Multiple Molecular Spiders With a Single Localized Source—the One-Dimensional Case

Extended Abstract

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Abstract. Molecular spiders are nanoscale walkers made with DNA enzyme legs attached to a common body. They move over a surface of DNA substrates, cleaving them and leaving behind product DNA strands, which they are able to revisit. Simple one-dimensional models of spider motion show significant superdiffusive motion when the leg-substrate bindings are longer-lived than the leg-product bindings. This gives the spiders potential as a faster-than-diffusion transport mechanism. However, analysis shows that single-spider motion eventually decays into an ordinary diffusive motion, owing to the ever increasing size of the region of cleaved products. Inspired by cooperative behavior of natural molecular walkers, we propose a model for multiple walkers moving collectively over a one-dimensional lattice. We show that when walkers are sequentially released from the origin, the collective effect is to prevent the leading walkers from moving too far backwards. Hence there is an effective outward pressure on the leading walkers that keeps them moving superdiffusively for longer times, despite the growth of the product region.

1 Introduction

Molecular walkers are nanometer-sized molecules that move over surfaces with tracks of chemical sites by means of chemical reactions. They provide a means to transport chemicals by non-diffusive directed motion. Molecular walkers are ubiquitous as a transport mechanism in biological systems [12], and many of the complex regulatory cellular processes are controlled by the actions of molecular walkers such as kinesin and dynein [7]. It has been demonstrated experimentally that these cellular molecular walkers work in teams, wherein their collective action leads to behaviors not possible for a single walker [3]. In addition, theoretical models predict that collective cooperative or competitive behavior of walkers is fundamentally different from the behavior of individual walkers [5, 6, 8].

Inspired by the potential for walker cooperation, we propose a model describing the collective behavior of teams of molecular walkers. Our model is based on synthetic walkers called *molecular spiders* [10] (Sec. 2). Molecular spiders have two or more enzymatic legs attached to a common body. The legs are deoxyribozymes—catalytic sequences of single-stranded DNA that can cleave complementary single-stranded DNA *substrates*. Spiders move over a surface coated with substrates, attaching to, cleaving, and detaching from the substrate sites. Spiders leave behind *product* strands, which are the lower portions of the cleaved surface-bound substrates. Experiments have shown

that this mechanism allows spiders to move directionally over nanoscale tracks of regularly spaced DNA substrates [9].

Antal and Krapivsky proposed a simple abstract model that describes spider motion in one dimension (1D) as a continuous-time Markov process [1, 2]. We call it the AK model, and describe it in Sec. 2.1. In previous work, we showed via computer simulation and analytical arguments that walkers in the AK model can move superdiffusively over significant times and distances [13]. However, analysis shows that the AK walkers always eventually end up slowing down and moving as an ordinary diffusive process. This can be explained by observing that spiders move superdiffusively only when there is a difference in residency times between substrates and products. When a walker is not attached to any substrates, its motion is unbiased and diffusive. As a walker moves, it creates an increasingly large region of products that is difficult to escape from, and diffusing within it eventually consumes most of the walker's time.

In this work, we propose that the collective action of many spiders simultaneously moving over a 1D surface can act to ameliorate the decay of the superdiffusive motion of certain (namely, leading) walkers. The exclusionary properties of spiders act to limit the effective size of the product sea, and prevent the furthermost walkers from moving too far backwards. In Sec. 3 we describe a model for multiple spiders interacting on an infinite 1D lattice. Using Kinetic Monte Carlo methods, we show that multi-spider systems exhibit significantly superdiffusive motion within the time bounds studied (Sec. 4). These preliminary results indicate that multi-spider systems exhibit behavior not seen in single-spider systems, and this behavior has the potential to be used to perform useful tasks in nanoscale computational and communication systems by providing a faster-than-diffusion mechanism of transport.

2 Molecular Spiders

Walkers in our model are nearly identical (except for a detail that arises only in multi-spider interactions, cf. Sec. 3) to the walkers of the AK model, which we summarize here (see Refs. [1, 13] for a complete treatment).

A molecular spider has a rigid, chemically inert body (such as streptavidin) and several flexible legs made of deoxyribozymes—enzymatic single-stranded DNA that can bind to and cleave complementary strands of a DNA substrate at the point of a designed ribonucleic base "impurity". When a spider is placed on a surface on which the appropriate DNA substrate has been deposited (or nanoassembled), the legs bind to the substrate and catalyze its cleavage, creating two product strands. The upper portion floats away in solution and we do not consider it further. The lower portion remains on the surface, and, because it is complementary to the lower part of the leg, there is some residual binding of the leg to the product, typically much weaker and shorter-lived than the leg-substrate binding. The leg kinetics are described by the five reactions in Eq. 1 relating legs (L), substrates (S), and products (P), in which we have folded the catalysis reaction and subsequent dissociation reactions into a single k_{cat} rate:

$$\begin{aligned} &\mathrm{L} + \mathrm{S} \underset{k_{\mathrm{S}}^-}{\overset{k_{\mathrm{S}}^+}{\rightleftarrows}} \mathrm{LS} \xrightarrow{k_{\mathrm{cat}}} \mathrm{L} + \mathrm{P} \\ &\mathrm{L} + \mathrm{P} \underset{k_{\mathrm{P}}^-}{\overset{k_{\mathrm{P}}^+}{\rightleftarrows}} \mathrm{LP} \end{aligned} \tag{1}$$

2.1 The Antal-Krapivsky Model

The Antal-Krapivsky model [1, 2] is a high-level abstraction. It represents molecular spiders as a (very uncommon kind of) random walker. Each walker has k legs (in the following results, $k = 2$), whose chemical activity is independent, but whose motion is constrained by their attachment to a common body; in the model, any two legs must be within distance s (in the following results, $s = 2$). The legs walk over sites on a regular 1D lattice, where each site is either a substrate or a product.

Mathematically, the AK model takes the form of a continuous-time Markov process, where the states of the system are given by the state of the lattice sites, and the state of the walker legs. All lattice sites are initially substrates and are only transformed to products when a leg detaches from the substrate (via catalysis). Thus the state of the lattice sites can be defined by the set $P \subset \mathbb{Z}$ of product sites. The state of the walker is completely defined by the set F of attached feet locations. Thus any state can be described as the pair (P,F).

We call F a *configuration* of the legs. The *gait* of a spider is defined by what configurations and what transitions between configurations are allowed in the model. In any state $(P,F) \in \Omega$, all k legs are attached. Together with the restriction that at most one leg may be attached to a site, this implies that

$$|F| = k. \tag{2}$$

Additionally, the legs are constrained by their attachment to a common body. If the spider has a point body with flexible, string-like legs of length $s/2$, then any two feet can be separated by at most distance s, thus

$$\max(F) - \min(F) \leq s. \tag{3}$$

The transitions in the process correspond to individual legs unbinding and rebinding. When a spider is in configuration F, any foot $i \in F$ can unbind and move to a nearest-neighbor site $j \in \{i+1, i-1\}$ to form a new configuration $F' = (F \setminus \{i\}) \cup \{j\}$, provided the new configuration does not violate one of the constraints of Eqs. 2 and 3. A transition $i \to j$ is called *feasible* if it meets these constraints. The feasible transitions determine the gait of the spider. The nearest-neighbor hopping combined with the mutual exclusion of legs leads to a shuffling gait, wherein legs can slide left or right if there is a free site, but legs can never move over each other, and a leg with both neighboring sites occupied cannot move at all. If the legs of such a spider were distinguishable, they would always remain in the same left-to-right ordering.

The rate at which feasible transitions take place depends on the state of the site i. If i is a product the transition rate is 1, but if i is a substrate the transition occurs at a slower rate $r < 1$. This is meant to model the realistically slower dissociation rates from substrates, corresponding to chemical kinetics where $k_{\text{cat}}/k_{\text{P}}^{-} = r < 1$. The effect of substrate cleavage is also captured in the transition rules. If for state (P,F), where $i \in F \setminus P$, the process makes the feasible transition $i \to j$, then the leg will cleave site i before leaving, and the new state will have $P' = P \cup \{i\}$.

The relation of the AK model to the chemistry of the spiders in Eq. 1 can be understood if one assumes the chemical rates are given as in Eq. 4:

$$\begin{aligned} k_{\text{S}}^{+} &= k_{\text{P}}^{+} = \infty \\ k_{\text{S}}^{-} &= 0 \\ k_{\text{P}}^{-} &= 1 \\ k_{\text{cat}} &= r < 1 \end{aligned} \tag{4}$$

The infinitely fast on-rates account for all legs always being attached; when a leg unbinds it will instantly rebind to some neighboring site. Thus the spider is modeled as jumping from configuration F to configuration F'.

2.2 Superdiffusive Motion of Single AK Spiders

To characterize the motion of spiders we use the notion of *superdiffusion*. Superdiffusive motion can be quantified by analyzing the mean squared displacement (MSD) of a spider as a function of time. For diffusion in a one-dimensional space with diffusion constant D, the mean squared displacement is given by Eq. 5.

$$\text{msd}(t) = 2Dt^{\alpha} \quad \begin{cases} \alpha = 0 & \text{stationary} \\ 0 < \alpha < 1 & \text{subdiffusive} \\ \alpha = 1 & \text{diffusive} \\ 1 < \alpha < 2 & \text{superdiffusive} \\ \alpha = 2 & \text{ballistic or linear} \end{cases} \tag{5}$$

We say that the spider is moving *instantaneously superdiffusively* at a given time t if

$$\alpha(t) = \frac{d(\log_{10} \text{msd}(t))}{d(\log_{10} t)} > 1. \tag{6}$$

Using Kinetic Monte Carlo simulations [4] of the Markov process we can estimate the MSD for the spider process for different parameter values by averaging over many realizations $x(t)$ of the process $X(t)$, where each $x(t)$ is a function from $t \in [0, t_{\text{max}}]$ to the state space Ω of the walker process, and $x(t) \sim X(t)$.

When $r < 1$, each spider process goes through three different regimes of motion defined by their instantaneous value for the exponent α of $\text{msd}(t)$. Initially spiders are at the origin and must wait for both legs to cleave a substrate before they start moving at all

and when $t < 1/r$ the process is essentially stationary; we call this largely unimportant period the *initial period*. After the spiders take several steps, walkers with $r < 1$ show a sustained period of superdiffusive motion over many decades in time. We call this the *superdiffusive period*, and define it as the period during which the instantaneous estimate of $\alpha > 1.1$. The cutoff of 1.1 is somewhat arbitrary but represents a threshold where spiders are moving significantly superdiffusively, in contrast to spiders with $r = 1$, which never have $\alpha > 1$. Finally, all spiders as predicted by Antal and Krapivsky will decay to an ordinary diffusion with $\alpha \approx 1$. This is called the *diffusive period* and is characterized by walkers mainly moving over regions of previously cleaved products, which makes the values of r irrelevant, since all walkers move with rate 1 over product sites.

To explain this behavior we observe that spiders with $s = 2$ and $k = 2$ always cleave all sites they move over since the AK model does not permit legs to change their effective ordering on the surface, and hence the walkers move with a shuffling gait consuming all products in the region they move over. This leads to the formation of a sharp boundary between a contiguous region of products called the *product sea*, and the remainder of the unvisited sites which are still substrates. The product sea has boundaries on either end, and only when the spider is at one of the boundaries can it be attached to substrates and hence affected by the parameter r.

To explain this behavior, we consider *boundary* and *diffusive* states. When the spider is in the boundary state, it moves ballistically towards unvisited sites; when it is in the diffusive state, its motion is ordinary diffusive. The transitions from the boundary state to diffusive state are independent of the previous state of the system before it entered the boundary state. However, the transitions from the diffusive state back to the boundary state depend on the size of the product sea that the spider has left behind, and this size increases with time. This explains the apparent superdiffusion at short times when the spider spends more time in the boundary state, and the decay to ordinary diffusion at long times, as the spider spends more and more of its time in the diffusive state.

There are two options to increase the superdiffusive effect of the spider motion: (1) decrease the effective size of the product sea, and hence the time needed to escape from it and return to the boundary; or (2) decrease the rate at which spiders leave the boundary. Here we focus on option (1), by means of localized release of spiders at the origin, which effectively fills the product sea with follower spiders, preventing the leading spiders from moving too far backwards away from the boundary. This works because spider legs cannot occupy the same site at the same time, and spiders walk with a shuffling gait, sliding left or right one site at a time, so a spider cannot jump over an adjacent spider. Thus, the presence of multiple spiders will restrict the motion of the spiders around them, potentially reducing the effective size of the product sea as seen by a walker at the boundary. Thus by releasing many spiders sequentially at the origin we can make the diffusive state of the leading spiders shorter and perhaps make their transition into the boundary state independent of the number of sites they have already cleaved; such a system would have the potential for asymptotically superdiffusive motion.

3 Multiple Spiders Model

Here we consider a system with multiple k-legged spiders. The surface remains exactly the same as in the AK model. Thus the state of the system can now be described as $X = (P, F_1, F_2, ..., F_N)$ where, by analogy with the AK model, $F_i \subset \mathbb{Z}$ is a set describing the state of the ith spider and N is the total number of spiders released onto the surface. As new spiders are released N grows with time. All spiders are exactly the same and so parameters $k = 2$ and $s = 2$ apply to all spiders:

$$|F_i| = k, \text{ for all } i. \tag{7}$$

$$\max(F_i) - \min(F_i) \leq s, \text{ for all } i. \tag{8}$$

To extend the chemical exclusionary properties of spider legs to multi-spider systems, we add the restriction that any site on the surface can be occupied by only one leg of any spider:

$$F_i \cap F_j = \emptyset, \text{ for all } i, j. \tag{9}$$

With multiple spiders on a single lattice, there are situations where a particular spider is completely blocked from movement when other spiders occupy the sites to its immediate left and right. Thus, to simplify the Markov process description, we introduce a slight change to the gait of the walker with respect to the AK model. When a leg detaches from a site i it can move not only to sites $i-1$ and $i+1$, but also back to site i. It chooses from any site in $\{i-1, i, i+1\}$ with equal probability, provided none of the new configurations violates the constraints of Eqs. 7, 8, and 9. Thus, even if sites $i-1$ and $i+1$ are occupied, the leg has somewhere to go. This change of the gait also makes the model more realistic, as the enzymatic leg of a real spider can always rebind to the site it just dissociated from.

All legs of all spiders move independently. As with a single spider, the constraints enforce that a leg is never detached for a finite amount of time, i.e., legs hop to neighboring sites or step back onto the previous site infinitely fast.

We start all experiments from a symmetric configuration with two spiders placed on the surface, one left of the origin with legs at $\{-3, -1\}$ and the other right of the origin with legs at $\{1, 3\}$. The initial set of products is $P = \{-2, -1, 0, 1, 2\}$; all other sites are substrates. The pair of sites $\{0, 1\}$ is the injection point for new spiders. A new spider is released whenever the injection point is unoccupied.

4 Simulation Results for Multiple Spiders

Similarly to our single-spider experiments [13] we use the Kinetic Monte Carlo method [4] to numerically sample traces of the multi-spider Markov process. We vary the chemical-kinetics rate r to see how it influences the motion. In case when $r = 1$ there is no effective difference between substrates and products.

4.1 Comparison of a Single AK Model Spider with a Single Spider of the Current Model

Recall from Sec. 3 that the action of individual spiders in the multi-spider model was modified to incorporate the possibility of a leg rebinding to the site it just detached from. This is a realistic modification of the model for single spiders, but as it represents a formal model change, we investigate its effects on the motion of single walkers. We compare the results of the AK model with the modified model permitting rebinding through KMC simulations, using $k = 2$, $s = 2$, and $r = 0.1$, and show the msd(t) estimates in Fig. 1. These results show substantially the same qualitative behavior. However, spiders with rebinding move at a constant-factor slower pace than the original model, as the transitions which lead to a rebinding do not move the walker in any direction. This effectively slower rate needs to be taken into account when comparing the motion of spiders in the multi-spider model to those in the AK model, but it does not fundamentally change anything about the characteristics of spider motion.

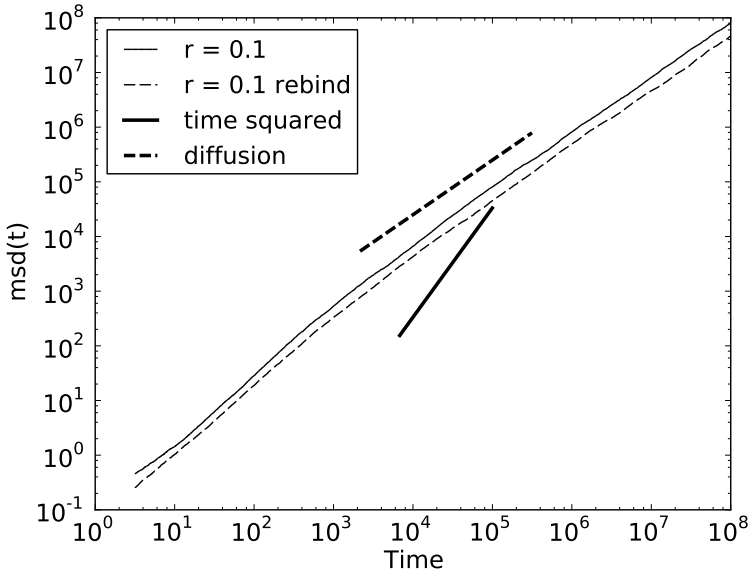

Fig. 1. Comparison of msd(t) for a single spider moving in the AK model and with the modified model permitting rebinding of a leg to its previous site.

4.2 Multiple Spiders Simulations

For each value of $r \in \{1, 0.5, 0.1, 0.05, 0.01, 0.005\}$ we used our KMC algorithm to simulate 1200 independent realizations of the multi-spider model described in Sec. 3. We used these realizations to sample the number of spiders and the position of each

of the spiders at regularly spaced time intervals. We define the position of a spider to be the mean of its attached leg positions (i.e., $\sum F_k/2$ for spider k). To ensure that each simulation trace provides a sample for each measured time, we run each simulation until time is at least $t_{\max} = 10^6$. We choose the measurement time points to be equispaced for the independent axis of the plots reported, so that for linear plots the successive time intervals have a constant difference, and for log axes, the successive time intervals have a constant ratio.

Observed Superdiffusion of the Leading Spiders. As discussed in Sec. 2.2, it is known that single spiders show transient superdiffusive behavior [13]. Single spiders with $r < 1$ move faster than ordinary diffusion for a significant time and distance, but eventually slow down and move as an ordinary diffusion. The leading spiders in the multi-spider model also initially move superdiffusively, but they reach higher values of α and thus they are closer to ballistic motion than single spiders at peak times; furthermore, the decay towards ordinary diffusion appears to be incomplete. Fig. 2 shows the estimate of msd(t) for the leading spider on a log-log plot for each measured r parameter value. In this plot, straight lines correspond to power laws, that is, to Eq. 5, and the parameter α is given by the slope. To show the instantaneous value of α, we use finite difference methods to estimate $\alpha(t)$ (Eq. 6), and Fig. 3 shows the result of using the Savitzky-Golay smoothing filter [11] on these estimates. Fig. 4 gives a comparison of $\alpha(t)$ for the single spider of the AK Model and the leading spider of the multi-spiders model.

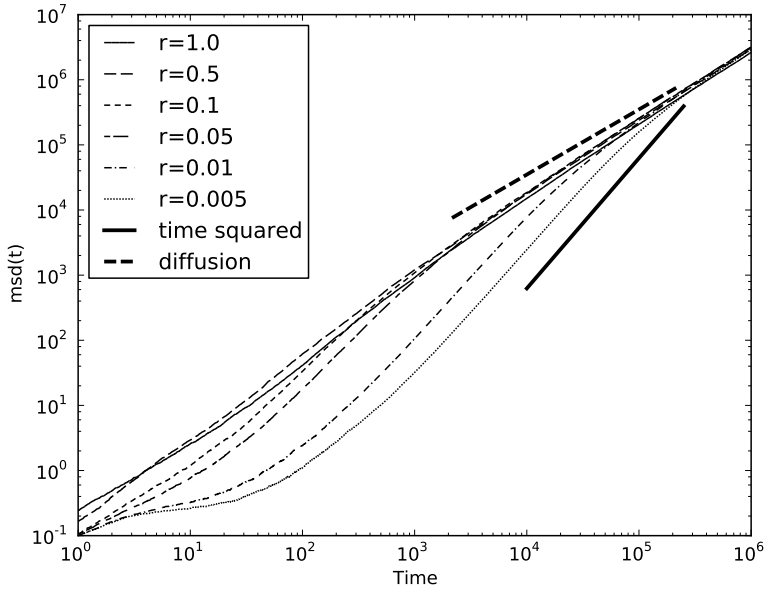

Fig. 2. Mean squared displacement for the leading spider in multi-spider simulations. Reference lines are shown for ordinary diffusion and ballistic motion.

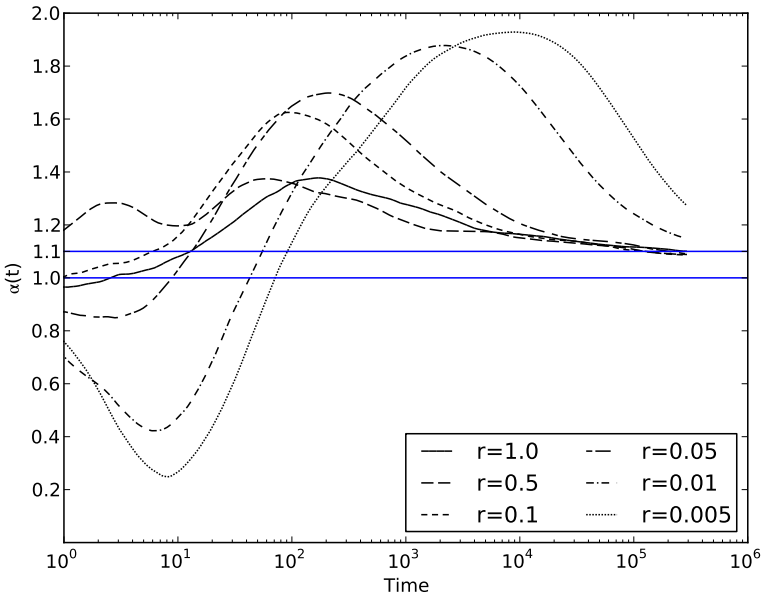

Fig. 3. Finite difference approximation of $\alpha(t)$ for the leading spider in multi-spider simulations. Horizontal lines define the threshold for ordinary diffusion at $\alpha = 1$ and our defined threshold for superdiffusion at $\alpha = 1.1$.

In Sec. 2.2 we explained that single spiders in the AK model have been observed to have three distinct regimes of motion defined by their value of $\alpha(t)$. There is an initial stationary regime before the walker starts moving, followed by a superdiffusive regime spanning many decades in time, and finally a diffusive regime as $\alpha(t)$ falls back to 1, where the walkers spend most of their time diffusing in the product sea. In contrast, for the leading spiders in the multi-spider model, the third regime is a gradual but incomplete shift towards diffusion. There is a decrease in $\alpha(t)$ at longer times (Fig. 3), but, at least within the simulated time bound of $t_{\max} = 10^6$, the motion remains superdiffusive. Unlike for the single-spider model, there are as yet no analytical results for the multi-spider model. The true behavior at greater times thus remains a matter for speculation, but we do notice a clearly different behavior than for single spiders within the simulated times (Fig. 4). Also note that, as in the single-spider model, decreasing values of r lead to increasingly superdiffusive behavior, but, unlike in the single-spider model, even spiders with $r = 1$ move superdiffusively. This is not unexpected, because even when $r = 1$ there is an exclusionary pressure exerted on the outermost spiders that prevents them from returning to the origin as would occur for single walkers with $r = 1$. However, as with the single spiders, when $r < 1$ we see a much enhanced superdiffusive effect, something not possible for a walker that does not transform sites irreversibly like the molecular spiders.

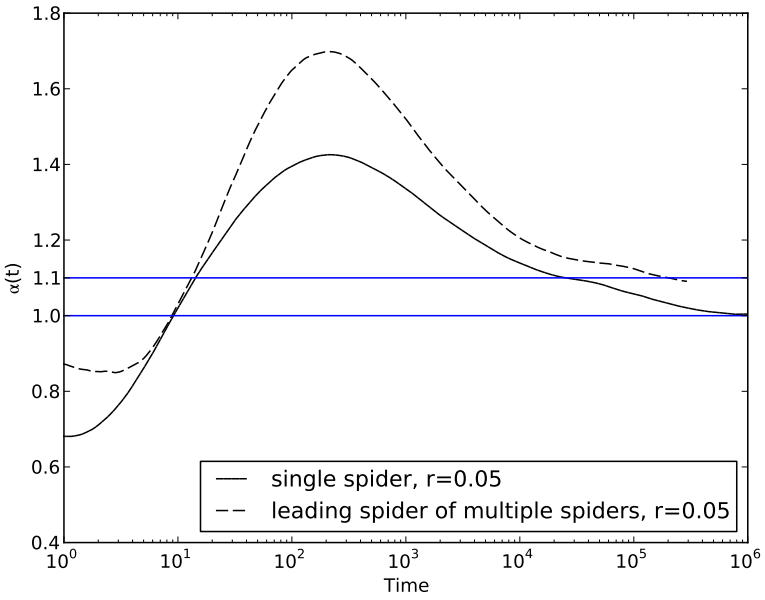

Fig. 4. Comparison of finite difference approximation of $\alpha(t)$ for the leading spider in multi-spider simulations and the single spider in simulations of the AK model.

Number of Released Spiders. Spiders in the multi-spider model are released at the origin *whenever possible*, so the number of spiders actually released by time t is a random variable of interest, and estimates for its mean are shown in Fig. 5 for each studied value of r.

We observe that the average number of spiders grows sublinearly. Thus, attempts to release spiders are often unsuccessful, because of interference from other spiders at the origin. This indicates that in one dimension spiders move away from the origin relatively slowly.

Density of Spiders. The density of spiders gives some insight into why the leading spiders move superdiffusively, even for $r = 1$, and why the number of spiders added does not grow linearly. We measure the density of spiders as the average probability for each site to be occupied by a spider at a particular time. Shown in Fig. 6 is the spider density at time $t_{\max}$. Clearly, spiders with $r = 0.05$ have spread out slightly farther, but both r-values show a much higher density of spiders arround the origin where new spiders are released. The evolution of this density through time can be seen in Fig. 7.

5 Discussion

Our analysis of the multi-spider model shows significant differences from the previous work on single spiders. The most fundamental difference is that (at least within the

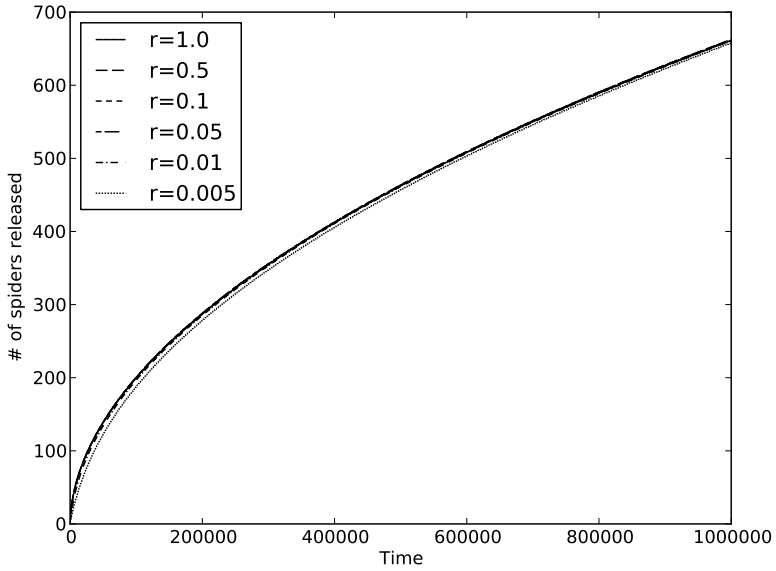

Fig. 5. Number of released spiders for multi-spider simulations.

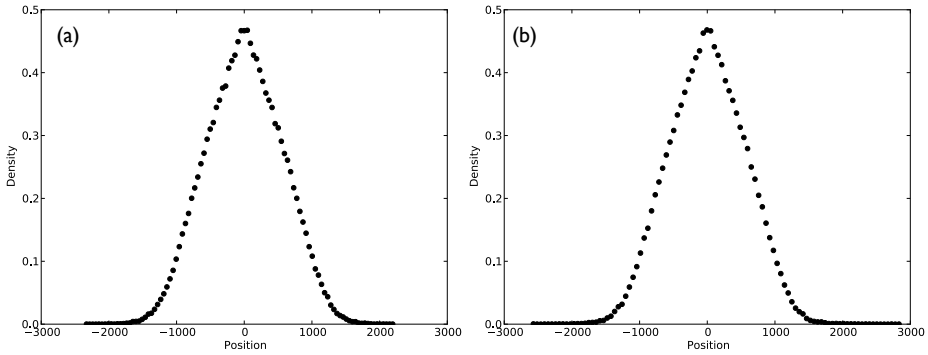

Fig. 6. Average spider density at $t_{\max}$, for $r = 1$ (a) and for $r = 0.05$ (b).

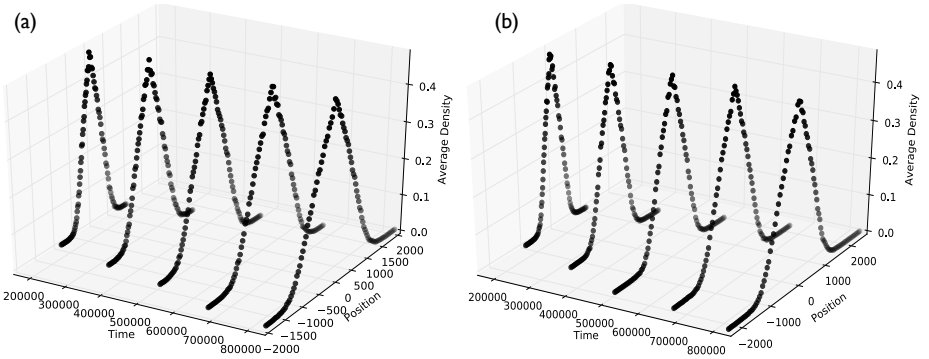

Fig. 7. Average spider density plotted at several instants, for $r = 1$ (a) and for $r = 0.05$ (b).

times simulated) walkers for all values of r move superdiffusively with $\alpha(t_{\max}) > 1.1$. However, as with the single-spider model, decreasing values of r lead to increasingly superdiffusive behavior. This is an essential property of molecular spiders that distinguishes them from many other types of molecular walkers. The spider superdiffusion depends on there being a residency-time bias between visited and unvisited sites (i.e., $r < 1$) and it also depends on the walkers having more than one leg. Thus, even a single spider shows some cooperative behavior between the two legs to enable an emergent superdiffusive effect. However, the interactions in the multi-spider model show an even more significant effect, and this can be attributed to the cooperative collective behavior of the swarm of walkers. The furthest walkers from the origin do all of the cleaving of sites, but the internal walkers act to exert a "pressure" on the outermost walkers, preventing them from moving backwards too far, and keeping their behavior superdiffusive.

There are many possibilities for adding stronger interactions between spiders that will potentially lead to even more pronounced emergent behaviors. However, the present work shows that even simple interactions, defined solely by an exclusion property that prevents multiple walkers from binding to the same site at once, can lead to motion that is faster than diffusion, at least over the finite times simulated. These results can be used to design collective spider transport systems that can perform useful tasks at the nanoscale.

Acknowledgments. This material is based upon work supported by the National Science Foundation under grant 0829896.

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