

Survival of an evasive prey

G. Oshanin^{a,b,1}, O. Vasilyev^{c,d}, P. L. Krapivsky^e, and J. Klafter^{f,g}

^aLaboratory J.-V. Poncelet, Unité Mixte Internationale 2615, Centre National de la Recherche Scientifique, Independent University of Moscow, Bolshoy Vlasyevskiy Pereulok 11, 119002 Moscow, Russia; ^bLaboratoire de Physique Théorique de la Matière Condensée, Unité Mixte de Recherche 7600, Centre National de la Recherche Scientifique, Université Pierre et Marie Curie, 4 Place Jussieu, 75252 Paris Cedex 5, France; ^cMax Planck Institut für Metallforschung, Heisenbergstrasse 3, D-70569 Stuttgart, Germany; ^dInstitut für Theoretische und Angewandte Physik, University of Stuttgart, D-70569 Stuttgart, Germany; ^eDepartment of Physics, Boston University, Boston, MA 02215; ^fSchool of Chemistry, Tel Aviv University, 69978 Tel Aviv, Israel; and ^gFreiburg Institute for Advanced Studies, University of Freiburg, 79104 Freiburg, Germany

Edited by Joshua Jortner, Tel Aviv University, Tel Aviv, Israel, and approved June 24, 2009 (received for review April 20, 2009)

We study the survival of a prey that is hunted by N predators. The predators perform independent random walks on a square lattice with V sites and start a direct chase whenever the prey appears within their sighting range. The prey is caught when a predator jumps to the site occupied by the prey. We analyze the efficacy of a lazy, minimal-effort evasion strategy according to which the prey tries to avoid encounters with the predators by making a hop only when any of the predators appears within its sighting range; otherwise the prey stays still. We show that if the sighting range of such a lazy prey is equal to 1 lattice spacing, at least 3 predators are needed in order to catch the prey on a square lattice. In this situation, we establish a simple asymptotic relation $\ln P_{\rm ev}(t) \sim (N/V)^2 \ln P_{\rm imm}(t)$ between the survival probabilities of an evasive and an immobile prey. Hence, when the density $\rho = N/V$ of the predators is low, $\rho \ll 1$, the lazy evasion strategy leads to the spectacular increase of the survival probability. We also argue that a short-sighting prey (its sighting range is smaller than the sighting range of the predators) undergoes an effective superdiffusive motion, as a result of its encounters with the predators, whereas a far-sighting prey performs a diffusive-type motion.

pursuit | chase | diffusion | superdiffusion | first-passage times

Pursuit-and-evasion problems have a long and fascinating history (1). The classical setup involves 2 agents—say, a merchant vessel pursued by a pirate ship that it desperately tries to evade. The goal for both is to choose a deterministic motion strategy, given their velocities and sighting ranges, that optimizes their respective chances of successful pursuit or evasion. Similar games between adversary species occur in different environmental or biological systems; coevolution of bacteria and phage or preypredator contests being just 2 examples (see e.g., refs. 2–5 for more details). The chief difference here is that the objects move less deterministically, their strategies are less "intelligent," and the number of interacting objects can be large. Such pursuer–evader contests are also assisted by some finite-range vision or smell.

In this paper, we investigate a class of pursuit-and-evasion problems involving a single evading prey that is being hunted by N predators (Fig. 1)—a variation of the classic princess-and-monster game (6). The predators perform independent nearest-neighbor random walks (RWs) on a finite square lattice (with V sites), and the prey is caught upon the first encounter with a predator. In such a situation, how should the prey move in order to maximize its chances of not being caught up to time t?

When the prey is blind, i.e. it has no information on predators' actual positions (its sighting range is zero), the best strategy is to stay still (7–9). The survival probability $P_{\text{imm}}(t)$ of this immobile prey is given by

$$P_{\rm imm}(t) \sim e^{-\alpha \rho t}$$
, [1]

where $\rho = N/V$, and α depends on the diffusion coefficient of the predators, the structure of the lattice (particularly, the dimensionality), and on the number of sites V.

The exponential decay shown in Eq. 1 is an ultimate asymptotic for a finite lattice. There is also an intermediate

asymptotic [which is the true asymptotic for infinitely large systems (10-12)]

$$P_{\text{imm}}(t) = e^{-\rho S(t)}, \qquad [2]$$

where S(t) is the mean number of distinct sites visited by a predator up to time t.

The behavior of S(t) crucially depends on the spatial dimension d. For nearest-neighbor RWs, S(t) grows according to (13)

$$S(t) \sim \left(\frac{8t}{\pi}\right)^{1/2}$$
 and $S(t) \sim \frac{\pi t}{\ln(t)}$, [3]

on 1-dimensional and 2-dimensional (2d) square lattices, respectively. In 3 (and higher) dimensions, S(t) grows linearly with time, $S(t) \sim t/G$, where G is the mean number of visits to the origin on an infinite lattice within an infinite time. (Hereinafter the symbol " \sim " signifies that we deal with the leading in time asymptotic behavior.)

The question we address is how the simplest evasion strategy affects the survival probability of a prey, having a finite sighting range r, hunted by N predators with sighting ranges R. The predators perform independent RWs and, as soon as a given predator appears within distance R from the prey, it changes the mode of motion and begins a direct chase, minimizing at each step a distance to the prey. The prey tries to avoid encounters with the predators by investing a minimal effort: Because the blind prey's best recourse is to stay still, we assume that the lazy prey does the same as long as all the predators are outside of its sighting range. Whenever predators appear within its sighting range, the prey instantaneously hops to the nearest-neighboring site, chosen at random but so that (i) the distance from the visible predators will increase, and (ii) no other predator will get inside the prey's sighting range. We emphasize that whenever the prey hops, the choice of the landing site is random modulo the validity of the above requirements.

We focus on the simplest situation in which the sighting ranges of the lazy prey and of the predators are both equal to just 1 lattice spacing. We find that in this case, instead of obeying Eqs. 1 and 2, the prey survival probability obeys:

$$P_{\rm ev}(t) \sim \begin{cases} e^{-Blpha\,
ho^3\,t} & {
m finite \, lattice} \\ e^{-B
ho^3\,S(t)} & {
m infinite \, lattice} \end{cases}$$
 [4]

where B is a numerical factor. The key feature is the replacement of the density ρ by ρ^3 . A rough explanation is that on the square lattice at least 3 predators must surround the prey in order to catch it. Hence, a very modest investment in effort pays back with a

Author contributions: G.O., O.V., P.L.K., and J.K. designed research, performed research, and wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. E-mail: oshanin@lptmc.jussieu.fr.

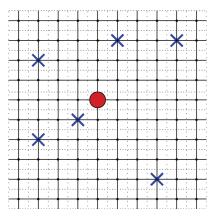


Fig. 1. Prey (circle) and predators (crosses) on a square lattice with V sites.

spectacular (several orders of magnitude) increase of the survival probability.

We also observe that, due to encounters with the predators, the prey performs long-range excursions on the lattice until the moment when it is captured. When (r,R)=(1,1), the motion of the prey is effectively a diffusive motion with the mean-squared displacement growing linearly with time and the diffusion coefficients dependent on the mean density of predators. Surprisingly enough, there is a qualitative change in the behavior when R>r; we show numerically that in the case (r,R)=(1,2), the mean-squared displacement grows as $t^{1.65}$, i.e. random motion of the prey is superdiffusive.

The Model and Numerical Results

The minimal model is defined as follows:

- 1. There are *N* predators on a square lattice with *V* sites and periodic boundary conditions. Predators are placed at random and the prey is initially at the origin of the lattice.
- Each predator performs a nearest-neighbor RW, the updates are made simultaneously, and the predators do not interact; e.g., there is no exclusion implying that a few predators can be at the same lattice site.
- 3. If a predator is on the nearest-neighboring site to the prey, it hops to that site and thereby the prey is caught.
- 4. Just before the predators hop, the prey checks the nearest-neighboring sites. If all four of them are empty, the lazy prey remains at the site. If some are occupied, the prey hops to the randomly chosen unoccupied nearest-neighboring site, provided all 4 sites neighboring the target one are unoccupied. If the latter happens, the predators chasing the prey still hop to the site that has been occupied by the prey.

Thus, for the minimal model, the sighting ranges of both prey and predators are equal to 1 lattice spacing, r=R=1. The generalization is obvious: The predator starts a direct chase when the distance to the prey is $\leq R$; the prey begins to move whenever there are predators within the range $\leq r$. By definition, the metric is Manhattan, so e.g. the site (x,y) is on distance |x|+|y| from the origin. We focus on the minimal model. (A few simulation results for the model with r=1, R=2 are presented in Fig. 5.)

We performed Monte Carlo simulations on a 100×100 square lattice with different numbers of predators. In Fig. 2, we plot the survival probability $P_{\rm ev}(t)$ of an evasive prey and compare it with the survival probability $P_{\rm imm}(t)$ of an immobile prey (*Inset*). Both types of prey display an exponential decay with time. The comparison reveals a pronounced difference (several orders of magnitude for sufficiently low density of predators) in the values of respective survival probabilities. In Fig. 3, we plot the numerical data for the characteristic decay rates $b(\rho)$ as a function of ρ . This figure shows

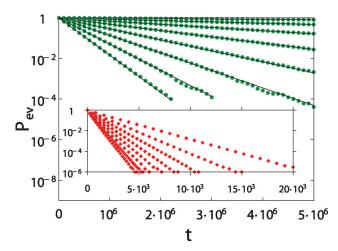


Fig. 2. Survival probability of an evasive prey on a square lattice with $V=10^4$ sites. The curves from top to bottom present the behavior of $P_{\rm ev}(t)$ when the density of the predators is $\rho=0.002,0.003,\ldots0.009$. Symbols denote results of numerical simulations and solid lines represent an exponential fit $\exp(-b(\rho)t)$. Inset shows the corresponding survival probability of an immobile prey.

that for an immobile prey, $b(\rho)$ is a linear function of ρ , $b(\rho) \sim \rho$, as it should be, whereas for the lazy evasive prey $b(\rho) \sim \rho^3$. This very different scaling explains why the survival probability of evasive prey is so much higher when $\rho \ll 1$.

In the following sections, we explain these findings. First, we consider an immobile prey and evaluate an exact expression for $P_{\text{imm}}(t)$ for finite lattices and in the thermodynamic limit. Then, we look on this problem from a different point of view and obtain $P_{\text{imm}}(t)$ by using a heuristic approach that reproduces correctly the temporal behavior of $P_{\text{imm}}(t)$ and gives a correct dependence of the characteristic decay times on V and other pertinent parameters, but predicts slightly different values for numerical factors. Next, we show that in order for the evasive prey to be captured, the predators must first appear in a special configuration in which the prey will be under a direct attack but cannot evade the predators. We specify such "stalemate" configurations and extend our heuristic approach to estimate $P_{\text{ev}}(t)$.

Survival of an Immobile Prey

To set up the scene, we start with a reminder of the so-called "target" problem (10–12), which describes the survival of an immobile prey in the presence of predators performing independent RWs. This is an exactly solvable problem, but existing theoretical descriptions are focused on the infinite systems. We determine

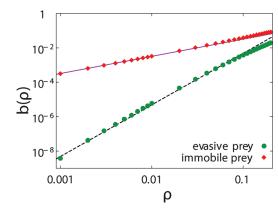


Fig. 3. Characteristic decay rates $b(\rho)$ as a function of ρ . Diamonds represent numerical data for an immobile prey, solid line is an analytic result given by Eq. 1 with $\alpha=1/G$, where G is given by Eq. 10. Circles represent numerical data for an evasive prey, whereas the dashed line is a fit $b(\rho)=4.82\,\rho^3$.

 $P_{\text{imm}}(t)$ for finite V by taking advantage of some already known results.

Let $\{X_n(t)\}$ denote a given realization of the trajectory of the n^{th} predator within the time interval [0,t] and $X_n(\tau)$ is its position at time $\tau \in [0,t]$. We suppose here that τ and t are integers.

An indicator function $\mathcal{P}(t)$ of the event—that within the time interval [0,t], neither of the N predators has visited the location of the prey—can be written down as

$$\mathcal{P}(t) = \prod_{n=1}^{N} \mathcal{P}(\{X_n(t)\}),$$
 [5]

where $\mathcal{P}(\{X_n(t)\}) = 1$ if $X_n(\tau) \neq 0$ for any $\tau \in [0,t]$ and 0 otherwise. Averaging Eq. 5, we obtain*

$$P_{\text{imm}}(t) = \left(\frac{1}{V} \sum_{X, X \neq 0} L(X, t)\right)^{N},$$
 [6]

where L(X,t) is the probability that a RW, starting at site X at time 0, has not yet visited the origin at time t. Explicitly, L(X,t) is defined [see, e.g., (14)] as

$$L(X,t) = \frac{1}{2\pi i} \oint \frac{dz}{z^{t+1}} \frac{1}{1-z} \left[1 - \frac{G(X,z)}{G(0,z)} \right],$$
 [7]

where the integral is near the origin of the z plane and G(X,z) is the lattice Green (generating) function of the probability G(X,t) to find a predator at site X at time t. From Eq. 7, we infer (see refs. 14 and 15) that

$$\sum_{X,X\neq 0} L(X,t) = V - S(t),$$
 [8]

and consequently,

$$P_{\text{imm}}(t) = \left(1 - \frac{1}{V}S(t)\right)^{N}.$$
 [9]

In the thermodynamic limit, $N \to \infty$ and $V \to \infty$ with $\rho = N/V$ kept constant, Eq. 9 reduces to Eq. 2. For finite lattices, the large-time behavior of S(t) is well known (see e.g., refs. 14 and 16). One finds that at sufficiently large times

$$S(t) \sim V[1 - e^{-t/VG}], G = \begin{cases} \frac{2V}{\pi^2}, & d = 1, \\ \frac{\ln(cV)}{\pi}, & d = 2, \end{cases}$$
 [10]

where c is a constant. For a square lattice, $c \approx 1.8456$. For d > 2, G is a constant, as mentioned in the introduction. Overall, we recover Eq. 1 with $\alpha = 1/G$.

We close this section with a remark that the target problem is closely related to the so-called narrow-escape problem, which arises in a number of biological processes, such as biochemical reactions in cellular microdomains (see e.g. refs. 17–19). Here, particles (ions, molecules, proteins, etc.) move randomly in a bounded domain (cell, compartment) enclosed by a boundary that is perfectly reflecting everywhere, except for a small window through which particles can escape. Within this context, one is interested to calculate the first-passage time density, which is defined as the time-derivative of the survival probability of a target placed at a position of the escape window in the presence of a particle diffusing in a bounded domain.

In a 2d circular domain of area V with reflecting walls containing a small escape window of size a (size of the target), the

survival probability of such an immobile target in the presence of N particles diffusing with diffusion coefficient D obeys (see ref. 18), for $V \gg a^2$,

$$P_{\text{imm}}(t) \sim \exp\left(-\rho \frac{\pi D t}{\ln(V/a^2)}\right).$$
 [11]

To match $P_{\rm imm}(t)$ given by Eq. 11 and our discrete-space calculations, we set D=1/4 and notice that the characteristic time of the decay in Eq. 11 is 4 times larger that the one defined by Eq. 1 with $\alpha=1/G$ determined by Eq. 10, meaning that an immobile prey located at the origin of a periodic lattice will typically be caught sooner than an immobile prey hiding at a reflective boundary. The corresponding characteristic time may be even larger if the boundary is not smooth and the prey is located in the corner or near a cusp (see ref. 18). Note, as well, that the target size a in Eq. 11 may be interpreted here as the sighting range of the predators; hence, Eq. 11 signifies that in 2d, dependence of the characteristic decay time on the predators' sighting range is logarithmically weak.

Survival of an Immobile Prey Revisited

We suppose from now on that t is a continuous variable, and predators perform continuous-time RWs with a pausing-time density $\Psi(t) = \exp(-t)$. Such a choice is for convenience only and would not cause any difference in the large-time behavior compared with discrete-time RWs.

Let T_1 be a random variable defining the time within the interval [0, t] when the origin has been occupied by 1 or more predators simultaneously. Then, $\mathcal{P}(t)$ in Eq. 5 reads

$$\mathcal{P}(t) = \begin{cases} 1, & T_1 \equiv 0, \\ 0, & T_1 > 0. \end{cases}$$
 [12]

Hence, once we know the probability density $P(T_1)$, we may find the survival probability $P_{\text{imm}}(t)$ of an immobile target from $P_{\text{imm}}(t) = P(T_1 = 0)$.

Occupancy time T_1 , i.e., a time spent on a given lattice site by 1 (or simultaneously k) random walkers, have been studied in a number of works (see e.g. refs. 20–22). An important result for us has been conjectured and verified numerically in ref. 21; it states that $P(T_1)$ is a Gaussian

$$P(T_1) \sim \exp\left(-\frac{(T_1 - \overline{T_1})^2}{2\sigma_1^2}\right),$$
 [13]

and thus is entirely defined by the first 2 moments of T_1 : mean value $\overline{T_1}$ and the variance $\sigma_1^2 = \overline{T_1^2} - \overline{T_1}^2$. Evidently, $\overline{T_1}$ grows linearly with t, and hence $T_1 = 0$ is a large deviation from the most probable value, such that, in principle, an assumption that $P(T_1)$ is Gaussian may not be valid in this domain. We proceed to show, however, that an estimate

$$P_{\text{imm}}(t) \sim P(T_1 = 0) \sim \exp\left(-\frac{\overline{T_1}^2}{2\sigma_1^2}\right)$$
 [14]

reproduces correctly the dependence of $P_{\text{imm}}(t)$ on time and other parameters; only numerical factors in the characteristic decay times are incorrect.

Let $\Psi_0(\tau)$ be the indicator function of the event that at time-moment τ none of N predators is at the origin:

$$\Psi_0(\tau) = \prod_{n=1}^{N} [1 - I(X_n(\tau))], I(X) = \begin{cases} 1, & X = 0 \\ 0, & X \neq 0. \end{cases}$$
 [15]

^{*}Actually, the factor before the sum is equal to 1/(V-1); because we are interested in large lattices, $V\gg 1$, we always write V instead of V-1.

Therefore, random variable T_1 is explicitly defined by

$$T_1 = \int_0^t d\tau \, (1 - \Psi_0(\tau)).$$
 [16]

The first moment of T_1 is now calculated to give

$$\overline{T_1} = \int_0^t d\tau \left[1 - \left(1 - \frac{z_{\tau}}{V} \right)^N \right], z_{\tau} = 1 - G_{\tau},$$
 [17]

where $G_{\tau} = G_{\tau}(0)$ is the probability that a RW, commencing at the origin, is at the origin at time-moment τ .

For the variance of T_1 , we find

$$\sigma_1^2 = \int_0^t d\tau_1 \int_0^t d\tau_2 \, \phi_{0,0}(\tau_1, \tau_2), \quad [18]$$

where $\phi_{0,0}(\tau_1, \tau_2)$ is the 2-time correlation function

$$\begin{aligned} \phi_{0,0}(\tau_1, \tau_2) &= \overline{\Psi_0(\tau_1) \, \Psi_0(\tau_2)} - \overline{\Psi_0(\tau_1)} \cdot \overline{\Psi_0(\tau_2)} \\ &= \left(1 - \frac{z_{\tau_1} + z_{\tau_2} - G_{|\tau_1 - \tau_2|} z_{\tau_2}}{V} \right)^N \\ &- \left(1 - \frac{z_{\tau_2}}{V} \right)^N \left(1 - \frac{z_{\tau_1}}{V} \right)^N. \end{aligned}$$
[19]

Consider first the behavior predicted by Eq. 14 in the thermodynamic limit. We find that

$$\phi_{0,0}(\tau_1, \tau_2) \sim \rho G_{|\tau_1 - \tau_2|},$$
 [20]

implying that the occupation of the origin (or any other lattice site) of an infinite lattice is a stationary process with long-range algebraic correlations. Curiously enough, this behavior resembles very much the behavior observed experimentally for "blinking" of nanoscale light emitters (23).

Integrating Eq. 20 and noticing that $\overline{T_1} \sim \rho t$, we obtain

$$\frac{\overline{T}_1^2}{2\sigma_1^2} \sim \rho \begin{cases} f_1 (8t/\pi)^{1/2}, & d = 1, \\ f \pi t / \ln(t), & d = 2, \\ f t / G', & d > 2, \end{cases}$$
[21]

where $f_1 = 3\pi/32$, f = 1/4 and $G' = \int_0^\infty d\tau \, G_\tau$. Note that G' has exactly the same meaning as G in Eq. 10; namely, it equals the mean number of visits to the origin of an infinite lattice by a continuous-time RW within an infinite time.

For finite but large V, from Eqs. 17 and 20 we find that in the leading in 1/V order

$$\overline{T_1} \sim \rho t, \, \sigma_1^2 \sim 2\rho \int_0^t d\tau_1 \int_0^{\tau_1} d\tau_2 \, \left(G_{\tau_1 - \tau_2} - \frac{1}{V} \right),$$
 [22]

which yields

$$\frac{\overline{T_1}^2}{2\sigma_1^2} \sim \frac{\rho t}{4} \begin{cases} \pi^2/2V, & d = 1, \\ \pi/\ln(V), & d = 2, \\ 1/G', & d > 2. \end{cases}$$
 [23]

Hence, both in the thermodynamic limit and for finite V, our approximate approach predicts correct (nontrivial in low dimensions) temporal evolution of $P_{\text{imm}}(t)$, and correct (nontrivial) dependence on V, but overestimates numerical factors in the characteristic decay times.

Survival of a Lazy Evasive Prey

We now can explain why the behavior of the survival probability becomes so markedly different when the prey is evasive. First, we note the obvious fact that the evasive prey cannot be captured by a single predator. On a square lattice, the evasive prey cannot be captured by 2 predators; i.e., a more collective effort is required. In order to catch the prey, the predators have to create a stalemate-type situation in which the prey can be attacked but cannot evade.

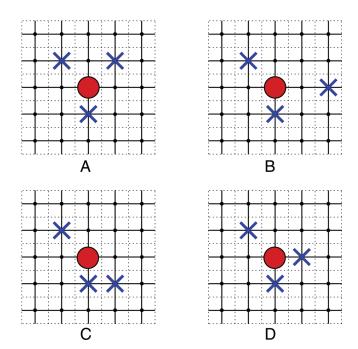


Fig. 4. Four basic stalemate configurations from which lazy prey cannot escape; the prey will be captured on the next step.

On the square lattice, 3 predators can do this job. Several such configurations created by 3 predators are depicted in Fig. 4.

When $\rho \ll 1$, we may consider only lowest-order "reaction events" which involve just 3 predators, as depicted in Fig. 4, and disregard higher-order configurations, involving 4 or more predators.

Due to the lazy evasion, the prey effectively performs a diffusive-type motion. A rigorous proof of this statement could be extremely challenging, and even quantifying the motion is not trivial, as the prey is eventually caught. If we limit ourselves to the realizations when the lazy prey has not been caught up to time t and consider the mean-squared displacement of the prey, we find that it grows linearly with time (see Fig. 5). Its diffusion coefficient $D \sim \rho$ (Inset in Fig. 5) and is small compared with the diffusion coefficient of the predators (which is $D_p=1/4$, according to our definition of the motion of the predators). There is also another indirect argument to ignore the motion of the prey. In low-dimensional systems, the

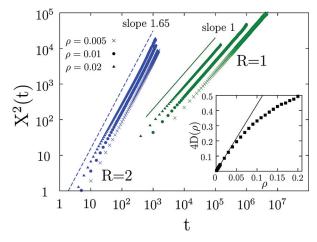


Fig. 5. Mean-squared displacement of an evasive prey until the moment of its capture. Shown are simulation results for the predator sighting ranges R=1 and R=2. (Inset) The effective diffusion coefficient (determined via relation $4D(\rho)=\overline{X^2(t)}/t$) of the prey for R=1. The solid line in the inset represents $D(\rho)\sim \rho$.

leading asymptotical behavior of the survival probability of the diffusive prey in the presence of diffusive predators is independent of the diffusion coefficient of the prey (24–27) as well as of the reaction probability (15). Hence, we neglect diffusive-type motion of the prey and suppose that it is immobile.

Thus, the most significant effect of the lazy evasion tactics is the change of the effective reaction order—the prey can be captured only when any 3 predators appear in a stalemate configuration. Summing up these arguments, we estimate $P_{ev}(t)$ of an evasive

$$\ln P_{\rm ev}(t) \sim A C \ln P_3(t)$$
. [24]

Here, C = 28 is the total number of stalemate configurations (see Fig. 4), and $P_3(t)$ is the survival probability of an immobile prey which is captured only by 3 or more predators; that is, the prey can coexist with 1 or 2 predators, and it is caught when 3 predators appear simultaneously at the site it occupies. The numerical factor A in Eq. 24 is unknown; it emerges because we approximately consider any stalemate configuration involving 3 predators as a simultaneous encounter of predators at the same site. (One can also envision that stalemate configurations have different weights.) We will extract the value of A from the fit to numerical data.

Following our heuristic interpretation of the survival probability of an immobile prey, we estimate $P_3(t)$ as

$$P_3(t) \sim \exp\left(-\frac{\overline{T_3}^2}{2\sigma_3^2}\right),$$
 [25]

where now T_3 is a random variable equal to the fraction of time within the interval [0,t] when the origin has been occupied by at least 3 predators simultaneously.

Next, we define the indicator functions:

$$\Psi_1(\tau) = \sum_{l=1}^{N} I(X_l(\tau)) \prod_{n=1, n \neq l}^{N} [1 - I(X_n(\tau))]$$
 [26]

and

$$\Psi_{2}(\tau) = \sum_{l=1}^{N} \sum_{p=1, p \neq l}^{N} I(X_{l}(\tau)) I(X_{p}(\tau)) \times \prod_{n=1, n \neq l, p}^{N} [1 - I(X_{n}(\tau))],$$
[27]

of the events that at time-moment τ , there is only 1 or only 2 predators at the origin, respectively. Then, T_3 is given by

$$T_3 = \int_0^t d\tau \left[1 - \Psi_0(\tau) - \Psi_1(\tau) - \Psi_2(\tau)\right],$$
 [28]

and its first 2 moments obey

$$\overline{T_3} = \int_0^t d\tau \left(1 - \left(1 - \frac{z_{\tau}}{V} \right)^N - \frac{Nz_{\tau}}{V} \left(1 - \frac{z_{\tau}}{V} \right)^{N-1} - \frac{1}{2} \frac{N(N-1)z_{\tau}^2}{V^2} \left(1 - \frac{z_{\tau}}{V} \right)^{N-2} \right)$$
[29]

and

$$\sigma_3^2 = \overline{T_3^2} - \overline{T_3}^2 = \int_0^t d\tau_1 \int_0^t d\tau_2 \sum_{i,j=0}^2 \phi_{i,j}(\tau_1, \tau_2), \quad [30]$$

where the 2-time correlation functions are defined by

$$\phi_{i,j}(\tau_1,\tau_2) = \overline{\Psi_i(\tau_1)\Psi_j(\tau_2)} - \overline{\Psi_i(\tau_1)} \cdot \overline{\Psi_j(\tau_2)}.$$
 [31]

In the leading in N/V order, $\overline{T_3}$ is simply

$$\overline{T_3} \sim \rho^3 t.$$
 [32]

For finite lattices, the 2-time correlation functions follow

$$\phi_{i,j}(\tau_1, \tau_2) \sim a_{i,j}(\rho) \left(G_{|\tau_1 - \tau_2|} - \frac{1}{V} \right),$$
 [33]

where $a_{ij}(\rho)$ are polynomials in ρ . After straightforward but tedious calculations, we find that in the leading in N/V order $\sum_{i,j} a_{i,j}(\rho) \sim \rho^3$ and hence, $\overline{T_3} \sim \rho^2 \overline{T_1}$ and $\sigma_3^2 \sim \rho^2 \sigma_1^2$. This finding implies that for sufficiently large times, the survival probability $P_3(t)$ of an immobile prey that can be captured when any 3 predators appear simultaneously on the site it occupies, and the survival probability $P_{imm}(t)$ of the target problem are related to each other

$$ln P_3(t) \sim \rho^2 ln P_{imm}(t).$$
[34]

Consequently, for finite square lattices $P_{ev}(t)$ of an evasive prey obeys

$$\ln P_{\rm ev}(t) \sim A C \rho^2 \ln P_{\rm imm}(t) \sim -A C \rho^3 \frac{\pi t}{\ln(cV)}.$$
 [35]

From the fit to numerical data, we get $A \approx 0.55$.

In a similar fashion, we find that for an infinitely large square lattice

$$\ln P_{\rm ev}(t) \sim -A C \rho^3 \frac{\pi t}{\ln(t)}.$$
 [36]

Eqs. 35 and 36 lead to the announced result in Eq. 4.

Discussion

We studied the survival of a prey in the presence of predators performing RWs on sites of a square lattice. We analyzed minimaleffort evasion tactics in which the prey tries to avoid predators by stepping away whenever a predator appears on one of the neighboring sites; otherwise the prey stays still. We showed that this strategy leads to the great enhancement of the survival probability in comparison with the stay-still strategy (7–9). More precisely, when the density ρ of the predators is small, the life expectancy of the immobile prey scales as ρ^{-1} whereas the minimal-evasion strategy results in a life expectancy of the order of ρ^{-3} .

Several interesting additional conclusions are as follows:

- (i) We assumed that the predators perform conventional RWs until the prey appears within their sighting ranges. Within this picture, the characteristic relaxation time of the survival probability of both an evasive and an immobile prey appears to be proportional to the factor G, which defines the mean number of returns to the origin within an infinite time during which a predator commences its random motion at the origin. In the case of a search for the prey by conventional RWs, in 2 dimensions G is large when V is large, because $G \sim \ln(V)$ but attains a finite value (as $V \to \infty$) for d > 2. Such a behavior is associated with the fact that the spatial dimension d=2 coincides with the fractal dimension of RWs. Playing on the side of the predators, it becomes clear that more efficient search for the prey in 2 dimensions will be realized when the predators' trajectories have a fractal dimension < 2 (i.e. the best option would be to perform ballistic motion).
- (ii) We focused on a particular situation (the minimal model) in which the sighting range of both the prey (r) and of the predators (R) were equal to 1 lattice spacing. When R > r, e.g. R = 2 and r = 1, we observed a different behavior: After the prey notices the predator, it can never escape from the sighting range of this predator. In this situation, as time increases, more and more predators turn from a random-search phase to the phase of the direct chase, so that the prey is accompanied by a tail of chasing predators. In our model, neither of the species is superior to the other

with respect to speed, and hence the predators who are directly chasing the prey are harmless—they just follow the prey but can never catch it, as long as the prey is not caged. We observed that in some realizations of the prey-predator contests on sufficiently small lattices, all N predators were directly chasing the prey which, however, survives to eternity. On the other hand, the predators who perform a direct chase: (a) block some possible directions for escape, such that it suffices now to meet just 1 randomly searching predator in order to create a stalemate configuration, and (b) exert some pressure on the prey, prompting it to move almost ballistically. Encounters with the predators who have not yet started a direct chase suppress pure ballistic motion, but still the prey performs effectively a superdiffusive motion, in contrast to the case when R = r. Here, the mean-square displacement $X^{2}(t)$ of the prey, until the moment it is caught, obeys $X^2(t) \sim t^z$ with $z \approx 1.65$ (see Fig. 5, R = 2 case), meaning that contrary to predators, whose random motion is recurrent in 2d and whose S(t) grows sublinearly with time (due to a logarithmic correction), the fractal dimension of the prey's trajectories $d_w \approx 1.2 < 2$, and the mean number of distinct sites it visits grows linearly with t. Thus, paradoxically, although the predators who are in a direct-chase phase are harmless to the prey, they force it to explore more new sites and, consequently, to die sooner. This interesting case bears further investigation.

- 1. Nahin P (2007) Chases and Escapes: The Mathematics of Pursuit and Evasion (Princeton Univ Press, Princeton)
- Weihs D, Webb PW (1984) Optimal avoidance and evasion tactics in predator-prey interactions. J Theor Biol 106:189–206.
- Miller GF, Cliff D (1994) Co-evolution of pursuit and evasion: Biological and gametheoretical foundations. Technical Report CSRP311 (University of Sussex, Brighton,
- Krapivsky PL, Redner S (1996) Kinetics of a diffusive capture process: Lamb besieged
- by a pride of lions. *J Phys A* 29:5347–5357. Redner S, Krapivsky P L (1999) Capture of the lamb: Diffusing predators seeking a
- diffusing prey. Amer J Phys 67:1277–1283. Isaacs R (1965) Differential Games: A Mathematical Theory with Applications to Warfare and Pursuit, Control and Optimization (Wiley, New York).
- Bray AJ, Majumdar SN, Blythe R (2003) A formal solution of a class of reaction-diffusion models: Reduction to a single-particle problem. *Phys Rev E* 67:060102.
- Moreau M, Oshanin G, Bénichou O, Coppey M (2003) Pascal principle for diffusion-controlled trapping reactions. *Phys Rev E* 67:045104.
- Moreau M, Oshanin G, Bénichou O, Coppey M (2004) Lattice theory of trapping
- reactions with mobile species. *Phys Rev E* 69:046101.

 Tachiya M (1983) Theory of diffusion-controlled reactions: Formulation of the bulk
- reaction rate in terms of the pair probability. *Radiat Phys Chem* 21:167–175. Blumen A, Zumofen G, Klafter J (1984) Target annihilation by random walkers. *Phys*
- Redner S, Kang K (1984) Kinetics of the 'scavenger' reaction. *J Phys A* 17:L451–L455. Dvoretzky A, Erdös P (1951) Some problems on random walks in space. In: *Proceed-*
- ings of the Second Berkeley Symposium on Mathematical Statistics and Probability, ed Neyman J, (Univ California Press, Berkeley) pp 353–367.

 14. Brummelhuis MJAM, Hilhorst HJ (1991) Covering of a finite lattice by a random walk.
- Physica A 176:387-408.

- (iii) There should be an optimal value of the prey sighting range r. Clearly, a sighting range that is too small would not result in an effective evasion. On the other hand, having a too-large r is not good either. If r exceeds the mean distance between the predators, the prey will always see predators attempting a move and thus would most likely stay still.
- (iv) Finally, we remark that our results shed some light on an interesting problem of first-passage times \tilde{t} to rare density fluctuations in diffusive systems. Within this context, one is interested to calculate the first passage time density $Q^{(k)}(\tilde{t})$ of the event when k out of N particles performing \widetilde{RWs} on a lattice appear for the first time \tilde{t} simultaneously on a specific lattice site (28). Our analysis suggests that for sufficiently large \tilde{t} the first passage time density obeys $\ln Q^{(k)}(\tilde{t}) \sim -\rho^k \tilde{t}/G$, with G defined by Eq. 10.

ACKNOWLEDGMENTS. We thank Ed Cox for inspiring our interest in this subject. We also acknowledge helpful discussions with Olivier Bénichou, Raphael Voituriez and Alexander Berezhkovskii on many aspects of sojourn and firstpassage time distributions in confined systems. This work was supported by Agence Nationale de la Recherche Grant Dynamique et Optimisation des Processus de Transport Intermittents (DYOPTRI) (to G.O.) and National Science Foundation Grants CHE-0532969 and CCF-0829541 (to P.L.K.). P.L.K. and J.K. acknowledge the hospitality of Laboratoire de Physique Théorique et Modèles Statistiques, Université Paris 11, and of Laboratoire de Physique de la Matière Condensée, Ecole Polytechnique.

- Bénichou O, Moreau M, Oshanin G (2000) Kinetics of stochastically gated diffusion-limited reactions and geometry of random walk trajectories. *Phys Rev E* 61:3388–3406.
 Weiss GH, Havlin S, Bunde A (1985) On the survival probability of a random walk in a finite lattice with a single trap. *J Stat Phys* 40:1572–9613.
 Grigoriev IV, Makhnovskii YA, Bereshkovskii AM, Zitserman VY (2002) Kinetics of
- escape through a small hole. *J Chem Phys* 116:9574–9577.

 Schuss Z, Singer A, Holcman D (2007) The narrow escape problem for diffusion in cellular microdomains. *Proc Natl Acad Sci USA* 104:16098–16103.

 Bénichou O, Voituriez R (2008) Narrow-escape time problem: Time needed for a particle to exit a confining domain through a small window. *Phys Rev Lett* 100:168105.
- Weiss GH, Shuler KE, Lindenberg K (1983) Order statistics for first passage times in diffusion processes. *J Stat Phys* 31:255–278.
- Bogunà M, Berezhkovskii AM, Weiss GH (2000) Occupancy of a single site by many random walkers. *Phys Rev E* 62:3250–3256.
 Bénichou O, Coppey M, Klafter J, Moreau M, Oshanin G (2003) On the joint residence
- time of N independent two-dimensional Brownian motions. *J Phys A* 36:7225–7231. Stefani FD, Hoogenboom JP, Barkai E (2009) Beyond quantum jumps: Blinking
- nanoscale light emitters. Phys Today 62(2):34–39. Bray AJ, Blythe R (2002) A exact asymptotics for one-dimensional diffusion with mobile traps. *Phys Rev Lett* 89:150601.
- Blythe R A, Bray A J (2003) Survival probability of a diffusing particle in the presence of Poisson-distributed mobile traps. *Phys Rev E* 67:041101.

 Oshanin G, Bénichou O, Coppey M, Moreau M (2002) Trapping reactions with ran-
- domly moving traps: Exact asymptotic results for compact exploration. Phys Rev E
- Yuste S B, Oshanin G, Lindenberg K, Bénichou O, Klafter J (2008) Survival probability of a particle in a sea of mobile traps: A tale of tails. Phys Rev E 78:021105
- Sanders DP, Larralde H (2008) How rare are diffusive rare events? Europhys Lett 82:40005-40011.