Does Greed Help a Forager Survive?

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We investigate the role of greed on the lifetime of a random-walking forager on an initially resource-rich lattice. Whenever the forager lands on a food-containing site, all the food there is eaten and the forager can hop $S$ more steps without food before starving. Upon reaching an empty site, the forager comes one time unit closer to starvation. The forager is also greedy—given a choice to move to an empty or to a food-containing site in its local neighborhood, the forager moves preferentially towards food. Surprisingly, the forager lifetime varies non-monotonically with greed, with different senses of the non-monotonicity in one and two dimensions. Also unexpectedly, the forager lifetime in one dimension has a huge peak for very negative greed.

Optimal foraging theory is a classic framework for modeling how a forager should continue to exploit local resource or move to new feeding grounds [1–17]. In this class of models, the goal is to formulate a criterion about which choice is optimal. Another perspective is to employ exotic search algorithms, such as Lévy walks [3], intermittent walks [9,13] and persistent random walks [14] to find resources. However, these models typically do not account for resource depletion in an explicit way.

Recently, an alternative description of foraging dynamics was developed in which the forager is unaffected by the presence or absence of food and always performs an unbiased random walk—the starving random walk [9–13]. When a forager lands on a food-containing site, all the food there is consumed. The forager can subsequently hop $S$ steps without again encountering food before it starves. However, if the forager lands on an empty site, the forager goes hungry and comes one time unit closer to starvation. Because there is no replenishment, resources are depleted by consumption and the forager is doomed to ultimately starve to death.

How does the forager lifetime $T$ depend on basic parameters—its metabolic capacity $S$ and the spatial dimension $d$? It was previously found that $T$ grows linearly with $S$ for $d = 1$, as $S^β$ with $β ≈ 1.9$ in $d = 2$, and as $\exp(S^ω)$ for $d ≥ 3$, with $ω ≈ 1/2$ in $d = 3$, and with $ω$ a gradually increasing function of $d$ for $d ≥ 3$ [15,16]. The full understanding of this dependence is still incomplete.

In this Letter, we investigate an ecologically motivated extension of the starving random walk in which the forager possesses a modicum of environmental awareness. Whenever the nearest neighborhood of a forager contains both empty and full (food-containing) sites, the forager preferentially moves towards the food (Fig. 1). We define this local propensity to move towards food as “greed”, which is quantified by a greediness parameter $−1 ≤ G ≤ 1$. For $G > 0$ a forager moves preferentially towards food, while for $G < 0$, the forager tends to avoid food. Naively, one might expect that increasing greed always increases the forager lifetime. However, we find that the forager lifetime varies non-monotonically in $G$ when $S$ is large, with opposite senses of the non-monotonicity in $d = 1$ and $d = 2$.

In $d = 1$, we implement greed as follows: when one neighbor of the forager contains food while the other is empty, the forager moves towards the food with probability $p = (1 + G)/2$; otherwise, the forager hops symmetrically (Fig. 1). For $d > 1$ the forager chooses one of the $k$ full sites in its neighborhood of $z$ sites with probability $p = (1 + G)/[(z − k)(1 − G) + k(1 + G)]$. The forager begins in the “Eden” condition where all sites initially contain food. As the foragers moves, it carves out a food-depleted region—the “desert”. As this desert grows, the forager typically spends longer times wandering within the desert and eventually starves.

Greed represents a particularly simple example of feedback between the environmental state and the forager motion, a mechanism that abounds in the microscopic world. Perhaps the best-known example is the run and tumble model of chemotaxis [17,18], in which a bacterium effectively swims up a concentration gradient of nourishment. In chemotaxis, however, the concentration of nutrients is fixed, while the starving forager model explicitly incorporates resource depletion.

**Heuristics for one dimension.** We provide a heuristic argument that predicts both the non-monotonic dependence of lifetime on greediness and a huge maximum for greediness $G ≈ −1$ (Fig. 2(a)). In $d = 1$, starvation proceeds in two stages: (i) The forager first carves a critical desert of length $L_c$ by repeatedly reaching either edge of the desert within $S$ steps after food is consumed. The critical length is defined by a forager of capacity $S$ typically starving if it attempts to cross a desert of this length. We denote the time to create this critical-length desert as $T_c$. (ii) Once the desert length reaches $L_c$, the
forager likely starves if it attempts to cross the desert. That is, the far side is unreachable and thus irrelevant. The time for this second stage is just the lifetime of a forager in a semi-infinite desert, $T_{S_{\infty}}$.

We now estimate the quantities $L_c$, $T_c$, and $T_{S_{\infty}}$. The time for a forager to reach food when it starts a unit distance from food in a desert of length $k$ is $t_1(k) \approx \frac{1 - p}{p} k$.

Therefore the time for the desert to grow to the critical length $L_c$ is

$$T_c = \sum_{k=1}^{L_c} t_1(k) \approx \frac{1 - p}{p} \frac{L_c^2}{2}.$$  \hspace{1cm} (1)

We determine $L_c$ by equating the typical time to cross a desert of this length, $t_x \approx \frac{2}{3} L_c^2 + \frac{4L_c^2}{3p}$ \cite{20}, to $S$. This gives two behaviors: $L_c \approx \sqrt{3S/2}$ for $p \gg 1/\sqrt{S}$, and $L_c \approx 3pS/4$ for $p \ll 1/\sqrt{S}$. Thus the time to reach the critical-length desert is

$$T_c \approx \begin{cases} \frac{3(1-p)S}{4p} & p \gg 1/\sqrt{S}, \\ \frac{9pS^2}{32} & p \ll 1/\sqrt{S}. \end{cases}$$  \hspace{1cm} (2)

For the semi-infinite geometry, a typical trajectory consists of segments where the forager moves ballistically into the food-containing region, interspersed by diffusive segments in the desert (Fig 3). As long as the diffusive segment lasts less than $S$ steps, the forager returns to the food/desert interface and a new cycle of consumption and subsequent diffusion begins. A ballistic segment of $m$ consecutive steps towards food (followed by a step away) occurs with probability $p^m(1 - p)$. The average time $t_b$ for this ballistic segment is $t_b = \sum_{m\geq1} m p^m (1 - p) = p/(1 - p)$. The probability $R$ for a diffusive segment to return to food within $S$ steps is the integral of the first-passage probability for a forager that starts at $x = 1$ to reach $x = 0$ within time $S$ \cite{21}:

$$R = \int_0^S dt \frac{e^{-1/4Dt}}{\sqrt{4\pi Dt^3}} = \text{erfc}(1/\sqrt{4DS}),$$

where $\text{erfc}(\cdot)$ is the complementary error function. The average number of returns is $\langle r \rangle = \sum_{r \geq 1} r R^r(1 - R) = R/(1 - R) \approx \sqrt{\pi S/2}$ for $S \to \infty$, where the asymptotics of the error function gives the final result, and we take the diffusion coefficient $D = \frac{1}{4}$. For a forager that does return within $S$ steps, the return time $t_r$ is thus

$$t_r = \frac{1}{R} \int_0^S dt \frac{1}{\sqrt{4\pi Dt^3}} e^{-1/4Dt} \approx \sqrt{\frac{2S}{\pi}} - 1.$$  \hspace{1cm} (3)

Two important consequences follow (Fig. 2(a)):
• When $S$ exceeds a critical value, it is easily seen that $T$ is decreasing with $p$, except for $p \to 0$ and $p \to 1$. Since $T$ diverges as $p \to 1$, the dependence of lifetime on greediness is non-monotonic!

• For $p \simeq 1/\sqrt{S}$, Eqs. (4) give a common lifetime $T \sim S^{3/2}$. A huge maximum for large $S$!

One-dimensional solution: We now outline an analytical solution for the forager lifetime that confirms and quantifies our heuristic picture given above. The probability $V_k$ that the forager has eaten $k$ times at the instant of starvation can be written as

$$V_k = [1 - F_k(S)] \prod_{j=2}^{k-1} F_j(S).$$  \hspace{1cm} (5)

Here $F_k(S)$ is the probability that a greedy forager escapes a desert of $k$ empty sites when the forager starts one lattice spacing from either edge. This quantity can, in turn, be written as

$$F_k(S) = \sum_{t=0}^{S} F_k(t),$$  \hspace{1cm} (6)

where $F_k(t)$ is the first-passage probability that the greedy forager, which is one lattice spacing from either edge of a desert of $k$ empty sites first reaches either edge at time $t$. Finally, the average forager lifetime is

$$T = \sum_{k \geq 0} \left[ \tau_1 + \tau_2 + \cdots + \tau_{k-1} \right] V_k + S,$$  \hspace{1cm} (7)

where

$$\tau_k = \sum_{t=0}^{S} t F_k(t) / \sum_{t=0}^{S} F_k(t).$$  \hspace{1cm} (8)

is the conditional average time for a greedy forager to successfully escape a desert of $k$ empty sites when it starts one lattice spacing from either edge.

Finally, we need the first-passage probability for a greedy forager, $F_k(t)$. This can be related to the first-passage probability $F_k(t)$ of a symmetric random walk by the convolution

$$F_k(t) = p \delta_{t,1} + (1 - p) \sum_{t' \leq t - 1} F_{k-2}(t') F_k(t - t' - 1).$$  \hspace{1cm} (9)

The first term accounts for a forager that reaches food in a single step. The second term accounts for the forager hopping to the interior of the interval. In this case, the walker is at $x = 2$ or $k - 2$ and hops symmetrically until it again reaches either $x = 1$ or $k - 1$. Thus the relevant first-passage probability is that for an unbiased random walk that starts at $x = 2$ or $k - 2$ on $[1, k - 1]$. Once the walker first reaches either $x = 1$ or $k - 1$, the process renews and the subsequent propagation involves $F_k$. Since one time unit is used in the first hop to the right, the walker must reach the boundary in the remaining time $t - t' - 1$ steps.

We solve Eq. (9) by introducing the generating functions

$$\tilde{f}_k(z) = \sum_{t \geq 1} f_k(t) z^t, \quad \tilde{F}_k(z) = \sum_{t \geq 1} F_k(t) z^t.$$

which leads to

$$\tilde{F}_k(z) = \frac{p z}{1 - (1 - p) z \tilde{F}_{k-2}(z)}. \quad (10)$$

We now use the well-known result for the Laplace transform of the first-passage probability [21]

$$\tilde{f}_k(s) = \text{sech} \sqrt{\frac{s}{D}} k \left[ \tanh \left( \sqrt{\frac{s}{D}} k \right) + \tanh \left( \sqrt{\frac{s}{D}} (k - 1) \right) \right],$$

$$\lim_{s \to 0} 1 - \sqrt{\frac{s}{D}} \tanh \sqrt{\frac{sk^2}{4D}} k + \cdots.$$  \hspace{1cm} (11)

Substituting this in (10) and converting the generating function to a Laplace transform by replacing $z \to 1 - s$, the Laplace transform of the first-passage probability for the greedy forager for $s \to 0$ and $k \to \infty$ is

$$\tilde{F}_k(s) = \left( 1 + \frac{1 - p}{p} \sqrt{\frac{s}{D}} \tanh \sqrt{\frac{sk^2}{4D}} \right)^{-1}. \quad (11)$$

We now use the above relations together with standard Laplace transform manipulations to determine $\tau_k$, $V_k$, and finally $T$ in the limiting cases of $p \gg 1/\sqrt{S}$ and $p \ll 1/\sqrt{S}$. In the former regime,

$$\tilde{F}_k(s) = \frac{1}{s} \tilde{F}_k(s) = \frac{1}{s} - \frac{1 - p}{p} \sqrt{\frac{1}{D s}} \tanh \sqrt{\frac{sk^2}{4D}} + \cdots.$$  \hspace{1cm} (12a)

whose Laplace inversion gives

$$F_k(S) = 1 - \frac{1 - p}{p} \sum_{j=0}^{4} e^{-D S \pi^2 (2j + 1)^2 / k^2}. \quad (12b)$$

Using standard Laplace transform manipulations, we finally obtain

$$\tilde{\tau}_k(s) \simeq -\frac{1}{s} \frac{\partial}{\partial s} \tilde{F}_k(s) = \frac{1 - p}{p} \tilde{\tau}_k(s; p = 1/2), \quad (13)$$

where the quantity on the right-hand side is the known escape time for the case of no greed, $p = 1/2$ [13,16]. Thus we obtain the fundamental relation between the escape times

$$\tau_k = \frac{1 - p}{p} \tilde{\tau}_k(p = 1/2). \quad (14)$$

Using these results for $F_L$ and $\tau_L$, we eventually obtain, for $p \gg 1/\sqrt{S}$ (see [20] for details),

$$T \simeq S \frac{1 - p}{p} \int_0^{\infty} \rho V_0 \int_0^{\infty} \frac{d\psi}{\psi} \sum_{j \geq 0} \frac{4}{\psi^2} \left[ 1 - e^{-\psi^2 [1 + \psi^2]} \right] + S. \quad (15)$$
where $v = (2j+1)/u$, $\theta = n/(\pi \sqrt{DS})$, with $n$ the number of sites visited by the forager at starvation, and

$$V_0 \approx \frac{4(1-p)}{p^2} \sum_{j \geq 0} e^{-w x^2} \cdot Q = \frac{2(1-p)}{p} \sum_{j \geq 0} E_1(u^2),$$

with $w = (2j+1)/\theta$, $E_1(x) = \int_1^\infty dt e^{-xt}/t$ the exponential integral. Because the function $V_0$ depends on $p$, the greedy forager lifetime $T$ does not merely equal $T$ for the non-greedy forager times the prefactor $(1-p)/p$. Our result (15) agrees with numerical simulations for large $S$ (Fig. 2(a)).

Deep in the negative greed regime $p \ll 1/\sqrt{S}$, Eq. (11) simplifies to

$$\bar{F}_k(s) \approx \left(1 + \frac{k}{2pD} s\right)^{-1}.$$  

(16)

Following the same steps as given above now leads to

$$T = \sum_{k \geq 1} \frac{k^2}{2pS} e^{-2pDS/k} \exp \left[-\int_1^k e^{-2pDS/x} dx\right] + S, \quad (17)$$

and the asymptotic evaluation of this integral gives (20)

$$T \approx S \frac{\sqrt{\pi}}{2} e^{-\frac{pS^2}{\ln(pS)^2}} + S. \quad (18)$$

The full form (17) and the asymptotic approximation, (18) match simulation results in the small-$p$ regime.

**Two Dimensions:** Surprisingly, simulations show that the forager lifetime again varies non-monotonically with (positive) greed, but in the opposite sense compared to one dimension (Fig. 2(b)). A perfectly greedy forager has a smaller lifetime than one that is not quite as avaricious. We can explain this feature quite simply: Suppose that a perfectly greedy forager is about to form such a closed loop (Fig. 4(a)). At this point, the forager has only two possible choices for the next step. One of them leads outside the incipient closed loop and the other leads inside. If the latter choice is made, a “moat” is created by the previous trajectory.

Once inside the moat, a perfectly greedy forager always consumes food in its nearest neighborhood. Ultimately, this interior food is mostly or completely depleted (the latter is shown in Fig. 4(c)). While the former case is more likely, the remaining food will be scarce and isolated. Thus the forager creates and then becomes trapped inside a (perhaps slightly imperfect) desert.

Conversely, if the greediness $G < 1$, a forager that encounters the moat from the interior can cross it with a non-zero probability and thereby reach food on the outside. This mechanism provides a route for the forager to escape the desert and survive longer than if it remained strictly inside. This argument indicates that the forager lifetime should be a decreasing function of $G$ as $G \to 1$, as confirmed by simulations (Fig. 2(b)). Also in stark contrast to one dimension, there is no peak in the forager lifetime for negative greed, at least for the values of $S$ that we were able to simulate.

To summarize, greed plays a paradoxical role in the lifetime of a greedy random-walking forager that moves preferentially towards local food for positive greediness, and away from local food for negative greediness. The lifetime depends non-monotonically on greediness when the forager capacity is sufficiently large and the sense of the non-monotonicity is opposite in one and two dimensions. In $d = 1$, the forager lifetime exhibits a huge maximum of the order of $S^{3/2}$ for $G \approx -1$, scales as $S^{1/2}/(1-G)$ for $G \to 1$, while $T \approx S$ throughout the rest of the range of $G$. We gave a heuristic argument to understand both the non-monotonicity and the peak.

A variety of questions remain open. Is there no peak in the lifetime for negative greed in two dimensions? What is the behavior of the lifetime in greater than two dimensions? Simulations are not useful here because the lifetime is extremely long for non-negligible greed and memory/computation time constraints become prohibitive. On a biological note, greed can be viewed as endowing a forager with a minimal information processing capability. A related mechanism is for the forager to perform a non-backtracking random walk (previous step is not retraced). The forager lifetime increases monotonically with the probability of not backtracking (Fig. 2(b); here $1 - G$ is a proxy for the backtracking probability) and perfect non-backtracking is superior to perfect greed. It would be useful to understand how to most effectively increase the forager lifetime with minimal information-processing enhancements to random-walk motion.

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