technical paper

Diffusing populations: Ghosts or folks? *

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SUMMARY: *Random walk phenomena abound in engineering contexts, from pedestrian traffic to cell motility in tissue engineering. We contrast two random walk models. The ghost model involves individuals who pass through each other unhindered. The folks model involves agents that interact by refusing to share the same location. Simple simulations reveal behaviour consistent with classical diffusion ideas. Using intuitive arguments, we demonstrate how the models are naturally associated with partial differential equations. Seductive opportunities for the misinterpretation of experimental data are discussed.*

1   INTRODUCTION

In a random walk model (Hughes, 1995; Berg, 1983), an agent moves in a sequence of random steps. Such models are easy to simulate and well-suited to student projects. Students can learn important ideas in a highly intuitive context, while the subject is still an area of active mathematical research. We are interested in applications of random walk models in biological contexts, especially cell motility in tissue engineering and developmental biology (Simpson et al, 2007; Tremel et al, 2009). This kind of discrete random walk model may also be referred to as a kind of cellular automata model. We show how simulation leads to insight and suggests connections to other modelling paradigms, and then show how these connections can be derived mathematically. The procedure is in a sense the reverse of the process of discretising a partial differential equation (PDE) for numerical computation.

We consider agents occupying sites of the square lattice. The possible locations of an agent are (i, j), where i and j are integer coordinates. When attempting to move, an agent at site (i, j) will always choose one of the four target sites $(i, j − 1)$, $(i, j + 1)$, $(i − 1, j)$ or $(i + 1, j)$. The way the site is chosen is described in table 1. The third column gives the probability of the choice being made. To simulate this process, for each step we draw a random number S uniformly distributed in the interval $0 \le S \le 1$. The fourth column in the table shows the interval in which the random number must fall for the target site to be chosen.

Here $−1 \le \rho_x \le 1$ and $−1 \le \rho_y \le 1$: these two parameters control the preferred direction of drift. For example, if $0 < \rho_x < 1$, the agent makes both left and right moves, but right moves are favoured. Elegant results are available for a single agent moving by this or other rules (Hughes, 1995) and there are many applications (Hughes, 1995; Berg, 1983). However, we shall be interested in the behaviour of crowds of agents. We consider two models which represent different extremes.

In the *ghost model*, agents do not interact at all. Two agents can step through each other, and there is no limit on how many agents can occupy the same site at any instant. Questions about the ghost model can be rephrased as equivalent questions for a single agent in a classical random walk process.

In the *folks model*, we never permit two agents to occupy the same site simultaneously. This captures an important aspect of many multi-agent systems, where volume constraints or territorial aggression lead to one agent excluding other agents from its immediate vicinity.

There are many ways to implement the ghosts and folks models. We always consider the case where there are N agents present, and we select an agent at random and deal with it, then we chose another agent and deal with it, and so on. Of course, sometimes the same agent will be chosen more than once in this process; but the average number of times that a given agent is chosen per time step will be unity. This protocol is described as *random sequential update* (Chowdhury et al, 2005).

When an agent is chosen, there is a probability P that it decides to attempt a move: we draw a random number R from the interval $0 \le R \le 1$ and the agent attempts to move if $R \le P$, and decides not to move

Table 1:   Algorithm by which an agent at site (i, j) selects a target site.

Move chosen	Target site	Probability	Where random number S falls
vertically down	$(i, j-1)$	$\dfrac{1-\rho_y}{4}$	$0 \le S < \dfrac{1-\rho_y}{4}$
vertically up	$(i, j+1)$	$\dfrac{1+\rho_y}{4}$	$\dfrac{1-\rho_y}{4} \le S < \dfrac{1}{2}$
horizontally left	$(i-1, j)$	$\dfrac{1-\rho_x}{4}$	$\dfrac{1}{2} \le S < \dfrac{1}{2} + \dfrac{1-\rho_x}{4}$
horizontally right	$(i+1, j)$	$\dfrac{1+\rho_x}{4}$	$\dfrac{1}{2} + \dfrac{1-\rho_x}{4} \le S \le 1$

otherwise. The value of P can be used to control the level of activity of the agents, with small P representing minimal motility, and $P = 1$ representing maximal motility.

For each agent offered an opportunity to move, another random number S is drawn. Motile ghosts always accept an opportunity to move according to table 1. Motile folks, however, move according to the rules in table 1 with the additional constraint that the target site must be empty. If the target site is occupied, the attempt to move is aborted. This rule is known as an asymmetric simple exclusion process (Liggett, 1999; Spitzer, 1970) and has been used as a model for traffic flow (Chowdhury et al, 2005) and biological cell motility (Sander & Deisboeck, 2002).

We also discretise time into unit increments. We will place agents on the square lattice at time $t = 0$ and then implement the rules at $t = 1, 2, 3, ...$ times. All our simulations and arguments can be easily generalised to arbitrary lattice spacings and arbitrary time increments, but we keep things simple here by choosing uniform lattice spacing and constant time steps.

2   SIMULATIONS

It is relatively easy to perform simulations of the motions of ghosts or folks, but what quantitative data would we like to extract from simulations? The trajectory of each agent is a sequence of coordinates (X_t, Y_t), starting from (X_0, Y_0), where t indexes the time step. For simplicity, we consider only the horizontal (x) component of the trajectory, but the vertical (y) component of the trajectory data may be analysed in the same way. We use angle brackets to denote the average or expected value over all possible agent motions. The (random) net x-displacement $X_t - X_0$ after t time steps and its expected value μ_t are given, respectively, by:

$$X_t - X_0 = \sum_{l=1}^{t}\left(X_l - X_{l-1}\right)$$

$$\mu_t = \left\langle X_t - X_0 \right\rangle = \sum_{l=1}^{t}\left\langle X_l - X_{l-1}\right\rangle \qquad (1)$$

The expected net displacement μ_t gives no information about statistical fluctuations. For this, we study the sum of squares of individual horizontal displacements and its expected value:

$$S_t = \sum_{l=1}^{t}\left(X_l - X_{l-1}\right)^2$$

$$\left\langle S_t \right\rangle = \sum_{l=1}^{t}\left\langle \left(X_l - X_{l-1}\right)^2 \right\rangle \qquad (2)$$

Periodic (cyclical) boundary conditions are imposed along both the horizontal and vertical boundaries. This means that, for example, an agent residing in the bottom row of the lattice that moves in the negative y direction will appear in the top row of the lattice.

2.1   Simulating single agents or one tagged ghost

Consider a system with only one agent, or a particular tagged agent in a swarm of ghosts; for simulations these scenarios are equivalent. Simulation data in figure 1 shows sample trajectories, with $P = 1$ and $(X_0, Y_0) = (20, 50)$ for 500 time increments. Each sample trajectory comes from a single simulation. The trajectory is irregular in shape and another simulation would look different in detail, although some similarities between successive simulations might be seen. Figure 1(a) shows unbiased motion ($\rho_x = \rho_y = 0$); note that we cannot assume that unbiased motion produces perfectly symmetric individual trajectories. Figure 1(c) shows a trajectory with a preference to drift to the right imposed on the agent in the parameters ($\rho_x = 0.5$, $\rho_y = 0$). This desire is reflected in the trajectory.

Let us try to quantify this behaviour. For a single agent or a tagged ghost, then all steps are equivalent and the expected displacement in a single step is the same for all steps; so we have:

$$\left\langle X_l - X_{l-1}\right\rangle = \left\langle X_1 - X_0\right\rangle = \mu_1$$

$$= P\left[-1 \cdot \frac{1-\rho_x}{4} + 1 \cdot \frac{1+\rho_x}{4}\right] = \frac{P\rho_x}{2} \qquad (3)$$
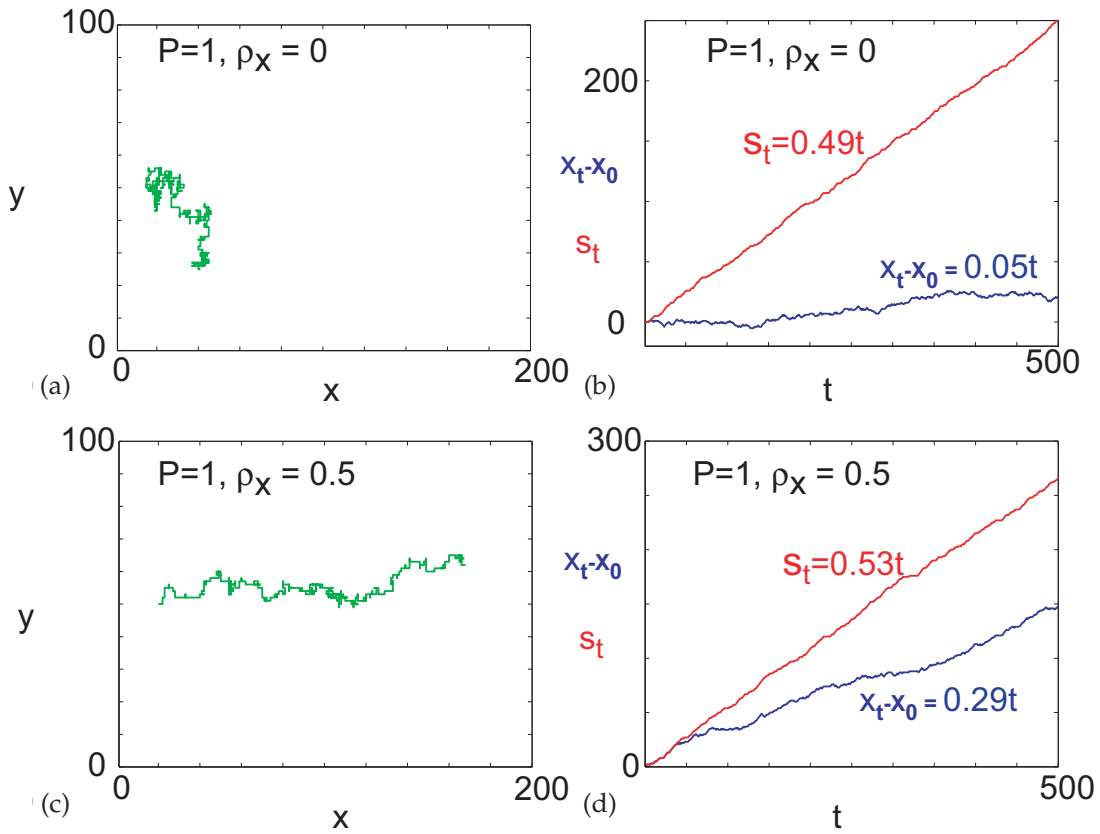
Figure 1: Trajectory data for a single isolated agent (or a tagged ghost within a population of ghosts) with $P = 1$. (a) The trajectory coordinates of an unbiased isolated agent initially located at (20, 50). (b) The corresponding evolution of $X_t - X_0$ and S_t. (c) The trajectory coordinates of a biased isolated agent, with $\rho_x = 0.5$, initially located at (20, 50). (d) The corresponding evolution of $X_t - X_0$ and S_t.

The factor of P accounts for the fact that not all opportunities to attempt a move are accepted by the agent. Thus, the average velocity component in the x direction is:

$$v_x = \frac{\mu_t}{t} = \mu_1 = \frac{P\rho_x}{2} \qquad (4)$$

In figure 1(b), we show $X_t - X_0$ from the trajectory with $\rho_x = 0$ given in figure 1(a). For this case $\mu_t = 0$, but we do not see $X_t - X_0 \equiv 0$: the agent makes excursions to the left ($X_t < X_0$) and to the right ($X_t > X_0$), but these are small compared to the duration of the process. For example, for this simulation a least-squares fit to a straight line constrained to pass through the origin gives $X_t - X_0 \approx 0.05t$. In figure 1(d), corresponding to the trajectory from figure 1(c) with $\rho_x = 0.5$, we have $\mu_t = 0.25t$, but for the simulation we find that $X_t - X_0 \approx 0.29t$. If instead of plotting single trajectories we take averages over many trajectories to compute an "average trajectory", then a plot of this average trajectory conforms more closely to the expected behaviour $\langle X_t \rangle = tP\rho_x/2$. Alternatively, we can run a single simulation over a much longer timescale and exploit a result known as the Strong Law of Large Numbers (Feller, 1971) that in this context says $X_t/t \to P\rho_x/2$ (in a well-defined sense appropriate to random systems) as $t \to \infty$.

The average velocity gives only a partial characterisation of the process: if it is found to be non-zero, it reveals the presence of bias, but we are unable to separate the values of P and ρ_x in the combination $v_x = P\rho_x/2$. What we need is a direct way to estimate P, which embodies the degree of motility of an agent. Consider the sum S_t of squared displacement increments and its average value (equation (2)). For a single agent or a tagged ghost, we have:

$$\left\langle (X_t - X_{t-1})^2 \right\rangle = P\left[(-1)^2 \cdot \frac{1-\rho_x}{4} + 1^2 \cdot \frac{1+\rho_x}{4} \right] = \frac{P}{2} \qquad (5)$$

and so

$$S_t = \frac{Pt}{2} \qquad (6)$$

Note that this is independent of the drift parameter ρ_x. If we average S_t over many simulations, or if we consider the limiting behaviour for one very long simulation, then the prediction of equation (6) will be a good approximation. In figure 1(b), we have $S_t \approx 0.49t$ for our single simulation with $\rho_x = 0$, while in figure 1(b), $S_t \approx 0.53t$ for our single simulation with $\rho_x = 0.5$. The simulations are consistent with the prediction that for our simulated cases, where $P = 1$, we should find $S_t \approx 0.5t$, independent of the value of ρ_x.

2.2   Tagged folks

If we tag one agent in a swarm of folks, equations (3) and (5) fail to hold, since some moves are aborted due to the interactions between agents. The value of μ_t is not known unless the position of all other agents at all times are known.

Trajectory data for populations of interacting agents differ from the trajectory data for a single agent. To demonstrate this, simulations are performed on a lattice where each site has been independently populated with probability $0 \leq C \leq 1$. For example, the lattice shown in figure 2 corresponds to $C = 0.25$.
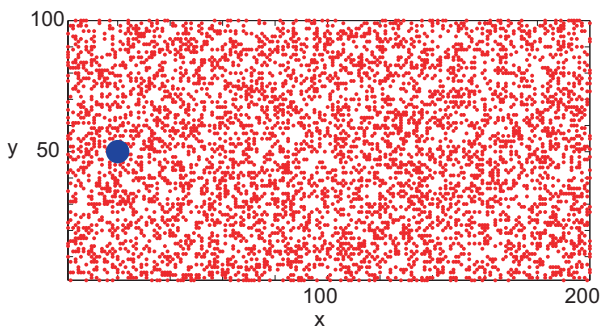

Figure 2:   A randomly populated lattice where each site is populated with $C = 0.25$. A tagged agent within the bulk population is located at (20, 50) is shown with an enlarged blue bullet.

To estimate the influence of the interactions between the agents, a tagged agent is introduced into the background population, such as the enlarged agent in figure 2. The tagged agent and the background agents behave identically. The system is allowed to evolve and we compute $X_t - X_0$ and S_t for the tagged agent. Results in figure 3 correspond to $C = 0.25$ and show both unbiased (figures 3(a) and (b)) and biased (figures 3(c) and (d)) simulations. In comparison with the results for a single agent in figure 1, we see that the rates of increase of $X_t - X_0$ and S_t are reduced when the background population are introduced. By performing a range of simulations and varying C, P and ρ_x, we find that the parameters that characterise an individual folk's motion are density dependent and are given by:

$$S_t(C) \approx \frac{P}{2}(1-C)$$

$$v_x(C) \approx \frac{P\rho_x}{2}(1-C) \tag{7}$$

where we have modified the notation for S_t and v_x to exhibit the value of C, the background concentration of folks. The influence of the interactions between agents in equation (7) appears through the factor $(1 - C)$. We note that these results are not derived rigorously, they are simply implied through our simulation data.
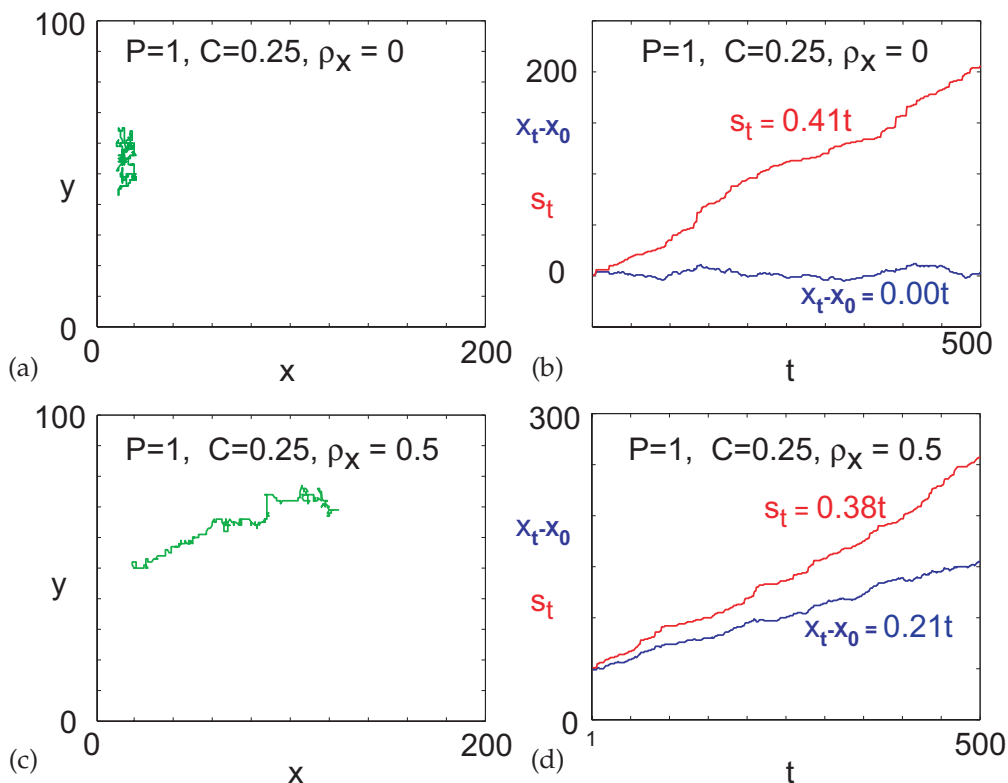

Figure 3:   Trajectory data for a tagged agent within a background population of interacting agents (folks) with $P = 1$. (a) The trajectory coordinates of an unbiased isolated agent initially located at (20, 50). (b) The corresponding evolution of $X_t - X_0$ and S_t. (c) The trajectory coordinates of a biased isolated agent, with $\rho_x = 0.5$, initially located at (20, 50). (d) The corresponding evolution of $X_t - X_0$ and S_t.

As expected, when $C = 0$, the behaviour is the same as for a single isolated agent, or a tagged ghost in a swarm of ghosts, but among genuine crowds ($C > 0$), individual ghosts do not behave like individual folks. Indeed, when the lattice is completely full and $C = 1$, for folks we have $v_x(1) = 0$ and $S_t(1) = 0$. This is intuitively reasonable since the tagged agent is unable to move at all on a completely occupied lattice.

3   PARTIAL DIFFERENTIAL EQUATION DESCRIPTION

We would like to consider average properties of a population of agents. A continuous-time, continuous-space description in terms of an agent density is natural. Here we show, using conservation of mass arguments, how the simple discrete random walk rules can be developed into a PDE description, often encountered in engineering applications.

In order to carry this out properly, we introduce a unit of length Δ called the lattice spacing and a unit of time τ called the time increment. (In our previous simulations, $\Delta = 1$ and $\tau = 1$.) An agent with integer coordinates (i, j) after k time increments will be deemed to be at position $(x, y) = (i\Delta, j\Delta)$ at time $t = k\tau$.

The ghosts and folks models will be considered separately, but in each case we shall average over each column of our square lattice to produce a one-dimensional model.

3.1   For ghosts

Let $\langle C_i^* \rangle$ be the averaged occupancy of any site in column i. Since any site can contain an unlimited number of agents, we normalise $\langle C_i^* \rangle$ by the maximum value across the lattice, defined as $C_i = \langle C_i^* \rangle / \langle C_i^* \rangle_{max}$, giving $0 \leq C_i \leq 1$.

A one-dimensional conservation of agent statement for the average occupancy of any site in column i between time t and $t + \tau$ is:

$$C_i(t+\tau) = C_i(t) + C_{i-1}(t)\frac{P(1+\rho_x)}{4} + C_{i+1}(t)\frac{P(1-\rho_x)}{4}$$
$$- C_i(t)\frac{P(1+\rho_x)}{4} - C_i(t)\frac{P(1-\rho_x)}{4} \tag{8}$$

The first term on the right of equation (8) is the averaged occupancy of any site in column i at time t, while the remaining four terms represent the change in occupancy of sites in column i due to transitions between sites in columns $(i - 1)$, i and $(i + 1)$. These remaining terms consist of two factors which can be interpreted as follows: (i) $P(1 \pm \rho_x)/4$ is the probability that an agent can step to the right and left, respectively; and (ii) $C_q(t)$ is the averaged occupancy of a site in column q at time t.

Dividing equation (8) by τ and rearranging, we obtain:

$$\frac{C_i(t+\tau) - C_i(t)}{\tau} = \frac{P}{4\tau}\left(C_{i-1}(t) - 2C_i(t) + C_{i+1}(t)\right)$$
$$- \frac{P\rho_x}{4\tau}\left(C_{i+1}(t) - C_{i-1}(t)\right) \tag{9}$$

As the terms on the right of equation (9) look similar to standard finite difference approximations (Chapra & Canale, 1998) (or using Taylor series expansions arguments), we rewrite equation (9) as:

$$\frac{C_i(t+\tau) - C_i(t)}{\tau} = \frac{P\Delta^2}{4\tau}\left(\frac{C_{i-1}(t) - 2C_i(t) + C_{i+1}(t)}{\Delta^2}\right)$$
$$- \frac{P\rho_x 2\Delta}{4\tau}\left(\frac{C_{i+1}(t) - C_{i-1}(t)}{2\Delta}\right) \tag{10}$$

By considering the limiting case where $\tau \to 0$ and $\Delta \to 0$ simultaneously while keeping Δ^2/τ constant (Codling et al, 2008), we replace the discrete derivatives with their continuous counterparts written in terms of a continuous variable $C(x, t)$:

$$\frac{\partial C}{\partial t} = D\frac{\partial^2 C}{\partial x^2} - V_x\frac{\partial C}{\partial x} \tag{11}$$

where

$$V_x = \lim_{\Delta,\tau\to 0}\left(\frac{P\rho_x}{2\tau}\right)$$
$$D = \lim_{\Delta,\tau\to 0}\left(\frac{P\Delta^2}{4\tau}\right) \tag{12}$$

The governing PDE for the non-interacting population of agents is an advection-diffusion equation. This equation is linear, which reflects the fact that the motile agents do not interact.

3.2   For folks

The averaging procedure will now be repeated for the folks model. Again, we average the occupancy of all sites within each column of the lattice giving C_i, which is the averaged occupancy of any site in column i. Since we permit a maximum of one agent per site, we have $0 \leq C_i \leq 1$ without any scaling. A one-dimensional conservation of mass statement for the average occupancy of any site in column i between time t and $t + \tau$ is:

$$C_i(t+\tau) = C_i(t) + C_{i-1}(t)\frac{P(1+\rho_x)}{4}\left(1 - C_i(t)\right)$$
$$+ C_{i+1}(t)\frac{P(1-\rho_x)}{4}\left(1 - C_i(t)\right)$$
$$- C_i(t)\frac{P(1+\rho_x)}{4}\left(1 - C_{i+1}(t)\right)$$
$$- C_i(t)\frac{P(1-\rho_x)}{4}\left(1 - C_{i-1}(t)\right) \tag{13}$$

The discrete conservation equation for the folks model is identical to the ghost model with the addition of an extra factor on each term associated with transitions between sites in columns $(i-1)$, i and $(i+1)$. The extra term, $1 - C_q(t)$, can be interpreted as the probability that a site in column q is unoccupied at time t. This extra term represents the interaction of agents as transitions are only allowed when the target site is empty.

Dividing equation (13) by τ and simplifying (Simpson et al, 2009a), we see that the conservation statement corresponds to an explicit finite difference approximation of a PDE written with $C(x, t)$ as the dependent variable, given by:

$$\frac{\partial C}{\partial t} = D \frac{\partial^2 C}{\partial x^2} - V_x \frac{\partial}{\partial x}\left[C(1 - C) \right] \qquad (14)$$

where the transport coefficients are given by equation (12).

Here we see that the PDE governing a swarm of folks is different from the PDE governing a swarm of ghosts through the appearance of a non-linear advection term. However, it is a real surprise that the diffusion term has a constant diffusivity, just as it did for the ghosts model – we might have expected it to reflect the exclusion of volume that we saw in the individual folks trajectories. We will comment more on this, after showing that equation (14) matches averaged simulation data very well.

Averaging the occupancy of sites across each column in the lattice allows us to reduce the two-dimensional random walk to a one-dimensional PDE. This differential equation is only valid for simulations where the initial average occupancy of all sites within every column on the lattice is a constant (Simpson et al, 2009a; 2009b). For more general initial conditions, it is possible to develop a two-dimensional conservation statement by averaging the occupancy of each site (i, j) across several identically prepared realisations to give $\langle C_{i,j} \rangle$. We leave this extension to two-dimensions as an exercise; the results can be checked with the conservation equations given elsewhere (Simpson et al, 2009a).

3.3 Comparing continuum and discrete models of folks

The PDE description given by equation (14) will now be tested by comparing the solution of equation (14) with density data extracted from the random walk simulations. Simulations with $0 \leq x \leq 250$, $0 \leq y \leq 20$, and $\Delta = \tau = 1$ are considered. For these simulations, periodic boundary conditions are imposed along the horizontal boundaries only. Reflecting boundary conditions are imposed on the vertical boundaries; this means that agents located in the left-most column are unable to move left, while agents in the right-most column are unable to move right. All simulations

that we consider are insensitive to the boundary conditions imposed on the vertical boundaries since we stop the simulations before such time that the agents touch the vertical boundaries. The initial distribution of agents has all sites with $90 \leq x \leq 110$ completely occupied.

Density data are extracted by averaging the occupancy of all sites across each column of the lattice, and then further averaging these estimates across 40 identically prepared realisations giving C_i for $i = 0, 1, ..., 250$. Scatter plots in figures 4(a) and 4(b) show a single realisation of an unbiased and biased simulation. Averaged density data are given in figures 4(c) and (d) showing the temporal evolution of the agent density profiles. The influence of the bias parameter is clear as the biased population is more effective in moving in the positive x direction than the unbiased population.

To compare the simulation density profiles with the solution of equation (14), we must obtain numerical solutions of equation (14). This can be done in several ways. For example, standard software for solving PDEs such as the MATLAB routine pdepe.m or the Numerical Algorithms Group routine d03pcf.f may be used. Alternatively, a finite difference approximation may be used. To do this, we replace the continuous spatial derivatives in equation (14) with a central difference approximation after discretising the domain $0 \leq x \leq 250$ with constant grid spacing δx. This leads a system of coupled non-linear first-order ordinary differential equations with t as the dependent variable. These ordinary differential equations are integrated using a backward Euler finite difference approximation (Chapra & Canale, 1998).

Numerical solutions of equation (14) with the same initial condition used in the discrete simulations are given in figured 4(e) and 4(f). Comparing these with the discrete averaged solutions, figures 4(c) and 4(d) show that the discrete and continuum profiles match very well. This confirms that the population-level evolution of the agent density is described by equation (14).

4 DISCUSSION AND CONCLUSIONS

We have outlined a description of two very different random walk models that can be implemented and analysed in order to give us deeper insight into the connection between individual-level random walk mechanisms and the collective population-level response. Computational methods to obtain population-level transport coefficients through agent tracking data are described, and data are presented showing how different estimates of diffusivities and drift velocities are obtained for both the ghost and folks random walk models. In parallel, a conservation statement, described by a PDE, is developed for the ghost and folks random walk models.
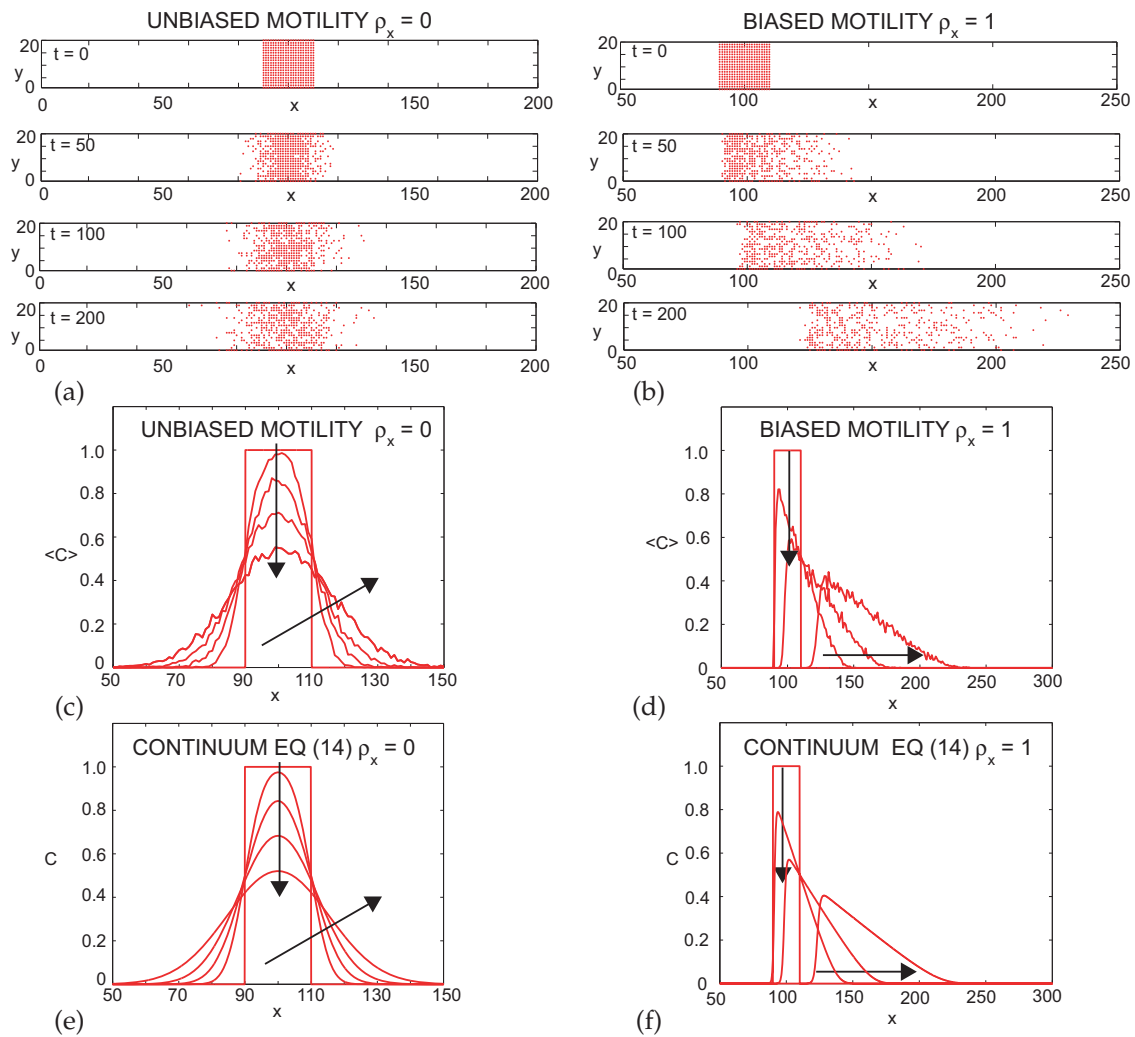
Figure 4: Comparison of population-level density information from simulating folks with solutions of the associated PDE. (a)-(b) Single realisations of unbiased ($\rho_x = 0$) and maximally biased ($\rho_x = 1$) folks. (c)-(d) Density data obtained from averaged occupancy across each column in the lattice, as well as across the 40 realisations, starting with the same initial conditions. The arrows indicate the direction of increasing time. (e)-(f) Numerical solutions of equation (14) with the same initial condition as the simulation data. The arrows indicate the direction of increasing time. Note: In (c) and (e), the profiles are given at $t = 0$, 50, 100, 200 and 400; in (d) and (f), the profiles are given at $t = 0$, 50, 100 and 200.

For unbiased motility ($\rho_x = 0$), both of the PDEs reduce to the linear diffusion (or heat) equation. This was a real surprise. It says that a swarm of unbiased folks behaves just like a swarm of unbiased ghosts. This is intriguing and unexpected given that the underlying random walk mechanism for ghosts and folks models are very different. However, by expanding each of the terms (equation (13)), we find that all the non-linear terms cancel out when $\rho_x = 0$, and the equation simplifies into equation (8); hence after taking the continuum limits, the swarm of folks satisfies the same PDE as a swarm of ghosts.

These results have bizarre consequences. If an individual interacting folk is tagged within a swarm of unbiased folks, the individual trajectory is affected by neighbourhood interactions – this can be observed from trajectory data. But at the population level, the distributions of the swarm of folks would be indistinguishable from a swarm of ghosts.

For biased motility, things are now different. Since the two PDEs are not identical, a swarm of biased folks behaves differently to a swarm of biased ghosts. The ghost population behaves like the standard linear advection-diffusion equation, which reflects the absence of interactions between the agents (Hughes, 1995; Berg, 1983). The folk population behaves like a non-linear advection-diffusion equation, due to their interactions. The advection term is non-linear and is similar to models used to represent traffic flow and Burgers' equation (Whitham, 1974).

These results provide great opportunities for data misinterpretation. If trajectory data is used to estimate the diffusivity from an interacting random walk mechanism, the density-dependent estimates given by equation (7) are inappropriate for describe the transport phenomena of the bulk population. This highlights the critical difference between self-diffusion of an individual within a population of

agents and bulk diffusion of the population. On the individual level, the interactions between agents is observed through the tracking data, yet when we consider the averaged behaviour of the population these interactions do not appear in the description of the population level behaviour.

There is much interest in understanding the connection between the microscopic description of individuals and the macroscopic description of populations. This brief exploration here illuminates many interesting and intriguing features. Such studies will help us understand the emergent behaviour of swarms of animals, cells and, indeed, perhaps even humans.

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Barry Hughes studied at the University of Queensland and the Australian National University, before undertaking postdoctoral work in the USA at the Universities of Rochester Maryland in the physical sciences, and the University of Minnesota in chemical engineering. He has held positions at the Australian National University and the Royal Military College, Duntroon, and has been at the University of Melbourne since 1986. His treatise *Random Walks and Random Environments* (2 volumes, Oxford University Press, 1995-1996) reflects longstanding interests in the applications of probabilistic modelling in physics and engineering. In recent years his interests have turned towards applications of probability in the social sciences and life sciences, and to mathematical modelling in developmental biology and other biological systems where cell motility is of paramount importance.

KERRY LANDMAN

Kerry Landman received her PhD from the University of Melbourne, and returned there after six years in the USA, during which she worked at MIT, the Environmental Protection Agency and Southern Methodist University. Her research interests are in mathematical modelling of a wide range of industrial, environmental, biological and medical phenomena. These include shape changes of red blood cells, indoor pollution by radon gas, heat loss in houses, consolidation and filtration of minerals waste, cooking of wheat grains for breakfast cereal manufacture, and the design of windscreen wipers. From 1993 to 1997, Kerry was the Director of the Mathematics-in-Industry Study Group.