

Exits in order: How crowding affects particle lifetimes

Catherine J. Penington,¹ Ruth E. Baker,² and Matthew J. Simpson¹

¹*School of Mathematical Sciences, Queensland University of Technology, Brisbane, Australia*

²*Mathematical Institute, University of Oxford, Radcliffe Observatory Quarter, Woodstock Road, Oxford, United Kingdom*

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Diffusive processes are often represented using stochastic random walk frameworks. The amount of time taken for an individual in a random walk to intersect with an absorbing boundary is a fundamental property that is often referred to as the particle lifetime, or the first passage time. The mean lifetime of particles in a random walk model of diffusion is related to the amount of time required for the diffusive process to reach a steady state. Mathematical analysis describing the mean lifetime of particles in a standard model of diffusion without crowding is well known. However, the lifetime of agents in a random walk with crowding has received much less attention. Since many applications of diffusion in biology and biophysics include crowding effects, here we study a discrete model of diffusion that incorporates crowding. Using simulations, we show that crowding has a dramatic effect on agent lifetimes, and we derive an approximate expression for the mean agent lifetime that includes crowding effects. Our expression matches simulation results very well, and highlights the importance of crowding effects that are sometimes overlooked. *Published by AIP Publishing.* [<http://dx.doi.org/10.1063/1.4953913>]

INTRODUCTION

Steady state models of diffusion are widely used in many applications, including physics,^{1,2} engineering,³ and life sciences.^{4–8} By definition, steady state conditions arise as a long-time limit of a transient process. Therefore, an implicit assumption in invoking these models is that time has progressed to infinity, $t \rightarrow \infty$. Since in reality it is impossible to wait an infinite amount of time, it is important to determine whether a sufficiently large amount of time has passed so that it is reasonable to use a steady state approximation.^{9–15} Sadly this important question is often overlooked.

In a discrete random walk model of diffusion with absorbing boundary conditions, the time to reach steady state is related to the mean particle lifetime, the average total time an individual remains in the system.^{11,12} Previous analysis of classical non-excluding random walk models is well known.^{16,17} However, many modern applications require descriptions of diffusive transport, such as models of the motion of pedestrians,¹⁸ animals,¹⁹ or biological cells,²⁰ involve individuals, often called agents, that cannot occupy the same space as another individual. This is known as volume exclusion or crowding.^{21,22}

Throughout this work, we refer to individuals in the standard non-excluding random walk model of diffusion as *particles*. This terminology leads us to consider mean particle lifetime, which has been studied extensively.^{11,12,16} Once crowding is introduced, we refer to individuals in the excluding random walk model of diffusion as *agents*. This naturally leads us to consider an expression for the mean agent lifetime, which has not been explored before.

Without any analysis, it is not obvious what effect crowding has on agent lifetimes. The effects of crowding are not always obvious. For example, the evolution of the

spatial distribution of particles in the standard unbiased non-excluding random walk is governed by the linear diffusion equation.¹⁶ It is surprising that the evolution of the spatial distribution of agents in an unbiased exclusion process is governed by the same linear diffusion equation.^{23,24} However, other features of these two different discrete models are very different. For example, the expected trajectories of agents in an exclusion model are very different to the expected trajectories of particles in a standard non-exclusion random walk.²⁵

While previous analysis has described mean particle lifetimes without crowding,^{11,12} in this work we investigate mean agent lifetimes, where agents have volume and cannot occupy the same space. This kind of model can be used to study ion conduction in narrow channels.^{26,27} We use averaged simulation results to demonstrate substantial differences between models with and without exclusion. Furthermore, we construct a new analytical expression for the mean particle lifetime that captures the main features of the simulation results.

MATHEMATICAL MODEL

We model the motion of individual random walkers on a finite, one-dimensional regular lattice, with lattice sites indexed $i = 1, 2, 3, \dots$. The lattice sites are a distance Δ apart, and the total lattice length is $L\Delta$, for a given number of sites, $L \in \mathbb{N}$. Each agent occupies a single lattice site, and we define an agent's position relative to the left boundary of the lattice, at $x = 0$. An agent occupying the i th lattice site is therefore at position $x = i\Delta$. At each discrete time step of duration, τ , individual agents are randomly chosen, without replacement, to attempt to move. This ensures that each agent attempts to move exactly once per time step, but the order in which the

agents attempt to move is random.²⁸ The chosen agent then attempts to step to site $i - 1$ with probability p_L , or to site $i + 1$ with probability p_R , or remains in the same position with probability $p_S = 1 - p_L - p_R$, with $p_L + p_R \leq 1$.

If an agent immediately adjacent to the left boundary, at lattice site $i = 1$, moves left, the agent is absorbed by the boundary and exits the system permanently. The right boundary is reflecting: if an agent at the right boundary attempts to move right, the move is aborted. We define the agent's lifetime as the time T until the agent is absorbed by the left boundary, and our aim is to find the expected value for the agent's lifetime depending on its starting position, $\mathbb{E}(T(x))$.

In the simplest version of the model, the non-exclusion model, agents move without interacting and there is no restriction on the number of agents at any one lattice site. This model has been studied in detail by many researchers,^{12,16,17} who have shown that the expected particle lifetime, $E(x)$, is given by the solution of the difference equation

$$p_L E(x - \Delta) + (p_L + p_R)E(x) + p_R E(x + \Delta) + \tau = 0. \quad (1)$$

When we consider x as a continuous variable, Equation (1) can be identified with the differential equation

$$D \frac{d^2 E}{dx^2} + V \frac{dE}{dx} + 1 = 0, \quad (2)$$

where

$$D = \lim_{\Delta, \tau \rightarrow 0} \frac{\Delta^2(p_L + p_R)}{2\tau}, \quad V = \lim_{\Delta, \tau \rightarrow 0} \frac{\Delta(p_L - p_R)}{\tau}. \quad (3)$$

These relations hold for finite choices of Δ and τ . For example, Ellery *et al.*¹² showed that the solution of Equation (2) matches simulation data with $\Delta = \tau = 1$.

In this manuscript, we extend known theory about mean particle lifetime to describe the mean lifetime of agents in an exclusion model. In the exclusion model, at most one agent can occupy a single lattice site at any time, and if an agent attempts to move to an already-occupied site then

the move is aborted. The probability that an agent at site i successfully moves left is $p_L \mathbb{P}(\text{site } i - 1 \text{ is unoccupied})$ and the probability that the agent successfully moves right is $p_R \mathbb{P}(\text{site } i + 1 \text{ is unoccupied})$.¹³⁻¹⁵

THE EFFECTS OF EXCLUSION

We are interested in a discrete space, discrete time random walk model. However, the average agent occupancy of lattice sites can often be well-approximated by a continuous function.²⁴ This average occupancy in a system where isolated agents move randomly without bias evolves according to a linear diffusion equation.²⁹

Ellery *et al.*¹² show that, for a non-excluding model where individuals move left or right with equal probability, the mean particle lifetime for an individual starting at position x is $E(x) = x(2L - x)/2D$, the solution to Equation (2) with $E(0) = 0$ and $dE/dx(L) = 0$. Since it is well established that the spatio-temporal distributions of agent or particle density in the unbiased exclusion and non-exclusion models obey the same linear diffusion equation,²⁹ we might be tempted to assume that Equation (2) also holds for the exclusion model. However, while the movement of the group as a whole is described by identical macroscopic equations, the average number of successful moves each individual makes is very different. This is because, in an exclusion model, the average movement of an agent depends on the surrounding agent density.

To demonstrate these features we perform simulations of models with and without exclusion, and with varying initial densities of agents. Figure 1 shows the resulting particle lifetimes, together with their mean value for each position x . The standard model without exclusion has the expected parabolic curve, $E(x) = x(2L - x)/2D$, but the variance in particle lifetimes is large at all starting positions. Some agents initially located towards the boundary at $x = L\Delta$ exit the

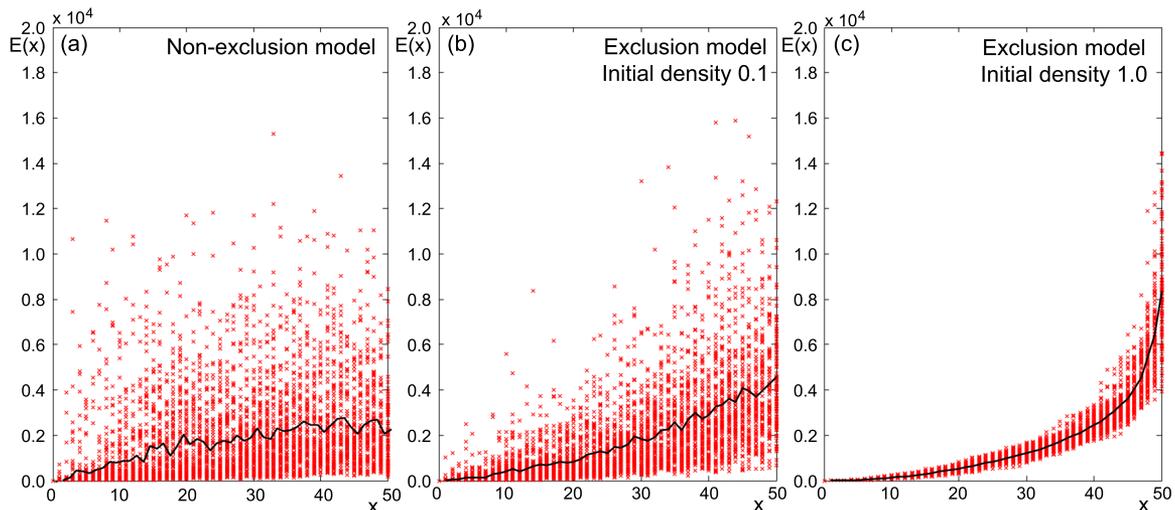


FIG. 1. Simulation data showing lifetime information about (a) particles with no exclusion, (b) agents with exclusion and an initial density of 0.1, or (c) agents with exclusion and an initial density of 1.0. In all cases, $\Delta = 1$, $\tau = 1$, and $L = 50$. Each red cross represents the lifetime of a single agent or particle at that starting location; the black lines are the mean for each starting position x . There are always 5000 particles or agents in total, across multiple simulations. In each simulation of (b), the starting position of each agent is chosen randomly, but the average initial density across the entire lattice is always 0.1. Each simulation of (a) and (c) begins with exactly one individual at each starting position.

system after less than 200 time steps, which is less than 10% of $E(x)$ for that position. At the opposite end of the lattice, near $x = 0$, some agents take more than 10 000 time steps to leave. In contrast, once exclusion is incorporated, the mean agent lifetime does not follow a parabolic curve with position, and the variance is smaller, as shown in Figures 1(b) and 1(c). The differences between the non-excluding and the exclusion models are obvious even with a low initial density, where agents do not interact often, and increase with initial density.

THEORY FOR EXCLUSION

As the excluding and non-excluding models give rise to very different mean lifetimes, we now develop new theory to explain the mean agent lifetime. To do this we consider a finite lattice, with length $L\Delta$, which is initially fully occupied by agents. While all our results are for this initial condition, we will discuss alternative initial conditions in the section titled "Discussion." At the beginning of each simulation, all potential moves are aborted by the presence of other agents, except for the agent at site $i = 1$, which is able to move left and exit the system. This must therefore be the first successful event to occur. Once this agent has exited the system, the agent at site $i = 2$ will have the opportunity to move left. The second agent may undergo a series of movement or rest events, but it will eventually leave the system when it resides at site $i = 1$ and attempts to move left. As agents exit the system the density of agents decreases, allowing more movement, but since two agents cannot occupy the same site at once they cannot overtake each other: the agents must remain in their original order. This means that the agents must exit the system in order. We therefore calculate the mean agent lifetime for a starting position $x = i\Delta$ by calculating the mean time for the i th agent to leave the system.

If $n - 1$ agents have left the system at time t , we use $E_n(t)$ to denote the remaining time until the n th agent exits the system. If the probability that the site x is occupied by an agent is equal to the average agent density at that site, $C(x, t)$, the probability that the left-most agent is at position $x = i\Delta$ can be approximated by

$$A(x, t) = C(x, t) \left(1 - \sum_{y=1}^{i-1} A(y, t) \right). \quad (4)$$

We can then calculate an approximate probability distribution for $E_n(t)$ by tracking the left-most agent as it moves towards the absorbing boundary.

In any time step, the probability that the left-most agent successfully moves left is p_L , since the target site is always vacant. However, a successful move right can only happen if target site is unoccupied. The probability of a successful move right is therefore

$$\begin{aligned} \mathbb{P}(\text{left-most agent at site } i \text{ moves right successfully}) \\ = p_R (1 - \mathbb{P}(\text{site } i + 1 \text{ is occupied by an agent})). \end{aligned} \quad (5)$$

A key element of our analysis is that we must approximate the probability that an agent occupies the lattice site $i + 1$ (the probability that the left-most agent has a neighbour). We

achieve this by introducing a function, f , which depends on the lattice site occupied by the left-most agent, i , the number of lattice sites in the system, L , and the number of agents not including the left-most remaining in the system, m , such that

$$\mathbb{P}(\text{left-most agent has a neighbour}) \approx f(m, i, L). \quad (6)$$

Calculating exit probabilities

Let $P(m, s, i, L)$ be the probability that the left-most agent takes s steps to leave the system if it starts at site i and there are m other agents remaining in a system with L lattice sites in total. We can then condition on the first step to obtain

$$\begin{aligned} P(m, s, i, L) = p_L P(m, s - 1, i - 1, L) \\ + (p_S + p_R f(m, i, L)) P(m, s - 1, i, L) \\ + p_R (1 - f(m, i, L)) P(m, s - 1, i + 1, L). \end{aligned} \quad (7)$$

The expected number of steps that the left-most agent takes to leave the system, $R(m, i, L)$, is therefore defined as

$$R(m, i, L) = \sum_{s \geq 1} s P(m, s, i, L), \quad (8)$$

and we sum Equation (7) over s to obtain the second-order difference equation

$$\begin{aligned} R(m, i, L) = p_L R(m, i - 1, L) \\ + (p_S + p_R f(m, i, L)) R(m, i, L) \\ + p_R (1 - f(m, i, L)) R(m, i + 1, L) + 1. \end{aligned} \quad (9)$$

Boundary conditions for Equation (9) can be found in a similar way: we know that the probability an agent takes one step to leave the system starting at site $i = 1$ is p_L , and if the agent takes more than one step to leave the system from site $i = 1$ then its next move cannot be left, so we obtain the following equation for $R(m, 1, L)$:

$$\begin{aligned} R(m, 1, L) = (p_S + p_R f(m, 1, L)) R(m, 1, L) \\ + p_R (1 - f(m, 1, L)) R(m, 2, L) + 1. \end{aligned} \quad (10)$$

For the other boundary, we know that if there are m other agents in the system they need m unique sites to occupy, so $f(m, (L - m), L) = 1$. Therefore we know that

$$\begin{aligned} R(m, (L - m), L) = p_L R(m, (L - m - 1), L) \\ + (1 - p_L) R(m, (L - m), L) + 1. \end{aligned} \quad (11)$$

Equations (9) and (11) can be reduced inductively to the first-order difference equation

$$\begin{aligned} R(m, i, L) = R(m, i - 1, L) + \frac{1}{p_L} \sum_{j=0}^{L-m-i} \left(\frac{p_R}{p_L} \right)^j \\ \times \left[\prod_{k=0}^{j-1} (1 - f(m, i + k, L)) \right], \end{aligned} \quad (12)$$

which can be solved using the left boundary condition, Equation (10), to give the following expression for $R(m, i, L)$:

$$R(m, i, L) = \frac{1}{p_L} \sum_{l=1}^i \sum_{j=0}^{L-m-l} \left(\frac{p_R}{p_L} \right)^j \left[\prod_{k=0}^{j-1} (1 - f(m, k + l, L)) \right]. \quad (13)$$

To calculate higher moments, we can define the family of functions $R^{(q)}(m, i, L)$ for $q \in \mathbb{N}$,

$$R^{(q)}(m, i, L) = \sum_{s \geq 1} s^q P(m, s, i, L), \quad (14)$$

where we note that $R^{(0)} \equiv 1$. We then obtain an equivalent equation to Equation (9), which can be solved in a similar manner to give the following expression for $R^{(q)}(m, x, L)$:

$$\begin{aligned} R^{(q)}(m, i, L) = & -\frac{1}{pL} \sum_{p=0}^{q-1} \binom{q}{p} (-1)^{q-p} \\ & \times \sum_{l=1}^i \sum_{j=0}^{L-m-l} \left(\frac{pR}{pL}\right)^j R^{(p)}(m, j+l, L) \\ & \times \prod_{k=0}^{j-1} (1 - f(m, k+l, L)). \end{aligned} \quad (15)$$

The new factor $\sum_{p=0}^{q-1} \binom{q}{p} (-1)^{q-p}$ appears in Eq. (15) as we are summing over s^q rather than s . The difference between consecutive time steps is now $s^q - (s-1)^q = \sum_{p=0}^{q-1} \binom{q}{p} (-1)^{q-p}$.

Approximating $f(m, i, L)$

To arrive at an approximate expression for f , we assume that the function depends on the average density of agents behind the left-most agent, $m/(L-i)$. We therefore plot estimated values of f obtained from averaged simulation results against the density for different values of i and L using MATLAB. Figure 2(a) shows the results graphically for all possible values of m when $i = 1$ and $L = 50$; results for other choices of i and L are similar and not shown here.

The frequency of neighbouring agents to the left-most agent appears to follow a power law in the average density behind the left-most agent. To investigate this further, we plot the frequency of left-most agent neighbours against average density behind the left-most agent ($m/(L-i)$) on a logarithmic scale. Figure 2(b) shows results for $x = 1$ and $L = 50$. The frequency appears to behave differently in two different regions: at lower densities, $\log(f)$ increases slowly with increasing agent density, while at higher densities $\log(f)$ increases more rapidly. Therefore a sensible choice for f is a piecewise function with two regions.

We know that $f(m, i, L) = 1$ when $m = L - i$, since at this point all lattice sites to the right of the left-most agent must be occupied and so the left-most agent must have a neighbour. Therefore, when the agent density behind the left-most agent is higher, the (piecewise) linear approximation must have the form $\log(f) = b \log(m/(L-i))$ for some parameter b . We observe that at lower agent densities the line has gradient close unity, so we consider the following piecewise linear approximation:

$$\log(f) = \begin{cases} y + a & y \leq \phi \\ b y & y > \phi \end{cases}, \quad (16)$$

where

$$y = \log\left(\frac{m}{L-i}\right), \quad \phi = \frac{a}{b-1}.$$

We fit estimates of $\log(f)$ from simulation data to Equation (16) for all possible values of m for fixed position x and system length L . The parameters a and b in Equation (16) are functions of i and L . We can therefore fit the values of a and b to curves for all possible values of position i for a fixed system length L . Figure 3 shows the results for $L = 30$; other choices of L give similar results and are not shown here. The parameter $a(i, L)$ appears to follow an exponential curve, so we fit it to the function

$$a(i, L) = \alpha e^{\beta i} + \gamma e^{\delta i}, \quad (17)$$

with four unknown parameters α , β , γ , and δ . The parameter $b(x, L)$ is fitted to the function

$$b(i, L) = g i^h, \quad (18)$$

with two unknown parameters g and h .

We now have six unknown parameters (α , β , γ , δ , g , h) that depend on the system length L . Unlike the left-most agent position and the number of agents remaining in the system, there is no limit to the possible size of L and so we cannot evaluate the parameters for every possible system length. We restrict our investigation to systems where $L = 10, 15, 20, \dots, 50$.

There appears to be no discernible trend in h across the range of L we examine, so we take the mean value and approximate $h \approx 0.78$. Using this value for h in Equation (18) we can obtain a slightly different best-fit values for g across the

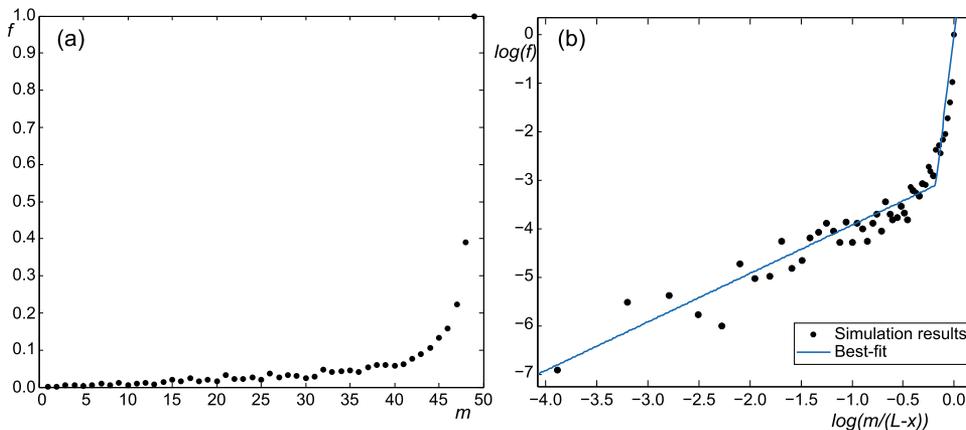


FIG. 2. (a) Frequency of neighbour to the left-most agent (black dots), for different numbers of agents remaining in the system (m). In this example, the left-most agent is at position $i = 1$ and the system length is $L = 50$. (b) Log-log plot of frequency of neighbour to the left-most agent as a function of average agent density behind the left-most agent. Black dots are simulation results, while the piecewise linear best-fit is shown in blue. In both figures, the simulation results are the averages of 1000 identically prepared simulations.

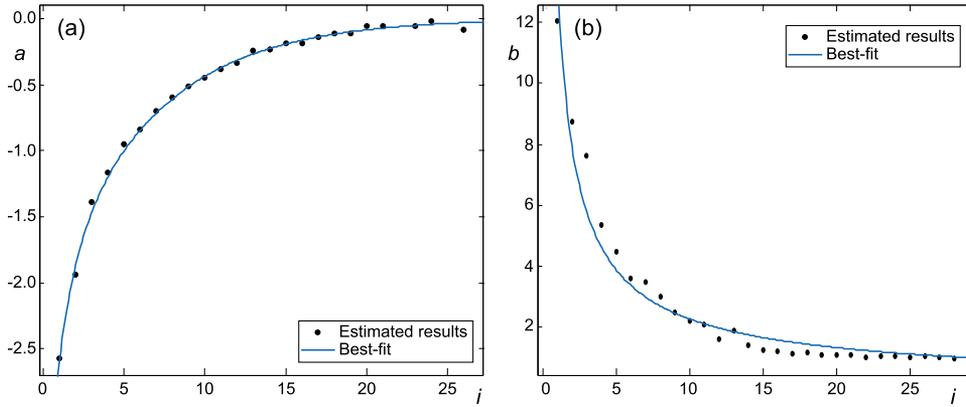


FIG. 3. Fitting (a) $a(i, L)$ and (b) $b(i, L)$ to curves across all possible positions i for a fixed system length $L = 30$. Black dots are estimated results from fitting Equation (16) to the simulated estimates for the unknown function f , while the best-fits are shown in blue.

range of L . The relationship between g and L is approximately linear, and we obtain $g \approx 0.35L + 3.1$.

Similarly, there appears to be no discernible trend in α across the range of L we consider, so we take the mean value, giving $\alpha \approx -2.23$. We use this value for α in Equation (17), and slightly adjust the best values for β . There is an approximately inverse relationship between β and L for the range of L we consider, and we find that $\beta \approx -6/L^{1.06}$.

If we use this approximation in Equation (17) we can again slightly adjust the best-fit values for γ , and discover that there is no discernible trend in γ across L . We therefore take the mean value, and approximate $\gamma \approx -1.81$. Finally, we make another adjustment of the best-fit values for δ based on the approximations for α , β , and γ , and find that the results fit the line $\delta = 0.031L - 2.1$.

In summary, combining Equations (16)–(18) with the approximations for α , β , γ , δ , g , and h , we obtain an approximation for f , namely

$$f(m, i, L) = \begin{cases} e^{\alpha} \left(\frac{m}{L-i} \right) & \text{if } m < e^{\phi}(L-i) \\ \left(\frac{m}{L-i} \right)^{\beta} & \text{otherwise} \end{cases}, \quad (19) \quad \text{and}$$

where

RESULTS

We can use the approximation given in Equation (19) for f in the expression for the expected time between agents to leave the system, $R(m, i, L)$, found in Equation (13). To find the expected lifetime of a particle as a function of its starting position, we define

$$T_T(i) = \text{Total lifetime of particle starting at position } x = i\Delta = \sum_{n=1}^i E_n(T_T(i-1)) \quad (20)$$

$$E(i) = \mathbb{E}(T_T(i)).$$

We then calculate

$$\begin{aligned} E(2) &= \sum_{t \geq 1} t \mathbb{P}(T_T(2) = t) = \sum_{r \geq 1} \sum_{s \geq 1} (r+s) \mathbb{P}(T_1(0) = r, T_2(r) = s) \\ &= \sum_{r \geq 1} r \mathbb{P}(T_1(0) = r) \left(\sum_{s \geq 1} \mathbb{P}(T_2(r) = s | T_1(0) = r) \right) + \sum_{s \geq 1} s \left(\sum_{r \geq 1} \mathbb{P}(T_2(r) = s | T_1(0) = r) \mathbb{P}(T_1(0) = r) \right) \\ &= \mathbb{E}(T_1(0)) + \sum_{s \geq 1} s \left(\sum_{r \geq 1} \mathbb{P}(T_2(r) = s | T_1(0) = r) \mathbb{P}(T_1(0) = r) \right). \end{aligned}$$

We use the approximation

$$\sum_{r \geq 1} \mathbb{P}(T_2(r) = s | T_1(0) = r) \mathbb{P}(T_1(0) = r) \approx \mathbb{P}(T_2(E(1)) = s), \quad (21)$$

and equivalent expressions for larger values of i to obtain an approximate expression for the expected lifetime of a particle from its starting position,

$$E(i) = \sum_{r=1}^i \sum_{y=1}^r A(y, E(i-1)) R(L-r, y, L), \quad (22)$$

where $A(y, t)$ is defined in Equation (4), $R(L-r, y, L)$ is defined in Equation (13), and $f(m, i, L)$ is defined in Equation (19).

The average lifetimes of agents at each starting position are estimated using 500 identically prepared realisations of

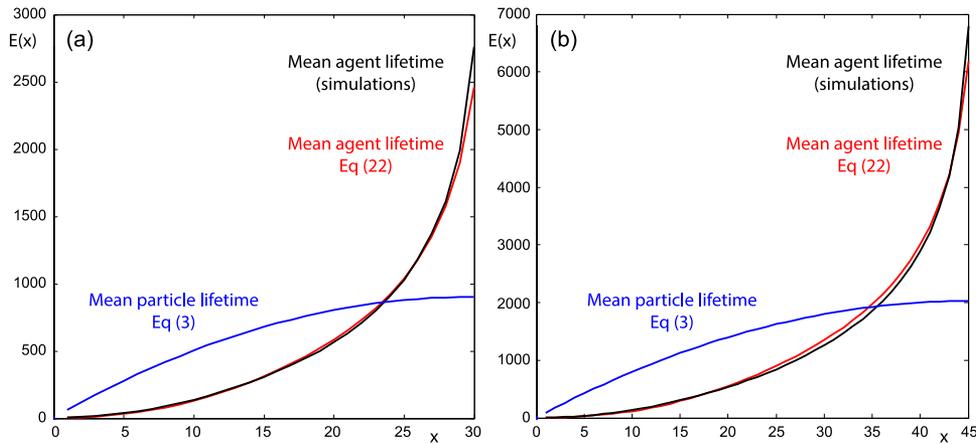


FIG. 4. Mean agent lifetimes by initial position for agents with an initial density of one agent at each lattice site, exiting the system on the left. Unit lattice spacing ($\Delta = 1$) and time-steps ($\tau = 1$) are always used. The lattice has (a) $L = 30$ or (b) $L = 45$ sites in total. The red line shows the average lifetime for particles over 500 (discrete) simulations, and the black line shows the solution to Equation (22) using the function $f(m, i, L)$ given in Equation (19). For comparison, the average particle lifetime for the non-excluding model is shown in blue. Note the different scales on each subfigure.

the stochastic simulation algorithm. Averaged lifetime data from the simulations are compared to the prediction of Equation (22), and match very well. Figure 4 shows the results for $L = 30$ and $L = 45$; other values of L also show good results.

Throughout this work we have always chosen $\Delta = \tau = 1$. In many ways the choice of Δ is arbitrary, since our choice of $\Delta = 1$ can always be re-scaled to any other value of Δ where appropriate. The choice of τ is more subtle. In the discrete model p_R is the probability that an isolated agent will step a distance Δ to the right during a time interval of duration τ . This means that any choice of p_R and τ such that the ratio p_R/τ is constant will lead to identical outcomes. Alternative results only arise by choosing a different value of the ratio p_R/τ or p_L/τ . We note that the method outlined here applies to arbitrary values of Δ and τ , and thus Equation (22) depends on both variables.

DISCUSSION

The mean particle lifetimes for the standard non-excluding model of diffusion are well known.¹⁶ The main aim of this work is to present an analogous expression, Equation (22), for the mean agent lifetime in an exclusion model with crowding. The mean lifetimes of individuals in excluding and non-excluding models are very different, as the results in Figures 1 and 4 clearly illustrate. For agents initially positioned towards the absorbing boundary, crowding reduces the mean agent lifetime as the presence of other agents reduces the probability that the agent will move away from the absorbing boundary. Non-excluding point particles often move through most of the systems' lattice sites before eventually reaching the absorbing boundary, while excluding agents tend to be herded towards the absorbing boundary by the agents behind them. If an agent begins the simulation far from the absorbing boundary, however, its lifetime can be significantly longer than a non-excluding particle in the same position, since the agents closer to the absorbing boundary take many steps to move out of the way.

Our expression for the mean agent lifetime matches simulation data extremely well for a range of system lengths, L . Figure 4 illustrates how closely the solution to Equation (22) matches the actual averaged values for the

range of starting positions. While our result in Equation (22) must still be calculated for any given starting position $x = i\Delta$ and lattice length L , the computation time for evaluating Equation (22) using the function $f(m, i, L)$ is significantly faster than performing repeated identically prepared stochastic simulations.

Our results in Figure 4 are for a model without a directional bias, $p_L = p_R$. However, all our analyses and Equation (22) are also valid for models with directional bias, where $p_L \neq p_R$.

Additionally, in this paper, we focus on estimating the mean agent lifetimes for the maximum possible initial density, $C(x, 0) = 1$. Extending this work to other initial conditions is possible, but would require an estimate of the number of agents to the left of any given position, x , to estimate the number of agents that must exit the system before the agent in question can exit. Different initial conditions might also require an alternative approximation for f . We leave this question for future investigation.

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