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Sampling rate effects on measurements of correlated and biased random walks

E.A. Codling[a,*,1], N.A. Hill[b]

[a]Department of Applied Mathematics, University of Leeds, Leeds LS2 9JT, UK
[b]Department of Mathematics, University of Glasgow, Glasgow G12 8QQ, UK

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Abstract

When observing the two-dimensional movement of animals or microorganisms, it is usually necessary to impose a fixed sampling rate, so that observations are made at certain fixed intervals of time and the trajectory is split into a set of discrete steps. A sampling rate that is too small will result in information about the original path and correlation being lost. If random walk models are to be used to predict movement patterns or to estimate parameters to be used in continuum models, then it is essential to be able to quantify and understand the effect of the sampling rate imposed by the observer on real trajectories. We use a velocity jump process with a realistic reorientation model to simulate correlated and biased random walks and investigate the effect of sampling rate on the observed angular deviation, apparent speed and mean turning angle. We discuss a method of estimating the values of the reorientation parameters used in the original random walk from the rediscretized data that assumes a linear relation between sampling time step and the parameter values.

Keywords: Biased random walk; Velocity jump process; Sampling rate; Animal dispersal

1. Introduction

The simple random walk model has been frequently used to describe the movement and dispersal of groups of animals or microorganisms (Skellam, 1951, 1973; Okubo, 1980). Possibly the simplest form of the two-dimensional random walk is when a walker is restricted to changing positions on a square lattice where there is equal probability of moving up, down, left and right at each step. Such a walk is uncorrelated as the direction of movement is completely independent of the previous direction moved and results in *Brownian* motion (Brown, 1828; Einstein, 1906). Bias can be introduced into the random walk by making the probability of moving in one particular direction more likely and a drift in this direction will be observed (Berg, 1983). A problem with these simple uncorrelated models is that they allow for effectively infinite propagation speeds (Okubo, 1980; Othmer et al., 1988), and the resulting diffusion equations are only valid as long time approximations to the true underlying behaviour.

A more realistic random walk model is one that includes correlation between successive steps, so that the random walk is in the *velocity* rather than the position. In one dimension it is possible to set up a simple correlated random walk on a line (*velocity jump process*) and derive the *telegraph equation* to describe the population density (Goldstein, 1951; Kac, 1974; Okubo, 1980). However, a similar method does not work in higher dimensions and it is not possible to derive an equation for the population density directly (Othmer et al., 1988; Hillen and Othmer, 2000; Codling and Hill, 2004).

*Corresponding author. Tel.: +353 91 730400; fax: +353 91 730470.
E-mail addresses: edd.codling@marine.ie (E.A. Codling), n.a.hill@maths.gla.ac.uk (N.A. Hill).
[1]Current address: Department of Zoology, University College Cork, Cork, Ireland

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It is not necessary to restrict the two-dimensional correlated random walk to a lattice and it is more realistic to use a continuous circular probability distribution for the choice of direction at each step. Given such a circular probability distribution for the reorientation at each step, it is possible to calculate the properties of a two-dimensional correlated and *unbiased* random walk at a given time such as the mean squared displacement (Tchen, 1952; Nossal and Weiss, 1974; Kareiva and Shigesada, 1983), the sinuosity or rate of turning (Dunn, 1983; Bovet and Benhamou, 1988), and the mean dispersal distance (Bovet and Benhamou, 1988; McCulloch and Cain, 1989; Byers, 2001; Codling, 2003).

In general however, similar methods do not work with *biased* and correlated two-dimensional random walks and it is much harder to calculate their statistics. Using a linear transport equation to describe the velocity jump process, Othmer et al. (1988) show how it is possible to calculate equations for the spatial moments of a random walk that has separate probability distributions for bias and correlation effects in the reorientation. This method has been extended by Codling and Hill (2004) to include a more realistic reorientation model that implicitly includes bias and correlation effects in the same probability distribution, although this method requires making several moment closure assumptions. A general theory for using velocity jump processes and deriving transport equations is discussed in Hillen and Othmer (2000); Othmer and Hillen (2002) and Hillen (2002).

If such random walk models are to be used to predict or analyse the spatial properties of real animal populations, then it is essential that we use accurate and realistic models for the movement and reorientation of each individual. Both the position jump and velocity jump processes result in discrete step-wise movement paths that are not necessarily realistic. Certain animals have been observed to move in a step-wise fashion, such as ovipositing butterflies moving from site to site (Kareiva and Shigesada, 1983), but most movements are observed to have a more continuous path (e.g. Hill and Häder, 1997). However, when observing and recording the trajectory of an animal it is usually necessary to impose a fixed sampling rate (the number of observations in a given time) or sampling length (the time or distance between successive observations) to discretize the continuous path. The best results will obviously come from observations using the smallest possible sampling lengths but it may not be possible to use such small sampling lengths due to experimental constraints or practical considerations. It is therefore of intrinsic interest to understand how the sampling rate imposed by an observer will affect the properties of the random walk and the subsequent conclusions that may be drawn. In general, by increasing the sampling length, the trajectory will initially appear more random as correlation effects are lost, while smoothing of the path will mean that the apparent speed will also decrease as the total length of the walk decreases. The fact that the apparent randomness in turning increases with sampling length led to the definition of sinuosity (Bovet and Benhamou, 1988) (see Section 4) and has also been exploited by Hill and Häder (1997) in their random walk on a circle (see Section 6). Hill and Häder (1997) used a range of sampling time steps to estimate the reorientation parameters of a continuously turning walk, such as the angular deviation per unit time (or sinuosity) and the amplitude of the mean turning angle (which is used to calculate the mean reorientation time). These parameters can then be used in continuum models for the behaviour of populations of swimming microorganisms where bioconvection patterns occur (Kessler, 1986; Hill et al., 1989; Vincent and Hill, 1996; Hill and Pedley, 2004). However, the method of estimating the parameters used by Hill and Häder (1997) relies on an ad hoc assumption of linear relations between the sampling time step and both the angular deviation and the amplitude of the mean turning angle. At small sampling time steps this is likely to be true but at larger sampling time steps this assumption will not hold, so it is essential to be able to quantify at what point the sampling time step becomes too large.

In this paper we investigate the effect of changing the sampling rate on the observed properties of both biased and unbiased simulated velocity jump processes and in particular how the sampling rate affects the angular deviation (sinuosity) and the apparent speed. We demonstrate that the method of Hill and Häder (1997) to estimate the reorientation parameters of a biased and continuously turning random walk is valid for small sampling time steps, and quantify when the method is likely to fail.

2. Spatial and temporal sampling

We are concerned with discrete *temporal* sampling of the trajectory, i.e. an observation is made every τ_s time units (where τ_s is the *sampling time step* and the *sampling rate* is given by $1/\tau_s$). This is in contrast to discrete *spatial* sampling where a section of the trajectory that is already known is split into steps of a fixed length L, as used by Bovet and Benhamou (1988). In situ observations of the movement of animals and microorganisms are likely to rely on temporal sampling. Spatial sampling can only be used when a sufficient length of the complete trajectory has already been observed and, as the data is purely spatial, it is not possible to observe waiting times or variable speeds of movement that may have occurred in the original movement. In both temporal and spatial sampling, as the sampling time step or length (τ_s or L) increases, an observer will lose more information about