



Flexible continuous-time modelling for heterogeneous animal movement

Keith J. Harris^a, Paul G. Blackwell^{b,*}

^a Infrastructure and Environment Research Division, School of Engineering, University of Glasgow, UK

^b School of Mathematics and Statistics, University of Sheffield, UK

ARTICLE INFO

Article history:

Received 6 August 2012

Received in revised form 21 January 2013

Accepted 23 January 2013

Available online 1 March 2013

Keywords:

Animal movement
Continuous time
Diffusion process
Spatial heterogeneity

ABSTRACT

We describe a flexible class of continuous-time models for animal movement, allowing movement behaviour to depend on location in terms of a discrete set of regions and also on an underlying behavioural state. We demonstrate the ability of these models to represent complex behaviour and spatial heterogeneity, as found in real movement studies, while retaining tractability and the conceptual advantages of a continuous-time formulation. We discuss the relationship between the models defined here and a range of important applications, both when movement behaviour is the main focus and when it is essentially a nuisance process, for example in spatially explicit capture–recapture.

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1. Introduction

This paper introduces a new continuous-time modelling framework for animal movement, which extends the models introduced by Dunn and Gipson (1977) and Blackwell (1997, 2003) by allowing for spatial heterogeneity. Movement models are important in understanding and analysing movement data from radio-tracking, GPS tags, etc. (e.g. Morales et al., 2004; McClintock et al., 2012), in the analysis of other data that need to take movement into account such as spatially explicit capture–recapture (e.g. Royle and Young, 2008; Tufto et al., 2012), and in formalising conceptual models involving movement, for example in understanding individual habitat use (e.g. Matthiopoulos, 2003).

Modelling movement is challenging because of the need to represent the strong autocorrelation between locations. One general approach that deals with this problem of dependency is to model animal movement in continuous time using a diffusion process like the bivariate Ornstein–Uhlenbeck (OU) process (Dunn and Gipson, 1977), perhaps with some additional underlying discrete behavioural state (Blackwell, 1997, 2003). This approach is limited, however, because it does not allow for the realistic possibility that animals move differently in the different habitats they utilise. Current approaches to including spatial heterogeneity in diffusion models by Ovaskainen (2004) and Ovaskainen et al. (2008) have some attractive features but also some limitations compared

with models described here; see Section 7 for a more detailed comparison. The novel modelling framework for animal movement presented here allows spatial heterogeneity to be incorporated into continuous-time models in a flexible and parsimonious way. These properties also simplify statistical inference, which is not the focus of this paper but is discussed briefly in Section 5.

Part of the motivation for this work is to facilitate thinking about movement in continuous rather than discrete time. In most of the recent literature, animal movement modelling is carried out in discrete time, especially in the context of statistical analysis. Discrete-time models represent the modelled individual's locations only at particular time instants, which are usually regularly spaced in time, and often correspond to the times at which observations have been made (or were intended to be made). Such models may be entirely appropriate if the discrete timescale is behaviourally meaningful, such as modelling daily locations to avoid complex intra-day effects when they are unimportant to the application. Ideally this would involve observations at a fixed time of day; Morales et al. (2004) do essentially this, but the times of their observations may vary by two hours in either direction, “depending on fix availability”, and they then make a linear correction to distance moved. Some studies use less frequent observations instead, for example by taking the ‘best’ of a burst of observations made every few days (Fuller et al., 1998; Martell et al., 2001), in which case a discrete-time model with 1-day time-steps *may* be appropriate, depending on the length of the observation cycle.

Meaningful models that are in a sense discrete-time models can also be obtained as approximations to continuous-time ones. That is, the model can be formulated in continuous time, and then the implied movement properties over particular intervals calculated.

* Corresponding author. Tel.: +44 114 2223719.

E-mail addresses: Keith.Harris@glasgow.ac.uk (K.J. Harris), p.blackwell@sheffield.ac.uk (P.G. Blackwell).

Our emphasis here is not necessarily on the exactness of calculations with continuous-time models, but on the coherence of the underlying description of movement, even if implemented only approximately.

In many cases, however, discrete-time models are formulated on a regular timescale dictated by the observation process, and therefore having no specific behavioural interpretation, though the approximate magnitude of the time interval will typically be chosen to be relevant to the behaviour of interest. There is then no guarantee that they correspond to a meaningful model on any other timescale, often making it impossible to combine data or compare results from different experiments or analyses, even on the same species. The diffusion models cited and developed here should help increase the prospects for coherent movement modelling.

In addition, there are situations where thinking about continuous time is essential. In ‘common sense’ terms, animal movement clearly takes place in continuous time, in that at any given instant, “everybody’s got to be somewhere” (Milligan, 1972); whatever the underlying ‘truth’, it seems natural and meaningful to think about animal locations at any time between observations, in the same way that continuous-time modelling (e.g. using differential equations) is natural in many areas of macroscopic physics. These intermediate locations can be crucial to the scientific questions of interest in a movement study; this is illustrated by recent work using Brownian bridge models to investigate utilisation distributions (Bullard, 1999; Horne et al., 2007), though the models there are much simpler than most of those discussed in the present paper. Of course, it is possible to have some representation of locations at intermediate times within models that are essentially ‘discrete time’, but by definition such representations treat intermediate times differently from those forming the main model, and they are often extremely simplified e.g. linear interpolation (Jonsen et al., 2005).

Throughout this paper, we concentrate on the most common case of two-dimensional movement for our terminology and examples. However, all of the models apply readily to movement in three dimensions, as arises naturally with aquatic or avian tracking, or in one dimension, of increasing importance in analysing depth-only data from diving marine mammals for instance. In fact, the nature of the vertical dimension of movement makes spatial heterogeneity all the more important in such cases.

In Section 2, we introduce our modelling framework, concentrating on spatial heterogeneity in movement; in Section 3 we extend it to allow more general behavioural states. In each case, we illustrate the range of possible movement behaviours that can be represented by showing some realisations of our models relevant to particular kinds of applications. Sections 4–6 address some technicalities relating to simulation, inference and higher-order models, and we then go on to discuss in Section 7 how our models relate to some of the existing models used in the applied literature and show how some of the latter can be represented or approximated by particular cases of our models.

2. Incorporating spatial heterogeneity into models for animal movement

2.1. Behaviour determined by region

We incorporate spatial heterogeneity into models for animal movement by partitioning the environment into a finite set of regions, and allowing the properties of the animal’s movement process to vary with the region it is in at any given instant. We limit ourselves to specific, tractable parametric forms for the process in each region. We do this by extending the continuous time threshold autoregressive models of Brockwell et al. (1991), Brockwell and Hyndman (1992), and Hyndman (1994) into two dimensions. The general p th-order autoregression is discussed in Section 6, but for

the moment we concentrate on the first order ($p = 1$) case, which is sufficient for a wide range of applications.

A discrete-time threshold autoregressive model partitions the real line into l intervals, and the process at time t , X_t , then satisfies one of l autoregressive equations depending on the interval in which X_{t-d} falls, with d a positive integer. The continuous time analogue of this model also partitions the real line into l intervals. However, in this case, the model is a diffusion process $X(t)$ that satisfies one of l stochastic differential equations, the equation satisfied at time t depending on the interval in which $X(t)$ falls. The form of these l SDEs is given by the following equation:

$$dX(t) = (b^{(i)}X(t) + c^{(i)})dt + \sigma^{(i)}dW(t), \quad r_{i-1} < X(t) < r_i,$$

where $-\infty = r_0 < r_1 < \dots < r_l = \infty$, each $\sigma^{(i)} > 0$ and $W(t)$ is standard Brownian motion. Here, if $X(t)$ is in the i th interval, say, then $b^{(i)}$ and $c^{(i)}$ determine the expected change in $X(t)$ over a short time increment, as a linear function of the current value, while $\sigma^{(i)}$ controls the variance about that expected value. Thus each of these l SDEs individually defines a continuous-time autoregressive process of order 1. A precise mathematical definition of the overall process $X(t)$ requires consideration of the behaviour at the boundaries; see Brockwell et al. (1991) for details.

Note that over a period of time spent in the i th interval, the process defined by an equation of the above form is simply a univariate Ornstein-Uhlenbeck process, with

$$X(t+s)|X(s) = x(s) \sim N(\mu + e^{bt}(x(s) - \mu), \Lambda(1 - e^{2bt}))$$

writing $b = b^{(i)}$ and defining $\mu = -c^{(i)}/b^{(i)}$, $\Lambda = -\sigma^{(i)2}/2b^{(i)}$.

These continuous-time threshold models naturally extend into two dimensions by partitioning the real plane into l regions R_1, \dots, R_l and modelling the movement in each region by a different bivariate diffusion process; the same applies in higher dimensions. We can think of this as representing an animal ‘behaving differently’ in different regions cf. the random behavioural switching of Blackwell (1997, 2003). This modelling approach is also an extension of the Dunn and Gipson (1977) model for animal movement, because their model corresponds to the case when the number of regions, l , is one.

In the two-dimensional case, over a time interval spent in the i th region, the process followed is a bivariate OU process, with

$$\mathbf{X}(t+s)|\mathbf{X}(s) = \mathbf{x}(s) \sim N(\boldsymbol{\mu} + e^{Bt}(\mathbf{x}(s) - \boldsymbol{\mu}), \Lambda - e^{Bt}\Lambda e^{B't})$$

where $\boldsymbol{\mu}$ is a 2×1 vector, B , Λ are now 2×2 matrices and B' is the transpose of B ; see Blackwell (1997) for discussion of the interpretation, and constraints on, these parameters.

In some cases it is useful to also allow simpler diffusion models of movement in a particular state; Brownian motion, with or without drift, can be regarded as a limiting case of the above OU process and can be included in these models where appropriate.

2.2. Example: foraging in two neighbouring patches

A simple example of this kind of model can represent the behaviour of an animal that spends its time foraging in two neighbouring habitat patches. (A more realistic representation is given in Section 3.2; the present version is purely illustrative.) A random diffusion that exhibits this behaviour is shown in Fig. 1. We see that in this case the real plane was partitioned into two regions by the vertical line $x = 0$ and that this boundary was crossed three times by the simulated movement pattern. In each region movement was modelled by a single bivariate OU process. The OU process associated with the left hand region had a centre of attraction at $(-2, 0)$, whereas the process associated with the right hand region had one at $(2, 0)$. These centres of attraction can be thought of as representing something that exerts an attracting influence on

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