



Minireview

Lévy flights in random searches

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Abstract

We review the general search problem of how to find randomly located objects that can only be detected in the limited vicinity of a forager, and discuss its quantitative description using the theory of random walks. We illustrate Lévy flight foraging by comparison to Brownian random walks and discuss experimental observations of Lévy flights in biological foraging. We review recent findings suggesting that an inverse square probability density distribution $P(\ell) \sim \ell^{-2}$ of step lengths ℓ can lead to optimal searches. Finally, we survey the explanations put forth to account for these unexpected findings. © 2000 Published by Elsevier Science B.V. All rights reserved.

1. Introduction: how to quantify search processes

Search processes can be highly complex phenomena [1,2]. Extensive experimental data exist for the special case of animal foraging, in which an animal optimizes its search for, say, food [3–6]. On the one hand, animals have a certain degree of “free will” to move and forage according to their choice. On the other, they are subject to certain physical and biological constraints which restrict their behavior, e.g. if a foraging

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animal does not eat food for a certain maximum time then it will die. Moreover, evolution has through natural selection led over time to highly efficient – even optimal – foraging strategies. According to *optimal foraging theory*, animals seek to maximize the returns (in calories, nutrients, etc.) on their labor in deciding how best to forage [7]. Since physical as well as neurophysiological and evolutionary factors come into play, foraging is a rich problem that continues to present multi-faceted and interdisciplinary challenges.

Why study foraging? Foraging is often understood to mean biological foraging, where the objects being sought are food sites, but it can be interpreted in a broader context. For example, the “hunt” for criminals by police authorities may be governed by processes identical — or at least related — to those found in animal foraging. Hence, the general foraging problem is potentially more important than may at first appear from a purely biological perspective. Indeed, quantifying the statistical properties of search patterns is of practical relevance not only in physics but also in theoretical ecology, industry, and conceivably even to problems such as the search for missing children. Very recently, foraging concepts have even found application in information technology (e.g., *information foraging theory* [8]).

The general problem of how to search efficiently for randomly-located “target sites” (e.g., food objects) can be quantitatively described using ideas developed in the study of random walks [9–13]. Indeed, it can be argued that statistical physics is ideally suited to the study of complex phenomena of this nature. Here we discuss the quantitative description of the foraging problem and survey recent developments in statistical physics relating to foraging.

2. Lévy and Brownian random walks

Random walks can be classified either as Brownian (B) random walks or Lévy (L) walks:

- (B) The step lengths ℓ_j have a characteristic scale, usually defined by the first and by the second moment (mean and variance, respectively) of the step length density distribution $P(\ell)$;
- (L) The step lengths have no characteristic scale, by which we mean that the second moment or even the first moment diverge and the distribution has self-affine properties: $P(\lambda\ell) \sim \lambda^{-\mu}P(\ell)$, $1 < \mu \leq 3$.

It is often possible to estimate experimentally the probability density distribution $P(\ell)$ of the step or flight lengths ℓ . Until recently it has often been assumed [9–12] that such a histogram of flight lengths $P(\ell_j)$ has a well-defined second moment. Hence arise Gaussian, Poisson and other classical distributions that lead to Brownian behavior. Indeed, it has generally been assumed a priori that foragers perform movements in their environments that correspond to normal diffusion. An essential feature of such random walks is that their mean square displacement increases linearly with the number of steps taken.

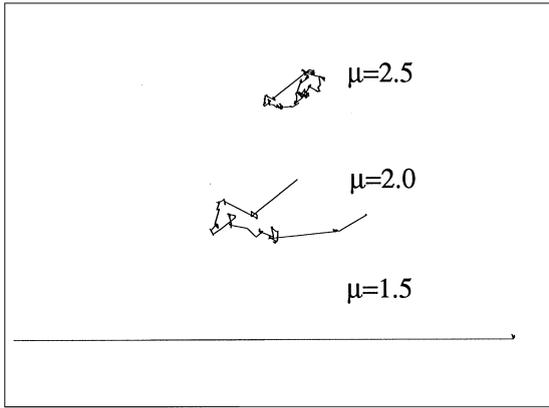


Fig. 1. 2-D random walks for $\mu = 2.5$, 2.0, and 1.5, respectively, with identical total lengths of 10^3 units. Micro-organisms, mammals, birds, and insects show episodes of approximately straight locomotion randomly interrupted by re-orientation events.

Recently, however, it has been questioned if this assumption is unnecessarily restrictive, and whether its predictions can be supported by existing experimental data [3–6,14]. To address this question, one can assume the more general Lévy distribution [11,12,15–17]

$$P(\ell_j) \sim \ell_j^{-\mu} \quad (1)$$

with $1 < \mu \leq 3$ where, in fact, Gaussian behavior is a special case for $\mu > 3$ [18]. Values $\mu \leq 1$ do not correspond to normalizable probability distributions. Apart from its intrinsic mathematical merit, as being the largest class of stable distributions, Lévy distributions have found useful applications in biology [11,12], and foraging studies specifically [3–6]. The mean square displacement of Lévy random walks grows with time as $t^{4-\mu}$ for $2 < \mu < 3$ and as t^2 for $\mu < 2$. Here t is the time of the walk with the assumption that a jump of length ℓ_j takes time $t = \ell_j$. Strictly speaking, Lévy flights are defined in [19,20] such that each jump regardless of its size takes one unit of time. Since in this article we consider flights of birds and insects, we use the term Lévy flights instead of Lévy walks throughout the paper. The behavior of Lévy flights is dominated by extremely long but rare step lengths. Such behavior corresponds to anomalous super-diffusive motion [11,12] (Fig. 1). Lévy flights have also been found to be associated with enhanced diffusion in chaotic systems and continuous-time models (see, for instance, Refs. [21–24]).

Microorganisms, insects, birds, and mammals have been found to follow a Lévy distribution of flight lengths or times (assumed to be proportional or at least correlated statistically) [3–6,14] (Fig. 2). Moreover, the exponent μ appears to be the same in many instances [14]. When the nectar concentration is low, the flight length distribution of bumble bees [14,25] decays like Eq. (1) with $\mu \approx 2$ (Fig. 2(a)). Similarly, the value

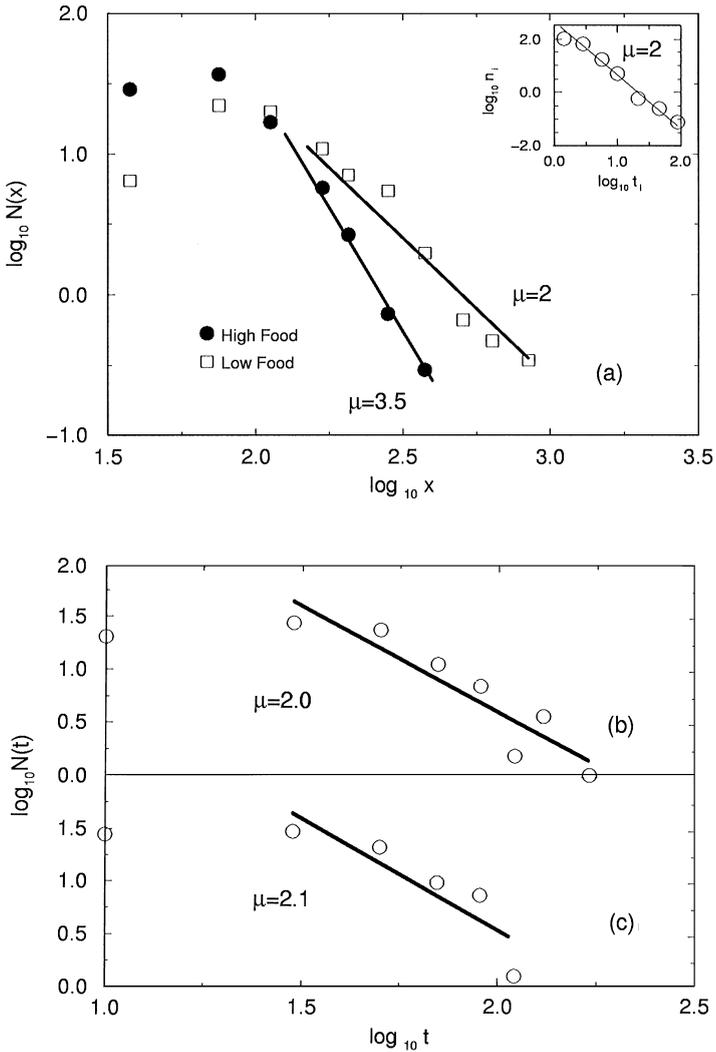


Fig. 2. Double log plot of the flight length percentage distributions for foraging bumble bees, digitized from Ref. [25]. Note the value $\mu \approx 2$ for low nectar concentration. The value $\mu \approx 3.5$ for ($\approx 10\times$) higher nectar concentrations in which long flights become very rare (see text) is also consistent with the theory. The inset displays a double log plot of the histograms of flight times (in 1 h intervals) for the Wandering Albatross [6]. (b) Double log plot of the foraging time (s) percentage distributions for deer in wild areas and (c) fenced areas.

$\mu \approx 2$ is also found for the foraging time distribution of the Wandering Albatross [6] (Fig. 2(a) (inset)) and deer (Fig. 2(b) and (c)) in both wild and fenced areas [14,26]. Even the value $2 \leq \mu \leq 2.5$ found for amoebas [4] supports the hypothesis that $\mu_{\text{opt}} = 2$ might be a universal value of the exponent in Lévy flight foraging. What, might we

ask, drives animals to this type of behavior and what benefits, if any, do they thus derive from Lévy flight motion?

3. Benefits of Lévy flights

Why flights lengths might follow a Lévy distribution rather than a Gaussian or Poisson distribution is of general interest. The reasons behind the experimentally observed Lévy flights in biological foraging have never been fully understood, but a number of studies have shed some light. Levandowsky et al. [3,4] have suggested reasons why microorganisms may perform Lévy flights in three dimensions (3-D), showing that a Lévy distribution is advantageous since the probability of returning to a previously visited site is smaller than for a Gaussian distribution, irrespective of the value of μ chosen [19]. A related explanation proposed by Shlesinger (see Ref. [6]) argues that foragers may perform Lévy flights because the number of new visited sites is much larger for n Lévy walkers than for n Brownian walkers [27–30]. The n Lévy walkers diffuse so rapidly that the competition for the resources (target sites) among themselves is greatly reduced relative to the competition encountered by the n Brownian walkers, who typically remain close to the origin, hence to each other. A Lévy flight strategy is also a good solution for the related problem where N radar stations search for M targets [31]. Yet another proposed hypothesis is that the fractal properties of the set of sites visited by a Lévy walker are related to scale invariant properties of the underlying ecosystem [6]. Specifically, a fractal distribution of target sites may explain the observed Lévy flights [6]. Very recently, there has been a study of how the search efficiency depends on the value μ of the Lévy exponent [14]. This study finds that there is an optimum value $\mu_{\text{opt}} = 2$ which can lead to optimal foraging when the target sites are randomly and sparsely distributed. Below, we discuss this latest development in greater detail.

By studying how the search efficiency varies with μ , one can compare different classes of foraging strategies characterized by unique values of μ . In the first case of “nondestructive foraging”, the forager can visit the same target site many times. Nondestructive foraging can occur in either of two cases: (i) if the target sites become temporarily depleted, or (ii) if the forager becomes satiated and leaves the area. In the second case of “destructive foraging”, the target site found by the forager becomes undetectable in subsequent flights. Consider the following idealized model that captures some of the essential dynamics of foraging in the limiting case in which predator-prey relationships are ignored, and learning is minimized. Assume that target sites are distributed randomly, and the forager behaves as follows (see Fig. 3):

(1) If there is a target site located within a “direct vision” distance r_v , then the forager detects it with certain probability and moves on a straight line to the detected target site.

(2) If there is no detected target site within a distance r_v , then the forager chooses a direction at random and a distance ℓ_j from the probability distribution, Eq. (1).

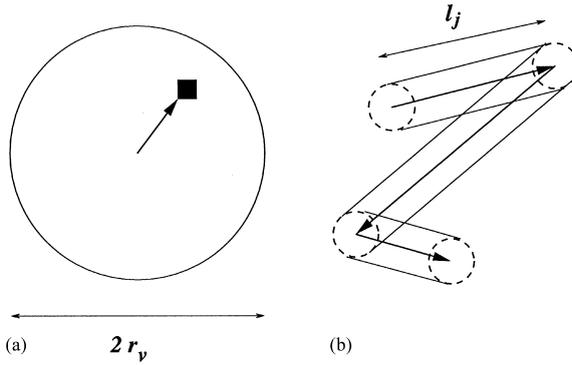


Fig. 3. Foraging strategy: (a) If there is a target site (full square) located within a “direct vision” distance r_v , then the forager detects it with certain probability and moves on a straight line to it. (b) If the forager does not detect a target site within a distance r_v , then the forager chooses a random direction and a random distance ℓ_j from the Lévy probability distribution $P(\ell_j) \sim \ell_j^{-\mu}$, and then proceeds as explained in the text.

It then incrementally moves to the new point, constantly looking for a target within a radius r_v along its way. If it does not detect a target, it stops after traversing the distance ℓ_j and chooses a new direction and a new distance ℓ_{j+1} , otherwise it proceeds to the target as in step (1). (Memory effects are discussed below). In the following we will assume for simplicity that the lower cutoff of the flight length distribution is equal to the vision radius r_v . This restriction may have biological motivation, since it is unreasonable for the forager to change the direction of the flight within the distance of the direct vision from the previous turning point.

One can solve this model as follows: let λ be the mean free path of the forager between successive target sites (for 2-D, $\lambda \equiv (2r_v\rho)^{-1}$ where ρ is the target site area density). The mean flight distance is

$$\langle \ell \rangle \approx \frac{\int_{r_v}^{\lambda} dx x^{1-\mu} + \lambda \int_{\lambda}^{\infty} x^{-\mu} dx}{\int_{r_v}^{\infty} x^{-\mu} dx} = \left(\frac{\mu - 1}{2 - \mu} \right) \left(\frac{\lambda^{2-\mu} - r_v^{2-\mu}}{r_v^{1-\mu}} \right) + \frac{\lambda^{2-\mu}}{r_v^{1-\mu}}. \quad (2)$$

The second term of this “mean field” calculation is an approximation because it assumes that the distances between successive sites are identically equal to λ , so that there are no flights longer than λ . A new target site is always encountered a maximum distance λ away from the previous target site, effectively resulting in a truncated Lévy distribution [32]. A more rigorous treatment that considers not only the mean value but also a Poisson distribution of the free paths does not seem to alter the results significantly and numerical simulations in which fluctuations are taken into account support the mean field picture (see discussion below).

One defines the search efficiency function $\eta(\mu)$ to be the ratio of the number of target sites visited to the total distance traversed by the forager, so that

$$\eta = \frac{1}{N \langle \ell \rangle}. \quad (3)$$

Here N is the mean number of flights taken by a Lévy forager in order to travel between two successive target sites. The value of N can be found analytically in 1-D case [33], when the Lévy flight starts from an arbitrary point x of the interval $[0, L]$ with absorbing boundaries (see Ref. [34] where similar problems are solved). The average number of flights taken by the walker before it is absorbed is given by the equation

$$N = C \left(\frac{x(L-x)}{r_v^2} \right)^{(\mu-1)/2}, \quad (4)$$

where the constant C does not depend on x , and L . For the Brownian random walk with all steps equal to r_v , which corresponds to $\mu > 3$ we recover the well-known equation $N = x(L-x)r_v^{-2}$.

Consider first the case of *destructive foraging*, when the target site is “eaten” or destroyed by the foraging animal and becomes unavailable in subsequent flights. This situation corresponds in terms of Eq. (4) to the case when the walker starts from the previously destroyed site that is about the same distance λ away from the two remaining target sites, so that $x = L - x = \lambda$. Hence, the mean number of flights N_d in case of destructive foraging is given by

$$N_d \sim (\lambda/r_v)^{\mu-1} \quad (5)$$

for $1 < \mu \leq 3$. Here $\mu - 1$ is the fractal dimension of the set of sites visited by a Lévy random walker [19]. Note that $N_d \sim (\lambda/r_v)^2$ for $\mu > 3$ (Brownian case). Consider the common case in which the target sites are “sparsely” distributed, defined by $\lambda \gg r_v$. Substituting Eqs. (2) and (5) into (3) one finds that the mean efficiency η has no maximum, with lower values of μ leading to more efficient foraging. Note that when $\mu = 1 + \varepsilon$ with $\varepsilon \rightarrow 0^+$, the fraction of flights with $\ell_j < \lambda$ becomes negligible, and effectively the forager moves along straight lines until it detects a target site.

Consider next the case of *nondestructive foraging* for sparsely distributed target sites. Since previously visited sites can then be revisited, the mean number N_d of flights between successive target sites in Eq. (5) overestimates the true number N_n for the nondestructive case. This situation corresponds in terms of Eq. (4) to the case when the walker starts from the small distance r_v from the previously visited site and the next site which is about distance λ away, i.e., $x = r_v$ and $L = \lambda$. Hence,

$$N_n \sim (\lambda/r_v)^{(\mu-1)/2} \quad (6)$$

for $1 < \mu \leq 3$. This result has also been systematically tested using simulations and found to become better and better as (λ/r_v) increases (cf. also Figs. 4(a) and (b)). Note that if $\lambda \gg r_v$ then $N_d \gg N_n$. Substituting Eqs. (2) and (6) into (3) and differentiating with respect to μ , one finds that the optimal efficiency $\eta = 1/(N_n \langle \ell \rangle)$ is achieved at

$$\mu_{\text{opt}} = 2 - \delta, \quad (7)$$

where $\delta \sim 1/[\ln(\lambda/r_v)]^2$. So in the absence of a priori knowledge about the distribution of target sites, an optimal strategy for a forager is to choose $\mu_{\text{opt}} = 2$ when λ/r_v is large but not exactly known.

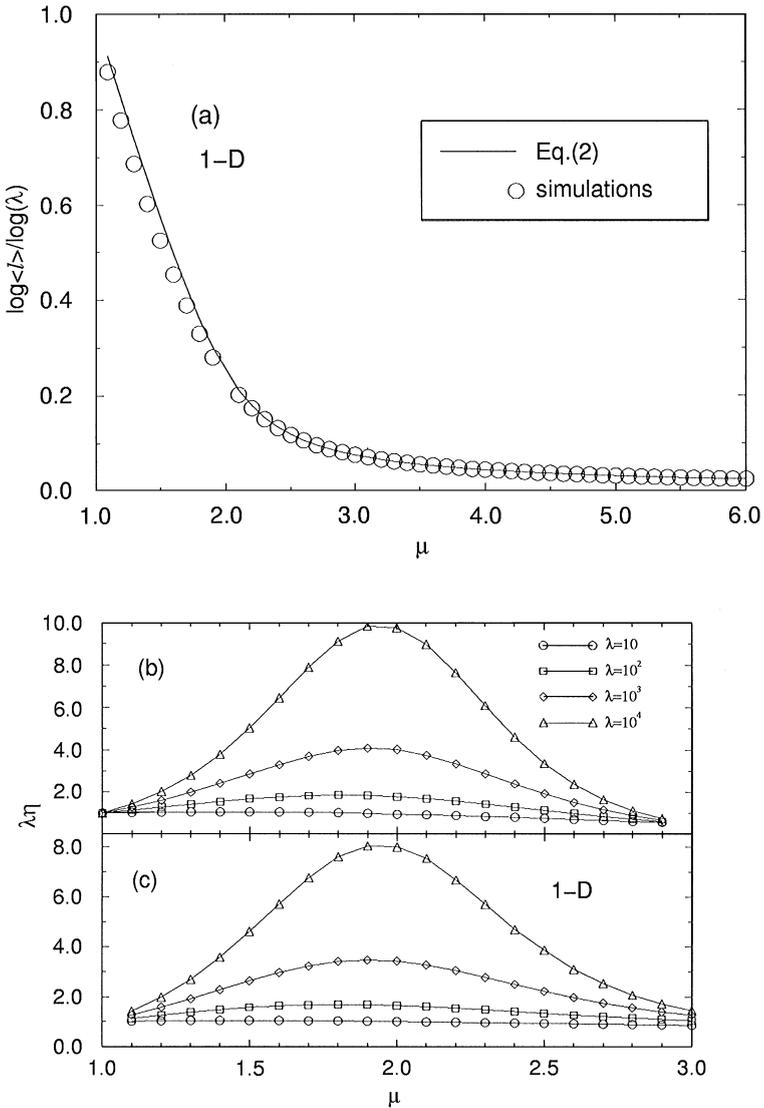


Fig. 4. (a) The ratio $\log\langle\ell\rangle/\log(\lambda)$ as a function of μ found from Eq. (2) and from simulations in 1-D, for the case $\lambda/r_v = 10^4$. (b) the product of the search efficiency η and the mean free path λ vs. μ in 1-D for different λ , found from Eqs. (2) and (3) ($r_v = 1$) for the case of nondestructive foraging and (c) from simulations. (d) $\eta\lambda$ found from simulations in 2-D for the case of non-destructive foraging with $\lambda = 5000$ ($r_v = 1$). In each case, $\mu_{\text{opt}} \approx 2$ emerges as an optimal value of the Lévy flight exponent. Inset: the food is distributed in patches of food-rich areas in an otherwise empty environment, for the case of non-destructive foraging. The effective value of the distribution exponent μ_m is obtained by computing $\mu_m = -d \log N(\ell)/d \log \ell$ from the histograms $N(\ell)$ of flight lengths. Only flights with $\log_{10} \ell < 4.5$ are considered in order to eliminate the effects of the periodic boundaries. Again, $\mu_m \approx 2$ seems to optimize the search efficiency.

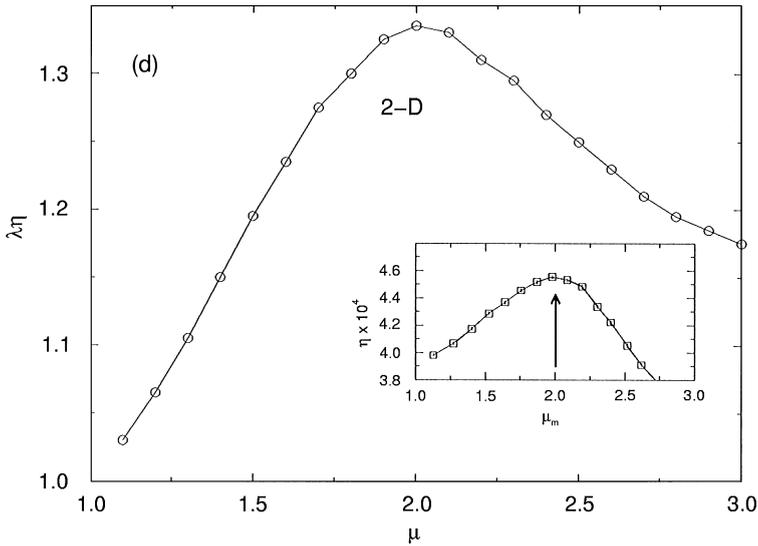


Fig. 4. Continued.

The above results are independent of the dimension of the foraging space. This is analogous to the behavior of random walks whose mean square displacement is proportional to the number of steps in any dimension [9,10]. Furthermore, Eqs. (5) and (6) describe the correct scaling properties even in the presence of short-range correlations in the directions and lengths of the flights. Short-range correlations can alter the width of the distribution $P(\ell)$, but cannot change μ , so these findings remain unchanged. Hence, learning, predator-prey relationships, and other short-term memory effects become unimportant in the long-time long-distance limit. Note also that for both destructive and nondestructive foraging, Brownian behavior, corresponding to $\mu \geq 3$, is significantly less efficient than Lévy flight motion. This finding suggests that a power law distribution of flight lengths may be *essential* for optimal foraging when the target sites are sparsely and randomly distributed. For completeness, consider also the case in which the target sites are plentiful, i.e., $\lambda \leq r_v$. Then $\langle \ell \rangle \approx \lambda$ and $N_d \approx N_n \approx 1$. Hence, η becomes independent of μ . This behavior does not correspond to Lévy flight foraging but is more similar to a Brownian random walk. The independence of η on μ is a direct consequence of the extreme rarity of long flights with $\ell_j > r_v$.

These theoretical results have been supported with numerical simulations which do not depend on approximations. Indeed, 1-D and 2-D simulations have been performed of the above model to study how η varies with μ for the case of nondestructive foraging by a single random walker. Fig. 4(a) shows that the mean flight paths estimated analytically and through simulations are consistent. For 1-D, the position of the maximum in η for the simulation agrees with the analytical results (Fig. 4(b)), and approaches $\mu_{\text{opt}} = 2$ as $\lambda \rightarrow \infty$ (Fig. 4(c)). These simulations were performed for a fixed interval of size λ with no disorder, since this is a valid simplification because there is no

significant difference between Poisson distributed λ and fixed λ , as discussed further below. The simulation results for 2-D nondestructive foraging also show maxima near $\mu_{\text{opt}} = 2$. Fig. 4(d) shows simulated foraging in a system of size $10^4 \times 10^4$ with $r_v = 1$, periodic boundary conditions, and $\lambda/r_v = 5 \times 10^3$, corresponding to a total number of 10^4 fixed target sites (of which the forager must find at least 10^2 sites), averaged over 10^2 initial configurations. (Care must be taken to avoid repetitive and endless jumping between two fixed sites closer than r_v to avoid spurious results.) Moreover, for destructive foraging with $\lambda \gg r_v$, simulations show that $\mu \rightarrow 1$ optimizes the efficiency as predicted. In contrast, if the target sites are densely distributed such that $\lambda \approx r_v$, then, as expected, we find no significant effect of varying μ . These findings agree with the theoretical predictions and raise the possibility that Lévy flight foraging with $\mu < 3$ may be confined to instances of low global target site concentration, since the principal advantage of choosing small μ – long flights – becomes negligible when there are ample target sites (see also Figs. 4(c) and 2(a)). We stress that such simulation results do not use the approximations inherent in Eq. (2) and effectively use a true distribution of free paths, thereby showing that such approximations do not alter the shape of the η curve, nor – most importantly – its maximum value near $\mu_{\text{opt}} = 2$. Our preliminary results show that this is still true in 3-D [33].

We also note that nondestructive foraging is more realistic than destructive foraging because in nature, flowers, berries, krill, fish, etc., are usually found in patches or clumps which are rarely completely depleted. Organisms are often in clusters for reproductive purposes. Sometimes such clusters have fractal shapes [35]. Thus an animal can revisit the same food patch many times, and a patch can restore itself by regrowth. Simulations of destructive foraging in patchy target site distributions give results consistent with nondestructive foraging for uniformly distributed target sites. As an illustrative example, Fig. 4(d) (inset) shows $\eta(\mu)$ found from simulating a patchy distribution of food. There are many small randomly distributed food-rich regions, each with radius R , outside of which there is no food to be found. To speed up the simulations, it was assumed that the forager performs a Lévy Flight only outside the region of radius R , and that it instead performs Brownian motion within, finding food at each site along the way separated by the local mean free path $\lambda = R/3$. The system size used was $10^5 \times 10^5$. A low patch area to system area ratio of $\pi \times 10^{-6}$ is achieved using a patch radius of $R = 10$, and a number of patches $n_p = 10^4$. Here, $\mu_m \equiv -d \log N(\ell) / d \log \ell$ was measured from the histogram $N(\ell)$ of flight lengths instead of using the parameter μ from the model. Such a histogram represents an experimentally observable distribution of flight lengths. Note that μ_m is consistent with the theoretically predicted value μ_{opt} .

Lévy flights in foraging suggest the existence of dispersal or redistribution kernels [36,37] which follow the Lévy distribution. Dispersal kernels are used in population biology and occur in integrodifference equations such as

$$n_t(x) = \int_{\Omega} K(x, y) f(n_t(y)) dy, \quad (8)$$

where $n_t(x)$ represents the population density in the generation t at location x , the nonlinear function f describes density dependent processes at a given position in space, and K is the kernel. Each value of μ is related to a different type of kernel, e.g. $\mu \geq 3$ corresponds to the normal (or similar) distribution, while $\mu = 2$ corresponds to a Cauchy distribution [38].

4. Prospects

Over the last decade there has been much progress in the study of Lévy flights in search processes. A re-examination of existing experimental data for evidence of Lévy flight behavior might be warranted, especially in the case of patchy food distributions. It would also be interesting to compare in greater detail the Lévy flight foraging in 2-D and 3-D. Finally, we also note that a fuller treatment of foraging that takes energy into account remains to be done.

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