Search in patchy media: Exploitation-exploration tradeoff

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How to best exploit patchy resources? We introduce a minimal exploitation-migration model that incorporates the coupling between a searcher's trajectory, modeled by a random walk, and ensuing depletion of the environment by the searcher's consumption of resources. The searcher also migrates to a new patch when it takes $\mathcal{S}$ consecutive steps without finding resources. We compute the distribution of consumed resources F_t at time t for this non-Markovian searcher and show that consumption is maximized by exploring multiple patches. In one dimension, we derive the optimal strategy to maximize F_t. This strategy is robust with respect to the distribution of resources within patches and the criterion for leaving the current patch. We also show that F_t has an optimum in the ecologically relevant case of two-dimensional patchy environments.

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I. INTRODUCTION

Optimizing the exploitation of patchy resources is a long-standing dilemma in a variety of search problems, including robotic exploration [1], human decision processes [2], and especially in animal foraging [3–6]. In foraging, continuous patch use [6,7] and random search [5,8] represent two paradigmatic exploitation mechanisms. In the former [Fig. 1(a)], a forager consumes resources within a patch until a specified depletion level, and concomitant decrease in resource intake rate, is reached before the forager moves to another virgin patch. In his pioneering work [6], Charnov predicted the optimal strategy to maximize resource consumption. This approach specifies how fitness-maximizing foragers should use environmental information to determine how completely a food patch should be exploited before moving to new foraging territory.

The nature of foraging in an environment with resources that are distributed in patches has been the focus of considerable research in the ecology literature (see, e.g., Refs. [6,9–20]); theoretical developments are relatively mature and many empirical verifications of the theory have been found. However, continuous patch-use models typically do not account for the motion of the searcher within a patch, and the food intake rate within a patch is given *a priori* [9,20,21], so that depletion is deterministic and spatially homogeneous.

Random search represents a complementary perspective in which the searcher typically moves by a simple or a generalized random walk. The search efficiency is quantified by the time to reach targets [Fig. 1(b)]. Various algorithms, including Lévy strategies [22], intermittent strategies [23–26], and persistent random walks [27], have been shown to minimize this search time under general conditions. However, these models do not consider depletion of the targets.

Issues that have been addressed to some extent in the above scenarios include the overall influence of resource patchiness (but see Refs. [11,13,18,19,28,29] for relevant work), as well as the coupling between searcher motion within patches and resource depletion; the latter is discussed in a different context than that given here in Ref. [30]. In this work, we introduce a minimal exploitation-migration model that accounts for the interplay between mobility and depletion from which we are able to explicitly derive the amount of consumed food F_t up to time t, determine the optimal search strategy, and test its robustness.

II. EXPLOITATION-MIGRATION MODEL

Each patch is modeled as an infinite lattice, with each site initially containing one unit of resource, or food. A searcher undergoes a discrete-time random walk within a patch and food at a site is completely consumed whenever the site is first visited. The searcher thus sporadically but methodically depletes the resource landscape.

Resources within a patch become scarcer and eventually it becomes advantageous for the searcher to move to a new virgin patch. We implement the scarcity criterion that the searcher leaves its current patch upon wandering for a time $\mathcal{S}$ without encountering food. Throughout this work, all times are rescaled by the (fixed) duration of a random-walk step. Thus $\mathcal{S}$ also represents the number of random-walk steps that the walker can take without finding food. This notion of a specified give-up time has been validated by many ecological observations [20,21,31,32]. The searcher therefore spends a random time T_i and consumes f_i food units in patch i, before leaving [Fig. 1(d)]. We assume, for simplicity, a deterministic migration time Z to go from one patch to the next. We define t_i as the time when the searcher arrives at patch $i+1$ and $\tau_i = t_i - t_{i-1}$ as the time interval between successive patch visits. The duration of phase i, which starts at t_{i-1} and consists of exploitation in patch i and migration to patch $i+1$, is $\tau_i \equiv T_i + Z$.

Our model belongs to a class of composite search strategies that incorporate (i) intensive search (patch exploitation) and (ii) fast displacement (migration) [33–35]; here we extend these approaches to account for resource depletion. In addition to

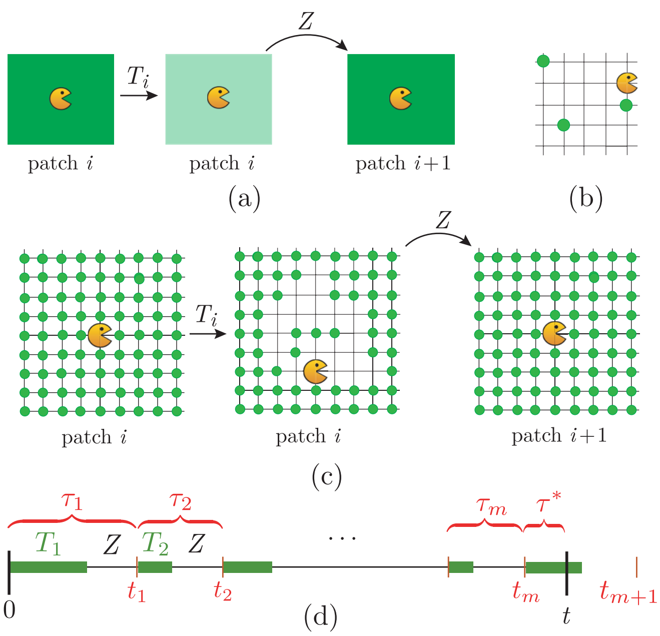

FIG. 1. (a) Continuous patch use: a searcher uniformly depletes patch i at a fixed rate for a deterministic time T and moves to a patch $i+1$ when patch i is sufficiently depleted. (b) Random search: a searcher seeks one or a few fixed targets (circles) via a random walk. (c) Our model: a searcher depletes resources within a patch for a random time T_i. (d) Model time history. Phase i, of duration τ_i, is composed of patch exploitation (duration T_i, shadowed) and migration (duration Z). The last phase is interrupted at time t, either during exploitation (shown here) or migration, and lasts τ^*.

its ecological relevance, this exploit-explore duality underlies a wide range of phenomena, such as portfolio optimization in finance [36], knowledge management and transfer [37], research and development strategies [2], and also everyday life decision making [38].

We quantify the exploitation efficiency by the amount of consumed food F_t up to time t. Note that F_t is also the number of distinct sites that the searcher visits by time t, which is known for Markovian random walks [39,40]. In our model, we need to track all previously visited sites in the current patch to implement the scarcity criterion, which renders the dynamics non-Markovian.

We will show that F_t admits a nontrivial optimization in spatial dimensions $d \leqslant 2$. If a random-walk searcher remains in a single patch forever (exploitation controlled; equivalently, $\mathcal{S} \to \infty$), then F_t, which coincides with the number of distinct sites visited in the patch, grows sublinearly in time, as $\sqrt{t}$ in $d = 1$ and as $t/\ln t$ in $d = 2$ [39]. On the other hand, if the searcher leaves a patch as soon as it fails to find food (migration controlled, $\mathcal{S} = 1$), F_t clearly grows linearly in time, albeit with a small amplitude that scales as $1/Z$. Thus F_t must be optimized at some intermediate value of $\mathcal{S}$, leading to substantial exploitation of the current patch before migration occurs.

III. AMOUNT OF FOOD CONSUMED

A. Formalism

To compute the amount of food consumed, let m be the (random) number of phases completed by time t, while the $(m+1)$th phase is interrupted at time t. Then F_t can be written as

$$F_t = f_1 + \cdots + f_m + f^*, \tag{1a}$$

where f^* denotes the food consumed in this last incomplete phase. Similarly, the phase durations $\{\tau_i\}$ satisfy the sum rule [Fig. 1(d)]

$$t = \tau_1 + \cdots + \tau_m + \tau^*, \tag{1b}$$

where again τ^* denotes the duration of the last phase. Since the food consumed and the duration of the ith phase, f_i and τ_i respectively, are correlated, the sum rule (1b) couples the f_i's and the number m of patches visited. The distinct variables f_i and τ_i are correlated and pairwise identically distributed, except for the last pair (f^*,τ^*) for the incomplete phase. We will ignore this last pair in evaluating F_t, an approximation that is increasingly accurate for large $\mathcal{S}$.

We now express the distribution of F_t in terms of the joint distribution of the food consumed in any phase and the duration of any phase, which we compute in $d = 1$. For this purpose, we extend the approach developed in Ref. [41] for standard renewal processes to our situation where f and τ are coupled. To obtain the distribution of F_t, it is convenient to work with the generating function $\langle e^{-pF_t}\rangle$, where the angle brackets denote the average over all possible searcher trajectories. This includes integrating over each phase duration, as well as summing over the number of phases and the food consumed in each patch. The generating function can therefore be written as

$$\langle e^{-pF_t}\rangle = \sum_{m=0}^{\infty} \int_{\mathbb{R}^m} dy_1 \ldots dy_m \sum_{n_1,\ldots,n_m} e^{-p(n_1+\cdots+n_m)} \times \Pr(\{n_i\},\{y_i\},m), \tag{2}$$

where we now treat the time as a continuous variable in the long-time limit. The second line is the joint probability that the food consumed in each patch is $\{n_i\}$, that each phase duration is $\{y_i\}$, and that m phases have occurred; we also ignore the last incomplete phase. From Fig. 1(d), the final time t occurs sometime during the $(m+1)$th phase, so that $t_m < t < t_{m+1}$.

We rewrite the joint probability as the ensemble average of the following expression, which equals 1 when the process contains exactly m complete phases of durations $\{y_i\}$, with n_i units of food consumed in the ith phase, and equals 0 otherwise:

$$\Pr(\{n_i\},\{y_i\},m) = \left\langle \prod_{i=1}^{m} \delta_{f_i,n_i}\delta(\tau_i - y_i) I(t_m < t < t_{m+1})\right\rangle, \tag{3}$$

with the indicator function $I(z) = 1$ if the logical variable z is true, and $I(z) = 0$ otherwise. We can compute the Laplace transform with respect to the time t of this joint probability (see Appendix A) from which the temporal Laplace transform of the generating function $\langle e^{-pF_t}\rangle$ is

$$\int_0^{\infty} dt\, e^{-st}\langle e^{-pF_t}\rangle = \frac{1-\langle e^{-s\tau}\rangle_1}{s(1-\langle e^{-pf-s\tau}\rangle_1)}. \tag{4}$$

Here $\langle e^{-pf-s\tau}\rangle_1$ is an ensemble average over the values (f,τ) for the amount of food consumed in a single phase and the duration of this phase; we use the subscript 1 to indicate such an average over a single phase. Equation (4) applies for any distribution of the pair (f,τ); in particular for any spatial dimension, search process, and distribution of food within patches.

B. Detailed results

We now make Eq. (4) explicit in $d=1$ by calculating $\langle e^{-s\tau-pf}\rangle_1$. For this purpose, we use the equivalence between exploitation of a single patch and the survival of a starving random walk [42,43]. In this latter model, a random walk is endowed with a metabolic capacity $\mathcal{S}$, defined as the number of steps the walker can take without encountering food before starving. The walker moves on an infinite d-dimensional lattice, with one unit of food initially at each site. Upon encountering a food-containing site, the walker instantaneously and completely consumes the food and can again travel $\mathcal{S}$ additional steps without eating before starving. Upon encountering an empty site, the walker comes one time unit closer to starvation.

In our exploitation-migration model, the statistics of (f,τ) for a searcher that leaves its current patch after $\mathcal{S}$ steps without finding food coincides with the known number of distinct sites visited and lifetime of a starving random walk with metabolic capacity $\mathcal{S}$ at the instant of starvation [42,43]. In Appendix B, we determine the full distribution of the pair (f,τ), from which we finally extract the quantity $\langle e^{-pf-s\tau}\rangle_1$ in Eq. (4), where $\tau=T+Z$, with T the (random) time spent in a patch and Z the fixed migration time. The final result is

$$\langle e^{-pf-s\tau}\rangle_1=\int_0^\infty d\theta\, P(\theta)\, e^{[-p\pi\theta\sqrt{\mathcal{S}/2}-s(Z+\mathcal{S})+Q(\theta)]},\qquad (5a)$$

where

$$Q(\theta)=\exp\left[4\int_0^\theta\frac{du}{u}\sum_{j=0}^\infty q_j\right],$$
$$q_j=\frac{1-e^{-[s\mathcal{S}+(2j+1)^2/u^2]}}{1+su^2\mathcal{S}/(2j+1)^2}-(1-e^{-(2j+1)^2/u^2}),$$
$$P(\theta)=\frac{4}{\theta}\sum_{j=0}^\infty e^{-(2j+1)^2/\theta^2}\exp\left[-2\sum_{k=0}^\infty E_1((2k+1)^2/\theta^2)\right],\qquad (5b)$$

and $E_1(x)=\int_1^\infty dt\, e^{-xt}/t$ is the exponential integral.

We now focus on the first two moments of F_t, whose Laplace transforms are obtained from the small-p expansion of Eq. (4). By analyzing this expansion in the small-s limit, the long-time behavior of these moments are (with all details given in Appendix C):

$$\frac{\langle F_t\rangle}{t}\sim\frac{\langle f\rangle}{\langle T\rangle+Z},$$
$$\frac{\mathrm{Var}(F_t)}{t}\sim\frac{\langle f\rangle^2\mathrm{Var}(T)}{(\langle T\rangle+Z)^3}+\frac{\mathrm{Var}(f)}{\langle T\rangle+Z}-2\frac{\langle f\rangle\mathrm{Cov}(f,T)}{(\langle T\rangle+Z)^2},\qquad (6)$$

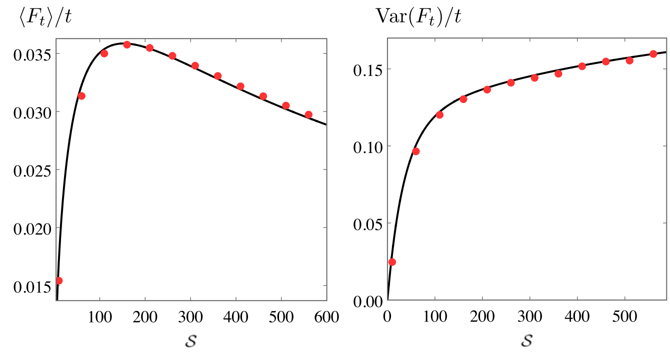

FIG. 2. (a) Scaled mean and (b) variance of the food consumed F_t at $t=5\times10^5$ steps. Points give numerical results and the curves are the asymptotic predictions in (7). The migration time Z between patches is 500 steps.

where $\mathrm{Var}(X)\equiv\langle X^2\rangle-\langle X\rangle^2$, $\mathrm{Cov}(X,Y)\equiv\langle XY\rangle-\langle X\rangle\langle Y\rangle$ and for simplicity, we now drop the subscript 1. From the small-p and small-s limits of Eqs. (5a) and (5b), the limiting behavior of the moments for $\mathcal{S}\gg1$ are

$$\frac{\langle F_t\rangle}{t}\simeq\frac{K_1\sqrt{\mathcal{S}}}{K_2\mathcal{S}+Z},$$
$$\frac{\mathrm{Var}(F_t)}{t}\simeq\left[\frac{K_3\mathcal{S}^3}{(K_2\mathcal{S}+Z)^3}+\frac{K_4\mathcal{S}}{K_2\mathcal{S}+Z}-\frac{K_5\mathcal{S}^2}{(K_2\mathcal{S}+Z)^2}\right],\qquad (7)$$

where the K_i are constants that are derived in Appendix D. The dependences $\langle f\rangle=K_1\sqrt{\mathcal{S}}$ and $\langle T\rangle=K_2\mathcal{S}$ have simple heuristic explanations (see also Ref. [43]): Suppose that the length of the interval where resources have been consumed reaches a length $\sqrt{\mathcal{S}}$. When this critical level of consumption is reached, the forager will typically migrate to a new patch because the time to traverse the resource-free interval will be of the order of $\mathcal{S}$. Thus, the resources consumed in the current patch will be of the order of the length of the resource-free region, namely $\sqrt{\mathcal{S}}$, while the time $\langle T\rangle$ spent in this patch will be of the order of the time $\mathcal{S}$ to traverse this region of length $\sqrt{\mathcal{S}}$.

The salient feature from Eq. (7) is that $\langle F_t\rangle$ has a maximum, which occurs when $\mathcal{S}=Z/K_2$, corresponding to $\langle T\rangle=Z$ (Fig. 2). That is, the optimal strategy to maximize food consumption is to spend the same time exploiting each patch and migrating between patches.

It is worth mentioning that we can reproduce the first of Eqs. (6) by neglecting correlations between f and T. In this case $\langle F_t\rangle$ is simply the average amount of food $\langle f\rangle$ consumed in a single patch multiplied by the mean number $t/(\langle T\rangle+Z)$ of patches explored at large time t. However, this simple calculational approach fails to account for the role of fluctuations, specifically the covariance between f and T, in the variance of F_t. In fact, the covariance term [last term in Eq. (6)] reduces fluctuations in food consumption by a factor three compared to the case where correlations are neglected.

IV. EXTENSIONS

The optimal strategy outlined above is robust and holds under quite general conditions, including, for example, (i) randomly distributed food within a patch, and (ii) searcher

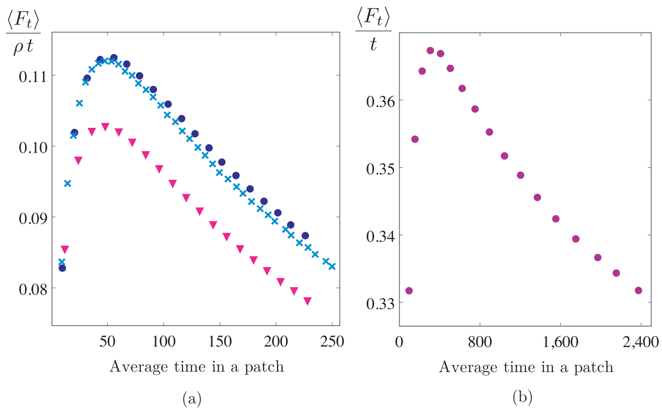

FIG. 3. Average food consumed in $d = 1$ when: (a) the distribution of food is Poisson distributed with density $\rho = 0.1$ ($\times$) and $\rho = 1$ ($\bullet$), as well as when the searcher has a constant probability at each step to leave the patch ($\blacktriangledown$); (b) average food consumed in $d = 2$ for food density $\rho = 1$. The interpatch travel time $Z = 50$ for all cases.

volatility. For (i), suppose that each lattice site initially contains food with probability ρ. To show that the optimal search strategy is independent of ρ, we again exploit the mapping onto starving random walks in the limit $\mathcal{S} \gg 1/\rho$. A density of food ρ corresponds to an effective lattice spacing that is proportional to $\rho^{-1/d}$, with d the spatial dimension. For large $\mathcal{S}$, this effective lattice spacing has a negligible effect on the statistics of the starving random walk. Both the mean lifetime and mean number of distinct sites visited are the same as in the case where the density of food equals 1. However, because the probability to find food at a given site is ρ, the amount of food consumed differs from the number of distinct sites visited by an overall factor ρ. Thus, the food consumed at time t [the first of Eqs. (7)] is simply

$$\frac{\langle F_t \rangle}{t} \simeq \rho \, \frac{K_1\sqrt{\mathcal{S}}}{K_2\mathcal{S} + Z}. \tag{8}$$

Consequently, the optimal search strategy occurs for the same conditions as the case where each site initially contains food [Fig. 3(a)].

For the second attribute, suppose that the searcher has a fixed probability λ to leave the patch at each step, independent of the current resource density, rather than migrating after taking $\mathcal{S}$ steps without encountering food. The residence time of the searcher on a single patch thus follows an exponential distribution with mean λ^{-1}. The exploitation of a single patch can now be mapped onto the evanescent random walk model, in which a random walk dies with probability λ at each step [44], and for which the mean number of distinct sites visited has recently been obtained in one dimension. Since Eq. (4), and thus Eqs. (6), still hold for any distribution of times spent in each patch, we can merely transcribe the results of Ref. [44] [in particular their Eq. (7) and the following text] to immediately find that the average food consumed at time t is

$$\frac{\langle F_t \rangle}{t} \sim \frac{\sqrt{\coth \lambda/2}}{Z + \lambda^{-1}}. \tag{9}$$

Now $\langle F_t \rangle$ is maximized for $1/\lambda \simeq Z$ in the $Z \gg 1$ limit. Again, the optimal strategy is to spend the same amount of time on average in exploiting a patch and in migrating between patches [Fig. 3(a)].

For the ecologically relevant case of two-dimensional resource patches, the average amount of food consumed is governed by a similar optimization as in $d = 1$ [Fig. 3(b)]. While the description of the two-dimensional case does not appear to be analytically tractable, we numerically find that the optimal strategy consists in spending somewhat more time exploiting a single patch rather than migrating between patches. This inclination arises because patch exploitation—whose efficiency is quantified by the average number of distinct sites visited by a given time—is relatively more rewarding in two than in one dimension [39,40].

V. SUMMARY

To summarize, we introduced a minimal exploitation-migration model that quantifies the couplings between searcher motion within patches, resource depletion, and migration to new patches. Our model may provide a first step to understand more realistic ecological foraging, where effects such as predation of the forager [45,46], heterogeneous travel times between patches [47], and more complex motions than pure random walks [48,49] are surely relevant. On the theoretical side, our model can also be viewed as a resetting process, in which a random walker stochastically resets to a new position inside a virgin patch. In contrast to existing studies [50–54], the times between resets are not given *a priori* but determined by the walk itself. This modification may open a new perspective in the burgeoning area of resetting processes.

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APPENDIX A: DERIVATION OF EQ. (4)

We first provide the details to relate the distribution of the amount of food F_t consumed by time t to the statistics of the amount of food f consumed in a single patch and the associated phase duration τ and thereby obtain Eq. (4). Next, in Appendix B, we determine the joint statistics of the time T spent in a patch and the quantity f of food consumed in this patch for the case of one-dimensional patches [Eqs. (5a) and (5b)]. For this calculation, we use the scarcity criterion that the searcher migrates to a new patch when it takes $\mathcal{S}$ steps without encountering food. This criterion maps the multipatch foraging problem onto the starving random walk model. In Appendix C, we extract the moments of F_t from Eq. (4) in the long-time limit to obtain Eq. (6). Combining all these elements ultimately gives Eqs. (7), as shown in Appendix D.

We first need to compute the quantity $\langle e^{-pf-s\tau}\rangle_1$ that appears as Eq. (4), as well as the moments of $\tau = T + Z$ and f that appear as Eqs. (6). Note that all the times in the problem—t, $\mathcal{S}$, Z, T_i, τ_i and t_i—are rescaled by the duration of a random-walk step. We start with the amount of food F_t consumed by time t, which is the sum of the amounts of food consumed during each of the m complete phases and the last incomplete phase

$$F_t = f_1 + \cdots + f_m + f^*. \tag{A1}$$

Since t occurs anytime during the last phase (either during the exploitation of the $(m+1)$th patch or during migration to the next patch), the statistics of the food consumed during the last incomplete phase, f^*, is different from those of all the other f_i's. In the long-time limit, f^* is negligible compared to the total amount of food consumed F_t, so we ignore f^* in (A1) henceforth.

As defined in Eq. (2), the generating function of F_t is

$$\langle e^{-pF_t}\rangle = \sum_{m=0}^{\infty}\int_{\mathbb{R}^m} dy_1\ldots dy_m \sum_{n_1,\ldots,n_m} e^{-p(n_1+\cdots+n_m)}\,\Pr(\{n_i\},\{y_i\},m). \tag{A2}$$

Here, the joint probability for the amount of food $\{n_i\}$ consumed in the ith patch, the times $\{y_i\}$ for the phase durations, and the number m of complete phases is

$$\Pr(\{n_i\},\{y_i\},m) = \left\langle \prod_{i=1}^{m} \delta_{f_i,n_i}\delta(\tau_i - y_i) I(t_m < t < t_{m+1})\right\rangle, \tag{A3}$$

where the indicator function $I(z) = 1$ if the logical variable z is true, and $I(z) = 0$ otherwise. Following Ref. [41], we compute the multiple Laplace transform of this joint probability with respect to the time t and the $\{y_i\}$. This Laplace transform is

$$\mathcal{L}_{t,y_1,\ldots,y_m}\Pr(\{n_i\},\{y_i\},m) \equiv \int_{(\mathbb{R}^+)^{m+1}} dt\, dy_1\ldots dy_m\, e^{-(st+u_1y_1+\cdots+u_my_m)}\Pr(\{n_i\},\{y_i\},m), \tag{A4a}$$

where s is the variable conjugate to t, and each u_i is conjugate to the corresponding y_i. Substituting in the definition (A3) for the joint probability, we obtain

$$\begin{aligned}\mathcal{L}_{t,y_1,\ldots,y_m}\Pr(\{n_i\},\{y_i\},m) &= \left\langle \int_0^{\infty} dt\, e^{-st}\, I(t_m < t < t_{m+1}) \prod_{i=1}^{m}\delta_{f_i,n_i} e^{-u_i\tau_i}\right\rangle \\ &= \left\langle \frac{e^{-st_m} - e^{-st_{m+1}}}{s}\prod_{i=1}^{m}\delta_{f_i,n_i}\, e^{-u_i\tau_i}\right\rangle.\end{aligned} \tag{A4b}$$

We now write t_m and t_{m+1} (the latter defines the end of the phase $m+1$, which happens after time t), as a function of the τ_i's:

$$t_{m+1} = t_m + \tau_{m+1} = \tau_1 + \cdots + \tau_{m+1}. \tag{A5}$$

Here τ_{m+1} is the duration of the $(m+1)$th complete phase (which is longer than the duration of the interrupted phase τ^*). Using these relations in (A4b) yields

$$\begin{aligned}\mathcal{L}_{t,y_1,\ldots,y_m}\Pr(\{n_i\},\{y_i\},m) &= \left\langle \frac{1 - e^{-s\tau_{m+1}}}{s}\prod_{i=1}^{m}\delta_{f_i,n_i}\, e^{-(u_i+s)\tau_i}\right\rangle, \\ &= \frac{1-\langle e^{-s\tau}\rangle_1}{s}\prod_{i=1}^{m}\left\langle\delta_{f_i,n_i}\, e^{-(u_i+s)\tau_i}\right\rangle,\end{aligned} \tag{A6}$$

where we use the independence of the phase durations in the second line. We now denote by $g(n,y)$ the joint probability that the searcher consumes an amount of food n during this phase and that this phase lasts a time y. We also define the Laplace transform of this joint probability with respect to y as $\hat{g}(n,s)$. We then rewrite the ensemble average in Eq. (A6) as a sum over the amount of food consumed in phase i and over all possible phase durations:

$$\left\langle\delta_{f_i,n_i}\, e^{-(u_i+s)\tau_i}\right\rangle_1 = \int_0^{\infty} dy_i' \sum_{n_i'=0}^{\infty} g(n_i',y_i')\, e^{-(u_i+s)y_i'}\,\delta_{n_i',n_i} = \hat{g}(n_i,s+u_i). \tag{A7}$$

Substituting Eq. (A7) into (A6) gives

$$\mathcal{L}_{t,y_1,\ldots,y_m}\Pr(\{n_i\},\{y_i\},m) = \frac{1-\langle e^{-s\tau}\rangle_1}{s}\prod_{i=1}^{m}\hat{g}(n_i,s+u_i). \tag{A8}$$

We now use the feature that shifting the Laplace variable corresponds to multiplication by an exponential factor in the time domain

$$\mathcal{L}_t(e^{-at}h(t)) \equiv \int_0^\infty dt\ e^{-st}e^{-at}h(t) = \hat{h}(s+a), \tag{A9}$$

to obtain the inverse Laplace transform (with respect to the variables u_i) of Eq. (A8):

$$\mathcal{L}_t \,\mathrm{Pr}(\{n_i\},\{y_i\},m) = \frac{1-\langle e^{-s\tau}\rangle_1}{s}\prod_{i=1}^{m} e^{-sy_i}\, g(n_i,y_i). \tag{A10}$$

We can now express simply the Laplace transform of F_t with respect to t using Eqs. (A2) and (A10)

$$\begin{aligned}\mathcal{L}_t\langle e^{-pF_t}\rangle &= \frac{1-\langle e^{-s\tau}\rangle_1}{s}\sum_{m=0}^{\infty}\left(\prod_{i=1}^{m}\int_0^\infty dy_i\sum_{n_i=0}^{\infty} e^{-pn_i-sy_i}g(n_i,y_i)\right)\\ &= \frac{1-\langle e^{-s\tau}\rangle_1}{s}\sum_{m=0}^{\infty}\left(\int_0^\infty dy\sum_{n=0}^{\infty}e^{-pn-sy}g(n,y)\right)^m.\end{aligned} \tag{A11}$$

The expression inside the parentheses is exactly the single-patch ensemble average $\langle e^{-pf-s\tau}\rangle_1$. Thus after performing the geometrical sum over m, we obtain Eq. (4):

$$\mathcal{L}_t\langle e^{-pF_t}\rangle = \frac{1-\langle e^{-s\tau}\rangle_1}{s(1-\langle e^{-pf-s\tau}\rangle_1)}. \tag{A12}$$

APPENDIX B: DERIVATION OF EQS. (5a) AND (5b)

Having derived the generating function of F_t in the Laplace domain [Eq. (4)], we now focus on the specific case of one dimension, in which the searcher uses the give-up criterion that it migrates to another patch upon taking $\mathcal{S}$ steps without encountering food. We first derive $\langle e^{-pf-sT}\rangle_1$, in the limit of large $\mathcal{S}$, that we trivially relate to $\langle e^{-pf-s\tau}\rangle_1$ using $\tau = T + Z$. Following [42], we treat the time T spent in a patch, which is normally an (integer) number of steps, as a continuous variable. We write the ensemble average $\langle e^{-pf-sT}\rangle_1$ as

$$\langle e^{-pf-sT}\rangle_1 = \int_0^\infty dy\sum_{n=0}^{\infty}e^{-pn-sy}\,h(y,n) = \sum_{n=0}^{\infty}P(n)e^{-pn}\int_0^\infty dy\, e^{-sy}\, h(y|n), \tag{B1}$$

where $h(y,n)$ is the joint probability for the searcher to spend a time y in a patch and consume n units of food. Additionally, $P(n)$ is the marginal probability that n units of food are consumed in a single patch when the searcher leaves the patch, integrated over all exploitation durations, and $h(y|n)$ is the conditional probability to spend a time y in the patch, given that n units of food have been consumed at the instant of starvation.

As discussed in Sec. III A, to evaluate $\langle e^{-pf-sT}\rangle_1$, we need to characterize the trajectory of a one-dimensional starving random walk that has visited n distinct sites at the instant of starvation (see Ref. [42]). This trajectory consists of $n-1$ successful returns to food at either end of a growing food-free interval and a final lethal excursion. A return to food is successful if it takes less than $\mathcal{S}$ steps, so the duration R_k of the kth return satisfies $R_k < \mathcal{S}$ for $k \in [2,n]$ and $R_{n+1} \geqslant \mathcal{S}$, corresponding to the walker dying before reaching one end of the interval. Each time the walker returns to one end of the interval, it eats the food there, so that the interval length grows by one lattice spacing to $(k+1)a$ after k returns (with a the lattice spacing). The lifetime of this walk is therefore $T = R_2 + \cdots + R_n + \mathcal{S}$. The integral in Eq. (B1) can thus be written as

$$\begin{aligned}\langle e^{-sT}|n\rangle_1 &\equiv \int_0^\infty dy\, e^{-sy}h(y|n) = \int_0^\infty dy\int_0^\infty dr_2\ldots\int_0^\infty dr_n e^{-sy}\delta(y-r_2-\cdots-r_n-\mathcal{S})\prod_{k=2}^{n}\mathrm{Pr}(r_k)\\ &= e^{-s\mathcal{S}}\prod_{k=2}^{n}\langle e^{-sR_k}\rangle_1 \equiv e^{-s\mathcal{S}}\ U_n,\end{aligned} \tag{B2}$$

where $\mathrm{Pr}(r_k)$ denotes the probability that the kth return to food lasts r_k steps. The average $\langle e^{-sR_k}\rangle_1$ is conditioned on the walker surviving until the kth return and can be expressed as

$$\langle e^{-sR_k}\rangle_1 = \frac{\int_0^{\mathcal{S}} dt\, e^{-st}\mathcal{F}_k(t)}{\int_0^{\mathcal{S}} dt\, \mathcal{F}_k(t)} \to \int_0^{\mathcal{S}} dt\ e^{-st}\mathcal{F}_k(t) \qquad \mathcal{S}\to\infty. \tag{B3}$$

Here $\mathcal{F}_k(t)$ is the first-passage probability that the walker first exits an interval of length ka at time t when starting a distance a from one end. The denominator is thus the probability that the walker survives until the kth return, i.e., it reaches either end of a food-free interval of length ka within $\mathcal{S}$ steps. For large $\mathcal{S}$, this survival probability equals 1 up to an exponentially small correction.

To complete the calculation of $\langle e^{-pf-sT}\rangle_1$, we need to evaluate the terms $\langle e^{-sR_k}\rangle_1$ that comprise U_n in Eq. (B2). In the long-time limit, corresponding to $s \to 0$ and specifically to $sR_k \ll 1$, each such term in U_n is close to 1. Thus, it is convenient to first compute $\ln U_n$ and then reexponentiate:

$$\ln U_n = \sum_{k=2}^{n} \ln\langle e^{-sR_k}\rangle = \sum_{k=2}^{n} \ln(1 + \langle e^{-sR_k} - 1\rangle). \tag{B4}$$

We now substitute the explicit expression for the first-passage probability [55]

$$\mathcal{F}_k(t) = \frac{4\pi D}{((k-1)a)^2} \sum_{j=0}^{\infty}(2j+1)\,\sin\frac{(2j+1)\pi}{k-1}\,\exp\left\{-\left[\frac{(2j+1)\pi}{(k-1)a}\right]^2 Dt\right\} \tag{B5}$$

with the diffusion constant $D = a^2/2$ for a one-dimensional lattice random walk, in Eq. (B3) to recast (B4) as

$$\ln U_n = \sum_{k=2}^{n} \ln\left[1 + \frac{4}{ku^2\mathcal{S}} \sum_{j=0}^{\infty}(2j+1)^2\left(\frac{1-e^{-(s\mathcal{S}+(2j+1)^2/u^2)}}{s+(2j+1)^2/(u^2\mathcal{S})} - \frac{1-e^{-(2j+1)^2/u^2}}{(2j+1)^2/(u^2\mathcal{S})}\right)\right], \tag{B6}$$

where $u \equiv \sqrt{2}\,k/(\pi\sqrt{\mathcal{S}})$. Since the argument of the logarithm is close to 1 for $\mathcal{S} \to \infty$, we expand to lowest order to give

$$\ln U_n \simeq \sum_{k=2}^{n} \frac{4}{ku^2\mathcal{S}} \sum_{j=0}^{\infty}(2j+1)^2\left(\frac{1-e^{-[s\mathcal{S}+(2j+1)^2/u^2]}}{s+(2j+1)^2/(u^2\mathcal{S})} - \frac{1-e^{-(2j+1)^2/u^2}}{(2j+1)^2/(u^2\mathcal{S})}\right). \tag{B7}$$

We now introduce $\theta \equiv \sqrt{2}\,n/(\pi\sqrt{\mathcal{S}})$ and take the continuum limit of Eq. (B7), using again $u = \sqrt{2}\,k/(\pi\sqrt{\mathcal{S}})$, to give

$$\ln U(\theta) \simeq 4\int_0^{\theta}\frac{du}{u}\sum_{j=0}^{\infty}\left\{\frac{1-e^{-[s\mathcal{S}+(2j+1)^2/u^2]}}{1+su^2\mathcal{S}/(2j+1)^2} - [1-e^{-(2j+1)^2/u^2}]\right\}. \tag{B8}$$

Furthermore, the distribution $P(n)$ that appears in Eq. (B1) was determined in the continuum limit in Ref. [42] in terms of the rescaled variable θ

$$P(\theta) = \frac{4}{\theta}\sum_{j=0}^{\infty} e^{-(2j+1)^2/\theta^2}\,\exp\left\{-2\sum_{k=0}^{\infty} E_1[(2k+1)^2/\theta^2]\right\}, \tag{B9}$$

where $E_1(x) \equiv \int_1^{\infty} dt\, e^{-xt}/t$ is the exponential integral function. We finally obtain

$$\langle e^{-sT-pf}\rangle_1 = \int_0^{\infty} d\theta\, P(\theta)\, e^{-p\pi\theta\sqrt{\mathcal{S}/2}-s\mathcal{S}}\,\exp\left\{4\int_0^{\theta}\frac{du}{u}\sum_{j=0}^{\infty}\left[\frac{1-e^{-[s\mathcal{S}+(2j+1)^2/u^2]}}{1+s\mathcal{S}u^2/(2j+1)^2} - (1-e^{-(2j+1)^2/u^2})\right]\right\}, \tag{B10}$$

and using the relation $\tau = T + Z$, we obtain Eqs. (5a) and (5b).

APPENDIX C: DERIVATION OF EQS. (6)

We now extract the moments of F_t in the long-time limit starting from Eq. (A12) [which coincides with (4)]. These moments are obtained by expanding the generating function for $p \to 0$:

$$\langle e^{-pF_t}\rangle = 1 - p\langle F_t\rangle + \frac{p^2}{2}\left\langle F_t^2\right\rangle + \cdots, \tag{C1}$$

where . . . denotes higher-order terms that are negligible as $p \to 0$. From (C1), the temporal Laplace transform is

$$\mathcal{L}_t\langle e^{-pF_t}\rangle = \frac{1}{s} - p\,\mathcal{L}_t\langle F_t\rangle + \frac{p^2}{2}\mathcal{L}_t\left\langle F_t^2\right\rangle + \cdots. \tag{C2}$$

We now straightforwardly expand Eq. (4) in a series in p to give

$$\mathcal{L}_t\langle e^{-pF_t}\rangle = \frac{1}{s}\left[1 - p\frac{\langle fe^{-s\tau}\rangle_1}{1-\langle e^{-s\tau}\rangle_1} + \frac{p^2}{2}\left(\frac{\langle f^2e^{-s\tau}\rangle_1}{1-\langle e^{-s\tau}\rangle_1} + \frac{2\langle fe^{-s\tau}\rangle_1^2}{(1-\langle e^{-s\tau}\rangle_1)^2}\right)\right] + \cdots. \tag{C3}$$

We identify the first two moments of F_t by comparing Eqs. (C2) and (C3), yielding, in the Laplace domain

$$\mathcal{L}_t\langle F_t\rangle = \frac{\langle f e^{-s\tau}\rangle_1}{s(1-\langle e^{-s\tau}\rangle_1)} \tag{C4a}$$

$$\mathcal{L}_t\langle F_t^2\rangle = \frac{1}{s}\left(\frac{\langle f^2 e^{-s\tau}\rangle_1}{1-\langle e^{-s\tau}\rangle_1} + \frac{2\langle f e^{-s\tau}\rangle_1^2}{(1-\langle e^{-s\tau}\rangle_1)^2}\right). \tag{C4b}$$

The long-time behavior of the moments is given by the small-s expansion of the above Laplace transforms:

$$\mathcal{L}_t\langle F_t\rangle = \frac{\langle f\rangle_1}{s^2\langle\tau\rangle_1} + \frac{1}{s}\left(\frac{\langle\tau^2\rangle_1\langle f\rangle_1}{2\langle\tau\rangle_1^2} - \frac{\langle f\tau\rangle_1}{\langle\tau\rangle_1}\right) + \cdots, \tag{C5a}$$

$$\mathcal{L}_t\langle F_t^2\rangle = \frac{2\langle f\rangle_1^2}{s^3\langle\tau\rangle_1^2} + \frac{1}{s^2}\left[\frac{2\langle f\rangle_1}{\langle\tau\rangle_1}\left(\frac{\langle\tau^2\rangle_1\langle f\rangle_1}{\langle\tau\rangle_1^2} - 2\frac{\langle f\tau\rangle_1}{\langle\tau\rangle_1}\right) + \frac{\langle f^2\rangle_1}{\langle\tau\rangle_1}\right] + \cdots, \tag{C5b}$$

where ... indicates lower-order terms in s as $s \to 0$. Note that two orders in s are necessary to calculate the variance of F_t, as the leading-order terms in s for $\langle F_t^2\rangle$ and $\langle F_t\rangle^2$ cancel. By performing the inverse Laplace transform, we finally obtain, in the limit $t\to\infty$,

$$\langle F_t\rangle = \frac{\langle f\rangle_1}{\langle\tau\rangle_1}t + \left(\frac{\langle\tau^2\rangle_1\langle f\rangle_1}{2\langle\tau\rangle_1^2} - \frac{\langle f\tau\rangle_1}{\langle\tau\rangle_1}\right) + \cdots, \tag{C6a}$$

$$\langle F_t^2\rangle = \frac{2\langle f\rangle_1^2}{\langle\tau\rangle_1^2}t^2 + \left[\frac{2\langle f\rangle_1}{\langle\tau\rangle_1}\left(\frac{\langle\tau^2\rangle_1\langle f\rangle_1}{\langle\tau\rangle_1^2} - 2\frac{\langle f\tau\rangle_1}{\langle\tau\rangle_1}\right) + \frac{\langle f^2\rangle_1}{\langle\tau\rangle_1}\right]t + \cdots. \tag{C6b}$$

This yields Eqs. (6), after using $\tau = T + Z$:

$$\langle F_t\rangle = \frac{\langle f\rangle_1}{\langle T\rangle_1 + Z}\,t + \cdots \tag{C7a}$$

$$\mathrm{Var}(F_t) = \left[\frac{\langle f\rangle_1^2\mathrm{Var}(T)}{(\langle T\rangle_1+Z)^3} + \frac{\mathrm{Var}(f)}{\langle T\rangle_1+Z} - \frac{2\langle f\rangle_1\mathrm{Cov}(f,T)}{(\langle T\rangle_1+Z)^2}\right]t + \cdots, \tag{C7b}$$

where the variance $\mathrm{Var}(f)$ and covariance $\mathrm{Cov}(f,T)$ of f and T were defined after Eq. (6).

APPENDIX D: DERIVATION OF EQS. (7)

Finally, we obtain $\langle f\rangle_1$, $\langle T\rangle_1$, $\mathrm{Var}(T)$, and $\langle fT\rangle_1$ that appear in Eq. (6) by taking the small-p and small-s limits of the Laplace transform:

$$\langle e^{-sT-pf}\rangle_1 = 1 - s\langle T\rangle_1 - p\langle f\rangle_1 + ps\langle Tf\rangle_1 + \frac{s^2}{2}\langle T^2\rangle_1 + \cdots, \tag{D1}$$

where ... denotes higher-order terms in p and s. Substituting Eq. (B10) in this expansion gives

$$\langle e^{-sT-pf}\rangle_1 = \left(1 - s\mathcal{S} + \frac{s^2}{2}\mathcal{S}^2\right)\int_0^\infty d\theta\, P(\theta)\left(1 - p\pi\theta\sqrt{\frac{\mathcal{S}}{2}} + \frac{(p\pi\theta)^2\mathcal{S}}{4}\right)\left(1 + s\mathcal{S}\mathcal{A}(\theta) + s^2\mathcal{S}^2\frac{2\mathcal{B}(\theta)+\mathcal{A}^2(\theta)}{2}\right) + \cdots, \tag{D2}$$

with

$$\mathcal{A}(\theta) \equiv \sum_{j=0}^\infty\int_0^\theta du\,\frac{4}{u}\left[\left(1+\frac{u^2}{(2j+1)^2}\right)e^{-(2j+1)^2/u^2} - \frac{u^2}{(2j+1)^2}\right],$$

$$\mathcal{B}(\theta) \equiv \sum_{j=0}^\infty\int_0^\theta du\,\frac{4}{u}\left[\frac{u^4}{(2j+1)^4} - \left(\frac{1}{2} + \frac{u^2}{(2j+1)^2} + \frac{u^4}{(2j+1)^4}\right)e^{-(2j+1)^2/u^2}\right]. \tag{D3}$$

Here we have also used the small-s expansion of the expression in the last exponential in Eq. (B10):

$$\frac{1-e^{-[s\mathcal{S}+(2j+1)^2/u^2]}}{1+u^2 s\mathcal{S}/(2j+1)^2} - (1-e^{-(2j+1)^2/u^2}) = s\mathcal{S}\left[\left(1+\frac{u^2}{(2j+1)^2}\right)e^{-(2j+1)^2/u^2} - \frac{u^2}{(2j+1)^2}\right] + s^2\mathcal{S}^2\left[\frac{u^4}{(2j+1)^4} - \left(\frac{1}{2}+\frac{u^2}{(2j+1)^2}+\frac{u^4}{(2j+1)^4}\right)e^{-(2j+1)^2/u^2}\right]\ldots,$$

From Eq. (D2), the moments of f are simply expressed in terms of the marginal distribution $P(\theta)$:

$$\langle f\rangle_1 = \pi\sqrt{\frac{\mathcal{S}}{2}}\int_0^\infty d\theta\,\theta\,P(\theta) \equiv K_1\sqrt{\mathcal{S}},$$

$$\langle f^2\rangle_1 = \frac{\pi^2\mathcal{S}}{2}\int_0^\infty d\theta\,\theta^2\,P(\theta),$$

$$\mathrm{Var}(f) = \langle f^2\rangle_1 - \langle f\rangle_1^2 = \frac{\pi^2\mathcal{S}}{2}\left[\int_0^\infty d\theta\,\theta^2\,P(\theta) - \left(\int_0^\infty d\theta\,\theta\,P(\theta)\right)^2\right] \equiv K_4\mathcal{S}. \tag{D4}$$

Similarly, identifying (D2) with (D1), we obtain

$$\langle T\rangle_1 = \left[1 - \int_0^\infty d\theta\,P(\theta)\mathcal{A}(\theta)\right]\mathcal{S} \equiv K_2\mathcal{S},$$

$$\langle T^2\rangle_1 = \left[1 + 2\int_0^\infty d\theta\,P(\theta)\left(\mathcal{B}(\theta) + \frac{1}{2}\mathcal{A}^2(\theta) - \mathcal{A}(\theta)\right)\right]\mathcal{S}^2,$$

$$\mathrm{Var}(T) = \left[\int_0^\infty d\theta\,P(\theta)\big(2\mathcal{B}(\theta) + \mathcal{A}^2(\theta)\big) - \left(\int_0^\infty d\theta\,P(\theta)\mathcal{A}(\theta)\right)^2\right]\mathcal{S}^2. \tag{D5}$$

Equation (D1) also yields

$$\langle fT\rangle_1 = \pi\sqrt{\frac{\mathcal{S}^3}{2}}\int_0^\infty d\theta\,P(\theta)\,\theta[1 - \mathcal{A}(\theta)],$$

$$\mathrm{Cov}(f,T) \equiv \langle fT\rangle_1 - \langle f\rangle_1\langle T\rangle_1 = \pi\sqrt{\frac{\mathcal{S}^3}{2}}\int_0^\infty d\theta\,P(\theta)\,\theta\left[\int_0^\infty d\varphi\,P(\varphi)\mathcal{A}(\varphi) - \mathcal{A}(\theta)\right]. \tag{D6}$$

Finally, we substitute these asymptotic expressions for the moments of f and T into Eq. (6) and obtain the constants K_1 to K_5 that appear in Eq. (7):

$$K_1 \equiv \frac{\pi}{\sqrt{2}}\int_0^\infty d\theta\,\theta\,P(\theta) \simeq 2.90\ldots,$$

$$K_2 \equiv 1 - \int_0^\infty d\theta\,P(\theta)\,\mathcal{A}(\theta) \simeq 3.27\ldots,$$

$$K_3 \equiv \frac{\pi^2}{2}\left[\int_0^\infty d\psi\,\psi\,P(\psi)\right]^2\left[\int_0^\infty d\theta\,P(\theta)(2\mathcal{B}(\theta) + \mathcal{A}^2(\theta)) - \left(\int_0^\infty d\theta\,P(\theta)\,\mathcal{A}(\theta)\right)^2\right] \simeq 16.1\ldots,$$

$$K_4 \equiv \frac{\pi^2}{2}\left[\int_0^\infty d\theta\,\theta^2\,P(\theta) - \left(\int_0^\infty d\theta\,\theta\,P(\theta)\right)^2\right] \simeq 1.78\ldots,$$

$$K_5 \equiv \pi^2\int_0^\infty d\psi\,\psi\,P(\psi)\int_0^\infty d\theta\,P(\theta)\,\theta\left[\int_0^\infty d\varphi\,P(\varphi)\mathcal{A}(\varphi) - \mathcal{A}(\theta)\right] \simeq 8.51\ldots, \tag{D7}$$

where the results are quoted to three-digit accuracy.

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