Optimizing a jump-diffusion model of a starving forager

Nikhil Krishnan and Zachary P. Kilpatrick

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Department of Applied Mathematics, University of Colorado, Boulder, Colorado 80309, USA

We analyze the movement of a starving forager on a one-dimensional periodic lattice, where each location contains one unit of food. As the forager lands on sites with food, it consumes the food, leaving the sites empty. If the forager lands consecutively on s empty sites, then it will starve. The forager has two modes of movement: it can either *diffuse*, by moving with equal probability to adjacent sites on the lattice, or it can *jump* to a uniformly randomly chosen site on the lattice. We show that the lifetime T of the forager in either paradigm can be approximated by the sum of the cover time τ_{cover} and the starvation time s, when s far exceeds the number n of lattice sites. Our main findings focus on the hybrid model, where the forager has a probability of either jumping or diffusing. The lifetime of the forager varies non-monotonically according to p_j, the probability of jumping. By examining a small system, analyzing a heuristic model, and using direct numerical simulation, we explore the tradeoff between jumps and diffusion, and show that the strategy that maximizes the forager lifetime is a mixture of both modes of movement. However, when extending the model to include time penalties for long-range movement, the forager's lifetime is no longer typically non-monotonic in p_j. Pure jumping is typically optimal when there is an upper bound on the time-penalty, but pure diffusion is optimal when jumping becomes too perilous. A mixed jump-diffusion strategy is recovered if a forager is allowed to avoid jumping if they will die mid-jump.

I. INTRODUCTION

Virtually all motile organisms must forage for resources such as food, habitats, or mates. Optimal foraging theory typically examines what strategies best balance search cost with reward [1]. An integral component of foraging is the balance between exploiting the known and/or nearby resources versus exploring one's broader environment for new resources [2]. Organisms typically deplete resources in their immediate vicinity over time [3], unless depletion is slow and resources are renewable [4]. Thus, organisms often invoke strategies in which they compare the known yield at their current location with distribution of yields from distant sites [5].

The predictions of theoretical models of foraging strongly depend on the information available to the forager. If foragers have partial knowledge of the statistical distribution of resources, optimal foraging strategies are usually straightforward to identify and typically balance an explore/exploit tradeoff [1, 6]. In contrast, foragers may possess no knowledge of their environment and may be incapable or unwilling to learn based on their foraging history [7]. Recent models along these lines study the dynamics of foragers moving in environments organized on a lattice, according to a random walk. Previous work has examined the effect of making the forager more or less likely to pursue food [8], making the forager wait before consuming food [9], and giving the forager a chance not to consume encountered food [10]. In particular, this recent work has studied the added constraint of starvation, whereby the forager cannot go longer than s steps without food. Exploration/exploitation tradeoffs are then determined by how search strategy parameters

shape the lifetime of the forager, corresponding to the number of steps until it starves.

Our model is similar to a starving forager executing a random walk developed in [7, 8]. We consider the movement of a forager on a one-dimensional periodic lattice with n sites, where each location contains one unit of food. If the forager lands on a site with food, the forager consumes the food, leaving the site empty. After the forager lands on s consecutive empty sites, it starves. Since the food is depleted and never regenerated, the forager will eventually starve, and can survive at most $s \cdot n$ steps, though the mean lifetime T is typically much less than this upper limit.

Recent analyses have focused on cases in which foragers only move locally, according to biased or unbiased random walks [7–9]. In contrast here, we explore the effects of allowing the forager to make large jumps. Food is typically distributed heterogeneously in an environment, and animals can adapt their foraging strategy as such [1]. For example, penguins alternate between foraging locally on patches of krill and moving ballistically between them [11]. One foraging strategy for this situation is a Lévy-type movement, where animals combine small-scale movements with long-distance displacements [12–15]. Our model will emulate this type of movement as follows.

Our forager has two modes of movement (Fig. 1A): it can either diffuse, by moving with equal probability to adjacent points on the lattice (Fig. 1B), or it can jump to a uniformly randomly chosen site on the lattice (Fig. 1C). In particular, we examine a hybridized approach, where the forager jumps with probability p_j, or diffuses with probability $1 - p_j$ (Fig. 1D). Providing our forager with both types of movement allows us to consider how much time the forager should spend exploiting a given location, and how frequently the forager should move to other locations. We demonstrate that the mean lifetime T of the

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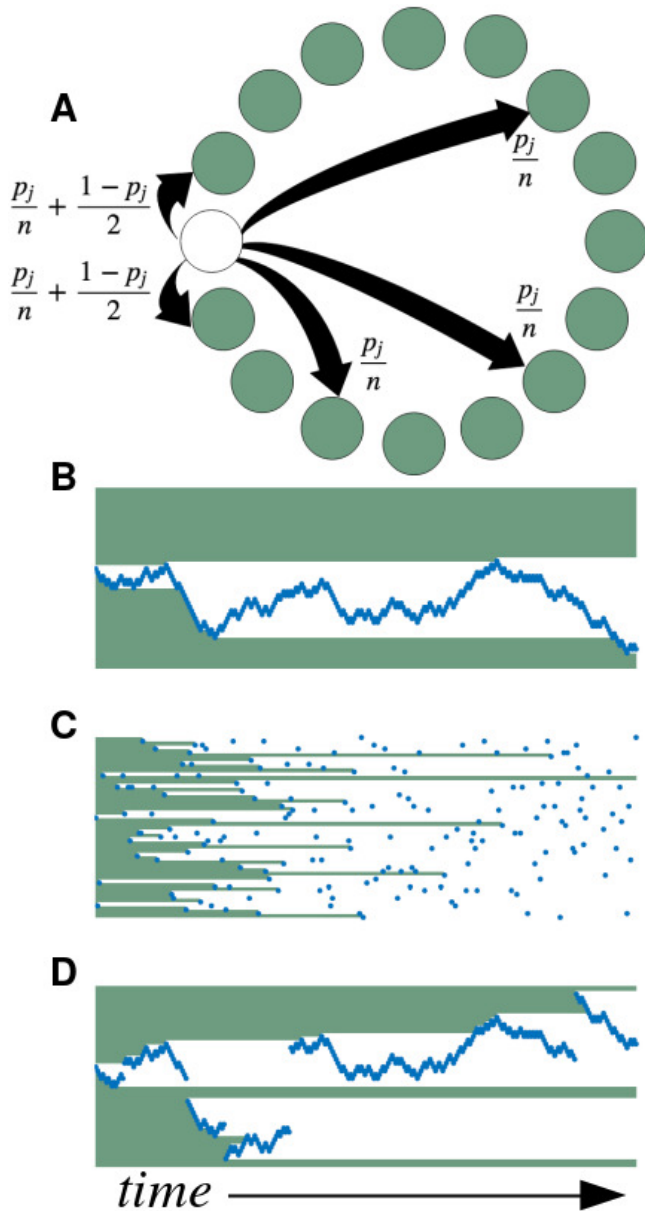* nikhil.krishnan@colorado.edu; zpkilpat@colorado.edu

FIG. 1. Jump-diffusion foraging model parametrized by p_j the probability of jumping. **A**. The forager moves to non-adjacent sites with probability $\frac{p_j}{n}$ and to adjacent sites with probability $\frac{p_j}{n}\frac{1-p_j}{2}$, accounting for the possibility of diffusion. **B**,**C**,**D**. Example forager paths (blue lines/dots) for $p_j = 0, 1, 0.03$. Green represents sites with food, while white represents empty sites.

forager varies non-monotonically with respect to p_j, and the forager's lifetime is maximized through a mixture of jumping and diffusion.

This work extends the recent studies of [7–9] by incorporating long-range motion into the dynamics of a starving forager. Those previous studies were primarily concerned with how additional considerations like greed or frugality could affect the lifetime of a starving forager that moves via local diffusion. Note that in the limit

of $p_j \to 0$ our model reduces to the basic form of those previous models.

Obtaining an explicit formula for the forager lifetime proves difficult, perhaps even intractable. Thus, we employ a number of alternative methods for gaining insight into how the mean forager lifetime T depends on model parameters. First, we study separately the two boundary cases of pure diffusion and pure jumping. In both cases, we can determine an upper bound for the forager lifetime as the sum of the cover time and survival time, and explicitly derive formulas for the forager lifetime. This reveals that a diffusive strategy is more advantageous when the survival time s is longer, whereas a jumping strategy is better for short survival times. Next, we analyze the jump-diffusion model in a very small environment (with $n = 4$ food sites) and short survival time ($s = 2$), showing mean lifetime is optimized by using a mix of jumping and diffusion. Finally, we analyze a jump-wait model, where we replace the diffusive behavior with waiting behavior where the forager remains in the same location until jumping. The qualitative performance of this model is similar to the jump-diffusion model, suggesting that foragers extend their lifetime by simply not consuming food when they have recently fed.

Our study concludes by considering several extensions of our model in which long-range jumps require more time than diffusion. In this extended model, the non-monotonicity of the forager lifetime in p_j mostly disappears. Typically, the forager does best when enacting a strategy of pure jumping in these cases. Although, when time penalties scale linearly with distance, pure diffusion becomes optimal, as most jumps result in death. In either case, a forager's lifetime can be lengthened by allowing a mixed jump-diffusion strategy whereby the forager only makes jumps that do not kill them and diffuse otherwise.

II. THE OPTIMAL JUMP RATE

To begin, we consider the full hybrid model, where the forager can both jump and diffuse. We will numerically determine the effect of p_j on the mean forager lifetime $T(n, s, p_j)$, while varying the environment size n and survival time s. Across a wide range of parameters, a mixture of jumping and diffusion ($0 < p_j < 1$) leads to higher values of T. For larger s relative to n, the value of p_j that maximizes T becomes smaller. This trend will be studied in detail by analyzing related models in subsequent sections. Numerical results are shown in Fig. 2. As shown in Fig. 2A, T is non-monotonic in p_j for different values of s, so there is an interior p_j that maximizes T. As we demonstrate in subsequent sections, a larger p_j (more jumping) causes the forager to consume food more rapidly, lowering the odds of starving between feedings, but depleting the resources more rapidly. Thus, the optimal p_j balances the tradeoff of slowing the rate of food consumption (decreasing p_j) with decreasing the probability of starving early on (increasing p_j). For lower
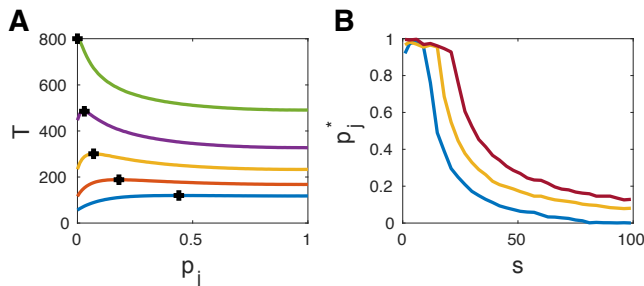
FIG. 2. **A**. Mean survival time T of a starving forager obeying jump-diffusion with jump rate p_j. Forager lifetime T varied nonmonotonically with p_j for $s = 320, 160, 80, 40, 20$ (top-to-bottom). The maximal lifetime is marked in black. Environment size $n = 40$. Means at each value of p_j are generated using 10^6 Monte Carlo simulations. **B**. The jump rate p_j that maximizes the forager lifetime primarily decreases as a function of s. Shown for $n = 400, 80, 20$ (top-to-bottom). Maxima are found using golden-section search [16] using 10^6 simulations per point.

values of s, there is a broad range of p_j values over which T is relatively unchanged. This suggests that the advantage gained by slowing the rate of food consumption is roughly counteracted by the increased probability of starvation. As the survival time s is increased, the optimal value of p_j decreases, since the forager becomes less likely to die between feedings (Fig. 2B). Utilizing diffusive motion (lower p_j) more often limits that rate at which food is consumed. On the other hand, as the size of the environment is increased (larger n), the optimal p_j increases. This is because there is more food initially available, so the forager can afford to increase the rate of food consumption to decrease their probability of starving.

Our interpretations of the mean lifetime T dependence on p_j, s, and n can be analyzed in further detail by considering a few different limiting cases and approximations of the jump-diffusion model. We begin by studying the behavior of the model at the two extremes of pure diffusion ($p_j = 0$: Fig. 1B) and pure jumping ($p_j = 1$: Fig. 1C). Our two main findings in this analysis are that (a) a diffusive forager covers the environment more slowly, decreasing the rate of food consumption as discussed above; and (b) jumping is a better strategy in large environments (large n) with lower survival times (small s). Indeed this is consistent with our numerical results above. We conclude with an analysis of two simpler models that demonstrate the same nonmonotonicity of T in p_j as shown in Fig. 2.

III.   COVER TIMES AT EXTREMES

Considering the boundary cases of pure diffusion $p_j = 0$ and pure jumping $p_j = 1$ allows us to derive explicit formulas for how model parameters, such as the environment size n and starvation time s impact the mean lifetime T of the forager. This can be approximated first

by calculating the mean cover time $\mathbb{E}(\tau_{cover})$ of the forager: the time it takes the forager to reach all of the food sites in the environment. This quantity plus the starvation time s constitutes an upper bound on the lifetime in general, but for large s it provides a reasonable approximation of

$$T(n, s, p_j) \approx s + \mathbb{E}(\tau_{cover}(n, p_j)). \tag{1}$$

This is because, when s is large, the forager generally consumes almost all of the food in the domain before dying, since it will typically have enough time between feeding to locate remaining food in the environment.

The mean cover time $\mathbb{E}(\tau_{cover})$ can be computed explicitly. If t_k denotes the time the kth piece of food is eaten, then $\tau_{cover} = t_n$, $t_1 = 0$, and by the linearity of expectation, we have:

$$\mathbb{E}(\tau_{cover}) = \sum_{k=2}^{n} \mathbb{E}(t_k - t_{k-1}). \tag{2}$$

In the case of both pure diffusion ($p_j = 0$) and pure jumping ($p_j = 1$), $\mathbb{E}(t_k - t_{k-1})$ can be explicitly calculated.

A.   Diffusion

We first consider the case where $p_j = 0$, so the forager moves only to adjacent sites. Following along the lines of [17], to calculate the cover time, we first consider the time between eating the kth piece of food and the $k-1^{\text{th}}$ piece of food. The kth piece of food here refers to the time-ordering of food consumption in a single foraging realization. Since the forager can only move to adjacent locations, after eating $k-1$ pieces of food, it must be on the boundary of a contiguous region of $k-1$ sites with no food – a desert [8]. If we label the current location of the forager as site 1, and the opposite end of the desert as site $k-1$, then the time to consume the kth piece of food is simply the hitting time of either site 0 or site k. We let f_i be the average time to hit either state 0 or state k starting at state i, as described by the recursion relation

$$f_i = \frac{1}{2}(f_{i-1} + 1) + \frac{1}{2}(f_{i+1} + 1) \tag{3}$$

with $f_0 = f_k = 0$. A detailed analysis of the time for a biased random walk to escape a finite interval is given in [18], where the lifetime of a starving greedy forager is studied. In that work, a parameter p determines the probability of moving towards a site containing food. Their results (given in Appendix B of [18]) reduce to ours for the unbiased random walk when $p = 1/2$. We can solve Eq. (3) for $f_i = i(k - i)$, and note that [19]

$$\mathbb{E}(t_k - t_{k-1}) = f_1 = k - 1, \tag{4}$$

so by plugging into Eqs. (1) and (2), we find

$$T(n, s, p_j = 0) \approx s + \frac{n(n-1)}{2}. \tag{5}$$

Note, this approximation is linear in s and quadratic in n, the size of the environment. Fig. 3A demonstrates that as s increases, Eq. (5) becomes more accurate, as the forager generally consumes almost all of the food in the environment. For this to be true, s must be nearly an order of magnitude larger than n. When s is too small, the forager will typically die before it can consume all of the food, so the cover time approximation breaks down.

B. Jumping

We next study the case in which the forager always jumps to a uniformly randomly chosen site on each timestep ($p_j = 1$). The cover time is then precisely the solution to the 'coupon collecting problem' [17]. Assume the forager has eaten $k-1$ pieces of food. There are then $n-(k-1)$ pieces of food remaining, and the time it takes to eat the kth piece of food is geometrically distributed:

$$(t_k - t_{k-1}) \sim \frac{(k-1)^{t-1}(n-k+1)}{n^t}.$$

Plugging this result into Eqs. (1) and (2) yields

$$T(n, s, p_j = 1) \approx s + n \sum_{k=1}^{n-1} \frac{1}{k}. \tag{6}$$

Fig. 3B shows the exact lifetime converges to this approximation as s is increased. Eq. (6) is again linear in s, but now scales much more slowly in n than in the case of pure diffusion. In the limit of large n, we can estimate the scaling in n as follows:

$$n \sum_{k=1}^{n-1} \frac{1}{k} \leq n \sum_{k=1}^{n} \frac{1}{k} \leq 2n \int_{1}^{n} \frac{dx}{x} = 2n \log(n).$$

In particular, if we compare the cover times of the two boundary cases, we see that $\tau_{cover}(p_j = 0) = \mathcal{O}(n^2)$ while $\tau_{cover}(p_j = 1) = \mathcal{O}(n \log(n))$. This shows that if the forager can consume almost all of the food, then for large n, it will live longer by diffusing rather than jumping. This suggests that as s increases, the optimal value of p_j goes to 0, and this is indeed the case.

IV. FORAGER LIFETIME AT EXTREMES

We now determine the exact formula for the lifetime of the forager. While the formula we derive actually applies to all values of $p_j \in [0, 1]$, we can only compute its constituent parts explicitly in the boundary cases $p_j \in \{0, 1\}$. Let X_k denote the time between eating the kth piece of food and the $k-1^{th}$ piece of food, where $X_1 = 0$, since the forager immediately consumes food at their initial position. The probability the forager, with starvation time s, consumes k pieces of food before starving thus equals

$$\mathbb{P}(k^* = k) = \mathbb{P}(X_1, ..., X_k \leq s, X_{k+1} > s), \tag{7}$$
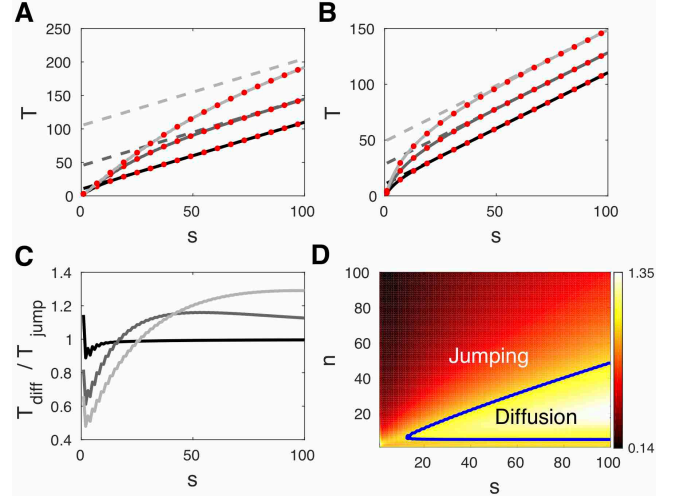

FIG. 3. **A**, **B**. Forager lifetime computed from Eq. (9) in the case of pure diffusion (**A**) and pure jumping (**B**). Cover time approximations (dashed lines) computed from Eq. (1) agree in the limit of large s: $n = 15, 10, 5$ for black, dark grey, and grey. Red dots are means computed using 10^6 numerical simulations. **C,D**. Ratio of forager lifetime for pure diffusion to forager lifetime for pure jumping: $T_{\text{diff}}/T_{\text{jump}}$. The contour on **D** marks where the ratio is one, marking the boundary between where jumping vs. diffusion is the better strategy.

so $k^* \in \{1, ..., n\}$ is a random variable arising from the stochastic movement and death of the forager. We can determine the distribution of k^* by first computing the cumulative distribution for each X_k:

$$F_k(s) = \mathbb{P}(X_k \leq s) = \sum_{j=1}^{s} \mathbb{P}(X_k = j), \quad F_{n+1}(s) = 0. \tag{8}$$

Note $F_1(s) \equiv 1$. Thus, $F_k(s)$ is the probability the forager survives long enough to consume the kth piece of food having consumed the $k-1^{th}$ piece of food. We also wish to know the probability that the forager eats exactly k pieces of food before dying. This is given by

$$\mathbb{P}(k^* = k) = \left(1 - F_{k+1}(s)\right) \prod_{j=1}^{k} \left(F_j(s)\right).$$

The forager lifetime in each case can be computed first by conditioning on consuming exactly k pieces of food, $T_k | k^* = k$, which is simply the time it takes to eat the k pieces of food, plus s steps more until starvation. The expected lifetime T is then given by marginalizing over all possible values of k^*:

$$T = \sum_{k=1}^{n} [T_k | k^* = k] \, \mathbb{P}(k^* = k) \tag{9}$$

$$= s + \sum_{k=1}^{n} \left(1 - F_{k+1}(s)\right) \prod_{j=1}^{k} F_j(s) \sum_{i=1}^{k} \mathbb{E}(X_i | X_i \leq s).$$

For the boundary cases of $p_j = 0$ and $p_j = 1$, we can derive an explicit formula for $\mathbb{P}(X_k = j)$ in Eq. (8), allowing us to explicitly calculate Eq. (9). In the limit of large s, we can approximate $F_j(s) = 1$ for all $j \leq n$ and reduce Eq. (9) to the sum of the expectations, $\mathbb{E}(X_i)$, which is the cover time upper bound given in Eq. (1).

A. Diffusion

We have a general Eq. (9) for $\mathbb{E}(T)$ that requires knowing $\mathbb{P}(X_k = j)$, the probability it takes j timesteps between consumption of the kth and $(k-1)^{th}$ pieces of food. In what follows, we demonstrate how to explicitly compute this probability mass function in the case of a diffusive forager. In the next subsection, we study the case of a forager that purely jumps.

When $p_j = 0$, the forager moves by diffusion to carve out a food desert, a simply connected region without any food. As before, we label the sites of the desert so that site 1 is where the forager begins after consuming the $(k-1)^{th}$ piece of food, and the other desert boundary is site $k-1$. Following [19, 20], we can determine the probability mass function of X_k.

Let $u_{\ell,j}$ be the probability that it takes exactly j steps to first hit site 0 from site ℓ. We then have the following recursion relation:

$$u_{\ell,j+1} = \frac{1}{2}u_{\ell-1,j} + \frac{1}{2}u_{\ell+1,j} \qquad (10)$$

$$u_{0,0} = 1, \ u_{j,0} = u_{0,j} = u_{k,j} = 0, \forall j > 0.$$

We then define the generating function

$$U_\ell(v) = \sum_{j=0}^{\infty} u_{\ell,j} v^j$$

and multiply Eq. (10) by v^{j+1}, so that by summing over j we obtain

$$U_\ell(v) = \frac{v}{2}U_{\ell-1}(v) + \frac{v}{2}U_{\ell+1}(v) \qquad (11)$$

$$U_0(v) = 1, \quad U_k(v) = 0.$$

The boundary conditions arise from the fact that the probability of hitting site 0 is $u_{0,0} = 1$ if starting there, but $u_{k,0} = 0$ if starting at the opposite food site. Considering solutions to Eq. (11) of the form $U_\ell(v) = \lambda^\ell(v)$, we obtain the characteristic equation

$$\lambda(v) = \frac{v}{2} + \frac{v}{2}\lambda^2(v).$$

This quadratic equation has two roots:

$$\lambda_\pm(v) = \frac{1 \pm \sqrt{1 - v^2}}{v}, \qquad (12)$$

assuming $0 < v < 1$. Each root is a particular solution to Eq. (11). It follows that there are some functions $A(v), B(v)$ so the general solution has the form

$$U_\ell(v) = A(v)\lambda_+^\ell(v) + B(v)\lambda_-^\ell(v). \qquad (13)$$

We can apply the boundary conditions $A(v) + B(v) = 1$ and $A(v)\lambda_+^k(v) + B(v)\lambda_-^k(v) = 0$ from Eq. (11) to determine $A(v)$ and $B(v)$. Finally, noting that by their definition, $\lambda_+(v)\lambda_-(v) = 1$, we have the explicit formula:

$$U_\ell(v) = \frac{\lambda_+^{k-\ell}(v) - \lambda_-^{k-\ell}(v)}{\lambda_+^k(v) - \lambda_-^k(v)}. \qquad (14)$$

To determine $u_{\ell,j}$, we will decompose $U_\ell(v)$ with partial fractions. To start, we make the change of variables $v = \sec\phi$. Applying this to Eq. (12) and Eq. (14), we find

$$\lambda_\pm(v) = \cos\phi \pm i\sin\phi, \quad U_\ell(v) = \frac{\sin(k-\ell)\phi}{\sin k\phi}.$$

The denominator of $U_\ell(v)$ is zero for $\phi_m = \frac{m\pi}{k}$, $m = 0,...k$, which correspond to $v_m = \sec\phi_m$. Furthermore, since the degree of the numerator exceeds the degree of the denominator by at most 1, $U_\ell(v)$ has a partial fraction decomposition with the form

$$\frac{\sin(k-\ell)\phi}{\sin k\phi} = Av + B + \frac{\rho_1}{v_1 - v} + ... + \frac{\rho_{k-1}}{v_{k-1} - v}. \qquad (15)$$

To determine the value of ρ_m, we multiply both sides by $v_m - v$, then take $v \to v_m$ (and $\phi \to \phi_m$):

$$\rho_m = \frac{\sin\frac{\ell\pi m}{k}\sin\frac{\pi m}{k}}{k\cos^2\frac{\pi m}{k}}.$$

By decomposing each fraction of Eq. (15) into a geometric series, we find that the coefficient of v^j (which is $u_{\ell,j}$) is given by

$$\sum_{m=1}^{k-1}\frac{\rho_m}{v_m^{j+1}} = \frac{1}{k}\sum_{m=1}^{k-1}\cos^{j-1}\left(\frac{\pi m}{k}\right)\sin\left(\frac{\ell\pi m}{k}\right)\sin\left(\frac{\pi m}{k}\right).$$

We are interested in two possibilities, associated with the site the forager hits next, $h_k \in \{0, k\}$. Either, the forager can start at site 1 and hit site 0 ($h_k = 0$, corresponding to $u_{1,j}$), or the forager can start at site 1 and hit site k ($h_k = k$), which by symmetry is identical to the forager starting at site $k-1$ and hitting site 0 (corresponding to $u_{k-1,j}$). The probability it takes j steps from consuming the $(k-1)^{th}$ to the kth food site is then the sum over the joint probabilities $\mathbb{P}(X_k = j, h_k)$. Thus, we have the following distribution for X_k:

$$\mathbb{P}(X_k = j) = \sum_{h_k = 0, k}\mathbb{P}(X_k = j, h_k) = u_{1,j} + u_{k-1,j}$$

$$= \frac{1}{k}\sum_{m=1}^{k-1}\cos^{j-1}\left(\frac{\pi m}{k}\right)\sin\left(\frac{\pi m}{k}\right) \qquad (16)$$

$$\times \left((1 - (-1)^m)\sin\left(\frac{\pi m}{k}\right)\right).$$

We can compute the corresponding conditional expectations and cumulative distributions in the standard way, and then use Eq. (9) to compute the expected lifetime

of the forager. For small values of s, the forager lifetime is initially super-linear in s, but that as s increases, the lifetime slowly converges to a linear function of s, as described by the cover time approximation (Fig. 3A). Furthermore, the lifetime $T(n, s, p_j = 0)$ is generally insensitive to n for small values of s. This is because the forager will rarely ever consume all the food in its environment in these cases.

B. Jumping

For $p_j = 1$, the time X_k between consuming the $(k-1)^{th}$ and k^{th} food site is geometrically distributed with success probability $[n - (k-1)]/n$. Specifically, $\mathbb{P}(X_k = j)$ is the probability of $j - 1$ visits to empty sites, each with probability $[k-1]/n$, followed by a visit to a food site, with probability $[n - (k-1)]/n$. Thus,

$$\mathbb{P}(X_k = j) = \left(\frac{k-1}{n}\right)^{j-1} \left(\frac{n-(k-1)}{n}\right).$$

We can compute the cumulative distributions and conditional expectations of a geometric random variable in the typical way, to yield the following formula for the forager lifetime from Eq. (9):

$$T(n, s, p_j = 1) = s + \sum_{k=1}^{n-1} \left(\frac{k+1}{n}\right)^s \prod_{j=1}^{k} \left(1 - \left(\frac{j}{n}\right)^s\right)$$
$$\times \sum_{i=1}^{k} \left[\frac{n}{n-i} + s + \frac{s}{(i/n)^s - 1}\right].$$

From Fig. 3B we again see that for small values of s the forager lifetime $T(n, s, p_j = 1)$ is initially super-linear in s and insensitive to n, but limits to the cover time approximation as s increases.

To compare the two strategies (pure diffusion vs. pure jumping), we compute the ratio $T_{\text{diff}}/T_{\text{jump}}$ of the forager lifetime for $p_j = 0$ to the forager lifetime for $p_j = 1$. For sufficiently large s, diffusion leads to longer lifetimes than jumping (Fig. 3C). This is because the diffusive forager will cover the environment more slowly than the jumping forager, so they will not consume food as quickly. Note, the ratio drops as we change $s = 1$ to $s = 2$, since in the case of pure diffusion (and $s = 1$) the forager will live at least two timesteps, whereas the pure jumper may not. As soon as $s = 2$, this effect becomes negligible. Furthermore, this drop in the ratio becomes less severe for larger values of n, since the jumper will almost always live at least two timesteps. In Fig. 3D, we display the ratio as a surface plot along both the s and n axis. Increasing s clearly expands the region (outlined) of n values, for which diffusion is a better strategy. Note that for very small values of n ($n \leq 5$) the cover time for diffusion is less than the cover time for jumping, leading to an advantage of jumping over diffusion at those parameter values.

When s is large relative to n, the diffusive forager benefits from a larger cover time, so for these small values of n, it is consistently more beneficial to jump rather than diffuse. On the other hand, when s is small compared to n, it is better to jump since this will decrease the likelihood of starving before much of the environment's food has been consumed.

This concludes our analysis in the case of pure diffusion ($p_j = 0$) or pure jumping ($p_j = 1$). We now turn to two simpler instantiations of the jump-diffusion model of the starving forager: one that considers a very small environment ($n = 4$) and another that considers replacing diffusion with waiting. Both of these models exhibit the same nonmonotonicity of the lifetime T with respect to p_j, and admit some explicit analysis.

V. TRACTABLE MODELS AND APPROXIMATIONS OF JUMP-DIFFUSION

Given our insights from the extreme cases $p_j \in \{0, 1\}$, we now consider the full hybrid model, where the forager can both jump and diffuse. We have seen that when s is large is relative to n, it is more advantageous to diffuse rather than jump. To obtain explicit expressions of this result, we will consider two simplifications. First, for a sufficiently small system (small n and s), the forager lifetime can be explicitly determined either by combinatorial methods or by analyzing the probability transition matrix for the system. Secondly, we will consider a model that replaces diffusion with waiting. This altered model still yields qualitatively similar results to the jump-diffusion model, lending credence to our theory that diffusion acts as a way to prevent premature resource depletion. Both of these models demonstrate that it is most beneficial for the forager to use a mixture of jumping and diffusing (or waiting), specifically that $T(n, s, p_j)$ has an interior maximum on $p_j \in [0, 1]$. Furthermore, in the case of the jump-wait model, we will see that the larger s is relative to n, the smaller the optimal value of p_j becomes, consistent with our results for the jump-diffusion model.

A. Small System

For a system of small enough size, the lifetime of the forager can be analytically determined, either by enumerating all possible outcomes or by analyzing an associated discrete-time Markov chain. Here, we consider a lattice with $n = 4$ sites, and a starvation time of $s = 2$. The combination of food and forager states can be described as a thirteen state Markov chain (Fig. 4A). State 1 corresponds to timestep 1, in which the starting site's food has been eaten. State 13 corresponds to the cemetery state, in which the forager has starved. Most of the remaining intermediate states are identical to at least one other state, when considering rotations, so there are only six el-
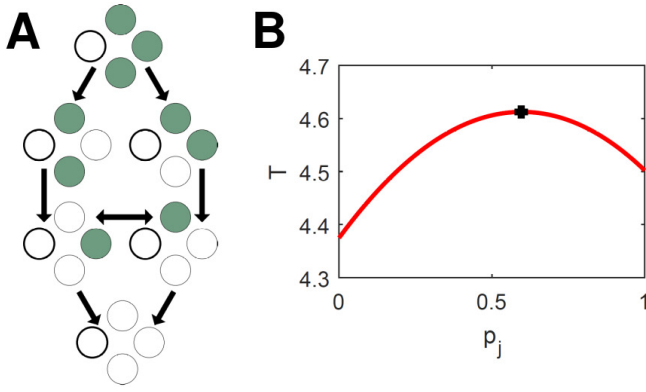
FIG. 4. Jump-diffusion model of foraging for small environment size and survival time ($n = 4$, $s = 2$). **A.** Enumeration of food/forager geometries for $n = 4$ and $s = 2$ system. The forager is always in the left (bold) site after a rotation of the system. The arrows denote admissible transitions between geometries. Note that since $s = 2$, every geometry can return to itself once. **B.** Expected forager lifetime T computed explicitly as a function of p_j, Eq. (17), has an interior maximum (black dot).

ementary "live" states plus the cemetery state. Note that the forager can transition from most state geometries to death, by landing on a site without food more than $s = 2$ times in a row. The nonzero entries of the associated transition matrix Q corresponding to the probabilities to transition from state i to j are given in Appendix A.

To calculate the forager lifetime, we compute the mean absorption time into the thirteenth state (the cemetery state) as a passage time problem for Markov chains [21]. Let us denote by v be the vector of all zeroes save the first entry which is one. Let $\mathbf{1}$ be a vector of all ones. Finally, let $\tilde{Q}$ be the sub-matrix of the preceding probability transition matrix excluding the cemetery state. The expected forager lifetime is then given by

$$T(4, 2, p_j) = \mathbf{1}^T (I - \tilde{Q}^T)^{-1} v.$$

We can also determine the expected forager lifetime $T(4, 2, p_j)$ by enumerating outcomes directly (see Appendix B), yielding the following polynomial:

$$T(4, 2, p_j) = -\frac{3}{512}p_j^6 - \frac{3}{256}p_j^5 + \frac{15}{256}p_j^4 \tag{17}$$

$$-\frac{11}{128}p_j^3 - \frac{39}{64}p_j^2 + \frac{25}{32}p_j + \frac{35}{8}, \tag{18}$$

which can be maximized numerically (Fig. 4B). With either method of computation, the maximal forager lifetime is $T^{\max} \approx 4.612$ at $p_j \approx 0.598$, demonstrating it is optimal for the forager to both jump and diffuse in this simple case. Examining Fig. 4A, we expect that the forager lifetime is lengthened by allowing the system to dwell in the intermediate states preceding the bottom cemetery state. This is the same intuition as in the large system: the optimal forager balances a reduction in their probability of starving before eating all the food with a reduction in the rate at which food is consumed.
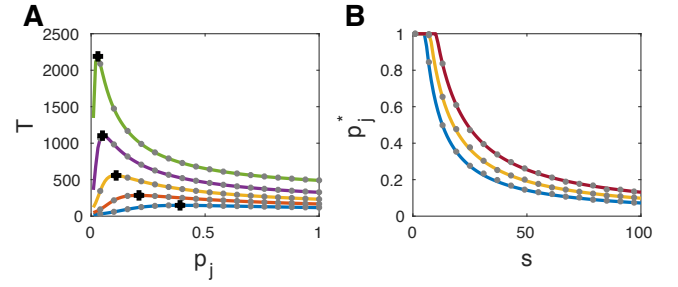

FIG. 5. Jump-wait model of foraging. **A** Forager lifetime as a function of p_j. The maximal lifetime is marked in black: $n = 40$ and $s = 320, 160, 80, 40, 20$ top-to-bottom as in Fig. 2A. Means computed using 10^6 numerical simulations per point are given by grey dots. **B** The value of p_j that maximizes the forager lifetime as a function of s: $n = 400, 80, 20$ top-to-bottom as in Fig. 2B. Maxima computed using golden-section search [16] using 10^6 simulations per point are given by grey dots.

B. A Jump-Wait Model

We now consider a modification of our jump-diffusion model which admits explicit analysis as a function of the jumping probability p_j. In this case, the forager remains at the same site (rather than diffusing) with probability $1 - p_j$. This mimics diffusion in food 'deserts,' which will generally arise in large domains when p_j is not too large. The forager can thus only consume food and reset their starvation clock by jumping. As we saw in our discussion of cover times, a diffusing forager covers the domain more slowly than a jumping forager. Waiting, just like diffusing, acts to slow the rate at which the forager consumes the food, providing qualitatively similar non-monotonic lifetimes in p_j (Fig. 5A).

In this case, we can obtain an analytic expression for the forager lifetime, by noting that the inter-feeding times X_k are geometrically distributed with success probability $p_j \frac{n - (k-1)}{n}$. This can be derived by noting that the probability that the forager lands on a piece of food is the probability that the forager jumps at all, p_j, multiplied by the probability that the forager lands on a site with food, $\frac{n - (k-1)}{n}$. The probability that $X_k = j$ is thus the probability of $j - 1$ visits to empty sites multiplied by the probability of a visit to a site with food:

$$\mathbb{P}(X_k = j) = \left(1 - p_j \frac{n - (k-1)}{n}\right)^{j-1} \left(p_j \frac{n - (k-1)}{n}\right).$$

The conditional expectation and cumulative distributions for a geometric random variable can be computed in the standard way, giving the forager lifetime from Eq. (9):

$$\mathbb{E}(T) = s + \sum_{k=1}^{n-1} \left[\left(\frac{p_j(k - n + 1) + n}{n} \right)^s \right. \tag{19}$$

$$\left. \prod_{\ell=1}^{k} \left(1 - \left(\frac{p_j(\ell - n) + n}{n} \right)^s \right) \right)$$

$$\sum_{i=1}^{k} \left[s + \frac{n}{(n-i)p_j} + \frac{s}{\left(\frac{p_j(i-n)+n}{n} \right)^s - 1} \right] \Bigg]$$

Taking a large s limit of this expression, we obtain:

$$\mathbb{E}(T) \approx s + \frac{n}{p_j} \sum_{k=1}^{n-1} \frac{1}{k}, \qquad (20)$$

which is exactly the approximation Eq. (1) for the mean cover time plus the starvation time s. The cover time is equal to that from the case of pure jumping, Eq. (5), scaled by $\frac{1}{p_j}$. This demonstrates that for sufficiently large s, the smaller the value of p_j, the longer the expected forager lifetime.

By examining Fig. 5A, we see that the jump-wait model shares important characteristics with the jump-diffusion model. The forager lifetime is non-monotonic in p_j and the optimal value of p_j decreases as s increases. Additionally, the optimal p_j decreases as a function of s, but increases as a function of n (Fig. 5B). Similar to the optimal p_j curves for the jump-diffusion model, the curves have sections of relatively rapid change for intermediate values of s. Thus, our findings for the jump-wait model again suggest that a starving forager can maximize their lifetime by balancing a decrease in the rate of food consumption (by lowering p_j) with an increase probability of surviving until most of the food is consumed (by increasing p_j).

VI.   JUMP-PENALTY MODELS

Up to this point, we have considered a model in which jumps and diffusive movements both take a single timestep. However, foragers exploring distant food patches typically require more time for these excursions [22]. Thus, we consider the effects of introducing a cost function associated with the jumps. Specifically, we consider two different cost functions: (i) a constant penalty, where each jump takes c timesteps, and (ii) a distance-based penalty function where each jump takes $c \cdot d$ timesteps for a distance d. During the jump, the forager cannot consume any food, and in the simplest version of this extended model, it may starve mid-jump if the jump cost is large enough. Thus, we also consider a model in which the forager only makes jumps if it will not starve mid-jump. In certain cases, models in which jumps are penalized have longer survival times, due to the inclusion of large epochs in which the agent is traveling and not exhausting the finite food supply.

A.   Constant Penalty

We begin by considering a constant penalty function. Any time the forager jumps, it takes $c \in \mathbb{N}$ timesteps to do so. This provides a benefit to the forager by limiting
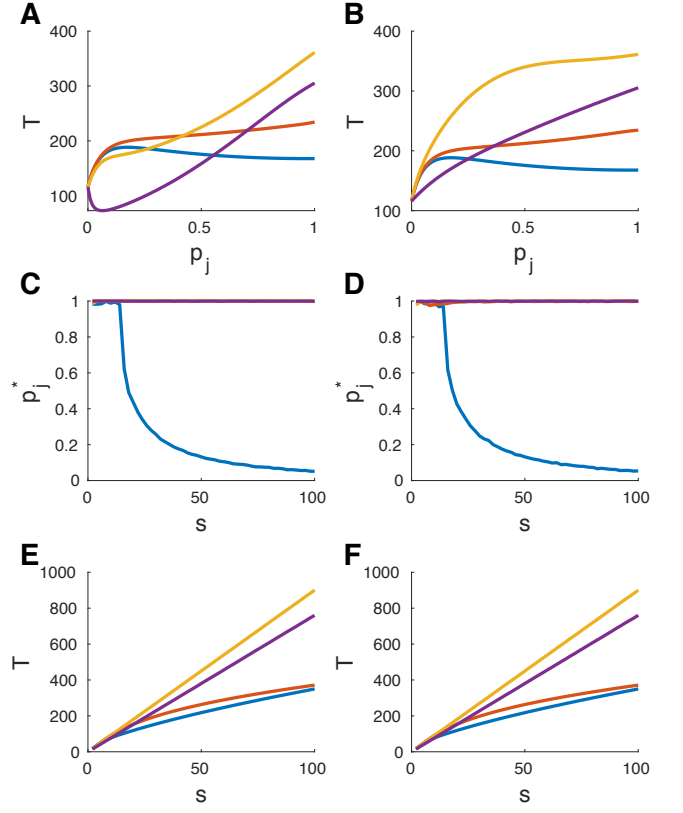

FIG. 6.   Jump-diffusion model of foraging with constant penalty c where the forager can (**A**,**C**,**E**) and cannot (**B**,**D**,**F**) starve during a jump. **A**,**B**. The expected lifetime of a forager as a function of p_j with $s = 40$. Means are computed with 10^6 numerical simulations per point. **C**,**D**. The optimal value of p_j as a function of s. Maxima are computed using golden-section search [16] with 10^7 simulations per point. **E**,**F**. The expected lifetime of a forager moving with the optimal p_j. Means are computed using 10^6 numerical simulations per point. $n = 40$ and blue, red, yellow, and purple correspond to $c(s) = 1, 2, s/2$, and s.

premature resource depletion, but every jump the forager makes brings it much closer to starvation. Despite these additional risks, it is more beneficial for the forager to jump than to diffuse for $c > 1$ (Fig. 6A,C). Thus, the added risk incurred by decreasing the number of jumps needed to starve the forager is outweighed by the slowing of food depletion. However, a larger c does not necessarily correspond to a greater lifetime. The forager lives longer with $c = \frac{s}{2}$ than for $c = s$ (Fig. 6E). This is because for $c = s$, any time the forager makes a jump to an empty site, it is guaranteed to starve, whereas with $c = \frac{s}{2}$, if the forager lands on an empty site, it can jump once more, substantially reducing its odds of starving.

In the case of pure jumping ($p_j = 1$) we can calculate an explicit formula for the forager's lifetime as long as c evenly divides s, following along similar lines to Section IV. Let $s = c \cdot q$, for $c, q \in \mathbb{N}$. Let us define the geometric

random variable X_k so that

$$\mathbb{P}(X_k = j) = \left(\frac{k-1}{n}\right)^{j-1}\left(\frac{n-(k-1)}{n}\right). \quad (21)$$

The equation for the lifetime is fairly similar to Eq. (9) with some modifications. Now, interfeeding times are given by $c \cdot X_k$ rather than X_k. Thus, the cumulative distribution of interfeeding times is computed by summing over Eq. (21):

$$F_k(s) = \mathbb{P}(c \cdot X_k \leq s) = \sum_{j=1}^{q}\mathbb{P}(X_k = j),$$

$$F_{n+1}(s) = 0, \quad (22)$$

where $q = s/c \in \mathbb{N}$ as assumed. It follows that if $F_k(s)$ is the probability the forager survives long enough to consume the kth piece of food after consuming the $(k-1)^{th}$ piece of food, then the probability the forager eats exactly k pieces of food is

$$\mathbb{P}(k^* = k) = \left(1 - F_{k+1}(s)\right)\prod_{j=1}^{k}\left(F_j(s)\right). \quad (23)$$

Finally, we calculate the conditional expectation, noting that $\mathbb{E}(c \cdot X_k | c \cdot X_k \leq s) = c \cdot \mathbb{E}(X_k | X_k \leq q)$. Replacing terms in Eq. (9) as such, and calculating the terms explicitly, using Eq. (21-23), we have the following result:

$$T(n, s, p_j = 1, c) = s + c \sum_{k=1}^{n-1}\left(\frac{k+1}{n}\right)^q \prod_{j=1}^{k}\left(1 - \left(\frac{j}{n}\right)^q\right)$$

$$\times \sum_{i=1}^{k}\left[\frac{n}{n-i} + q + \frac{q}{(i/n)^q - 1}\right].$$

Indeed, the theoretical curves generated from $T(n, s, p_j = 1, c)$ match precisely with the results from numerical simulations in Fig. 6E when $p_j = 1$.

We can also consider an alteration to this model where the forager will not jump if it can die mid-jump. If the forager has $s_{current}$ steps left until starvation, then if $s_{current} < c$, the forager will strictly diffuse until it finds another piece of food or starves. If $s_{current} \geq c$, the forager will jump with probability p_j and diffuse with probability $1 - p_j$, exactly as before. This addition does not affect the optimal value of p_j (Fig. 6B,D,F). For $c = 1$, the inability to die does not matter, since as long as the forager is alive, $s_{current} > 1 = c$. Furthermore, for $c > 1$, the addition of not being able to take a fatal jump does not make jumping any less favorable, so the optimal p_j continues to be 1.

B. Distance-Based Penalty

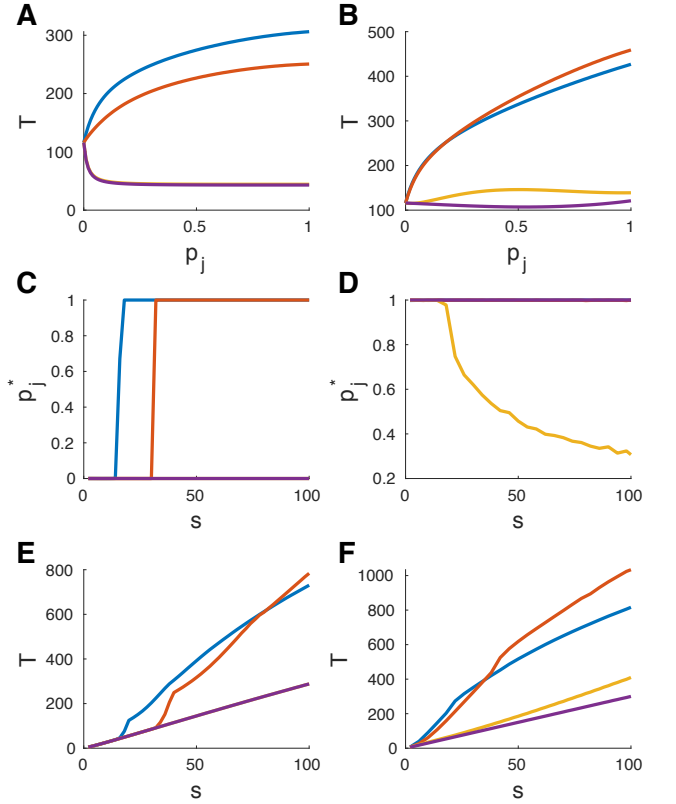We now consider a penalty function for the jump that depends on the distance traveled d. If we enumerate

FIG. 7. Jump-diffusion model of foraging with distance based penalty $c \cdot d$ where the forager can (**A**,**C**,**E**) and cannot (**B**,**D**,**F**) starve during a jump. **A**,**B**. The expected lifetime of a forager as a function of p_j with $s = 40$. Means are computed with 10^6 numerical simulations per point. **C**,**D**. The optimal value of p_j as a function of s. Maxima are computed using golden-section search [16] with 10^7 simulations per point. **E**,**F**. The expected lifetime of a forager moving with the optimal p_j. Means are computed using 10^6 numerical simulations per point. $n = 40$ and blue, red, yellow, and purple correspond to $c(s) = 1, 2, s/2,$ and s.

our sites on the periodic lattice so that site i is adjacent to sites $i \pm 1$, for $i = 2, ...n$ and so site 1 and site n are adjacent, then the distance between sites x and y are $d(x, y) = \min(|x - y|, n - |x - y|)$. The number of timesteps for a jump from site x to site y is then given by $c \cdot d(x, y)$. Note that for c large enough, the average lifetime is a monotone decreasing function of the jump probability (Fig. 7A). From Fig. 7C, we see that for small values of s, it is better to solely diffuse, regardless of c. If s is small compared to the average jump penalty ($\approx c \cdot n/4$), the forager will likely starve mid-jump, possibly even on the first jump. However, for s sufficiently large compared to the average jump penalty, the benefits of slower food consumption become apparent. As in the case of constant jump penalties, the perils of dying mid-jump are outweighed by the slowed rate of food depletion. At this point the optimal strategy flips, and it is optimal to purely jump, which results in more rapid growth of the optimal survival time T as a function of s

(Fig. 7E). However, this never occurs for $c = \frac{s}{2}, s$, since the forager has a very small probability of surviving a jump, so it is always better to diffuse.

We can calculate the lifetime of the forager in the case where $p_j = 1$ and $c = s$ explicitly. When $c = s$, the forager can only survive jumps if it jumps to an adjacent site that still contains food. Since it takes zero time to jump to the site it is currently at, the forager essentially has $n - 1$ choices each time it needs to jump. For the first jump, it can survive if it jumps to either of the two adjacent sites, with probability $\frac{2}{n-1}$. If it jumps to any other site with probability $\frac{n-3}{n-1}$, it will starve mid-jump in s timesteps. For the forager to survive $s \cdot k$ steps for $1 < k < n$, it must survive the first jump with probability $\frac{2}{n-1}$ (by jumping to the either of the two adjacent sites), it must survive $k - 2$ jumps with probability $\frac{1}{n-1}$ (by jumping to the one adjacent site with food), and then it must starve with probability $\frac{n-2}{n-1}$ (jumping to any site other than the adjacent site with food). The forager will live $s \cdot n$ steps if it survives the first jump with probability $\frac{2}{n-1}$, and it survives $n - 1$ jumps each with probability $\frac{1}{n-1}$. The expected lifetime is

$$T(n, s, p_j = 1, c = s) = s\frac{n-3}{n-1}$$
$$+ 2s(n-2)\sum_{k=2}^{n-1} k\left(\frac{1}{n-1}\right)^k + \frac{2sn}{(n-1)^n}.$$

It is clear from Fig. 7C that it is always better to diffuse for such large values of the penalty scaling c.

We can also consider a modification to the model where the forager will only execute a jump if it does not starve mid-jump. In models discussed prior to this one, the forager jumps by selecting a uniformly randomly distributed site on the full domain to jump to (Fig. 1A). In the modified model we consider now, a jumping forager restricts the space of possible next site locations to the set $V = \{y : c \cdot d(x,y) \leq s_{current}\}$, where $d(x,y)$ is the distance between the current x and next possible y site. This restriction prevents the forager from dying mid-jump. If $V = \{x\}$, then the forager will only diffuse until it consumes another piece of food, or it starves. The inability to die mid-jump substantially alters optimal strategy (Fig. 7B,D). For small values of s, it is now optimal to strictly jump for $c = 1, 2$, since the forager cannot make a jump that it will not survive. Thus, jumping outperforms diffusion for even smaller s. Even more altered is the optimal strategy for $c = s$. The forager is only permitted to move to neighboring sites, which will typically have a probability $1/2$ of containing food, as a desert is carved out in the forager's wake. Now that the forager survives a jump with probability no less than $\frac{1}{2}$ instead of $\frac{1}{n-1}$, it is always optimal to jump. Finally, for $c = \frac{s}{2}$, the optimal values of p_j look qualitatively similar to the optimal values of p_j in the original model (Fig. 2B). Lifetimes are longer when c is relatively small as compared to s (Fig. 7F). However, once s becomes large

enough that the forager can comfortably reach the entire domain, the optimal strategy for $c = 2$ leads to longer lifetimes than $c = 1$.

We can again calculate the forager lifetime in the case of pure jumping with $c = s$. The forager is guaranteed to survive at least the first jump. Every subsequent jump is survived with probability $\frac{1}{2}$ if it jumps to the adjacent site with food. Otherwise, it will starve upon reaching the empty adjacent site. Thus, the proability that the forager lives $c \cdot k$ timesteps is $\frac{1}{2^{k-1}}$ for $1 < k < n - 1$. To survive $s \cdot n$ steps, the forager needs to survive the first jump with probability 1, and $n - 2$ subsequent jumps each with probability $\frac{1}{2}$. The expected forager lifetime is

$$T(n, s, p_j = 1, c = s) = s\sum_{k=2}^{n-1} \frac{k}{2^{k-1}} + \frac{sn}{2^{n-2}} = s(3 - 2^{2-n}),$$

which matches the points generated from numerical simulations in Fig. 7F.

VII. DISCUSSION

We have extended the recently-developed starving forager model [7] to account for the possibility of long-range motion via jumping. The combination of these two modes of movement is related to Lévy-type motion often found in the dynamics of motile organisms' foraging strategies [12]. By analyzing cover times, we have shown that jumping consumes food more rapidly than diffusion. This provides an explanation for why a mixture of jumping and diffusion is optimal: excessive jumping leads to rapid food depletion, excessive diffusion leads to earlier starvation of the forager who gets stuck in food 'deserts.' In a sense, the forager optimally balances exploration (via jumping) and exploitation (via diffusion) when using a mixture of these modes of movement. This explanation is further validated by the qualitative similarities of the jump-diffusion and jump-wait models. In either model: Making s larger or n smaller lead to situations in which the forager maximizes their lifetime by diffusing more, while the converse corresponds to more jumping being optimal.

The non-monotonicity of the forager's lifetime in p_j breaks down when considering a model with time-penalized jumping. For constant time penalties, foragers obtain the longest lifetime by practicing pure jumping. The advantage formerly gained by diffusing, the slowing of food consumption, is now accomplished via the time penalties: No food is consumed while the forager is in the midst of a jump. When jumps are penalized as a function of their distance, pure diffusion becomes optimal, as most jumps will result in sudden death. However, if foragers enact a strategy of not jumping if it causes them to die, the best strategy is then for foragers to make long-distance jumps unless they will die mid-jump, in which case they diffuse. This more sophisticated strategy recovers an exploration/exploitation tradeoff that depends

on the the forager's nearness to starvation.

Our model of a starving forager with a mixture of movement modes suggests several other possible extensions. Throughout this work, jumping has represented movement with equal probability to any lattice site. However, a forager executing a jump may more often select a site that is further away, to avoid revisiting empty sites. They may also be less likely to make extremely large jumps. This would suggest a model where the jump process is associated with a nonuniform distribution of jump distances. Our extension to a model that considers distance-penalized jumping has partially incorporated such a strategy by only allowing jumps below a certain distance, when the forager wishes to avoid starvation. However, we could also consider strategies whereby the forager only takes jumps above a certain size, to try and promote movement out of food deserts.

Our work has also only considered a periodic one-dimensional lattice environment. The behavior of the forager in higher dimensions is still open, and it would be interesting to see how the forager lifetime depends on domain size and geometry in higher dimensions (e.g., plane, torus, or sphere). Another relevant extension would be for the forager to retain some information about its previous actions. For example, p_j could increase, as the number of steps without food increases. This would provide a strategy in which the forager only executes long range movement if they are starving, which will probably limit the rate at which food is consumed and increase the overall lifetime T. Our model could also incorporate greed (or anti-greed) as a parameter [8]. As shown in previous work, the lifetime of foragers increases in one-dimensional environments if their diffusion is biased away from food. This finding mirrors our own conclusion, that foragers maximize their lifetime by balancing a reduction in the probability of early starvation with the conservation of resources.

Appendix A: Transition matrix for small system

We define the states of the small system with $n = 4$ sites and survival time $s = 2$ according to the relative location of the forager and the arrangement of food sites remaining. This numbers thirteen distinct states, with a transition matrix Q for the update of the state vector $S_{t+1} = Q^T S_t$ where $Q_{1,2} = Q_{1,3} = Q_{2,3} = Q_{2,13} = Q_{9,10} = Q_{9,11} = Q_{10,11} = \frac{p_j}{4}$, $Q_{1,5} = Q_{2,5} = Q_{9,8} = \frac{2-p_j}{2}$, $Q_{3,4} = Q_{4,13} = Q_{7,8} = \frac{p_j}{2}$, $Q_{3,9} = Q_{4,9} = Q_{7,10} = Q_{7,11} = Q_{8,11} = \frac{2-p_j}{4}$, $Q_{5,6} = Q_{5,7} = Q_{6,7} = Q_{6,13} = \frac{1}{2}$, $Q_{8,13} = \frac{2+p_j}{4}$, $Q_{10,13} = \frac{4-p_j}{4}$, $Q_{11,12} = Q_{12,13} = Q_{13,13} = 1$. Note that the thirteenth state is the absorbing cemetery state.

Appendix B: Calculating $T(4, 2, p_j)$

With a four site geometry, the forager has two types of movement. It can either move to the opposite site or remain at the current site both with probability $p_+ = \frac{p_j}{4}$ or it can move to a specific adjacent site with probability $p_- = \frac{2-p_j}{4}$. For brevity, we denote $\mathbb{P}(T(4, 2, p_j) = i)$ as p_i, and enumerate all possible paths

$$p_2 = p_+^2, \qquad p_3 = \frac{p_-}{2} + 4p_+^3$$
$$p_4 = p_+ p_3 + 2(p_-^2 + p_- p_+)(2p_-^2 + 3p_- p_+ + 4p_+^2) + 2(p_+ p_-)(2p_-^2 + 6p_- p_+ + p_+^2)$$
$$p_5 = p_+(2(p_-^2 + p_- p_+)(2p_-^2 + 3p_- p_+ + 4p_+^2) + 2(p_+ p_-)(2p_-^2 + 6p_- p_+ + p_+^2)) + 2(p_-^3 + p_-^2 p_+ + p_- p_+^2) + (1/2)p_-(2p_-^2 + 3p_- p_+ + 4p_+^2) + 4p_- p_+^2(2p_-^2 + 6p_- p_+ + p_+^2)$$
$$p_6 = 2(p_-^2 + p_- p_+)(3p_- p_+) + 2p_- p_+(2p_-^2 + p_+^2) + p_+ 2(p_-^3 + p_-^2 p_+ + p_- p_+^2) + p_-(p_-^2 + p_+ p_-) + 4p_+^3 p_- + p_+((1/2)p_-(2p_-^2 + 3p_- p_+ + 4p_+^2) + 4p_- p_+^2(2p_-^2 + 6p_- p_+ + p_+^2))$$
$$p_7 = (3/2)p_-^2 p_+ + 4p_+^2 p_-(2p_-^2 + p_+^2) + p_+(2(p_-^2 + p_- p_+)(3p_- p_+) + 2p_- p_+(2p_-^2 + p_+^2)) + p_+(p_-(p_-^2 + p_+ p_-) + 4p_+^3 p_-)$$
$$p_8 = p_+((3/2)p_-^2 p_+ + 4p_+^2 p_-(2p_-^2 + p_+^2))$$

We have $\mathbb{E}(T(4, 2, p_j)) = \sum_{i=2}^{8} i p_i$ which yields Eq. (17).

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