

Optimal escape-and-feeding dynamics of random walkers: Rethinking the convenience of ballistic strategies

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Excited random walks represent a convenient model to study food intake in a media which is progressively depleted by the walker. Trajectories in the model alternate between (i) *feeding* and (ii) *escape* (when food is missed and so it must be found again) periods, each governed by different movement rules. Here, we explore the case where the escape dynamics is adaptive, so at short times an area-restricted search is carried out, and a switch to extensive or ballistic motion occurs later if necessary. We derive for this case explicit analytical expressions of the mean escape time and the asymptotic growth of the depleted region in one dimension. These, together with numerical results in two dimensions, provide surprising evidence that ballistic searches are detrimental in such scenarios, a result which could explain why ballistic movement is barely observed in animal searches at microscopic and millimetric scales, therefore providing significant implications for biological foraging.

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I. INTRODUCTION

Identifying the strategies which minimize the time of a random walk to reach one or a set of targets represents a problem of wide interest that can be used to study search algorithms on networks [1,2], the control of robotic units and/or microswimmers [3,4], or binding processes on folding polymers [5], to name a few applications. Many authors, however, put a special focus on the implications on biological foraging [6]. Then one implicitly assumes that searching efficiently could represent a significant evolutionary force for living organisms, so those optimal strategies would have been probably selected and should be then experimentally observed in biological movement patterns. The Lévy foraging hypothesis, which has stimulated a great debate both in biology and in physics [7–10], is a paradigmatic example, but one can find many others as in the optimal tumbling frequencies of *E. coli* [11,12], the pollination flights of bumblebees [13,14], or the optimal soaring of birds through thermal winds [15].

That a ballistic strategy (that is, moving straightforward in a random direction until hitting the target) is optimal under many conditions is a widely rooted idea in the field [16,17]. This stems from (i) the intuitive idea that such a strategy minimizes path overlap, and (ii) the fact that the mean first-passage time through the boundary of a finite domain, if the walk consists of a random sequence of flights of characteristic duration τ , decreases monotonically with τ (see, e.g., Ref. [18]). However, ballistic search patterns under uncertainty are rare in nature and very few organisms seem to adopt such a strategy. Reference books in ecology [19,20] claim that most animal searches rather combine two phases: (i) an area-restricted process in which the organism wanders around in its immediate vicinity looking for nearby resources, and (ii) an extensive phase in which larger and larger motion scales

are subsequently introduced to reach further regions. Both phases are used alternatively in higher organisms as a result of information acquisition, which has been modeled in the past through intermittent random walks, Lévy flights, or similar approaches [21,22]. Alternatively, optimization mechanisms based on the idea of restarting the search from the original point have also been discussed in the literature (see, e.g., Refs. [23–27]). For simpler (microscopic or millimetric) organisms, however, the search mechanisms are less flexible and are mainly regulated by biochemical or neuronal responses to food deprivation that get progressively activated [28,29], leading to nonstationary patterns [30]. In particular, for the well-studied case of the nematode *C. elegans* it is observed [31] that an initial area-restricted search (if food was available until recently) leads progressively to a more extensive exploration as food deprivation persists.

On the other hand, signals or cues (as chemical gradients, visual or mechanical signals, or even cognitive maps) represent the main force driving animal foraging. A random search often represents just a temporary process that finishes (or fades out) as soon as those signals are detected. A rough (but meaningful) approach to this is given by the excited random walk (ERW) model [32,33]. In its original formulation, the walker moves in a discrete media of cells containing food, which is consumed by the walker as it reaches there. The walker then moves to the nearest-neighbor cell containing food with a probability $p > 1/2$, leaving an empty path behind. However, with probability $1 - p$ the walker will turn back to the empty region. Then it will start an *escape* process driven by a homogenous ($p = 1/2$) rule until food is reached again, and then *feeding* starts again. As long as food is depleted, a growing empty region of size $l(t)$ will be dynamically generated, making the escape process more and more difficult.

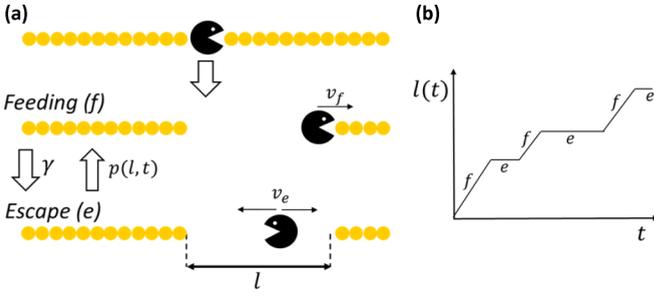


FIG. 1. Schematic picture of the ERW dynamics considered. (a) The 1D domain is initially full of food (upper panel) and is depleted through successive feeding periods at speed v_f separated by escape periods. (b) Time dynamics of $l(t)$, which grows uniformly for feeding (marked as f) and stays constant during the escape (marked as the e phase).

Previous works on the ERW have revealed some of the properties of this depletion process (see Refs. [34,35] for a review). The mean number of depleted cells is known to grow asymptotically as $\sim\sqrt{t}$ in one dimension (1D), and as $\sim t$ for two and higher dimensions [36–38]. The shape of the time distribution to reach a given cell has been provided in Ref. [39]. Alternatively, extensions of the model to the continuous case [40], or assuming that food is only partially depleted and/or it can be renewed [41], have been explored. Finally, recent works [42–47] have studied the properties of the food intake if assuming that the excursions through the empty region involve a risk to die for the walker.

In the present paper we extend the ERW framework to the case where the *escape* rule followed by the walker is not merely a classical isotropic walk (or Brownian motion, its continuous counterpart), but the individual is able to implement an adaptive strategy to escape. Our main focus will be then on asking how the escape strategy can be optimized to increase the food intake, determined by $l(t)$. In Sec. II we present our general ERW framework and prove that it can be formally derived within a continuous-time random walk (CTRW) framework. In Sec. III we describe the escape strategies that are considered in the present work, which are aimed at testing the convenience of ballistic searches within the context presented. In Sec. IV we derive the mean escape time for such a family of strategies and prove that, contrary to the intuitive belief, ballistic movement is not necessarily a good escape strategy. This argument is further supported by the dynamics of the empty region $l(t)$ left by the walker both in 1D (for which an asymptotic analytical expression is provided) and 2D (numerical results), as reported in Sec. V. Section VI, finally, contains the summary and the conclusions of our findings.

II. GENERAL FRAMEWORK

Specifically, we consider a continuous (both in time and space) model (see Fig. 1) in which the walker feeds at a constant speed v_f until food is missed and the process is interrupted, which happens at a rate γ . Then an *escape* process from the empty region occurs that will be governed by $p(l, t)$, which is the distribution of escape times from an empty region

of size l , if starting at a small distance x_0 from the boundary, given a particular escape strategy. The feeding dynamics is then driven by the set of master equations

$$\begin{aligned}\frac{\partial \rho_f}{\partial t} &= -v_f \frac{\partial \rho_f}{\partial l} - \gamma \rho_f + \int_0^t \gamma p(l, t-t') \rho_f(l, t') dt', \\ \frac{\partial \rho_e}{\partial t} &= \gamma \rho_f - \int_0^t \gamma p(l, t-t') \rho_f(l, t') dt'.\end{aligned}\quad (1)$$

Here, $\rho_f(l, t)$ represents the probability density of the walker being in the feeding phase at time t , provided that the empty region has size l . Equivalently, $\rho_e(l, t)$ is the probability density of the walker being in the empty region at time t , given l . Hence, they satisfy $\int_0^\infty (\rho_f + \rho_e) dl = 1$ for any t , and the initial conditions read $\rho_f(l, t=0) = \delta(l)$, $\rho_e(l, t=0) = 0$. The *advective* term in the first equation stands for the uniform growth of l at speed v_f during *feeding*, and the other terms correspond to the switching between feeding and escape. The statistics of $l(t)$ can be easily obtained from the solution of (1); for instance, its n th moment will read $\langle l^n \rangle = \int_0^\infty l^n (\rho_f + \rho_e) dl$.

A. Derivation of Eqs. (1)

While the meaning of all the terms in (1) is rather intuitive, we now show for the sake of completeness that this set of equations can be formally derived from a CTRW scheme. Apart from the probability densities $\rho_f(l, t)$ and $\rho_e(l, t)$ above, we then need to introduce $j_f(l, t)$ and $j_e(l, t)$ as the probabilities that the walker switches to the feeding or to the escape phase exactly at time t .

For the feeding phase we impose that the walker makes the size l increase at a constant speed v_f , and such a process will terminate only when the signal is missed, which happens at a constant rate γ . Then we can write

$$\rho_f(l, t) = \int_0^t j_f(l - v_f t', t - t') e^{-\gamma t'} dt', \quad (2)$$

where the exponential term $e^{-\gamma t'}$ represents the probability that the depletion period, which started at time $t - t'$, has not finished yet at time t . Similarly we can write an equivalent expression for the escape state:

$$\rho_e(l, t) = \int_0^t j_e(l, t - t') g(l, t') dt'. \quad (3)$$

In this expression $g(l, t')$ represents the probability that the individual has not been able to escape from the empty region after a time t' trying, so it is related to the escape time distribution $p(l, t)$ through $g(l, t) = \int_t^\infty p(l, t') dt'$.

Finally, we can write the transition equations that determine how the individual switches from the *escape* to the *depletion* state once the escape is completed, and how it switches from depletion to escape when an error in the signal detection occurs. These two equations read, respectively,

$$j_f(l, t) = \int_0^t j_e(l, t - t') p(l, t') dt' + \delta(t) \delta(l) \quad (4)$$

and

$$j_e(l, t) = \int_0^t j_f(l - v_f t', t - t') \gamma e^{-\gamma t'} dt', \quad (5)$$

where we have introduced the initial condition in the last term of (4), assuming that initially $l = 0$ and the individual starts in the depletion state.

The system of equations (2)–(5) can be simplified if we use a Laplace transform in time and a Fourier transform in l space. To keep the notation simple, we will identify whether functions are in real space or in Laplace and Fourier space simply by writing explicitly their arguments (l, t in real space, or k, s in Fourier and Laplace space, respectively). By applying both transforms in (2) and (5) we obtain

$$j_e(k, s) = \gamma \rho_f(k, s) = \frac{\gamma j_f(k, s)}{s + \gamma + ikv_f}, \quad (6)$$

which after rearranging terms and inverting only the Fourier transform leads to

$$(s + \gamma)j_e(l, s) = \gamma(s + \gamma)\rho_f(l, s) = -v_f \frac{\partial j_e(l, s)}{\partial l} + \gamma j_f(l, s). \quad (7)$$

On the other side, applying the Laplace transform in (3) and (4) we have

$$\rho_e(l, s) = j_e(l, s) \frac{1 - p(l, s)}{s}, \quad (8)$$

$$j_f(l, s) = j_e(l, s)p(l, s) + \delta(l). \quad (9)$$

Now, it is easy to check that combining (7) and (9) one obtains

$$s\rho_f(l, s) - \delta(l) = -v_f \frac{\partial \rho_f(l, s)}{\partial l} - \gamma \rho_f(l, s) + \gamma p(l, s)\rho_f(l, s), \quad (10)$$

which is the Laplace transform of the first equation in (1). Similarly, combining (6) and (8) we find the Laplace transform of the second equation in there,

$$s\rho_e(l, s) = \gamma \rho_f(l, s) - \gamma p(l, s)\rho_f(l, s). \quad (11)$$

This shows that the CTRW scheme is formally equivalent to the framework presented above.

III. ADAPTIVE ESCAPE DYNAMICS

The information about the escape strategy is then contained within $p(l, t)$. For simplicity, here we restrict our study to a simple family of two-stage strategies. When the walker misses food and enters into the empty region (stage 1) it will carry out flights of speed v_e and random directions whose duration is determined by a termination rate α_1 . This rule for stage 1 is intended to represent an intensive (area-restricted) search. Finally, at a given rate w the walker decides to switch its strategy to a new one (stage 2) based on longer flights (thus governed by a termination rate $\alpha_2 \ll \alpha_1$) also in random directions at speed v_e . Actually, to keep our discussion simple, we will focus on the limit case $\alpha_2 \rightarrow 0$, so in practice a ballistic motion rule is implemented after the area-restricted search of stage 1 is left. Our main interest lies then in exploring whether there is an optimal switching rate w from stage 1 to stage 2 that maximizes food intake by the walker. Obviously, the cases $w \rightarrow 0$ and $w \rightarrow \infty$ correspond to the extreme cases of an area-restricted (Brownian-like) strategy and a ballistic strategy, respectively.

Finding $p(l, t)$ requires solving the escape (or first-passage) problem from a finite interval of size l (at least in 1D) for the case of a particle initially at a small distance from the boundary, that is, $x_0 \rightarrow 0$. As far as we know, this specific problem has yet to be explored for the two-stage strategies described, though similar cases have been reported in the literature. For example, the case of intermittent searches has been analyzed in Refs. [21, 48–50]. Here, we will adapt the method in Ref. [50] to our case. Since all the processes involved in the escape strategy (flight terminations and switching from stage 1 to 2) are Markovian and so they are governed by constant rates, we are allowed to write renewal equations for the functions $p_1(l, t)$ and $p_2(l, t)$, which correspond to the escape time distributions while the particle is at stage 1 or 2, respectively [thus $p_1(l, t) + p_2(l, t) = p(l, t)$]. These two renewal equations read

$$q_1(l, t|x_0) = p_1(l, t) + \int_0^t p_1(l, t - t')q_1(l, t'|l)dt', \quad (12)$$

$$q_2(l, t|x_0) = p_2(l, t) + \int_0^t p_2(l, t - t')q_2(l, t'|l)dt' + \int_0^t p_1(l, t - t')q_{12}(l, t'|l)dt'. \quad (13)$$

Here, $q_1(l, t'|x_0)$ and $q_2(l, t'|x_0)$ represent the probability density of being at the boundaries of the interval for a walker moving according to the rules in stage 1 and stage 2, respectively, given the initial position x_0 . On its turn, $q_{12}(l, t'|x_0)$ is the probability density of being at the boundary provided that the motion started from x_0 at stage 1 and it has subsequently switched to stage 2. In consequence, the meaning of Eq. (12) is as follows: The probability of reaching the boundary while being at stage 1 corresponds to those trajectories that hit the boundary then for the first time [first term on the right-hand side (rhs)] plus those that hit it at a previous time $t - t'$ and then follow its path from the boundary (second term on the rhs). In Eq. (13) an extra term appears on the rhs; this is because we need to separate the trajectories contributing to $q_2(l, t|x_0)$ that hit the boundary for the first time at a previous time $t - t'$ while being already in stage 2 (second term on the rhs) from those that hit it while still being at stage 1 (third term on the rhs).

Taking into account that both stages 1 and 2 are assumed, as described above, to satisfy the telegrapher's processes with different termination rates α_1 and α_2 , the corresponding probability densities will satisfy the telegrapher's equations coupled through a switching from stage 1 to 2:

$$\frac{\partial q_1}{\partial t} + \frac{1}{\alpha_1} \frac{\partial^2 q_1}{\partial t^2} = \frac{v_e^2}{\alpha_1} \frac{\partial^2 q_1}{\partial x^2} - wq_1, \quad (14)$$

$$\frac{\partial q_{12}}{\partial t} + \frac{1}{\alpha_2} \frac{\partial^2 q_{12}}{\partial t^2} = \frac{v_e^2}{\alpha_2} \frac{\partial^2 q_{12}}{\partial x^2} + wq_1. \quad (15)$$

So, the functions q_1 and q_{12} in (12) and (13) are the solution of the system (14) and (15) for $x = l$, when computed within the interval $(0, l)$ with periodic boundary conditions and an initial condition x_0 at stage 1. Finally, the case of $q_2(t|x_0)$ will correspond to the solution of (15) but removing the coupling (that is, the last term on the rhs) and imposing instead the initial condition x_0 for stage 2.

IV. MEAN ESCAPE TIME FROM THE EMPTY REGION

An explicit analytical solution to the problem (12)–(15) can be found in Laplace space. In particular, Eqs. (12) and (13) can be written as

$$p(l, s) = \frac{q_1(l, s|x_0)}{1 + q_1(l, s|l)} + \frac{q_1(l, s|x_0)}{1 + q_2(l, s|l)} - \frac{q_1(l, s|x_0)q_{12}(l, s|l)}{[1 + q_1(l, s|l)][1 + q_2(l, s|l)]}, \quad (16)$$

where we identify whether a function is written in Laplace space just by explicitly indicating its Laplace argument s instead of time t . The exact expression for $p(l, s)$ reached in this specific case is too long to be reproduced here (see Appendix A). Instead, we can compute the mean hitting time as $\langle T \rangle = \partial p(l, s) / \partial s|_{s=0}$, which yields (for $\alpha_2 = 0$)

$$\langle T \rangle = \left[\frac{l}{2v_e} + \frac{\alpha_1 + w}{\alpha_1 w} \right] \times \left[1 + \frac{\sqrt{\alpha_1 + wh(l - x_0)}}{\sqrt{w[h(l) - 2] - \sqrt{\alpha_1 + wh(l)}}} \right]. \quad (17)$$

This expression [where we have defined $h(x) \equiv 1 + e^{-\sqrt{w(\alpha_1 + w)x}/v_e}$] represents the first main result of the present work, since it already provides valuable information about the starting questions posed. We note that in the limit $w \rightarrow 0$ this mean escape time reduces, after some simplifications, to $\langle T \rangle = l/2v_e + \alpha_1 x_0(L - x_0)/v_e^2$, which is the well-known result for the case of a simple telegrapher's process [18]. On the other side, $w \rightarrow \infty$ leads to $\langle T \rangle = l/2v_e$, the expected solution for a ballistic search path.

Also, the escape probability P_∞ of the walker, provided we introduce a constant death rate r while being in the escape phase, can be computed from our results above. This will be simply given by $P_\infty = p(l, s = r)$, in agreement with recent works (see Refs. [51,52]).

If we plot the mean escape time in (17) as a function of w for different values of x_0 and l (Fig. 2), we observe that for x_0/l small enough, there is an intermediate w which minimizes $\langle T \rangle$. For a search process on an interval of a fixed size starting from one extreme $x_0 = 0$, it is well known that such an optimal exists at $w = 2v_e/l$ [53]. However, it is not trivial how this translates into a system where l grows with time, since then the optimal w decreases with time, too. For this reason, it is particularly interesting to see that the range of w values for which $\langle T \rangle$ lies below $l/2v_e$ (which is the ballistic limit) becomes larger as l increases. This is rather surprising since one normally expects ballistic strategies to outperform Brownian-like strategies. However, we observe that when both strategies are combined sequentially, then it is beneficial to postpone the transition to ballistic movement up to very long times in order to optimize the escape process.

We can also plot the results for P_∞ to confirm that view. This is done in the inset of Fig. 2, which shows P_∞ for the same parameters as in the main figure, with $r = v_e/l$. As can be seen, the probability to escape before dying is larger for smaller w provided that x_0/l is small enough. These results also recover the limits $\lim_{w \rightarrow 0} P_\infty = \exp(-\sqrt{r\alpha_1}x_0/v_e)$ and $\lim_{w \rightarrow \infty} P_\infty = \exp(-rx_0/v_e)/2$ expected for a mortal ran-

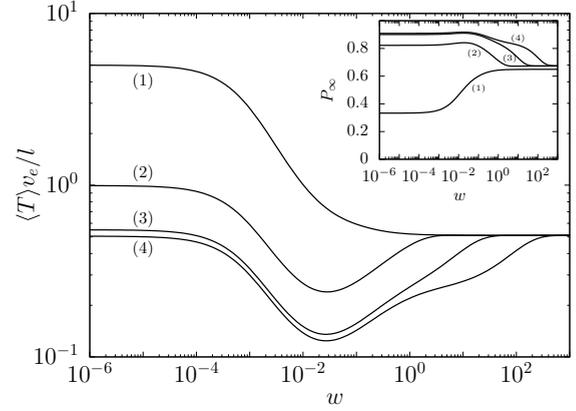


FIG. 2. Nondimensional mean escape time as a function of the switching rate w for different values of the ratio x_0/l as follows: (1) $x_0/l = 10^{-1}$, (2) $x_0/l = 10^{-2}$, (3) $x_0/l = 10^{-3}$, (4) $x_0/l = 10^{-4}$. In all cases we use $l = 100$, $v_e = \alpha_1 = \gamma = 1$. Inset: Survival probability of the walker in the escape phase for a constant mortality rate $r = v_e/l$. The values of the parameters are the same as those used for the main figure.

dom walk in the diffusive and the ballistic limit, respectively [51,52].

V. DYNAMICS OF FOOD INTAKE

Taking into account the previous results, we expect that as long as food is consumed and therefore l becomes larger, then ballistic strategies should be progressively postponed or avoided for maximizing the food intake. To compute this, we can introduce the expression for $p(l, s)$ into (1) in order to reveal the statistical properties of $l(t)$. While an exact and general expression is unattainable, we can focus on the long-time (and so small- s and large- l) regime. Then, one can expand $p(l, s)$ for s small and a simple expression for the mean size of the empty region is reached (the details are given in Appendix B) in the form

$$\langle l \rangle \approx \sqrt{\frac{2v_f v_e}{\gamma} \left(1 + \sqrt{\frac{\alpha_1 + w}{w}} \right) t}. \quad (18)$$

This expression, which represents our second main result, recovers the expected scaling $\langle l \rangle \sim t^{1/2}$ found in previous works on the ERW. Moreover, it shows that as we approach the ballistic limit ($w \rightarrow \infty$) the food intake will be largely independent of w , and it will depend only on the walker speeds v_f , v_e , and the error rate γ . On the contrary, for $w \rightarrow 0$ we obtain the nontrivial scaling $\langle l \rangle \sim w^{-1/4}$. This is relevant since it confirms that asymptotically ballistic strategies should be suppressed in order to maximize the average intake. In Fig. 3 we provide a comparison of the result in (18) (dotted lines) to the values obtained from simulations for the random-walk realization of the ERW described above (symbols), showing a perfect agreement in the asymptotic regime. Also, the inset in Fig. 3 shows explicitly the existence of the optimal w for long times. Note that the specific value of the optimal w is time dependent, such that it decreases with time and remarkably it goes to zero for $t \rightarrow \infty$, which is logical since this implies $l \rightarrow \infty$ and then ballistic

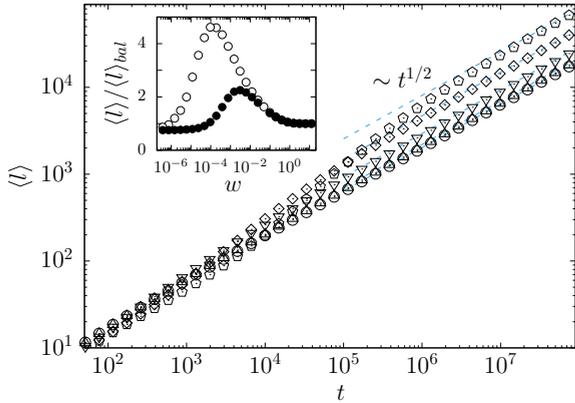


FIG. 3. Mean size of the depleted region as a function of time for different values of the switching rate w , as follows: circles ($w = 10$), triangles ($w = 1$), inverted triangles ($w = 0.1$), diamonds ($w = 0.01$), pentagons ($w = 0.001$). The dotted lines correspond to the corresponding asymptotic expression derived in (18). Inset: Mean food intake relative to the ballistic escape case for long times ($t = 10^5$ for solid symbols, $t = 10^7$ for open symbols) as a function of w . In all cases we use $v_f = v_e = \alpha_1 = \gamma = 1$.

strategies become largely inefficient. For this reason, Fig. 3 shows for intermediate times that a fast switch to ballistic motion (that is, a large w) can still maximize $\langle l \rangle$, but the situation changes as the asymptotic regime $l \rightarrow \infty$ is fully reached.

We now pose the question of whether the conclusions analytically obtained here in 1D can be extended to two or higher dimensions, as topologically the problem becomes rather different then. For dimensions higher than 1 the empty region left by the individual is no longer a regular interval with a characteristic size l but takes a complex (fractal-like, in general) shape. So, to provide a fair comparison with the 1D case we implement the following numerical scheme in 2D. We assume food is initially located at every node of a regular lattice of unit size, and then we allow the walker to move according to the same rules as above, that is, movement in a constant direction at speed v_f while feeding such that with rate γ the food is missed, and then a escape phase starts which is governed by a double telegrapher's process at speed v_e , with short flights at short times (stage 1) that switch irreversibly (with rate w) to arbitrarily long flights (stage 2). The walker will be able to detect the food located at the nearest node of the lattice in case it has not been already depleted. In that case the feeding phase is kept, or initiated, and the food is removed from that site. Now, instead of $l(t)$ we rather compute the number of depleted food nodes as a function of time $N(t)$ to measure food intake.

The corresponding results (Fig. 4) confirm that ballistic strategies ($w \rightarrow \infty$) are also detrimental in 2D. This can be justified by checking that the fractal-like regions left empty with a ballistic strategy are more space filling (see the movies provided in the Supplemental Material [54]). Then ballistic flights often require traveling from one extreme of the empty region to the other, which represents a significant waste of time. In consequence, we find again that food intake does not increase monotonically with w (see the inset in Fig. 4) but an

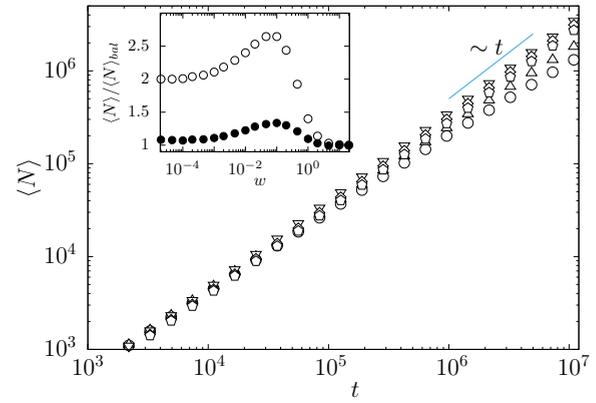


FIG. 4. Food intake $\langle N \rangle$ in two dimensions (as defined in the main text) as a function of time for different values of the switching rate w , as follows: circles ($w = 10$), triangles ($w = 1$), inverted triangles ($w = 0.1$), diamonds ($w = 0.01$), pentagons ($w = 0.001$). Inset: Mean food consumed at long times relative to the ballistic escape case, for long times ($t = 10^5$ for solid symbols, $t = 10^7$ for open symbols) as a function of w . In all cases we use $v_f = v_e = \alpha_1 = \gamma = 1$.

optimal switching rate is found, which slowly decays to zero as time increases. In Fig. 4 one can see that for small w the food intake approaches the asymptotic scaling $N \sim t$, as in the standard ERW, while for large w the scaling is eventually lost and becomes sublinear. As the empty region grows, longer and inefficient crossings through that region will dominate the escape process, so $N \sim l \sim \sqrt{t}$ should be expected for extremely long times (we have not been able to reach that limit numerically, but up to $t = 10^7$ the sublinear behavior starts to appear clearly).

VI. DISCUSSION

As a whole, the results from the two previous sections provide robust evidence that ballistic strategies are not convenient in the context of spaces homogeneously filled with food, or resources, that are progressively depleted by the walker. We stress that this situation reflects a case that could be really significant for smaller organisms in nature, since search mechanisms in those cases could be more focused on *recovering* a lost signal than on starting a blind search in an empty space, which is the scenario most typically studied in random search theory.

Finally, one could wonder what is the role of Lévy flights and other well-studied search strategies within the context presented. The fact that Lévy flights optimize searches in the limit $x_0/l \rightarrow 0$ for one-dimensional homogeneous domains is well known. Then, since our escape-and-feeding process is a sequence of many of these situations for increasing values of l , we expect that the Lévy flight will also represent the global optimum, though an explicit expression for $\langle l \rangle$ is probably unattainable in that case (actually, there is some evidence that microscopic organisms could be able to exhibit scale-invariant motion [55,56]). So, while the strategy presented here probably does not represent a global optimum to the search problem, it has the power to explain why ballistic strategies are not observed in simple organisms, where

correlated or persistent (often nonstationary) random walks are rather the rule. Nevertheless, we note that our arguments seem to remain valid still in 2D (Fig. 4), where the global optimality of Lévy flights stops holding [57]. Moreover, it is still likely that an adaptive (time-decreasing) value of w would yield even higher food intakes, as the optimum w decays progressively for $t \rightarrow \infty$. Such an adaptive strategy probably should be able to outperform Lévy flights, as happens for informed random walks (in which the walker has some

minimum information about the domain scales) [53]. These and other questions remain to be explored in forthcoming works in which the general ERW scheme presented here can be satisfactorily applied.

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APPENDIX A: DERIVATION OF THE MEAN ESCAPE TIME $\langle T \rangle$

Expressions (14) and (15) can be transformed to Laplace space

$$s \left(\frac{s - \delta(x_0)}{\alpha_1} + 1 \right) q_1(x, s|x_0) - \delta(x_0) = \frac{v^2}{\alpha_1} \frac{\partial^2 q_1(x, s|x_0)}{\partial x^2} - w q_1(x, s|x_0), \quad (\text{A1})$$

$$s \left(\frac{s}{\alpha_2} + 1 \right) q_{12}(x, s|x_0) = \frac{v^2}{\alpha_2} \frac{\partial^2 q_{12}(x, s|x_0)}{\partial x^2} - w q_{12}(x, s|x_0), \quad (\text{A2})$$

so they admit an explicit solution within the interval $(0, l)$ with periodic boundary conditions (see, e.g., Ref. [58]):

$$q_1(l, s|x_0) = \frac{1}{2} \sqrt{\frac{s+w+\alpha_1}{s+w}} \frac{\cosh \left[\frac{(s+w)(s+w+\alpha_1)}{v_e} \left(\frac{l}{2} - x_0 \right) \right]}{\sinh \left[\frac{(s+w)(s+w+\alpha_1) l}{2 v_e} \right]}, \quad (\text{A3})$$

$$q_{12}(l, s|x_0) = \frac{w}{2v_e} \left(\frac{h_1(s) \cosh \left[\frac{s}{v_e} \left(\frac{l}{2} - x_0 \right) \right]}{\sinh \left[\frac{s l}{2 v_e} \right]} + \frac{h_2(s) \cosh \left[\frac{\sqrt{(s+w)(s+w+\alpha_1)}}{v_e} \left(\frac{l}{2} - x_0 \right) \right]}{\sinh \left[\frac{\sqrt{(s+w)(s+w+\alpha_1) l}}{2 v_e} \right]} + \frac{h_3(s) \cosh \left[\frac{s+\alpha_1}{v_e} \left(\frac{l}{2} - x_0 \right) \right]}{\sinh \left[\frac{(s+\alpha_1) l}{2 v_e} \right]} \right), \quad (\text{A4})$$

where we have already considered $\alpha_2 = 0$ for the sake of simplicity, and we have defined

$$h_1(s) = \frac{(2s+w)(s+\alpha_1) + \alpha_1^2}{(2s+\alpha_1)[s(\alpha_1+2w) + w(\alpha_1+w)]}, \quad (\text{A5})$$

$$h_2(s) = \frac{-\alpha_1(2s+w+\alpha_1)\sqrt{s+w+\alpha_1}}{\sqrt{s+w}[s(2w+\alpha_1) + w(w+\alpha_1)][\alpha_1(s+\alpha_1) - w(2s+w+\alpha_1)]}, \quad (\text{A6})$$

$$h_3(s) = \frac{s(2s+w+2\alpha_1)}{(2s+\alpha_1)[\alpha_1(s+\alpha_1) - w(2s+w+\alpha_1)]}. \quad (\text{A7})$$

Finally, we also need the explicit expression for $q_2(l, s|x_0)$. As mentioned in the main text, this comes from the solution of the equation

$$\frac{\partial q_2(x, t|x_0)}{\partial t} + \frac{1}{\alpha_2} \frac{\partial^2 q_2(x, t|x_0)}{\partial t^2} = \frac{v^2}{\alpha_2} \frac{\partial^2 q_2(x, t|x_0)}{\partial x^2}. \quad (\text{A8})$$

Transforming to the Laplace space, the explicit solution in the interval $(0, l)$ with periodic conditions reads (again in the limit $\alpha_2 \rightarrow 0$)

$$q_2(l, s|x_0) = \frac{\cosh \left[\frac{s}{v} \left(\frac{l}{2} - x_0 \right) \right]}{2 \sinh \left(\frac{s l}{2 v} \right)}. \quad (\text{A9})$$

Now, if one replaces expressions (A3), (A4), and (A9) into Eq. (16) of the main text, one reaches an exact (but lengthy) expression for $p(l, s)$ that contains all the statistical properties of the escape process.

APPENDIX B: DERIVATION OF $\langle l \rangle$

As mentioned in the main text, the long-time limit of the escape-and-depletion process necessarily implies that l will be large, too, if compared to the characteristic scales of motion involved (that is, v_e/γ , v/w , and v/α_1).

Thus, the limits of s small and l large can be carried out together. Note from (A3), (A4), and (A9) that the dependence of $f(l, s)$ on l is always through functions of the type $\tanh [b(s)l/v_e]$ (provided $x_0 \rightarrow 0$), with different forms of the function $b(s)$. One can thus approximate $\tanh [b(s)l/v_e] \approx 1$ for l large [except when $b(s)$ is such that $\lim_{s \rightarrow 0} b(s) = 0$, where this is expanded to first

order in $s \rightarrow 0$]. Applying this, the whole expression for $p(l, s)$ simplifies, under these two limits, to $p(l, s) \approx a_1(s) - a_2(s)sl/v_e$, where

$$a_1(s) = 1 + \frac{\alpha_1^2(w + \alpha_1) + (2\alpha_1^3 - 6w^2\alpha_1 - 3w^3)\sqrt{w(w + \alpha_1)}}{w\alpha_1[w + \alpha_1 + \sqrt{w(w + \alpha_1)}](w^2 + w\alpha_1 - \alpha_1^2)}s, \quad (\text{B1})$$

$$a_2(s) = \frac{1}{2\left(1 + \sqrt{\frac{w+\alpha_1}{w}}\right)}\left[1 - \frac{w + \alpha_1}{w\alpha_1}s\right], \quad (\text{B2})$$

where the required normalization condition $a_1(0) = 1$ is satisfied.

These expressions are to be introduced into the system (1) once this is transformed to Laplace space, which reads

$$\begin{aligned} \rho_f(l, s) - 1 &= -v_f \frac{\partial \rho_f(l, s)}{\partial l} + \gamma \rho_f(l, s)[p(l, s) - 1], \\ \rho_e(l, s) &= -\gamma \rho_f(l, s)[p(l, s) - 1]. \end{aligned} \quad (\text{B3})$$

Once the form of $p(l, s)$ is explicitly introduced here and the Fourier transform (from l space to k space) is carried out, the mean value of l can be computed from $\langle l \rangle = -i\partial_k[\rho_f(k, s) + \rho_e(k, s)]_{k=0}$. By following these steps one finds

$$\langle l \rangle = \sqrt{\frac{\pi i v_f v_e}{2\gamma a_2(s) s^3}} \exp\left[-\frac{i v_e[-s + \alpha_1(a_1(s) - 1)]^2}{2v_f \alpha_1 a_2(s) s}\right] \operatorname{erfc}\left[\frac{\sqrt{v_e}[-s + \alpha_1(a_1(s) - 1)]}{\sqrt{2i v_f \alpha_1 a_2(s) s}}\right], \quad (\text{B4})$$

which, at first order in the long-time limit ($s \rightarrow 0$), becomes expression (18) in the main text.

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