# Are Lévy strategies in intermittent search processes advantageous?

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Intermittent search processes switch between local Brownian search events and ballistic relocation phases. We demonstrate analytically and numerically in one dimension that when relocation times are Lévy distributed resulting in a Lévy walk dynamics, the search process significantly outperforms the previously investigated case of exponentially distributed relocation times: The resulting Lévy walks reduce oversampling and thus further optimize the intermittent search strategy in the critical situation of rare targets. We also show that a searching agent, that uses the Lévy strategy, is much less sensitive to the target density, which would require considerably less adaptation by the searcher.

Search processes | random processes | optimization | Lévy walk | movement ecology

#### Introduction

Random search processes occur in many areas, from chemical reactions of diffusing reactants [1] to the foraging behavior of bacteria and animals [2, 3]. Of general importance is the search efficiency. Brownian search in one and two dimensions involves frequent returns to an area, leading to oversampling. Higher efficiency, for instance, can be achieved by facilitated diffusion in gene regulation [4] or by controlled motion in foraging [2, 3]. From theoretical and data analysis Lévy strategies, in which the searching agent performs excursions whose length is drawn from distributions with a heavy tail

$$\lambda(x) \simeq |x|^{-1-\alpha},$$
[1]

for  $0 < \alpha < 2$  were shown to be advantageous [5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16]: occasional long excursions assist in exploring previously unvisited areas and significantly reduce oversampling.

As an alternative to Lévy search, intermittent strategies have been introduced to improve the efficiency of diffusive search [17, 18, 19, 20]. Intermittent search requires that the searcher occasionally shifts focus from the search and concentrates on fast relocation. The relocation phase implies that the searcher is wasting time in the short run as the target cannot be spotted during it. However, the overall search efficiency is improved by introducing the searcher to previously unexplored areas [17, 18, 19, 20].

In Refs. [18, 19] relocation events were assumed to occur in a random direction for exponentially distributed time spans, giving rise to a Markovian process. We show here analytically and numerically in one dimension that this is only a partial solution to oversampling, as eventually the central limit theorem (CLT) reduces the process to a Brownian random walk with jumps on the scale of  $v\tau_2$ , where  $\tau_2$  is the typical time spent in a relocation event. In practice, revisits can be reduced by adjusting the average time spent in search and relocation phases to the density of targets. Lévy strategies on the other hand fundamentally circumvent the CLT and we here demonstrate a twofold advantage of them over the exponential distribution: Lévy walk in-

termittent processes find the target faster than exponential strategies in the critical case of rare targets, and their performance is much less dependent on adapting to the target density.

#### Intermittent search with Lévy relocations

Generalizing the model from Ref. [19], we consider two phases: The search phase scanning for the target by diffusive motion with diffusivity D. With probability per time  $\tau_1^{-1}$  the searcher switches to the relocation phase, during which it moves ballistically with velocity v in a random direction [19]. The relocation time is drawn from the waiting time distribution  $\psi(t)$ , which will be considered to be exponential or Lévy stable. The purpose of relocations is to move as quickly as possible away from the area that has just been searched, and thus the searcher is not scanning for the target in this phase. To compare with previous results we take a closed cell approach: the search is performed on an interval of length L with periodic boundary conditions, corresponding to regularly spaced targets with density 1/L. The model can be formulated as an equation for the probability density P(x, t) for the position x of the searcher in the search phase:

$$\frac{\partial P}{\partial t} = \frac{1}{\tau_1} \int_{-L/2}^{L/2} dx' \int_0^\infty dt' W(x - x', t - t') P(x', t') \\ -\frac{1}{\tau_1} P(x, t) + D \frac{\partial^2 P}{\partial x^2} - p_{\rm fa}(t) \delta(x).$$
[2]

The role of the last term on the right hand side is to remove the particle when it arrives at the target placed at x = 0. The density  $p_{fa}(t)$  thus represents the first arrival time at the target, which is determined implicitly by the absorbing boundary condition P(x = 0, t) = 0. The term proportional to the diffusivity D describes the local Brownian motion in the search phase. The term  $-\tau_1^{-1}P(x,t)$  removes the searcher from location x with rate  $\tau_1^{-1}$ . The searcher is then relocated according to the integral expression in which the kernel W(x,t) is the joint probability density of making a relocation of length x during a time t. It is defined by

$$W(x,t) = \frac{\psi(t)}{2} \sum_{n=-\infty}^{\infty} \delta(|x+nL| - vt) .$$
 [3a]

Here the  $\delta$ -coupling enforces that the distance traveled in time t is vt, and the sum over n renders W(x,t) L-periodic in x.  $\psi(t)$  is related to the spatial distribution of the relocations  $\lambda(x)$  by

$$\psi(t) = 2v\lambda(vt).$$
 [3b]

The jump length distribution  $\lambda(x)$  is assumed to be symmetric around x = 0 (no orientational memory).

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The search efficiency is quantified by the mean search time

$$\langle t \rangle = \int_0^\infty dt \, t p_{\rm fa}(t).$$
 [4]

To obtain  $\langle t \rangle$  we Fourier expand

$$P(n,t) = \int_{-L/2}^{L/2} dx \, e^{ik_n x} P(x,t),$$
 [5]

where n is an integer with corresponding wavenumber  $k_n = 2\pi n/L$ , and Laplace transform, where

$$P(n,u) = \int_0^\infty dt \, e^{-ut} P(n,t).$$
 [6]

We find

$$uP(n,u) - \delta_{n,0} = \frac{1}{\tau_1} W(n,u)P(n,u) - \frac{1}{\tau_1}P(n,u) - Dk_n^2 P(n,u) - p_{\rm fa}(u).$$
 [7]

The initial distribution is uniform, P(x, t = 0) = 1/L, since the searcher initially has no information on the target position. Isolating P(n, u), summing over n (note that  $\sum_{n} P(n, u) = P(x = 0, u) = 0$ ), we find for  $p_{\text{fa}}(u)$ ,

$$p_{\rm fa}(u) = \left\{ \sum_{n=-\infty}^{\infty} \frac{u + [1 - \psi(u)]/\tau_1}{u + Dk_n^2 + [1 - W(n, u)]/\tau_1} \right\}^{-1} .$$
 [8]

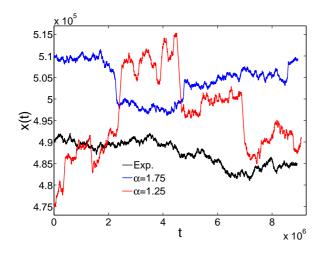
In Laplace space the mean search time  $\langle t \rangle$  yields from expansion of  $p_{\rm fa}$  at small u since  $p_{\rm fa}(u) \sim 1 - \langle t \rangle u + \ldots$  From the average time  $\tau_2$  spent in a single relocation event ( $\psi(u) \sim 1 - \tau_2 u + \ldots$ ), one obtains

$$\langle t \rangle = \sum_{n=1}^{\infty} \frac{2(\tau_1 + \tau_2)}{D\tau_1 k_n^2 + 1 - \lambda(k_n)}.$$
 [9a]

Here,

$$\lambda(k_n) = W(n, u = 0) = \int_{-\infty}^{\infty} dx \ e^{ik_n x} \lambda(x) \qquad [9b]$$

is the Fourier transform of the relocation length distribution  $\lambda(k) = \int_{-\infty}^{\infty} dx \ e^{ikx} \lambda(x)$ , at the discrete wavenumbers  $k_n = 2\pi n/L$ . We



**Figure 1.** *x*-*t* diagram with exponential and Lévy relocations, with  $\tau_1 = 37$ ,  $\tau_2 = 200$ , D = 1, v = 0.1, and  $L = \infty$ .

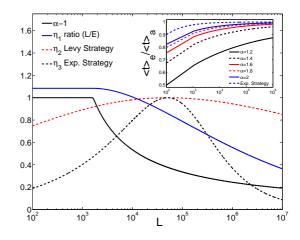
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now use Eq. (9a) to determine the search efficiency of (i) Lévy and (ii) exponentially distributed relocations:

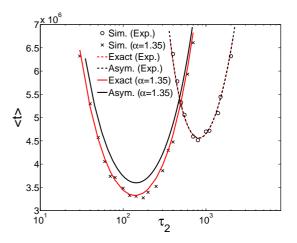
(i) For Lévy distributed relocations we use the symmetric Lévy stable law with characteristic function [21]

$$\lambda(k) = \exp\left\{-\sigma^{\alpha}|k|^{\alpha}\right\}, \quad \sigma = \frac{\pi v \tau_2}{\left[2\Gamma(1-1/\alpha)\right]}.$$
 [10]

From this closed expression the asymptotic form (1) follows. The index  $\alpha$  is restricted to  $1 < \alpha < 2$  so that the mean relocation time  $\tau_2$  is finite. Fig. 1 depicts trajectories for cases of exponential and Lévy relocations, distinguishing the Lévy case with its occasional long relocations.



**Figure 2.** Solid lines: optimal  $\alpha$ , and ratio  $\eta$  of search times for optimal  $\alpha$  vs. exponential strategy, as function of L. Dashed lines: ratio  $\eta = \langle t \rangle_{L,\tau_i(L)} / \langle t \rangle_{L,\tau_i(L_0)}$  of optimal vs. fixed  $\tau_i$  search times as a function of L for exponential and  $\alpha = 1.25$  Lévy strategies ( $L_0 = 5 \times 10^4$ ). The values are calculated using asymptotic Eqs. (14) and (18), and corresponding optimal  $\tau_1$  and  $\tau_2$  [22]. Inset: Convergence of the asymptotic  $\langle t \rangle_a$  (Eqs. (14) and (18)) towards the exact  $\langle t \rangle_e$  (Eq. (9a)) with L for asymptotically optimal  $\tau_i$ . D = 1, v = 1 for all curves.



**Figure 3.** Mean search time for Lévy ( $\alpha = 1.35$ ) and exponential strategies as function of  $\tau_2$  at asymptotically optimal  $\tau_1$  ( $\tau_1 = 37.2$  for Lévy and  $\tau_1 = 411$  for exponential). We chose  $L = 10^5$ , D = 1, v = 1. Simulations versus exact (Eq. (9a)) and asymptotic (Eqs. (14) and (18)) theory.

We introduce three approximations valid for large L:

(a) Assume that  $v\tau_2 \gg \sqrt{D\tau_1}$ , i.e., that the mean relocation distance is much longer than the average distance scanned in a typical search phase. We will see that this is self-consistent with the obtained optimal values of  $\tau_1$  and  $\tau_2$  that have the same *L*-scaling for large *L*. This assumption means that  $D\tau_1k_n^2$  and  $\lambda(k_n)$  are to a good approximation non-zero at different *n*, and we expand

$$\frac{1}{D\tau_1 k_n^2 + 1 - \lambda(k_n)} \sim \frac{1}{D\tau_1 k_n^2 + 1} + \frac{1}{1 - \lambda(k_n)} - 1.$$
 [11]

(b) Assuming that the search range  $\sqrt{D\tau_1}$  is much smaller than *L*, we replace the sum over the first term on the right hand side of Eq. (11) by an integral, yielding

$$\sum_{n=1}^{\infty} \frac{1}{D\tau_1 k_n^2 + 1} \sim \int_0^{\infty} \frac{1}{D\tau_1 k_n^2 + 1} dn = \frac{L}{4\sqrt{D\tau_1}}.$$
 [12]

(c) Since  $\lambda(k_n) \sim 1 - \sigma^{\alpha} |k_n|^{\alpha}$  at small values of  $k_n$   $(k_n \to 0$  at n = 1 in the limit of large L) we approximate the last two terms of Eq. (11). Namely the contribution from the singularity at small n dominates the sum,

$$\sum_{n=1}^{\infty} \left[ \frac{1}{1 - \lambda(k_n)} - 1 \right] \sim \left( \frac{L}{2\pi\sigma} \right)^{\alpha} \zeta(\alpha).$$
 [13]

Here  $\zeta(\alpha) = \sum_{n=1}^{\infty} n^{-\alpha}$  is the Riemann  $\zeta$  function.

Collecting (a) to (c), Eq. (9a) is approximated by

$$\langle t \rangle \sim 2(\tau_1 + \tau_2) \left[ \frac{L}{4\sqrt{D\tau_1}} + \left( \frac{L}{2\pi\sigma} \right)^{\alpha} \zeta(\alpha) \right].$$
 [14]

For honest comparison between Lévy and exponential strategies, we determine the respective optimal  $\tau_1$  and  $\tau_2$ . Solving  $\partial \langle t \rangle / \partial \tau_1 = 0$  and  $\partial \langle t \rangle / \partial \tau_2 = 0$  simultaneously, we obtain from Eq. (14) that at large L

$$\tau_1 \sim (b/a^{\alpha})^{1/(\alpha-1/2)}$$
,  $\tau_2 \sim (b/\sqrt{a})^{1/(\alpha-1/2)}$ , [15]

where (using  $\Omega \equiv \sqrt{1+4(\alpha-1)\alpha})$ 

$$a = (1+\Omega)/(2[\alpha-1]),$$

$$b = 2\sqrt{D} \left[2\alpha + \Omega - 3\right] \zeta(\alpha) L^{\alpha-1} \left[\frac{\Gamma\left(1-\alpha^{-1}\right)}{\pi^2 v}\right]^{\alpha}$$
[16b]

such that the optimal  $\tau_i$  scale with L like  $L^{(\alpha-1)/(\alpha-1/2)}$ . According to Eq. (14),  $\langle t \rangle$  will then scale like  $L^{(3\alpha-2)/(2\alpha-1)}$ , implying that for large L the more efficient search will occur for  $\alpha$  close to 1. However, the prefactor to the L-scaling diverges as  $\alpha \to 1$ , so the optimal choice of  $\alpha$  will be somewhat larger than 1 for any finite L, as demonstrated in Fig. 2. The inset of Fig. 2 shows the validity of the approximate  $\langle t \rangle$  for optimal  $\tau_i$ .

(ii) For exponentially distributed relocation with

$$\psi(t) = \tau_2^{-1} e^{-t/\tau_2}, \qquad [17]$$

approximations (a) to (c) also apply, with  $\sigma = v\tau_2$ . The corresponding results for  $\langle t \rangle$  and optimal  $\tau_i$  obtain by replacing  $\Gamma(1 - 1/\alpha)$  by  $\pi/2$  and taking  $\alpha = 2$ :

$$\langle t \rangle \sim \frac{\tau_1 + \tau_2}{12} \left[ \frac{6L}{\sqrt{D\tau_1}} + \left( \frac{L}{v\tau_2} \right)^2 \right],$$
 [18]

$$\tau_1 \sim \left(D/\left[18v^4\right]\right)^{1/3} L^{2/3}/2, \quad \tau_2 \sim 2\tau_1.$$
 [19]

These expressions agree with those of Ref. [19, 23].

Footline Author

#### Performance of Lévy intermittent search

The search time  $\langle t \rangle$  for exponential strategies scales like  $L^{4/3}$  for optimal  $\tau_1$  and  $\tau_2$ , proving that Lévy strategies with  $1 < \alpha < 2$  are increasingly more efficient than the exponential strategies for decreasing target density. In Fig. 3 we show  $\langle t \rangle$  as function of relocation time  $\tau_2$ .

An additional advantage of Lévy strategies is due the scaling  $\tau_i \simeq L^{(\alpha-1)/(\alpha-1/2)}$  of the optimal  $\tau_i$ : for  $\alpha$  close to unity the optimal strategy becomes insensitive to the target density. This means that it is less important for the searcher to have advance knowledge of the density of targets  $L^{-1}$  if it follows a small  $\alpha$  Lévy strategy, since it can choose  $\tau_i$  that are almost optimal over a broad range of densities. This point is illustrated in Fig. 2.

To understand better the  $\alpha$ -dependence of the Lévy strategy we study the first arrival density  $p_{\rm fa}(t)$  for large L, where again  $L \gg v\tau_2 \gg \sqrt{D\tau_1}$ . We consider times much longer than one relocation-search cycle such that  $\psi(u) \sim 1 - \tau_2 u + \ldots$ , and rewrite Eq. (8) as

$$p_{\rm fa}(u) \sim \frac{1}{u} \frac{\tau_1}{\tau_1 + \tau_2} \frac{1}{W_0(u)} \frac{1}{L} ,$$
 [20]

where we have introduced the term

$$W_0(u) = \frac{1}{L} \sum_{n=-\infty}^{\infty} \frac{1}{u + Dk_n^2 + [1 - W(n, u)]/\tau_1} .$$
 [21]

The last expression can be simplified following similar approximations as for  $\langle t \rangle$  before. The separation of length scales leading to approximation (a) allows us to write

$$W_0(u) \sim \frac{\tau_1}{L} \sum_{n=-\infty}^{\infty} \left[ \frac{1}{D\tau_1 k_n^2 + 1} + \frac{1}{\tau_1 u + 1 - W(n, u)} - 1 \right].$$
[22]

For the last two terms in Eq. (22) the contribution at small n again dominate the sum (approximation (c)); expanding W(n, u) at small  $k_n$  and u produces  $W(n, u) \sim 1 - \sigma^{\alpha} |k_n|^{\alpha} - \tau_2 u$ . Collecting the results, we find

$$W_0(u) \sim \frac{\tau_1}{L} \sum_{n=-\infty}^{\infty} \left[ \frac{1}{D\tau_1 k_n^2 + 1} + \frac{1}{(\tau_1 + \tau_2)u + \sigma^{\alpha} |k_n|^{\alpha}} \right].$$
[23]

We focus on times short enough such that the *L*-periodicity of the problem does not yet play a role, so that Laplace space  $u \gg (\sigma^{\alpha}|k_n|^{\alpha})/(\tau_1 + \tau_2)$  at n = 1. In this approximation we replace the sum  $L^{-1}\sum_{n=-\infty}^{\infty}$  by the integral  $\int_{-\infty}^{\infty} dk_n/(2\pi)$ , obtaining

$$W_0(u) \sim \frac{1}{2\sqrt{D\tau_1^{-1}}} + \frac{\tau_1/[\alpha \sin(\pi/\alpha)\sigma]}{[u(\tau_1 + \tau_2)]^{1-1/\alpha}}.$$
 [24]

For shorter times (corresponding to larger u) we discard the subdominant second term in Eq. (24). Laplace inversion of Eq. (20) then produces

$$p_{\rm fa}(t) \sim 2\sqrt{D\tau_1} / \left[ L(\tau_1 + \tau_2) \right].$$
 [25]

At later times (smaller u) the second term in Eq. (24) dominates, and the plateau (25) turns into

$$p_{\rm fa}(t) \sim \frac{\alpha}{2} \left[ \sin\left(\frac{\pi}{\alpha}\right) \right]^2 \frac{v\tau_2}{L \left(\tau_1 + \tau_2\right)^{1/\alpha} t^{1-1/\alpha}}.$$
 [26]

The crossover between these two regimes occurs when the values of expressions (26) and (25) become equal, i.e., at

$$t \sim (\tau_1 + \tau_2) \left\{ \alpha [\sin(\pi/\alpha)]^2 v \tau_2 / \left[ 4\sqrt{D\tau_1} \right] \right\}^{\alpha/(\alpha-1)}.$$
 [27]

PNAS | Issue Date | Volume | Issue Number | 3

### Discussion

In Eq. (25),  $2\sqrt{D\tau_1}$  is the average length scanned in a search event. Division by *L* yields the probability to find the target during this phase, and  $1/(\tau_1 + \tau_2)$  is the rate at which the search phase itself occurs. A crucial part in this interpretation is that the probability of searching in a previously scanned area is negligible. This assumption will break down at some point because of the searcher's lack of orientational memory. The searcher will then begin to revisit explored regions with a reduced probability of finding the target as a result. This causes the crossover to the power-law behavior (26). Fig. 4 shows the turnover from plateau to inverse power-law of the first arrival. At even longer times, finite size effects cause a turnover to an exponential decay.

From Eq. (26) the advantage of having  $\alpha$  close to unity at large L becomes evident: the presence of rare but long relocation events reduces the risk of rescanning already visited areas which will be important for large L. However, the downside to choosing an  $\alpha$ -value too close to 1 is that an increased amount of very long relocations implies an increased amount of very short ones too, as the average distance is fixed by  $v\tau_2$  [24]. This means that the crossover to the less favorable situation described by Eq. (26) happens earlier, so that larger  $\alpha$  becomes more efficient for shorter search times relevant at smaller L.

Intermittent strategies are beneficial when purely diffusive search would slow down over time due to the increasing returns to previously scanned areas (oversampling). Choosing an exponential strategy for relocations, however, only partially solves this problem: At times  $t \gg \tau_2$ , the CLT governs, leading to oversampling on a typical scale  $v\tau_2$ . Conversely, Lévy-intermittent strategies are not bound to the CLT, rendering them a more amenable solution to reduce oversampling and therefore advantageous in the search for rare targets. Although less pronounced, the problem of oversampling still occurs in two dimensional search studied in [18]. Lévy strategies are expected to improve the search efficiency in this case, as well; however, as to what extent remains to be established quantitatively.

Based on our results we advocate that intermittent strategies should not be thought of as alternatives to Lévy strategies. In contrast, the synergistic combination of intermittent search and Lévy relocation strategies turns out to be beneficial. Moreover, a given Lévy walk intermittent search strategy (with fixed  $\tau_i$ ) is almost optimal over a wide range of sparse target densities, which might be a strategic advantage for creatures that have limited abilities to adjust their search parameters.

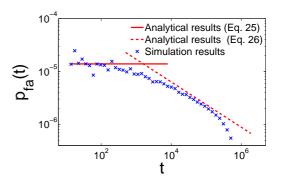
We note, however, that the small scaling exponent of  $\langle t \rangle$  with L for the Lévy strategy is not a result of the Lévy part of the strategy alone. To explain what we mean by this we will define the pure Lévy strategy as a strategy where the searcher only quickly tests his immediate neighborhood for the target at the end of each relocation. Thus we assume that  $\tau_1$  has a small finite value (alternatively the target could have a small finite size and  $\tau_1 = 0$ ) and only consider optimization of the strategy with respect to  $\tau_2$ . Doing this we find from our analytic asymptotic result that the optimal  $\tau_2$  scales with L as  $L^{1-1/\alpha}$  and that this results in a scaling  $\langle t \rangle \simeq L^{2-1/\alpha}$ . A scaling which increases faster with L for any  $\alpha > 1$  compared with the result where  $\tau_1$  is also optimized. And it is only an improvement over the optimized exponential strategy when  $\alpha < 3/2$ . Without any optimization the Lévy strategy would result in  $\langle t \rangle \simeq L^{\alpha}$ , a scaling that that is still

better than for the optimized exponential strategy when  $\alpha < 4/3$ .

A remark on the recent discussion about the empirical observation of Lévy distributions of relocation lengths in animal foraging is in order. Thus, while the original publications provided evidence of long-tailed relocation lengths in accordance with theoretical considerations [7, 8, 6], a reanalysis of the data reveals that the original data contained few extreme events for the flight times after removal of which the data no longer unequivocally allow an interpretation as Lévy pattern [25]. In that paper also few other previous claims of Lévy foraging patterns were invalidated. This has caused some uncertainty about the general relevance of Lévy search patterns in animal foraging [26]. Among the recent criticisms of reference [25] we refer to the consideration of finite size effects of real trajectories in reference [27] that were shown to reestablish the validity of a Lévy based search mechanism for the albatross flight. It is our belief that Lévy search models show a distinct advantage over strategies governed by the central limit theorem. However, it will require considerably larger data sets to be able to tell for sure whether typically animals use a specific search strategy. The value of this and similar theoretical studies is to provide a framework for the analysis of data that are being collected now or in the future. The robustness of the search efficiency of Lévy strategies to changing target densities, as demonstrated here for the first time, appears to be a key concept in the discussion of search mechanisms, and potentially an important evolutionary advantage.

Our analysis relies on the assumption that each relocation is pointed toward a random direction. This will be a good model for "non-intelligent" search, similar to bacterial movement in absence of chemical or temperature gradients during which tumbling motion changes with directed motion [2]. Intelligent creatures will improve the target search by partial or complete memory, avoiding previously visited locations. It will be interesting to study in more detail models with search memory.

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**Figure 4.** First arrival density versus time. The crosses are simulation data, while the straight lines are the intermediate regimes of Eq. (25) and Eq. (26). Parameters are:  $\tau_1 = 35$ ,  $\tau_2 = 50$ ,  $L = 10^4$ ,  $\alpha = 1.75$ , v = 1 and D = 1.

- von Smoluchowski M (1916) Drei Vorträge über Diffusion, Brownsche Bewegung und Koagulation von Kolloidteilchen (Three presentations on diffusion, Brownian motion, and coagulation of colloidal particles), *Physikal. Zeitschr.* 17 557-585.
- 2. Berg HC (1993) Random walks in biology (Princeton University Press, Princeton).
- 3. Bell WJ (1991) Searching Behaviour (Chapman & Hall, London).
- von Hippel PH, Berg OG (1989) Facilitated target location in biological systems, J. Biol. Chem. 264, 675-678. (1989) Facilitated target location in biological systems.
- Shlesinger MF, Klafter J (1986) in On growth and form, eds Stanley HE, Ostrowsky N (Martinus Nijhoff Publishers, Amsterdam), pp. 279-283.
- Viswanathan GM, Afanasyev V, Buldyrev SV, Murphy EJ, Prince PA, Stanley HE (1996) Lévy flight search patterns of wandering albatrosses, *Nature* 381 413-415.
- Viswanathan GM, Buldyrev SV, Havlin S, da Luz MGE, Raposo EP, Stanley HE (1999), Optimizing the success of random searches, *Nature* 401, 911-914.
- Faustino CL, Silva LR, Luz MG, Raposo EP, Viswanathan GM (2007) Search dynamics at the edge of extinction: Anomalous diffusion as a critical survival state. *EPL (Europhysics Letters)* 77 30002.
- Reynolds AM, Frye MA (2007) Odor tracking in Drosophila is consistent with an optimal intermittent scale-free search *PLoS ONE* 2(4) e354.
- Brown CT, Liebovitch LS, Glendon R (2007) Léy flights in Dobe Ju/'hoanso foraging patterns, Human Ecology 35 129-138.
- 11. Atkinson RPD, Rhodes CJ, Macdonald DW, Anderson RM (2002) Scale-free dynamics in the movement patterns of jackals, *OIKOS* **98**, 134-140.
- Ramos-Fernandez G, Mateos JL, Miramontes O, Cocho G, Larralde H, Ayala-Orozco B (2003) Lévy walk patterns in the foraging movements of spider monkeys (Ateles geoffroyi), *Behav. Ecol.* Sociobiol. 55, 223-230.
- Bartumeus F (2007) Lévy processes in animal movement: an evolutionary hypothesis, Fractals 15, 151-162.
- Lomholt MA, Ambjörnsson T, Metzler R (2005) Optimal target search on a fast-folding polymer chain with volume exchange *Phys. Rev. Lett.* 95, 260603.

- Bartumeus F, Catalan J, Fulco, UL, Lyra ML, Viswanatham, GM (2002) Optimizing the encounter rate in biological interactions: Lévy versus Brownian strategies, *Phys. Rev. Lett.* 88, 097901.
- 16. Sims DW et al. (2008) Nature 451, 1098.
- Bénichou O, Coppey M, Moreau M, Suet P-H, Voituriez R (2005) Optimal search strategies for hidden targets *Phys. Rev. Lett.* 94, 198101.
- Bénichou O, Loverdo C, Moreau M, Voituriez R (2006) Two-dimensional intermittent search processes: an alternative to Lévy flight strategies *Phys. Rev. E* 74, 020102R. Reviewed in: Shlesinger MF (2006) Mathematical physics: search research, *Nature (London)* 443, 281-282.
- Bénichou O, Coppey M, Moreau M, Voituriez R (2006) When losing time becomes efficient, *Europhys. Lett.* 75, 349-354.
- Oshanin G, Wio HS, Lindenberg K, Burlatsky SF (2007) Intermittent random walks for an optimal search strategy: one-dimensional case, J. Phys. Cond. Mat. 19, 065142.
- Metzler R, Klafter J (2000) The random walk's guide to anomalous diffusion: a fractional dynamic approach, *Phys. Rep.* 339, 1-77.
- 22. Allowing  $\alpha$  to range between 1 and 2.
- Note the typo in the expression for (t) in Eq. (5) of Ref. [19]: coth(1/[2αL]) should be coth(αL/2).
- 24. Corresponding to the stronger pronounciation of the central part around x = 0 of stable laws for decreasing  $\alpha$ .
- Edwards AM, Phillips RA, Watkins NW, Freeman MP, Murphy EJ, Afanasyev V, Buldyrev SV, da Luz, MGE, Raposo EP, Stanley HE, Viswanathan GM (2007) Revisiting Léy flight search patterns of wandering albatrosses, bumblebees and deer, *Nature (London)* 449 1044-1048.
- 26. Travis J (2007) Do wandering Albatrosses care about math?, Science 318 742-743.
- Boyer D, Miramontes O, Ramos-Fernández G (2008) Evidence for biological Lévy flights stands, E-print arXiv:0802.1762.