Role of Depletion on the Dynamics of a Diffusing Forager

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Abstract.

We study the dynamics of a *starving random walk* in general spatial dimension d. This model represents an idealized description for the fate of an unaware forager whose motion is not affected by the presence or absence of resources. The forager depletes its environment by consuming resources and that dies if it wanders too long without finding food. In the exactly-solvable case of one dimension, we explicitly derive the average lifetime of the walk and the distribution for the number of distinct sites visited by the walk at the instant of starvation. We also give a heuristic derivation for the averages of these two quantities. We tackle the complex but ecologically-relevant case of two dimensions by an approximation in which the depleted zone is assumed to always be circular and which grows incrementally each time the walk reaches the edge of this zone. Within this framework, we derive a lower bound for the scaling of the average lifetime and number of distinct sites visited at starvation. We also determine the asymptotic distribution of the number of distinct sites visited at starvation. Finally, we solve the case of high spatial dimensions within a mean-field approach.

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1. Introduction

The *starving random walk* represents an idealized description for the dynamics of a forager without any sensory awareness who randomly searches for food in an environment that is depleted by the foraging process itself [1]. In this model, the forager undergoes an unbiased nearest-neighbor random walk on a regular d-dimensional lattice, in which each lattice site initially contains one food unit. The walk has a metabolic capacity, or intrinsic starvation time $\mathcal{S}$, which is defined as the number of steps that the walk can travel without encountering food before starving to death. Each time the walk lands on an empty site, it comes one time unit closer to starvation. However, if the walk lands on a site that contains food, the food is instantaneously and completely consumed, and the walk can again travel $\mathcal{S}$ additional steps without encountering food before starving.

Our goal in this work is to quantitatively account for the phenomenon of starvation, in which an organism fails to find resources before it expends its own metabolic reserves and starves to death. This search for resources is an essential task of all living organisms [2–10], in which the resource could be nourishment, an abode, or a particular individual. Here we view the resource as food that is gradually depleted through consumption by foragers; the ecologically relevant situation where the resource is replenished has also been investigated [11]. Search for a resource has been extensively studied for an omniscient forager that has full knowledge of its environment (see, e.g., [2–4]). In this setting, the basic objective is to determine the criterion that optimizes the foraging process. Our focus is on the complementary case where the forager has no environmental knowledge nor the ability to learn about its environment. Because the resource is gradually depleted by the forager, the ultimate fate of the forager is to necessarily starve.

An important aspect of the starving random walk is that it moves in the same manner, irrespective of its distance to food sources, as well as whether or not it has recently encountered food. This feature contrasts with the *excited* random walk [12–18], in which the walk continues to move in the same direction when it encounters food and wanders randomly when it does not. While the excited random walk exhibits surprising properties, the starving random walk is also quite phenomenologically rich. The salient feature of the starving random walk is that its mortality is coupled to its gradually depleting environment. In this sense the starving random walk also differs from *mortal* random walk models [19–22], in which a walk spontaneously dies at a fixed rate, independent of its trajectory.

We will investigate two basic questions: (i) How long does a forager live? (ii) What is the spatial extent of the region explored by a forager before it starves? The behaviors of two quantities depend in an essential way on the metabolic capacity $\mathcal{S}$ and the spatial dimension d, as previously discussed in [1]. Here, we provide details of the derivation of these results, as well as qualitative arguments to support our analytical and numerical results.

We will first treat the case of one dimension, where the problem is amenable to a full analysis (Sec. 2). For any $d \leq 2$, the forager tends to carve out a compact depleted spatial region—which we define as the "desert"—because of the recurrence of the random walk [23, 24], and then starve before it can escape this desert. As a consequence, the forager lifetime grows slowly with $\mathcal{S}$—linearly in $\mathcal{S}$ for $d = 1$ and as $\mathcal{S}^z$ with $z \approx 1.9$ for for the ecologically relevant case of $d = 2$, as will be presented in Sec. 3. We also introduce a circular approximation to provide a lower bound for the lifetime and number of sites visited at the instant of starvation in $d = 2$.

As the spatial dimension increases, the transience of the random walk implies the forager is less likely to return to previously depleted sites. Consequently, the lifetime of the forager should be an increasing function of the dimension for a fixed metabolic capacity $\mathcal{S}$. Thus a starving random walk is long-lived for $d > 2$; simulations suggest that the average survival time grows as $\exp(\mathcal{S}^\omega)$, with $\omega \approx \frac{1}{2}$ in $d = 3$ and with ω a gradually increasing function of the spatial dimension [1].

In Sec. 4, we present a mean-field approximation in which successive visits to food-containing sites are uncorrelated; this description corresponds to the starving random walk model in the limit of $d = \infty$. Here, we solve for the first-passage probability for the walk to starve, from which we find that the average forager lifetime grows exponentially with $\mathcal{S}$. We close with some concluding remarks in section 5. Calculational details for the distribution of visited sites and the average lifetime in one and two dimensions are presented in the Appendices.

2. One Dimension

The evolution of the system in one dimension is schematically illustrated in Fig. 1. As the walk moves, a region of length $L(t)$ that is devoid of food—the desert—is carved out. The survival of the walk is controlled by the interplay between its wandering and going hungry in the desert interior and reaching the edge of this desert to consume food. We are interested in the average of the lifetime of the walk and of the number of distinct sites visited by the walk, as well as the distribution of the latter at the moment of starvation. Because of the simplicity of one dimension, these properties can all be calculated explicitly. It is instructive, however, to begin with an intuitive argument for the lifetime and number of distinct sites visited.

2.1. Heuristic approach

In one dimension, the walk clears out a desert whose length grows sporadically by steps of a single lattice spacing a (Fig. 1). We estimate the average walk lifetime by partitioning a typical trajectory into three stages:

(i) The walk first carves out a desert of a "dangerous" critical length L_c—duration T_1.

(ii) The walk returns M times to the same edge of the desert—duration T_2.

(iii) The walk wanders for too long inside the desert and dies—duration T_3.

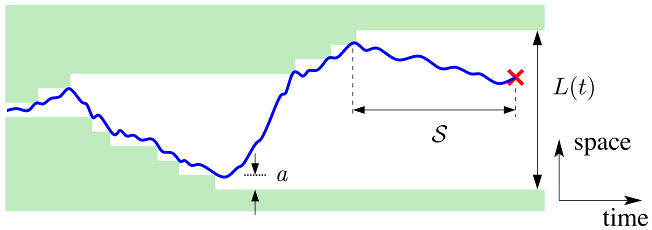


Figure 1. Space-time evolution of a one-dimensional random walk that clears out an interval—the desert—where food (shaded) has been eaten. Whenever the walk reaches a food-containing site, the food is consumed and the desert grows by one lattice spacing a. The walk starves ($\times$) when it travels $\mathcal{S}$ steps without encountering food.

During stage (i), the walk successively reaches either edge of the desert and extends it by one lattice spacing as long as the average crossing time

$$t_{\rm cross} = \frac{L^2 - a^2}{6D} \tag{1}$$

is less than the metabolic capacity $\mathcal{S}$. Equation (1) applies for a walk that starts a distance a from one edge of a desert of length L and reaches the other side [25]. We define the critical desert length $L_c \equiv n_c\, a$ by the condition that the walk typically starves when it attempts to cross the desert. This gives $t_{\rm cross} = \mathcal{S}$, or

$$L_c \simeq \sqrt{6D\mathcal{S}} \tag{2}$$

in the large-$\mathcal{S}$ limit. When the length of the desert equals ka, the average time t_k needed to reach *either* edge of the desert when starting a distance a from one edge is [25]

$$t_k = \frac{(k-1)a^2}{2D}\,. \tag{3}$$

Thus the duration T_1 of the first stage of a typical trajectory is the sum of these average return times t_k until the desert reaches the critical length $L_c \equiv n_c\, a$:

$$T_1 \simeq \sum_{k=1}^{n_c} \frac{a^2 k}{2D} \simeq \frac{L_c^2}{4D} = \tfrac{3}{2}\mathcal{S}\,. \tag{4}$$

During stage (ii), the walk likely starves if it attempts to cross the desert. Thus it continues to survive only if it makes repeated excursions to the same side of the desert. Suppose that the walk is at the left edge at the end of stage (i). The walk will typically return M times to this edge before attempting to cross the desert, which results in its starvation. The probabilities that the walk *eventually* hits the left edge or the right edge of a desert of length L when starting a distance a from the left edge are, respectively, [25]

$$p_- = \frac{L-a}{L} \qquad\qquad p_+ = \frac{a}{L}\,, \tag{5}$$

and the conditional first-passage time to the left edge is

$$t_- = \frac{aL}{6D}\Big(2 - \frac{a}{L}\Big)\,. \tag{6}$$

The probability Π_k that a random walk hits the left edge k times before hitting the right edge, starting from a desert of length L_c, therefore is

$$\begin{aligned}\Pi_k &= \frac{L_c - a}{L_c} \times \frac{L_c}{L_c + a} \times \frac{L_c + a}{L_c + 2a} \times \ldots \times \frac{L_c + (k-2)a}{L_c + (k-1)a} \times \frac{a}{L_c + ka} \\ &= \frac{a(L_c - a)}{[L_c + (k-1)a](L_c + ka)} \,. \end{aligned} \tag{7}$$

The first $k-1$ terms in the product give the probabilities for the walk to successively hit the left edge; after each such event the interval grows by a. The last factor is the probability to hit the right edge when the interval has reached length $L_c + ka$. It is straightforward to verify that this probability distribution is normalized, $\sum_{k\geq 0} \Pi_k = 1$. Because $\Pi_k \sim k^{-2}$ for large k, the average number of same-side excursions until the right edge is reached, $\sum_{k\geq 0} k\,\Pi_k$, is infinite. Nevertheless, the *typical* number M of same-side excursions is meaningful. This quantity can be defined as the median number of such excursions, so that $\sum_{0\leq k\leq M} \Pi_k = 1/2$. This gives

$$\sum_{0\leq k\leq M} \frac{a(L_c - a)}{(L_c + (k-1)a)(L_c + ka)} = 1 - \frac{L_c - a}{L_c + Ma} = \frac{1}{2} \,. \tag{8}$$

Thus for an interval of length L_c, the right edge will typically be reached after $M \sim L_c/a$ consecutive same-side excursions to the left edge. This condition defines the end of the stage (ii). Its duration T_2 is the sum of the average conditional return times to the same edge of the desert when starting one lattice spacing away from this edge:

$$T_2 \simeq \sum_{k=L_c/a}^{L_c/a+M} \frac{ka^2}{3D} \simeq \frac{L_c^2}{2D} = 3\,\mathcal{S} \,. \tag{9}$$

Finally, in stage (iii), the walk fails to return to the left edge of the desert within $\mathcal{S}$ steps. The duration T_3 of this terminal stage is exactly $\mathcal{S}$ steps.

We therefore estimate of the average lifetime τ of the starving random walk as

$$\tau \simeq T_1 + T_2 + T_3 \simeq 5.5\,\mathcal{S} \tag{10}$$

compared to the exact asymptotic value of $3.27686\ldots\mathcal{S}$ that will be derived in the next section (see also [1]). Note that T_1, T_2 and T_3 are comparable when $\mathcal{S} \to \infty$. Moreover, the above heuristic approach gives the average number of distinct sites visited $\langle \mathcal{N} \rangle$ as

$$\langle \mathcal{N} \rangle \simeq \frac{L_c}{a} + M \simeq 2\frac{\sqrt{6D\mathcal{S}}}{a} \simeq 3.4641\,\sqrt{\mathcal{S}} \,, \tag{11}$$

compared to the exact asymptotic value of $2.9022\ldots\sqrt{\mathcal{S}}$ [1] that we will also derive in the next section.

2.2. Exact probabilistic approach

We now calculate the average number of distinct sites visited by the walk and its distribution at the instant when the walk starves, as well as its average lifetime. We then provide explicit results by an asymptotic analysis.

For an unbiased n-step nearest-neighbor random walk in one dimension, the average number of distinct sites visited, which is also the span of the walk divided by the lattice spacing a, asymptotically grows as $S_n \sim \sqrt{8n/\pi} \approx \sqrt{2.55\,n}$ [24]. The new feature for starving random walks is that there cannot exist excursions of more than $\mathcal{S}$ consecutive steps in the previous history in which the walk does not encounter food. Thus a long-lived starving random walk spends less time roaming within the interior of a desert than an unrestricted random walk. As a consequence, the number of distinct sites visited by starving random walks should be larger than that for unrestricted random walks at the same time.

To determine the number of distinct sites visited and its distribution at the instant of starvation, we define $V(\mathcal{N})$, the probability that a random walk has visited $\mathcal{N}$ distinct sites when starvation occurs. We may express this probability as

$$V(\mathcal{N}) = \mathcal{F}_2\,\mathcal{F}_3\,\mathcal{F}_4\ldots\mathcal{F}_{\mathcal{N}}(1-\mathcal{F}_{\mathcal{N}+1})\,, \tag{12}$$

where

$$\mathcal{F}_k = \int_0^{\mathcal{S}} dt\, F_k(t)\,,$$

with $F_k(t)$ the first-passage probability to either edge of an interval of length ka when the walk starts a distance a from one edge. That is, an interval of length ka has to be generated, then an interval of length $(k+1)a$, then $(k+2)a$, etc., each within a time $\mathcal{S}$, until the final interval length is reached.

The details of this derivation are given in Appendix A; we make contact with the discrete nearest-neighbor random walk by setting the diffusion coefficient $D = a^2/2$. From the asymptotic result given in Eq. (A.8), the average number of visited sites at the starvation time is, in the large $\mathcal{S}$ limit,

$$\langle\mathcal{N}\,\rangle = \sum_{\mathcal{N}\geq 1} \mathcal{N}V(\mathcal{N}) \simeq \mathcal{N}^* \int_0^\infty \theta\, V(\theta)\, d\theta\,, \tag{13}$$

where we take the continuum limit and express the distribution of visited sites in terms of the scaled variable $\theta = \mathcal{N}/\mathcal{N}^*$, with $\mathcal{N}^* = \pi\sqrt{D\mathcal{S}}/a$. Using the explicit form for the distribution $V(\theta)$ in Eq. (A.8) and computing this integral numerically gives

$$\langle\mathcal{N}\rangle \simeq 1.3065\,\mathcal{N}^* \approx 2.9022\,\sqrt{\mathcal{S}} \qquad\qquad \mathcal{S} \gg 1. \tag{14}$$

We now turn to the average lifetime τ, which we write as

$$\tau = \sum_{n=0}^{\infty} \big(\tau_1+\tau_2+\cdots+\tau_n+\mathcal{S}\big)V(n)\,. \tag{15}$$

Here τ_n is the average return time for the random walk to hit either edge of the interval in the $n^{\rm th}$ excursion, conditioned on the walk hitting either edge before it starves, while the term $\mathcal{S}$ accounts for the final excursion in which the walk starves. By definition

$$\tau_n = \frac{\int_0^{\mathcal{S}} dt\ t\ F_n(t)}{\int_0^{\mathcal{S}} dt\, F_n(t)} = \frac{\int_0^{\mathcal{S}} dt\ t\ F_n(t)}{\mathcal{F}_n}\,, \tag{16}$$

with $\mathcal{F}_n = \int_0^{\mathcal{S}} dt\, F_k(t)$. The calculation of τ_n and subsequently τ are presented in Appendix B and the final result is

$$\tau \simeq 3.26786\ \mathcal{S} \qquad\qquad \mathcal{S} \gg 1. \tag{17}$$

Thus the average lifetime of a starving random walk also scales linearly in $\mathcal{S}$. Roughly speaking, the same amount of time is spent in carving out a desert to reach the critical length, then in enlarging it always via the same edge, before finally attempting (and failing) to cross this desert. The underlying distributions of visited sites and lifetimes are visually similar and are characterized by a well-defined peak near the average value and an exponential large-argument tail.

3. Two Dimensions

Two dimensions is the ecologically relevant situation because of the obvious connection to the movement of land foragers. This case is also theoretically interesting because $d = 2$ is the critical dimension between recurrence and transience of random walks [23–25]. Four sample trajectories of starving random walks at the instant of starvation are given in Fig. 2 for metabolic capacity $\mathcal{S} = 500$ to show the types of trajectories that arise. A walk survives if it never makes an excursion of more than $\mathcal{S}$ steps anytime in its past history without encountering food. Thus the effect of starvation is to progressively bias the ensemble of random walks as time increases. For fixed $\mathcal{S}$, a short-lived trajectory is relatively compact so that a desert is quickly carved out within which the walk starves. Conversely, a long-lived walk typically has a ramified trajectory to ensure that the walk remains close to food-containing sites and thus is unlikely to starve.

The starvation constraint on the trajectories is highly non-trivial and we have been unable to solve the problem by exact methods. Thus we turn to simulations and crude approximations to elucidate some basic properties of starving random walks in two dimensions.

3.1. Simulation results

Our simulations are typically based on 10^6 realizations of nearest-neighbor random walks that wander until they starve, for metabolic capacities $\mathcal{S}$ between 10 and 2000. For each walk, we record the time at the instant of starvation, the position of the walk, and the number of distinct sites visited (equal to the amount of food that the walk has eaten). From these data, we reconstruct the underlying distributions of these quantities.

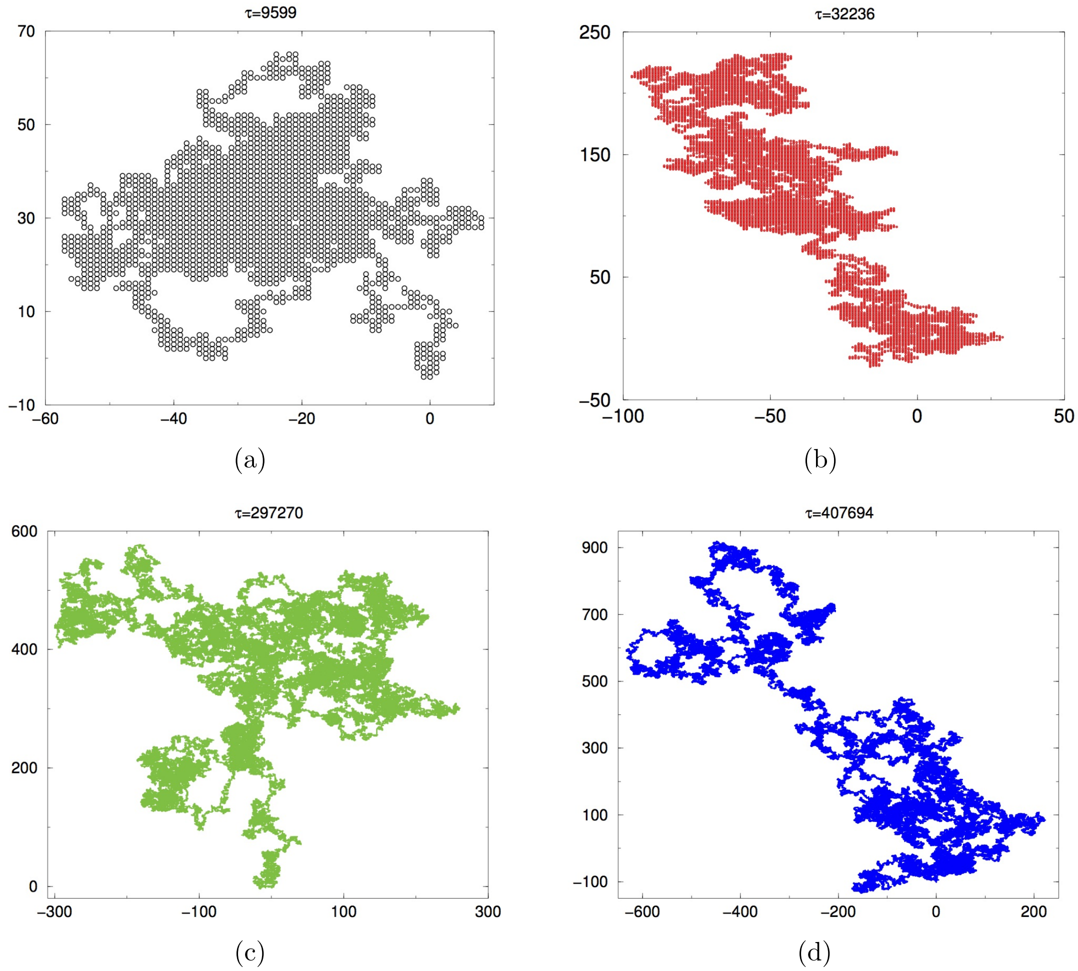
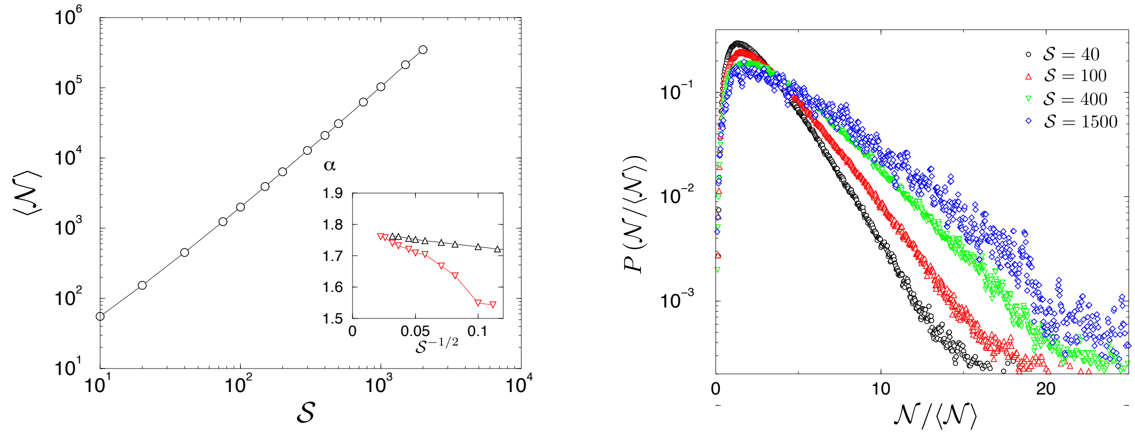


Figure 2. Example random-walk trajectories for $\mathcal{S} = 500$ with the lifetime τ of each walk indicated. (a), (b): Short-lived walks. (c), (d) Long-lived walks.

A plot of the average number of distinct sites visited at starvation (Fig. 3) is suggestive of the algebraic behavior $\langle \mathcal{N} \rangle \sim \mathcal{S}^{\alpha}$. While a naive linear fit to the data on a double logarithmic scale gives $\alpha \approx 1.66$, there is a systematic upward curvature in the data of $\ln\langle \mathcal{N} \rangle$ versus $\ln \mathcal{S}$. We account for this curvature by defining two types of $\mathcal{S}$-dependent exponents: (a) a local exponent that is obtained from the slopes of four adjacent data points in a window that is moved to progressively larger $\mathcal{S}$, and (b) a running exponent that is obtained by successively deleting the first point, the first two points, the first three points, etc. in the data. These two $\mathcal{S}$-dependent exponents both appear to extrapolate to the common value $\alpha \approx 1.8$ (Fig. 3(a) inset). (For the average lifetime and the root-mean-square displacement, we use only the running exponent because it has smaller fluctuations.) The closeness of this exponent to 2 and the fact that $d = 2$ is the critical dimension of random walks may indicative that the true dependence of $\langle \mathcal{N} \rangle$ on $\mathcal{S}$ is quadratic but modified by a logarithmic correction.

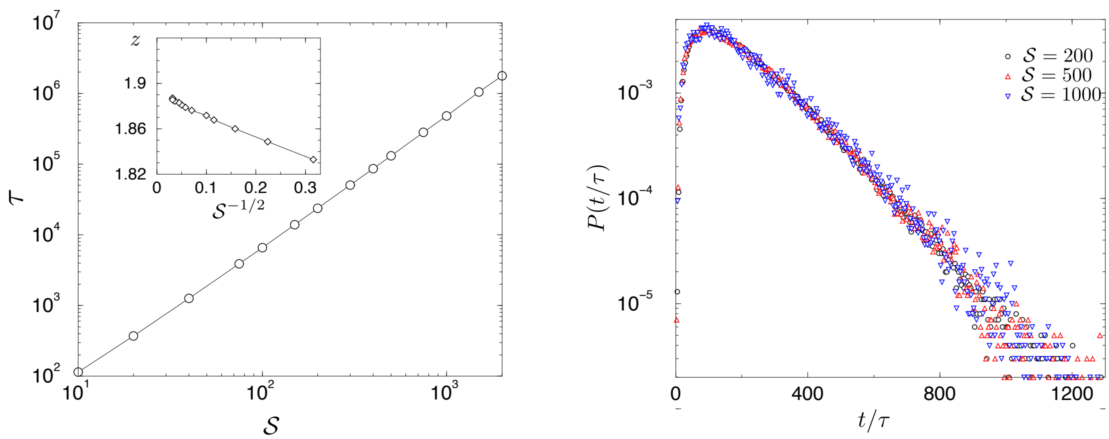
Perhaps the most surprising aspect of this data is that the distribution of distinct sites visited at the instant of starvation does not satisfy single-parameter scaling, as



(a) (b)

Figure 3. (a) Average number of distinct sites visited for 10^6 realizations of starving random walks at the starvation time as a function of $\mathcal{S}$. The curve through the points is a guide for the eye. The inset shows the local exponent ($\triangle$) and the running exponent (∇). (b) The scaled distribution of number of distinct sites visited for 4 representative value of $\mathcal{S}$. The data have been averaged over a 15-point range and only every fifth data point is displayed. All data are based on 10^6 for each value of $\mathcal{S}$.

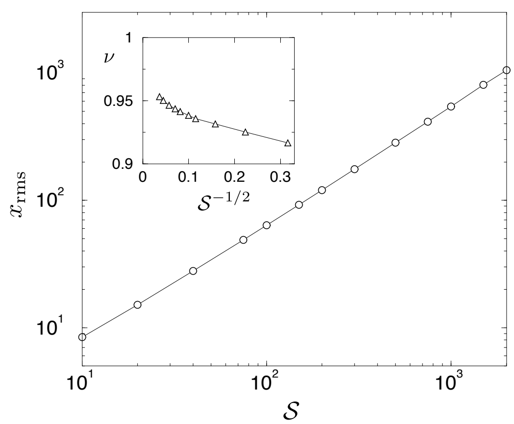
initially reported in [1]. This is in stark contrast to the cases of $d = 1$ and $d = 3$, where this same distribution does obey single-parameter scaling. This lack of scaling indicates that two dimensions represents a unique situation.



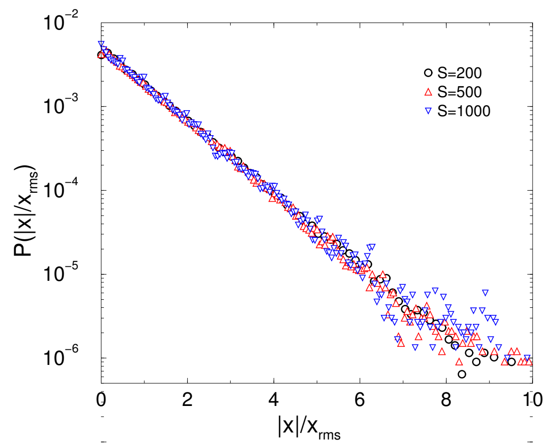
(a) (b)

Figure 4. (a) Average lifetime of starving random walks in $d = 2$ as a function of $\mathcal{S}$. The inset shows the running exponent. (b) The scaled distribution of lifetimes $P(t/\tau)$ for 3 representative values of $\mathcal{S}$. Data are based on 10^6 realizations for each $\mathcal{S}$.

The dependence of the average walk lifetime τ on $\mathcal{S}$ is shown in Fig. 4. Again, there is a small and systematic upward curvature of the data of τ versus $\mathcal{S}$ on a double logarithmic scale. Thus we employ the same analysis as that used for the number of distinct sites visited, to estimate that the asymptotic exponent for the lifetime extrapolates to a value near 1.9 (inset to Fig. 4(a)) The closeness of this exponent estimate to 2 is again suggestive that perhaps the dependence of τ on $\mathcal{S}$ may be modified by a logarithmic correction. The distribution of lifetimes for different values of $\mathcal{S}$ collapse onto a single universal curve, with an exponential long-time decay, when each distribution is scaled by the average lifetime τ (Fig. 4(b)). This contrasts with the lack of scaling displayed by the distribution of visited sites.



(a)



(b)

Figure 5. (a) Average rms displacement of a single coordinate for starving random walks at the instant of starvation in $d = 2$ as a function of $\mathcal{S}$. The inset shows the running exponents in the main plot. (b) Scaled distribution of this rms displacement for 3 representative values of $\mathcal{S}$. Data are based on 10^6 for each value of $\mathcal{S}$.

Finally, we study the root-mean-square displacement of a single Cartesian coordinate $x_{\rm rms} \equiv \sqrt{\langle x^2 \rangle}$ and its distribution at the instant of starvation. As shown in Fig. 5(a), it appears that $x_{\rm rms} \sim \mathcal{S}^{\nu}$, with ν close to 1. This dependence accords with naive expectations based on the dependence of τ on $\mathcal{S}$. Namely, if $x_{\rm rms} \sim \mathcal{S}$ and $\tau \sim \mathcal{S}^2$, and furthermore, the distribution of lifetimes is sharply peaked about its most probable value, then we should expect that $x_{\rm rms} \sim \sqrt{\tau}$, which is the same scaling of rms displacement versus time as an unrestricted random walk. Finally, Fig. 5(b) shows the scaled distribution of the absolute value of a single coordinate at the instant of starvation. The distributions for different $\mathcal{S}$ all collapse onto a universal curve that decays exponentially, in contrast to the Gaussian decay of a pure random walk. This distinction stems from the difference between the ensemble of trajectories of a starving random walk and that of an unconstrained random walk. Indeed, the long-lived trajectories for a starving random walk are more ramified and more spatially extended than for a pure random walk, as the walk needs to remain close to resources to survive.

3.2. Circular approximation: heuristic approach

Because of the typically labyrinthine desert geometry in two dimensions, it does not seem feasible to determine the properties of two-dimensional starving random walks exactly. Thus we develop an approximation that is based on the assumption that the desert remains circular at all times. While obviously crude (compare with Fig. 2), this approximation provides a lower bound for the average lifetime at starvation because a circular desert is the most unfavorable geometry for the walk to survive.

We now adapt the heuristic argument given in 2.1 for one dimension to this circular approximation. Each time the walk hits the edge of the desert, it eats one unit of food, which we take to be a small patch of area a^2, with a the lattice spacing. After each meal, the area of the desert increases by a^2 so that its radius after n meals is $R_n = \sqrt{na^2/\pi}$. Moreover, we assume that after reaching the desert boundary, the walk starts a distance a from the enlarged boundary to begin another excursion (Fig. 6), as on the lattice.

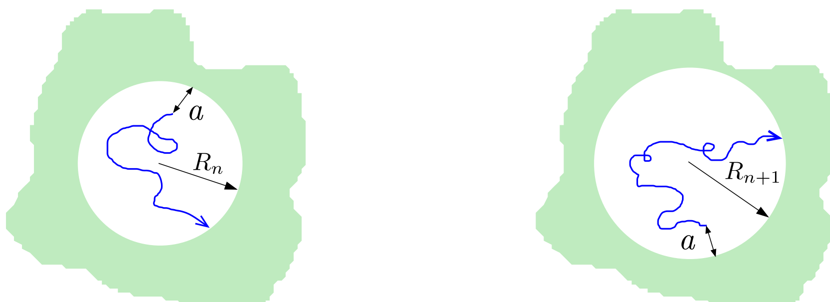


Figure 6. Schematic illustration of the evolution of the desert in the circular approximation. When the random walk hits the boundary, it is restarted a distance a from the newly enlarged boundary.

Following Sec. 2.1, we again decompose a typical trajectory into three phases:

(i) The walk carves out a circular desert of a "dangerous" radius R_c.

(ii) After R_c is reached, the walk makes M excursions into the desert without starving.

(iii) The walk wanders too deeply into the desert and starves.

The desert radius reaches a dangerous value R_c when the average time to go from the edge to the center is roughly one-half of the metabolic capacity $\mathcal{S}$. This typically corresponds to the average conditional time to reach a small disk in the center of the desert without having touched its edge, at the radius R_c, starting from a radius $R_c - a$ [25]. This gives the criterion

$$\frac{R_c^2}{4D} \simeq \frac{\mathcal{S}}{2},$$

from which $R_c = \sqrt{2D\mathcal{S}}$.

We now estimate the time to reach this critical radius. When the desert is subcritical, a forager typically survives an excursion no matter where it exits the desert.

For a walk that starts at radius $R_n - a$, the time to reach the edge of the desert is $t_n \sim aR_n/2D$. The number of meals n_c that the forager must eat for the desert to reach the critical radius is determined from $\pi R_c^2 = n_c a^2$, or $n_c = 2\pi D\mathcal{S}/a^2$. Thus the duration of phase (i) is the sum of the excursion times until the critical radius is reached:

$$T_1 = \sum_{n<n_c} t_n = \sum_{n<n_c} \frac{aR_n}{2D} \simeq \frac{a}{3D}\sqrt{\frac{a^2}{\pi}}\, n_c^{3/2} \sim \frac{D^{1/2}}{a}\,\mathcal{S}^{3/2}\,. \tag{18}$$

As we will show, the duration of phases (ii) and (iii) are negligible compared to phase (i). Phase (iii) has duration $\mathcal{S}$ by definition. For phase (ii), if we know the typical number M of times that the walk returns to the edge of the desert of initial radius R_c before starving, then its duration is given by

$$T_2 = \sum_{n=n_c}^{n_c+M} R_n \simeq \int_{n_c}^{n_c+M} \sqrt{n}\, dn \;\propto\; (n_c{+}M)^{3/2} - n_c^{3/2}\,. \tag{19}$$

While we are unable to determine M, we can provide an upper bound that we write as M_+. Suppose that the desert radius remains fixed at R_c each time the walk returns to the boundary. The number of returns M_+ in this case is strictly greater than M. To estimate M_+, we need the probability $\mathcal{E}$ that the walk does not starve in this fixed-size desert between two consecutive returns to the edge of the desert. We estimate $\mathcal{E}$ as the probability that the walk does not reach the core of the desert, which we take as a small disk of radius b that is much less than R_c. This quantity is just the splitting probability for a walk that starts at radius $R_c - a$ to return to radius R_c before reaching radius b. For unconstrained diffusion, this splitting probability is given by [25]

$$\mathcal{E} = \frac{\ln\left[(R_c - a)/b\right]}{\ln\left(R_c/b\right)} \simeq 1 - \frac{C}{\sqrt{\mathcal{S}}\,\ln\mathcal{S}} \quad \text{for } \mathcal{S} \gg 1. \tag{20}$$

with C a constant of order 1 as long as $b \ll R_c$. The probability that the walk returns k times to the outer boundary R_c before starving is $\Pi_k = \mathcal{E}^k\,(1-\mathcal{E})$. Hence the average number M_+ of returns to this boundary is

$$M_+ = \sum_{k=0}^{\infty} k\,\Pi_k = \frac{\mathcal{E}}{1-\mathcal{E}} \;\propto \sqrt{\mathcal{S}}\,\ln\mathcal{S}\,. \tag{21}$$

Since we previously showed that $n_c \propto \mathcal{S}$, we have $M < M_+ \ll n_c$. Thus Eq. (19) yields

$$T_2 \propto M\sqrt{n_c} < \mathcal{S}\ln\mathcal{S}\,. \tag{22}$$

Thus phase (ii) has negligible duration compared to that of phase (i), so that the average lifetime τ of the walk in the circular approximation scales as $\mathcal{S}^{3/2}$. Similarly, the number M of returns to the edge of the desert during phase (ii) is negligible compared to the number n_c of such returns during phase (i), so that $\langle\mathcal{N}\rangle$, the average number of distinct sites visited in the circular approximation scales as $\mathcal{S}$.

3.3. Circular approximation: microscopic approach

We now determine the distribution $V(\mathcal{N})$ of the number of distinct sites visited at starvation in the circular approximation and then extract the average lifetime and the average number of distinct sites visited. As in one dimension, we write $V(\mathcal{N})$ as

$$V(\mathcal{N}) = \mathcal{F}_2\,\mathcal{F}_3\,\mathcal{F}_4 \ldots \mathcal{F}_{\mathcal{N}}(1-\mathcal{F}_{\mathcal{N}+1})\,,$$

where again $\mathcal{F}_k = \int_0^{\mathcal{S}} dt\, F_k(t)$, with $F_k(t)$ the first-passage probability at time t to any point of the circular boundary of radius R_k when the walk starts a distance a from this boundary. Following a similar approach as in the case of one dimension (see Appendix C), we obtain the following expression for the distribution of visited sites at the instant of starvation‡

$$V(\theta,\mathcal{S}) \simeq \frac{2\pi}{a}\sqrt{\frac{D\mathcal{S}}{\theta}}\sum_{k=1}^{\infty} e^{-j_k^2/\theta}\exp\left\{-\frac{4\pi}{a}\sqrt{D\mathcal{S}\theta}\sum_{m=1}^{\infty}\left[e^{-j_m^2/\theta}-\sqrt{\frac{\pi}{\theta}}\,j_m\,\mathrm{erfc}\left(\frac{j_m}{\sqrt{\theta}}\right)\right]\right\} \tag{23}$$

where $\theta \equiv \mathcal{N}a^2/(\pi D\mathcal{S})$. Because of the simultaneous appearance of $\mathcal{S}$ and θ, this distribution of the number of distinct sites visited does not obey single-parameter scaling, as mentioned in Sec. 3.1.

A numerical evaluation of (23) is not straightforward because the sums converge slowly and it appears that average number of distinct sites visited grows as

$$\langle\mathcal{N}\rangle \sim \mathcal{S}^{\beta} \tag{24a}$$

with $\beta \simeq 0.9$. This value roughly accords with the scaling that was obtained from the heuristic circular approximation. Using the circular approximation, we may also deduce the average lifetime of the walk (Appendix D). Subject to the same convergence issues as in the number of distinct sites visited, the lifetime appears to grow as

$$\tau \sim \mathcal{S}^{\gamma} \tag{24b}$$

with $\gamma \simeq 1.4$. This exponent estimate is also close to that obtained in the heuristic circular approximation.

The exponents in Eqs. (24a) and (24b) are substantially smaller than the corresponding values obtained by numerical simulations, $\beta \approx 1.8$ and $\gamma \approx 1.9$. Thus the circular approximation is a relatively weak lower bound for the starving random walk on the lattice. This disparity is not unexpected because the true shape of the desert is generally quite ramified (Fig. 2). Such a desert shape allows the walk to eat much more often than in the circular approximation. In spite of the imprecise numerical results, the circular approximation gives a lower bound for $\langle\mathcal{N}\rangle$ and τ in two dimensions, where the complex desert shape seems to render an exact calculation unfeasible. The circular approximation also captures the two-parameter scaling for the distribution of the number of distinct sites visited, a property that does not exist in one dimension.

‡ Equation (23) corrects errors in the corresponding formula in [1].

4. Infinite-Dimensional Limit

For large spatial dimension d, an N-step random walk visits $A\,N$ distinct sites on average [23, 24], with A a constant that approach 1 as $d \to \infty$. Thus the depletion of the environment plays an insignificant role as the walk typically visits new (food-containing sites) at each step. We therefore investigate the starvation dynamics for large d under the assumption that the walk hits a previously visited or a previously unvisited site at each step with time-independent probabilities λ and $1-\lambda$ respectively. For a hypercubic lattice in $d \gg 1$ dimensions, a naive estimate for the probability λ is just the backtracking probability $1/(2d)$. The relevant point is that λ is very small in the high-dimensional limit.

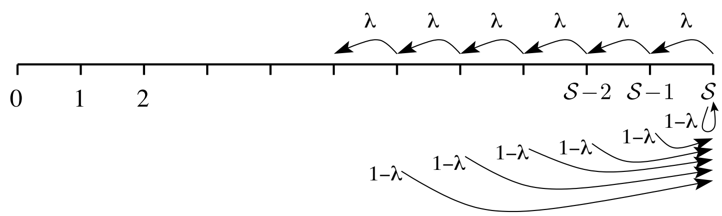


Figure 7. Evolution of a high-dimensional random walk in "starvation space". A walk at position n can survive n additional steps without encountering food.

Under the assumption that visits to full or empty sites are independent events with the probabilities given above, the time until the walk starves undergoes a stochastic process in a one-dimensional "starvation space"— an interval of length $\mathcal{S}$. When the origin is reached in this starvation space, it corresponds to the starvation of the walk on the lattice (Fig. 7). A walk at site n in starvation space can wander n additional steps on the lattice without encountering food before it starves. When the walk hits a previously visited (empty) site in physical space, the time to starvation decreases by one. This corresponds to a hop to the left (with probability λ) in starvation space. Conversely, when the random walk hits a new (food-containing) site, it can wander an additional $\mathcal{S}$ steps on the lattice until starvation occurs. This corresponds to an immediate hop to site $\mathcal{S}$ in starvation space with probability $1-\lambda$.

Based on this picture, we compute t_n, the average time until the walk starves when starting from position n in starvation space. These average starvation times satisfy the backward equations [25]:

$$\begin{aligned} t_1 &= (1-\lambda)t_{\mathcal{S}} + 1\,, \\ t_n &= \lambda t_{n-1} + (1-\lambda)t_{\mathcal{S}} + 1 \qquad\qquad 2 \le n \le \mathcal{S}\,. \end{aligned} \tag{25}$$

In the equation for t_n, the first term accounts for hopping to a previously-visited site, in which case the walk can wander $n-1$ additional steps before starving. The second term accounts for hopping to a new food-containing site, in which case the walk can wander $\mathcal{S}$ more steps before starving. The last term accounts for the time elapsed for a single step. We use the first equation to eliminate t_1 in the recursion for t_2, and thereby determine t_2 in terms of $t_{\mathcal{S}}$. Repeating this elimination gives each t_n in terms of $t_{\mathcal{S}}$, and ultimately the closed equation for $t_{\mathcal{S}}$

$$t_{\mathcal{S}} = \frac{1}{\lambda^{\mathcal{S}}}\left(\frac{1-\lambda^{\mathcal{S}}}{1-\lambda}\right). \tag{26}$$

In the (unrealistic) limit of $\lambda \to 1$, the average starvation time approaches $\mathcal{S}$, while, for the relevant high-dimensional limit where $\lambda \to 0$, the average starvation time grows exponentially with $\mathcal{S}$.

We may also solve for the probability that the walk starves at a given time. Let $Q_n(t)$ be the probability that a walk at time t can wander without food for an additional n steps before starving. This probability obeys the recursion

$$\begin{aligned}
&F(t) = \lambda Q_1(t-1)\,, \\
&Q_n(t) = \lambda Q_{n+1}(t-1) && 1 \le n \le \mathcal{S}-1\,, \\
&Q_{\mathcal{S}}(t) = (1-\lambda)\big[Q_{\mathcal{S}}(t-1) + Q_{\mathcal{S}-1}(t-1) + \ldots + Q_1(t-1)\big]\,.
\end{aligned} \tag{27a}$$

The first equation accounts for a walk that is one time step from starvation and hops to an empty site, and thus gives the first-passage probability that the walk dies at time t. The second equation accounts for processes in which a walk hops to an empty site and thus moves one time unit closer to starvation. The last equation accounts for events in which a walk hops from any point in starvation space to a full site. When this occurs, the walk can survive $\mathcal{S}$ additional time units without eating before it starves.

We impose the initial condition $Q_n(t\!=\!0) = \delta_{n,\mathcal{S}}$, corresponding to the walk being fully sated at the outset. To solve Eqs. (27a), we multiply each equation by z^t, and sum from $t = 1$ to ∞. In terms of the the generating function $Q_n(z) = \sum_{t\ge 0} Q_n(t) z^t$, we obtain the algebraic equations

$$\begin{aligned}
&F(z) = \lambda z Q_1(z)\,, \\
&Q_n(z) = \lambda z Q_{n+1}(z) && 1 \le n \le \mathcal{S}-1\,, \\
&Q_{\mathcal{S}}(z) = 1 + z(1-\lambda)\sum_{1\le k\le \mathcal{S}} Q_n(z)\,.
\end{aligned} \tag{27b}$$

Solving these equations, the generating function for the first-passage probability is

$$F(z) = \frac{(z\lambda)^{\mathcal{S}}(1-\lambda z)}{1 - z\big[1-(1-\lambda)(\lambda z)^{\mathcal{S}}\big]}\,. \tag{28}$$

Notice that $F(z\!=\!1) = 1$, which means that the sum of the first-passage probability over all times equals 1. Thus the walk eventually must starve. One can also readily verify that the average first-passage time given in (26) is reproduced by

$$\langle t\rangle = \sum tF(t) = z\frac{\partial F(z)}{\partial z}\bigg|_{z=1}\,. \tag{29}$$

Because $F(z)$ has a simple pole at $z = z_c \approx 1 + (1-\lambda)\lambda^{\mathcal{S}}$ to lowest order, the first-passage probability decays exponentially with time. The characteristic decay time of the first-passage probability is given by z_c^{-1}, which has the same scaling as the average first-passage time given in Eq. (26).

Finally, we determine the distribution of the number of sites visited by the walk on the lattice. The essential ingredient to determine this distribution is the return probability R_n, namely, the probability for a walk that starts from site n in starvation space to reach $\mathcal{S}$ without first hitting 0. Each such return corresponds to the random walk visiting a new site on the physical lattice without starving. These return probabilities satisfy the recursion

$$\begin{aligned} &R_1 = (1-\lambda)\,, \\ &R_n = (1-\lambda) + \lambda R_{n-1} \qquad\qquad 2 \le n \le \mathcal{S}\,. \end{aligned} \tag{30}$$

In the equation for R_n, the first term accounts for the walk hitting a previously unvisited site, in which case the walk is at site $\mathcal{S}$ in starvation space, while the second term accounts for the walk hitting an empty site, in which case the walk is at site $n-1$ in starvation space.

The solution to this recursion is simply $R_n = 1-\lambda^n$. From these return probabilities, we now infer the distribution of distinct sites visited at starvation. For a walk that starts at site $\mathcal{S}$ in starvation space, the probability that $\mathcal{N}$ distinct sites are visited on the lattice before the walk starves is simply given by

$$P(\mathcal{N}) = R_{\mathcal{S}}^{\mathcal{N}}(1-R_{\mathcal{S}})\,. \tag{31}$$

This equation expresses the fact that to visit $\mathcal{N}$ distinct sites on the lattice, the walk must visit a full site $\mathcal{N}$ times, each within $\mathcal{S}$ steps, before the walk staves. From this result, the average number of distinct sites visited before the walk starves is

$$\langle\mathcal{N}\rangle = \frac{R_{\mathcal{S}}}{1-R_{\mathcal{S}}} = \lambda^{-\mathcal{S}}(1-\lambda^{\mathcal{S}})\,. \tag{32}$$

As might be expected in this mean-field description, the average lifetime given in Eq. (26) and the average number of distinct sites visited before starving are the same up to an overall constant factor of $1-\lambda$, and both grow exponentially with the metabolic capacity $\mathcal{S}$. These long-lived trajectories in large spatial dimension arise from the low probability to encounter a previously visited site.

5. Summary and Discussion

The starving random walk model represents a minimalist description for the consumption of a depleting resource by an unaware forager. While there is much literature on optimizing the search for resources by a rational forager that possesses complete knowledge of its environment (see, e.g., [2–10]), the complementary starving random walk model in which the forager has no propensity to move toward food and no environmental knowledge seems mostly unexplored. The fundamental parameters for a starving random walk are its metabolic capacity $\mathcal{S}$, namely, the number of steps that the walk can wander in a row without food before starving to death, and secondarily the spatial dimension d. The latter parameter enters because of the non-trivial dimension dependence of visits to distinct sites for random walks.

We solved the starving random walk model in one dimension by probabilistic methods to give the average lifetime of the walk, the average number of distinct sites visited at the instant of starvation, and the distribution of the latter. Qualitatively, a forager carves out a growing desert until the desert reaches a dangerous critical length of the order of $\sqrt{D\mathcal{S}}$. When this length is reached, the walk can still survive if it returns to the same side of the desert, but starves when it attempts to cross to the other side. From this picture, the average number of distinct sites visited at the instant of starvation, which is the same as the total amount of consumed food, scales as $\sqrt{\mathcal{S}}$, while the average lifetime scales as $\mathcal{S}$.

In the ecologically relevant case of two dimensions, a probabilistic solution for the lifetime and number of distinct sites visited remains an open challenge. By numerical simulations, both the average number of distinct sites visited and the average lifetime appear to scale algebraically with $\mathcal{S}$, with an exponent close to 1.8 for the former quantity and exponent close to 1.9 for the latter. The spatial probability distribution of starving random walks is exponential rather than the Gaussian for a pure random walk. This difference reflects the feature that a long-lived starving random walk remains close to the source of food, which means that it should explore a ramified and more spatially extended region than a pure random walk. We provided a (weak) lower bound for the average lifetime and number of distinct sites visited within a circular approximation. The two-dimensional case is particularly challenging, as the distribution of the distinct sites visited does not obey single-parameter scaling [1] and the relation between the geometry of the carved out desert and the lifetime of the walk is not yet resolved.

In greater than two dimensions, the transience of the random walk means that visits to new (i.e., food containing) sites occur at a fixed rate. Thus a starving random walk is much more long lived for $d > 2$ than in $d \leq 2$. Indeed, we previously found [1] that the average lifetime τ grows as $\exp(\mathcal{S}^{\omega})$, with $\omega \approx \frac{1}{2}$ in $d = 3$ and with ω slowly growing with d. Simulation results up to 5 dimensions suggest that β is a continuously growing function of dimension [1] and β reaches the mean-field value of 1 only when $d \to \infty$. Preliminary numerical simulations indicate that the distribution of times between visits to distinct sites has a slower than exponential decay for spatial dimensions $d > 2$ and only gradually approaches an exponential decay for $d \to \infty$ [26]. These features suggest that the critical dimension of the starving random walk problem may be infinite.

Thus starving random walks represent a new type of non-equilibrium process in which the dynamics is controlled by the times *between visits to distinct sites* in a random walk. While much is known about the average number of distinct sites visited and its underlying distribution for random walks [23, 24], little appears to be known about the times between visits to new sites, as well as the distribution of times between such visits. This aspect of the starving random walk model is very much worth exploring.

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Appendix A. Distribution of the number of distinct sites visited in one dimension

For a random walk that starts at $x = a$ within an interval of length $L = ka$ with both ends absorbing, the concentration at position x at time t is

$$c(x,t) = \frac{2}{ka} \sum_{n\geq 1} \sin\frac{n\pi x}{ka}\, \sin\frac{n\pi}{k}\, \exp\left[-\left(\frac{n\pi}{ka}\right)^2 Dt\right]. \tag{A.1}$$

The flux leaving the interval at time t is therefore

$$\begin{aligned} F_k(t) &= D\left(c'\big|_{x=0} - c'\big|_{x=ka}\right) \\ &= \frac{2D}{ka} \sum_{n=1}^{\infty} \frac{n\pi}{ka} \sin\frac{n\pi}{k}\,(1-\cos n\pi)\, \exp\left[-\left(\frac{n\pi}{ka}\right)^2 Dt\right], \\ &= \frac{4\pi D}{(ka)^2} \sum_{n=0}^{\infty} (2n+1)\, \sin\frac{(2n+1)\pi}{k}\, \exp\left[-\left(\frac{(2n+1)\pi}{ka}\right)^2 Dt\right]. \end{aligned} \tag{A.2}$$

We rewrite the sum over odd integers n as the sum over all integers $2n+1$. Thus the integrated flux that leaves the interval up to time $\mathcal{S}$ is

$$\mathcal{F}_k = 1 - \frac{4}{\pi} \sum_{n\geq 0} \frac{1}{2n+1} \sin\frac{(2n+1)\pi}{k}\, \exp\left[-\left(\frac{(2n+1)\pi}{ka}\right)^2 D\mathcal{S}\right]. \tag{A.3}$$

We now need to compute the product $\prod_{2\leq k\leq \mathcal{N}} \mathcal{F}_k \equiv U(\mathcal{N})$ that appears in (12). Taking the logarithm, we have

$$\ln U(\mathcal{N}) = \sum_{k=2}^{\mathcal{N}} \ln\left\{1 - \frac{4}{\pi}\sum_{n} \frac{\sin[(2n+1)\pi/k]}{2n+1}\, \exp\left[-\big((2n+1)\pi\big)^2 D\mathcal{S}/(ka)^2\right]\right\}. \tag{A.4}$$

We convert the sum to an integral, introduce the scaled variable $z = n/\sqrt{\mathcal{S}}$, and replace $\sin[(2n+1)\pi/k]/(2n+1)$ by π/k; this latter approximation applies in the limit of large $\mathcal{S}$. These steps lead to

$$\ln U(\mathcal{N}) \simeq \sqrt{\mathcal{S}} \int_0^{\mathcal{N}/\sqrt{\mathcal{S}}} dz\, \ln\left\{1 - \frac{2}{\pi}\,\frac{2\pi}{z\sqrt{\mathcal{S}}} \sum_{n\geq 0} \exp\left[-\frac{\big((2n+1)\pi\big)^2 D}{(az)^2}\right]\right\}. \tag{A.5}$$

We expand the logarithm, which again applies for large $\mathcal{S}$, and ultimately obtain

$$\begin{aligned}\ln U(\mathcal{N}) &\simeq -4\int_0^{\mathcal{N}/\sqrt{\mathcal{S}}}\frac{dz}{z}\sum_{n\geq 0}\exp\left[-\frac{\big((2n+1)\pi\big)^2 D}{(az)^2}\right],\\ &= -2\sum_{n\geq 0}\mathrm{E}_1\big((2n+1)^2/\theta^2\big)\,,\end{aligned} \tag{A.6}$$

where $\theta \equiv \mathcal{N}a/(\pi\sqrt{D\mathcal{S}})$ and $\mathrm{E}_1(x)\equiv\int_1^\infty dt\, e^{-xt}/t$ denotes the exponential integral.

Similarly, the factor $1-\mathcal{F}_{\mathcal{N}+1}$ in (12) has the $\mathcal{S}\to\infty$ asymptotic behavior

$$1-\mathcal{F}_{\mathcal{N}+1}\simeq\frac{2}{\pi}\sum_{n\geq 0}\frac{2a}{\theta\sqrt{D\mathcal{S}}}\,e^{-(2n+1)^2/\theta^2}\,. \tag{A.7}$$

Finally, using Eq. (12), the distribution of the scaled variable θ is

$$V(\theta)=\frac{4}{\theta}\exp\left[-2\sum_{n\geq 0}\mathrm{E}_1\big((2n+1)^2/\theta^2\big)\right]\sum_{n\geq 0}e^{-(2n+1)^2/\theta^2}\,. \tag{A.8}$$

We use this form in Eq. (13) to compute the average number of distinct sites visited at the instant of starvation.

Appendix B. Average lifetime τ in one dimension

Using the results of the Appendix A, we write the numerator in Eq. (16) as

$$\mathcal{G}_k\equiv\int_0^{\mathcal{S}}dt\;t\;F_k(t)=\frac{4\pi D}{(ka)^2}\sum_{j=0}^{\infty}(2j+1)\sin\left[\frac{(2j+1)\pi}{k}\right]\int_0^{\mathcal{S}}dt\;t\;e^{-\beta t}\,, \tag{B.1}$$

with $\beta\equiv\big[(2j+1)\pi\big]^2 D/(ka)^2$. For large k, we approximate the sine function by its argument and then perform the temporal integral to give

$$\begin{aligned}\mathcal{G}_k &\simeq \frac{4\pi D}{(ka)^2}\,\frac{\pi}{k}\sum_{j=0}^{\infty}(2j+1)^2\left[\frac{k^2a^2}{(2j+1)^2\pi^2 D}\right]^2\left[1-e^{-\beta\mathcal{S}}(1+\beta\mathcal{S})\right]\,,\\ &\simeq \frac{4ka^2}{\pi^2 D}\sum_{j=0}^{\infty}\frac{1}{(2j+1)^2}\left[1-e^{-\beta\mathcal{S}}(1+\beta\mathcal{S})\right]\,.\end{aligned} \tag{B.2}$$

To leading order in $\mathcal{S}$, the denominator in (16) is subdominant, so that we have $\tau_k\simeq\mathcal{G}_k$. We now define $\mathcal{T}_n\equiv\sum\limits_{k=1}^{n}\tau_k$. Using Eq. (B.2), we again convert the sum over k to an integral and introduce the scaled variable $u=ka/(\pi\sqrt{D\mathcal{S}})$ to give

$$\mathcal{T}_n\simeq\mathcal{S}\int_0^{na/(\pi\sqrt{D\mathcal{S}})}du\,u\sum_{j=0}^{\infty}\frac{4}{(2j+1)^2}\left\{1-e^{-(2j+1)^2/u^2}\left[1+\left(\frac{2j+1}{u}\right)^2\right]\right\}\,. \tag{B.3}$$

From Eq. (15), we write

$$\tau = \sum_{n=0}^{\infty} \mathcal{T}_n V(n) + \mathcal{S}\,. \tag{B.4}$$

Introducing $\theta = na/(\pi\sqrt{D\mathcal{S}})$ and replacing the sum over n by an integral, we obtain

$$\tau \simeq \mathcal{S}\int_0^{\infty} d\theta\, V(\theta)\int_0^{\theta} du\, u\sum_{j=0}^{\infty}\frac{4}{(2j+1)^2}\left\{1-e^{-(2j+1)^2/u^2}\left[1+\left(\frac{2j+1}{u}\right)^2\right]\right\}+\mathcal{S}\,, \tag{B.5}$$

and using Eq. (A.8), the average lifetime is $\tau \simeq 3.27686\ldots\,\mathcal{S}$.

Appendix C. The distribution $V(\mathcal{N})$ in the circular approximation

Consider a random walk that starts a distance a from the boundary of a circle of radius $R_k \equiv \sqrt{k/\pi}\,a$. For $k \leq 3$, the radius is smaller than a, so for these cases the walk starts from the center of the circle. We neglect this detail in the following. The probability to first reach the boundary at time t is given by [25]

$$F_k(t) = \frac{2D}{R_k^2}\sum_{m=1}^{\infty} j_m\, e^{-Dtj_m^2/R_k^2}\ \mathrm{J}_0\Big(j_m\Big(1-\frac{a}{R_k}\Big)\Big)\Big/\mathrm{J}_1(j_m)\,, \tag{C.1}$$

with J_0 and J_1 the Bessel functions of order 0 and 1, and j_m the m^{th} zero of J_0. Integrating this expression for $0 \leq t \leq \mathcal{S}$, the probability $\mathcal{F}_k$ to reach the boundary before starving is then§

$$\mathcal{F}_k = 1 - 2\sum_{m=1}^{+\infty} e^{-D\mathcal{S}j_m^2/R_k^2}\ \mathrm{J}_0\Big(j_m\big(1-\sqrt{\pi/k}\big)\Big)\Big/\big[j_m\,\mathrm{J}_1(j_m)\big]\,. \tag{C.2}$$

As in one dimension, we need $U(\mathcal{N}) = \prod_{1\leq k\leq \mathcal{N}} \mathcal{F}_k$. We start by taking its logarithm

$$\ln U(\mathcal{N}) = \sum_{k=1}^{\mathcal{N}} \ln\left\{1 - 2\sum_{m=1}^{+\infty} e^{-D\mathcal{S}j_m^2/R_k^2}\ \mathrm{J}_0\left(j_m\big(1-\sqrt{\pi/k}\big)\right)\Big/\big[j_m\,\mathrm{J}_1(j_m)\big]\right\}. \tag{C.3}$$

We again convert the sum to an integral, expand the logarithm and use

$$\frac{\mathrm{J}_0\left(j_m\big(1-\sqrt{\pi/k}\big)\right)}{\mathrm{J}_1(j_m)} \sim j_m\sqrt{\frac{\pi}{k}} \tag{C.4}$$

when $\mathcal{S}$ and consequently k become large. This yields

$$\ln U(\mathcal{N}) \simeq -4\sqrt{\pi\mathcal{N}}\sum_{m=1}^{+\infty}\left[e^{-D\pi\mathcal{S}j_m^2/(\mathcal{N}a^2)} - \sqrt{\frac{D\mathcal{S}}{\mathcal{N}}}\,\frac{\pi j_m}{a}\,\mathrm{erfc}\Big(\sqrt{\frac{D\pi\mathcal{S}}{\mathcal{N}}}\,\frac{j_m}{a}\Big)\right]. \tag{C.5}$$

§ Eq. (C.2) corrects a misprint in the corresponding equation in [1].

Similarly, the term $1-\mathcal{F}_{\mathcal{N}+1}$ has the following asymptotic behavior in the large $\mathcal{S}$ limit

$$1-\mathcal{F}_{\mathcal{N}+1}\simeq\sqrt{4\frac{\pi}{\mathcal{N}}}\sum_{k=1}^{+\infty}e^{-D\pi\mathcal{S}j_k^2/(\mathcal{N}a^2)}\,. \tag{C.6}$$

Finally, the distribution of the number of distinct sites visited at starvation is given by

$$\begin{aligned}V(\mathcal{N})\simeq&\sqrt{\frac{4\pi}{\mathcal{N}}}\sum_{k=1}^{+\infty}e^{-D\pi\mathcal{S}j_k^2/(\mathcal{N}a^2)}\\&\times\exp\left\{-4\sqrt{\pi\mathcal{N}}\sum_{m=1}^{+\infty}\left[e^{-D\pi\mathcal{S}j_m^2/(\mathcal{N}a^2)}-\sqrt{\frac{D\mathcal{S}}{\mathcal{N}}}\,\frac{\pi j_m}{a}\,\mathrm{erfc}\Big(\sqrt{\frac{D\pi\mathcal{S}}{\mathcal{N}}}\frac{j_m}{a}\Big)\right]\right\}\,.\end{aligned} \tag{C.7}$$

Introducing the variable $\theta=\mathcal{N}a^2/(\pi D\mathcal{S})$, we obtain Eq. (23).

Appendix D. Average lifetime in the circular approximation

As in one dimension, we write the numerator in Eq. (16) as

$$\mathcal{G}_k\equiv\int_0^{\mathcal{S}}dt\ t\ F_k(t)=\frac{2D\pi}{ka^2}\int_0^{\mathcal{S}}dt\,t\sum_{m=1}^{\infty}j_m\frac{\mathrm{J}_0\left(j_m\big(1-\sqrt{\pi/k}\big)\right)}{\mathrm{J}_1(j_m)}\ e^{-\pi Dj_m^2t/(ka^2)}\,, \tag{D.1}$$

with j_m the $m^{\rm th}$ zero of the Bessel function J_0. For large k, we again substitute (C.4) in the above integrand and then perform the temporal integral to give

$$\mathcal{G}_k\simeq\frac{2a^2}{D}\sqrt{\frac{k}{\pi}}\sum_{m=1}^{\infty}\frac{1}{j_m^2}\left[1-\left(1+\frac{\pi Dj_m^2\mathcal{S}}{ka^2}\right)e^{-\pi D\mathcal{S}j_m^2/(ka^2)}\right]\,. \tag{D.2}$$

To leading order in $\mathcal{S}$, we still have $\tau_k\simeq\mathcal{G}_k$. We then define $\mathcal{T}_n\equiv\sum_{k=1}^{n}\tau_k$, use $\tau_k\simeq\mathcal{G}_k$, with $\mathcal{G}_k$ given in (D.2), and convert the sum to an integral to give

$$\mathcal{T}_n\simeq\frac{2a^2}{D}\int_0^n dk\sqrt{\frac{k}{\pi}}\sum_{m=1}^{\infty}\frac{1}{j_m^2}\left[1-\left(1+\frac{\pi Dj_m^2\mathcal{S}}{ka^2}\right)e^{-\pi D\mathcal{S}j_m^2/(ka^2)}\right]\,. \tag{D.3}$$

Changing to the variable $u=ka^2/(\pi D\mathcal{S})$ leads to

$$\mathcal{T}(\theta)\simeq\frac{2\pi\sqrt{D}\,\mathcal{S}^{3/2}}{a}\int_0^{\theta}\frac{du}{\sqrt{u}}\sum_{m=1}^{\infty}\left[\frac{u}{j_m^2}-\left(1+\frac{u}{j_m^2}\right)e^{-j_m^2/u}\right]\,, \tag{D.4}$$

where $\theta\equiv na^2/(\pi D\mathcal{S})$. Using Eq. (15), we write

$$\tau=\sum_{n=0}^{\infty}\mathcal{T}_nV(n)+\mathcal{S}\simeq\int_0^{\infty}\mathcal{T}(\theta)V(\theta,\mathcal{S})+\mathcal{S}\,. \tag{D.5}$$

with $V(\theta,\mathcal{S})$ given in Eq. (23). We finally obtain

$$\tau\simeq\mathcal{S}+\frac{2\pi\sqrt{D}\,\mathcal{S}^{3/2}}{a}\int_0^{\infty}d\theta\ V(\theta,\mathcal{S})\int_0^{\theta}\frac{du}{\sqrt{u}}\sum_{m=1}^{\infty}\left[\frac{u}{j_m^2}-\left(1+\frac{u}{j_m^2}\right)e^{-j_m^2/u}\right]\,. \tag{D.6}$$

[1] O. Bénichou and S. Redner, Phys. Rev. Lett. **113**, 238101 (2014).

[2] E. L. Charnov, Theor. Popul. Biol. **9**, 129 (1976).

[3] J.W. Bell, Searching Behaviour, the Behavioural Ecology of Finding Resources, Animal Behaviour Series (Chapman and Hall, London, 1991).

[4] W.J. O'Brien, H.I. Browman, and B.I. Evans, Am. Sci. **78**, 152 (1990).

[5] L.D. Kramer and R.L. McLaughlin, Am. Zool. **41**, 137 (2001).

[6] J.P. Anderson, D.W. Stephens, and S.R. Dunbar, Behav. Ecol. **8**, 307 (1997).

[7] P. Knoppien and J. Reddingius, J. Theor. Biol. **114**, 273 (1985).

[8] D.W. Stephens and J.R. Krebs, *Foraging Theory*, (Princeton University Press, Princeton, NJ, 1986).

[9] G.M. Viswanathan et al., Nature (London) **381**, 413 (1996); G.M. Viswanathan et al., Nature (London) **401**, 911 (1999).

[10] M. Levandowsky, J. Klafter, and B.S. White, Bull. Mar. Sci. **43**, 758 (1988).

[11] M. Chupeau, O. Bénichou, and S. Redner, Phys. Rev. E **93**, 032403 (2016).

[12] M. Perman and W. Werner, Probab. Theory Relat. Fields **108**, 357 (1997).

[13] B. Davis, Probab. Theory Relat. Fields **113**, 501 (1999).

[14] R. Pemantle, Probability Surveys, **4** 1 (2007).

[15] I. Benjamini and D. B. Wilson, Electr. Commun. Probab. **8**, 86 (2003).

[16] O. Angel O, I. Benjamini, and B. Virag, Electr. Commun. Probab. **8**, 66 (2003).

[17] M. P. W. Zerner, Probab. Theory Relat. Fields **133**, 98 (2005).

[18] T. Antal and S. Redner, J. Phys. A **38**, 2555 (2005).

[19] J. Stat. Phys. **134**, 307 (2009).

[20] R. F. Bonner, R. Nossal, S. Havlin, and G. H. Weiss, J. Opt. Soc. Am. A **4**, 423 (1987).

[21] S. B. Yuste, E. Abad, and K. Lindenberg, Phys. Rev. Lett. **110**, 220603 (2013).

[22] E. Abad, S. Yuste, and K. Lindenberg, Phys. Rev. E **88**, 062110 (2013).

[23] W. Feller, *An Introduction to Probability Theory and Its Applications*, (Wiley, New York, 1968).

[24] G. H. Weiss, *Aspects and Application of the Random Walk*, (North-Holland, Amsterdam, 1994).

[25] S. Redner, A Guide to First-Passage Processes (Cambridge University Press, Cambridge, England, 2001).

[26] O. Bénichou, M. Chupeau, and S. Redner, unpublished.