



This is a repository copy of *Continuous time resource selection analysis for moving animals*.

White Rose Research Online URL for this paper:  
<http://eprints.whiterose.ac.uk/148566/>

Version: Accepted Version

---

**Article:**

Wang, Y., Blackwell, P.G. [orcid.org/0000-0002-3141-4914](https://orcid.org/0000-0002-3141-4914), Merkle, J.A. et al. (1 more author) (2019) Continuous time resource selection analysis for moving animals. *Methods in Ecology and Evolution*. ISSN 2041-210X

<https://doi.org/10.1111/2041-210x.13259>

---

This is the peer reviewed version of the following article: Wang, Y. , Blackwell, P. , Merkle, J. and Potts, J. (2019), Continuous time resource selection analysis for moving animals. *Methods Ecol Evol*. Accepted Author Manuscript. doi:10.1111/2041-210X.13259. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions.

**Reuse**

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

**Takedown**

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing [eprints@whiterose.ac.uk](mailto:eprints@whiterose.ac.uk) including the URL of the record and the reason for the withdrawal request.



[eprints@whiterose.ac.uk](mailto:eprints@whiterose.ac.uk)  
<https://eprints.whiterose.ac.uk/>

# Continuous time resource selection analysis for moving animals

Y. Wang<sup>1</sup>, P.G. Blackwell<sup>1</sup>, J.A. Merkle<sup>2</sup> and J.R. Potts<sup>1\*</sup>

<sup>1</sup> School of Mathematics and Statistics, University of Sheffield, Hicks Building, Hounsfield Road, Sheffield  
S3 7RH, UK

<sup>2</sup> Wyoming Cooperative Research Unit and Department of Zoology and Physiology, University of Wyoming,  
Laramie, WY, USA

\* Correspondence: E-mail: j.potts@sheffield.ac.uk

**Short title:** Continuous time resource selection analysis

**Word Count:** 7000

# Abstract

12

13 1. Resource selection analysis (RSA) seeks to understand how spatial abundance covaries with environ-  
14 mental features. By combining RSA with movement, step selection analysis (SSA) has helped uncover  
15 the mechanisms behind animal relocations, thereby giving insight into the movement decisions underly-  
16 ing spatial patterns. However, SSA typically assumes that at each observed location, an animal makes  
17 a ‘selection’ of the next observed location. This conflates observation with behavioural mechanism and  
18 does not account for decisions occurring at any other time along the animal’s path.

19

20 2. To address this, we introduce a continuous time framework for resource selection. It is based on  
21 a switching Ornstein-Uhlenbeck (OU) model, parameterised by Bayesian Monte Carlo techniques. Such  
22 OU models have been used successfully to identify switches in movement behaviour, but hitherto not  
23 combined with resource selection. We test our inference procedure on simulated paths, representing both  
24 migratory movement (where landscape quality varies according to season) and foraging with depletion  
25 and renewal of resources (where the variation is due to past locations of the animals). We apply our  
26 framework to location data of migrating mule deer (*Odocoileus hemionus*) to shed light on the drivers of  
27 migratory decisions.

28

29 3. In a wide variety of simulated situations, our inference procedure returns reliable estimations of  
30 the parameter values, including the extent to which animals trade-off resource quality and travel dis-  
31 tance (within 95% posterior intervals for the vast majority of cases). When applied to the mule deer data,  
32 our model reveals some individual variation in parameter values. Nevertheless, the migratory decisions  
33 of most individuals are well-described by a model that accounts for the cost of moving and the difference  
34 between instantaneous change of vegetation quality at source and target patches.

35

36 4. We have introduced a technique for inferring the resource-driven decisions behind animal movement  
37 that accounts for the fact that these decisions may take place at any point along a path, not just when the  
38 animal’s location is known. This removes an oft-acknowledged but hitherto little-addressed shortcom-  
39 ing of stepwise movement models. Our work is of key importance in understanding how environmental  
40 features drive movement decisions and, as a consequence, space use patterns.

## 41 1 Introduction

42 Resource selection is a fundamental tool for understanding the drivers behind spatial distributions of  
43 animals (Manly *et al.* (2002)). Applications not only include estimation of the distribution and abun-  
44 dance of species, but also prediction of species diversity, representation of interactions of species, and

45 identification of key spatial features of the landscape (e.g. Chetkiewicz & Boyce (2009), Lendrum *et al.*  
46 (2012), Boyce (2006), McLoughlin *et al.* (2010)). Furthermore, the role of movement as a primary cause  
47 of spatial patterning is becoming increasingly evident (Cagnacci *et al.* (2010), Thurfjell *et al.* (2014))  
48 and formally integrated into the resource selection framework (Moorcroft & Barnett (2008), Avgar *et al.*  
49 (2016)). This has diverse applications including home range formation (Merkle *et al.* (2017)), compe-  
50 tition (Vanak *et al.* (2013)), disease spread (Merkle *et al.* (2018)), territorial interactions (Potts *et al.*  
51 (2014b)), and predator-prey dynamics (Bastille-Rousseau *et al.* (2015)).

52 Step Selection Analysis (SSA) has provided the main tool for incorporating movement into resource  
53 selection (Fortin *et al.* (2005), Forester *et al.* (2009), Thurfjell *et al.* (2014)). It relies on comparing move-  
54 ment between two successive location fixes (called a ‘step’) with various possible steps potentially avail-  
55 able to the animal. As well as explicitly incorporating movement into the resource selection framework,  
56 SSA has recently been extended to estimate movement and resource selection parameters simultaneously,  
57 termed integrated step selection analysis (iSSA; Avgar *et al.* (2016)). The iSSA procedure corrects for  
58 any error implicit in the choice of distribution for ‘available’ steps, and can be used to parameterise a  
59 mechanistic model of animal movement. In addition, appropriate modelling of resource selection at the  
60 level of the individual step can link it to the long-term utilisation distribution (Michelot *et al.* (2018)).

61 However, both SSA and iSSA implicitly assume that movement decisions occur on the same scale as  
62 the observation frequency (McClintock *et al.* (2014)), or the scale of a regular subsample of the observa-  
63 tions (Potts *et al.* (2014c)). These assumptions may result in misleading interpretations of inferences from  
64 data, and in particular make it tricky to work with irregularly sampled data (McClintock *et al.* (2014),  
65 Thurfjell *et al.* (2014)). To avoid these issues, it makes sense to model the animal path as a continuous  
66 track, where decisions may have occurred at any point along that track, then fit this continuous-time  
67 model to the data.

68 Continuous-time modelling frameworks for animal movement have existed for some time. An early  
69 example is that of Blackwell (1997). There, a switching Ornstein-Uhlenbeck (OU) process was proposed,  
70 which is flexible enough to capture a wide range of animal movement patterns, and has thus gained  
71 increasing popularity over the years. It has the advantage of being amenable to rigorous and efficient  
72 parameterisation by data using Bayesian Monte Carlo methods (Blackwell (2003)) and has recently been  
73 extended to incorporate spatial heterogeneity (Harris & Blackwell (2013), Blackwell *et al.* (2016)). This  
74 opens the question as to whether it can be combined with resource selection analysis (RSA) to model  
75 animal decisions as they move in continuous time.

76 Several continuous-time models have already been developed to incorporate resource selection. John-  
77 son *et al.* (2008) was one of the first such studies. This study proposed various possible models for the  
78 distribution of a location along path, conditional on the knowledge of all previous locations. However,  
79 although the models themselves were defined in continuous time, they all model movement from one

80 measured location to the next, so do not account for the possibility of behavioural changes between  
81 location fixes.

82 On the other hand, the approach of Hanks *et al.* (2015) does deal with between-observation be-  
83 havioural switches. This method discretises space into a lattice and models movement as jumps between  
84 neighbouring lattice sites, building on previous work by Hooten *et al.* (2010) and Hanks *et al.* (2011).  
85 Behavioural switches are possible at any nearest-neighbour jump, not just those that correspond to mea-  
86 sured locations. However, the implicit assumption of the model in Hanks *et al.* (2015) is that the spatial  
87 scale of discretisation represents the scale of behavioural decisions. In reality, animal movement decisions  
88 may play out on multiple scales, with localised considerations (e.g. moving around a small obstacle or  
89 over a fence) balanced with longer-term goals (e.g. moving to the next foraging patch or continuing  
90 a migratory journey). Furthermore, this technique only considers movement in response to proximate  
91 resources (e.g. a local resource gradient). In reality, animals may be attracted to resources that are quite  
92 some distance away, due to long-term memory processes. A continuous-time framework is needed that  
93 is flexible enough to account for such a variation of possibilities.

94 Here, we extend the switching OU framework of Blackwell *et al.* (2016) to incorporate resource  
95 selection in two separate ways. The first considers resources as objects that have an attractive pull  
96 on animals, which may take place over a considerable spatial scale (e.g. in migratory cases). If it is  
97 beneficial to move to a new area to gain access to better resources, taking into consideration the cost of  
98 moving there, then the animal becomes attracted to that area. In mathematical terms, this corresponds  
99 to a switch in the OU process. Otherwise, the animal stays in the vicinity of its current position. At  
100 any point, the best possible attractor on the landscape could switch, causing the animal to change its  
101 movement mode. We consider cases both where the landscape undergoes seasonal changes and where  
102 the quality of resources depends upon the past positions of the animal (through resource depletion and  
103 renewal).

104 The second modification is implemented separately from the first and takes a rather different ap-  
105 proach to modelling animal movement. Here, rather than assuming the animal assesses the whole land-  
106 scape and moves towards the most desirable goal, we assume that the animal considers only proximate  
107 aspects of the terrain and, as such, has a tendency to move up the resource gradient. This is similar to  
108 Hanks *et al.* (2015) but framed within a switching random walk framework. In doing this, the animal's  
109 path does not need to be discretised (as in Hanks *et al.* (2015)). However, by using efficient Bayesian  
110 Monte Carlo methods developed over a series of papers (Blackwell (2003), Harris & Blackwell (2013),  
111 Blackwell *et al.* (2016)), inference is still possible within a reasonable time-frame. We compare our frame-  
112 work with that of Hanks *et al.* (2015), testing for both speed and precision of inference by application  
113 to paths simulated from the model proposed in this paper.

114 We tested our modelling and inference method on both simulated and real trajectories. The simu-

115 lated trajectories model (a) migratory behaviour, (b) movement due to resource depletion and renewal  
116 in both patchy and lattice landscapes, and (c) resource-gradient following in a fixed (lattice) landscape.  
117 Real trajectories were measured from mule deer (*Odocoileus hemionus*) migrations in the Greater Yel-  
118 lowstone Ecosystem. Our simulation analysis demonstrates the ability of our method to infer parameters  
119 with reasonable accuracy. The application to mule deer data demonstrates that migratory timings may  
120 be explained by a simple trade-off between resource quality and travel distance. We include, in the Sup-  
121 porting Information, code for performing inference and simulating all trajectories used in this manuscript  
122 (instructions are found in Supplementary Appendix H).

## 123 2 Methods

### 124 2.1 Modelling framework

125 In this section, we model movements in response to the environment in two scenarios. In the first  
126 situation, we assume that animals have complete knowledge of the environment and bias their movements  
127 towards the most attractive location in space. Then we consider the other extreme, where animals only  
128 have information about local conditions.

#### 129 2.1.1 Movements in response to resource change in the whole landscape

130 A commonly used continuous-time movement model is the OU process, which describes a biased random  
131 walk with drift towards an attraction centre. The general formalism is given as follows

$$d\mathbf{x}(t) = B(\mathbf{x}(t) - \boldsymbol{\mu}(t))dt + \Lambda d\mathbf{W}(t). \quad (1)$$

132 Here,  $\mathbf{x}(t)$  is the animal's location at time  $t$  in  $n$ -dimensional space,  $\boldsymbol{\mu}(t)$  is the attraction centre at time  
133  $t$ ,  $B$  is an  $n$  by  $n$  matrix controlling the tendency towards the attraction centre,  $\Lambda$  is the covariance  
134 matrix, and  $\mathbf{W}(t)$  is an  $n$ -dimensional Wiener process. Under the process given by Equation (1), the  
135 probability of an animal being at location  $\mathbf{x}(t + \tau)$  at time  $t + \tau$ , given that it was at  $\mathbf{x}(t)$  at time  $t$ , is

$$\mathbf{x}(t + \tau) | \mathbf{x}(t) \sim MVN(\boldsymbol{\mu}(t) + e^{B\tau}(\mathbf{x}(t) - \boldsymbol{\mu}(t)), \Lambda - e^{B\tau} \Lambda e^{B'\tau}), \quad (2)$$

136 where  $\tau$  is a (small) time interval and  $MVN$  stands for "Multi-variate normal".

137 Throughout this paper, we work in two dimensions, so that  $B$  and  $\Lambda$  are  $2 \times 2$  matrices. Furthermore,  
138 we assume  $B = -bI$  and  $\Lambda = vI$  with  $b, v > 0$  and  $I$  the  $2 \times 2$  identity matrix, so that there is  
139 no correlation between the horizontal and vertical coordinates. Larger  $b$  leads to a stronger tendency  
140 toward the attraction centre and faster approach to the attraction centre when far away from it, while

141 larger  $v$  induces a wider range of wandering near the central point. Hence we refer to  $b$  as the *drift*  
 142 *coefficient* and  $v$  the *diffusive coefficient*.

143 To determine the attraction centre  $\boldsymbol{\mu}(t)$  in the OU process in Equation (2), a function is incorporated  
 144 into our modelling framework to evaluate the attractiveness of a location or an item in space. For this,  
 145 we choose a commonly used functional form known as a *resource selection function* (RSF) and defined  
 146 as follows (Boyce *et al.* (2002))

$$w(\mathbf{x}) = \exp(\beta_1 z_1(\mathbf{x}) + \beta_2 z_2(\mathbf{x}) + \cdots + \beta_k z_k(\mathbf{x})), \quad (3)$$

147 where  $\mathbf{x}$  is a location in space,  $\mathbf{z}(\mathbf{x}) = (z_1(\mathbf{x}), \cdots, z_k(\mathbf{x}))$  is the vector of predictor covariates, consisting  
 148 of possible factors affecting selection decision – for example, some kind of vegetation, predator pressure,  
 149 distance to a road, etc. (Manly *et al.* (2002)) – and  $\beta_1, \cdots, \beta_k$  are coefficients representing the relative  
 150 weight of each factor. We assume that the animal has complete knowledge of the available space and  
 151 decides its destination  $\boldsymbol{\mu}(t)$  at time  $t$  by comparing the attractiveness of all potential target locations,  
 152 given by Equation (3) (cf. Avgar *et al.* (2017)), then moves towards the most attractive destination.  
 153 That is,

$$\boldsymbol{\mu}(t) = \boldsymbol{\mu}_i \quad \text{where} \quad w(\boldsymbol{\mu}_i) = \max_{j \in \Omega} w(\boldsymbol{\mu}_j). \quad (4)$$

154 Here,  $\boldsymbol{\mu}_i$  is the centre of a resource unit, which may be a patch or an item, and  $\Omega$  indexes the collection  
 155 of all resource units, which is finite. In most typical situations,  $\boldsymbol{\mu}(t)$  will be unique, because Equation  
 156 (3) will normally involve continuous covariates, and so each resource unit  $\boldsymbol{\mu}_j$  is likely to have a different  
 157 value of  $w(\boldsymbol{\mu}_j)$  associated to it. In this study, we only consider such situations, so there is never an  
 158 arbitrary choice between resource units of precisely equivalent quality.

### 159 2.1.2 Movements following local resource gradient

160 The OU model described above assumes the animal has complete knowledge of the landscape when  
 161 making a decision. At the other extreme, we might assume that the animal only has proximate knowledge  
 162 of the landscape. For this, we model animals as following the local resource gradient. This can be  
 163 described by a process  $\mathbf{x}(t)$  satisfying a stochastic differential equation with constant drift term (Preisler  
 164 *et al.* (2004))

$$d\mathbf{x}(t) = \alpha \boldsymbol{\rho}(t) dt + \boldsymbol{\Sigma} d\mathbf{W}(t), \quad (5)$$

165 where  $\alpha$  is a governing the drift speed,  $\boldsymbol{\rho}(t)$  is a unit vector representing the direction of drift,  $\boldsymbol{\Sigma}$  is  
 166 an  $n \times n$  matrix controlling the diffusive aspects of movement. Here we use a two-dimensional (Euler-  
 167 Maruyama) approximation of the conditional distribution of the process defined by Equation (5), which

168 is valid for small  $\tau$ . This is given as follows

$$\mathbf{x}(t + \tau) | \mathbf{x}(t) \sim MVN(\mathbf{x}(t) + \alpha \boldsymbol{\rho}(t) \tau, \boldsymbol{\Sigma} \tau), \quad (6)$$

169 where  $\mathbf{x}(t)$  is the animal's position at time  $t$ . We assume  $\boldsymbol{\Sigma} = \sigma^2 I$  where  $I$  the  $2 \times 2$  identity matrix and  
 170  $\sigma$  is a scalar constant. The model in Equation (6) contrasts with that of Equation (2) in that the former  
 171 assumes animals respond to a local resource gradient, whereas the latter models animals as choosing a  
 172 target location from the landscape to move towards.

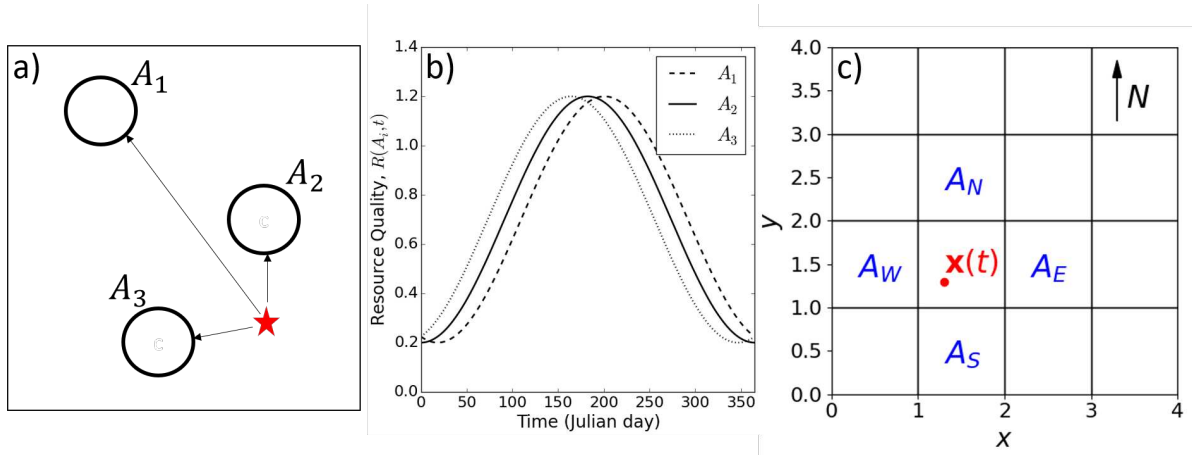


Figure 1: Panel (a) illustrates the patch selection model (Equations 1-4). Assume the animal is at the red star. In this simplified illustration, there are just three possible patches it can choose to move towards,  $A_1$ ,  $A_2$ , and  $A_3$  (in real situations there may be many more). The animal's choice is determined by both the patch quality, which may vary over time, and the distance to the patch. Panel (b) gives example curves of how the patch quality of each patch may vary over time, each in the format of Equation (11). Panel (c) illustrates the gradient following model (Equations 5-8). The animal is located at position  $\mathbf{x}(t)$  at time  $t$ . Patches  $A_N$ ,  $A_W$ ,  $A_E$  and  $A_S$  are the adjacent squares to the patch where the animal is located.  $N$ ,  $W$ ,  $E$ ,  $S$  stand for the north, west, east and south respectively. When calculating the resource gradient in the nearby area of  $\mathbf{x}(t)$ , the resource qualities in the four adjacent patches are considered, which means the animal only assesses resource qualities in neighbouring areas to determine its moving direction.

173 We assume that animals move in a rasterised landscape, that is, one subdivided into a square or  
 174 rectangular lattice. Hereafter we will consider a square lattice for simplicity. We determine the drift  
 175 direction  $\boldsymbol{\rho}(t)$  in Equation (6) by considering the resource qualities in the four adjacent squares (North,  
 176 East, South, West) to the one where the animal is located. Here, the resource gradient is given as follows  
 177 (cf. Preisler *et al.* (2013)):

$$\nabla w(\mathbf{x}(t)) := \left( \frac{w(A_E) - w(A_W)}{\Delta x}, \frac{w(A_N) - w(A_S)}{\Delta y} \right), \quad (7)$$



178 where  $\mathbf{x}(t)$  is the animal’s position at time  $t$ ,  $w(A_E)$ ,  $w(A_W)$ ,  $w(A_N)$ , and  $w(A_S)$  are the resource  
179 selection weightings (Equation 3) for the adjacent patches  $A_E$ ,  $A_W$ ,  $A_N$  and  $A_S$  in the east, west, north,  
180 and south respectively (Figure 1). We use  $\Delta x$  to denote the distance between the centres of patches  $A_E$   
181 and  $A_W$  while  $\Delta y$  is the distance from the north patch to the south patch. Notice that, whilst there are  
182 also diagonally adjacent squares (NW, NE, SE, SW), it is sufficient to use just four to define the resource  
183 gradient, as shown in Equation (7). Then the vector  $\boldsymbol{\rho}(t)$  in Equation (6) is defined as the normalised  
184 vector of  $\nabla w(\mathbf{x})$ ,

$$\boldsymbol{\rho}(t) = \frac{\nabla w(\mathbf{x}(t))}{|\nabla w(\mathbf{x}(t))|}. \quad (8)$$

185 Note that we model our drift speed as constant ( $\alpha$ ) rather than letting it vary with the magnitude of  
186  $\nabla w(\mathbf{x})$ . This means that the average speed of the animal across a time interval  $\tau$  is kept constant, rather  
187 than being allowed to become arbitrarily large. However, the model could easily be adjusted so that  
188  $\boldsymbol{\rho}(t) = \nabla w(\mathbf{x})$  if the user believes that to be more appropriate for their particular study species.

### 189 2.1.3 Locations between observations

190 In each of the above movement models, we assume that the animal can potentially make a decision  
191 to reassess its movement state at any instant in continuous time. To represent this, reassessments  
192 occur according to a Poisson point process with rate  $\kappa$ , as in Blackwell *et al.* (2016) (see Appendix  
193 A in Supporting Information). This process means that the time intervals between reassessments are  
194 exponentially distributed with parameter  $\kappa$ . At each reassessment time, we deterministically decide the  
195 movement state, which is defined by either the attraction centre  $\boldsymbol{\mu}(t)$  in Equation (2) or direction  $\boldsymbol{\rho}(t)$  in  
196 Equation (6). The movement state is decided by comparing the relative quality of resources in different  
197 patches, using Equations (3-4), or calculating the resource gradient using Equation (7).

198 The fact that the choice of target location is deterministic, based on a complex evaluation of the  
199 environment, contrasts with the stochastic switching of Blackwell *et al.* (2016), where the transition  
200 rates are relatively simple functions of habitat and time. One could, in principle, extend our model so  
201 that animals choose an attraction centre with a probability, based on the relative quality of each site.  
202 However, this introduces extra model complexity that may not increase realism, so we have chosen to  
203 model a deterministic switching process for simplicity.

## 204 2.2 Inference by Markov chain Monte Carlo algorithm

205 Having constructed the modelling frameworks, we use a Markov chain Monte Carlo (MCMC) algorithm,  
206 based on Blackwell *et al.* (2016), to parameterise the models from movement data. For details of the  
207 algorithm, see Appendix A in Supporting Information.

208 The MCMC algorithm comprises two main parts, one of which updates the movement trajectory by

209 simulation and the other updates parameters. To take into consideration the fact that animals can make  
 210 a decision to move at any time, we augment the observed data with points where the animal might have  
 211 changed its destination. In every iteration, we select an interval from the observed data and generate  
 212 a simulated path consisting of points where the switches of destinations might happen during the time  
 213 of the selected interval. Subsequently, we compare this simulated path with the selected interval in  
 214 existing trajectory by calculating the Hastings ratio, conditional on observed data points. After deciding  
 215 whether to accept the proposal trajectory or not, we update the parameters conditional on the accepted  
 216 trajectory (see Blackwell *et al.* (2016) for details).

## 217 **2.3 Simulations**

218 We test the MCMC algorithm on four classes of movement models. The first models migration, so  
 219 we assume that the animal moves in response to seasonally changing resource qualities. In the second  
 220 and third types of model, the resource quality depletes and renews according to the animal’s foraging  
 221 patterns. The last is a gradient-following model, where the animal only compares resource qualities in  
 222 the surrounding area to decide its direction.

### 223 **2.3.1 Migration model**

224 The first test of our inference method (Section 2.2) uses a very simple model of migration, whereby the  
 225 decision to migrate is a trade-off between the quality of a patch, which may be a destination range or  
 226 a stopover site, and how far it is away from the animal. Although migratory routes tend to be fixed,  
 227 the decision as to when to move to the next patch is not. Rather it is determined by how the quality  
 228 of patches over the migratory route are changing over time (e.g. due to green-up). We hypothesise that  
 229 movement to the next patch will occur when the animal will make sufficient foraging gains from the  
 230 next patch to make the movement worth while. The decision to migrate is thus caused by patch quality  
 231 varying over time, so we use an adjusted form of Equation (3), which includes time as a variable:

$$w(\boldsymbol{\mu}, t) = \exp(\beta_1 R(\boldsymbol{\mu}, t) + \beta_2 |\boldsymbol{\mu} - \mathbf{x}(t)|), \quad (9)$$

232 where  $\mathbf{z}(\boldsymbol{\mu}, t) = (R(\boldsymbol{\mu}, t), |\boldsymbol{\mu} - \mathbf{x}(t)|)$  is the vector of predictor covariates with  $R(\boldsymbol{\mu}, t)$  the resource quality  
 233 in a potential target location  $\boldsymbol{\mu}$  and  $\mathbf{x}(t)$  the animal’s position at time  $t$ . We assume  $\beta_1 > 0$  and  $\beta_2 < 0$ ,  
 234 representing the animal’s inclination for resources and aversion to distant places. Note that a similar  
 235 quality/distance trade-off for patch selection was also used by Mitchell & Powell (2004) in the slightly  
 236 different context of modelling home range formation.

237 In practice, since our aim is to use the patch that maximises Equation (9) as the movement centre,  
 238 comparing the value of Equation (9) is equivalent to comparing a constant multiple of its exponent.

239 Moreover, we can only infer  $\beta_1/\beta_2$  from data instead of inferring  $\beta_1$  and  $\beta_2$  simultaneously, because any  
 240 proposed values for  $\beta_1$  and  $\beta_2$  with ratio close to  $\beta_1/\beta_2$  will lead to the same attraction centre. Therefore,  
 241 it suffices to consider a simplified version of Equation (9) as follows

$$w(\boldsymbol{\mu}, t) = \exp(\beta R(\boldsymbol{\mu}, t) - |\boldsymbol{\mu} - \mathbf{x}(t)|), \quad (10)$$

242 where  $\beta = -\beta_1/\beta_2$  is termed the *resource coefficient*.

243 Our model landscape consists of  $N$  non-overlapping patches, denoted by  $A_i$ ,  $i \in \{1, \dots, N\}$ . The  
 244 centre of patch  $A_i$  is denoted by  $\boldsymbol{\mu}_i = (x_i, y_i)$  with  $y_1 \leq y_2 \dots \leq y_N$ , ordered by latitude. We assume the  
 245 resource quality changes periodically over the year and shifts corresponding to the latitude. The resource  
 246 quality  $R(A_i, t)$  in patch  $A_i$  at time  $t$  (Julian day) is assumed to be a cosine function with period 365  
 247 days and shift controlled by  $(y_i - y_1)/(y_N - y_1)$ , the relative latitude difference:

$$R(A_i, t) = a \cos\left(\frac{2\pi}{365}t - \frac{y_i - y_1}{y_N - y_1}\pi\right) + m, \quad (11)$$

248 where  $a$  and  $m$  are the amplitude and mean of resource quality and  $y_i$  is the  $y$ -coordinate of the centre  
 249 of  $A_i$  (Figure 1b).

250 We generated migration trajectories by sampling from the model described above with various values  
 251 of the drift coefficient,  $b$ , the diffusion coefficient,  $v$ , and the resource coefficient,  $\beta$  in the following ranges:  
 252  $0.1 \leq b \leq 0.8$ ,  $2 \leq v \leq 30$ , and  $1.5 \leq \beta \leq 8.5$ . These are chosen to produce simulations showing migration  
 253 patterns on a  $90 \times 160$  unit<sup>2</sup> landscape with 10 randomly generated non-overlapping food patches. These  
 254 implicitly include the winter and summer ranges and stopover sites between them.

255 We tested the MCMC algorithm on these simulations with resource qualities being given *a priori*.  
 256 We used a normally distributed prior for each parameter value with a mean equal to the real parameter  
 257 value and a standard deviation of 2. Example output is given in Figure 2a, illustrating migration from  
 258 the winter range in the south to the summer range in the north and back to the south over a year. We  
 259 used the MCMC algorithm to infer drift and diffusion coefficients ( $b$  and  $v$  respectively) from the OU  
 260 process in Equation (2), together with the resource coefficient,  $\beta$ , from the RSF in Equation (10). To  
 261 investigate the effectiveness of the MCMC algorithm when dealing with missing data, we carried out the  
 262 inference using every 5th data point, shown as red triangles in Figure 2a. We also investigated the effect  
 263 of finer rarification for certain simulated datasets from our study. This made very little difference to the  
 264 inference (details in Supplementary Appendices D-E).

### 265 **2.3.2 Depletion-renewal models in a patchy landscape**

266 In Section 2.3.1, we assumed that animals do not contribute in any significant way to the change of  
 267 resource quality (e.g. Illius *et al.* (2002)). In this section, we assume that the resource quality changes

268 according to the residential time of the animal in a food patch (e.g. Mitchell & Powell (2007), Van Moorter  
 269 *et al.* (2009)). As in the migration model, we describe a situation where an animal moves in pursuit  
 270 of quality food using the combination of the OU process and a RSF, introduced in Section 2.1.1. For  
 271 example, this may represent how an animal forages in its home range with complete knowledge of the  
 272 environment (e.g. Ford (1983)). As in Section 2.3.1, to test our inference method in a simple case, we  
 273 assume that the decision to move to a patch is a trade-off between the quality of a patch and the distance  
 274 to it and use the RSF given by Equation (10).

275 We simulate movements using Equations (2-4) in a landscape with food patches  $A_i$ ,  $i \in \{1, \dots, N\}$ ,  
 276 assuming that the resources either are consumed (if the animal is present) or renewed (otherwise).  
 277 Specifically, if the animal is foraging in patch  $A_i$  at time  $t$ , that is,  $\mathbf{x}(t) \in A_i$ , then the resource quality  
 278  $R(A_i, t)$  in patch  $A_i$  decreases exponentially while those in other patches grow logistically, so that (Ford  
 279 (1983), Van Moorter *et al.* (2009))

$$R(A_j, t + \tau) = \begin{cases} R(A_j, t)e^{-d_j\tau} & \text{if } j = i, \\ \frac{K_j R(A_j, t)e^{r_j\tau}}{K_j + R(A_j, t)(e^{r_j\tau} - 1)} & \text{for } j \neq i, \end{cases} \quad (12)$$

280 where  $d_j$ ,  $r_j$  and  $K_j$  are the depletion rate, growth rate and carrying capacity in patch  $A_j$  respectively  
 281 and  $\tau$  is a (short) time-step. For simplicity, here we assume that the growth and depletion rates and the  
 282 carrying capacity are the same in each patch, and thus denoted  $r$ ,  $d$  and  $K$  respectively.

283 We tested the inference procedure on simulations generated with various values of the drift coefficient,  
 284  $b$ , the diffusion coefficient,  $v$ , and the resource coefficient,  $\beta$  in the following ranges:  $0.05 \leq b \leq 0.5$ ,  
 285  $1700 \leq v \leq 3500$  and  $0.5 \leq \beta \leq 5$ . We used a  $2000 \times 2000$  unit<sup>2</sup> landscape with 10 randomly generated  
 286 non-overlapping food patches. Figure 2b shows an example of simulated trajectories of movements  
 287 depending on resource depletion or renewal in a patchy landscape. We tested the MCMC algorithm with  
 288 growth ( $r$ ), depletion rate ( $d$ ), and carrying capacity ( $K$ ) being given. We used a normally distributed  
 289 prior for each parameter value with a mean equal to the real parameter value and a standard deviation  
 290 of 2. We then inferred  $b$  and  $v$  in the OU process (Equation 2) and  $\beta$  in Equation (10) using the Bayesian  
 291 Monte Carlo algorithm. In principle, one could attempt to infer all five parameters ( $r, d, K, b, v$ ) using  
 292 our inference procedure, but we found that it was not usually possible to obtain precise inference in  
 293 this case, so we would advise users to try to measure  $r, d$ , and  $K$  directly. An example of such a direct  
 294 method is given by Fortin *et al.* (2002).

### 295 2.3.3 Depletion-renewal models in a raster landscape

296 Although there are many real-life situations where resource patches are disjoint and known (e.g. Merkle  
 297 *et al.* (2014), Sawyer & Kauffman (2011)), often resources change continuously over the landscape and

298 are represented in data by a square grid (a.k.a. raster; e.g. Potts *et al.* (2014a)). To test whether our  
299 inference procedure is effective at determining resource attraction in such situations, we model movement  
300 on a square grid of resources that deplete and renew over time. In this case, the centre of each square in  
301 the grid is a potential attraction centre of the OU process (Equation 2).

302 We started each simulation with homogeneous resource type in every square, which shares the same  
303 carrying capacity,  $K$ , depletion and growth rates,  $d$  and  $r$ , across the land (e.g. Figure 2c). The initial  
304 resource quality was equal to the carrying capacity and the resource quality in time  $\tau$  from time  $t$  forward  
305 was calculated using Equation (12) in Section 2.3.2. We tested our inference procedure on simulations  
306 of the model in Equations (2-4) generated with  $0.05 \leq b \leq 0.14$ ,  $0.05 \leq v \leq 0.5$  and  $0.2 \leq \beta \leq 2$  on  
307 a  $3 \times 3$  grid composed of unit squares. We carried out the MCMC algorithm on the assumption that  
308  $d$ ,  $r$  and  $K$  are known and attempted to infer the movement coefficients  $b$  and  $v$  in the OU process in  
309 Equation (2) and the resource coefficient  $\beta$  in Equation (10). As for the other simulations, we used a  
310 normally distributed prior for each parameter value with a mean equal to the real parameter value and  
311 a standard deviation of 2.

#### 312 **2.3.4 Gradient-following models**

313 When landscape rasters are large, it may not be computationally feasible to test every square to see if  
314 it is an attractive centre. Instead, we take a different modelling approach, assuming that the animal  
315 tends to move up the local resource gradient, rather than towards a prime destination. This means that  
316 animals are predominantly using local perception rather than memory (cf. Bracis & Mueller (2017)).  
317 Figure 2d illustrates such a trajectory in a landscape with three different resource qualities, which are  
318 assumed to be static.

319 Here, the movement process is described by Equation (6) with direction corresponding to the resource  
320 gradient calculated using Equations (7) and (8). We define the RSF in Equation (7) to be the resource  
321 quality at a square. The parameters to be inferred are  $\alpha$  and  $\sigma$  for the drift term and covariance matrix  
322 in Equation (6). We tested the MCMC algorithm on simulations constructed with  $0.1 \leq \alpha, \sigma \leq 1$  on a  
323  $10 \times 10$  grid consisting of unit squares with 3 resource qualities. As with the other simulated trajectories,  
324 we used a normally distributed prior for each parameter value with a mean equal to the real parameter  
325 value and a standard deviation of 2. We also compared our framework with that of Hanks *et al.* (2015),  
326 testing for both inference speed and precision by application to simulated paths (details in Supplementary  
327 Appendix G). In total, for our study we analysed 45 simulated paths for the Migration model, 30 for  
328 the Patch depletion/renewal model, 30 for the Raster depletion/renewal model, and 20 for the Gradient  
329 following model.

## 2.4 A case study of mule deer data in the Greater Yellowstone

### Ecosystem

We used GPS collar data from 28 adult ( $> 1.5$  years of age) female mule deer captured using a netgun fired from a helicopter near Cody, Wyoming (USA). Collars (ATS, Iridium, Isanti, Minnesota, USA) were programmed to take a fix every 2 hours, and we used data collected from March-August 2016. All deer were captured following protocols consistent with the University of Wyoming standards.

Before employing the MCMC inference procedure introduced in Section 2.2, we identified foraging patches by grouping data points where an animal stayed within a 3-km radius area for at least 3 days. Subsequently, the average longitude and latitude of locations inside the patches were regarded as the attraction centre (Figure 4a). For our data, these patches were quite straightforward to identify, being obvious just by looking at the location data (Figure 4a; Supplementary Video SV1), and the deer have high fidelity to these sites (Sawyer & Kauffman, 2011). However, this may not be true for all datasets on migratory movement. For each attraction centre, we extracted the values of the normalised difference vegetation index (NDVI) and instantaneous rate of green-up (IRG) for Julian days 1 to 250 from the corresponding pixels in the images (Figures 4c). NDVI and IRG data were compiled from the MODIS satellite based on the methods of Bischof *et al.* (2012) and Merkle *et al.* (2016).

Our model is based on Equation (10) for decision making and the OU process in Equation (2) for movement, and can be written out in full as follows

$$\mathbf{x}(t + \tau) | \mathbf{x}(t) \sim MVN(\boldsymbol{\mu}(t) + e^{-b\tau}(\mathbf{x}(t) - \boldsymbol{\mu}(t)), vI(1 - e^{-2b\tau})), \quad (13)$$

$$\boldsymbol{\mu}(t) = \operatorname{argmax}_{i \in \Omega} [\exp(\beta R(\boldsymbol{\mu}_i, t) - |\boldsymbol{\mu}_i - \mathbf{x}(t)|)], \quad (14)$$

where  $\Omega$  indexes the set of attraction centres (centres of the foraging patches). We used our MCMC algorithm to parameterise two different models from data. The first was the NDVI Model, where  $R(\boldsymbol{\mu}_i, t)$  is the NDVI value of patch  $i$  at time  $t$ . The second was the IRG Model, where  $R(\boldsymbol{\mu}_i, t)$  is the IRG value of patch  $i$  at time  $t$ . We used the Deviance Information Criterion (DIC) (Spiegelhalter *et al.* (2002)) for model selection.

## 3 Results

### 3.1 Testing MCMC inference on simulations

#### 3.1.1 Migration model

Figure 3a shows the posterior distributions derived by applying MCMC inference on the trajectory shown in Figure 2a. The posterior distributions captured the real values of parameters used in simulations to a good degree of accuracy with the real values lying within a 95% quantile interval of the posterior distributions, indicated by black dashed lines in Figure 3a.

When applying the MCMC algorithm on the migration model, the sampling chains converged within similar numbers of iteration in about 20 minutes (on a single thread of an i5 2.0GHz processor in a Windows desktop) regardless of various values for parameters used in simulation (Figure S1 in the Supporting Information). It took longer for the chains to converge when the number of proposed switching points increases (Figure S2a,b). However, the performance of estimation was not affected by the amount of proposed points (Figure S2c-e). Although the value of increasing  $\kappa$  was insignificant here, it might become important when the frequency of state switch is much higher than observation.

As one would expect, the chains converged faster when the initial value of the drift coefficient,  $b$ , was closer to the real value, in cases when the diffusion coefficient,  $v$ , and the resource coefficient,  $\beta$ , were fixed at real values (Figures S3a,b). However, the initial value of  $v$  had little impact on converging time (Figures S3c,d), while the chains converged faster when the initial value of  $\beta$  was near the real value (Figures S3e,f).

As for accuracy, the real values of  $b$ ,  $v$  and  $\beta$  were within 95% central posterior intervals of the estimated values for about 2/3, 4/5 and 1/2 simulations respectively (Figure S4, Table S1). (See Appendices B, F in Supporting Information for more details.) However, where they did deviate from these intervals the deviations were generally quite small (a discrepancy of less than about 25% in all cases).

#### 3.1.2 Resource depletion-renewal models in a patchy landscape

The 95% central posterior interval of each posterior distribution in Figure 2b contains the real values (Figure 3b), showing that our inference procedure has good accuracy in this case.

The algorithm was able to converge within 26,000 iterations (approximately 55 minutes) in most cases (Figure S5 in the Supporting Information). It took longer for the chains to converge when the initial value of  $b$  was far away from the real value, whereas the initial values of  $v$  and  $\beta$  had little influence on the time before converging (Figure S6). While  $b$  and  $v$  were captured by 95% central posterior intervals for most cases,  $\beta$  was overestimated when the values of  $v$  or  $\beta$  used in simulations were higher (Figure S7, Table S1) (See Appendix C in Supporting Information for more details.)

### 383 3.1.3 Resource depletion-renewal models in a raster landscape

384 For the case shown in Figure 2c, the posterior distributions captured parameters successfully, as shown  
385 in Figure 3c, despite that it is not straightforward to identify the attraction centres simply by eyeballing  
386 the trajectory.

387 In general, the convergence time of the algorithm was independent of the values of coefficients used  
388 in simulations (Figures S8 in the Supporting Information). However, starting the algorithm with initial  
389 values closer to real values usually led to faster convergence, as one would expect (Figure S9).

390 The performance of the MCMC algorithm using every 5th data point was similar to that using  
391 every 3rd point, but the discrepancy between sample means of  $\beta$  and real values was lower when more  
392 observations were considered (Figures S10,11,12). (See Appendix D in Supporting Information for more  
393 details.)

### 394 3.1.4 Gradient-following models

395 In the case shown in Figure 2d, the posterior distributions successfully captured the real values within  
396 95% central posterior intervals.

397 The value of the drift speed,  $\alpha$ , used to generate a simulated trajectory had no obvious impact on  
398 the time when MCMC chains converged (Figure S13a in the Supporting information). On the other  
399 hand, the chains tended to converge quicker when larger  $\sigma$  was used in simulation (Figure S13b). There  
400 was no clear relationship between the convergence time and initial values for the MCMC algorithm when  
401 inferring parameters from the simulation in Figure 2d (Figure S14). Initial values near real values did  
402 not guarantee faster convergence. On the contrary, the algorithm converged after fewer iterations when  
403 the initial values of  $\alpha$  were more than 10 times larger than the real value (Figure S14b). This might  
404 result from the slower convergence of the sampling chain of  $\sigma$ , which dominated the overall converging  
405 time, and fluctuations in the chains caused by the augmentation of data points. In general, the accuracy  
406 of estimating  $\sigma$  improved significantly when more data points were used in the inference procedure, while  
407 the accuracy of estimating  $\alpha$  was less affected by the density of data (Figures S15,16). (See Appendix  
408 E in Supporting Information for more details.) Our comparison with the method of Hanks *et al.* (2015)  
409 reveals that our method shows that our method is more precise (e.g. the posterior standard deviation of  
410  $\alpha$  was more than an order of magnitude smaller than the equivalent measure from the model of Hanks  
411 *et al.* (2015)) on data simulated from our model.

## 412 3.2 Applying MCMC inference on the mule deer data

413 When fitting the IRG Model to the deer data, the MCMC algorithm converged for 27 of the 28 individuals,  
414 whereas the NDVI Model only converged for 9. This gives some preliminary indication that the NDVI



415 model is not a good model for these data. In the 9 cases where both the NDVI and IRG Models led to  
416 convergent MCMC results (e.g. No. 4, Table 1), the DIC was used to determine the better model. This  
417 reveals that the NDVI Model is a better fit for one of the deer (No. 10) and the IRG Model for the other  
418 eight (Table 1), confirming our preliminary indications. For those cases where MCMC chains converged,  
419 we used the posterior mean of  $\beta$  of the best fit model to calculate the simulated departure dates of  
420 migration, shown together with the real departure dates in Table 1. The estimated departure dates were  
421 defined to be the dates when a switch of movement centre had occurred according to the RSF. The  
422 observed departure dates were the dates when locations occurring outside a patch and towards another  
423 patch were first observed. The agreement was generally good, suggesting that, when a model can be  
424 fitted to the data, the timing of migration can be explained by a simple trade-off between relative NDVI  
425 or IRG values and the distance between successive patches, but usually IRG is a better measurement to  
426 use (Figure 5).

427 However, for one individual (No. 21, Table 1), the inference procedure estimated that the individual  
428 left a patch, and was attracted to it again for a very short time soon after migrating. This is probably  
429 not a behavioural feature, though, since it was not observed in the data. Rather, this is likely to be a  
430 quirk resulting from small up-and-down fluctuation in the IRG around the time of migration.

431 Figure 4a gives an example migratory path of an individual, which can be compared with the  
432 simulated path from the best-fit model (Figure 4b). Supplementary Video SV1 shows an animation of  
433 both these paths superimposed (red dots are the observed locations and blue are simulated). In the  
434 best-fit model, the attraction centre changed from  $\mu_1$  to  $\mu_2$  on the 126th day of the year (Table 1). This  
435 is very close to the actual date of departure from winter range observed from data and is marked by an  
436 arrow in Figure 4c. Finally, the posterior distributions for this example are given in Figure 4d, where  
437 we observe a significant difference between the posterior mean and zero for each parameter ( $p < 10^{-5}$ ).

## 438 4 Discussion

439 We have constructed models of resource selection in continuous time, based on a switching random walk  
440 process, and parameterised using a Bayesian Monte Carlo algorithm. We have demonstrated that our  
441 method can be applied in a wide range of scenarios, including both movements driven by the evaluation  
442 of resources at the landscape scale, and those that simply follow local resource gradients. In broad terms,  
443 our model animals first (a) assess location and quality of different resources (either proximately or across  
444 the whole landscape), to decide the general direction of movement, then (b) move according to a process  
445 that incorporates not only the resource-based decision, but also some stochasticity to account for any  
446 unknown factors governing movement. Such stochastic continuous-time models allow us to make use  
447 of well-developed, flexible inference procedures (Blackwell *et al.* (2016)). When applying our inference

No.	simulated departure date (the NDVI Model)	simulated departure date (the IRG Model)	observed departure date	$\Delta$ DIC
4	128	<b>126</b>	125	167.58
6	138	<b>134</b>	133	117.25
10	<b>124,132</b>	124, 132	123,128	141.79
11	127,152	<b>126, 151</b>	125,149	182.79
13	148	<b>142</b>	140	75.53
18	130,158	<b>124,158</b>	123,157	97.84
20	135,146	<b>134,146</b>	133,145	54.27
21	152	<b>149,150,150</b>	144	185.09
25	142	<b>141</b>	140	496.41
1	–	100,151	132,150	
2	–	153	147	
3	–	126,158	125,154	
5	–	143	142	
7	–	151	148	
8	–	157	154	
9	–	147	144	
12	–	146	140	
14	–	140	139	
15	–	149	139	
16	–	101,138,148	112,136,147	
17	–	142	139	
22	–	149	146	
23	–	134	133	
24	–	140	139	
26	–	125,141	124,137	
27	–	148	128	
28	–	134	131	

Table 1: The comparison of models for the mule deer data. For cases where the switch of movement centre occurred on two days, the numbers for the Julian dates are separated with a comma. Figures in bold indicate the model with smaller DIC value on that individual.

448 algorithm to simulated data, where all the parameter values governing the movement are known, we  
449 were able to estimate the input parameters, including those governing the trade-off between maximising  
450 resource intake and minimising travel costs, with good accuracy. As such, our method can reliably  
451 capture important aspects of the processes underlying movement decisions.

452 Our framework can be viewed as generalising ideas from several previous studies. The study of  
453 Hanks *et al.* (2015) developed a gradient following algorithm that allows for behavioural switches between  
454 observed locations. This is similar to our gradient-following model, yet relies upon discretising the path  
455 into presence or absence on pixels of a square lattice, whereas ours considers the full, continuous path. A  
456 comparison of our method with that of Hanks *et al.* (2015) on a path simulated from our model revealed  
457 that in this case our method is more precise. However, this is not surprising, as we would expect a better  
458 fit from a model that accurately mimics the true movement process. Employing the model in Hanks *et al.*  
459 (2015), Brennan *et al.* (2018) attempted better understanding of habitat preferences by considering the  
460 impact of corridor choice on speed during migration, while we focus on the movement direction decided  
461 by identifying the destination. Breed *et al.* (2017) gives a model of patch-to-patch movement, based on  
462 a switching OU process, but where only the decision to *leave* a patch depends on environmental features.  
463 Ours generalises this by modelling patch-to-patch movements as dependent on the source patch, the  
464 target patch, and the distance between them.

465 In this study, we have examined gradient-following and patch selection models separately. In prin-  
466 ciple, it would be possible to combine these. One would begin by writing down a stochastic differential  
467 equation that combines the processes in Equations (1) and (5) then derive from these the distribution of  
468 movement across a short time-interval (similar to Equations 2 and 6). This distribution can then be fed  
469 into the inference algorithm described in Section 2.2. Of course, such a model would be more complex  
470 than those described here, so would likely require more running time and a good dataset to achieve  
471 accurate inference.

472 We have focused on a few simple situations where the main factor in movement decisions is resource  
473 quality. However, being based on a resource selection function (RSF), our framework has potential  
474 to incorporate as wide a variety of movement covariates as in traditional resource- or step-selection  
475 analysis. For example, topography (Potts *et al.* (2014c)), interactions between animals (Vanak *et al.*  
476 (2013)), memory effects (Merkle *et al.* (2017)), barriers and corridors (Panzacchi *et al.* (2016)) have  
477 all been incorporated into step-selection analysis and so could, in principle, be incorporated into our  
478 modelling framework.

479 Classical step selection analysis tends to examine resource selection from one measured location to  
480 the next (Thurfjell *et al.* (2014)). However, it has occasionally been used to measure patch-to-patch  
481 movements (e.g. Merkle *et al.* (2014)) and this is similar in flavour to our patch-based models. On the  
482 other hand, our raster-based models are more appropriate for studies where distinct patches are less

483 clear. In this case, it is often far less clear what spatio-temporal scales are being used by the animal  
484 to make selection decisions. However, to use step selection analysis, one is forced either to make an  
485 *a priori* choice of scale or perform a complicated model selection procedure (Bastille-Rousseau *et al.*  
486 (2018)). Our approach has the advantage that the spatio-temporal scale of decision-making emerges  
487 from the interface between the landscape and the movement processes, and is not tied to the frequency  
488 of the location data. In addition, the flexibility of the switching random walk framework means that  
489 our models have potential to include variation in behavioural modes in different parts of space (Harris &  
490 Blackwell (2013)) or in different states such as encamped and exploratory states (Morales *et al.* (2004)).

491 Indeed, the switching OU framework used here has recently been used to model state-switching  
492 correlated random walks (Michelot & Blackwell (2019)). This makes use of the same code base as the  
493 code used for inference here, so is ready to be combined with our models. Furthermore, although we  
494 have developed our techniques for use with single animal tracks, there is ongoing work to incorporate  
495 collective movement and animal interactions into the switching OU framework (Niu *et al.* (2016)), which  
496 could be important for the study of mule deer (Sawyer *et al.*, 2006). Therefore we intend for future  
497 studies to factor group movement into continuous-time resource selection.

498 To demonstrate how our techniques can be applied to real data, we assessed the underlying mecha-  
499 nisms behind migration in mule deer. Our results support two hypotheses related to migration. First is  
500 the Forage Maturation Hypothesis, which posits that as plants grow herbivores face a trade-off between  
501 forage quality and quantity and therefore will select forage patches at intermediate stages of growth  
502 (Fryxell (1991), Hebblewhite *et al.* (2008)). Second is the Green Wave Hypothesis (Drent *et al.* (1978)),  
503 which is the spatial manifestation of the Forage Maturation Hypothesis (Merkle *et al.* (2016)). The  
504 Green Wave Hypothesis posits that animals migrate to acquire high-quality foods that are propagated  
505 as resource waves in space and time. For migratory herbivores, resource waves often correspond to the  
506 onset of spring along the migration route (Aikens *et al.* (2017)). The Green Wave Hypothesis has been  
507 tested in a variety of species of both birds and mammals (van Wijk *et al.* (2012), Kölzsch *et al.* (2015),  
508 Merkle *et al.* (2016)).

509 We used a model where the animal trades-off the relative quality of resources at source and target  
510 locations with the effort of moving from one to the other (using distance between patches as a proxy for  
511 effort). We used two proxies for resource quality of a patch: NDVI and IRG. The former represents an  
512 index of green forage biomass, and the latter represents an index of intermediate forage biomass (Bischof  
513 *et al.* (2012)). Similar to the findings of Aikens *et al.* (2017) and Merkle *et al.* (2016) for mule deer, our  
514 results suggest that the movements of most individual mule deer could be explained by IRG. The use  
515 of growth *rate* (IRG), rather than *absolute* quality of biomass (NDVI) suggests that movement is caused  
516 predominantly by the *process* of change, i.e. green-up. This is consistent with the idea of ‘surfing a green  
517 wave’: tracking the places at which rate of change is greatest. Note that for one individual, however,

518 the model using NDVI did fit better (No. 10, Table 1). Nonetheless, the resulting best-fit models  
519 tend to anticipate the migratory times well (Table 1, Figure 5), and simulated paths are qualitatively  
520 similar to the real paths (Supplementary Video SV1). Therefore our method has potential to test various  
521 hypotheses explaining migratory movement, and resource-driven movement in general.

522 In conclusion, we have developed a flexible framework for continuous-time inference of resource  
523 selection decisions in moving animals. The switching random-walk model, combined with Bayesian  
524 Monte Carlo inference, generalises several previous methods, and has potential to be extended to a wide  
525 range of scenarios. Whilst the inference speed is sufficient for paths of several hundred data-points, it  
526 may prove too slow with modern-era tracks that can contain millions (Hays *et al.* (2016)). Therefore a  
527 significant future challenge would be to develop either methods for speeding-up inference significantly  
528 (Kálmán filters may be an appropriate technique here: e.g. Fleming *et al.* (2017)), or rarefying high-  
529 resolution data to extract key locations in the path that represent animal decisions (Potts *et al.* (2018)).  
530 Indeed, the key limiting factor for speed is the number of MCMC samples required for convergence.  
531 Better data, sampled at behaviourally-meaningful locations, may have a clearer signal thus requiring  
532 less time for the MCMC procedure to converge, even if the datasets might be larger. In summary,  
533 our framework represents an important methodological step in understanding resource-use decisions by  
534 moving animals.

## 535 Acknowledgements

536 This work is supported in part by a scholarship provided by Ministry of Education of Taiwan (YW).  
537 We thank Mu Niu and Théo Michelot for contributions to the code that we adapted in building our  
538 inference procedure. Collection of the mule deer data was supported by the Wyoming Game and Fish  
539 Department, the Nature Conservancy of Wyoming, and the Knobloch Family Foundation. We thank two  
540 anonymous reviewers, an associate editor and the senior editor, Bob O'Hara, for comments that have  
541 helped improve the manuscript.

## 542 Author Contributions

543 JRP, PGB conceived and designed the research; YW performed the research; JAM provided data; PGB  
544 provided code for inference; YW, JRP led the writing of the manuscript. All authors contributed critically  
545 to the drafts and gave final approval for publication.

## 546 Data Accessibility

547 Data used in this manuscript are archived on Data Dryad at doi:10.5061/dryad.f9p3dq4.

## 548 References

549 1.

550 Aikens, E.O., Kauffman, M.J., Merkle, J.A., Dwinell, S.P., Fralick, G.L. & Monteith, K.L. (2017).  
551 The greenscape shapes surfing of resource waves in a large migratory herbivore. *Ecol. Lett.*, 20,  
552 741–750.

553 2.

554 Avgar, T., Lele, S.R., Keim, J.L. & Boyce, M.S. (2017). Relative Selection Strength: Quantifying  
555 effect size in habitat- and step-selection inference. *Ecol Evol*, 7, 5322–5330.

556 3.

557 Avgar, T., Potts, J.R., Lewis, M.A. & Boyce, M.S. (2016). Integrated step selection analysis: bridging  
558 the gap between resource selection and animal movement. *Methods Ecol Evol*, 7, 619–630.

559 4.

560 Bastille-Rousseau, G., Murray, D.L., Schaefer, J.A., Lewis, M.A., Mahoney, S.P. & Potts, J.R. (2018).  
561 Spatial scales of habitat selection decisions: implications for telemetry-based movement modelling.  
562 *Ecography*, 41, 437–443.

563 5.

564 Bastille-Rousseau, G., Potts, J.R., Schaefer, J.A., Lewis, M.A., Ellington, E., Rayl, N., Mahoney,  
565 S. & Murray, D.L. (2015). Unveiling trade-offs in resource selection of migratory caribou using a  
566 mechanistic movement model of availability. *Ecography*, 38, 1049–1059.

567 6.

568 Bischof, R., Loe, L.E., Meisingset, E.L., Zimmermann, B., Van Moorter, B. & Mysterud, A. (2012).  
569 A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? *Am.*  
570 *Nat.*, 180, 407–424.

571 7.

572 Blackwell, P.G. (1997). Random diffusion models for animal movement. *Ecol Modell*, 100, 87–102.

573 8.

574 Blackwell, P.G. (2003). Bayesian inference for Markov processes with diffusion and discrete compo-  
575 nents. *Biometrika*, 90, 613–627.

- 576 9.  
577 Blackwell, P.G., Niu, M., Lambert, M.S. & LaPoint, S.D. (2016). Exact Bayesian inference for animal  
578 movement in continuous time. *Methods Ecol Evol*, 7, 184–195.
- 579 10.  
580 Boyce, M.S. (2006). Scale for resource selection functions. *Diversity Distrib.*, 12, 269–276.
- 581 11.  
582 Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K. (2002). Evaluating resource selection  
583 functions. *Ecol Modell*, 157, 281–300.
- 584 12.  
585 Bracis, C. & Mueller, T. (2017). Memory, not just perception, plays an important role in terrestrial  
586 mammalian migration. *Proc. R. Soc. B*, 284, 20170449.
- 587 13.  
588 Breed, G.A., Golson, E.A. & Tinker, M.T. (2017). Predicting animal home-range structure and  
589 transitions using a multistate Ornstein-Uhlenbeck biased random walk. *Ecology*, 98, 32–47.
- 590 14.  
591 Brennan, A., Hanks, E.M., Merkle, J.A., Cole, E.K., Dewey, S.R., Courtemanch, A.B. & Cross, P.C.  
592 (2018). Examining speed versus selection in connectivity models using elk migration as an example.  
593 *Landscape Ecol*, 33, 955–968.
- 594 15.  
595 Cagnacci, F., Boitani, L., Powell, R.A. & Boyce, M.S. (2010). Animal ecology meets GPS-based  
596 radiotelemetry: a perfect storm of opportunities and challenges. *Phil. Tran. R. Soc. B*, 365, 2157–  
597 2162.
- 598 16.  
599 Chetkiewicz, C.L.B. & Boyce, M.S. (2009). Use of resource selection functions to identify conservation  
600 corridors. *J. Appl. Ecol.*, 46, 1036–1047.
- 601 17.  
602 Drent, R., Ebbinge, B. & Weijand, B. (1978). Balancing the energy budgets of arctic-breeding geese  
603 throughout the annual cycle: a progress report. *Verh. Ornithol. Ges. Bayern.*, 23, 239–264.
- 604 18.  
605 Fleming, C.H., Sheldon, D., Gurarie, E., Fagan, W.F., LaPoint, S. & Calabrese, J.M. (2017). Kálmán  
606 filters for continuous-time movement models. *Ecol. Inform.*, 40, 8–21.

- 607 19.  
608 Ford, R.G. (1983). Home range in a patchy environment: optimal foraging predictions. *Integr. Comp.*  
609 *Biol.*, 23, 315–326.
- 610 20.  
611 Forester, J., Im, H. & Rathouz, P. (2009). Accounting for animal movement in estimation of resource  
612 selection functions: sampling and data analysis. *Ecology*, 90, 3554–3565.
- 613 21.  
614 Fortin, D., Beyer, H., Boyce, M.S., Smith, D., Duchesne, T. & Mao, J.S. (2005). Wolves influence elk  
615 movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86, 1320–1330.
- 616 22.  
617 Fortin, D., Fryxell, J.M. & Pilote, R. (2002). The temporal scale of foraging decisions in bison. *Ecology*,  
618 83, 970–982.
- 619 23.  
620 Fryxell, J.M. (1991). Forage quality and aggregation by large herbivores. *Am. Nat.*, 138, 478–498.
- 621 24.  
622 Hanks, E.M., Hooten, M.B. & Alldredge, M.W. (2015). Continuous-time discrete-space models for  
623 animal movement. *Ann. Appl. Stat.*, 9, 145–165.
- 624 25.  
625 Hanks, E.M., Hooten, M.B., Johnson, D.S. & Sterling, J.T. (2011). Velocity-based movement modeling  
626 for individual and population level inference. *PLOS ONE*, 6, e22795.
- 627 26.  
628 Harris, K.J. & Blackwell, P.G. (2013). Flexible continuous-time modelling for heterogeneous animal  
629 movement. *Ecol Modell*, 255, 29–37.
- 630 27.  
631 Hays, G., Ferreira, L., Sequeira, A., Meekan, M., Duarte, C., Bailey, H., Bailleul, F., Bowen, W.,  
632 Caley, M. & Costa, D. (2016). Key questions in marine megafauna movement ecology. *Trends Ecol.*  
633 *Evol.*, 31, 463–475.
- 634 28.  
635 Hebblewhite, M., Merrill, E. & McDermid, G. (2008). A multi-scale test of the forage maturation  
636 hypothesis in a partially migratory ungulate population. *Ecol. Monogr.*, 78, 141–166.



637 29.

638 Hooten, M.B., Johnson, D.S., Hanks, E.M. & Lowry, J.H. (2010). Agent-based inference for animal  
639 movement and selection. *J Agric Biol Environ Stat*, 15, 523–538.

640 30.

641 Illius, A.W., Duncan, P., Richard, C. & Mesochina, P. (2002). Mechanisms of functional response and  
642 resource exploitation in browsing roe deer. *J. Anim. Ecol.*, 71, 723–734.

643 31.

644 Johnson, D.S., Thomas, D.L., Ver Hoef, J.M. & Christ, A. (2008). A general framework for the  
645 analysis of animal resource selection from telemetry data. *Biometrics*, 64, 968–976.

646 32.

647 Kölzsch, A., Bauer, S., Boer, R., Griffin, L., Cabot, D., Exo, K.M., van der Jeugd, H.P. & Nolet,  
648 B.A. (2015). Forecasting spring from afar? Timing of migration and predictability of phenology along  
649 different migration routes of an avian herbivore. *J. Anim. Ecol.*, 84, 272–283.

650 33.

651 Lendrum, P.E., Anderson Jr., C.R., Long, R.A., Kie, J.G. & Bowyer, R.T. (2012). Habitat selection  
652 by mule deer during migration: effects of landscape structure and natural-gas development. *Ecosphere*,  
653 3, 82.

654 34.

655 Manly, B., McDonald, L., Thomas, D., McDonald, T. & Erickson, W. (2002). *Resource selection by*  
656 *animals: statistical analysis and design for field studies*. 2nd edn. Springer Netherlands.

657 35.

658 McClintock, B.T., Johnson, D.S., Hooten, M.B., Ver Hoef, J.M. & Morales, J.M. (2014). When to be  
659 discrete: the importance of time formulation in understanding animal movement. *Movement Ecol*, 2.

660 36.

661 McLoughlin, P.D., Morris, D.W., Fortin, D., Vander Wal, E. & Contasti, A.L. (2010). Considering  
662 ecological dynamics in resource selection functions. *J. Anim. Ecol.*, 79, 4–12.

663 37.

664 Merkle, J.A., Cross, P., Scurlock, B.M., Cole, E., Courtemanch, A., Dewey, S. & Kauffman, M.J.  
665 (2018). Linking spring phenology with mechanistic models of host movement to predict disease trans-  
666 mission risk. *J. Appl. Ecol.*, 55, 810–819.

- 667 38.  
668 Merkle, J.A., Fortin, D. & Morales, J.M. (2014). A memory-based foraging tactic reveals an adaptive  
669 mechanism for restricted space use. *Ecol Lett*, 17, 924–931.
- 670 39.  
671 Merkle, J.A., Monteith, K.L., Aikens, E.O., Hayes, M.M., Hersey, K.R., Middleton, A.D., Oates, B.A.,  
672 Sawyer, H., Scurlock, B.M. & Kauffman, M.J. (2016). Large herbivores surf waves of green-up during  
673 spring. *Proc. R. Soc. B*, 283, 20160456.
- 674 40.  
675 Merkle, J.A., Potts, J.R. & Fortin, D. (2017). Energy benefits and emergent space use patterns of an  
676 empirically parameterized model of memory-based patch selection. *Oikos*, 126.
- 677 41.  
678 Michelot, T. & Blackwell, P.G. (2019). State-switching continuous-time correlated random walks.  
679 *Methods in Ecology and Evolution*.
- 680 42.  
681 Michelot, T., Blackwell, P.G. & Matthiopoulos, J. (2018). Linking resource selection and step selection  
682 models for habitat preferences in animals. *Ecology*. Accepted Author Manuscript.
- 683 43.  
684 Mitchell, M.S. & Powell, R.A. (2004). A mechanistic home range model for optimal use of spatially  
685 distributed resources. *Ecol. Modell.*, 177, 209–232.
- 686 44.  
687 Mitchell, M.S. & Powell, R.A. (2007). Optimal use of resources structures home ranges and spatial  
688 distribution of black bears. *Anim. Behav.*, 74, 219–230.
- 689 45.  
690 Moorcroft, P. & Barnett, A. (2008). Mechanistic home range models and resource selection analysis:  
691 a reconciliation and unification. *Ecology*, 89, 1112–1119.
- 692 46.  
693 Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E. & Fryxell, J.M. (2004). Extracting more out  
694 of relocation data: building movement models as mixtures of random walks. *Ecology*, 85, 2436–2445.
- 695 47.  
696 Niu, M., Blackwell, P.G. & Skarin, A. (2016). Modeling interdependent animal movement in continuous  
697 time. *Biometrics*, 72, 315–324.

- 698 48.  
699 Panzacchi, M., Van Moorter, B., Strand, O., Saerens, M., Kivimäki, I., St. Clair, C.C., Herfindal, I.  
700 & Boitani, L. (2016). Predicting the *continuum* between corridors and barriers to animal movements  
701 using Step Selection Functions and Randomized Shortest Paths. *J. Anim. Ecol.*, 85, 32–42.
- 702 49.  
703 Potts, J.R., Bastille-Rousseau, G., Murray, D.L., Schaefer, J.A. & Lewis, M.A. (2014a). Predicting  
704 local and non-local effects of resources on animal space use using a mechanistic step selection model.  
705 *Methods Ecol Evol*, 5, 253–262.
- 706 50.  
707 Potts, J.R., Börger, L., Scantlebury, D.M., Bennett, N.C., Alagaili, A. & Wilson, R.P. (2018). Finding  
708 turning-points in ultra-high-resolution animal movement data. *Methods Ecol. Evol.*, Accepted Author  
709 Manuscript.
- 710 51.  
711 Potts, J.R., Mokcross, K. & Lewis, M.A. (2014b). A unifying framework for quantifying the nature  
712 of animal interactions. *J. R. Soc. Interface*, 11, 20140333.
- 713 52.  
714 Potts, J.R., Mokcross, K., Stouffer, P. & Lewis, M.A. (2014c). Step selection techniques uncover the  
715 environmental predictors of space use patterns in flocks of amazonian birds. *Ecol Evol*, 4, 4578–4588.
- 716 53.  
717 Preisler, H.K., Ager, A.A., Johnson, B.K. & Kie, J.G. (2004). Modeling animal movements using  
718 stochastic differential equations. *Environmetrics*, 15, 643–657.
- 719 54.  
720 Preisler, H.K., Ager, A.A. & Wisdom, M.J. (2013). Analyzing animal movement patterns using  
721 potential functions. *Ecosphere*, 4, 1–13.
- 722 55.  
723 Sawyer, H. & Kauffman, M.J. (2011). Stopover ecology of a migratory ungulate. *J. Anim. Ecol.*, 80,  
724 1078–1087.
- 725 56.  
726 Sawyer, H., Nielson, R.M., Lindzey, F. & McDONALD, L.L. (2006). Winter habitat selection of mule  
727 deer before and during development of a natural gas field. *The Journal of Wildlife Management*, 70,  
728 396–403.

729 57.

730 Spiegelhalter, D.J., Best, N.G., Carlin, B.P. & Van Der Linde, A. (2002). Bayesian measures of model  
731 complexity and fit. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 64,  
732 583–639.

733 58.

734 Thurfjell, H., Ciuti, S. & Boyce, M.S. (2014). Applications of step-selection functions in ecology and  
735 conservation. *Movement Ecol*, 2, 4.

736 59.

737 Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M.S. & Gaillard, J.M. (2009).  
738 Memory keeps you at home: a mechanistic model for home range emergence. *Oikos*, 118, 641–652.

739 60.

740 Vanak, A., Fortin, D., Thakera, M., Ogdene, M., Owena, C., Greatwood, S. & Slotow, R. (2013).  
741 Moving to stay in place - behavioral mechanisms for coexistence of african large carnivores. *Ecology*,  
742 94, 2619–2613.

743 61.

744 van Wijk, R.E., Kölzsch, A., Kruckenberg, H., Ebbinge, B.S., Müskens, G.J. & Nolet, B.A. (2012).  
745 Individually tracked geese follow peaks of temperature acceleration during spring migration. *Oikos*,  
746 121, 655–664.

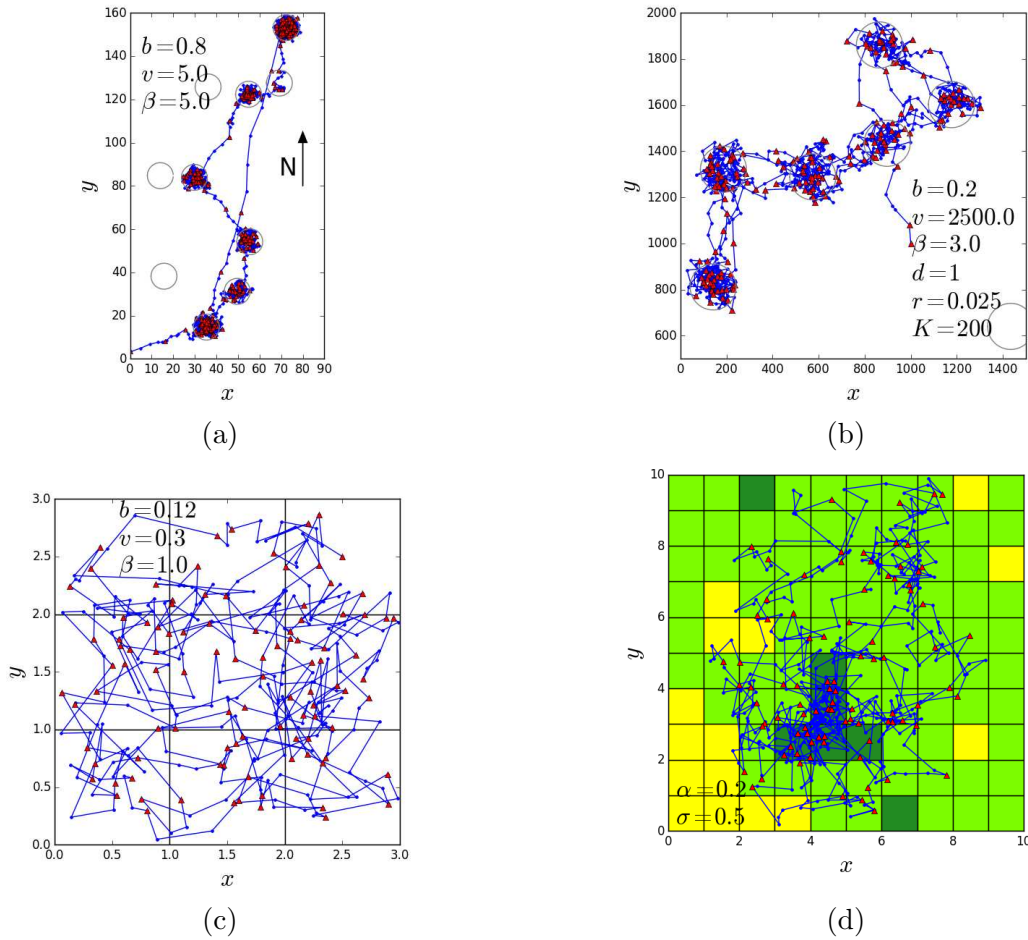


Figure 2: Simulations corresponding to (a) the Migration model (Section 2.3.1), (b) the Patch depletion/renewal model (Section 2.3.2), (c) the Raster depletion/renewal model (Section 2.3.3), and (d) the Gradient following model (Section 2.3.4). The blue dots and line segments show the whole set of data points, and the red triangles are those used in the MCMC algorithm. (a) A simulated trajectory of migration during one year using the OU process in Equation (2) and RSF in Equation (10) with resource quality in Equation (11). The animal moves towards the north from patches in the south and comes back to the south. (b) A simulated trajectory in a patchy landscape with the resource depletion-renewal model. The resource quality changes according to Equation (12) and the movement process is given by Equations (2) and (10). (c) A simulated trajectory in a homogeneous raster landscape with the resource depletion-renewal model. The resource quality changes according to Equation (12) and the movement process is given by Equations (2) and (10). (d) A simulation of movement following resource gradient, according to Equations (6) and (7). The different colours in the landscape represent different resource types. Dark green, light green and yellow stand for high, medium and low resource quality respectively.

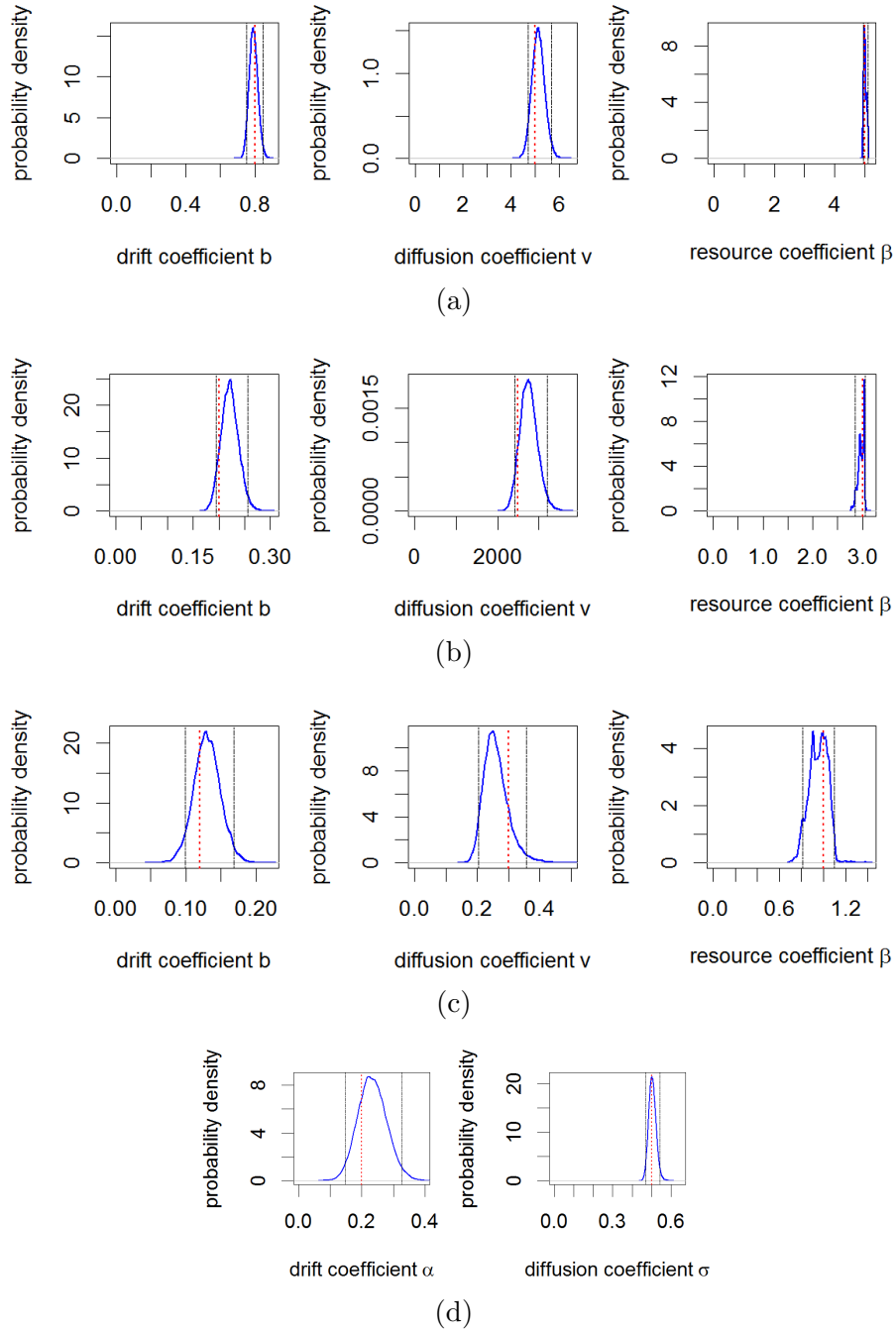


Figure 3: Posterior distributions of parameters obtained by applying the MCMC inference procedure to the simulated trajectories in Figure 2. Red dotted lines indicate real values used in simulations and black dashed lines shows 95% quantile intervals. Panel (a) uses the Migration model (Figure 2a). Panel (b) uses the Patch depletion/renewal model (Figure 2b). Panel (c) uses the Raster depletion/renewal model (Figure 2c). Each of (a-c) show the inferred posterior distributions of the movement coefficients,  $b$  and  $v$ , from Equation (2) and the resource coefficient,  $\beta$ , from Equation (10). Panel (d) uses the Gradient following model (Figure 2d) and shows the posterior distribution of the drift and diffusion coefficients ( $\alpha$  and  $\sigma$ , respectively) from Equation (6).

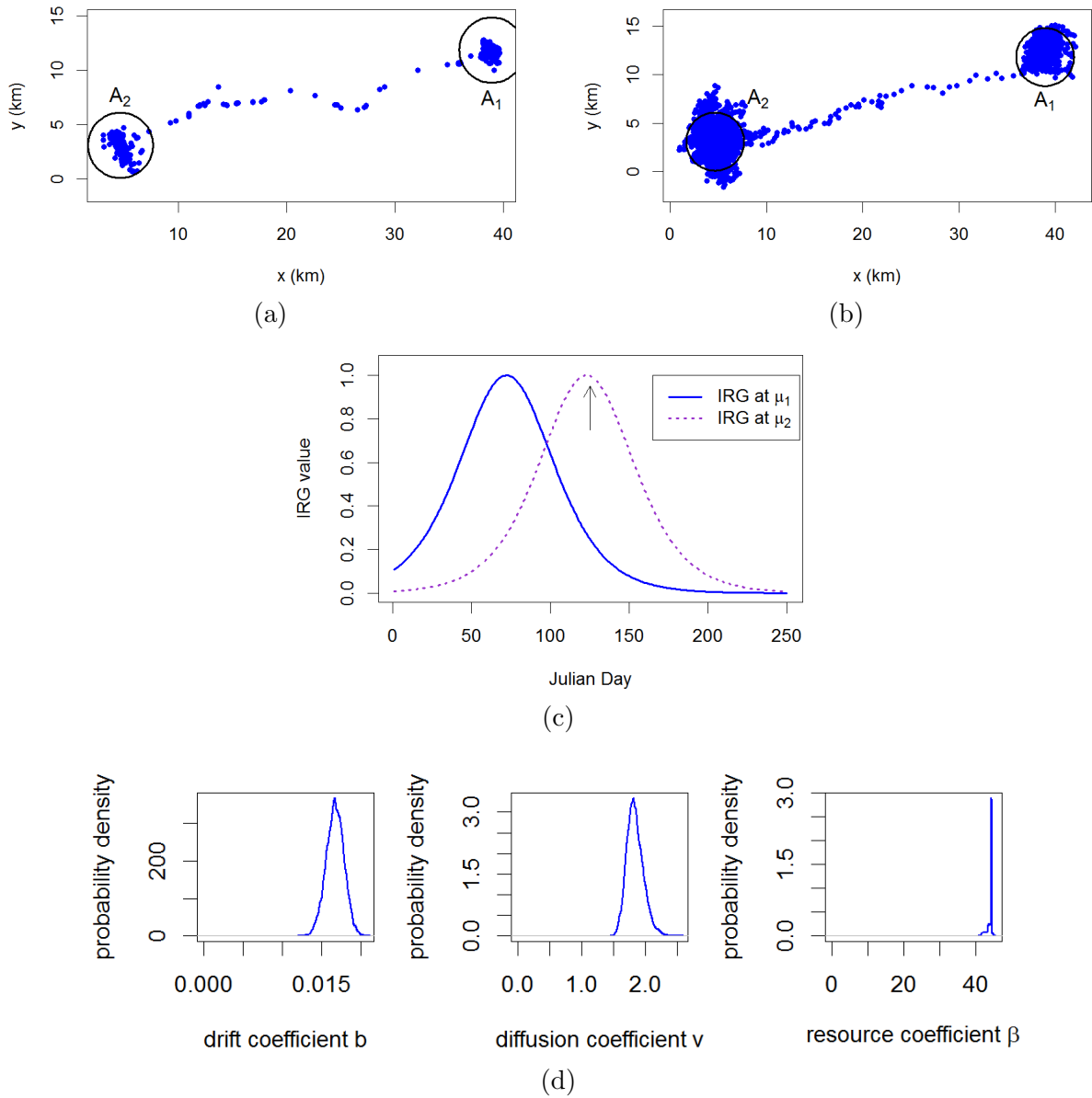


Figure 4: A case study of mule deer data. (a) The migration trajectory of mule deer No. 4. The blue dots are observed locations collected between March and August 2016. The circles  $A_1$  and  $A_2$  are foraging patches where the mule deer spent more than two weeks. (b) A simulated trajectory of mule deer migration, generated using posterior means derived from analysing the data of deer No. 4 with the IRG model. (c) The IRG values at  $\mu_1$  and  $\mu_2$ , the centres of patches  $A_1$  and  $A_2$  illustrated in Figure 4a. The arrow indicates the date when the mule deer left patch  $A_1$ . (d) The posterior distributions derived by applying the MCMC algorithm on the trajectory of mule deer No. 4, shown in Figure 4a, with the IRG model.

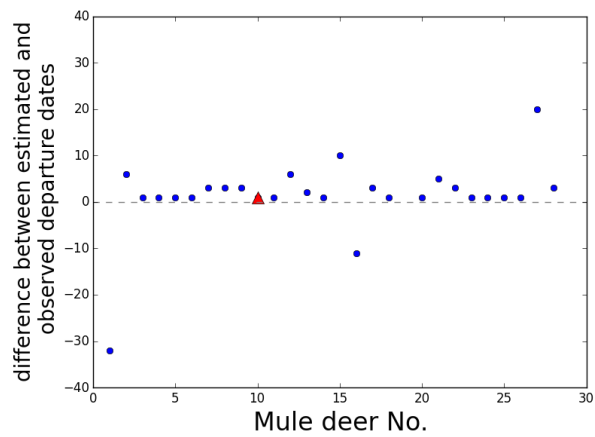


Figure 5: A comparison between the estimated and observed dates when leaving winter ranges. Blue dots show the cases where the IRG Model fitted the data better, while the red triangle represents the case where the NDVI Model was better (No. 10, Table 1). Markers above and below the horizontal dashed line indicate that the estimated departure date was later and earlier than the observed date respectively.