

Lifetime of a greedy forager with long-range smell

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Abstract – We study a greedy forager who consumes food throughout a region. If the forager does not eat any food for S time steps it dies. We assume that the forager moves preferentially in the direction of greatest smell of food. Each food item in a given direction contributes towards the total smell of food in that direction, however the smell of any individual food item decays with its distance from the forager. We study both power-law decay and exponential decay of the smell with the distance of the food from the forager. For power-law decay, we vary the exponent α governing this decay, while for exponential decay we vary λ also governing the rate of the decay. For power-law decay we find, both analytically and through simulations, that for a forager living in one dimension, there is a critical value of α , namely α_c , where for $\alpha < \alpha_c$ the forager will die in finite time, however for $\alpha > \alpha_c$ the forager has a nonzero probability to live infinite time. We calculate analytically the critical value, α_c , separating these two behaviors and find that α_c depends on S as $\alpha_c = 1 + 1/\lceil S/2 \rceil$. We find analytically that at $\alpha = \alpha_c$ the system has an essential singularity. For exponential decay we find analytically that for all λ , the forager has a finite probability to live for infinite time. We also study, using simulations, a forager with long-range decaying smell in two dimensions (2D) and find that for this case the forager always dies within finite time. However, in 2D we observe indications of an optimal α (and λ) for which the forager has the longest lifetime.

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Introduction. – Animals seeking food or resources spread out over a region often must move throughout the region in order to obtain the desired resources. The question of whether such foraging can be performed in an optimal manner to maximize the animal's lifetime or likelihood of finding food has received significant attention [1–4]. Many earlier studies argue that to be optimal such searching should be done stochastically [5–7] and that random walks or Lévy flights can be used to model this behavior [8–12]. Several models for a forager's movement behavior have been proposed including based on stimuli, memory, and cues from fellow foragers [4,13–15].

Recent work has suggested a new model where a forager carries out a random walk, yet the food is explicitly consumed until the forager starves to death [16,17]. In this model, the forager begins at some point on a lattice with each site containing food. The forager then moves and eats the food at the discovered site, leaving no remaining food there. It continues to move throughout the region either returning to sites without food or eating food at

new discovered sites. If the forager goes S steps without eating, it starves to death. Notably, this process leads to inherent desertification [18,19], as the forager eventually creates a desert of visited sites among which it moves until starvation. Later work expanded this to cases where the food renews after some time [20], where the forager eats only if it is near starvation [21,22], and where the forager walks preferentially in the direction of a *nearby* site with food (greed) [23,24].

Indeed, this recent extension of the random forager to include “greed” incorporates the fact that the forager has knowledge of its surroundings [7,25,26]. However, it only considers very short-range knowledge of the surroundings. Here we extend the starving forager models to a forager with an explicit sense of *smell* that extends to potentially longer ranges [27]. We assume that the contribution of an individual food site to the overall smell in a given direction decays with its distance d from the forager. While actual patterns of odor diffusion are turbulent and vary in time in highly complex ways [28], we simplify to consider two

realistic cases: power-law decay with distance and exponential decay. Power laws have been found to arise in the context of odor regarding perceptions and concentrations, in particular in the well-known Steven's Law [29,30]. Likewise, in applied settings, guidelines for setback distances for odorous agricultural factories, have been set based on a power-law decay of concentration with distance [31]. At the same time, both power-law and exponential decay were found in recent experiments on odor patterns depending on the type of wind, threshold concentration, and other conditions [28]. We therefore consider both cases in order to better understand the possible behavior of our model. After calculating the total smell (based on either power-law or exponential decay), we assume that the forager walks probabilistically in each direction proportional to the total smell in that direction.

Our model begins with a lattice with sites all containing food. The forager starts at some site and at each site it visits, it consumes all the food leaving behind a site with no remaining food. If the forager goes S time steps without visiting a site containing food, it starves to death. The forager is biased to walk in the direction of food, however as opposed to [23] where only food at the nearest site was considered, we also consider food at more distant sites in determining the forager's preferred trajectory. Thus at each time step the forager calculates the total "smell", F , emanating from each possible direction and weights its likelihood to walk in a particular direction based on the total smell in that direction. The total smell is found by calculating the smell from all sites in that direction weighted either by a power law with exponent α or by an exponential function with decay rate λ . The forager then moves in each direction probabilistically with likelihood according to the fraction of total smell in that direction. We are then primarily interested in the quantity T , defining the total number of steps that the forager survives before starving to death.

One dimension with power-law decay. – Like earlier studies [16,23,32], we begin with the case of one dimension, see fig. 1. This case is more tractable to analytic solutions and provides intuition for the more ecologically relevant case of two dimensions.

We assume that the forager begins at the center of a one-dimensional lattice of length l with periodic boundary conditions. For power-law decay, we define the total smell of food in a given direction as

$$F = \sum_{d=1}^{l/2} \frac{\delta_d}{d^\alpha}, \quad (1)$$

where d is the distance of the forager from the site being considered, δ_d is 1 if the site contains food and 0 otherwise, and α controls the decay with distance. Ideally, we are interested in the limit of $l \rightarrow \infty$, but we will start by considering a finite l and then take the limit $l \rightarrow \infty$.

For one dimension there are two directions of smell, denoted as F_R to the right and F_L to the left. The forager

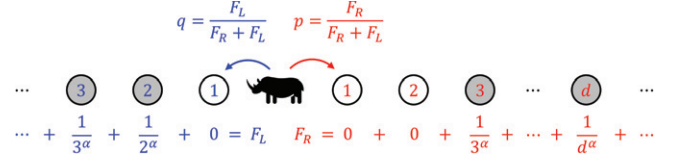


Fig. 1: Model demonstration in 1D. We show the likelihood of the forager to walk in a given direction based on the amount of food in that direction. In one dimension there are two directions with smells F_R and F_L . The probability to walk right (left) is then given by $p(q)$ as defined in the figure for power-law decay.

moves with probability proportional to the smell such that

$$\begin{cases} p = \frac{F_R}{F_R + F_L}, \\ q = \frac{F_L}{F_R + F_L}, \end{cases} \quad (2)$$

where p, q are the probability to walk right or left, respectively (see fig. 1).

We present simulation results for the system described above in fig. 2(a) for different S and measure the mean forager lifetime T as a function of α . Until $\alpha \approx 1$ the forager has a short lifetime (below ≈ 100), see fig. 2(b). This is because, for small α the forager considers unreachable far away food, causing the forager to essentially carry out an unbiased random walk as in [16].

In contrast, above some α , α_c , which decreases with S , the forager consumes all (or most) food in the system, *i.e.*, $T \approx 10\,000 = l$ (see fig. 2(a)). This is since for sufficiently large α , once the forager takes one step in either direction, it will then mainly consider only its immediate neighbors. The previously visited site will be empty, while the other site will be filled, thus the forager will move towards the filled site. This will happen nearly every time step and the forager will continue moving in the same direction and eating food at new sites. In the limit $\alpha \rightarrow \infty$, our results approach those of [23] with perfect greed.

Using the intuition gained above, we now consider $l \rightarrow \infty$. For this case, after eating, the forager will be at the edge of a semi-infinite line of food in one direction. Therefore the smell in the direction of this line is

$$F = \sum_{d=1}^{\infty} \frac{1}{d^\alpha} = \zeta(\alpha), \quad (3)$$

where $\zeta(\alpha)$ is the Riemann-Zeta function (RZF).

This mapping to the ζ function allows us to simulate an infinite system since rather than looping over an infinite amount of food, we can subtract from $\zeta(\alpha)$ those locations which do not have food. Thus if x_0 is the current forager location and the maximal (minimal) location reached is $x_{\max}(\min)$, then

$$F_i = \zeta(\alpha) - \sum_{d=1}^{x_{\max}(\min) - x_0} \frac{1}{d^\alpha}, \quad (4)$$

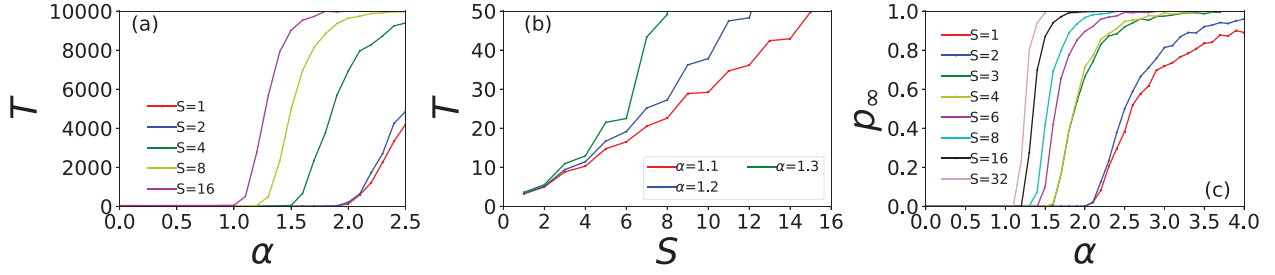


Fig. 2: Greedy forager with power-law decaying smell in one dimension, eq. (1). (a) Simulation results for the mean lifetime of the forager, T , as a function of α for several S values for a one-dimensional line of $l = 10^4$ sites with periodic boundary conditions. All points are averaged over 1000 runs. (b) T , the forager lifetime, as a function of S for several fixed α . We choose α values just above 1 in order to obtain finite values of T . We observe an even-odd alternating pattern. (c) We plot the probability of the forager to live for an infinite time, p_∞ . In practice, we carry out 1000 realizations and find the fraction that approach to $T = 10^7$, which is our cutoff for $T \rightarrow \infty$.

where i is either R or L . After calculating F_R and F_L , we use eq. (2) to obtain the probability to move in each direction.

In fig. 2(b) we show the forager lifetime, T , as a function of S for values of α slightly above 1, where the forager lifetime is finite. The even-odd alternating steps in the forager lifetime are due to the fact that if a forager has eaten for several steps in one direction and then takes one step away from the food, it will also not eat on the next step since both locations next to it will be empty. Thus, the forager requires at least 3 steps to return to new food (one to step away from the food, one to step back to its original location, and a third step to reach the new food). This is similarly true for taking n steps away from the food and therefore only odd S increase the lifetime significantly.

For the infinite l case we can expect that for sufficiently large α the forager will survive for infinite time (in practice, we set some cutoff time). In fig. 2(c), we plot the likelihood, p_∞ that the forager will have a lifetime above the cutoff *vs.* α for different values of S . Defining p_∞ as the order parameter, we observe a critical value of α , α_c , for which the forager lives an infinite lifetime. As we will demonstrate below, the reason for this phase transition is that for sufficiently large α , after the forager consumes food in one direction for several time steps, it will be faced with a desert in one direction and an infinite line of food in the other direction. Therefore, if α is large, the forager will have very high (and increasing) probability to continue moving towards the food and consuming all the available food. We note that it is somewhat surprising that α_c changes with S as typically critical exponents are independent of the values of microscopic parameters [33].

Theoretical calculation of α_c . Having observed that the forager could live for $T \rightarrow \infty$ steps, we aim to calculate the lowest value of α , α_c , that this occurs. We define α_c such that for $\alpha > \alpha_c$ the probability to live forever ($T \rightarrow \infty$) is $p_\infty > 0$ and the average number of distinct sites visited (food consumed), is $\langle N \rangle \rightarrow \infty$, while for $\alpha < \alpha_c$, $p_\infty = 0$. If a forager lives forever, it will do so by almost always moving in the same direction, creating

a desert of length D between itself and food on the other side of the desert. After a large number of steps where the forager remains alive it will reach a point where D is very large. The behavior in this limit will determine if the forager can live forever.

To derive p_∞ we will calculate the likelihood ϕ of the forager to survive until its next meal given that it just ate. We note that ϕ depends on D and that each time the forager eats a meal, the size of the desert will increase by 1, $D \rightarrow D + 1$. We can now recognize that p_∞ , the probability of the forager to live forever, is

$$p_\infty = \prod_{D=1}^{\infty} \phi_D, \quad (5)$$

where ϕ_D represents the value of ϕ for a given D . Equation (5) essentially explains that the likelihood for the forager to live for an infinite time is the product of its likelihood to reach its next meal every time. Next, we calculate the values of ϕ_D . Without loss of generality, we assume that the forager has so far moved to the left and thus after its most recent meal, the desert of size D is to its right. Between meals, the forager will wander and its distance x from the next meal, just past the edge of the desert, will vary. To calculate ϕ_D , we must first determine the likelihood of the forager to move either towards or away from the edge of the desert. As in fig. 1 we denote as $p_D(x)$ the probability to move right (further into the desert) given that the desert is of size D and that the forager is at distance x from the desert's edge. Likewise, $q_D(x)$ is the likelihood to move left or towards the edge of the desert of size D .

In the limit of large D , we approximate $p_D(x) = F_R/(F_R + F_L) \approx F_R/F_L$ since the forager is far from the food at the opposite end of the desert (right side) and $F_R \ll F_L$. For a given value of x , F_L will be the same for any value of D . Thus, all that remains to find $p_D(x)$, is to determine

$$F_R = \sum_{n=D-x}^{\infty} \frac{1}{n^\alpha}. \quad (6)$$

This sum can be approximated by the integral

$$F_R \approx \int_{D-x}^{\infty} n^{-\alpha} dn = \frac{(D-x)^{1-\alpha}}{\alpha-1}.$$

To leading order this implies the scaling $F_R \sim D^{1-\alpha}$ and so

$$p_D(x) \sim F_R/F_L \sim D^{1-\alpha}. \quad (7)$$

This scaling relationship is important for the remainder of the derivation and so we verify it for $x = 1$ in fig. A.1 of the supplementary material [SupplementaryMaterial.pdf](#) (SM).

We now return to ϕ_D and its complement $1 - \phi_D$. We consider “paths of starvation” *i.e.*, those paths along which the forager will fail to consume its next meal and die. These paths must end at $x > 0$ and thus they include only paths with equal or more steps to the right than to the left. This means that at least $k = \lceil S/2 \rceil$ steps must be to the right where $\lceil \cdot \rceil$ is the nearest integer above the number. Since $p_D(x) \ll 1$, we only consider the leading term which consists of paths with the minimum number of steps to the right. Using eq. (7), we can write

$$1 - \phi_D \sim p_D^k q_D^{S-k} \sim D^{(1-\alpha)k}, \quad (8)$$

where p_D^k represents k steps to the right and q_D^{S-k} represents $S - k$ steps to the left. Knowing the scaling of ϕ_D , we can now evaluate p_∞ using eq. (5). We estimate p_∞ by converting the product in eq. (5) to a sum of logarithms as

$$\begin{aligned} \ln p_\infty &= \sum_{D=1}^{\infty} \ln \phi_D \\ &\approx \sum_{D=1}^{D_0-1} \ln \phi_D + \sum_{D=D_0}^{\infty} \ln(1 - AD^{(1-\alpha)k}), \end{aligned}$$

where A is a constant prefactor, D_0 is a large arbitrary value of D such that eq. (7) is true, and for $D \geq D_0$ we have from eq. (8) that $AD^{(1-\alpha)k} \ll 1$. Thus,

$$\ln p_\infty \approx -B - A \sum_{D=D_0}^{\infty} D^{(1-\alpha)k}, \quad (9)$$

with $B = \sum_{D=1}^{D_0-1} \ln \phi_D$ being another constant factor. The result in eq. (9) depends on if the sum diverges to negative infinity. If the RHS of eq. (9) diverges then when exponentiating we will find that $p_\infty = 0$, whereas if the sum remains a finite negative number, then $p_\infty > 0$. Which case occurs will depend on the value of $(1-\alpha)k$ such that

$$\ln p_\infty = \begin{cases} -\infty, & (\alpha-1)k \leq 1, \\ -C(\alpha), & (\alpha-1)k > 1, \end{cases}$$

where $C(\alpha)$ is some finite value resulting from the infinite sum. Finally, we can obtain

$$p_\infty = \begin{cases} 0, & \alpha \leq 1 + \frac{1}{k}, \\ e^{-C(\alpha)}, & \alpha > 1 + \frac{1}{k}. \end{cases} \quad (10)$$

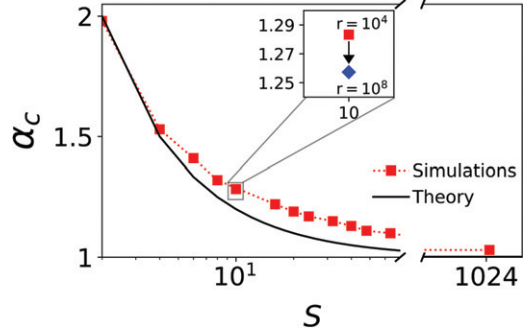


Fig. 3: Critical value of α_c for power-law decay of smell. Theory and simulations of α_c as a function of S . The simulations suggest values of α_c slightly larger than those calculated by the theory, yet this is likely due to the finite number of realizations, $r = 10^4$, for each point and the likelihood of a single realization to reach $T \rightarrow \infty$ may be less than this value near α_c . In the inset, we show that increasing the number of realizations (to 10^8) leads to a decrease in the calculated value of α_c , closer to the analytic result of eq. (11).

Thus, we find $p_\infty > 0$ for

$$\alpha > \alpha_c = 1 + \frac{1}{\lceil S/2 \rceil}. \quad (11)$$

We show our analytic result compared to simulations in fig. 3. We note that in the limiting case $S = 1$ then $\alpha_c = 2$, and for S large $\alpha_c \rightarrow 1$. The slight discrepancy between the theory and simulations is observed because the measured α_c only represents an upper bound for the true value of α_c . This is since we only considered a finite number of realizations. For example in the case of 10^4 realizations, we examine if in any one realization the forager’s lifetime reaches the cutoff ($T = 10^7$) and if so we assume $p_\infty < 10^{-4} = 1/10^4$. However, we cannot actually measure $p_\infty \rightarrow 0$. At the same time, we do find that increasing the number of realizations leads to a lower upper bound. Second, another reason for the deviation is that in eq. (8), we only considered the leading term. For the infinite limit, this will be correct, however given that in the simulations we could only measure finite $p_\infty > 0$, the later terms will affect our determination of α_c and lead us to obtain higher values than would be found in the infinite case.

As $\alpha \rightarrow \alpha_c^+$, it can be found that $C(\alpha) \sim \frac{1}{\alpha - \alpha_c}$, since approximating the sum in eq. (9) as an integral gives $C(\alpha) \approx -B - A \int_{D_0}^{\infty} x^{(1-\alpha)k} dx \sim AD_0^{(\alpha-\alpha_c)k} / ((\alpha_c - \alpha)k)$. Thus we can obtain the scaling relationship near criticality, where $p_\infty \rightarrow 0$, as

$$p_\infty \sim \exp\left(-\frac{b}{\alpha - \alpha_c}\right), \quad (12)$$

where b is some positive constant. This implies that p_∞ undergoes a continuous transition at α_c (see fig. A.2 in the SM), and that at α_c there is an essential singularity. In the appendix, we show that there is also a transition in T as the same value of α_c .

One dimension with exponential smell decay. –

We next consider the scenario in which the smell decays with the distance exponentially as $e^{-\lambda d}$ where λ determines the rate of decay. For this case, eq. (1) becomes

$$F = \sum_{d=1}^{l/2} \exp(-\lambda d). \quad (13)$$

In this case the average lifetime diverges for any positive value of λ . We can see this by first noting that eq. (5) remains true, whereas eq. (7) must be modified for the exponential case. We note

$$F_R \approx \int_{D-x}^{\infty} e^{-\lambda n} dn = \frac{e^{-\lambda(D-x)}}{\lambda},$$

which implies that the correctly modified form of eq. (7) is

$$p_D(x) \sim F_R/F_L \sim e^{-\lambda D}. \quad (14)$$

Equation (8) will then become

$$1 - \phi_D \sim p_D^k q_D^{S-k} \sim e^{-\lambda k D}. \quad (15)$$

and eq. (9) is

$$\ln p_{\infty} \approx -B - A \sum_{D=D_0}^{\infty} e^{-\lambda k D}. \quad (16)$$

The RHS of eq. (16) is finite for any positive λ . Therefore when isolating to obtain p_{∞} by exponentiating both sides of the equation, we find that $p_{\infty} > 0$ for all $\lambda > 0$. Likewise, this implies that $\langle \mathcal{N} \rangle$ and T will be infinite for $\lambda > 0$. Thus, in one dimension, exponential decay of smell with distance leads to an infinite expected lifetime for all cases, unlike power-law decay where the expected lifetime may be finite or infinite depending on α .

Two dimensions. – We will now consider the more ecologically relevant case of two dimensions. There are now 4 possible directions (on a square lattice) that the forager can move. We assume that food located at distance $(\Delta x, \Delta y)$ from the forager contributes (for power-law decay of smell) $\frac{1}{\sqrt{(\Delta x^2 + \Delta y^2)^\alpha}} (\frac{\Delta x}{\sqrt{\Delta x^2 + \Delta y^2}}, \frac{\Delta y}{\sqrt{\Delta x^2 + \Delta y^2}})$ to the smell. We sum all of the smells in the positive and negative directions of x and y and stochastically choose one of the 4 proportionally to their smell (see fig. 4).

Results. We begin with the case of power-law decaying smell. To gain more intuition into the effect of smell, we convert to polar coordinates where the distance from an individual food item is $(r \cos \theta, r \sin \theta)$, with $r = \sqrt{x^2 + y^2}$ and $\theta = \tan^{-1}(\frac{y}{x})$. We can then approximate the total upper smell, u , with the integral $\int_0^\pi \int_{r_0}^\infty 1/r^\alpha \sin \theta r dr d\theta = 2 \int_{r_0}^\infty r^{1-\alpha} dr$. This integral diverges for $\alpha \leq 2$ and the same will be true for the lower, left, and right directions. Thus, for $\alpha \leq 2$ our model converges to the model of the uniformly random walker forager [16] since there is infinite smell in all directions. As for the one-dimensional

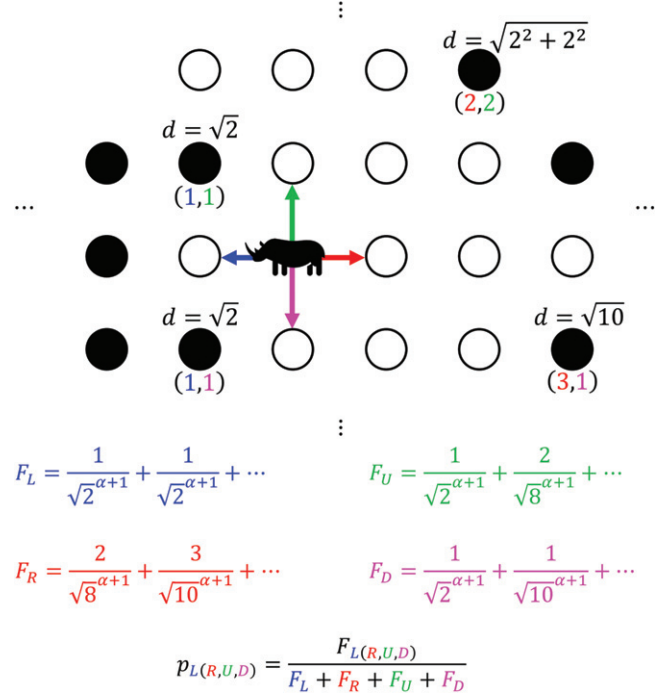


Fig. 4: Model demonstration in 2D. In 2D there are four possible directions, F_L, F_R, F_U, F_D , and $d = \sqrt{\Delta x^2 + \Delta y^2}$. The probability, p_i , to walk in each direction is proportional to its smell.

case, here too when $\alpha \rightarrow \infty$ the forager will behave like the completely greedy forager smelling only the nearest neighbors [23].

Unfortunately, our useful idea in one dimension where we recognized that the entire tail of the smell is $\zeta(\alpha)$ will not work in two dimensions since the forager need not walk in an orderly manner, but rather can “snake” throughout a region. Therefore analytic results are difficult for 2D and in our simulations we simulate a finite-size system of size $l \times l$ with periodic boundaries. Previous work on percolation and other systems have shown that periodic boundary conditions generally lead a system to converge to the infinite limit at smaller system sizes than using non-periodic boundaries [33]. In our case, we expect this to be true as well since for periodic boundaries, the forager can reach food on the other side of the boundary, which is more similar to the situation if the system extended forever.

We begin by examining the finite-size effects on the lifetime of the forager for fixed S and α near $\alpha = 2$. For $l \rightarrow \infty$, we expect that for $\alpha \leq 2$, the forager lifetime should be constant and equal to the random case [16]. Since the simulations are heavy, we set a maximum distance up to which we will consider the impact of food, whereas food at greater distances will be ignored. Figure 5(a) shows that for $\alpha = 1.9 < 2$, the forager lifetime decreases significantly as this maximal smell range increases. This can be understood by recognizing that the far away food must be considered in order for the sum to approach ∞ in all directions. We choose 250 as our

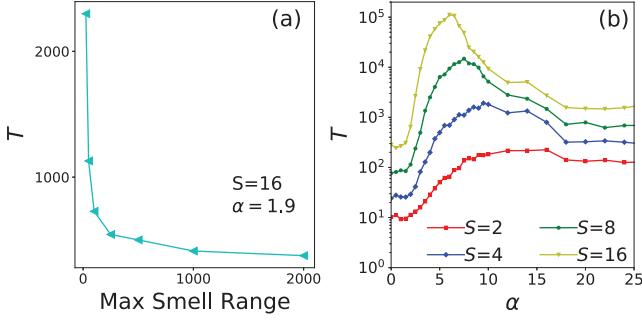


Fig. 5: Plots for a forager with power-law decaying long-range smell in two dimensions. (a) We show that varying the maximum smell range significantly affects the forager’s lifetime and thus one must carry out larger computations to assess the finite size issues. For smell range ≤ 1000 the system size is $10^3 \times 10^3$, while for 2000 it is $2 \cdot 10^3 \times 2 \cdot 10^3$. In (b) we show the mean lifetime of the forager, T , as a function of S for a two-dimensional space of $10^3 \times 10^3$ sites with periodic boundary conditions. All points are averaged over 100 realizations.

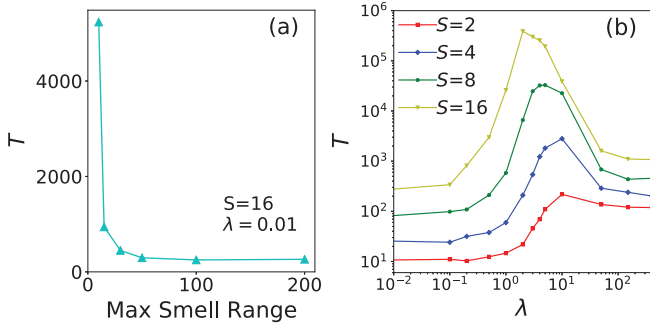


Fig. 6: Plots for a forager with long-range exponentially decaying smell in two dimensions. (a) For the exponential case, the maximal smell range quickly converges when we set 100 as the maximal smell range. In (b) we show the mean lifetime of the forager, T , as a function of S for exponential decay in two dimensions. All points are averaged over 100 realizations.

linear-size limit, since it balances between being reasonably computationally feasible and giving results that are sufficiently close to those expected for the infinite limit.

In fig. 5(b) we plot the forager lifetime as a function of α for different values of S . We observe that from $\alpha = 0$ until $\alpha \approx 2$ the forager lifetime is constant, as expected. This is since the smell in each direction is diverging and thus the forager moves randomly. As α further increases, we see that the forager lifetime increases and reaches a peak before dropping to a constant value for large α . This constant value for large α is the limit of total greed in [23]. There, it was found that near the limit of total greed in 2 dimensions, the forager lifetime actually decreases as the forager becomes more greedy because the forager forms deserts and becomes “trapped” inside them. These traps play a similar role here with intermediate α optimally avoiding them.

In fig. 6 we present results for exponential decay in two dimensions. Now the smell will be given by $e^{-\lambda d}(\frac{\Delta x}{d}, \frac{\Delta y}{d})$, where $d = \sqrt{\Delta x^2 + \Delta y^2}$. We first assess how using a maximum smell range affects our results and we find that in contrast to the power-law case of fig. 5(a), for the exponential case the result converges for a smaller value of the smell range (fig. 6(a)). We thus choose 100 as our cutoff for the smell range for the exponential results. For the case of large λ our results converge to those of the perfectly greedy forager, whereas for small λ we obtain the results of a random walking forager. Similar to what was found for power-law decay, for exponential decay we also find a peak in the forager lifetime with a particular value of λ that appears to depend on S . Here too, this peak is related to the creation of “traps” if λ is too small.

Discussion. – We have studied a forager that walks preferentially according to the smell of food in a given direction. For power-law decay of smell in one dimension, above a certain critical α_c , the forager can live for infinite time and almost always walks in the same direction. The value of α_c decreases with the time, S , that the forager can live without food. However, for exponential decay of smell with distance, for all values of $\lambda > 0$, there is a finite likelihood for the forager to live forever. In the two-dimensional case, we find optimal values of both α and λ for which the forager lifetime is maximal. Overall, our results provide intuition on how long-range smell affects the lifetime of a forager. Further work could compare these results to experimental measurements, which also might lead to additional extensions to the model such as exploring cases where originally only some sites contain food (possibly in unequal amounts) and incorporating the fact that food often appears in “patches” [26]. Likewise, multiple foragers living in the region could be considered with all of them depleting food sources [15].

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