Universality classes of foraging with resource renewal

M. Chupeau,[1] O. Bénichou,[1] and S. Redner[2]

[1] *Laboratoire de Physique Théorique de la Matière Condensée (UMR CNRS 7600), Université Pierre et Marie Curie, 4 Place Jussieu, 75255 Paris Cedex France*

[2] *Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA*

We determine the impact of resource renewal on the lifetime of a forager that depletes its environment and starves if it wanders too long without eating. In the framework of the minimal starving random walk model with resource renewal, there are three universal classes of behavior as a function of the renewal time. For sufficiently rapid renewal, foragers are immortal, while foragers have a finite lifetime otherwise. In one dimension, there is a third regime, for sufficiently slow renewal, in which the lifetime of the forager is independent of the renewal time. We outline an enumeration method to determine the mean lifetime of the forager in the mortal regime.

PACS numbers: 05.40.Jc, 87.23.Cc

What is the impact of renewal of resources on the state of a forager? If the environment is harsh and resources regenerate slowly, then foragers may be confronted by perpetual scarcity. Thus a forager may often go hungry or even starve. Conversely, in an abundant environment where resources are quickly replenished, a forager may never experience starvation risk. Our goal is to map out the states of a forager as a function of the renewal time within the framework of the minimal "starving random walk" model [1] that we define below.

The random walk model has been frequently invoked to describe the motion of foraging animals [2–4], as well as a wide variety of classic applications [5–9]. In the wild, foraging animals can die from many causes, such as diseases or old age [10]. The underlying dynamics from these causes of death can be described by a "mortal" random walk that dies according to a specified lifetime distribution [12–14]. This model has a wide range of applications, such as the diffusion of light in human tissue [15], and biologically-inspired search problems [16]. However, another important contributor to mortality of a forager is that it may be unsuccessful in its search for food within its habitat [11]. Thus the age at which a forager dies is also determined by its trajectory and the amount of available resources. This coupling between the lifetime of a living organism and its trajectory, along which environmental resources are depleted, defines a nontrivial class of random-walk problems—including the starving random walk model—that are largely unexplored.

In the original starving random walk model [1], a random walk irreversibly depletes its environment during its wanderings, and starves if it remains too long in a resource-depleted region. Initially, each lattice site contains one food unit. Whenever a forager, which undergoes a random walk, arrives at a full site, the food is completely eaten. Once depleted, a site remains empty. Whenever the forager arrives at an empty site, it does not eat. If the forager wanders $\mathcal{S}$ steps without eating, it starves. Here we view $\mathcal{S}$ as the metabolic capacity of the forager—the amount of time it can live without food before starving. Asymptotic expressions for the walker lifetime and the territory visited at the starvation time

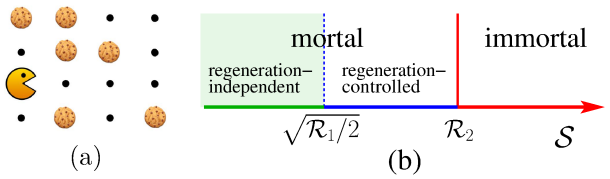

Figure 1: (a) Starving random walk with resource renewal in $d = 2$. Each lattice site initially contains food that the forager eats whenever it reaches an occupied site. The forager starves if it wanders $\mathcal{S}$ steps without eating. Food reappears on empty sites after a given renewal time. (b) Phase diagram showing the three regimes of behavior. The shaded zone, where the lifetime is independent of renewal rate, occurs only $d = 1$; the two other regimes arise for any d. The thresholds between these regimes are given by Eqs. (1) and (6).

were given in one dimension [1]. Estimates for these two quantities in dimensions $d \geqslant 3$ and a lower bound for the territory visited at starvation in $d = 2$ were also given. These results provide a first step in quantifying the interplay between the trajectory of a forager and the consumption of food and their effect on the lifetime of the forager.

However, the natural resources being consumed—preys, plants, water, and nutrients—typically obey their own dynamics. In particular, consumed resources usually do not disappear permanently [17, 18]. Instead, they typically regenerate a certain time after they have been depleted [19–21]. This basic fact motivates our study of starving random walks with renewal of resources (Fig. 1(a)).

As we will discuss, resource renewal substantially modifies the properties of a starving random walk. Using extreme trajectory arguments, we will argue that the correlations induced by the coupling between the trajectory of a forager, its metabolic capacity $\mathcal{S}$, and the dynamics of the resources lead to three universal regimes of behavior that are determined by $\mathcal{S}$ and the bounds $\mathcal{R}_1$ and $\mathcal{R}_2$ of the support of the renewal time distribution, but are insensitive to the shape of this distribution. We will

first demonstrate the existence of a transition between an immortal regime, in which the forager cannot starve, no matter what its trajectory, and a mortal regime, where the forager must eventually starve. Both regimes arise in any spatial dimension. We also show that a third regime arises in one dimension, in which renewal is so slow that the forager lifetime is the same as in the case of no renewal. We also develop an enumeration method that yields the exact value of the mean lifetime of a forager in the mortal regime.

Let us first investigate starving random walks with deterministic renewal in one dimension. Such a deterministic mechanism describes plants that grow at a fixed rate [22], and reaches an edible size a fixed time after having been previously defoliated. Food that is eaten at time step t reappears at time $t+\mathcal{R}$, with $\mathcal{R}$ an integer. In each time step, the time elapsed since an empty site was depleted is increased by one and food appears at any site where this time equals $\mathcal{R}$. As part of this same time step, the walker hops to one of its nearest neighbors. If the site contains food, which may have appeared just before the walker arrives, the food is eaten. We call the set of empty sites, which may or may not be connected because of renewal, the "desert".

Immortality. For a forager with metabolic capacity $\mathcal{S} \in \mathbb{N}$, we now determine the range of the renewal times for which immortality arises. A forager is immortal if it survives forever on any trajectory, and, in particular, on the most unfavorable trajectories. The set of such trajectories is infinite, but they all possess the common pattern (see Fig. 2) that the walker depletes two sites in a row at one end of the desert, before wandering within the desert as long as possible until being sure, because of resource renewal, to land on a food-containing site [23]. It takes $\mathcal{R}$ time steps before food reappears on one of these two sites (Fig. 2). Thus, roughly speaking, when $\mathcal{R} < \mathcal{S}$, the forager necessarily survives. The precise criterion actually is $\mathcal{R} \leq \mathcal{R}^*$, with

$$\mathcal{R}^* = \begin{cases} \mathcal{S} & \mathcal{S} \text{ even}, \\ \mathcal{S}+1 & \mathcal{S} \text{ odd}, \end{cases} \tag{1}$$

due to the even-odd oscillations of a nearest-neighbor random walk [23]. This result can be immediately extended to probabilistic renewal and to higher dimensions. In the former case, suppose that each empty site is replenished in a time τ, with τ drawn from a continuous distribution with support $[\mathcal{R}_1, \mathcal{R}_2] \subset \mathbb{R}^+$. The immortality regime arises if $\mathcal{R}_2 \leq \mathcal{R}^*$, that is, if a depleted site does not remain empty more than $\mathcal{R}^*$ steps.

In higher dimensions, the most unfavorable trajectories described above still have the same character outlined above, so that the immortality criterion is the same as in one dimension. Similarly, the forager is immortal in any spatial dimension and for any distribution of renewal times, whenever the upper bound of this distribution satisfies $\mathcal{R}_2 \leq \mathcal{R}^*$. Note that if the upper bound $\mathcal{R}_2$ is infinite, so that replenishment on some sites can take an arbitrarily long time, then immortality cannot occur. However, in plants adapted to grazing, renewal always happens in a time of the order of days or weeks [19, 24].

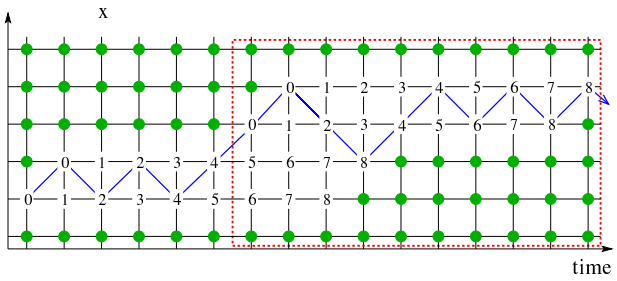

Figure 2: Illustration of the common pattern (inside the dashed rectangle) of all extremal trajectories for renewal time $\mathcal{R} = 9$. This pattern consists of depleting two consecutive sites at one end of the desert. The forager wanders inside this desert which gradually shortens until it reaches length 2. The pattern ends when the walker is sure to land on a food-containing site. Green dots denote food-containing sites and the numbers give the ages of each site.

On the other hand, when $\mathcal{R}_2 > \mathcal{R}^*$, the forager is mortal and thus eventually starves with probability 1 because there now exist trajectories that lead to starvation. These trajectories again involve the forager first carving out a desert and then wandering strictly within this desert so that renewal does not reach the forager before it starves. By their very construction, such trajectories are achieved with non-zero probability. From classical results about Markov chains (see, e.g., [25]), every trajectory will eventually generate a configuration for which the forager starves. Thus in all spatial dimensions there are two regimes of behavior—immortality and mortality. The boundaries between these regimes depend only on the metabolic capacity $\mathcal{S}$ of the forager and the upper bound of the renewal-time distribution $\mathcal{R}_2$, but not on its shape.

Mean Lifetime in the Mortal Regime. Using the Markov chain formalism, we can, in principle, determine the mean lifetime of the forager by enumerating the configurations of the system as the forager wanders. A configuration is defined as the location and age of each empty site in the desert, the position of the forager in the desert, and the number of time steps elapsed since the forager last ate. Here the age of an empty site is the time since the food was last consumed at this site. Thus a newly empty site has age 0, while a site that will regenerate at the next step has age $\mathcal{R}-1$. Because the desert has a finite size, the number of configurations is finite. We can therefore write the transition matrix that describes the evolution of the system at each step of the forager and thereby extract its mean lifetime.

We illustrate this enumeration for the simple case of $\mathcal{S} = 2$ and $\mathcal{R} = 3$ in one dimension. There are five distinct configurations (Fig. 3). State ① arises after the first step, and the evolution of the system from one state to another is illustrated in Fig. 3. The associated transition

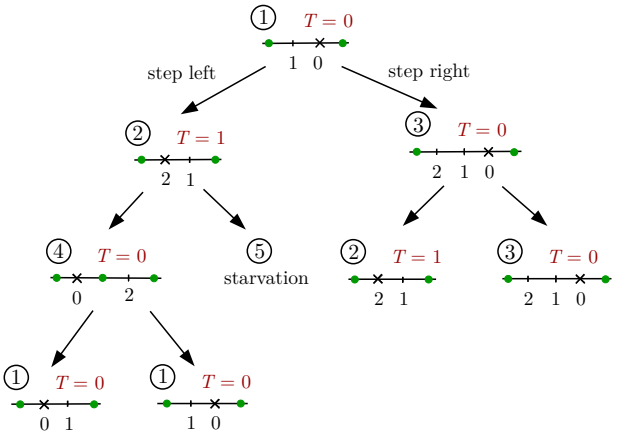

Figure 3: State space of the system for metabolic capacity $\mathcal{S} = 2$ and deterministic renewal time $\mathcal{R} = 3$. The circled numbers denote the distinct states and T is the time elapsed since the forager last ate.

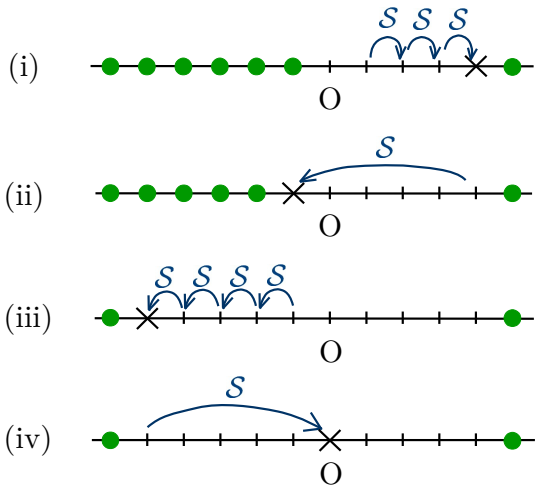

Figure 4: Optimal trajectory for a forager to live the longest and still be able to return the origin O, with $\mathcal{S} = 5$. (i) The forager eats a site on the right edge of the desert every $\mathcal{S}$ steps until carving the largest semi-desert that it can cross. (ii) The forager crosses the desert. (iii) Reflection of stage (i). (iv) The forager crosses the left semi-desert to reach the origin. Such an excursion lasts $\mathcal{R}^\dagger$ steps (Eq. (6)).

matrix is

$$\begin{pmatrix} 0 & 0 & 1 & 0 & 0 \\ 1/2 & 0 & 0 & 1/2 & 0 \\ 0 & 1/2 & 0 & 0 & 0 \\ 1/2 & 0 & 0 & 1/2 & 0 \\ 0 & 1/2 & 0 & 0 & 1 \end{pmatrix} \equiv \begin{pmatrix} Q & 0 \\ V & I \end{pmatrix} \tag{2}$$

where the states are listed in order ①–⑤, with

$$Q = \begin{pmatrix} 0 & 0 & 1 & 0 \\ 1/2 & 0 & 0 & 1/2 \\ 0 & 1/2 & 0 & 0 \\ 1/2 & 0 & 0 & 1/2 \end{pmatrix}, \tag{3}$$

and $V = (0, \frac{1}{2}, 0, 0)$. We define the matrix (see [25])

$$N \equiv (I - Q^+)^{-1} = \begin{pmatrix} 2 & 2 & 1 & 2 \\ 1 & 2 & 1 & 1 \\ 2 & 2 & 2 & 2 \\ 1 & 2 & 1 & 3 \end{pmatrix}, \tag{4}$$

where Q^+ is the transpose of Q. Each entry N_{ij} in this matrix is the average time that a system, which ultimately reaches starvation, spends in configuration j when it starts from configuration i [25]. From this matrix we can extract the mean absorption time t_i starting from the state i. These are given by

$$\begin{pmatrix} t_1 \\ t_2 \\ t_3 \\ t_4 \end{pmatrix} = N \begin{pmatrix} 1 \\ 1 \\ 1 \\ 1 \end{pmatrix} = \begin{pmatrix} 7 \\ 5 \\ 8 \\ 7 \end{pmatrix}. \tag{5}$$

The mean lifetime of the forager is then $t_1 + 1 = 8$, because after the first step, the system is necessarily in the state ①. In principle, this method can be extended to higher dimensions and also to probabilistic renewal with a bounded support of renewal times. In practice, this approach quickly becomes intractable because the number of possible configurations becomes prohibitively large when both $\mathcal{R}$ and $\mathcal{S}$ are large. Note also that if the support of the distribution of renewal times is unbounded, the approach given here fails because the number of configurations is infinite. Nevertheless, this approach gives a well-defined prescription for computing the average time until the forager starves.

Renewal Independent Regime. In one dimension, the mortal regime class can be divided in two subclasses: (a) forager lifetime dependent on $\mathcal{R}$, and (b) renewal independence—lifetime independent of $\mathcal{R}$. Clearly, as $\mathcal{R}$ increases, the forager lifetime decreases and approaches the no-renewal limiting value as $\mathcal{R} \to \infty$. Does this decrease stop when $\mathcal{R}$ reaches a finite critical value $\mathcal{R}^\dagger$, or does the decrease continue as $\mathcal{R} \to \infty$? To resolve this question, we determine if there is at least one trajectory for which the forager can return to a replenished site without starving. If there is such a trajectory, then renewal is relevant, as the lifetime of the forager depends on the renewal time.

We first treat the case of deterministic renewal. For a forager to return to a site on which food is renewed requires: (i) living long enough for such a renewal to occur and (ii) staying sufficiently close to this site to reach it without starving. These two attributes are most easily satisfied for a site (which we take as the origin) at which food has just been eaten and is surrounded by full sites. We determine the largest value of $\mathcal{R}$ for which the forager can return to this origin after the food at this site has been renewed.

To return to the origin without starving imposes the

constraint that the forager does not stray more than $\mathcal{S}$ steps from the origin. Moreover, to maximize the time that the forager wanders, it should eat only when it really needs to, that is, every $\mathcal{S}$ steps. The trajectory on which the forager lives the longest while staying within $\mathcal{S}$ steps of the origin therefore consists of the following components (Fig. 4): (i) The forager creates a semi-desert of length $\mathcal{S}$ on one side, say to the right, of the origin. During this creation of the semi-desert, the forager eats by moving to a previously unvisited site only every $\mathcal{S}$ steps. (ii) The forager successfully crosses this semi-desert, which is the longest possible for which a successful traversal is possible. (iii) The forager creates a mirror image semi-desert of length $\mathcal{S}$ to the left of the origin. (iv) The forager crosses this left semi-desert and fetches the regenerated food at the origin.

The duration of this excursion is roughly $2\mathcal{S}^2$, as the forager has eaten $2\mathcal{S}$ times when it returns to the origin. A careful enumeration [23] of the above sequence of moves gives the maximal renewal time $\mathcal{R}^\dagger$ with

$$\mathcal{R}^\dagger = \begin{cases} 2\mathcal{S}^2 - 3\mathcal{S} + 4 & \mathcal{S} \text{ even}, \\ 2\mathcal{S}^2 - \mathcal{S} + 1 & \mathcal{S} \text{ odd}. \end{cases} \tag{6}$$

For $\mathcal{R} \leq \mathcal{R}^\dagger$, a forager has a non-zero probability to eat food at a site where renewal has occurred. Conversely, for $\mathcal{R} > \mathcal{R}^\dagger$, a forager cannot reach any replenished site, so that renewal has no impact on the forager lifetime. Hence the mean lifetime does not gradually converge to the limiting no-renewal value, but rather reaches this value for $\mathcal{R} = \mathcal{R}^\dagger + 1$. Thus we infer the existence of a renewal-independent regime (Fig. 1) for the lifetime of the forager. For probabilistic renewal, the renewal-independent regime still arises if the lower bound of the support of the distribution of renewal times obeys $\mathcal{R}_1 > \mathcal{R}^\dagger$, that is, if every depleted site remains empty for at least $\mathcal{R}^\dagger$ steps.

In contrast to the immortality transition, the transition to the renewal-independent regime does not occur in higher dimensions. In this case, a forager can live for an arbitrarily long time and still return to the origin without starving, because it does not need to cross the desert as in one dimension. Thus the renewal time—no matter how long—always affects the lifetime of the forager. These results are summarized in the phase diagram of Fig. 1(b), which is our key result.

To summarize, renewal has a dramatic effect on starving random walks. There exist three regimes of behavior as a function of the renewal time $\mathcal{R}$: (i) an immortal regime where a forager can live forever, (ii) a mortal regime where the forager lifetime is finite and depends on $\mathcal{R}$, and (iii) a renewal-independent mortal regime where renewal does not affect the lifetime of a forager. The latter arises only in one dimension, in which the average forager lifetime equals the value obtained in the absence of any renewal. In contrast, regimes (i) and (ii) arise in any spatial dimension and are universal with respect to the distribution of renewal times. The transitions between them depend only on the bounds of the support of the renewal-time distribution and not on its shape. Much of this new phenomenology is determined by the times between visits to distinct sites in a random walk, an as yet unexplored feature of site visitation statistics of random walks. Finally, we outlined an enumeration method to determine the mean forager lifetime in the mortal regimes (ii) and (iii). Average values of other basic observables, such as the number of distinct sites visited at starvation, the number of sites in the desert, the time spent in a certain configuration, can also be extracted from this approach.

Immortality is the main new feature that arises as a result of the renewal of resources. Thus if a wandering organism can survive without food longer than the time needed for resources to be replenished, its lifetime is no longer limited by starvation but rather by external constraints (such as predation, diseases, life expectancy of the species, etc.). We speculate that perhaps the metabolic capacity of a given species is determined by the characteristic time for regeneration of resources.

We acknowledge NSF Grant No. DMR-1205797 (S. R.) and ERC starting Grant No. FPTOpt-277998 (O. B.) for partial support of this research.

[1] O. Bénichou and S. Redner, Phys. Rev. Lett. **113**, 238101 (2014).
[2] H. C. Berg, *Random walks in biology* (Princeton University Press, 1993).
[3] F. Bartumeus, M. G. E. da Luz, G. Viswanathan, and J. Catalan, Ecology **86**, 3078 (2005).
[4] E. A. Codling, M. J. Plank, and S. Benhamou, Journal of the Royal Society Interface **5**, 813 (2008).
[5] G. H. Weiss and R. J. Rubin, Adv. Chem. Phys **52**, 363 (1983).
[6] B. D. Hughes, *Random walks and random environments* (Clarendon Press Oxford, 1996).
[7] D. Ben-Avraham and S. Havlin, *Diffusion and reactions in fractals and disordered systems* (Cambridge University Press, 2000).
[8] A. Okubo and S. A. Levin, *Diffusion and ecological problems: modern perspectives*, Vol. 14 (Springer Science & Business Media, 2013).
[9] G. I. Bell and S. Glasstone, *Nuclear Reactor Theory.*, Tech. Rep. (Division of Technical Information, US Atomic Energy Commission, 1970).
[10] S. B. Fey, A. M. Siepielski, S. Nusslé, K. Cervantes-Yoshida, J. L. Hwan, E. R. Huber, M. J. Fey, A. Catenazzi, and S. M. Carlson, Proceedings of the National Academy of Sciences **112**, 1083 (2015).
[11] A. Sinclair, H. Dublin, and M. Borner, Oecologia **65**, 266 (1985).
[12] S. Yuste, J. Ruiz-Lorenzo, and K. Lindenberg, Phys.

Rev. E **74**, 046119 (2006).
[13] S. B. Yuste, E. Abad, and K. Lindenberg, Phys. Rev. Lett. **110**, 220603 (2013).
[14] E. Abad, S. Yuste, and K. Lindenberg, Phys. Rev. E **88**, 062110 (2013).
[15] R. Bonner, R. Nossal, S. Havlin, and G. Weiss, JOSA A **4**, 423 (1987).
[16] B. Meerson and S. Redner, Phys. Rev. Lett. **114**, 198101 (2015).
[17] G. C. Evans, *The quantitative analysis of plant growth*, Vol. 1 (Univ of California Press, 1972).
[18] G. Lemaire, in *International Grassland Congress*, Vol. 19 (SBZ São Paulo, 2001) pp. 29–37.
[19] W. B. McCallum, Botanical Gazette **40**, 97 (1905).
[20] W. G. Harrison, in *Primary productivity in the sea* (Springer, 1980) pp. 433–460.
[21] M. Fenner, *Seeds: the ecology of regeneration in plant communities* (Cabi, Wallingford, UK, 2000).
[22] R. O. Erickson, Annual Review of Plant Physiology **27**, 407 (1976).
[23] Supplemental Information.
[24] D. Briske, in *The Ecology and Management of Grazing Systems*, edited by J. Hodgson and A. I. (Eds) (CAB International, Wallingford, UK, 1996) Chap. 2, pp. 37–67.
[25] C. M. Grinstead and J. L. Snell, *Introduction to probability* (American Mathematical Soc., 2012)
.