Supplementary Material for Depletion-Controlled Starvation of a Diffusing Forager

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We wish to determine $P(N)$, the probability that a random walker has visited $\mathcal{N}$ distinct sites when it starves. This probability is expressed as

$$P(N) = Q_2 Q_3 Q_4 \ldots Q_{N}(1 - Q_{N+1}),$$

(1)

where $Q_j = \int_0^S dt F_j(t)$, and $F_j(t)$ is the probability that the walker reaches either end of an interval of length $ja$ (with $a$ the lattice spacing) within $t$ steps when starting a distance $a$ from one end. Each $Q_j$ accounts for the interval growing from length $j - 1 \rightarrow j$ because the walker reaches either endpoint within $S$ steps, while the factor $Q_{N+1}$ accounts for the last excursion in which the walker starves. It is expedient to express the the visitation probability in terms of the scaled number of distinct sites visited, $\theta = a \mathcal{N} / (\pi \sqrt{DS})$. We now provide the essential steps to go from Eq. (1) to (2) in the manuscript.

In the long-time limit, we use the continuum expression for $F_j(t)$ \cite{1}:

$$F_j(t) = \frac{4 \pi D}{(ja)^2} \sum_{n \geq 0} (2n + 1) e_n(j/\sqrt{t}) \sin \lambda_{j,n},$$

(2)

where $D \equiv a^2/2$ is the diffusivity of the corresponding continuous process, $\lambda_{j,n} = (2n + 1)\pi/j$, and

$$e_n(j/\sqrt{t}) \equiv \exp \left[ - (2n + 1)^2 \pi^2 Dt/(ja)^2 \right].$$

(3)

Consequently,

$$Q_j = \int_0^S dt F_j(t) = 1 - \frac{4}{\pi} \sum_{n \geq 0} \frac{e_n(j/\sqrt{S}) \sin \lambda_{j,n}}{2n + 1}.$$ 

(4)

This expression for $Q_j$, together with Eq. (1), provides a formal solution for the distribution of the number of distinct sites visited at the starvation time.

To obtain the explicit result, we start by taking the logarithm of the function defined by

$$U_N \equiv \prod_{2 \leq j \leq N} Q_j.$$ 

(5)

This gives

$$\ln U_N = \sum_{2 \leq j \leq N} \ln \left[ 1 - \frac{4}{\pi} \sum_{n \geq 0} \frac{e_n(j/\sqrt{S}) \sin \lambda_{j,n}}{2n + 1} \right].$$

(6)

We now convert the outer sum to an integral, introduce the variable $z = j/\sqrt{S}$, and, for $S \gg 1$, replace $\sin \lambda_{j,n}/(2n + 1)$ by $\pi/j$. These steps give

$$\ln U_N \approx \sqrt{S} \int_0^{N/\sqrt{S}} dz \ln \left[ 1 - \frac{4}{z \sqrt{S}} \sum_{n \geq 0} e_n(z) \right].$$

(7)

Expanding the logarithm, which applies for large $S$, gives

$$\ln U_N \approx -4 \int_0^{N/\sqrt{S}} \frac{dz}{z} \sum_{n \geq 0} e_n(z) = -4 \sum_{n \geq 0} \frac{E_1([2n + 1]^2/\theta^2)}{2 \theta^2},$$

(8)

where $\theta = a \mathcal{N} / (\pi \sqrt{DS})$ is the scaled number of distinct sites visited and $E_1$ is the exponential integral, which is defined as $E_1(x) = \int_1^{\infty} dt e^{-xt}/t$.

Similarly, the factor $1 - Q_{N+1}$ in (1) has the limiting behavior for $S \gg 1$

$$1 - Q_{N+1} \approx \sum_{m \geq 0} \frac{4a}{\pi \theta \sqrt{DS}} e^{-(2n+1)^2/\theta^2},$$

(9)

Substituting Eqs. (8) and (9) in (1) leads to Eq. (2) in the manuscript.

[1] S. Redner, A Guide to First-Passage Processes (Cambridge University Press, Cambridge, England, 2001).
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We study the starvation of a lattice random walker in which each site initially contains one food unit and the walker can travel $S$ steps without food before starving. When the walker encounters food, it is completely eaten, and the walker can again travel $S$ steps without food before starving. When the walker hits an empty site, the time until the walker starves decreases by 1. In spatial dimension $d = 1$, the average lifetime of the walker $\langle \tau \rangle \propto S$, while for $d > 2$, $\langle \tau \rangle \simeq \exp(S^{\omega})$, with $\omega \to 1$ as $d \to \infty$; the latter behavior suggests that the upper critical dimension is infinite. In the marginal case of $d = 2$, $\langle \tau \rangle \propto S^{z}$, with $z \approx 2$. Long-lived walks explore a highly ramified region so they always remain close to sources of food and the distribution of distinct sites visited does not obey single-parameter scaling.

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Searching for a randomly located resource is an essential task of all living organisms \cite{1}. Examples include searching for nourishment, an abode, or a particular individual. Stochastically driven search processes also underlie diffusion-controlled reactions \cite{11} and a variety of physiological processes \cite{12}. In all these examples, the time for a successful search is the typical metric that the organism is trying to optimize. A related aspect of stochastic search is the tradeoff between continued exploitation of a familiar resource or the exploration of new domains for potentially more fruitful resources \cite{13}.

An important theme in biological foraging \cite{1–3} is the notion of optimality. Given an environment with heterogeneously distributed resources and a predatory organism that has full environmental knowledge and makes intelligent decisions, the marginal value theorem \cite{1} provides a specific criterion about whether the forager should continue to exploit current resources or move to new territory. Our focus, in this Letter, is on a different aspect of foraging in that we ascribe zero intelligence to the forager and it is the depletion of the environmental resource that determines when the forager dies.

In our model, the forager is a random walker that gradually depletes the resource contained in a medium as it moves. The medium is a $d$-dimensional lattice with a unit of food initially at each site. The walker is endowed with an intrinsic starvation time $\mathcal{S}$, defined as the number of steps it can take without encountering food before starving to death. If the walker encounters a food-containing site, the walker instantaneously and completely consumes the food and can again travel $\mathcal{S}$ additional steps without eating before starving. Each time the walker encounters an empty site, it comes one time unit closer to starvation. Our goal is to understand the interplay between the amount of the resource consumed and how long the random walker can survive before starving.

We focus on two key observables of starving random walks: the average lifetime $\langle \tau \rangle$ and the average number $\langle N \rangle$ of distinct sites visited when starvation occurs. In dimension $d = 1$, $\langle \tau \rangle \propto \mathcal{S}$ and we determine the distribution of $\mathcal{N}$ at starvation, $P(\mathcal{N})$. For $d > 2$, the transience of the random walk leads to $\tau$ scaling as $\exp(\mathcal{S}^{\omega})$, with $\omega \to 1$ as $d \to \infty$. When successive visits to new sites are uncorrelated, corresponding to $d = \infty$, we find $\tau \sim e^{kS}$, with $k$ given in terms of the probability to visit a new site. In $d = 2$, numerical simulations suggest that $\tau \simeq \mathcal{S}^{z}$, with $z \approx 2$. We develop a mean-field approximation for $d = 2$ that gives a rigorous lower bound for $\tau$ and suggests that $P(\mathcal{N})$ does not obey single-parameter scaling, as seen in our simulations.

Our mortality mechanism differs from previous models in which a random walker can die or be absorbed at a fixed rate, independent of its location \cite{14–17}. Here, the lifetime distribution of a random walker is not given \textit{a priori} but is generated by the random-walk trajectory, which renders the problem highly nontrivial. It is worth mentioning the related problem of the “excited” random walk, in which the hopping of the walker depends on whether it has just encountered food or an empty site \cite{18–23}. While the excited random walk has surprising behavior, we will show that even when the motion of the walker is not explicitly affected by the environment unusual properties arise.

One dimension. As the walker moves, an interval devoid of food—a desert—is gradually carved, and the survival of the walker is controlled by the interplay between wandering within the desert and reaching food at the edge of this desert (Fig. 1). For a starving random walker to survive for times beyond its intrinsic lifetime $\mathcal{S}$, excursions of more than $\mathcal{S}$ steps without food cannot occur in its past history. A long-lived walk must therefore spend less time wandering in the interior of a desert than unre-
restricted walks. Thus, the mean number of distinct sites visited should be larger than that for unrestricted random walks of the same number of steps \( N \).

We first determine \( P(N) \), the probability that a random walker has visited \( N \) distinct sites when it starves. This probability can be expressed as

\[
P(N) = Q_2 Q_3 Q_4 \cdots Q_N (1 - Q_{N+1}),
\]

where \( Q_j = \int_0^S dt F_j(t) \), and \( F_j(t) \) is the probability that the walker reaches either end of an interval of length \( ja \) (with \( a \) the lattice spacing) at step \( t \) when starting a distance \( a \) from one end. Each \( Q_j \) accounts for the interval growing from length \( j - 1 \rightarrow j \) because the walker reaches either end point within \( S \) steps, while the factor \( Q_{N+1} \) accounts for the last excursion in which the walker starves. It is expedient to express the visitation probability in terms of the scaled number of distinct sites visited, \( \theta = aN/\langle j\rangle \). In the Supplemental Material, we show that, when \( S \gg 1 \), \( P(\theta) \) is (Fig. 2)

\[
P(\theta) \simeq \frac{4}{\theta} \sum_{m \geq 0} \exp \left\{ -\frac{(2m+1)^2}{\theta^2} - \frac{2}{\theta^2} \frac{E_1\left(\frac{(2m+1)^2}{\theta^2}\right)}{E_1(1)} \right\},
\]

where \( D \equiv a^2/2 \) is the diffusivity of the corresponding continuous process and \( E_1(x) \equiv \int_x^\infty \frac{dt}{t} e^{-t} \) denotes the exponential integral. From Eq. 2, the average number of visited sites at the starvation time is

\[
\langle N \rangle \simeq \frac{\pi \sqrt{DS}}{a} \int_0^\infty \theta P(\theta) d\theta \approx A \sqrt{S},
\]

with \( A \approx 2.9022 \).  

The average lifetime \( \langle \tau \rangle \) of starving random walks is formally given by

\[
\langle \tau \rangle = \sum_{j \geq 1} \left( \langle \tau_j \rangle + \langle \tau_{j+1} \rangle + \cdots + \langle \tau_{j+S} \rangle \right) P(j),
\]

where \( \langle \tau_j \rangle \) is the average time for the random walk to hit either end of the interval in the \( j^{th} \) excursion, conditioned on the walker hitting either end before it starves, while the factor \( S \) accounts for the final excursion that causes the walker to starve. By definition

\[
\langle \tau_j \rangle = \frac{\int_0^S dt \int_0^S dt F_j(t)}{\int_0^S dt F_j(t)}.
\]

The numerator, defined as \( N_j \), reduces to

\[
N_j = \frac{4\pi D}{(ja)^2} \sum_{n \geq 0} (2n+1) \sin \lambda_{j,n} \int_0^S dt t e^{-\beta t},
\]

with \( \lambda_{j,n} \equiv (2n+1)\pi/j \) and \( \beta \equiv \lambda_{j,n}/(ja)^2 \).

For large \( j \), we approximate the sine function by its argument and perform the temporal integral to give

\[
\langle \tau \rangle \simeq \frac{4a^2}{\pi^2 D} \sum_{n \geq 0} \frac{1}{(2n+1)^3} \left[ 1 - e^{-\beta S(1 + \beta S)} \right]
\]

for \( S \gg 1 \). Using this in Eq. \ref{nu} gives \( \langle \tau \rangle \simeq 3.26786 S \).

These results for the distinct sites visited and the lifetime agree with numerical simulations shown in Fig. \ref{fig:3}.  

**Infinite dimension.** For \( d = \infty \), the probabilities of hitting a previously visited or previously unvisited site equal \( \lambda \) and \( 1 - \lambda \), respectively, with \( \lambda \) a constant. Schematically, the time until the walker starves undergoes one-dimensional hopping in “starvation space”—an interval of length \( S \)—and starvation occurs when 0 is reached.
A particle at site \( n \) in starvation space can wander \( n \) additional steps in physical space without encountering food before starving. When the walker hits a previously visited site in physical space, the time to starvation decreases by one time unit, corresponding to a hop to the left with probability \( \lambda \) in starvation space. When the random walker encounters a new food-containing site, it can wander an additional \( S \) steps until starvation occurs, corresponding to a long-range rightward hop to site \( S \) in starvation space with probability \( 1 - \lambda \).

\[
\begin{align*}
0 & \quad 1 \quad 2 \quad S-1 \quad S \quad S+1 \\
\lambda & \quad \lambda & \quad \lambda & \quad 1-\lambda & \quad 1-\lambda & \quad 1-\lambda
\end{align*}
\]

**FIG. 4:** Evolution of a high-dimensional random walk in starvation space. A particle at position \( n \) in this space can survive \( n \) additional steps without encountering food.

Using this equivalence to hopping in starvation space, we now compute \( t_n \), the average time until the walker starves when starting from site \( n \). These starvation times satisfy the recursions [20]

\[
\begin{align*}
t_{n} & = 1 + \lambda t_{n-1} + (1 - \lambda)t_{S}, \quad 2 \leq n \leq S; \\
t_{1} & = 1 + (1 - \lambda)t_{S},
\end{align*}
\]

from which

\[
t_{S} = \langle \tau \rangle = \frac{1}{\lambda S} \left( \frac{1 - \lambda S}{1 - \lambda} \right). \tag{9}
\]

The high-dimensional limit corresponds to \( \lambda \to 0 \), for which the average starvation time grows exponentially with \( S \), in contrast to the linear dependence for \( d = 1 \).

We may also obtain the distribution of the number of distinct sites visited by the walker in physical space at the starvation time. For this quantity, we need the probability \( R_n \) that the walk reaches \( S \) without first hitting 0, when starting from site \( n \) in starvation space. Each such return corresponds to the random walker visiting a new site in physical space without starving. These return probabilities satisfy the recursions

\[
\begin{align*}
R_{n} & = 1 - \lambda + \lambda R_{n-1}, \quad 2 \leq N \leq S, \\
R_{1} & = 1 - \lambda,
\end{align*}
\]

with solution \( R_n = 1 - \lambda^n \).

For a walker that starts at site \( S \) in starvation space, the probability that \( N \) distinct sites are visited before the walker starves is given by

\[
P(N) = (R_S)^N (1 - R_S), \tag{11}
\]

from which the average number of distinct sites visited before the walker starves is

\[
\langle N \rangle = \frac{R_S}{1 - R_S} = \lambda^{-S} (1 - \lambda^S). \tag{12}
\]

**Dimensions \( d > 2 \).** A random walk is transient, so new sites are visited at a nonzero rate [26, 28] and it is unlikely for a walker to first create a local desert and then wander within this desert until it starves. Thus the survival time should be much longer than in \( d = 1 \) for the same \( S \). As a check, we simulate starving random walks on a periodic hypercubic lattice where each site initially contains one food unit. We choose the lattice size so that wraparound effects are negligible. A random walk dies when it takes \( S \) consecutive steps without encountering food. We find \( \ln \langle \tau \rangle \sim S^\omega \) with \( \omega \approx 0.54, 0.73, \) and 0.81 in \( d = 3, 4, 5 \) (Fig. 5). Even though the walk is transient, so that the rate of visiting new sites is nonzero, temporal correlations between successive visits to new sites [29] lead to \( \langle \tau \rangle \) deviating from the mean-field result [30]. The systematic trend in the exponent estimates suggests that the upper critical dimension is \( d_c = \infty \).

**Two dimensions.** The most relevant case is that of two dimensions, which lies at the boundary between recurrence and transience. Numerical data indicate that both \( \langle N \rangle \) and \( \langle \tau \rangle \) scale as \( S^2 \), albeit with substantial preasymptotic corrections. This behavior is consistent with rigorous bounds for these quantities [29]. Sample random-walk trajectories are shown in Fig. 6 for intrinsic lifetime \( S = 500 \). Trajectories of short-lived walks are compact, while those of long-lived walks are quite stringy so that the walker remains close to food-containing sites. Strikingly, the underlying distribution for \( N \) violates single-parameter scaling (Fig. 7). To explain this feature, we give a mean-field description for the evolution of the desert that relies on the assumption that it always remains circular. When the walker comes to the edge of the desert and eats a morsel of food, we assume that the desert becomes a slightly enlarged circle with an area that is increased by \( a^2 \). After \( n \) visits to the edge of the desert and immediately after the walker has eaten, the radius of the desert is \( R_n = a \sqrt{n/\pi} \) and the walker is a distance \( a \) from the edge. Equation (11) still holds and
$Q_j$ can be shown to be given by

$$Q_j = 1 - 2 \sum_{k=0}^{\infty} \frac{J_0(\sqrt{\pi/j} \alpha_k)}{\alpha_k J_1(\alpha_k)} e^{-D_S \pi \alpha_k^2 / j a^2},$$

(13)

where $\alpha_k$ is the $k$th zero of the Bessel function $J_0$. We then follow the same analysis as in one dimension to give

$$P(N) \simeq \exp \left\{ -\frac{2 D \pi S}{a^2} \sum_{j=0}^{\infty} \frac{\theta e^{-\alpha_j^2/\theta} - \alpha_j^2 E_1(\alpha_j^2/\theta)}{\alpha_j J_1(\alpha_j)} \right\} \times 2 \sum_{j=0}^{\infty} e^{-\alpha_j^2/\theta} \alpha_j J_1(\alpha_j).$$

(14)

The simultaneous appearance of multiple parameters, $D$, $N$, and the scaling variable $\theta = aN/(\pi \sqrt{DS})$, shows that the above expression for $P(N)$ does not satisfy single-parameter scaling, as is observed in our simulation shown in Fig. 7.

FIG. 6: Example two-dimensional trajectories for $S = 500$. The lifetime $\tau$ of each walk is indicated. Note the very different spatial scales.

FIG. 7: The scaled distribution of number of distinct sites visited for four representative values of $S$. The data have been averaged over a 15-point range and only every fifth data point is displayed. Data are based on $10^6$ realizations for each $S$.

To summarize, starving random walks represent a minimalist description for the consumption of a depleting resource by a stochastic searcher. The motion of the walker is limited by the number of steps $S$ that it can take without encountering food before starving. The spatial dimensionality plays a crucial role in the dynamics, as the lifetime of a starving random walker grows faster than algebraically in $S$ for $d > 2$ and algebraically with $S$ for $d \leq 2$. We also obtained comprehensive results for the starvation dynamics in $d = 1$. The two-dimensional case is particularly challenging, as the distribution of the distinct sites visited does not obey single-parameter scaling and the region visited by the random walker is spatially complex. Many challenges remain to understand all of the statistical properties of this intriguing model, including the properties of starving random walks at fixed time and the connection between the walk lifetimes and the geometry of the desert, as illustrated in Fig. 6.

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[1] E. L. Charnov, Theor. Pop. Biol. 9, 129 (1976).
[2] P. Knoppien and J. Reddingius, J. Theor. Biol. 114, 273 (1985).
[3] D. W. Stephens and J. R. Krebs, Foraging Theory (Princeton University Press, Princeton, NJ, 1986).
[4] M. Levandowski, J. Klafter, and B. S. White, Bull. Marine Sci. 43, 758 (1988).
[5] W. J. O’Brien, H. I. Browman, and B. I. Evans, Am. Sci. 78, 152 (1990).
[6] J. W. Bell, Searching Behaviour, the Behavioural Ecology of Finding Resources, Animal Behaviour Series (Chapman and Hall, London, 1991).
[7] G. M. Viswanathan et al., Nature (London) 381, 413 (1996); 401, 911 (1999).
[8] J. P. Anderson, D. W. Stephens, and S. R. Dunbar, Behav. Ecol. 8, 307 (1997).
[9] L. D. Kramer and R. L. McLaughlin, Am. Zool. 41, 137 (2001).
[10] O. Bénichou, C. Loverdo, M. Moreau, and R. Voituriez, Rev. Mod. Phys. 83, 81 (2011).
[11] S. A. Rice, in Diffusion-Limited Reactions, Comprehensive Chemical Kinetics Vol. 25, edited by C. H. Bamford, C. F. H. Tipper, and R. G. Compton (Elsevier, New York, 1985).
[12] O. G. Berg and C. Blomberg, Biophys. Chem. 4, 367 (1976).
[13] T. Gueudré, A. Dobrinevski, and J.-P. Bouchaud, Phys. Rev. Lett. 112, 050602 (2014).
[14] M. Tachiya, Chem. Phys. Lett. 69, 605 (1980)
[15] R. F. Bonner, R. Nossal, S. Havlin, and G. H. Weiss, J. Opt. Soc. Am. A 4, 423 (1987).
[16] A. B. Kolomeisky and M. E. Fisher, Physica (Amsterdam) 279A, 1 (2000).
[17] S. B. Yuste, E. Abad, and K. Lindeberg, Phys. Rev. Lett. 110, 220603 (2013).
[18] M. Perman and W. Werner, Probab. Theory Relat. Fields 108, 357 (1997).
[19] B. Davis, Probab. Theory Relat. Fields 113, 501 (1999).
[20] I. Benjamini and D. B. Wilson, Electron. Commun. Probab. 8, 86 (2003).
[21] O. Angel O, I. Benjamini, and B. Virag, Electron. Commun. Probab. 8, 66 (2003).
[22] M. P. W. Zerner, Probab. Theory Relat. Fields 133, 98 (2005).
[23] T. Antal and S. Redner, J. Phys. A 38, 2555 (2005).
[24] See Supplemental Material at [http://link.aps.org/supplemental/10.1103/PhysRevLett.000.000000] for the derivation of $P(\theta)$.
[25] For the unrestricted random walk after $N = S$ steps, $\langle N \rangle \approx \sqrt{8S/\pi} \approx 1.5957\sqrt{S}$, see [27, 28].
[26] S. Redner, A Guide to First-Passage Processes (Cambridge University Press, Cambridge, England, 2001).
[27] G. H. Weiss, Aspects and Applications of the Random Walk (North-Holland, Amsterdam, 1994).
[28] B. D. Hughes, Random Walks and Random Environments (Clarendon, Oxford, 1995), Vol. 1.
[29] O. Bénichou and S. Redner, unpublished.