



ELSEVIER

Contents lists available at ScienceDirect

## Journal of Theoretical Biology

journal homepage: [www.elsevier.com/locate/jtbi](http://www.elsevier.com/locate/jtbi)

## On time scale invariance of random walks in confined space

Daniel Bearup<sup>a,\*</sup>, Sergei Petrovskii<sup>b</sup><sup>a</sup> Institute for Chemistry and Biology of the Marine Environment, University of Oldenburg, 26111 Oldenburg, Germany<sup>b</sup> Department of Mathematics, University of Leicester, Leicester LE1 7RH, UK

## HIGHLIGHTS

- We consider the effects of time scale on Brownian random walks in confined space.
- For reflective boundaries the drift and diffusion rates are usually unaffected.
- For other impenetrable boundaries these properties vary with the time step.
- Similar effects are observed for absorbing boundaries.

## ARTICLE INFO

## Article history:

Received 30 June 2014

Received in revised form

21 October 2014

Accepted 21 November 2014

Available online 4 December 2014

## Keywords:

Individual movement

Boundary effect

Self similarity

Brownian motion

Diffusion

## ABSTRACT

Animal movement is often modelled on an individual level using simulated random walks. In such applications it is preferable that the properties of these random walks remain consistent when the choice of time is changed (time scale invariance). While this property is well understood in unbounded space, it has not been studied in detail for random walks in a confined domain. In this work we undertake an investigation of time scale invariance of the drift and diffusion rates of Brownian random walks subject to one of four simple boundary conditions. We find that time scale invariance is lost when the boundary condition is non-conservative, that is when movement (or individuals) is discarded due to boundary encounters. Where possible analytical results are used to describe the limits of the time scaling process, numerical results are then used to characterise the intermediate behaviour.

© 2014 Elsevier Ltd. All rights reserved.

## 1. Introduction

Movement is always present in wild populations. Even species which are usually individually immobile, such as plants or sessile animals, have some means of dispersal in space, i.e. seed dispersal or a motile life stage. Naturally this movement can have significant effects on population dynamics, particularly if movement mediates interactions, such as predation, between species (Murray, 1989; Turchin, 1998; Mendez et al., 2014; Sheratt et al., 1995; Adamson and Morozov, 2012). Consequently it is beneficial, where possible, to incorporate the effects of movement into mathematical models of populations.

One approach to modelling movement attempts to account for all stimuli that may influence an individual's behaviour (Grimm and Railsback, 2005; Moorcroft and Barnett, 2008). These models can be quite complex and may require detailed information about

the individual's environment (Preisler et al., 2013). As such they are typically used to simulate individual movement tracks rather than population level behaviour. For studies of whole populations (consisting of large numbers of individuals) simpler approaches, describing average rather than specific behaviour i.e. mean field models, are usually needed. The diffusion equation is perhaps the most commonly used mean field model (Turchin, 1998; Berg, 1983).

The microscopic theory connecting these approaches is the framework of random walks (Codling et al., 2008); for example, the diffusion equation describes the behaviour of the simplest random walk, Brownian motion. By approximating movement by random walks, with known parameters, it is possible to extract the generic effects of movement. For example, a dispersal rate for the population can be derived and used to parameterise diffusion–reaction equations to model spatiotemporal population dynamics (Mendez et al., 2014; Turchin and Thoeny, 1993). Optimal foraging patterns and encounter rates, with predators or traps, (even in relatively complex environments) have been studied in a similar way (Viswanathan et al., 1999; Bartumeus et al., 2005; Petrovskii et al., 2012; Potts et al., 2014).

\* Corresponding author. Tel.: +49 441 7983 612.

E-mail address: [daniel.bearup@uni-oldenburg.de](mailto:daniel.bearup@uni-oldenburg.de) (D. Bearup).

Many random walk models are implemented in discrete time, that is each step takes a finite, non-zero period of time,  $\Delta t$ . It is clearly preferable that the generic properties of the random walk be insensitive to this parameter (scale invariance). Random walks generated by stable distributions have this property in unbounded space (Sornette, 2003). However, despite the ubiquity of boundaries in nature, the effects of time scaling in confined space have not been extensively studied. The only previous study on this subject that we are aware of, by Hernández Garcia et al. (1987), considers a model system which is not related to animal movement. It demonstrates that random walks with identical characteristics in unbounded space behave measurably differently in a bounded space.

In this paper we undertake a more detailed study of this phenomenon using the drift and diffusion rates of individuals performing a Brownian walk in a bounded space. Section 2 introduces a model framework for individual movement in a bounded space and particularly focuses on how boundaries may be implemented. In a one dimensional system the effects of these boundaries can be described analytically in certain limiting cases. This is discussed in detail in Section 3. Intermediate cases are investigated using numerical simulations. These results are extended to more realistic two dimensional geometries in Section 4. Finally Section 5 summarises these results and discusses their wider relevance.

## 2. Random walks in a bounded space

The size of individuals, relative to the typical dispersal distances, is usually negligible. Consequently we treat an individual's position as a point,  $\mathbf{R}(t) = (x, y)$ , and its movement path as a continuous, curvilinear, track in space. However it is relatively rare for individuals to be monitored in anything approaching real time. Instead an individual's location may be recorded on an hourly, or even daily, basis depending on the species traits. Thus the true path is approximated by a series of line segments  $(\{\Delta \mathbf{r}_i\})$ , Fig. 1, each representing displacement in a fixed time period,  $\Delta t$  (Turchin, 1998). Typically the movement represented by each line segment arises from responses to a multitude of stimuli. Consequently, even if these responses are deterministic, the combined response is likely to be complicated. It is for problems of this type, replacing a complicated deterministic description with a simpler probabilistic one, that statistical mechanics was developed (Balescu, 1975). Thus we simulate movement paths, at a given sampling rate, as random walks by drawing these line segments from a suitably parameterised probability distribution. We will consider Brownian random walks, generated by line segments with normally distributed components, i.e. in two dimensions  $\Delta \mathbf{r} = (\Delta x, \Delta y)$  with  $\Delta x, \Delta y \sim \mathcal{N}(0, \sigma^2)$ .

In this work we are particularly interested in the average movement behaviour of a population of identical individuals

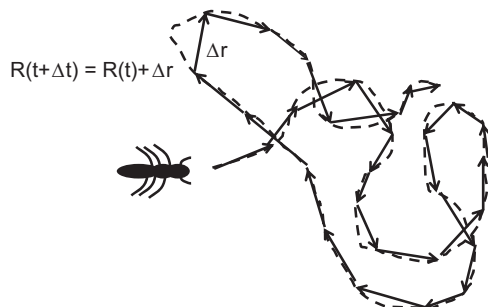


Fig. 1. Discretisation of a continuous path using line segments. An individual's position, denoted by  $\mathbf{R}(t)$ , changes, over a period  $\Delta t$ , by a line segment,  $\Delta \mathbf{r}$ .

performing the same movement pattern. This is typically characterised by two processes: drift, a movement biased in a particular direction, and diffusion, the spread of the population in space, cf. Codling et al. (2008). The rates of these processes can be calculated from the mean and mean square displacements of the individuals as follows. The mean displacement is given by

$$\langle \Delta \mathbf{R}(t) \rangle = \sqrt{\mu_x^2 + \mu_y^2}, \tag{1}$$

where  $\mu_x$  and  $\mu_y$  are the mean displacements in the  $x$  and  $y$  directions respectively. That is

$$\mu_x = \iint_{\Omega} (x - x_0) g(x, y) dx dy, \tag{2}$$

where  $g(x, y)$  is the position probability density function (pdf) of the population and  $\Omega$  is the (two dimensional) domain in which the individuals move ( $\mu_y$  is defined analogously). The mean square displacement is given by

$$\langle \Delta \mathbf{R}^2(t) \rangle = \iint_{\Omega} \left( \sqrt{(x - x_0)^2 + (y - y_0)^2} \right)^2 g(x, y) dx dy. \tag{3}$$

The drift rate,  $A$ , and the diffusion coefficient,  $D$ , in a two dimensional space are related to these properties as follows (Einstein, 1905):

$$A = \frac{\langle \Delta \mathbf{R}(t) \rangle}{t}, \quad D = \frac{\langle \Delta \mathbf{R}^2(t) \rangle - \langle \Delta \mathbf{R}(t) \rangle^2}{4t}. \tag{4}$$

In unbounded space a Brownian random walk has no drift,  $A=0$ , and second moment given by  $\langle \Delta \mathbf{R}^2(t) \rangle = 2n\sigma^2$ , where  $n = t/\Delta t$  and  $\sigma^2$  is the variance of the underlying distribution. Thus the diffusion coefficient is

$$D = \frac{\sigma^2}{2\Delta t}. \tag{5}$$

This relationship allows us to rescale the random walk while preserving  $D$ . For an alternative time scale,  $\tilde{\Delta t} = a\Delta t$ , we obtain the same dispersal rate by taking  $\tilde{\sigma}^2 = a\sigma^2$ .

However, when an individual encounters a boundary, its movement is modified by that encounter, see Fig. 2. For instance, a barrier which the individual cannot cross, requires that the individual remain within the domain. This interaction clearly reduces the total displacement of that individual and thus its effective speed. Alternatively, encountering a trap will cause the individual to be removed from the population. In this case its movement should no longer contribute to the overall dispersal of the population.

Moreover, the impact of these boundaries may not remain the same under the time-scaling process outlined above. For a relatively coarse time scale, with associated relatively large  $\sigma^2$ , each encounter with a boundary must necessarily introduce a

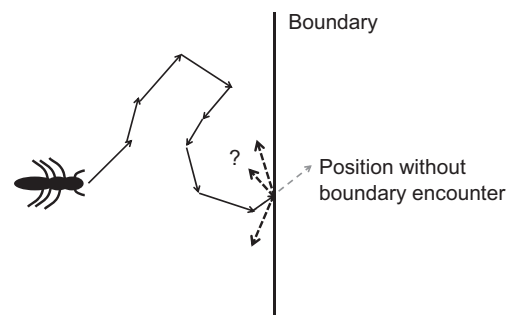


Fig. 2. Sketch of the effect of encountering a boundary. A line segment which crosses the boundary is split into two segments, movement prior to the boundary encounter and movement after this event. The bold arrows show possible movement directions after the encounter.

Download English Version:

<https://daneshyari.com/en/article/6370163>

Download Persian Version:

<https://daneshyari.com/article/6370163>

[Daneshyari.com](https://daneshyari.com)