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REVIEW

Random walk models in biology

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Mathematical modelling of the movement of animals, micro-organisms and cells is of great relevance in the fields of biology, ecology and medicine. Movement models can take many different forms, but the most widely used are based on the extensions of simple random walk processes. In this review paper, our aim is twofold: to introduce the mathematics behind random walks in a straightforward manner and to explain how such models can be used to aid our understanding of biological processes. We introduce the mathematical theory behind the simple random walk and explain how this relates to Brownian motion and diffusive processes in general. We demonstrate how these simple models can be extended to include drift and waiting times or be used to calculate first passage times. We discuss biased random walks and show how hyperbolic models can be used to generate correlated random walks. We cover two main applications of the random walk model. Firstly, we review models and results relating to the movement, dispersal and population redistribution of animals and micro-organisms. This includes direct calculation of mean squared displacement, mean dispersal distance, tortuosity measures, as well as possible limitations of these model approaches. Secondly, oriented movement and chemotaxis models are reviewed. General hyperbolic models based on the linear transport equation are introduced and we show how a reinforced random walk can be used to model movement where the individual changes its environment. We discuss the applications of these models in the context of cell migration leading to blood vessel growth (angiogenesis). Finally, we discuss how the various random walk models and approaches are related and the connections that underpin many of the key processes involved.

Keywords: angiogenesis; chemotaxis; diffusion; dispersal; navigation; random walk

1. INTRODUCTION

The basis of random walk theory can be traced back to the irregular motion of individual pollen particles, famously studied by the botanist Brown (1828), now known as *Brownian motion*. Classical works on probability have been in existence for centuries, so it is somewhat surprising that it was only at the beginning of the twentieth century that a random walk was described in the literature, when the journal *Nature* published a discussion between Pearson (1905) and Rayleigh (1905). Physicists, such as Einstein (1905, 1906) and Smoluchowski (1916), were then drawn to the subject and many important fields, such as random processes, random noise, spectral analysis and stochastic equations, were developed during the course of research on random walks. Random walk theory was further developed with the mean-reversion process (Uhlenbeck & Ornstein 1930).

The first simple models of movement using random walks are uncorrelated and unbiased. In this context, uncorrelated means the direction of movement is completely independent of the previous directions moved: the location after each step taken in the random walk is dependent only on the location in the previous step and the process is Markovian with regard to the location (Weiss 1994). Unbiased means there is no preferred direction: the direction moved at each step is completely random. Assuming that movement in any direction is allowed, this process is essentially Brownian motion and such models can be shown to produce the standard diffusion (or heat) equation.

Correlated random walks (CRWs) involve a correlation between successive step orientations, which is termed 'persistence' (Patlak 1953). This produces a local directional bias: each step tends to point in the same direction as the previous one, although the

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influence of the initial direction of motion progressively diminishes over time and step orientations are uniformly distributed in the long term (Benhamou 2006). Since most animals have a tendency to move forwards (persistence), CRWs have been frequently used to model animal paths in various contexts (e.g. Siniff & Jessen 1969; Skellam 1973; Kareiva & Shigesada 1983; Bovet & Benhamou 1988; Turchin 1998).

A global directional bias can be introduced by making the probability of moving in a certain direction greater, leading to the drift–diffusion (or advection–diffusion) equation. Paths that contain a consistent bias in the preferred direction or towards a given target are termed biased random walks (BRWs), or biased and CRWs (BCRWs) if persistence is also observed. The bias may be due to the fixed external environmental factors (e.g. bottom heavy micro-organisms moving upwards under gyrotaxis; Hill & Häder 1997), to spatially varying factors, such as chemical gradients (Alt 1980; Othmer *et al.* 1988), to mean-reversion mechanisms, such as movement within a home range (Blackwell 1997), or to a choice of direction by individuals at each step (Benhamou 2003). The target direction and strength of bias are not necessarily fixed over the whole path and may vary with location and time (e.g. fish larvae aiming for a reef; Codling *et al.* 2004). When the target direction is fixed for all individuals in the population, it is possible to quantify the direction, functional form and magnitude of the introduced bias (Hill & Häder 1997; Codling & Hill 2005*a*). However, due to the localized directional bias (persistence) in CRW, it is a non-trivial problem to distinguish between the CRW and BCRW when individuals have different target directions (Benhamou 2006).

In the context of population redistribution, uncorrelated random walks are classed as position jump processes (Othmer *et al.* 1988). In general, they are valid only for large time scales and can be thought of as an asymptotic approximation to the true equations governing movement that include correlation effects. In turn, the CRW and BCRW are often referred to as velocity jump processes (since the process involves random changes in velocity) and have been extensively studied leading to a general framework to describe these processes (Othmer *et al.* 1988; Hillen & Othmer 2000; Hillen 2002; Othmer & Hillen 2002).

The random walks discussed in this paper can have either a fixed or variable step length. In the case of a variable step length, only walks where the distribution of step lengths has finite variance (e.g. the exponential distribution) are considered. By the central limit theorem, this means that, after a sufficient length of time, the location coordinate of an individual walker on any axis converges to a Gaussian distribution. A different type of random walk that has generated much recent interest is the *Lévy walk*, in which the distribution of step lengths is heavy tailed, i.e. has infinite variance. In this case, the walk exhibits scale-invariant (i.e. fractal) characteristics. Several recent studies (Viswanathan *et al.* 1996, 2000) have claimed that Lévy walks provide a suitable model for animal movements, although this is still the subject of some controversy (Benhamou 2007; Edwards *et al.* 2007; James & Plank 2007) and they may not be as generally applicable as once thought. In fact, many of the observed patterns that are attributed to Lévy processes can be generated by a simpler composite random walk process where the turning behaviour is spatially dependent (Benichou *et al.* 2006; Benhamou 2007). A full review of Lévy walks is outside the scope of this paper.

Our aim in this review paper is to produce a comprehensive reference that can be used by both mathematicians and biologists. Other books and review papers are available in this field (e.g. Weiss 1994; Turchin 1998; Okubo & Levin 2001; Hillen 2002), but we have yet to find one paper including all the key results while also explaining how the models used in different biological contexts are related to one another. Random walk theory is generally applied in two main biological contexts (although these are by no means exclusive and there are many other relevant contexts): the movement and dispersal of animals and micro-organisms, and chemotaxis models of cell signalling and movement. As we aim to demonstrate in this review, most of the modelling approaches used in these different contexts are based on the same underlying models. The paper is split into two main sections. In §2, the fundamental theory and equations of random walks are introduced, and the central ideas of bias and persistence are developed in some detail. Section 3 reviews the use of random walks in relation to animal and cell movements, by showing how the theory can be used to predict information about rates of spread and tortuosity, and movements that are governed by chemical signalling agents (or other stimuli). We discuss the benefits and limitations of the different approaches used, and the connections that underpin the models and results. We briefly explain some of the more complex models available in the literature, where relevant. Our aim is to be comprehensive but not exhaustive; the reader is referred to key papers for further details and extensions of the basic ideas.

2. FUNDAMENTALS OF RANDOM WALKS

The simple isotropic random walk model (SRW) is the basis of most of the theory of diffusive processes. The walk is isotropic, or unbiased, meaning that the walker is equally likely to move in each possible direction and uncorrelated in direction, meaning that the direction taken at a given time is independent of the direction at all preceding times. Using this model, it is straightforward to derive an equation for the probability density function (PDF) for the location of the walker in one dimension, either by considering the limit as the number of steps gets very large or by using a difference equation (we illustrate these approaches in §§2.1 and 2.2). In §§2.3 and 2.4, we show how the SRW is extended to higher dimensions and, in §2.5, we discuss the general properties of diffusive processes and some limitations of models that use such an approach. In §2.6, we give a simple example of a random walk to a barrier to demonstrate how the SRW can form the basis of more complex models of movement.

An important extension to the SRW is the CRW, in which there is a persistence in the walker's direction of movement. In §2.7, an equation, known as the telegraph equation, describing the simplest one-dimensional CRW is derived and, in §2.8, its relation to the standard diffusion process is discussed. In §2.9, we demonstrate how this analysis can be extended to include bias in the global direction of movement. However, in two (or more) dimensions a similar analysis (for both the unbiased and biased cases) does not lead to a closed-form equation for the probability density in space and time. We discuss this problem and its implications in §2.10.

2.1. The simple isotropic random walk

Consider a walker moving on an infinite one-dimensional uniform lattice (i.e. a line split into discrete points). Suppose the walker starts at the origin ($x=0$) and then moves a short distance δ either left or right in a short time τ. The motion is assumed to be completely random, so the probabilities of moving both left and right are 1/2. After one time step, the walker can either be at a distance δ to the left or right of the origin, with probability 1/2 each. After the next time step, the walker will either be at a distance 2δ to the left or right of the origin (with probability 1/4 each) or will have returned to the origin (with probability 1/2). Note that, after an even (odd) number of steps, the walker can only be at an even (odd) distance away from the origin. Continuing in this way, the probability that a walker will be at a distance $m\delta$ to the right of the origin after n time steps (where m and n are even) is given by

$$\begin{aligned} p(m,n) &= \left(\frac{1}{2}\right)^n \begin{pmatrix} n \\ \dfrac{n-m}{2} \end{pmatrix} \\ &= \frac{n!}{2^n((n+m)/2)!((n-m)/2)!}. \end{aligned} \tag{2.1}$$

This is a form of the binomial distribution, with mean 0 and variance n. For large n, this converges to a normal (or Gaussian) distribution so, after a sufficiently large amount of time $t=n\tau$, the location $x=m\delta$ of the walker is normally distributed with mean 0 and variance $\delta^2 t/\tau$. Taking the limit $\delta,\ \tau\to 0$ such that $\delta^2/\tau=2D$, where D is a constant known as the diffusion coefficient, gives the PDF for the location of the walker after time t

$$p(x,t) = \frac{1}{\sqrt{4\pi Dt}}\exp\left(\frac{-x^2}{4Dt}\right). \tag{2.2}$$

Note that this is the fundamental solution of the *diffusion equation* (see §2.2).

Useful time-dependent statistics of this process are the mean location $E(X_t)$ and the mean squared displacement (MSD) $E(X_t^2)$, defined as

$$\left.\begin{aligned} E(X_t) &= \int_{-\infty}^{\infty} xp(x,t)\,\mathrm{d}x, \\ E(X_t^2) &= \int_{-\infty}^{\infty} x^2 p(x,t)\,\mathrm{d}x. \end{aligned}\right\} \tag{2.3}$$

Note that here, and throughout the paper, we adopt the convention that random variables are denoted by upper case letters (e.g. X, Θ), while the possible numerical values of these variables are denoted by lower case letters (e.g. x, θ; see Grimmett & Stirzaker 2001). For the one-dimensional solution (2.2), it is easy to show that $E(X_t)=0$ and $E(X_t^2)=2Dt$. The first result illustrates the absence of a preferred direction or bias (on average there is no overall movement in any direction), while the second result illustrates the standard property of a diffusive process—that MSD increases linearly with time. This contrasts with a system or process where the signal propagates as a wave (ballistic movement), in which MSD increases linearly with t^2 (Murray 1993; Okubo & Levin 2001). This relationship between MSD and D, and its equivalence in higher dimensions (see §2.3), is extremely important as it provides a means of estimating from empirical data the diffusion coefficient D that is used in many mathematical models of spatial population dynamics and diffusive processes.

2.2. A BRW with waiting times

It is also a standard procedure (Lin & Segel 1974; Okubo & Levin 2001) to derive the governing equation for a SRW using a difference equation, and subsequently solve to find solutions of the form (2.2). This method also allows more complex processes to be modelled as part of the random walk and we illustrate this in the following example by including both a preferred direction (or bias) and a possible waiting time between movement steps.

Consider a walker moving on a one-dimensional lattice, where, at each time step τ, the walker moves a distance δ to the left or right with probabilities l and r, respectively, or stays in the same location ('waits'), with probability $1-l-r$ (the isotropic random walk in §2.1 has $r=l=1/2$ and there is no waiting time). Now, if the walker is at location x at time $t+\tau$, then there are three possibilities for its location at time t: (i) it was at $x-\delta$ and then moved to the right, (ii) it was at $x+\delta$ and then moved to the left, and (iii) it was at x and did not move at all. Thus we have

$$\begin{aligned} p(x,t+\tau) &= p(x,t)(1-l-r) + p(x-\delta,t)r \\ &\quad + p(x+\delta,t)l. \end{aligned} \tag{2.4}$$

We now assume that τ and δ are small, so (2.4) can be expressed as a Taylor series about (x, t). This gives the partial differential equation (PDE)

$$\frac{\partial p}{\partial t} = -\frac{\delta\epsilon}{\tau}\frac{\partial p}{\partial x} + \frac{k\delta^2}{2\tau}\frac{\partial^2 p}{\partial x^2} + O(\tau^2) + O(\delta^3), \tag{2.5}$$

with $\epsilon=r-l$; $k=l+r$; and where $O(\tau^2)$ and $O(\delta^3)$ represent higher order terms. Now let $\delta,\tau\to 0$ in such a way that the following limits are positive and finite (compare with §2.1):

$$u=\lim_{\delta,\tau\to 0}\frac{\delta\epsilon}{\tau},\qquad D=k\lim_{\delta,\tau\to 0}\frac{\delta^2}{2\tau}. \tag{2.6}$$

The requirement that δ^2/t remains positive and finite as δ, $\tau\to 0$ implies that the difference $\epsilon=r-l$ between the probabilities of moving left and right must be proportional to δ, and that $\epsilon\to 0$ as δ, $\tau\to 0$. Hence, the probabilities r and l are not fixed, but vary with the spatial and temporal step sizes such that the above limits exist. Under these limits, the $O(\tau^2)$ and $O(\delta^3)$ terms in (2.5) tend to zero, giving

$$\frac{\partial p}{\partial t}=-u\frac{\partial p}{\partial x}+D\frac{\partial^2 p}{\partial x^2}. \tag{2.7}$$

This is called the drift–diffusion (or advection–diffusion) equation: the first term on the right-hand side represents drift due to the bias in the probability of moving in the preferred direction and the second term represents diffusion. If we set $r=l=1/2$, then we get $u=0$ and (2.7) reduces to the basic diffusion equation (which has solution (2.2)). Equation (2.7) is a special case of the Fokker–Planck equation (see §2.4) where the diffusion coefficient D is constant. Similarly, multiplying (2.7) by the total population size gives an equation of similar form for the number density of the population (assuming that all individuals act independently of each other), which is a special case of Fick's equation, with constant diffusion coefficient D (see Okubo & Levin 2001).

It is worth noting that, owing to the waiting time between movements, the value of the diffusion constant D is smaller ($k=l+r<1$ in this case) than that in §2.1 and hence, as expected, diffusion is less rapid. Note also that, due to the way the limits are taken in (2.6), the term $\epsilon=r-l$ must tend to zero in order to obtain a finite drift rate u.

The solution of (2.7) subjected to the initial condition $p(x,0)=\delta_{\mathrm{d}}(x)$ (the Dirac delta function), which means that the walker is at $x=0$ at time $t=0$, is (Montroll & Shlesinger 1984; Grimmett & Stirzaker 2001)

$$p(x,t)=\frac{1}{\sqrt{4\pi Dt}}\exp\left(\frac{-(x-ut)^2}{4Dt}\right), \tag{2.8}$$

which is similar to (2.2), except for the drift term in the exponential, which shifts the centre of the Gaussian distribution from $x=0$ to $x=ut$.

The mean location and the MSD can be easily calculated by substituting (2.8) into (2.3). Alternatively, it is possible to calculate the moments directly from the governing PDE (2.7). This is a technique that is particularly useful in more complex models when the governing differential equation is known, but the solution for $p(x,t)$ may be difficult or impossible to find (see §3.5). First, we multiply equation (2.7) either by x (to find mean location) or by x^2 (to find MSD) and integrate by parts. Then, using the definitions in (2.3), the fact that

$$\int_{-\infty}^{\infty}p(x,t)\,\mathrm{d}x=1$$

and making the reasonable assumption that $p(x,t)$ and its first two derivatives with respect to x tend to zero as $|x|\to\infty$, we get

$$E(X_t)=ut,\qquad E(X_t^2)=u^2t^2+2Dt. \tag{2.9}$$

Note that, in contrast to the isotropic (unbiased) random walk in §2.1, the MSD of a diffusion process with drift has $E(X_t^2)\sim t^2$ (when t is large), so the signal propagates as a wave. For such a process, the statistic

$$\sigma_t^2=\int_{-\infty}^{\infty}(x-E(X_t))^2p(x,t)\,\mathrm{d}x, \tag{2.10}$$

which measures the dispersal about the mean location $E(X_t)$, is a more appropriate measure than $E(X_t^2)$, which measures the dispersal about the origin. For (2.7), we get $\sigma_t^2=2Dt$, which is linear in time and hence characteristic of a standard diffusive process.

2.3. The BRW in higher dimensions

A similar derivation to that in §2.2 can be completed using an N-dimensional lattice to give the standard drift–diffusion equation

$$\frac{\partial p}{\partial t}=-\boldsymbol{u}\cdot\nabla p+D\nabla^2 p, \tag{2.11}$$

where $\boldsymbol{u}$ is the average drift velocity (now an N-dimensional vector); ∇ is the gradient operator; and ∇^2 is the Laplacian. Assuming an initial Dirac delta function distribution $p(\boldsymbol{x},0)=\delta_{\mathrm{d}}(x_1),\dots,\delta_{\mathrm{d}}(x_N)$ (i.e. the walker starts at $\boldsymbol{x}=\boldsymbol{0}$), (2.11) has the following solution (Montroll & Shlesinger 1984; Grimmett & Stirzaker 2001):

$$p(\boldsymbol{x},t)=\frac{1}{(4\pi Dt)^{N/2}}\exp\left(\frac{-|\boldsymbol{x}-\boldsymbol{u}t|^2}{4Dt}\right). \tag{2.12}$$

Figure 1*a*,*b* shows the PDF and some sample paths of a BRW on a two-dimensional lattice. The moments of the probability distribution can be calculated in a similar way to §2.2. The mean location is $E(\boldsymbol{X}_t)=\boldsymbol{u}t$. The MSD is defined in N dimensions by

$$\begin{aligned}E(R_t^2)&=\int_{\mathbb{R}^N}|\boldsymbol{x}|^2p(\boldsymbol{x},t)\,\mathrm{d}\boldsymbol{x}\\&=\int_{\mathbb{R}^N}(x_1^2+\cdots+x_N^2)p(\boldsymbol{x},t)\,\mathrm{d}x_1\ldots\mathrm{d}x_N\end{aligned} \tag{2.13}$$

with $R_t=|\boldsymbol{X}_t|$ and, for (2.12), is given by

$$E(R_t^2)=|\boldsymbol{u}|^2t^2+2NDt. \tag{2.14}$$

It is interesting to note that, if two-dimensional movement is not restricted to a lattice (box 1), then diffusion in the direction of the bias is lower than that in the perpendicular direction (see ch. 2 of Codling 2003; Coscoy *et al.* 2007). This result is not always properly considered in spatial population dynamics models, where diffusion is usually assumed to be the same in all directions even when there is an average drift in a particular direction.

2.4. The Fokker–Planck equation

It is also possible to extend the SRW in two (or more) dimensions to include movement probabilities that are spatially dependent. This results in the Fokker–Planck equation for $p(x,y,t)$ (Okubo & Levin 2001). Suppose that an individual moves on a two-dimensional lattice. At each time step τ, an individual can move a distance δ either up, down, left or right with probabilities dependent on location, given by $u(x,y)$, $d(x,y)$, $l(x,y)$ and $r(x,y)$,

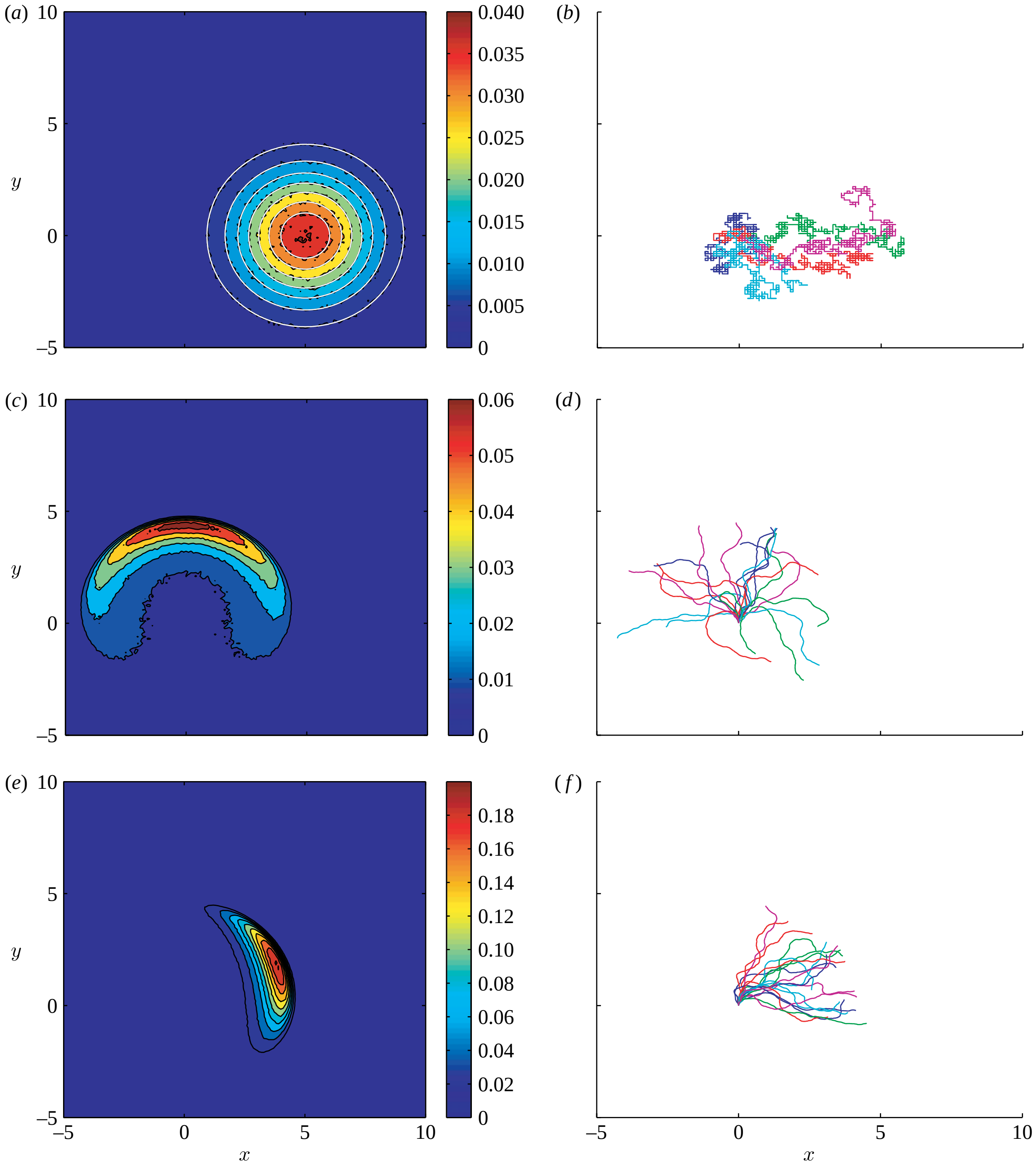

Figure 1. (*a*,*c*,*e*) PDFs and (*b*,*d*,*f*) sample paths of different random walks. (*a*,*b*) A lattice BRW with probabilities of moving a distance δ right or left of $\tau(D/\delta^2 \pm u/(2\delta))$ and up or down of $\tau D/\delta^2$. (*c*,*d*) A non-lattice CRW with probabilities of turning an angle δ_θ clockwise or anticlockwise of $\tau\sigma_0^2/(2\delta_\theta^2)$. (*e*,*f*) A non-lattice BCRW with probabilities of turning clockwise or anticlockwise of $\tau(\sigma_0^2/(2\delta_\theta^2) \pm \theta/(2B\delta_\theta))$ (cf. the linear reorientation model of §3.4). In the BRW and BCRW, the global preferred direction is $\theta_0=0$; in the CRW and BCRW, the initial direction is $\theta=\pi/2$ and the walker moves with constant speed v. In all cases, the walker starts at $(x, y)=(0, 0)$ at $t=0$ and is allowed to move until $t=10$. The PDFs $p(x, y, t=10)$ were calculated from 10^6 realizations of the walk. In (*a*), the white lines show the contours of the corresponding theoretical PDF (2.12). In the sample paths for the BRW, at each step the walker either stays still or moves right, left, up or down by a distance δ. In the CRW and BCRW, at each step the walker's direction of motion θ either stays the same or turns clockwise or anticlockwise by an angle δ_θ, and the walker's movement is given by the vector $v\tau(\cos\theta, \sin\theta)$. Parameter values: $D=0.2$, $u=0.5$, $\sigma_0^2=0.5$, $B=2.5$, $v=0.5$.

respectively (with $u+d+l+r\leq 1$), or remain at the same location with probability $1-u(x, y)-l(x, y)-d(x, y)-r(x, y)$. We now use a difference equation as in §2.2, expand as a Taylor series and define the following parameters:

$$b_i = \lim_{\delta,\tau,\epsilon_i\to 0} \frac{\epsilon_i\delta}{\tau}, \qquad a_{ii} = \lim_{\delta,\tau\to 0} \frac{k_i\delta^2}{2\tau}, \qquad (i=1,2),$$

with $\epsilon_1=r-l$; $\epsilon_2=u-d$; $k_1=r+l$; and $k_2=u+d$. (As these parameters are spatially dependent, we also need to define partial spatial derivatives of a and b in the same limit.) Now, taking appropriate limits as δ, τ, ϵ_1, $\epsilon_2\to 0$, such that $\epsilon_1\delta/\tau$, $\epsilon_2\delta/\tau$, $k_1\delta^2/(2\tau)$ and $k_2\delta^2/(2\tau)$ all tend to constants, gives

$$\frac{\partial p}{\partial t} = -\nabla\cdot(\boldsymbol{u}p) + \nabla\cdot(\boldsymbol{D}\nabla p), \qquad (2.15)$$

Box 1. Stepping off the lattice.

The simple random walk models discussed in §2 are mostly restricted to N-dimensional lattices so that there are only a finite number of choices of direction at each time step. A more realistic model allows for a continuous choice of direction. In two dimensions, this means that the walker is allowed to move in any direction θ on the unit circle. Linear statistical measures cannot be used because any angular value θ is only defined modulo 2π, so θ and $\theta+2\pi$ correspond to the same direction. Instead, circular distributions can be used to draw random angles for either the direction of movement (in an SRW or BRW) or turning angle (in a CRW or BCRW) at each step of a two-dimensional random walk.

Useful moments of a circular distribution (with PDF $f(\theta)$) are the mean cosine c and the mean sine s, defined as

$$c = E(\cos \Theta) = \int_{-\pi}^{\pi} \cos \theta f(\theta)\,\mathrm{d}\theta, \qquad s = E(\sin \Theta) = \int_{-\pi}^{\pi} \sin \theta f(\theta)\,\mathrm{d}\theta.$$

The mean angle is given by $\theta_0=\arctan(s/c)$ if $c>0$ and by $\theta_0=\arctan(s/c)+\pi$ if $c<0$, and the mean vector length r as $r=(s^2+c^2)^{1/2}$, which gives a measure of how peaked the distribution is about the mean angle (Mardia & Jupp 1999).

Commonly used circular distributions are (Batschelet 1981; Mardia & Jupp 1999) as follows:

— The von Mises distribution

$$f(\theta) = M(\theta; \theta_0, \kappa) \equiv \frac{1}{2\pi I_0(\kappa)} \mathrm{e}^{\kappa \cos(\theta-\theta_0)},$$

where I_0 denotes the modified Bessel function of the first kind and order 0, defined by $I_m(\kappa)=\frac{1}{2\pi}\int_{-\pi}^{\pi} \cos m\theta \mathrm{e}^{\kappa \cos \theta}\,\mathrm{d}\theta$. The mean vector length for this distribution is $r=I_1(\kappa)/I_0(\kappa)$.

— The wrapped normal distribution

$$f(\theta) = W(\theta; \theta_0, \sigma) \equiv \frac{1}{\sigma\sqrt{2\pi}} \sum_{k=-\infty}^{\infty} \exp\left(-\frac{(\theta-\theta_0+2\pi k)^2}{2\sigma^2}\right).$$

The mean vector length for this distribution is $r=\mathrm{e}^{-\sigma^2/2}$, where sigma is the standard deviation of the linear normal distribution before wrapping.

— The wrapped Cauchy distribution

$$f(\theta) = C(\theta; \theta_0, r) \equiv \frac{1}{2\pi} \left(\frac{1-r^2}{1+r^2-2r\cos(\theta-\theta_0)}\right).$$

The wrapped normal distribution is the standard normal distribution 'wrapped' around a unit circle, and is hence easy to interpret and simulate. The von Mises distribution is easier to deal with analytically, however, and is similar to the wrapped normal distribution with the same mean cosine, so is often used instead of the wrapped normal. The wrapped Cauchy distribution is more peaked, with fatter tails than the von Mises and wrapped normal (Mardia & Jupp 1999).

In three-dimensional space, a second angular direction ϕ must also be specified, and spherical distributions defined (Fisher *et al.* 1987). Spherical distributions and data are difficult to deal with (which may be the reason why many movement studies are restricted to two dimensions), although it is possible to use a vector-based approach (e.g. Uttieri *et al.* 2007).

with

$$\boldsymbol{u}(x, y) = \begin{pmatrix} b_1(x, y) \\ b_2(x, y) \end{pmatrix},$$

$$\boldsymbol{D}(x, y) = \begin{pmatrix} a_{11}(x, y) & 0 \\ 0 & a_{22}(x, y) \end{pmatrix}.$$

Equation (2.15) is an example of the Fokker–Planck diffusion equation, which is similar to the two-dimensional drift–diffusion equation (2.11), except that the drift rate and the diffusion coefficient now depend on location. In principle, equation (2.15) can be solved if the dependence of $\boldsymbol{u}$ and $\boldsymbol{D}$ on (x, y) are known, but this is usually possible only in the simplest cases. A similar derivation can also be completed for a random walk process where movement is not restricted to a lattice (box 1). This leads to a governing equation similar to (2.15), although the off-diagonal terms, a_{12} and a_{21}, in the diffusion matrix $\boldsymbol{D}$ may be non-zero due to the covariance in the movement direction (it becomes possible to move some distance in both the x and y directions at each step; see ch. 2 of Codling 2003, for further details).

2.5. *General diffusive properties and model limitations*

Closer inspection of the diffusion equation solutions (2.2) and (2.8) shows that the following important property holds: $p(x, t)>0$ for all locations x and all positive times t. Hence, for any positive time (no matter how small), there is a positive probability of being at *any* finite location.

In practice, the probability of being at an exceptionally large distance away from the origin after an infinitesimal time step is extremely small. However, the fact that this property of 'infinite propagation speed' exists suggests that the limiting process involved in deriving the governing equation of the SRW model has some limitations. As shown in §2.2, to derive the governing equation of a simple BRW, we take limits assuming that

$\delta^2/\tau = 2D$ is constant as $\delta, \tau \to 0$ (where δ is the distance moved at each time step τ). Clearly, if this property holds then, in the same limit, we get $\delta/\tau \to \infty$, i.e. the effective instantaneous speed is infinite (Okubo & Levin 2001). The solution of the diffusion equation should hence be considered only as an asymptotic approximation, valid for large times ($t \gg \tau$), of equations that more accurately describe the correlations in movement and finite speeds that are present when considering movement at shorter time scales.

A more detailed discussion of the infinite propagation speed in diffusive processes can be found in Okubo & Levin (2001), while in §2.7 we present a simple model based on a velocity jump process (rather than a position jump process), which avoids this problem.

2.6. Random walks with a barrier

To model movement in a confined domain, one can introduce a repelling or reflecting barrier into the random walk: a walker reaching the barrier will automatically turn around and move away in the opposite direction. Similarly, to model movement where walkers leave the system upon reaching a given point, one can introduce an absorbing barrier. Models such as these are not only appropriate to model movement in space, but they are also suited to modelling development and growth where critical life stages are reached (Pitchford & Brindley 2001; Pitchford *et al.* 2005; Mullowney & James 2007) and to 'integrate and fire' models of nerve responses (Iyengar 2000). These are examples of *first passage time* (or *first hitting time*) problems, in which the distribution of the time taken to reach an absorbing barrier is of primary interest (Condamin *et al.* 2007).

The simple example of an absorbing barrier given below is adapted from an example by Grimmett & Stirzaker (2001). Suppose we have a one-dimensional random walk process that satisfies the drift–diffusion equation (2.7) for $x>0$. Suppose the walker starts at location $x = x_0 > 0$, and there is an absorbing barrier at $x=0$ such that, if the walker reaches the point $x=0$, it is removed from the system. The appropriate boundary and initial conditions in this case are

$$p(0,t) = 0 \quad t \geq 0, \tag{2.16}$$

$$p(x,0) = \delta_{\mathrm{d}}(x - x_0) \quad x \geq 0. \tag{2.17}$$

The solution to (2.7) with initial condition (2.17) is simply given by (2.8) with x replaced by $x - x_0$. The solution to (2.7), which takes into account both conditions (2.16) and (2.17), can be found by extending a result from Grimmett & Stirzaker (2001). This may then be used to derive the PDF of the time T_{a} until the absorption of the walker. At time t, either the walker has been absorbed or its location has PDF given by $p(x,t)$, and hence

$$\Pr(T_{\mathrm{a}} \leq t) = 1 - \int_0^\infty p(x,t)\,\mathrm{d}x = 1 - \Psi\left(\frac{ut + x_0}{\sqrt{2Dt}}\right) + \Psi\left(\frac{ut - x_0}{\sqrt{2Dt}}\right)\mathrm{e}^{-ux_0/D}, \tag{2.18}$$

where $\Psi(x) = (1/\sqrt{2\pi})\exp(-x^2/2)$ is the PDF of the standard normal distribution function $N(0,1)$. Differentiation of (2.18) with respect to t gives the PDF of the absorbing time T_{a}

$$f_{T_{\mathrm{a}}}(t) = \frac{x_0}{\sqrt{4\pi D t^3}} \exp\left(\frac{-(x_0 + ut)^2}{4Dt}\right). \tag{2.19}$$

From (2.18), it is easy to see that the probability of absorption taking place in a finite time ($T_{\mathrm{a}} < \infty$) is given by

$$\Pr(T_{\mathrm{a}} < \infty) = \begin{cases} 1 & \text{if } u \leq 0, \\ \mathrm{e}^{-ux_0/D} & \text{if } u > 0. \end{cases} \tag{2.20}$$

Thus, the walker is certain to be absorbed within a finite time if there is no overall drift or if there is a drift towards the barrier ($u \leq 0$). If there is a drift away from the barrier, there is still a possibility of the walker being absorbed (because the random walk process allows for individual steps towards the barrier, even though steps away from the barrier are more likely), but this probability decreases exponentially as the rate of drift u, or the initial distance x_0 from the barrier, increases. Conversely, if the rate of diffusion D increases, the probability of absorption will increase.

A similar analysis is possible for a reflecting barrier (Grimmett & Stirzaker 2001) and the SRW model can be extended or analysed in many other ways. Montroll & Shlesinger (1984) give a good review of the general theory of random walks and discuss a wide variety of ideas and problems.

2.7. CRWs and the telegraph equation

A CRW takes into account short-term correlations in the direction of movement. In most cases, this means that the walker is more likely to move in the same or a similar direction to its previous movement direction. This tendency to continue in the same direction is known as persistence (Patlak 1953; see for example figure 1*d*). By explicitly including persistence and a fixed speed of movement in the random walk process, the problem of infinite propagation speed discussed in §2.5 is avoided (see also the discussion in Turchin 1998). The location at each step of the random walk is no longer a Markov process (as it depends on the sequence of previous locations). Hence the usual framework for describing a CRW is a *velocity jump process*, in which the variable following a Markov process is the walker's velocity rather than the location (Othmer *et al.* 1988).

Consider a population of individuals moving either left or right along an infinite line at a constant speed v. Denote the density of right- and left-moving individuals at location x and time t by $\alpha(x,t)$ and $\beta(x,t)$, respectively. The total population density is $p(x,t) = \alpha(x,t) + \beta(x,t)$. At each time step τ, each individual either changes direction and moves a distance δ in this new direction (with probability $r = \lambda\tau$), or moves a distance δ in the previous direction (with probability $q = 1 - \lambda\tau$). Hence, turning events occur as a Poisson process with rate λ. If we take a forward time step, then the number density of individuals at location x moving right and left, respectively, is given by

$$\alpha(x,t+\tau) = (1-\lambda\tau)\alpha(x-\delta,t) + \lambda\tau\beta(x-\delta,t), \quad (2.21)$$

$$\beta(x,t+\tau) = \lambda\tau\alpha(x+\delta,t) + (1-\lambda\tau)\beta(x+\delta,t). \quad (2.22)$$

Expanding these as Taylor series and taking the limit δ, $\tau \to 0$ such that $\delta/\tau = v$ gives

$$\frac{\partial\alpha}{\partial t} = -v\frac{\partial\alpha}{\partial x} + \lambda(\beta-\alpha), \quad (2.23)$$

$$\frac{\partial\beta}{\partial t} = v\frac{\partial\beta}{\partial x} - \lambda(\beta-\alpha). \quad (2.24)$$

Adding (2.23) and (2.24) and differentiating with respect to t, and subtracting (2.23) from (2.24) and differentiating with respect to x, respectively, give

$$\frac{\partial^2(\alpha+\beta)}{\partial t^2} = v\frac{\partial^2(\beta-\alpha)}{\partial x\,\partial t}, \quad (2.25)$$

$$\frac{\partial^2(\beta-\alpha)}{\partial x\,\partial t} = v\frac{\partial^2(\alpha+\beta)}{\partial x^2} - 2\lambda\frac{\partial(\beta-\alpha)}{\partial x}. \quad (2.26)$$

Finally, substituting (2.26) into (2.25), and using (2.23), (2.24) and the fact that $\alpha+\beta = p$ give

$$\frac{\partial^2 p}{\partial t^2} + 2\lambda\frac{\partial p}{\partial t} = v^2\frac{\partial^2 p}{\partial x^2}. \quad (2.27)$$

Equation (2.27) is an example of the telegraph equation, so called because it was originally studied by Lord Kelvin in relation to signals propagating across the transatlantic cable (Goldstein 1951). Goldstein (1951) was the first to show that the equation is also the governing equation of this special type of random walk process. Kac (1974) also completed a similar analysis to that shown previously, and hence this general type of movement process is often termed the Goldstein–Kac model. More recently, Shlesinger (2003) has demonstrated that a random walk with a coupled space–time memory can also be used to derive (2.27).

Note that, although (2.27) describes a correlated movement process, the random walk is globally unbiased in the sense that there is no overall preferred direction, simply a tendency for individuals to persist in their present direction of motion (a localized bias). Although the original process uses a fixed time step τ, the mean time between turning events, $\bar{\tau} = 1/\lambda$, is different since the telegraph process does not have a turning event at every time step.

Equation (2.27) can be solved given the initial conditions $p(x,0)$ and $(\partial p/\partial t)(x,0)$, but the full solution is quite complex (see Morse & Feshbach 1953, for details). Since there is a fixed speed v, the solution does not imply infinite propagation speeds (as found with the solutions (2.2) and (2.8) of the diffusion equation).

It is possible to use a similar method to that used in §2.2 to derive equations for the moments of the solution: $E(X_t) = 0$ and

$$E(X_t^2) = \frac{v^2}{\lambda}\left(t - \frac{1}{2\lambda}\left(1-\mathrm{e}^{-2\lambda t}\right)\right). \quad (2.28)$$

For small t (i.e. $t \approx 1/\lambda$), $E(X_t^2) \sim O(v^2t^2)$, which is characteristic of a wave propagation process; for large t, $E(X_t^2) \sim O(v^2t/\lambda)$, which is characteristic of a diffusion process (box 2).

2.8. Diffusion limit of the telegraph equation

In §2.1, we showed that the diffusion coefficient of a SRW is $D = \delta^2/(2\tau)$, where δ is the distance moved at each jump and τ is the time step between jumps. Since the telegraph turning process is a Poisson process of intensity λ, the mean time between turning events is $\bar{\tau} = 1/\lambda$ and the average distance moved between turning events is $\bar{\delta} = v/\lambda$. Hence the effective diffusion coefficient for the telegraph process is indeed given by

$$D = \frac{\bar{\delta}^2}{2\bar{\tau}} = \frac{v^2}{2\lambda}. \quad (2.29)$$

Thus, the 'diffusion limit' of the telegraph process consists of letting $\lambda \to \infty$ and $v \to \infty$, while maintaining v^2/λ as a constant (equivalent to letting $\tau \to 0$ and $\delta/\tau \to \infty$, while maintaining δ^2/τ as a constant in the SRW). We can therefore argue that, as $\lambda \to \infty$, both the uncorrelated SRW and the correlated telegraph process tend to the same limit. This is equivalent to the large time-limiting solutions of both processes being the same, due to short-term correlation effects becoming less evident at large time scales (more detailed analysis and discussion can be found in Othmer et al. 1988; Hillen & Othmer 2000; Okubo & Levin 2001; Hillen 2002; Othmer & Hillen 2002). This limiting process is also known as the 'parabolic limit' of the telegraph process (box 3).

2.9. The biased telegraph equation

The derivation of the biased one-dimensional telegraph equation is similar to the unbiased case, except that we use different turning probabilities depending on the direction of movement. Denoting the probability of turning by $r_1 = \lambda_1\tau$ for right-moving individuals and $r_2 = \lambda_2\tau$ for left-moving individuals, it can be shown that the governing equation, called the biased telegraph equation, is

$$\frac{\partial^2 p}{\partial t^2} + (\lambda_1+\lambda_2)\frac{\partial p}{\partial t} + v(\lambda_2-\lambda_1)\frac{\partial p}{\partial x} = v^2\frac{\partial^2 p}{\partial x^2}. \quad (2.30)$$

Comparing with (2.27), it can be seen that the presence of bias in the process introduces a drift term into the governing equation. If $\lambda_1 > \lambda_2$ then an individual is more likely to turn if right moving and hence there will be a drift to the left (and vice versa). If $\lambda_1 = \lambda_2$ then (2.30) reduces to the unbiased form given in (2.27). As with the unbiased case, it is straightforward to calculate the moments directly from (2.30), but the details are omitted.

Note that, in this example, the bias is introduced through the different rate of turning in each direction, which is a form of *klinokinesis*; this contrasts with the uncorrelated BRW in §2.2, where the bias came about through the probability of moving in each direction, which is a form of *taxis* (see §3.8).

2.10. The telegraph equation in higher dimensions

In §2.5, the solution to the two-dimensional diffusion process with or without drift was shown to be valid only

Box 2. Anomalous diffusion.

As discussed in §§2 and 3, the MSD $E(R_t^2)$, defined in (2.13), for a typical diffusive random walk is linearly related to time (or number of steps) as in (2.14). However, there are situations where dispersal may not be diffusive, and the MSD is not linear in time but instead has some other power-law relationship. Such situations are known as *anomalous diffusion* (e.g. Weeks *et al.* 1996). The key parameter is the value of μ that is observed in the relation $E(R_t^2) \sim t^{\mu}$. There are five possible situations to consider.

- $\mu=0$. This corresponds to a stationary process with no movement over the period of observation.
- $0<\mu<1$. This situation is known as *sub-diffusion* since MSD increases at a slower rate than in the case of standard diffusion. Such situations typically occur when waiting times between steps are included in the models of movement (e.g. Weeks *et al.* 1996; although a model with waiting times may not always be sub-diffusive, see §2.2), or if the spatial domain is constrained in some way (Coscoy *et al.* 2007), e.g. with the presence of a barrier (as in §2.6).
- $\mu=1$. This is the standard relation between MSD and time for diffusive movement.
- $1<\mu<2$. This situation is known as *super-diffusion* since MSD increases at a faster rate than in the case of standard diffusion (although not so fast as with ballistic movement). Such situations typically occur when the step lengths in the walk are drawn from a distribution with infinite variance. Such a process is known as a Lévy walk and has been extensively studied by physicists and more recently ecologists (Viswanathan *et al.* 1996) although its general applicability to animal movement is still open to debate (Benhamou 2007; Edwards *et al.* 2007).
- $\mu=2$. In this situation, the movement is described as *ballistic* or *wavelike*, and MSD increases quadratically with t. This corresponds to the absolute displacement (cf. MDD) increasing linearly with time, which is a standard property of a wave process. In such cases, the characteristic backtracking and random movement associated with diffusive processes is not present, and each individual effectively moves in a straight line (in a random direction) away from the origin for the whole time period. (Note that, as seen is §2.2, MSD scales with t^2 for large t in a BRW; here, we are concerned only with an unbiased movement process.)

These five cases are the only possibilities that can be observed for an individual moving with a finite speed; $\mu>2$ does not correspond to anything meaningful in this context. It should also be noted that an observed path may appear to belong to several of the above categories, depending on the time period of the observation and the spatial scale used. For example, correlated movement may appear ballistic for small t, but diffusive at large t (with highly correlated movement taking a longer time to appear diffusive than movement with low correlation). Hence, care should always be taken before classifying any particular path as belonging to one of the cases above (Coscoy *et al.* 2007).

Box 3. Hyperbolic or parabolic?

A linear second-order PDE can be written in the form

$$a\frac{\partial^2 u}{\partial x^2}+2b\frac{\partial^2 u}{\partial x\,\partial y}+c\frac{\partial^2 u}{\partial y^2}+d\frac{\partial u}{\partial x}+e\frac{\partial u}{\partial y}+fu+g=0,$$

where $u(x, y)$ is a function of both x and y (which could represent, for example, space and time). If $ac-b^2<0$ then the PDE is classed as *hyperbolic*. By contrast, if $ac-b^2=0$ then the PDE is *parabolic* and if $ac-b^2>0$ then the PDE is *elliptic*.

Hyperbolic and parabolic equations have been extensively studied and there is a large body of theory available, which deals with solving such equations (and also examines their relationship with each other), mainly relating to problems arising in physics. However, in our case it is interesting to note that, using the above definitions, the drift–diffusion equation (2.8) derived from a position jump processes is parabolic, while the telegraph equations, (2.27) and (2.30), and other velocity jump processes (see §3.5) are hyperbolic.

The relationship between the limiting processes involved in the movement model and the governing hyperbolic and parabolic equations has been discussed in more detail by, for example, Othmer *et al.* (1988), Hillen & Othmer (2000), Hillen (2002) and Othmer & Hillen (2002).

as a long-time approximation. One can introduce correlation by completing a similar derivation as in §2.7, but working with a two-dimensional lattice rather than a line. There are now four possible directions of movement: right, left, up and down. Initially, we assume that the probability of turning is independent of the direction of movement (so there is no bias). As before, we assume a constant speed v. We split the population into individuals moving in each of the four directions $\alpha_1, \ldots, \alpha_4$. At each time step τ, an individual can turn $\pi/2$ rad anticlockwise or clockwise (with probabilities $\lambda_1\tau$ and $\lambda_2\tau$, respectively), turn π rad (with probability $\lambda_3\tau$), or continue in the previous direction (with probability $1-(\lambda_1+\lambda_1+\lambda_3)\tau$).

Completing a similar analysis to §2.7 leads to a set of differential equations for each of the sub-populations moving in the four directions. Further manipulation similar to that in §2.7 then leads to

$$\begin{aligned}\frac{\partial^2 p}{\partial t^2} =& v^2\left(\frac{\partial^2(\alpha_2+\alpha_4)}{\partial x^2}+\frac{\partial^2(\alpha_1+\alpha_3)}{\partial y^2}\right)\\ &-v(\lambda_1+\lambda_2+2\lambda_3)\frac{\partial p}{\partial t}+(\lambda_2-\lambda_1)\\ &\times\left(\frac{\partial(\alpha_3-\alpha_1)}{\partial x}-\frac{\partial(\alpha_4-\alpha_2)}{\partial y}\right).\end{aligned} \tag{2.31}$$

This has a similar form to the one-dimensional telegraph equation (2.27), but the system cannot be written in terms of the total population p. It is possible to find solutions to the individual equations for $\alpha_1, \ldots, \alpha_4$, but it is not possible to solve directly for p. The two-dimensional telegraph equation does exist and can be solved, but it is not the limiting equation to the CRW process we have described above. Recent work by Keller (2004) may go some way to solving this problem, but other methods have also been developed to directly calculate the statistics of interest, such as mean location and MSD as we show in §3.

3. RANDOM WALKS AS MODELS OF ANIMAL AND CELL MOVEMENT

It was demonstrated in §2 how expressions may be derived for the PDF, $p(\boldsymbol{x}, t)$, of an uncorrelated random walk in one or more dimensions where the motion is either a purely random or a biased diffusive process. If $p(\boldsymbol{x}, t)$ is known, it is straightforward to calculate the moments such as the mean location, $E(\boldsymbol{X}_t)$, or MSD, $E(R_t^2)$. Animal and cell movements are often characterized by some directional correlation (persistence) and, unfortunately, with a CRW, it is not usually possible to calculate $p(\boldsymbol{x}, t)$ directly, or even to derive a system of differential equations for $p(\boldsymbol{x}, t)$. Variations of the telegraph equation can be used to model a one-dimensional CRW and $p(\boldsymbol{x}, t)$ (and associated moments) can be found. However, as discussed in §2.10, it is still a non-trivial problem to derive a solution for $p(\boldsymbol{x}, t)$ for a CRW in higher dimensions (Othmer et al. 1988; Hillen 2002; Keller 2004). Nevertheless, it is, in many cases, still possible to calculate statistics of the CRW directly through the analysis of paths, as discussed in §§3.1 and 3.2. In §3.3, some measures of the tortuosity of a path are introduced and their relation to MSD is discussed.

The situation is slightly more complex when movement is both correlated and biased in a global preferred direction (i.e. a BCRW). In §3.4, we discuss how it is possible to detect bias in observed paths when there is either a fixed global preferred direction (as in gyrotaxis where bias is due to gravity) or when the preferred direction is individual dependent (as in navigation to a fixed target in space). Simple extensions of the BRW model are also discussed. In §3.5, we introduce a generalized mass-balance equation (the transport equation) that describes hyperbolic movement and discuss how this can be used as a general framework for modelling BCRW.

In general, for organisms moving in an environment that is varying spatially and/or temporally, transition probabilities will depend explicitly on the time t and walker's location $\boldsymbol{x}$. Typically, this dependence is via some 'control signal', such as a chemical substance, light, heat, humidity or odour. A control signal can stimulate the organism in four main ways: the stimulus may be an attractant (or repellent), providing a directional bias that stimulates the organisms to migrate up (or down) a concentration gradient field, or may be an inducer (or inhibitor), causing the rate of diffusive unbiased movement to increase (or decrease). Of course, a specific stimulus may combine more than one of these four properties, and it is not always straightforward to distinguish between the different effects, and the underlying mechanisms responsible for them, on the basis of experimental observations (Cai et al. 2006).

As a further complication, it is common for migrating cells to modify their own chemical environment by producing or degrading the control substance. For example, the slime mould *Dictyostelium discoideum* secretes cyclic adenosine monophosphate (cAMP), which acts as a chemoattractant, leading to the aggregation of cells from a wide area (Höfer et al. 1995); certain types of bacteria secrete slime trails, which provide directional guidance for other cells (Othmer & Stevens 1997). In §3.6, the basic theory of reinforced random walks (RRWs) is introduced, together with some models for the transition probabilities which lie at the heart of the RRW description. Some applications of RRW modelling are reviewed in §3.7. Finally, in §3.8, the link between non-lattice random walks and tactic and kinetic movement mechanisms is discussed.

3.1. Mean squared displacement of CRWs

The MSD, defined in N dimensions by (2.13), gives a measure of the spatial spread of the population with time and, owing to its relationship with the diffusion coefficient D via, for example (2.14), is of great importance to those studying dispersal in biological systems (Okubo & Levin 2001). Interestingly, however, many of the results discussed in this section were first derived through studies in molecular chemistry. The growth and space-filling properties of polymer chains and larger molecules have been modelled as a CRW by, for example, Tchen (1952) and Flory (1969), who both derived equations for MSD. Tchen (1952) also demonstrated the important result that the location coordinates after a large number of steps of a CRW are normally distributed.

Taylor (1921) derived the following expression for the MSD in a one-dimensional correlated walk (see also Tchen 1952; Flory 1969; Hanneken & Franceschetti 1998; Okubo & Levin 2001). Suppose the walker takes a series of steps y_j ($j=1, \ldots, n$) of constant length ($|y_j|=\delta$). A correlation is explicitly introduced between the directions of successive steps (although this correlation propagates in a gradually diminishing way through the Markov process). As the number of steps n becomes large, the MSD for this discrete process tends asymptotically to

$$E(X_n^2) \sim n\delta^2 \frac{1+\gamma}{1-\gamma}, \quad \text{with} \quad \gamma = \frac{E(y_j y_{j+1})}{\delta^2}, \qquad (3.1)$$

where we use the notation $E(X_n^2)$ to distinguish from $E(X_t^2)$, the MSD in a random walk in continuous time as discussed in §2. The parameter $0<\gamma<1$ gives a measure of persistence (Patlak 1953). If γ is close to 1, the walk is highly correlated and will result in long straight movements. There is still no overall preferred direction or bias with this process and, after a long time, the average movement will appear diffusive since the correlation to the original direction of movement is lost (after large n, $E(X_n^2)$ increases linearly with n, which is characteristic of a diffusive process, see box 2). Conversely, if γ is close to 0, the process appears to be diffusive very quickly since correlation to the original direction of movement is lost almost immediately. In this case, (3.1) reduces to $E(X_n^2) \approx n\delta^2$, which is comparable with the result $E(X_t^2)=2Dt$, as derived in §2.1 for the isotropic SRW.

Kareiva & Shigesada (1983) were the first to set up and analyse a generalized model of a two-dimensional CRW for animal movement that included a variable step length and a general angular distribution for the direction moved at each step (see also Skellam 1973; Nossal & Weiss 1974; Lovely & Dahlquist 1975; Hall 1977; Dunn 1983; Marsh & Jones 1988). The CRW consists of a series of discrete steps of length L_j and direction Θ_j. The length L_j of the jth move and the turning angle $\Phi_j = \Theta_{j+1} - \Theta_j$ are assumed to be random variables with no autocorrelation or cross-correlation (and no correlation between step length and step direction). The CRW thus consists of a series of independent draws from the step length PDF, $p(l)$, and the turning angle PDF, $g(\phi)$ (box 1), for each step (i.e. the process is a first-order Markov chain, see Grimmett & Stirzaker (2001)). We define the mean cosine c and mean sine s of the turning angle as (see also box 1)

$$\left.\begin{aligned} c &= E(\cos \Phi) = \int_{-\pi}^{\pi} \cos\phi\, g(\phi)\,\mathrm{d}\phi, \\ s &= E(\sin \Phi) = \int_{-\pi}^{\pi} \sin\phi\, g(\phi)\,\mathrm{d}\phi. \end{aligned}\right\} \qquad (3.2)$$

In a CRW, the mean vector length $0<r=(c^2+s^2)^{1/2}<1$ provides a measure of the degree to which the direction of movement is correlated. If $r\approx 1$, the movement is highly correlated; if $r\approx 0$, the movement is close to being uncorrelated (cf. γ in the previous example). The value of the mean sine of turning angles s gives a measure of the relative probability of clockwise and anticlockwise turns. In random search movements used by animals, clockwise and anticlockwise turns are often balanced, so s and thereby the mean turning angle ϕ_0 (defined by $\tan\phi_0 = s/c$) are zero, and the correlation may be expressed only by the mean cosine of turns c.

Using this model, Kareiva & Shigesada (1983) derived the following equation for the MSD after n steps

$$E(R_n^2) = nE(L^2) + 2(E(L))^2 \times \left(\frac{n(c-c^2-s^2)-c}{(1-c)^2+s^2} + \frac{2s^2+(c^2+s^2)^{(n+1)/2}\gamma}{((1-c)^2+s^2)^2} \right), \qquad (3.3)$$

with

$$\gamma = ((1-c)^2 - s^2)\cos((n+1)\phi_0) - 2s(1-c)\sin((n+1)\phi_0).$$

It is worth noting that equation (3.3) contains the expression r^{n+1}, which is the directional correlation at order $n+1$ (i.e. between any two steps that are n steps apart). Since $r<1$, this correlation decreases progressively as n increases (i.e. for increasingly distant steps).

The general result (3.3) reduces to a much simpler form in particular cases. For example, if there is no persistence (i.e. the walk is uncorrelated), then $g(\phi)$ has a uniform density and both c and s are zero, and (3.3) reduces to $E(R_n^2) = nE(L^2)$ (cf. (2.14) with no drift, $\boldsymbol{u}=\boldsymbol{0}$ and with $N=2$). As mentioned, a more realistic case is when organisms exhibit equal probabilities of turning clockwise or anticlockwise, so $g(\phi)$ is symmetric about $\phi_0=0$ (although it is worth noting that this is not always the case—for example, bacteria can exhibit an inherent rotational bias due to the handedness of their flagellar motor). In the case of equal turning probabilities, we get $s=0$ and (3.3) may be written in terms of the coefficient of variation b of the step length L ($b_2 = E(L^2)/(E(L))^2 - 1$)

$$E(R_n^2) = (E(L))^2 \left(n\left(\frac{1+c}{1-c} + b^2\right) - \frac{2c(1-c^n)}{(1-c)^2} \right). \qquad (3.4)$$

This formula relates changes in $g(\phi)$ or $p(l)$ with consequent changes in MSD, and also highlights the difference between the MSD of a CRW with a fixed step length l and that with a variable step length with mean $E(L)=l$. It is immediately clear from (3.4) that, for $c<1$, the MSD is always larger when the step length is variable ($b>0$) than when it is fixed ($b=0$). The effect of variability in the step length on MSD can be quite significant. For example, in a random walk where the step lengths are drawn from an exponential distribution, we get $b=1$. Hence, as $c\rightarrow 0$, the MSD becomes almost twice as large as the MSD of a random walk with fixed step length.

In the case of random walks with bias, it can be more complicated to derive expressions for MSD. It is possible to write down the MSD of an uncorrelated BRW using a similar approach to the above. Consider a walk consisting of steps of length L_j and direction Θ_j (note the important difference between the direction of movement Θ_j and the turning angle $\Phi_j = \Theta_{j+1} - \Theta_j$), whose mean sine is zero and whose mean cosine is q. After n steps, the MSD is given by (Marsh & Jones 1988; Benhamou 2006)

$$E(R_n^2) = nE(L^2) + n(n-1)q^2(E(L))^2. \qquad (3.5)$$

This is comparable with (2.14), consisting of a component due to bias that scales with n^2 and that due to diffusion that scales with n.

An equation for MSD in a biased velocity jump process can be generated for both the one-dimensional case and higher dimensions, using a generalized transport equation (see §3.5). However, these are special cases of a BCRW where the turning events occur as a Poisson process. In the case of a BCRW with a fixed time step between turning events (where the spatial step lengths can be either fixed or variable), it remains an open problem to calculate a direct equation for MSD.

3.2. Mean dispersal distance of unbiased CRWs

The MSD, defined in (2.13), is of interest to ecologists and biologists owing to its relation to the diffusion coefficient D via (2.14). The MSD is also a statistic that is reasonably mathematically tractable, as illustrated in §3.1. However, because the MSD deals with the squared dispersal distance, it has been suggested that a more intuitive statistic is the mean dispersal distance (MDD; Bovet & Benhamou 1988; McCulloch & Cain 1989; Wu *et al.* 2000; Byers 2001). The MDD of a dispersing population is defined in N dimensions as

$$\begin{aligned} E(R_t) &= \int_{\mathbb{R}^N} |\boldsymbol{x}| p(\boldsymbol{x}, t)\, \mathrm{d}\boldsymbol{x} \\ &= \int_{\mathbb{R}^N} \sqrt{x_1^2 + \cdots + x_N^2}\, p(\boldsymbol{x}, t)\, \mathrm{d}x_1 \ldots \mathrm{d}x_N. \end{aligned} \quad (3.6)$$

Note that $E(R_t)$ is the mean of the absolute dispersal distance and is not the same as $E(\boldsymbol{X}_t)$, the mean location. The presence of an absolute value in (3.6) causes problems and means that calculating the MDD directly is mathematically very difficult (McCulloch & Cain 1989; Wu *et al.* 2000; Byers 2001). Owing to the way the squared dispersal distance is averaged across the population in the respective definitions, as can be seen by comparing (2.13) and (3.6), the MDD is not simply the square root of the MSD. However, the MSD and MDD are related and this fact can be exploited to give a direct equation for MDD.

Consider a two-dimensional, unbiased, CRW with mean step length $E(L)$, and a symmetrical about zero (i.e. zero mean sine) probability distribution $g(\phi)$ for the turning angle at each step. After a sufficiently large number of steps n, the location coordinates X_n and Y_n are independently normally distributed with equal variance. Bovet & Benhamou (1988) used this to derive the following approximate relationship between MDD and MSD:

$$E(R_n) = \frac{\sqrt{\pi E(R_n^2)}}{2}. \quad (3.7)$$

Combining this with equation (3.4) for MSD gives a formula for MDD. Strictly, this approximation is only valid for large n. Nevertheless, it is a good match to simulated data even for small values of n, at least in the case where the turning angles are distributed according to a zero-centred wrapped normal distribution, provided the complete equation (3.4) is used rather than the asymptotic formula for large n (in which case the second term in (3.4) becomes negligible; Benhamou 2004, 2006). Relying on complicated empirical formulae, such as those proposed by Wu *et al.* (2000) and Byers (2001), seems to be unnecessary.

As discussed in §2.7, it is possible to derive differential equations for the MSD of a BCRW where the times between turning events are distributed as a Poisson process but, owing to the presence of an absolute value in (3.6), this approach cannot be used to derive an equation for the MDD of a BCRW. This remains an open problem but, for particular cases, it may be possible to use the result of Bovet & Benhamou (1988), together with an equation for the MSD derived from a moment closure method (see Codling 2003).

3.3. Tortuosity of CRWs

The *tortuosity* of a path describes the amount of turning in a given space or time. Clearly, tortuosity is related to the MSD and MDD: highly tortuous paths will spread out in space slowly (small MSD), while straight paths will spread out in space quickly (high MSD). Hence, it can be useful to measure and study the tortuosity of observed paths in order to understand the processes involved, estimate the area searched by an organism and predict spatial dispersal. Several measures of tortuosity are available but most have some limitations.

The *straightness index* (sometimes called the *net-to-gross displacement ratio*) is a relative measure that compares the overall net displacement G of a path with the total path length T (Batschelet 1981). For example, if a random walk starts at location (x_0, y_0) and, after n steps with lengths l_j $(j=1, \ldots, n)$, ends at (x_n, y_n), then the straightness index is given by

$$\frac{G}{T} = \frac{|(x_n - x_0, y_n - y_0)|}{\sum_{j=1}^{n} l_j}. \quad (3.8)$$

This number must lie between 0 and 1, where 1 corresponds to movement in a straight line (the shortest distance between two points) and 0 corresponds to a random walk that returns to the origin. The straightness index is intuitively easy to understand and is also straightforward to compute. Benhamou (2004) shows how it can act as an unbiased estimator of orientation efficiency in a BCRW, both in cases with an ‘infinite’ goal (fixed directional bias) and in cases with a goal at a finite distance (so that the directional bias changes with each step).

Unfortunately the straightness index is not a reliable measure of tortuosity of a CRW, because the mean of G corresponds to the MDD and hence increases with the square root of n. Consequently, the ratio G/T tends to zero as the number of steps increases (Benhamou 2004). Thus, when observing a CRW and measuring the straightness index, a different result will be found depending on the number of steps considered (the total time observed or the total path length used). It is, therefore, very difficult to compare the tortuosity of different CRWs using this method, unless they all consist of a similar number of steps.

The tortuosity of a CRW corresponds to the amount of turning associated with a given path length and, in some way, measures its long-term diffusion potential. On this basis, Benhamou (2004) defined the path *sinuosity* in terms of the mean step length and MSD after a large number of steps as $S=2(nE(L)/E(R_n^2))^{1/2}$. Using equation (3.4) simplified by removing the second term on the right-hand side, which becomes negligible in the long term, gives

$$S = 2\left(E(L)\left(\frac{1+c}{1-c}+b^2\right)\right)^{-1/2}, \qquad (3.9)$$

where c is the mean cosine of turns and b is the coefficient of variation of step lengths (see §3.1). With this formulation, the path sinuosity S of a (two-dimensional) CRW can be very simply related to the diffusion coefficient D by $D=v/S^2$, where v is the mean speed. Hence, in the simplest case where step lengths are constant ($b=0$ and $E(L)=l$), the sinuosity for a CRW with particular values of c and l is exactly the same as an SRW ($c^*=0$) with a step length $l^*=l(1+c)/(1-c)$. In other words, both types of random walk have the same long-term diffusion potential. This equivalence makes sense as it is quite obvious that the tendency to continue moving in the previous direction not only depends on the persistence, usually defined by the value of c (Patlak 1953), but also on the step length. The particular form of (3.9) makes it possible to get a simple and intuitive formulation of sinuosity in the case where step lengths are constant and turning angles are drawn from a wrapped normal distribution with null mean and variance $\sigma^2=-2\ln(c)$ (box 1). When the turning angle variance is low enough to prevent too much wrapping ($\sigma<1.2$ rad, i.e. $c>0.5$), the ratio $(1+c)/(1-c)$ is approximately equal to $4/\sigma^2$ and (3.9) reduces to $S=\sigma/\sqrt{l}$ (Bovet & Benhamou 1988).

Equation (3.9) can be applied directly to actual paths when animals naturally move in a discrete way (e.g. a bee flying from one flower to another), provided the basic requirements of a CRW are respected (independence of step lengths and turns). For animals moving in a continuous way, the path is usually *discretized* when recorded (i.e. the raw data consist of a set of locations rather than of a continuous track), and can be rediscretized for analysis purposes. (Re)discretization has been shown to alter the turning angle and step length distributions, and hence involves the use of corrected formulae (Bovet & Benhamou 1988; Benhamou 2004; Codling & Hill 2005*a*). Note that rediscretization can be done either spatially (Bovet & Benhamou 1988), which is easier to fit with the analysis above, or temporally (Codling & Hill 2005*a*), which is perhaps more natural for experiments in the field.

It has also been proposed to measure the tortuosity of animals' random search paths by a fractal dimension. This would be useful for actual paths that can be reliably represented using fractioned Brownian motion, which is a fractal movement model where the persistence is related to the fractal dimension through the use of a parameter called the Hurst coefficient. To our knowledge, however, it has not yet been shown that this kind of model can provide a better representation of animals' random search paths than CRW, whose true fractal dimension is equal to 2 for two-dimensional movements (i.e. they will eventually fill the entire plane) for any positive sinuosity (for $S=0$, the CRW reduces to a straight line, with fractal dimension equal to 1). Applying the classical 'divider' method, initially developed to measure the fractal dimension of fractal lines, the CRW provides pseudo-fractal dimension values (Turchin 1998; Benhamou 2004), which correspond to indirect measures of the mean cosine of turns c (Nams 1996, 2005). These pseudo-fractal values cannot reliably estimate the path tortuosity of a CRW, which depends not only on the mean cosine of turns c, but also on the mean step length $E(L)$ and coefficient of variation b.

3.4. Bias in observed paths

The next step up in model complexity from a CRW is a BCRW. We will deal with modelling approaches for BCRWs in §§3.5 and 3.6, while in this section we will consider the ways in which bias may be detected in an observed path (see also Coscoy *et al.* 2007). Assuming the simplest possible environment and behaviour, there are two main ways in which individuals may respond to a signal and hence introduce bias into their movement. Firstly, there may be a fixed sensory gradient such that the preferred direction is always the same for all individuals at all locations in space (e.g. micro-organisms moving under the influence of gravity). Secondly, there may be a target or point source fixed in space, such that the preferred direction is towards a fixed point (e.g. animals searching for a food source). Note that the first scenario can be considered as a special case of the second where the target is fixed at infinity.

In order to parametrize continuum models of bioconvection in micro-organisms (Kessler 1986; Hill & Pedley 2005), Hill & Häder (1997) analysed the paths of swimming algae undergoing *gyrotaxis* (upward swimming due to a gravitational torque) or *phototaxis* (swimming towards a light source). In both situations, it was assumed that the preferred absolute direction of movement was independent of location (i.e. a 'target at infinity'), but that the *turning angle* was dependent on the most recent direction of movement. To help inform experimental observations, Hill & Häder (1997) set up a random walk on the unit circle as follows: at each time step τ, the walker makes a small turn δ clockwise with probability $a(\theta)$ or anticlockwise with probability $b(\theta)$, or continues in the same direction with probability $1-a(\theta)-b(\theta)$. Following a similar method to that used in §2.2 and taking the limit $\delta, \tau\to 0$ such that δ^2/τ is constant yields the Fokker–Planck equation for the PDF $p(\theta, t)$ of travelling in direction θ at time t

$$\frac{\partial p}{\partial t} = -\frac{\partial}{\partial \theta}(\mu_0(\theta)p) + \frac{1}{2}\frac{\partial^2}{\partial \theta^2}(\sigma_0^2(\theta)p), \qquad (3.10)$$

where $\mu_0(\theta)$ and $\sigma_0^2(\theta)$ are, respectively, the unit mean and variance of the turning rate,

$$\begin{aligned}\mu_0(\theta) &= \lim_{\tau\to 0}\frac{1}{\tau}E(\Theta(t+\tau)-\Theta(t))\\ &= \lim_{\delta,\tau\to 0}\frac{\delta}{\tau}(a(\theta)-b(\theta)),\\ \sigma_0^2(\theta) &= \lim_{\tau\to 0}\frac{1}{\tau}\mathrm{Var}(\Theta(t+\tau)-\Theta(t))\\ &= \lim_{\delta,\tau\to 0}\frac{\delta^2}{\tau}(a(\theta)+b(\theta)).\end{aligned}$$

As with the movement probabilities for a BRW in §2.2, the probabilities $a(\theta)$ and $b(\theta)$ are required to be such that both these limits exist (see for example the turning probabilities for the BCRW in figure 1). Note that μ_0 is the mean *net* change in θ per unit time, which will be zero if there is no directional bias $(a(\theta)=b(\theta))$, as opposed to the mean *absolute* turning rate, which is always positive. Hence μ_0 is a measure of the directional response of the organism to stimuli, whereas σ_0^2 (sometimes called the angular diffusivity) measures the random turning component; both parameters are required to parametrize continuum models of bioconvection (Kessler 1986; Hill & Pedley 2005).

By rediscretizing the observed paths and binning the data, Hill & Häder (1997) estimated σ_0^2 using a similar method to Bovet & Benhamou (1988; as σ_0^2 is essentially the same measure as sinuosity, see §3.3), and also the functional form of μ_0. For gyrotaxis, a sinusoidal reorientation model was found to fit well: $\mu_0(\theta, t)=-\sin(\theta-\theta_0(t))/B$, where $\theta_0(t)$ is the preferred direction and B is the average time taken to reorient to the preferred direction. If both σ_0^2 and θ_0 are assumed to be constant then the steady state of the Fokker–Planck equation (3.10) is a von Mises distribution (box 1). This sinusoidal response was predicted by Kessler (1986) and can be explained by the gravitational torque that acts on the individual alga: the torque is zero if the alga is moving in the preferred direction or in the opposite direction, and is the greatest when the alga is moving perpendicular to the gravitational force. For phototaxis, a better fit was given by a simple linear response: $\mu_0(\theta, t)=-(\theta-\theta_0(t))/B$. This case is more generally applicable since there are only a few physical situations likely to result in a sinusoidal response. However, if both σ_0^2 and θ_0 are allowed to be variable, then the steady state of the Fokker–Planck equation (3.10) is more complicated (Hill & Häder 1997).

This ad hoc method used by Hill & Häder (1997) was tested using simulations by Codling & Hill (2005*a*) and found to be valid (allowing for smoothing errors not accounted for by Hill & Häder (1997) and assuming that sinuosity is low enough to avoid 'wrapping' problems leading to an underestimate of σ_0^2 (Bovet & Benhamou 1988; Benhamou 2004)). Note that this method allows for both the functional form of the bias response to be estimated and the relevant parameters (mean reorientation time and angular diffusivity) to be quantified.

The situation is more difficult when the preferred direction changes with spatial location (and is thus individual dependent), a common scenario when animals are moving towards a target in space. The main problem in such a scenario is distinguishing between localized bias due to forward persistence and true biased movement towards a target. This is particularly true if there is more than one target or if the target moves in space. Benhamou (2006) suggested a new procedure based on the backward evolution of the beeline distance from the end of the path (the goal) to each animal's preceding locations. This procedure is efficient, as it requires only a small sample of short paths for detecting a possible orientation component, but is not perfect as there remains a relatively high (approx. 30%) probability of misidentifying a true CRW as a BCRW. This type I error can be reduced by considering together a number of paths assumed to be of the same kind.

The above scenarios assume that bias is introduced through reorientation towards the preferred direction. However, there are many other ways to model mechanisms that produce a directional drift, including the case where the mean turning rate is null and the directional bias comes about through variations in σ_0^2 (see Benhamou 2006, and §3.8). For example, the classical *run-and-tumble* behaviour observed in chemotactic bacteria is usually modelled through a low rate of turning when moving in the preferred direction (runs) and a high rate of turning (tumbles) otherwise (Berg 1983). We discuss the relation between these various mechanisms in §3.8.

3.5. The transport equation and general hyperbolic models of movement

In §2.7, it was shown how the telegraph process could be used in one dimension to model a CRW and how this resulted in a hyperbolic governing equation (box 3). A similar process does not produce a closed equation in two or more dimensions, but it is still possible to work with a generalized hyperbolic governing equation to model the CRW and BCRW (velocity jump processes) in higher dimensions. Othmer *et al.* (1988) introduced the idea of a governing mass balance equation, the *linear transport equation*, which can be used to describe the movement and reorientation of cells (and animals; see also Alt 1980).

Let $p(\boldsymbol{x}, \boldsymbol{v}, t)$ be the density function for individuals moving in N-dimensional space, where $\boldsymbol{x}\in\mathbb{R}^N$ is the location of an individual and $\boldsymbol{v}\in\mathbb{R}^N$ is its velocity. The total number density of individuals at location $\boldsymbol{x}$, regardless of velocity, is given by integrating p over all possible velocities

$$n(\boldsymbol{x}, t) = \int_{\mathbb{R}^N} p(\boldsymbol{x}, \boldsymbol{v}, t)\,\mathrm{d}\boldsymbol{v}. \tag{3.11}$$

We assume that $p(\boldsymbol{x}, \boldsymbol{v}, t)\to 0$ as $|\boldsymbol{x}|\to\infty$ and that changes in an individual's velocity occur as a Poisson process of intensity λ, where λ may be depending on location $\boldsymbol{x}$ or other variables. Thus, λ^{-1} is themean time between changes in direction. We define the *reorientation kernel* $T(\boldsymbol{v}, \boldsymbol{v}')$ as the probability of a change in velocity from $\boldsymbol{v}'$ to $\boldsymbol{v}$, given that a reorientation occurs, which must be non-negative and normalized so that $\int T(\boldsymbol{v}, \boldsymbol{v}')\,\mathrm{d}\boldsymbol{v} = 1$ for all $\boldsymbol{v}'$. We assume that $T(\boldsymbol{v}, \boldsymbol{v}')$ is independent of the time between jumps. It can be shown that the governing equation, known as the *linear transport equation*, for this process is (Othmer *et al.* 1988)

$$\frac{\partial p}{\partial t} + \boldsymbol{v}\cdot\nabla_{\boldsymbol{x}} p = -\lambda p + \lambda \int_{\mathbb{R}^N} T(\boldsymbol{v}, \boldsymbol{v}') p(\boldsymbol{x}, \boldsymbol{v}', t)\,\mathrm{d}\boldsymbol{v}'. \quad (3.12)$$

(Note that $\nabla_{\boldsymbol{x}}$ denotes the spatial gradient operator $(\partial/\partial x_1, \dots, \partial/\partial x_N)$.)

In general, we are interested in the first few velocity moments (as from these we can calculate the statistics of interest such as $E(\boldsymbol{X}_t)$ and $E(R_t^2)$), including the number density $n(\boldsymbol{x}, t)$ introduced in (3.11), and the average velocity $\boldsymbol{u}(\boldsymbol{x}, t)$, which is defined by

$$n(\boldsymbol{x}, t)\boldsymbol{u}(\boldsymbol{x}, t) = \int_{\mathbb{R}^N} p(\boldsymbol{x}, \boldsymbol{v}, t)\boldsymbol{v}\,\mathrm{d}\boldsymbol{v}.$$

Integrating (3.12) over $\boldsymbol{v}$ gives an evolution equation for n in terms of $\boldsymbol{u}$

$$\frac{\partial n}{\partial t} + \nabla_{\boldsymbol{x}}\cdot(n\boldsymbol{u}) = 0. \quad (3.13)$$

Similarly, multiplying (3.12) by $\boldsymbol{v}$ and integrating over $\boldsymbol{v}$ gives

$$\begin{aligned} \frac{\partial (n\boldsymbol{u})}{\partial t} + \int_{\mathbb{R}^N} v\nabla_{\boldsymbol{x}}\cdot(\boldsymbol{v}p)\,\mathrm{d}\boldsymbol{v} \\ = -\lambda n\boldsymbol{u} + \lambda \iint_{\mathbb{R}^{2N}} T(\boldsymbol{v}, \boldsymbol{v}')\boldsymbol{v}p(\boldsymbol{x}, \boldsymbol{v}', t)\,\mathrm{d}\boldsymbol{v}'\,\mathrm{d}\boldsymbol{v}. \end{aligned} \quad (3.14)$$

It is worth noting that equation (3.12) describes a general process, of which many of the basic random walk models discussed previously are special cases. For example, in one spatial dimension, and under the assumption that individuals move with constant speed v, there are only two possible velocities: $+v$ and $-v$. With the additional assumption that the turning frequency λ is constant, it can be shown that (3.13) and (3.14) reduce to equations (2.25) and (2.26) derived in §2.7, which lead to the one-dimensional telegraph equation.

The transport equation also provides a natural extension of the basic telegraph process to two dimensions, without the need to restrict the population to a lattice as in §2.10. Retaining the assumptions of constant turning frequency λ and constant speed v, an individual's velocity may be described simply by the angle θ between its direction of motion and the positive x_1-axis. The appropriate density function is now $p(\boldsymbol{x}, \theta, t)$. The transport equation (3.12) reduces to

$$\begin{aligned} \frac{\partial p}{\partial t} + v(\cos\theta, \sin\theta)\cdot\nabla_{\boldsymbol{x}} p \\ = -\lambda p + \lambda \int_{-\pi}^{\pi} T(\theta, \theta') p(\boldsymbol{x}, \theta', t)\,\mathrm{d}\theta'. \end{aligned} \quad (3.15)$$

Othmer *et al.* (1988) used the following example to illustrate how a random walk in an external field can be modelled using (3.15). Suppose individuals are moving with a taxis-inducing gradient in the direction $\theta_0 = 0$ (i.e. the positive x_1-direction), under the assumption that the gradient influences only the reorientation kernel $T(\theta, \theta')$. Suppose also that the reorientation kernel $T(\theta, \theta')$ is the sum of a symmetric probability distribution $h(\phi)$, where $\phi = \theta - \theta'$, and a bias term $k(\theta)$ that results from the taxis-inducing gradient. Since the gradient is directed along the x_1-axis, the bias term takes its maximum at $\theta = 0$ and is symmetric about $\theta = 0$. Thus

$$T(\theta, \theta') = h(\theta - \theta') + k(\theta). \quad (3.16)$$

The quantities

$$\lambda_0 = \lambda\left(1 - \int_{-\pi}^{\pi} h(\phi)\cos\phi\,\mathrm{d}\phi\right)$$

and

$$C_{\mathrm{I}} = \frac{\lambda}{\lambda_0}\int_{-\pi}^{\pi} k(\theta)\cos\theta\,\mathrm{d}\theta \le 1,$$

respectively, measure the relative turning rate and the net effect of bias due to the taxis-inducing gradient in the direction $\theta_0 = 0$.

Assuming that all individuals start at the origin $(0, 0)$, with initial directions uniformly distributed around the unit circle, one can derive a system of differential equations, known as *moment equations*, for the statistics of interest. For the above choice of $T(\theta, \theta')$, this system is straightforward to solve (Othmer *et al.* 1988; Codling 2003). The mean velocity and mean location are given by

$$E(\boldsymbol{V}_t) = vC_I(1 - \mathrm{e}^{-\lambda_0 t})(\cos\theta_0, \sin\theta_0),$$

$$E(\boldsymbol{X}_t) = vC_I\left(t - \frac{1}{\lambda_0}(1 - \mathrm{e}^{-\lambda_0 t})\right)(\cos\theta_0, \sin\theta_0).$$

The MSD is given by

$$\begin{aligned} E(R_t^2) = \frac{2v^2}{\lambda_0}\Big((1 - 2C_I^2)t - C_I^2 t\mathrm{e}^{-\lambda_0 t} \\ + \frac{(3C_I^2 - 1)}{\lambda_0}(1 - \mathrm{e}^{-\lambda_0 t}) + \frac{C_I^2\lambda_0 t^2}{2}\Big), \end{aligned}$$

and the mean squared dispersal about the average location by

$$\begin{aligned} \sigma_t^2 = \frac{2v^2}{\lambda_0}\Big((1 - C_I^2)t - 2C_I^2 t\mathrm{e}^{-\lambda_0 t} + \frac{(2C_I^2 - 1)}{\lambda_0}(1 - \mathrm{e}^{-\lambda_0 t}) \\ + \frac{C_I^2}{2\lambda_0}(1 - \mathrm{e}^{-2\lambda_0 t})\Big). \end{aligned}$$

The choice of reorientation kernel in (3.16) is crucial in the above analysis as it results in a closed system of differential equations for the statistics of interest. Codling & Hill (2005*b*) used an arguably more realistic reorientation kernel based on a single symmetric distribution with mean turning angle dependent on the direction of movement (see §3.4). However, this results in a 'cascade' of higher moment equations and further assumptions to close the system need to be made.

A general discussion of the issues relating to the moment closure of systems of moment equations resulting from transport equations is given in Hillen (2002). The transport equation can be developed further to allow more complex scenarios to be modelled (spatially dependent parameters, etc.) although this is likely to make finding a closed-form solution more difficult. The hyperbolic movement model has been used in the place of diffusion models to create *reaction–transport* systems (Hillen 1996, 2002), which can be used in place of the classical reaction–diffusion models (Turing 1952; Murray 1993) used in pattern formation and developmental biology.

3.6. Reinforced random walks

The types of processes whereby walkers modify the chemical environment of themselves and of other individuals in the population have led modellers of cell locomotion to employ the theory of RRWs, which allows the walker to modify (reinforce) the transition probabilities associated with the grid points, or interval, it traverses (Davis 1990). The most common way of representing a one-dimensional RRW is the so-called master equation

$$\begin{aligned}\frac{\partial}{\partial t}p(x,t) = {} & T^{+}(x-\delta,t)p(x-\delta,t) \\ & + T^{-}(x+\delta,t)p(x+\delta,t) - (T^{+}(x,t) \\ & + T^{-}(x,t))p(x,t).\end{aligned} \tag{3.17}$$

Here, $T^{-}(x,t)$ and $T^{+}(x,t)$ are called the transition rates from x to $x-\delta$ and x to $x+\delta$, respectively, and, in general, depend on location x and time t. Equation (3.17) is in the form of a continuous-time jump process as it is continuous in time and discrete in space. This is closely related to equation (2.4) (which is described as a discrete time jump process) for a simple nearest-neighbour walk. Typically, the random walk is simulated by choosing a fixed time step τ. The left and right transition probabilities for each time step may then be calculated as $\tau T^{\pm}(x,t)$.

There are many possible models for the transition rates $T^{\pm}$ in terms of the concentration $w(x,t)$ of a control substance, such as the 'local model', 'barrier model' and 'normalized barrier model' proposed by Othmer & Stevens (1997). For a specific choice of transition rates, the continuum limit of the master equation (3.17) can often be found by a similar method to that used to obtain equation (2.5), and may usually be written in the form

$$\frac{\partial p}{\partial t} = \frac{\partial}{\partial x}\left(d(w)\frac{\partial p}{\partial x} - \chi(w)p\frac{\partial w}{\partial x}\right), \tag{3.18}$$

by an appropriate choice of the diffusivity $d(w)$ and the chemotactic sensitivity $\chi(w)$ (if $\chi(w)>0$ the cells will move up a gradient in w and vice versa if $\chi(w)<0$). (Note that (3.18) is a one-dimensional version of the Fokker–Planck equation (2.15).) This is convenient from a modelling perspective as it allows the relationship between a particular choice of transition rates, which model individual cell behaviour on a microscopic scale, and the macroscopic behaviour at a population level to be seen via the functional forms of $d(w)$ (which describes the effects of the control substance on random motility) and $\chi(w)$ (which describes directional effects).

In the local model of Othmer & Stevens (1997), the transition rates depend only on the local concentration of control substance: $T^{-}(x,t) = T^{+}(x,t) = \rho F(w(x,t))$ for some constant ρ and positive function F, called the transition probability function. Taking the limit $\delta \to 0$ and $\rho \to \infty$, such that $D = \rho\delta^2$ is a constant, leads to a continuum limit equation (3.18) with diffusivity $d(w) = DF(w)$ and chemotactic sensitivity $\chi(w) = -D(\mathrm{d}F/\mathrm{d}w)$. Hence, as well as modulating the rate of random motility, the control substance provides a directional bias because the cell is more likely to move from an area of high motility to low motility than vice versa.

In the barrier model, the transition rates depend on the concentration of control substance in the interval to be traversed: $T^{\pm}(x,t) = \rho F(w(x \pm \delta/2, t))$. Hence, the cell can sense concentrations at $x \pm \delta/2$ (so δ is the effective sensory range of the cell) and uses these to decide its direction of movement. The continuum limit equation is (3.18) with diffusivity $d(w) = D\tau(w)$ and chemotactic sensitivity $\chi(w) = 0$. Hence, the control substance has an effect of random motility, as in the local model, but there is no directional bias. This is expected because the transition probability from x to $x+\delta$, determined by the control substance concentration at $x+\delta/2$, is the same as the transition probability from $x+\delta$ to x, so there is no directional bias.

In the normalized barrier model, the transition rates are as in the barrier model, but are normalized so that $T^{+} + T^{-}$ is a constant,

$$T^{\pm}(x,t) = 2\rho\frac{F\left(w\left(x \pm \frac{\delta}{2}, t\right)\right)}{F\left(w\left(x \pm \frac{\delta}{2}, t\right)\right) + F\left(w\left(x \pm \frac{\delta}{2}, t\right)\right)}. \tag{3.19}$$

The cell again senses concentrations at $x \pm \delta/2$, but the normalization means that the probability of moving left plus the probability of moving right is constant. Hence the decision 'when to move' is independent of the decision 'where to move' and the mean waiting time at a point is constant (Othmer & Stevens 1997). This is reflected in the fact that the diffusivity in the continuum limit equation (3.18) is a constant D, but the chemotactic sensitivity is $\chi(w) = D(1/F(w))(\mathrm{d}F/\mathrm{d}w)$, so there is a directional bias.

The actions of the control substance under each of these three models are summarized in table 1. Note that the normalized barrier model represents a control substance that is an attractant or repellent, whereas the barrier model represents an inducer or inhibitor. The local model allows both the motility and the directional bias to be varied. However, the constraint on the relationship between $d(w)$ and $\chi(w)$ in the local model means that the substance must either be an inducer and a repellent, or an inhibitor and an attractor, which is not always realistic. Motivated by this limitation, the normalized barrier model may be generalized to allow for a variable mean waiting time (VMWT). This may be achieved in two ways. Firstly, the transition rates take the form (3.19), but ρ is

Table 1. Summary of the biological interpretation of different models for the RRW transition rates, in terms of the non-directional ($d(w)$) and directional ($\chi(w)$) effects of the control substance.

model	$d(w)$	$\chi(w)$	control substance action
local	$DF(w)$	$-D(\mathrm{d}F/\mathrm{d}w)$	inducer & repellent (if $\mathrm{d}F/\mathrm{d}w>0$) inhibitor & attractant (if $\mathrm{d}F/\mathrm{d}w<0$)
barrier	$DF(w)$	0	inducer (if $\mathrm{d}F/\mathrm{d}w>0$) inhibitor (if $\mathrm{d}F/\mathrm{d}w<0$)
normalized barrier	D	$D(1/F(w))(\mathrm{d}F/\mathrm{d}w)$	attractant (if $\mathrm{d}F/\mathrm{d}w>0$) repellent (if $\mathrm{d}F/\mathrm{d}w<0$)
VMWT1	$D\rho(w)$	$D(\rho(w)/F(w))(\mathrm{d}F/\mathrm{d}w)$	inducer (if $\mathrm{d}\rho/\mathrm{d}w>0$) inhibitor (if $\mathrm{d}\rho/\mathrm{d}w>0$) attractant (if $\mathrm{d}F/\mathrm{d}w>0$) repellent (if $\mathrm{d}F/\mathrm{d}w<0$)
VMWT2	$G(w)$	$D(1/F(w))(\mathrm{d}F/\mathrm{d}w)$	inducer (if $\mathrm{d}G/\mathrm{d}w>0$) inhibitor (if $\mathrm{d}G/\mathrm{d}w<0$) attractant (if $\mathrm{d}F/\mathrm{d}w>0$) repellent (if $\mathrm{d}F/\mathrm{d}w<0$)

permitted to be a function of the control substance concentration w (Plank 2003). This results in a diffusivity of $d(w)=D\lambda(w)$ and a chemotactic sensitivity of $\chi(w)=D\rho(w)(1/F(w))(\mathrm{d}F/\mathrm{d}w)$, thus allowing both non-directional (random) and directional effects of the control substance to be specified independently. A second possible method is to combine the normalized and unnormalized barrier models by taking the transition rates as

$$T^{\pm}(x,t)=\rho\left(\frac{2F(w(x\pm\delta/2,t))}{F(w(x-\delta/2,t))+F(w(x+\delta/2,t))}+\frac{G(w(x\pm\delta/2,t))}{D}-1\right), \tag{3.20}$$

for some positive function G (Plank *et al.* 2004). Under this model, $d(w)=G(w)$ and $\chi(w)=D(1/F(w))(\mathrm{d}F/\mathrm{d}w)$, so again the non-directional and directional actions of the control substance may be chosen independently. Both these models (termed VMWT1 and VMWT2, respectively) are summarized in table 1.

Partial differential equations of the form (3.18) have been studied analytically for certain choices of the functions $\chi(w)$ and $d(w)$ and of the dynamics for w. For example, Keller & Segel (1971) obtained travelling wave solutions and Rascle & Ziti (1995) obtained similarity solutions in the case where chemotactic sensitivity is inversely related to w, and the control substance is consumed linearly by the cells. Othmer & Stevens (1997) considered three main cases of cell behaviour, which they termed 'aggregation' (meaning solutions in which the cell density aggregates to a finite positive value in certain regions), 'blow-up' (cell density tends to infinity in finite time) and 'collapse' (cell density tends to zero everywhere). Analogous results for the discrete RRW were originally shown by Davis (1990), and were linked to the continuum-level results by Plank (2003). Analytical conditions for the cases of aggregation, blow-up and collapse were developed by Levine & Sleeman (1997) and further theoretical work on mixed parabolic–hyperbolic equations was done by Takase & Sleeman (2002).

3.7. Applications of reinforced random walks

The theory of RRWs has been presented in terms of one-dimensional walks for simplicity, but is straightforward to extend to higher dimensions. Furthermore, the actions of multiple control substances $(w_1, \ldots, w_n)$ can be modelled by taking the transition probability function τ to be of the form $F(w)=F_1(w_1)\ldots F_n(w_n)$ (Levine *et al.* 2001). Under the normalized barrier model, this leads to a sum of n chemotactic terms in the continuum limit equation (3.18).

RRWs have been used to model the movement of myxobacteria (Othmer & Stevens 1997) and the migration of endothelial cells during tumour-induced angiogenesis (growth of new blood vessels; Levine *et al.* 2001; Sleeman & Wallis 2002; Plank & Sleeman 2003). These studies adopted the normalized barrier model, chiefly because this models a control substance that offers a directional stimulus (which is of prime importance for successful angiogenesis), but has no direct effects on cell motility. Nevertheless, the growth factors regulating angiogenesis do also influence cell motility and an extension to a VMWT model, which allows for both directional and non-directional effects, was proposed by Plank *et al.* (2004). A non-lattice RRW, similar to that outlined in §3.4, was subsequently used (Plank 2003; Plank & Sleeman 2004) to model angiogenesis in two and three dimensions. In addition to choosing an appropriate functional form for the reorientation rate $\mu_0(\theta)$, one must define the preferred direction θ_0. In the case of a chemoattractant, the natural choice is to define θ_0 to be in the direction of increasing chemical concentration (i.e. in the same direction as ∇w), which may be a function of the cell's location $\boldsymbol{x}$ and time t.

In models such as these, the control substance(s) may be assumed to be in a steady state, or the random walk model for cell movement may be coupled to one or more time-dependent PDEs for the concentration of the control substance(s). If the cells modulate their chemical environment by producing or consuming control substances, these PDEs will contain source/sink terms depending on cell density. In the case of angiogenesis, the basic cellular motion driving capillary growth is modelled by a random walk, but further rules must be specified to allow for capillary branching and looping (anastomosis). In addition to the transition probabilities, each cell has a probability, which may depend on local control substance concentration, of branching to create two daughter capillaries. If a capillary tip collides with an existing vessel, an anastomosis is formed and the colliding cell ceases to take part in the random walk.

An alternative to the RRW approach described above is to take a continuum Fokker–Planck equation of the form (3.18) as the starting point. This may be discretized using standard techniques to obtain a finite-difference equation of the form (2.4) (with the obvious extension to higher dimensions), which can be used to identify the relevant transition probabilities of moving left and right, and staying still. This method was developed by Anderson *et al.* (1997) to model nematode movement and has since been used to study tumour angiogenesis (Anderson & Chaplain 1998) and tumour cell invasion (Anderson *et al.* 2000), and to distinguish between the inhibitory and repellent effects of a signalling molecule called 'Slit' in experimental work (Cai *et al.* 2006). The random walk model for angiogenesis has also been coupled to a flow model to study the effects of blood flow and nutrient delivery in a nascent capillary network (McDougall *et al.* 2006).

Both the 'bottom-up' approach of the RRW and the 'top-down' approach of discretizing a PDE have the same governing equation (3.18) in the continuum limit. However, the two methods will, in general, result in random walks with different transition probabilities, illustrating the fact that, usually, there is not a unique random walk model corresponding to a given continuum equation. The RRW method has the advantage that the transition probabilities are derived mechanistically from the underlying biology, using a transition probability model of the type summarized in table 1, rather than via a mathematical discretization and normalization procedure (see Plank & Sleeman 2004, for details).

3.8. Biological orientation mechanisms

There are two main types of mechanisms for movement in response to a stimulus. Kinesis refers to the situation where the organism samples only the stimulus intensity at a single point and modulates its speed of movement (orthokinesis or *O*-kinesis) or its path sinuosity (klinokinesis or *K*-kinesis) accordingly. The terms *O*-kinesis and *K*-kinesis were first defined by Gunn *et al.* (1937) in terms of linear and angular speeds, but the redefinition of *K*-kinesis in purely spatial terms (Benhamou & Bovet 1989), by using sinuosity rather than rate of change of direction, has led to a much clearer view of the properties of kineses. By contrast, taxis is where the organism is able to detect a preferential direction of movement, and bias its turns accordingly, without necessarily altering its overall speed of movement or rate of turning.

The random walks described above are all couched in terms of transition rates, which are implicitly assumed to be under the full control of the migrating organism. This raises questions concerning the information that the organism requires in order to be able to exert this control, and the probable realism of assuming that such information is available. In the case of the barrier-type models (see §3.6), it is clear that the walker needs at least two sensors in order to compute the transition rates 'on the spot' (i.e. without moving); this type of mechanism is referred to as tropotaxis. The same is also true for the non-lattice random walk (§3.5) if the walker needs to resolve the target direction θ_0, for example by measuring ∇w. The same taxis may also be produced if the organism has only one sensor (or many sensors that are too close together to allow it reliably to detect differences), but moves its body in various directions to sample the local variations in stimulus; this is termed klinotaxis. In its simplest form, taxis does not incorporate a correlation between successive step directions, and hence corresponds to a BRW: individuals directly settle their local direction with respect to the target direction. More realistic taxis models can be obtained in the form of BCRW by introducing such a directional correlation (Benhamou & Bovet 1992; Benhamou 1994). The result of the taxis is then determined by the relative weights of the local directional bias (persistence, which controls the motility) and the global directional bias (goal attractiveness, which controls the advection), and by the level of random noise in the system.

By contrast, the local model in §3.6 comes under the category of kinesis, as opposed to taxis, because the walker measures only the stimulus intensity at a single point in order to compute the transition rates. Although the probabilities of moving in different directions are always equal at any given time, this mechanism results in an effective directional bias towards areas of low motility, illustrating the fact that a kinetic mechanism can produce a directional bias.

There are two working modes of kinesis (Benhamou & Bovet 1989): absolute (A) and differential (D). The movement is controlled, in A mode, with respect to the local stimulus intensity experienced at any given location or, in D mode, with respect to the change in stimulus intensity experienced during a step (e.g. through sensory adaptation). Both AO-kinesis and AK-kinesis are space-use mechanisms for exploiting patchy environments, enabling the animal to reduce locally the diffusion coefficient ($D=v/S^2$) of its movement (by decreasing mean speed v or increasing the sinuosity S) in the most suitable areas (Benhamou & Bovet 1989). Unlike AO-kinesis, however, AK-kinesis is able, when applied to a gradient field, to generate a slight drift in the gradient direction based on simple differences in angular diffusivity (σ_0^2), with a null mean turning rate $(\mu_0=0)$. This property was used by Jamon & Bovet (1987) to account for the homing behaviour of mice. However, the advection component is very weak (and accordingly most animals get lost), so that AK-kinesis cannot be considered as an efficient orientation mechanism. By contrast, DK-kinesis can reach 90% of the efficiency of a pure taxis (BRW; although taxis with persistence can outperform it in a noisy environment because persistence can be used to smooth the noise (Benhamou & Bovet 1992)). Indeed the so-called chemotaxis of bacteria (Alt 1980; Berg 1983) is mainly a DK-kinesis where the sinuosity is modulated through step length rather than turning angle variance (called a run-and-tumble mechanism). Finally, DO-kinesis seems to have no biological applications.

4. CONCLUSION

The field of random walks is a large and growing area of applied mathematics that is being increasingly used to model biological systems, notably in ecology (animal movements) and pathophysiology (cell movements in, for example, blood vessel formation and cancer cell invasion). In this review paper, the fundamental mathematical theory behind the unbiased and biased, and uncorrelated and CRWs has been developed. Limitations and extensions of these basic models have been discussed, and the progress and pitfalls associated with the application of random walk models to biological scenarios have been examined. A notable advantage of random walk models lies in their ability to distinguish, in a systematic way, underlying mechanisms (such as persistence, kineses and taxes) from observed data, in a way that would not be possible without the insight that rigorous mathematics provides. As a result of this, understanding of the various movement mechanisms that occur in nature has been greatly improved.

Research in the area of random walks is far from complete. There remains a wealth of mathematical problems relating to random walks that have yet to be solved (for example, formulae for the MSD and MDD in a general BCRW) and, of course, an almost endless supply of biological systems that are amenable to modelling using random walk techniques. We have discussed very simple environmental interactions (relating to simple changes in transition probabilities in a RRW) but, in reality, most animals (and many micro-organisms) are highly developed and able to interact extensively with their environment to optimize search strategies. Furthermore, most of the simple models discussed here implicitly assume homogeneous (or at most very simple heterogeneous) environments, whereas most real environments are highly complicated with barriers and differential terrain over all three dimensions that will affect movement behaviour and speed (Vuilleumier & Metzger 2006). Distinguishing between changes in behaviour due to environmental or spatial interactions simply by observing and analysing movements will always be difficult without further biological information. In general, we have considered only movements at an individual level, with population-level effects being subsequently extrapolated under the assumption that there are no interactions between individuals. However, in reality, these interactions can have an important effect on the overall behaviour and subsequent dispersal or orientation of a population (Couzin *et al.* 2005; Codling *et al.* 2007). Statistical techniques for the analysis of simple CRWs, for instance by measuring their MSD or their tortuosity, are relatively well developed, but there is little work in this area for the more general case of reinforced random walks. This is a potential avenue for future research.

One of the main issues that is causing many notable problems in the literature is the confusion between observed *pattern* and the underlying *process* that generated it. For example, Benhamou (2006) illustrated the high error rate in distinguishing between localized and global bias, while Parrish *et al.* (2002) and Codling *et al.* (2007) showed that it was very difficult to distinguish between individuals independently orienting towards a common target and an interacting group. Another example is aggregation, i.e. the increase in animal density in some places. This has often been considered as a mechanism, but is just a pattern that can be generated by two kinds of mechanisms: exploitation mechanisms (e.g. AO- and AK-kinesis) by which the animals spend more time in certain places and directional mechanisms (e.g. DK-kinesis and taxis) by which animals orient towards these places. This confusion between pattern and process has arguably led to many of the results in the literature (e.g. Viswanathan *et al.* 1996, 2000) interpreting animal movement as a Lévy process, a different class of random walk outside the scope of this review paper. Recent studies (Benhamou 2007; Edwards *et al.* 2007; Plank & James in press) have suggested that the Lévy model is less applicable than first thought and hence a better modelling approach may be to use extensions of the random walk models discussed here.

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Glossary

Ballistic movement: movement in which the *mean squared displacement* is linear with t^2.

Bias: preference for moving in a particular direction.

Biased random walk (*BRW*): random walk with *bias* but no *persistence.*

Biased and correlated random walk (*BCRW*)*:* random walk with *bias* and *persistence.*

Brownian motion: purely random movement first observed in the movement of pollen grains by Brown (1828).

Chemotactic sensitivity: the amount of directional *bias* (or *taxis*) induced by a control substance.

Correlated random walk (*CRW*)*:* random walk with *persistence.*

Diffusion: the spontaneous random movement of particles, resulting in net migration from an area of high concentration to that of low concentration.

Diffusion coefficient (*D*)*:* see *diffusivity.*

Diffusivity: the rate at which spontaneous random movements of particles occurs. For simple Brownian motion, diffusivity is defined as the ratio of the square of the distance moved in a short time step to the length of the time step.

Dirac delta function ($\delta_{\mathrm{d}}(x)$): function such that $\delta_{\mathrm{d}}(x)=0$ for $x\neq 0$ and the total area under the function is 1.

Displacement: straight-line distance between the start and endpoints of a *path.*

First passage (*or hitting*) *time:* first time that a walker arrives at a specified *location.*

Kinesis: non-directional response to a stimulus (cf. *taxis*).

Klinokinesis: type of *kinesis* in which the walker alters its *sinuosity* in response to a stimulus.

Location: coordinates of a walker at a certain time.

Markov process: process in which the probability of future states depends only on the present state, and not on the past state of the process.

Mean dispersal distance (*MDD*)*:* mean of the absolute *displacement* of all individuals in the population.

Mean squared displacement (*MSD*)*:* mean of the squared *displacement* of all individuals in the population.

Path: an ordered set of *location* coordinates for a walker.

Persistence: tendency to keep moving in the same direction, resulting in a correlation between successive step directions.

Position jump process: random walk in which the walker's *location* undergoes a series of discrete jumps.

Probability density function (*PDF*)*:* at time t, $p(x, t)\delta$ is equal to the probability of being between x and $x+\delta$ as $\delta\to 0$.

Reinforced random walk (*RRW*)*:* random walk in which the walker modifies the *transition probabilities* associated with its present *location*, e.g. by secreting a chemoattractant.

Simple random walk (*SRW*)*:* random walk with no *bias* or *persistence.*

Sinuosity: a measure of the *tortuosity* of a random walk.

Step length: distance (or time) moved in a straight line before changing direction.

Straightness index: ratio of the net *displacement* to the total distance travelled.

Taxis: directional (or oriented) response to a stimulus (cf. *kinesis*). Examples include chemotaxis, phototaxis, gyrotaxis.

Tortuosity: the amount of turning associated with a *path.*

Transition probability: probability of moving one *location* to another in a *position jump process*, or of changing from one velocity to another in a *velocity jump process.*

Turning angle: angle turned between successive steps.

Velocity jump process: random walk in which the walker's velocity (i.e. speed and direction) undergoes a series of discrete jumps.