

## Dynamical Robustness of Lévy Search Strategies

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We study the role of dynamical constraints in the general problem of finding the best statistical strategy for random searching when the targets can be detected only in the limited vicinity of the searcher. We find that the optimal search strategy depends strongly on the delay time  $\tau$  during which a previously visited site becomes unavailable. We also find that the optimal search strategy is always described for large step lengths  $\ell$  by a power-law distribution  $P(\ell) \sim \ell^{-\mu}$ , with  $1 < \mu(\tau) \leq 2$ . Our findings appear to remain valid even if arbitrary energy costs of locomotion are considered.

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Quantifying random search patterns has been a challenging interdisciplinary problem [1,2] that is attracting growing interest [3–9]. The practical relevance of the problem spans areas that include theoretical physics, information technology (information foraging theory [10]), industrial processes, and theoretical ecology [1,2,5]. Fundamental aspects of random search problems can be explained in terms of Lévy walks and Lévy flights [11,12]. In particular, the random search problem of finding the most efficient strategy of searching for randomly located objects (targets) whose exact locations are not known *a priori* has motivated several studies [3–5,13]. A conventional way of modeling random search is to assume the searcher performs a random walk in which the direction of each step is independent of previous steps and the length  $\ell$  of each step is taken from a distribution  $P(\ell)$ .

In the biological literature, studies usually tend to assume that  $P(\ell)$  is a Poisson or some other short-tailed distribution with finite variance. In this case the motion of the searcher becomes equivalent to regular diffusion as described by a Gaussian probability density. A recent study [4] proposed that  $P(\ell)$ , for many species, may have long power-law tails:

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

In the case  $1 < \mu < 3$ , the variance of this distribution diverges, extremely long steps dominate the motion of the searcher, and the probability density of its displacement converges in the asymptotic  $\ell \rightarrow \infty$  limit to a Lévy stable density with index  $\alpha = \mu - 1$ . In stable probability densities, after a large number of steps the distribution of the resulting composed step has the same step distribution as the original distribution, with identical behaviors in the tails. Lévy stable densities thus provide a generalization of the Gaussian stable density. In addition, an important parameter of  $P(\ell)$  is the characteristic length  $\ell_0$ , which

determines the lower cutoff of the power-law distribution (1), below which it becomes essentially constant. In this case,  $\ell_0$  is related to the proportionality coefficient in the power-law decay by

$$\ell_0 = \lim_{\ell \rightarrow \infty} \left[ P(\ell) \frac{\ell^\mu}{\mu - 1} \right]^{1/(\mu-1)}, \quad (2)$$

and represents the persistence length of the random walk, being also associated, in the context of animal foraging, with the inertia of the animal motion.

Here we assume that in general a forager can be modeled by a random walk in which the distribution of steps is given by Eq. (1), with the parameter  $1 < \mu \leq 3$  [14]. The natural question that arises concerns how to determine the optimal value of  $\mu$  that provides the maximal amount of targets (e.g., food) found per unit length traveled by the searcher. The studies in Refs. [4, 5, 13, 16, 17] have shown that if target sites are sparse and can be visited any number of times (unrestricted, nondestructive search), then  $\mu_{\text{opt}} = 2$  leads to the optimal search strategy. However if a target site can be visited only once (destructive search), then  $\mu$  takes on an optimal value  $\mu_{\text{opt}} \rightarrow 1$ , corresponding essentially to rectilinear ballistic motion between targets, since there is no advantage in returning to a previously visited site. In addition, experimental data on foraging for different animal species appear to agree with the theoretical predictions [3–5,13].

One advantage of a statistical analysis approach relates to how it can lead to general and robust results, independently of the peculiarities of the particular system studied. For the random search problem, the findings concerning the optimal strategy appear to be valid for any dimension of the foraging space [5,13] and seem to be mainly independent of the presence of short-range correlations arising from phenomena such as learning and predator-prey relationships [16]. Nevertheless, only from

the dynamical details of specific real systems can one infer relevant parameters that may be important for their characterization. For animal foraging especially, the dynamical search details can give the biologist studying a particular species information about the environment or metabolic aspects of the species. Hence, in this work we investigate the influence of two dynamical aspects relevant to the general random search problem.

We first study the role of the delay time  $\tau$  during which a previously visited site becomes unavailable for future visits. There are two general kinds of strategies. If a found site regenerates very quickly, then the best strategy involves waiting near the site for it to regenerate, leading to Brownian motion. However, if there is no advantage in waiting for the previously found site to regenerate, and if target sites are not likely to be found in the immediate vicinity of the searcher, then we find that the best search strategy always involves power laws, with the optimal exponent restricted to the interval  $1 < \mu_{\text{opt}}(\tau) \leq 2$ . Specifically, we find that  $\mu \approx 2$  for  $\tau \rightarrow 0$  (nondestructive limit) and  $\mu \rightarrow 1$  for  $\tau \rightarrow \infty$  (destructive limit). In this regime we also find that space-limited Gaussian strategies [14] (corresponding to  $\mu \geq 3$ ) lead to rather inefficient searches. In the context of animal foraging this result is also related to the problem of target revisitability and accounts for the fact that realistic targets cannot be revisited an infinite number of times, nor do they necessarily disappear forever in nature. We then also show that the introduction of an arbitrary (energetic) cost function assigned to the search trajectory does not change the optimal value  $\mu_{\text{opt}}$ , although in some cases its presence significantly limits the range of physically meaningful values for  $\mu$  [17].

To introduce the delay time  $\tau$ , we modify the foraging model proposed in Ref. [4] by allowing the searcher to look for randomly distributed sites according to the following three locomotion rules:

(A) If there are target sites located within a “direct vision” distance  $r$  (which in principle can be larger than  $\ell_0$ ), the forager detects one of them with some probability and then moves on a straight line to the detected site.

(B) If no target sites within  $r$  are detected, the searcher chooses a direction at random and a step length  $\ell_j$  from the probability distribution (1), and then moves with constant velocity  $v$  to the new point, constantly looking for a target site within a distance  $r$  along its way. If the searcher does not detect a site, it stops after traversing the distance  $\ell_j$  and chooses a new direction and a new distance  $\ell_{j+1}$ ; otherwise, it proceeds to the target as in Rule (A).

(C) In the case a target site is detected by applying Rules (A) or (B), it becomes unavailable for future visits during a time  $\tau$ , after which it regenerates.

Rule (A) is essentially based on a short-range detection mechanism of target sites, constituting the short flight length regime. On the other hand, Rule (B) actually

involves a random search and governs the intermediate and long flight regimes. So, for Rule (B) to apply the characteristic spacing  $\lambda$  of the target-site Poisson distribution should considerably exceed  $r$ , i.e.,  $\lambda \gg r$ . This represents the cases of low and intermediate concentrations of target sites. In contrast, when target sites are plentiful, searches of type (B) become rare and the foraging process is driven by the detection events (A), with a Poisson distribution.

In Rule (B) the searcher truncates its path if it finds a target site within the distance  $r$  along its way, so the effective probability distribution in fact corresponds to a so-called “truncated Lévy distribution” [18] with finite moments, the cutoff length being associated with  $\lambda$  [4,18], even though the convergence to Gaussian behavior occurs only after an extremely large number of steps [18]. Indeed, this upper cutoff emerges naturally in real systems, due to their finite sizes, or, in the case of animal foraging, due to biological constraints which, e.g., can lead the animal to starve to death if no food site is located within a certain maximum range.

As was shown in the one-dimensional case (see p. 155 of Ref. [15]), for any power-law tailed distribution, if the forager starts from a point  $x = z\lambda$  of an interval  $[0, \lambda]$ , where  $0 < z < 1$ , and if  $\lambda/\ell_0 \rightarrow \infty$ , then the optimal strategy is achieved provided

$$\mu_{\text{opt}} = 2 + \frac{2}{\ln z} + o\left(\frac{1}{\ln z}\right). \quad (3)$$

We can relate the distance  $z\lambda$  to the velocity of the forager and the time of recovery of the target site, where

$$z = \frac{v\tau}{\lambda}. \quad (4)$$

If  $\tau \rightarrow 0$ , then  $z \rightarrow 0$ ,  $\ln z \rightarrow -\infty$ , and therefore  $\mu_{\text{opt}} = 2$ . When  $z > 1/e^2$ , Eq. (3) gives  $\mu < 1$ , which corresponds to the motion along a straight line with constant velocity (nonlocalized regime).

In the case of  $d$  dimensions, the exact solution of the average total flight distance is not known; however, the results obtained in the one-dimensional case should still have validity, since in  $d$  dimensions the forager moves along a one-dimensional corridor of cross section proportional to  $r^{d-1}$ . The average length  $\lambda$  of this corridor between two target sites plays the role of the length of the one-dimensional interval

$$\lambda \sim \frac{1}{\rho r^{d-1}}, \quad (5)$$

where  $\rho$  is the density of the target sites. This quantity is equivalent to the mean free path in the problem of gas diffusion.

Equation (3) was obtained in Ref. [15] using hypergeometric functions. To illustrate the one-dimensional derivation in simple terms, we approximate the average length of the step by the expression calculated [4]

for a power-law distribution  $P(\ell > x) = (\ell_0/x)^{\mu-1}$  for  $x > \ell_0$ ,  $P(\ell > x) = 1$  for  $x \leq \ell_0$ ,

$$\langle \ell \rangle \approx \frac{\lambda^{2-\mu}}{\ell_0^{1-\mu}} + \frac{\mu-1}{2-\mu} \left( \frac{\lambda^{2-\mu} - \ell_0^{2-\mu}}{\ell_0^{1-\mu}} \right), \quad (6)$$

truncated at larger distances by  $\lambda$  and at small distances by  $\ell_0$ . For  $\mu < 2$  this expression is dominated by the upper cutoff  $\lambda$ . For  $\mu > 2$  it is dominated by the lower cutoff  $\ell_0$ . We take the  $d$ -independent scaling of the average number of steps before the forager finds a target site as [15]

$$N_s \sim \left[ \frac{x(\lambda-x)}{\ell_0^2} \right]^{(\mu-1)/2}, \quad (7)$$

where the initial position of the forager is  $x = v\tau$ .

The average length  $\langle L \rangle$  traveled by the forager before it reaches a target site can be approximated as a product of the average step length and the average number of steps

$$\langle L \rangle = N_s \langle \ell \rangle, \quad (8)$$

so that, by introducing Eq. (7) with  $z = x/\lambda$ , we get

$$\langle L \rangle = \lambda \left[ \frac{1 - (\lambda/\ell_0)^{(\mu-2)}(\mu-1)}{2-\mu} \right] (z - z^2)^{(\mu-1)/2}. \quad (9)$$

If  $\lambda z/\ell_0 \gg 1$  and  $\mu < 2$ , then  $\langle L \rangle$  can be approximated as

$$\langle L \rangle \approx \frac{\lambda}{2-\mu} (z - z^2)^{(\mu-1)/2}, \quad (10)$$

which has a minimum at

$$\mu = 2 + \frac{2}{\ln(z - z^2)}, \quad (11)$$

thus coinciding with Eq. (3) for small  $z$  [19].

Figure 1 displays two-dimensional simulation results as a function of  $\tau$ . When target sites are allowed to be visited at any time ( $\tau \rightarrow 0$ ; unrestricted, nondestructive limit), a power-law long-distance Lévy distribution with  $\mu = \mu_{\text{opt}} \approx 2$  optimizes the search, in agreement with Eqs. (3) and (11). In contrast, for  $\tau \gg 1$  the maximum in  $\eta$  tends to downshift towards  $\mu = 1$ , corresponding to rectilinear ballistic motion between targets (destructive limit). Qualitatively similar results are found for one-dimensional searches.

An entirely different strategy arises if  $r \gg \ell_0$  or  $\lambda \sim r$ , in which cases Rule (A) fairly dominates over Rule (B), thus leading to optimal Gaussian searches ( $\mu_{\text{opt}} \geq 3$ ). In particular, for  $r \gg \ell_0$  waiting near the old site until it regenerates becomes competitive. Therefore,  $\mu_{\text{opt}} \approx 2$  arises as a compromise between the  $\mu = 1$  (by exploring new sites without trying to return to visited sites) and the  $\mu \geq 3$  (wait near the visited site for it to regenerate) strategies.

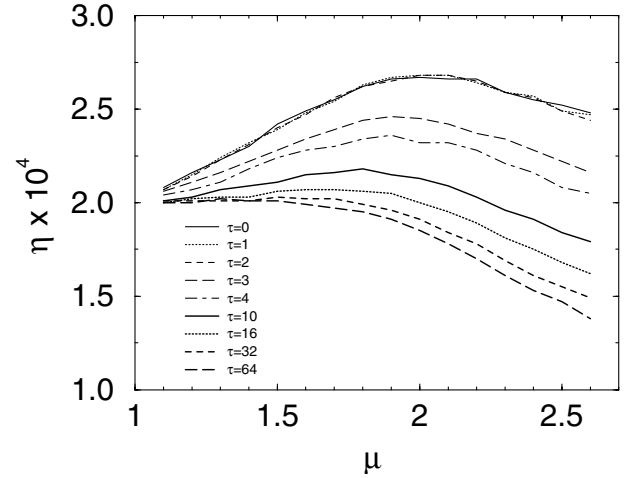


FIG. 1. Efficiency  $\eta$  vs  $\mu$  in two-dimensional searches, for several values of  $\tau$ ,  $r = \ell_0 = 1$ ,  $v = 1$ , and target area density  $\rho = 10^{-4}$  ( $\lambda \gg r$ ). When target sites are allowed to be visited at any time ( $\tau \rightarrow 0$ ), a power-law long-distance Lévy distribution with  $\mu = \mu_{\text{opt}} \approx 2$  optimizes the search, in agreement with Eqs. (3) and (11). In contrast, for  $\tau \gg 1$ , the maximum in  $\eta$  tends to downshift towards  $\mu = 1$ , corresponding to rectilinear ballistic motion between targets. Qualitatively similar results are found for one-dimensional searches.

The above discussion, based on a statistically defined efficiency function, does not take into account the influence of dissipative phenomena that might be important in realistic searches such as animal foraging. We therefore introduce an arbitrary locomotion energy cost function  $f(\langle L \rangle)$ , assigned to the average distance traveled between two target sites and conditioned only by being monotonically increasing. The new efficiency function is now  $\eta_E = \langle E \rangle / \langle L \rangle$ , where the average total length of the walk,  $\langle L \rangle$ , can be approximated [20] by the product  $N\langle L \rangle$ , where  $N$  denotes the mean number of visited sites. The mean net energy  $\langle E \rangle$  gained by the searcher in finding randomly distributed target sites (e.g., calories, nutrients, etc. in the case of animal foraging) is similarly written as  $\langle E \rangle = N\langle E_s \rangle$ , with  $\langle E_s \rangle = \varepsilon - f(\langle L \rangle)$  the net mean energy gained per target site found, and  $\varepsilon$  the gross mean energy gained per target. Here a natural constraint,  $\langle E \rangle > 0$ , emerges since the average energy cumulated in the foraging must be positive.

By writing

$$\eta_E = (\varepsilon - f) \eta, \quad (12)$$

where  $\eta = 1/\langle L \rangle$  is the statistical efficiency (defined as the number of targets found divided by total distance traveled [4]), the extremization of  $\eta_E$  implies  $F(\eta)d\eta/d\mu = 0$ , with  $F(\eta) = \varepsilon - f - \eta df/d\eta$ . The possible extrema of  $\eta_E$  thus arise either from the extrema of  $\eta$  or from the zeros of  $F$ . Regarding the latter, we recall the energy constraint  $\langle E_s \rangle = \varepsilon - f > 0$  and observe that  $df/d\eta < 0$ , since  $f$  is an increasing function

of  $\langle L \rangle = 1/\eta$ . Therefore,  $F > 0$  and the extrema of  $\eta_E$  coincide with those of the statistical efficiency  $\eta$ . Finally, since  $d^2\eta_E/d\mu^2 < 0$  at the extrema points, they are characterized as maxima of the energy efficiency. However, although the introduction of an arbitrary cost function does not change the results for the optimal value  $\mu_{\text{opt}}$ , its presence might significantly limit the range of acceptable values for  $\mu$  due to the energy constraint  $\langle E \rangle > 0$ .

In summary, we have found that the best search strategy for a searcher to follow is strongly dependent on the target-site revisitability delay time  $\tau$  during which a previously visited site becomes unavailable for future visits. When there is no advantage in waiting for the previously found site to regenerate, and when target sites are not likely to be found in the immediate vicinity of the searcher, then we find that the best search strategy always involves power laws, with the optimal exponent restricted to the interval  $1 < \mu_{\text{opt}}(\tau) \leq 2$ . Specifically, we find that  $\mu \approx 2$  for  $\tau \rightarrow 0$  (nondestructive limit) and  $\mu \rightarrow 1$  for  $\tau \rightarrow \infty$  (destructive limit). In this regime we also find that space-limited Gaussian strategies [14] (corresponding to  $\mu \geq 3$ ) lead to rather inefficient searches. The optimal value  $\mu_{\text{opt}}$  remains robust with respect to the introduction of an arbitrary cost function assigned to the search trajectory so long as  $\ell_0 \geq r$  and does not depend on the details of the dissipative process. Nevertheless, the presence of such energetic constraints significantly limits the range of acceptable values for  $\mu$ .

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