Lévy flight random searches in biological phenomena

G.M. Viswanathan[a,*], F. Bartumeus[a,b,c], Sergey V. Buldyrev[d],
J. Catalan[c], U.L. Fulco[a], Shlomo Havlin[d,e], M.G.E. da Luz[f],
M.L. Lyra[a], E.P. Raposo[g], H. Eugene Stanley[d]

[a] *Departamento de Física, Universidade Federal de Alagoas, 57072-970, Maceió–AL, Brazil*
[b] *Departament d'Ecologia, Facultat de Biologia, Universitat de Barcelona, Diagonal 645,*
08028 Barcelona, Spain
[c] *Centre d'Estudis Avançats de Blanes, CSIC, Accès a Cala St. Francesc. s/n 17300 Blanes, Spain*
[d] *Center for Polymer Studies and Department of Physics, Boston University, Boston, MA 02215, USA*
[e] *Gonda-Goldschmied Center and Department of Physics, Bar Ilan University, Ramat Gan, Israel*
[f] *Departamento de Física, Universidade Federal do Paraná, 81531-990, Curitiba–PR, Brazil*
[g] *Laboratório de Física Teórica e Computacional, Departamento de Física,*
Universidade Federal de Pernambuco, 50670-901, Recife–PE, Brazil

Abstract

There has been growing interest in the study of Lévy flights observed in the movements of biological organisms performing random walks while searching for other organisms. Here, we approach the problem of what is the best statistical strategy for optimizing the encounter rate between "searcher" and "target" organisms—either of the same or of different species—in terms of a limiting generalized searcher–target model (e.g., predator-prey, mating partner, pollinator–flower). In this context, we discuss known results showing that for fixed targets an inverse square density distribution of step lengths can optimize the encounter rate. For moving targets, we review how the encounter rate depends on whether organisms move in Lévy or Brownian random walks. We discuss recent findings indicating that Lévy walks confer a significant advantage for increasing encounter rates only when the searcher is larger or moves rapidly relative to the target, and when the target density is low.
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* Corresponding author. Fax: +55-82-214-1645.
  E-mail address: gandhi@fis.ufal.br (G.M. Viswanathan).

1. Introduction: the random search problem

An important application of two-species reaction–diffusion processes relates to the problem of what is the best statistical strategy for a searching organism [1,2] to adopt in order to find randomly located "targets" [3–5]. This application to biological phenomena is important because living organisms need to interact with individuals of other species (e.g., for obtaining food) or of their own species (e.g., in sexual reproduction). Biological interactions can be inter-specific, the most common being a trophic interaction between a consumer and a consumable, adopting the form of predation, parasite infection or mutual rewarding (e.g., flowers and pollinators), but also occur between individuals of the same species, the case of mating being particularly relevant. A null encounter rate can have a disastrous effect on essential biological processes such as feeding and sexual reproduction, while an optimized encounter rate could in principle confer significant advantages to the searchers or targets. The general problem of how to optimize the encounter rate is challenging partially because the searchers typically have a certain degree of "free will" to move and search according to their choice. On the other hand, they are subject to physical and biological constraints which restrict their behavior.

The richness of the problem is also due to the "ignorance" of the searchers concerning the locations of the randomly located targets. However, even if the positions of all target sites were completely known in advance by a "demon" as resourceful as Laplace's, the problem of what sequential order to visit the sites in order to reduce the energy costs of locomotion is itself rather challenging: the famous "traveling salesman" optimization problem. The ignorance of the target site locations, however, introduces yet another level of difficulty and renders the problem unsuited to deterministic search algorithms that do not use some element of randomness. Indeed, only a statistical approach to the search problem can deal adequately with the element of ignorance.

2. Lévy vs. Brownian searching

2.1. Fixed targets

In our general approach to the encounter rate problem, we distinguish the two interacting organisms either as a "searcher" (e.g., predator, forager, parasite, pollinator, male) or a "target" (e.g., prey, food, female). The searcher "consumes" targets, and we seek the optimal search strategy to maximize encounter rates. Recently, studies [3,4] have shown that the optimal strategy for a searcher looking for sparsely and randomly distributed fixed targets that can be visited any number of times is an inverse square power-law distribution of flight lengths, corresponding to Lévy flight motion [2–4]. In this case of "non-destructive" searching, the searcher can visit the same target site many times due to either of two reasons: (i) if the target sites become temporarily depleted, or (ii) if the forager becomes satiated and leaves the area. In the case of "destructive" searching, when the target found by the searcher becomes undetectable in subsequent flights, it was shown that the optimal strategy is for the searcher effectively to move

along straight lines between finding targets. Note that in both these cases of destructive and non-destructive searching, a Lévy strategy leads to a higher encounter rate than a Brownian strategy. Indeed, Lévy search strategies are experimentally observed [3]. However, not all organisms opt for a Lévy strategy always [3,5]. The question thus arises as to under which conditions a Lévy search strategy becomes *significantly* better than a Brownian strategy.

2.2. Moving targets

Very recently, there has been a study of how the relative advantage of Lévy searching depends—in a complex (and perhaps hierarchical) manner—on variables such as target density, the type of target movement and the target-to-searcher size and velocity ratios r and v. Below we discuss this latest development in greater detail, focusing on the theoretically important case of one dimensional (1-D) systems, in which diffusion-induced density fluctuations away from the mean field behavior are more relevant than in the (computationally more expensive) 2-D and 3-D cases. Another reason for studying the 1-D case is that the benefits of Lévy searching—at least for fixed target [3]—are mainly independent of the number d of spatial dimensions, for reasons that are analogous to how quantities such as the mean square displacement of Brownian and Lévy random walks are d-independent. Furthermore, many organisms do actually perform searches over nearly 1-D space, e.g., fish species that search in coastal or river ecosystems, and species that search in grassland–forest interfaces.

The simulated systems consisted of a single searcher and a single moving target in an interval of size L, under periodic boundary conditions. By varying the system size, effectively the target densities can also be varied. These "organisms" move with constant scalar velocity, but with random directions and step lengths ℓ_j chosen from a generalized Lévy probability density distribution with a power-law tail: $P(\ell_j) \sim \ell_j^{-\mu}$. For $\mu \geqslant 3$ the motion is equivalent to Brownian random walks, because the mean square displacement scales linearly with time, while for $\mu = 2$ the scaling becomes quadratic in time. Generally the encounter rate is defined as the number of encounters per unit volume swept. In a 1-D scenario the definition has to be adapted such that the encounter rate is the mean number of encounters per distance swept, which in this case will be the total distance traveled. This definition of the encounter rate is essentially identical to the definition of search efficiency used in Ref. [3]. Model variables are all dimensionless. There are different combinations of target-to-searcher velocity ratios v and size ratios r for Lévy ($\mu_t = 2$) and Brownian ($\mu_t = 3$) targets. For each of these scenarios, we can study the encounter rate for the cases in which the searcher performs Lévy ($\mu_s = 2$) and Brownian ($\mu_s = 3$) random walks. To evaluate the best search behavior, one defines γ as the ratio between the encounter rates for the Lévy and the Brownian searchers moving in identical environments and traversing identical total distances. A value $\gamma > 1$ represents a benefit for the searcher adopting a Lévy strategy over a Brownian strategy.

Fig. 1 is a grey-scale plot of the value of γ against r and v for Lévy and Brownian targets. White corresponds to large $\gamma > 2.5$ while black to $\gamma \leqslant 1$. For larger L (i.e., lower target densities), Lévy searching becomes better than Brownian for a wider range
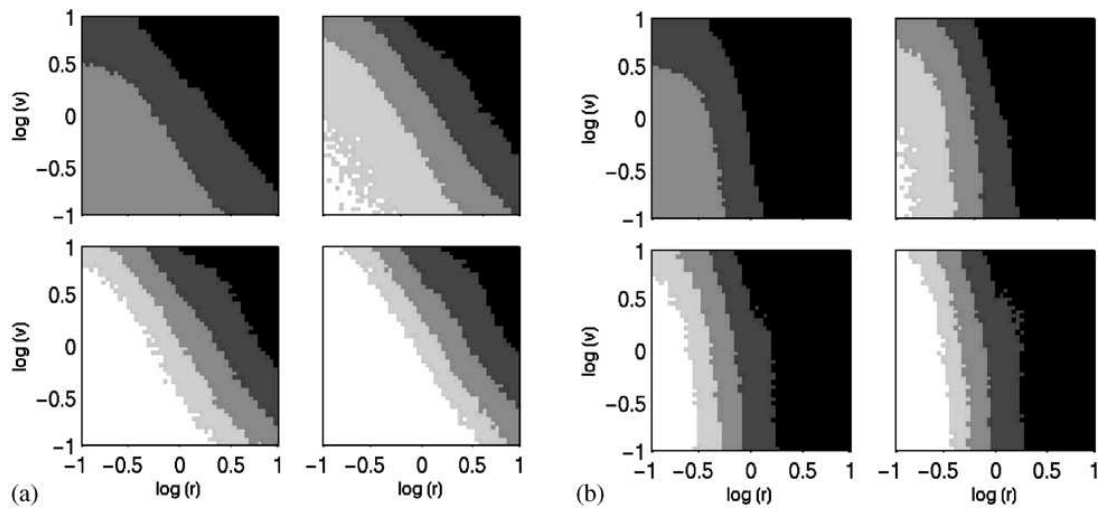
Fig. 1. Grey-scale graph showing γ as a function of r and v for (a) Brownian targets and (b) Lévy targets. Each set of four graphs corresponds to increasing system size $L = 25$, $L = 50$, $L = 75$, and $L = 100$ from top-left to bottom-right. The areas in white correspond to the case in which Lévy searching is significantly advantageous ($\gamma > 2.5$) while black indicates no advantage [5].

of size and velocity ratio combinations. High target densities recover Brownian searcher strategies as optimal. For Brownian target motion (Fig. 1(a)), the white area expands diagonally from left-bottom (small r, v) to right-top (large r, v) as system size increases (following the set of four graphs). In Lévy target motion scenarios (Fig. 1(b)), the white area expands more vertically. Therefore, size and velocity ratios r and v can both be considered as equally important in order to define the optimal search strategy for Brownian targets, in contrast to when searching for Lévy targets.

3. Discussion

A new result with biological implications has thus been uncovered: the qualitative movement of targets is also important for knowing which search strategy is best. Generally, it is clear that for Brownian targets, searchers larger and faster than their targets render Lévy searchers more efficient than Brownian searchers. However, the contrary is true for searchers smaller and slower than their targets. Lévy targets effectively "screen" size ratio effects, and, in this case, the best type of searching motion mainly depends on velocity ratios: for searchers faster than their targets, Lévy searching is optimal; while for searchers slower than their targets, Brownian searching is better.

Since environmental and biological situations in nature are highly variable, it is conceivable that different optimal search strategies should naturally evolve. From Fig. 1 it is clearly seen that Lévy motion does not lead to significantly higher encounter rates always, except only for scarce, small and slow target scenarios. An important consequence of this result is that we can expect Brownian motion to have evolved naturally as one possible optimal search strategy. The optimal type of searching mo-

tion depends in a complex (and perhaps hierarchical) manner on variables such as target density, the type of target movement and the size and velocity ratios between searchers and targets (r, v). As expected, Lévy motion is not beneficial to the searcher for small L. This situation corresponds to high target density in the real world, hence our results are consistent with known results for fixed targets [3] showing that Lévy searching confers no advantages unless the target density is low. For a wide range of proposed scenarios (r and v ratios), low target densities enhance the benefits of Lévy searching.

For a given target density, the type of target motion is important in order to choose the best search strategy (Fig. 1). For Brownian targets, velocity and size ratios between target and searchers are equally important and have a (more or less) symmetrical effect on the optimal strategy. Lévy motion in targets diminishes what may be called the "target density effect". Although a lower target density also improves Lévy searching, this density effect is not as dominant when targets move in a super-diffusive manner [5]. In low density and Lévy target scenarios, Brownian searchers still have acceptable efficiencies (Fig. 1(b)). The non-relevance of size and the reduction of the "target density effect" for the optimal search strategy when searching for Lévy targets renders the Brownian search strategy optimal in the specific situations in which searchers are slower than their targets even for low target densities (Fig. 1(b)). Some examples could be parasitic insects or planktonic searchers.

Relative size also plays an important role in the choice of optimal strategy, being more importand for Brownian than for Lévy targets. For high values of r the best searching strategy is mainly dependent on the relative velocity and L, regardless of the type of terget movement, as can be seen from the similarities of Figs. 1a and 1b for large r. Prey to predator size ratios are far from being unity in Nature (e.g., in planktonic organisms [5]). The "effective size" of the searcher or target could even be larger than the actual geometrical diameter or maximum body length. For the searcher, it can be defined as the distance up to which a target (or its wake) enters its influential area, defined by different chemical, mechanical or visual types of perception involved in any searching and detection interaction process, or just the feeding currents or concentration gradients generated by predators. The effective size of targets could be any chemical, mechanical or visual wake (or cue) left by preys.

In summary, the faster and the more super-diffusive the target motion, the less advantageous it is to adopt a Lévy strategy, hence the greater the advantage for Brownian and slow searchers. For such targets, the most efficient search strategy is not to move at all, because the preys will come by themselves! Hence, emerges the ambushing strategy.

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