, 0.06) for the high-speed

485   exploratory state. Due to tortuosity in the movement path, there was some uncertainty

486   in state assignments for transitory movements among centers of attraction. We suspect

487   these indirect paths are related to environmental cues or ocean currents. There was also

488   some state assignment uncertainty for movements in the vicinity of the Abertay and

489   Dogger Bank centers of attraction. This could be attributable to a potential foraging

490   area in the offshore sandbanks near the Abertay haul-out site, responses to prey

491   movement in the Dogger Bank foraging area, and missing location data during "dry" or

492   prolonged diving periods. Further model structure, including additional movement

493   behavior states or environmental covariates, may be required to better explain these

494   movements.

495   Given the reliability of locations using hybrid-GPS transmitters, we were not

496   particularly concerned about spatio-temporal measurement error for these data. We

497   were far more concerned about irregularly-observed and missing data because we were

498   unable to obtain locations while the seal was hauled out or underwater. Error terms (in

499   meters) were relatively small, with posterior medians for $\hat{\sigma}_x = 562$ (95% HPDI: 511 -

500   620) and for $\hat{\sigma}_y = 255$ (95% HPDI: 233 - 276). Similar to Patterson et al. (2010), the

501   larger value for σ_x reflects the prevalence of east-west movements between haul-out

502   and foraging sites. There were several instances where small, but non-negligible,

503   differences were found between observed and predicted locations (Figure 3a), but we

504   believe these instances are more likely attributable to some deficiencies in the model

505   than to location measurement error.

506   Previous studies on individual seal movement (Jonsen et al. 2005, Johnson et al.

507   2008, Breed et al. 2009, Patterson et al. 2010) limited models to simple and correlated

508   random walks among haul-out and foraging areas. Based on posterior estimates and

509   probabilities for simple (0% of posterior model probabilities), correlated (0%), biased

510   (82%), and both biased and correlated (18%) random walk mixture models, we found

511   overwhelming evidence that including bias (or drift) towards centers of attraction better

512   explained seal movement than simple or correlated random walks. This result strongly

513   supports the recognized ability of grey seals to rely on navigational capabilities for

514   directed (and not simply correlated) movement among haul-out colonies and foraging

515   patches.

516   Correlations among parameters and the large number of latent variables made

517   the development of a model fitting algorithm a computational challenge. To help

518   diagnose convergence, we examined a series of additional chains with overdispersed

519   initial values. With poor starting values for $\left(X_z^*, Y_z^* \right)$ and $\left(X_t, Y_t \right)$, we found the

520   algorithm could diverge or get caught in local maxima. However, we achieved similar

521   results for chains covering a range of reasonable starting values. Even with reasonable

522   starting values, it required about five million iterations before chains appeared to

523   converge. The centers of attraction do not necessarily need to be located on the

524   predicted movement path, but we found mixing and performance were greatly improved

525   by this prior specification for the coordinates of the centers of attraction $\left(X_z^*, Y_z^* \right)$. We

526   also believe it is reasonable to assume that centers of attraction are visited (and hence

527   located along the predicted path).

528   At the expense of some biological realism, we chose to keep this example

529   relatively simple to demonstrate the application of this methodology to a general

530   audience. If our intended audience were limited to marine mammalogists, we would

531   have incorporated additional model complexity and prior information to better reflect

532   the biology of grey seals. Similar to Johnson et al. (2008), we could have included an

533   additional "dry" state for movement during periods when the seal was (presumably) out

534   of water (e.g., smaller step lengths). Alternatively, landscape covariates could have

535 been used for specifying "haul-out" movement states when the seal was located on land.

536 We also could have constrained transition probabilities to make switches between states

537 less likely until the seal reached the vicinity of the current center of attraction. Not only

538 would refinements such as these add biological realism, but they would likely improve

539 mixing and convergence of the RJMCMC algorithm.

540 DISCUSSION

541 With the development of an intuitive framework for modeling animal movement,

542 ecologists may better appreciate the applicability of mechanistic, inferential movement

543 models to a wide variety of species and conditions. We have proposed a discrete-time,

544 continuous-space, and discrete-state conceptualization of the individual animal

545 movement process to facilitate the biological interpretation of distinct movement

546 behaviors and associated parameters. We believe its mathematical simplicity and focus

547 on ecology can make the application of bespoke movement models more

548 straightforward for non-statisticians. This "tool-box" of model components allows

549 researchers to construct custom-built mechanistic movement models for the species of

550 interest, while providing a means to compare weights of evidence in support of specific

551 hypotheses about different movement behaviors.

552   Perhaps most appealing is the ease with which new components can be added

553 to the nested model-building tool-box. While more components can lead to a large

554 number of potential models to choose from, the framework can accommodate the

555 additional model selection uncertainty in a straightforward quantitative manner. As

556 demonstrated in our grey seal example, this approach enabled the simultaneous

557 investigation of numerous hypotheses about seal movement, including the use of

558 navigation and time allocations to different movement behavior states. To our

559 knowledge, this is the first methodology utilizing model weights for selection and multi-

560 model inference in the mechanistic movement model literature.

561   Although our main goal has been to present this suite of model-building tools,

562 a serious study of animal movement should include some additional assessments of

563 goodness of fit. Morales et al. (2004) and Dalziel et al. (2010) briefly explore this topic,

564 including the use of posterior predictive checks and probes to test whether the fitted

565 models are consistent with emergent properties of the movement process (e.g.,

566 autocorrelation patterns in displacements and habitat use). However, an assessment of

567 absolute goodness of fit remains a daunting task for mechanistic movement models. In

568 the absence of classical tests of goodness of fit, it is particularly important that the

569 model set be selected with care utilizing the best biological information available for

570 reliable inference. Conditional on this candidate model set, model comparisons (e.g.,

571 based on posterior model probabilities or other model selection criteria) can provide

572 some assessment of the relative goodness of fit.

573   There remain many potential extensions to the modeling framework beyond

574 those already identified. In the grey seal example, we included two exploratory

575 movement states not associated with any center of attraction, but additional spatially-

576 unassociated states that differ in their movement properties (and associated state

577 parameters) may be incorporated (*sensu* Morales et al. 2004, Jonsen et al. 2005, Breed

578 et al. 2009). These additional states could be used to further differentiate among

579 exploratory movements (e.g., dispersal or search strategies) that have unique

580 distributions for step length and the degree of correlation between successive

581 movements.

582   We reiterate that centers of attraction do not necessarily refer to a single location

583 in space. Rather, they can refer to any entity to which animals move in response to.

584   This includes immobile entities such as habitat patches, but also mobile entities such as

585   conspecifics or prey. Any given entity (or group of entities) could therefore be used to

586   define a different behavior state for movement towards, away from, or within each

587   entity. Potential centers of attraction can also be dynamically incorporated within an

588   individual's portfolio as its habitat is explored, thus allowing for explicit modeling of

589   the effects of past experience on movement. Instead of centers of attraction, centers of

590   repulsion (where $-1 < \rho_z \leq 0$) may be particularly useful for demonstrating avoidance

591   behaviors related to encounters with conspecifics, predators, or undesirable habitats.

592   From a behavioral ecology perspective, perhaps most promising is the potential

593   for modeling movement state transition probabilities. By incorporating physiological or

594   environmental covariate information into the framework, one can investigate hypotheses

595   about the timing and motivations behind various movement behaviors as individuals

596   respond to changes in the internal and external environment (Morales et al. 2010).

597   Biotelemetry data (e.g., metabolic rate) or time of year (e.g., breeding season) are

598   among many factors that may help explain changes in movement behavior. Instead of

599   relying solely on trajectories, ancillary data may also be helpful in the assignment of

600   movement states. For example, additional landscape or seascape information may have

601   better explained the indirect movements between the two haul-out colonies in our grey

602   seal analysis. Recent advances, such as animal-borne accelerometers (Wilson et al.

603   2008, Holland et al. 2009, Payne et al. 2010), will likely provide additional ways to

604   distinguish among different types of movement (e.g., predator hunting and feeding).

605   There are also many ways by which memory can be incorporated into movements and

606   state transitions. Here we only explored two such mechanisms for memory, including

607   Markov processes for state transitions and the existence of spatial locations that are

608   committed to memory because they are (presumably) associated with specific goals.

609   The locations of centers of attraction are typically assumed to be known based

610   on prior knowledge or qualitative assessments of the data. Indeed, one could relatively

611   easily predict the coordinates of the three centers of attraction in our grey seal example

612   using only the naked eye or previous studies. However, we envision more complicated

613   movement paths where it is very difficult to identify or differentiate between potential

614   centers. We believe a quantitative means for estimating the location of centers and their

615   associated strengths of attraction (or repulsion), such as that proposed here, improves

616   our ability to extract reliable information from novel or more complex movement paths.

617   For simplicity, we chose to specify three centers of attraction in our grey seal

618   example. Although we found strong evidence of bias towards all three of these centers,

619   if any center z receives little support for bias (e.g., $\rho_{z,t} \approx 0$ for all δ_t), alternative models

620   removing such centers should be explored because state z essentially becomes an

621   uncorrelated exploratory state. This may have undesirable consequences, including

622   confounded exploratory states and poor MCMC mixing. Ideally, the model could be

623   extended to accommodate an unknown number of centers and reduce any need for ad-

624   hoc assessments of the appropriate number of centers. This would require an additional

625   parameter for the number of centers and (state-specific) movement parameters for each

626   potential center. Similar to the multi-model inference procedure used here, a reversible

627   jump MCMC algorithm could be utilized to estimate the number of centers of attraction.

628   This potential extension constitutes the focus of current research.

629   Additional information or structural complexity could also be specified in the

630   observation process of the state-space model. For example, Jonsen et al. (2005)

631   specified informative priors for measurement error parameters based on previously

632   published records of location estimation error for Argos-tagged grey seals. State-

633   dependent error or correlation terms (e.g., utilizing a multivariate normal error

27

634 distribution) could also be incorporated. Although a great deal of previous effort in the

635 analysis of animal location data has focused on the observation process, we expect

636 greater emphasis on the movement process as the quality of location data continue to

637 improve (e.g., with advances in GPS technology).

638   Although other approaches (e.g., Blackwell 2003, Jonsen et al. 2005, Johnson et

639 al. 2008) could potentially be extended to include the various types of movement

640 accommodated by our multi-state model, we chose to extend the basic methodology of

641 Morales et al. (2004) because of its intuitive appeal to ecologists and wildlife

642 professionals. The discrete-time, continuous-space approach of Jonsen et al. (2005) can

643 accommodate correlated and uncorrelated exploratory movements, but it does not

644 include biased or area-restricted movements related to specific locations or habitats. An

645 additional limitation of the correlated random walk approach of Jonsen et al. (2005) is a

646 lack of independence between direction and step length, resulting in higher-order auto-

647 correlations than found in standard correlated random walks. Our approach assumes

648 independence between direction and step length for each movement behavior state, but

649 a joint distribution including correlations could potentially be incorporated if deemed

650 appropriate (e.g., specifying shorter step lengths when movement is away from the

651 current center of attraction).

652   The continuous-time, continuous-space approaches of Blackwell (2003) and

653 Johnson et al. (2008) do allow correlated movements and "drift" that can (potentially)

654 be related to specific locations (*sensu* Kendall 1974, Dunn and Gipson 1977).

655 However, Blackwell (2003) assumes movement behavior states are known and Johnson

656 et al. (2008) only include a single state with known covariates, hence neither approach

657 includes an estimation framework for both movement state and switching behavior.

658 Although satisfying from a mathematical and theoretical perspective, we believe the

659 often difficult interpretation of continuous-time movement parameters (e.g., those

660 related to Ornstein-Uhlenbeck and other diffusion processes) can in practice be

661 discouraging to applied ecologists wishing to use or extend these methods. This may

662 change as ecologists become more familiar with the principles of mechanistic

663 movement models and computer software makes these approaches more accessible.

664   Unlike continuous-time movement process models, the primary disadvantage of

665 a discrete-time approach is that the time scale between state transitions must be chosen

666 based on the biology of the species and the frequency of observations. For any

667 continuous- or discrete-time approach to be useful, the temporal resolution of the

668 observed data must be relevant to the specific movement behaviors of interest. The

669 timing and frequency of observations must therefore be carefully considered when

670 designing telemetry devices and data collection schemes.

671   To encourage the broader application of movement models in ecology, user-

672 friendly software for the analysis of animal location data is needed. Ovaskainen et al

673 (2008) and Johnson et al. (2008) provided important first steps in accessible software by

674 creating DISPERSE and the R package CRAWL to perform the complicated

675 computations the models respectively require. Despite its relative mathematical

676 simplicity, the large number of parameters and latent variables inherent to our modeling

677 framework also makes implementation a computational challenge. We therefore

678 provide code for the full state-space formulation of our model (see *Supplement*) and are

679 currently developing a software package for general use by practitioners (Milazzo et al.

680 in prep.).

681   By making individual movement models more accessible and readily

682 interpretable to ecologists, we ultimately hope progress can be made towards linking

683 animal movement and population dynamics at the interface of behavioral, population,

684   and landscape ecology (Morales et al. 2010). Although the mechanistic links between

685   animal movement and population dynamics are theoretically understood, fitting

686   population-level models to data from many individuals will pose considerable

687   mathematical and computational challenges. Scaling individual movement models up

688   to population-level processes therefore remains a very promising avenue for future

689   research.

690   ACKNOWLEDGMENTS

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854 APPENDIX A

855 Strength of bias for the wrapped Cauchy distribution as a function of distance to a

856 center of attraction (Ecological Archives XXXX-XXX-A1).

857 APPENDIX B

858 Reversible jump Markov chain Monte Carlo algorithm for the multi-state random walk

859 model (Ecological Archives XXXX-XXX-A2).

860 APPENDIX C

861 HTML animation of Figure 3 (Ecological Archives XXXX-XXX-A3).

862 SUPPLEMENT

863 Computer code and data for implementing the reversible jump Markov chain Monte

864 Carlo algorithm for the multi-state random walk model (Ecological Archives XXXX-

865 XXX-A4).

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878 Table 1. Parameter definitions and (uninformative) prior specifications for a Bayesian

879 analysis of grey seal location data using the multi-state 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 $z = 1,2,3$.	$\text{Unif}(0,1)$
υ_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 (m) of the Weibull distribution for step length of states $z = 1,2,3,4,5$.	$\text{Unif}(0,14400)$
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 (m) for scale and shape parameters of the Weibull distribution for step length of center of attraction states $z = 1,2,3$.	$\text{Unif}(0,400000)$
σ_x^2	Measurement error variance for easting coordinates of	$\Gamma^{-1}(10^{-3}, 10^{-3})$

	observed locations $\left(x_{t,i}, y_{t,i} \right)$.	
σ_y^2	Measurement error variance for northing coordinates of observed locations $\left(x_{t,i}, y_{t,i} \right)$.	$\Gamma^{-1}\left(10^{-3}, 10^{-3} \right)$
$\psi_{[k,\cdot]}$	The kth row vector of the state transition probability matrix, with each element $\left(\psi_{k,i} \right)$ corresponding to the switching probability from state k at time t - 1 to state i = 1,2,3,4,5 at time t.	Dirichlet(1,1,1,1,1)

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882 Table 2. Posterior model probabilities (PMP) for strength of attraction (q_z) and

883 correlation $(\eta_z$ and $\upsilon_z)$ parameters for a grey seal in the North Sea. For each parameter,

884 a '1' indicates presence in the model. The bottom row indicates the marginal posterior

885 probabilities (MPP) for each parameter. Centers of attraction correspond to the Farne

886 Islands haul-out site $(z=1)$, Abertay haul-out site $(z=2)$, and Dogger Bank foraging

887 site $(z=3)$. Other states correspond to high-speed $(z=4)$ and low-speed $(z=5)$

888 exploratory states. Results are for models with a PMP of at least 0.02.

PMP	Model							
	q_1	q_2	q_3	η_1	η_2	η_3	υ_4	υ_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

889   Table 3. Model-averaged posterior summaries for strength of attraction

890     $\left(r_z,\ q_z,\ m_z,\ \text{and}\ \tau \right)$, correlation $\left(\eta_z, \upsilon_z,\ \text{and}\ \phi_0 \right)$, step length $\left(a_z, b_z,\ \text{and}\ d_z \right)$,

891   observation error $\left(\sigma_x\ \text{and}\ \sigma_y \right)$, and state transition probability $\left(\psi_{k,i} \right)$ parameters.

892   Summaries include posterior medians and 95% highest posterior density intervals

893   (HPDI), conditional on the parameter being present in the model. Posterior means are

894   reported for state transition probabilities. Center of attraction states correspond to the

895   Farne Islands haul-out site $\left(z = 1 \right)$, Abertay haul-out site $\left(z = 2 \right)$, and Dogger Bank

896   foraging site $\left(z = 3 \right)$. The high-speed $\left(z = 4 \right)$ and low-speed $\left(z = 5 \right)$ exploratory states

897   are not associated with a center of attraction.

		95% HPDI	
Parameter	Estimate	Lower	Upper
Strength of attraction parameters			
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

Correlation parameters			
η_1	0.00	0.00	0.01
η_2	0.00	0.00	0.00
η_3	0.00	0.00	0.01
υ_4	0.16	0.00	0.63
υ_5	0.01	0.00	0.04
ϕ_0	0.06	3.47	3.13
Step length parameters			
$a_{1,1}$	10497.04	10026.35	10990.62
$a_{2,1}$	11052.65	10631.82	11524.23
$a_{3,1}$	10859.38	10503.77	11194.52
a_4	5188.94	4755.68	5644.98
a_5	1902.68	1601.28	2230.24
$b_{1,1}$	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	1576.19	1152.39	2077.87
d_2	5583.09	3694.29	6552.00
d_3	1425.98	1016.81	2722.62
$a_{1,2}$	1908.44	1369.26	2529.56

$a_{2,2}$	2061.91	1760.39	2333.18
$a_{3,2}$	2480.05	1572.07	5811.18
$b_{1,2}$	4.93	1.26	18.97
$b_{2,2}$	24.70	16.45	30.00
$b_{3,2}$	2.77	1.04	5.83
Observation error parameters			
σ_x	562.32	510.92	619.68
σ_y	254.62	233.42	276.44
State transition probability parameters			
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
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

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910   Figure 1. Simulated time-series of animal location data using three centers of attraction

911   from multi-state (a) biased random walk; (b) biased correlated random walk; and (c)

912   biased correlated random walk with an exploratory state. The strength of bias towards

913   the corresponding center of attraction at each time step t, $z_t = 1,2,3$, is a function of the

914   Euclidean distance between the current location and the center of attraction.

915

916   Figure 2. Observed locations for a grey seal as it traveled clockwise among a foraging

917   area in the North Sea and haul-out sites on the eastern coast of Great Britain.

918

919   Figure 3. Predicted locations, movement behavior states, and coordinates of three

920   centers of attraction for a grey seal in the North Sea and eastern coast of Great Britain.

921   Estimated movement states for the predicted locations (solid colored circles) correspond

922   to the Farne Islands haul-out site (red), Abertay haul-out site (green), Dogger Bank

923   foraging site (blue), or spatially-unassociated high-speed (light blue) and low-speed

924   (magenta) exploratory states. Solid yellow circles indicate the estimated coordinates of

925   the three centers of attraction, and solid black circles indicate observed locations in (a).

926   Uncertainty in the estimated state ($< 95\%$ posterior probability) is indicated by smaller

927   hollow circles within predicted locations in (a). Uncertainty in estimated coordinates

928   are indicated by symmetric 95% credible intervals for predicted locations in (b). An

929   animated version of this figure is available online (see *Appendix C*).

930

931   Figure 4. Model-averaged strength of bias $\left(\rho_z \right)$ to three centers of attraction as a

932   function of distance from a grey seal in the North Sea. Center of attraction states

933   correspond to the Farne Islands haul-out site (red), Abertay haul-out site (green), and

934   Dogger Bank foraging site (blue). Dashed lines indicate symmetric 95% credible

935   intervals. Lines terminate at the maximum distance at which the seal was assigned to

936   each respective center of attraction state.

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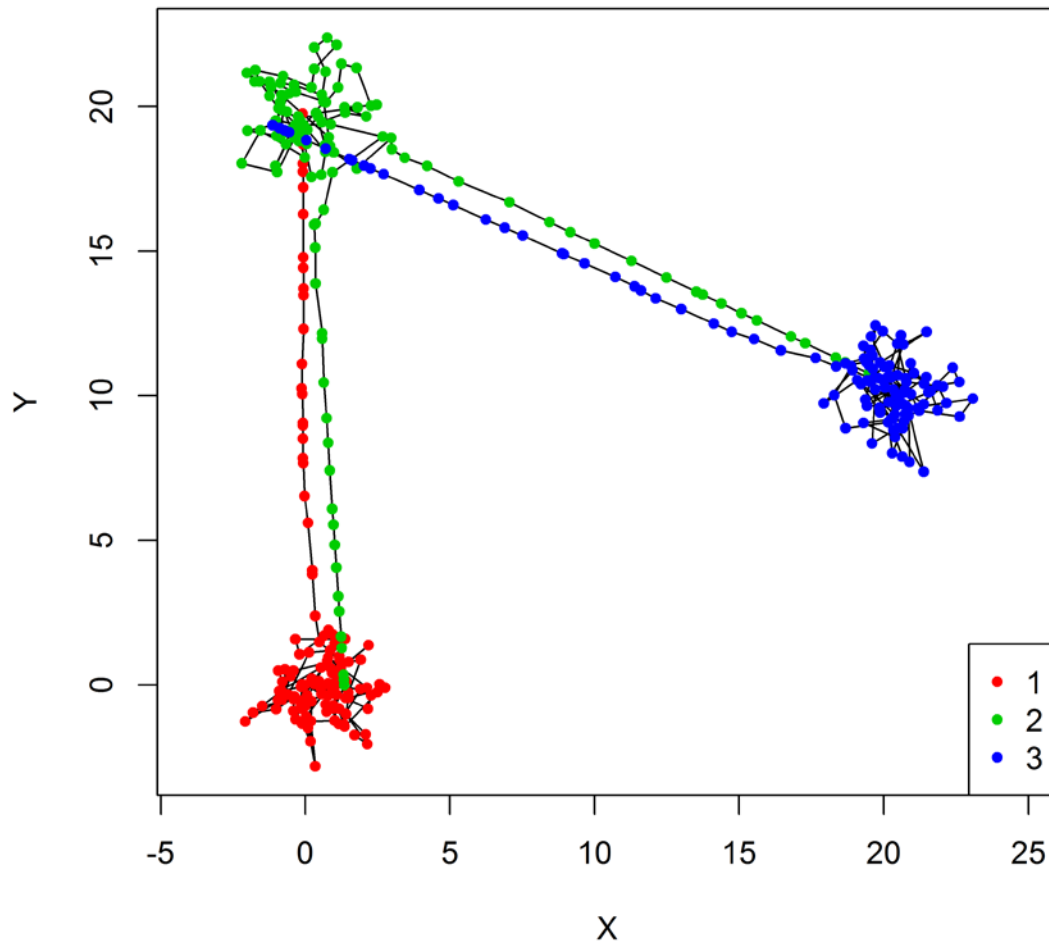948

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960   Figure 1.

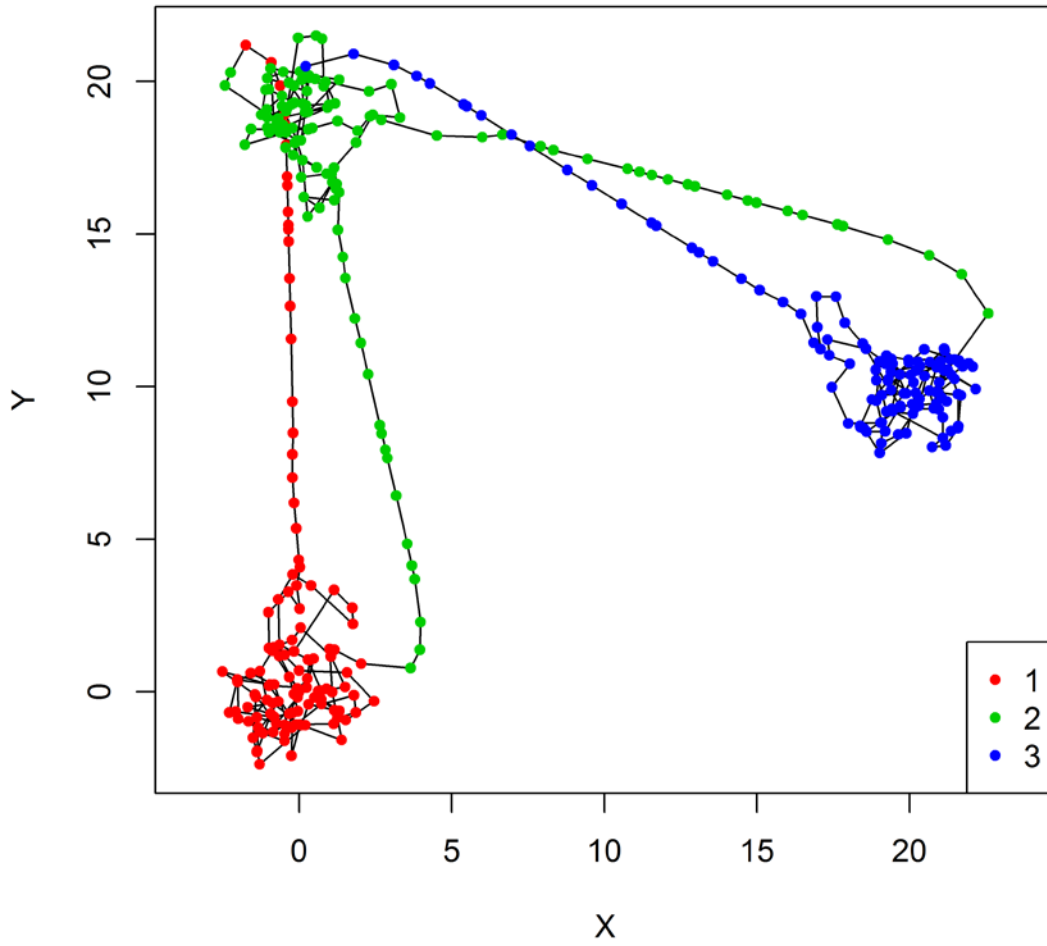961   (a)
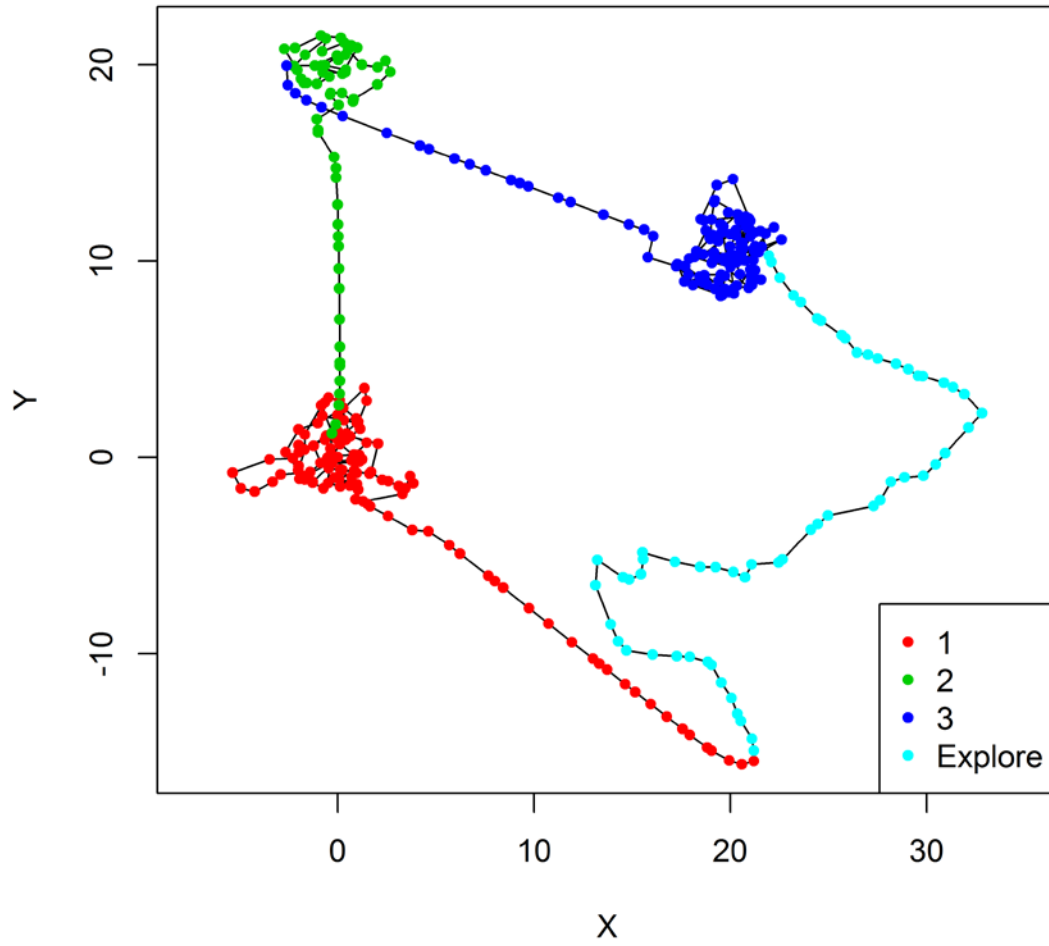

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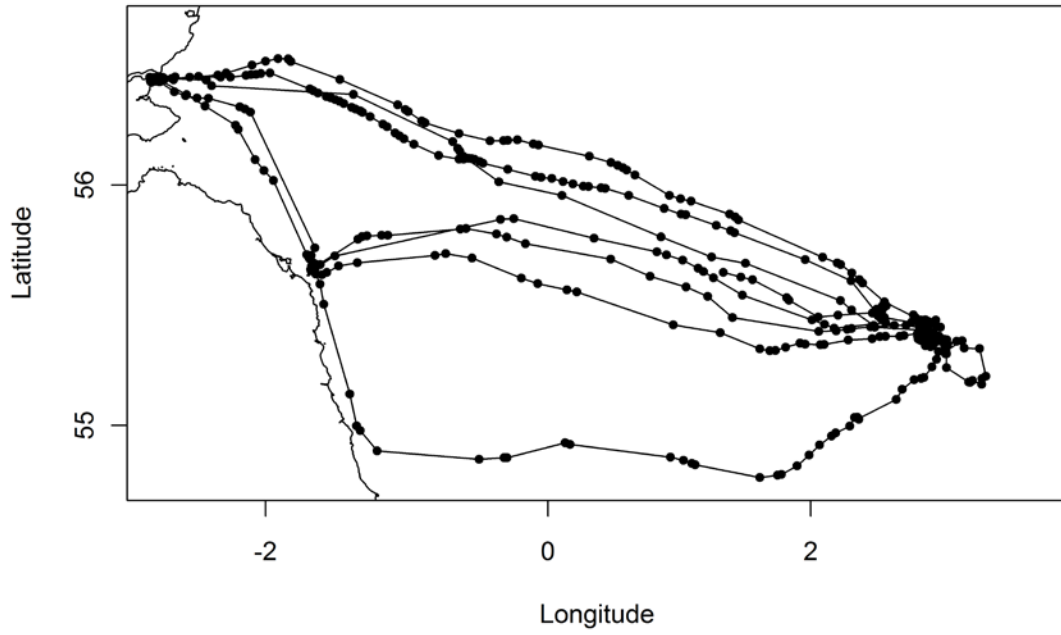
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990   Figure 2.

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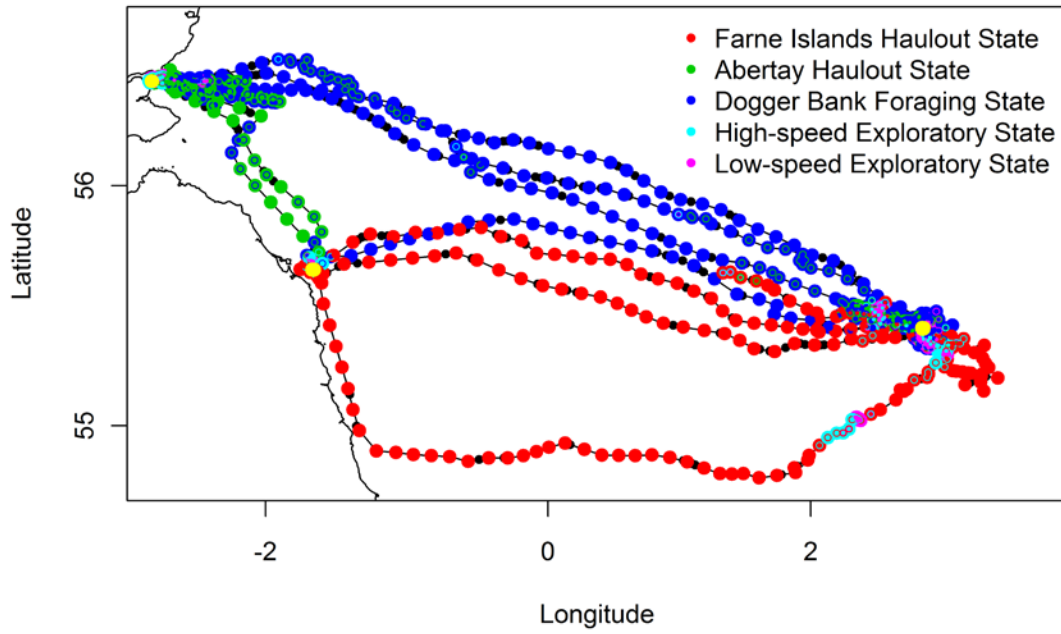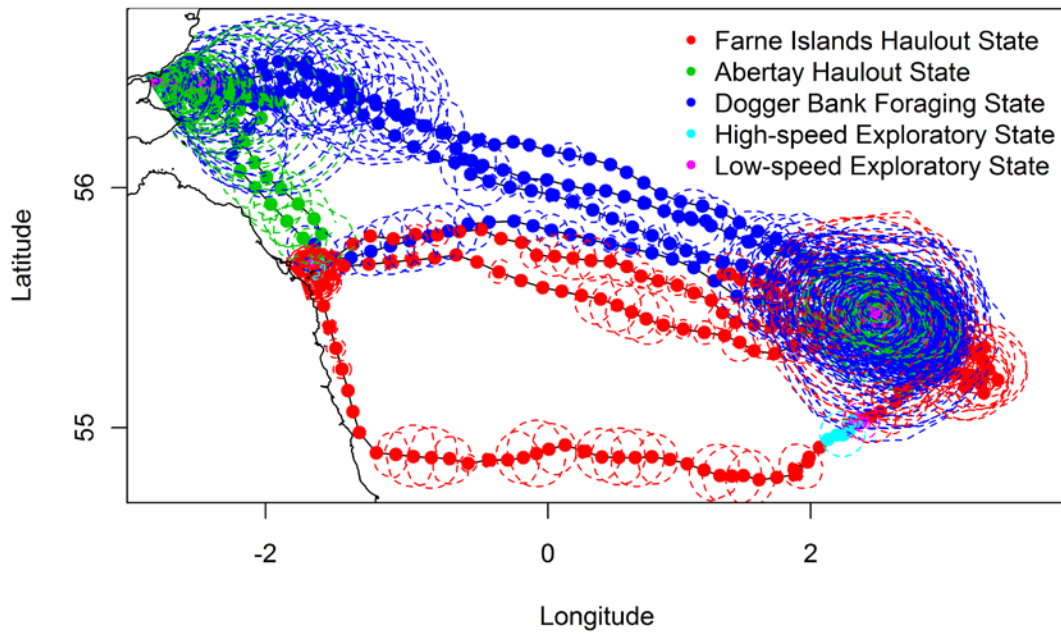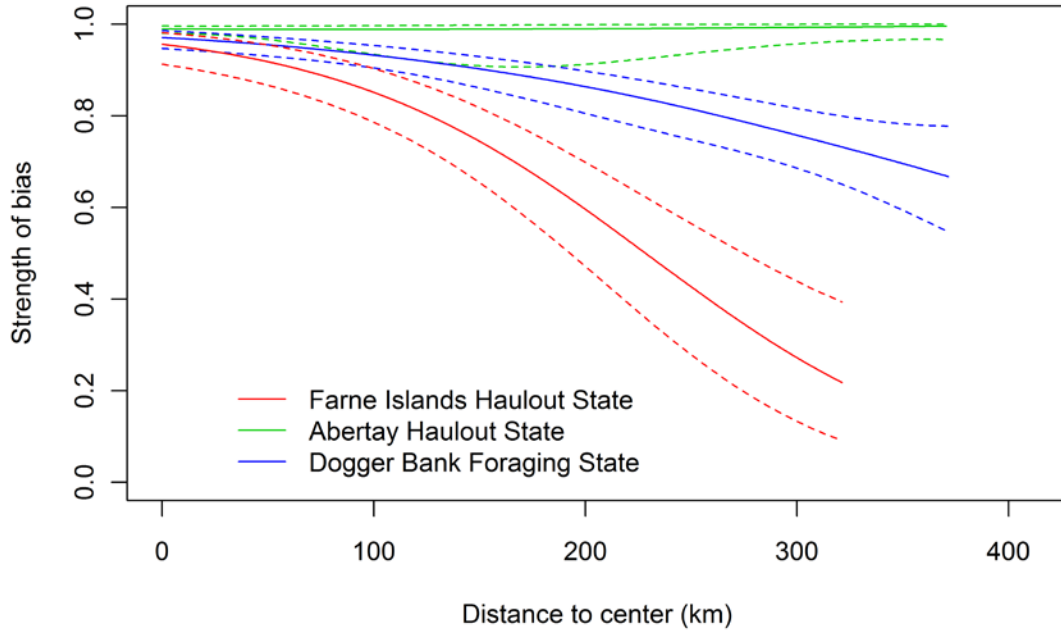1006   (a)

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1010   Figure 4.

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