Review

Lévy flights and superdiffusion in the context of biological encounters and random searches

G.M. Viswanathan [a],[*],[1], E.P. Raposo [b], M.G.E. da Luz [c]

[a] *Instituto de Física, Universidade Federal de Alagoas, 57072-970 Maceió, AL, Brazil*
[b] *Laboratório de Física Teórica e Computacional, Departamento de Física, Universidade Federal de Pernambuco, 50670-901 Recife, PE, Brazil*
[c] *Departamento de Física, Universidade Federal do Paraná, 81531-990 Curitiba, PR, Brazil*

Abstract

We review the general problem of random searches in the context of biological encounters. We analyze deterministic and stochastic aspects of searching in general and address the destructive and nondestructive cases specifically. We discuss the concepts of Lévy walks as adaptive strategies and explore possible examples. We also review Lévy searches in other media and spaces, including lattices and networks as opposed to continuous environments. We analyze empirical evidence supporting the Lévy flight foraging hypothesis, as well as the more general idea of superdiffusive foraging. We compare these hypothesis with alternative theories of random searches. Finally, we comment on several issues relevant to the practical application of models of Lévy and superdiffusive strategies to the general question of biological foraging.
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[*] Corresponding author.
  E-mail address: Gandhi.Viswanathan@pq.cnpq.br (G.M. Viswanathan).
[1] Present address: Consortium of the Americas for Interdisciplinary Science, University of New Mexico, 800 Yale Blvd. NE, Albuquerque, NM 87131, USA.

1. Biological encounters

Biological encounters typically involve a diffusive aspect, movement, as well as a reactive component, such as eating or mating. They thus represent a special case of reaction–diffusion processes with relevance not only in physics and chemistry, but also for understanding diverse phenomena in geology, biology, and even social sciences. Two-species reaction–diffusion models can be used to describe many ecological systems [1–9]. In particular, one important application relates to the general problem of regulating encounter rates between organisms. It represents a scientifically important issue of broad interest because living organisms need to interact with individuals of other species or of their own. To a large extent, biological interactions fall into two general categories: (i) inter-specific interaction, typically a trophic interaction between a consumer and a consumable, adopting the form of predation, parasite infection or mutual rewarding (e.g., flowers and pollinators); and (ii) interaction between individuals of the same species, e.g., mating or territorial competition. Thus, factors conditioning encounter rates between organisms are believed to play a crucial role in the ecological constraints important in the evolution of life [9]. These interactions can involve many potential factors and multiple ecological adaptive pathways [10].

Search strategies represent one of the most important factors that can modulate the rate of encounters. Hence, considering the above context, strategy choices can become essential in determining the fitness of a given species. This possibility is rendered further plausible because searches—and locomotion in general—require the expenditure of metabolic energy. Inefficient search could deplete energy reserves and lead to rates of encounters below a minimum acceptable threshold.

The framework of the search problem [9] distinguishes between two kinds of interacting organisms. They are either a "searcher", e.g., forager, predator, parasite, pollinator, the active gender in the search activity involved in the mating process, or else they are a "target", e.g., prey, food, the passive gender in the mating activity. Regarding the nature of the searching drive, in certain instances it can be guided almost entirely by external cues, either by the cognitive (memory) or detective (olfaction, vision, etc.) skills of the searcher. However, in many situations the movement is not-oriented [11], thus becoming in essence a stochastic process. Therefore, in such cases [12] (and even when a small deterministic component in the locomotion exists [12,13]) it is a random search that defines the final outcomes of biological encounters.

Generally, we can state the random search problem in terms of the following question: what is the most efficient strategy for searching randomly located objects whose exact locations are not known *a priori*? Performing efficient searches is not a trivial or straightforward task for a number of reasons. On the one hand, the searchers typically have a certain degree of "free will" to move and search according to their choice. By "free will" we refer not to contra-causal
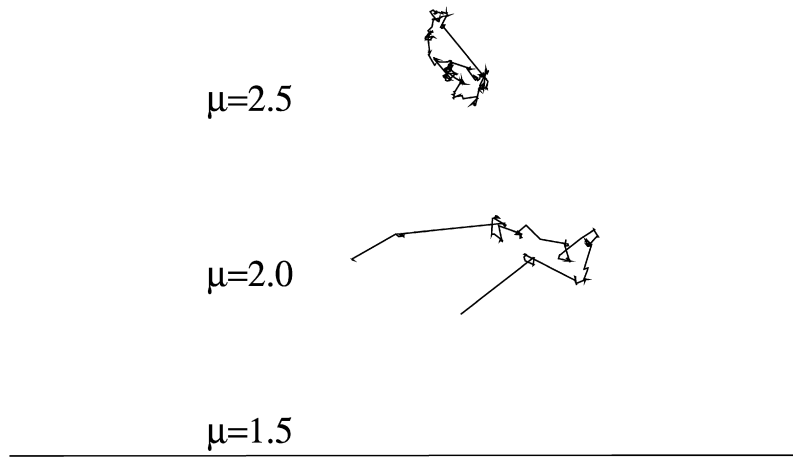
Fig. 1. Illustration of Lévy walks with different values of μ. Values close to unity lead to ballistic paths, whereas values closer to $\mu = 3$ lead to more Brownian behavior. The variance of the flight lengths diverges below $\mu = 3$.

behavior but rather to the degree of autonomy commonly seen in human beings and other organisms. On the other hand, organisms are subject to certain physical and biological constraints, which restrict their modes of action. For example, a predator cannot search for so long without finding food, or it will perish.

The inherent complexity and dynamical richness implied by the random search problem carries over to the application to biological encounters. All these are exactly the points we shall address in the present review.

2. The Lévy flight foraging hypothesis

The Lévy flight foraging hypothesis states that since Lévy flights (actually, truncated Lévy flights; see below) optimize random searches, biological organisms must have therefore evolved to exploit Lévy flights [8]. A Lévy flight is a process where at each time step j the random walker makes an instantaneous jump ℓ_j chosen from a probability density function $P(\ell)$ which has a power law tail in the long-distance regime:

$$P(\ell) \sim \ell^{-\mu}, \tag{1}$$

with $1 < \mu \leqslant 3$. For $\mu < 3$ the second moment of $P(\ell)$ diverges and for $\mu < 2$ the first moment also diverges. Lévy walks and flights lead to superdiffusion, i.e., the mean squared displacement of the position of the walker,

$$\langle x^2 \rangle \sim t^{2H}, \tag{2}$$

scales superlinearly with time t. In other words, Lévy flights allow $H > 1/2$. This contrasts with diffusive walks for which the Hurst exponent H equals 1/2 (Fig. 1).

Lévy flights and walks have scale invariant and fractal properties. A "zoom" of a part of a true Lévy walk trajectory will reveal a substructure with statistically identical properties except for cutoffs. In other words, Lévy walks "look" the same on any scale, except for cutoffs. Their diffusive properties do not depend on the scale. We discuss the difference between Lévy flights and walks in Section 9.

One central concept concerns the use of μ to compare superdiffusive Lévy searches with Brownian searches involving normal diffusion. By comparing the search efficiencies as one varies μ, we can obtain an idea about how much advantage can be gained by exploiting diffusivity and stochasticity in this specific manner.

3. The statistical approach to random searches

One reason underlying the richness of the random search problem concerns the "ignorance" of the locations of the randomly located "targets". Contrary to conventional wisdom, however, the lack of complete information does not necessarily lead to greater complexity. As an illustrative example, let us consider the case of complete information. If the positions of all target sites are known in advance, then the question of what sequential order to visit the sites so to
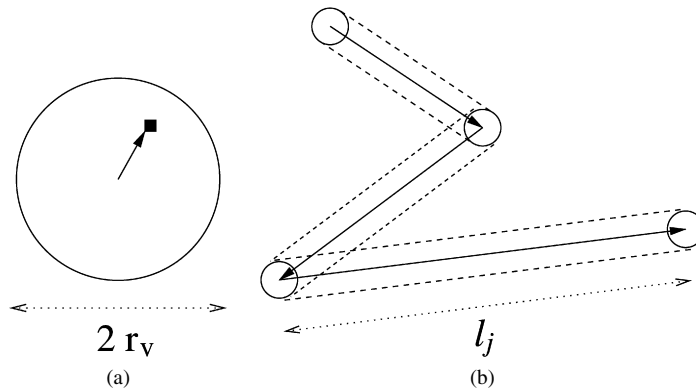
Fig. 2. A foraging model. (a) If there is a target site (full square) located within a distance r_v, then the forager moves on a straight line to it. (b) If there is no target site within r_v, then the forager chooses a random direction and a distance ℓ_j from $P(\ell_j)$, and then proceeds as explained in the text.

reduce the energy costs of locomotion itself becomes a rather challenging problem: the famous "traveling salesman" optimization problem [14]. The ignorance of the target site locations, however, considerably modifies the problem and renders it not amenable to be treated by purely deterministic computational methods [13]. Indeed, as expected the random search problem is not particularly suited to search algorithms that do not use some element of randomness.

For the reasons discussed above, only a statistical approach to the search problem can deal adequately with the element of ignorance. This conclusion is equivalent to saying that incomplete information renders the problem underdetermined, so that probabilistic or stochastic strategies become unavoidable. Therefore, it has been argued [14] that statistical physics is ideally suited to the study of complex phenomena of this nature [15]. Indeed, the general problem of how to search efficiently for randomly-located target sites can be quantitatively described [8,9,15] using ideas developed in the context of random walks, a standard problem approached by the methods of statistical physics [16,17].

A general and idealized model, capturing the essence of the above discussed statistical view, but at the same time preserving the main dynamical aspects of searches—in the limiting context in which predator–prey relationships can be ignored and learning is minimized—can be formulated as follows. (Here we are not going to discuss more complex landscapes, but we mention that such cases can also be of interest.) See, e.g., comments in [12,18,19] and also in references therein. Assume that target sites are distributed randomly. The searcher then behaves as follows (see Fig. 2):

(1) If there is a target site located within a "direct vision" distance r_v, then the forager moves on a straight line to the nearest target site.
(2) If there is no target site within a distance r_v, then the forager chooses a direction at random and a distance ℓ_j from a probability distribution $P(\ell_j)$. 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).

The above rules, nevertheless, are not enough to fully formulate the problem. Indeed, models of animal searches need to take into consideration the different kinds of foraging. Perhaps the most important difference concerns what happens to the targets. Do they regenerate? Do they move? The extreme situations correspond to destructive and nondestructive foraging. In the case of "non-destructive search", the forager can visit the same target site many times. Nondestructive (as opposed to destructive, see below) searches 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 search", the target site found by the forager becomes undetectable in subsequent flights. Finally, the most general intermediate static situation corresponds to regenerative foraging, in which the targets reappear and become available again after some finite typical time. Regenerative searches might be the most realistic type of search.

4. Efficiency of Lévy random searches: analytical results

The model defined in Section 3, for $P(\ell_j)$ given by Eq. (1), can be analytically solved in a "mean-field"-like approach as follows. Let λ be the mean free path of the forager between successive target sites randomly distributed. In a two-dimensional landscape, $\lambda \equiv (2r_v\rho)^{-1}$ where ρ is the target site area density. The mean flight distance is thus

$$\langle \ell \rangle \approx \frac{\int_{r_v}^{\lambda} dx \, x^{1-\mu} + \lambda \int_{\lambda}^{\infty} x^{-\mu} \, dx}{\int_{r_v}^{\infty} x^{-\mu} \, dx} = \left(\frac{\mu - 1}{2 - \mu} \right) \left(\frac{\lambda^{2-\mu} - r_v^{2-\mu}}{r_v^{1-\mu}} \right) + \frac{\lambda^{2-\mu}}{r_v^{1-\mu}}. \tag{3}$$

The second term above is an approximation since it assumes that the distances between successive sites are at most 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 [20]. As we discuss below, this truncation effect may play an important role in the context of experimental studies.

We can define 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. Since this distance is equal to the product of the total number of flights and the mean flight length $\langle \ell \rangle$,

$$\eta = \frac{1}{N\langle \ell \rangle}, \tag{4}$$

where N is the mean number of flights taken by a Lévy forager in order to find two successive target sites.

Consider first the case of *destructive search*, when the target site is "eaten" or destroyed by the searching animal and becomes unavailable in subsequent flights. The mean number of flights N_d taken to cover an average distance λ between two successive target sites scales as

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

for $1 < \mu \leqslant 3$, whereas $N_d \sim (\lambda/r_v)^2$ for $\mu > 3$ (normal diffusion). One can arrive at this expression by noting that for a Lévy flight the pseudo mean squared displacement $\langle |x|^{\delta} \rangle^{2/\delta}$ scales with time t as $\sim t^{2/\alpha_L}$, where $\alpha_L = \mu - 1$ denotes the Lévy index and $\delta < \alpha_L$. Identifying N_d with t and λ with the (pseudo) root mean square displacement corresponding to a target, one obtains the above result.

Consider the common scenario in which the target sites are "sparsely" distributed, defined by $\lambda \gg r_v$. Substituting Eqs. (3) and (5) into (4) one finds that the mean efficiency η has no maximum, with lower values of μ leading to more efficient searches. Actually, when $\mu = 1 + \epsilon$ with $\epsilon \to 0^+$, 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 search* 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. We assume that $N_n \sim N_d^{1/2}$ holds generally, so it follows that

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

for $1 < \mu \leqslant 3$, whereas $N_n \sim \lambda/r_v$ for $\mu > 3$ (again, Brownian, normal diffusion). Indeed, it has been proven that Eq. (6) is in fact rigorous [21]. This result has been found to become better and better as (λ/r_v) increases. Note that if $\lambda \gg r_v$ then $N_d \gg N_n$. Substituting Eqs. (3) and (6) into (4), one has that the optimal efficiency η is achieved at

$$\mu_{\text{opt}} = 2 - \delta, \tag{7}$$

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

We can further generalize this result to the intermediate regenerative foraging regime. We can associate [22,23] the non-destructive and destructive cases with the random search problems with typical target-regeneration delay times $\tau \to 0$ and $\tau \to \infty$, respectively. The equations for N_d and N_n then become special cases of a more general equation for N_r for regenerative targets. Note that N_r must increase monotonically with τ (for fixed μ and λ/r_v). Thus, for a general $\tau \geqslant 0$ we can define an arbitrary function $\Gamma(\tau)$, where $\Gamma \to 2$ as $\tau \to 0$, and $\Gamma \to 1$ as $\tau \to \infty$, such that

$\Gamma(\tau)$ decreases monotonically with τ and $N_r \sim \lambda^{(\mu-1)/\Gamma}$. Maximization of $\eta(\mu)$ implies [22]

$$\{1 - (\lambda/r_v)^\delta\}\Gamma + \{(\Gamma - 1)(\lambda/r_v)^\delta + 1 - \delta\}\delta \ln[\lambda/r_v] = 0, \qquad (8)$$

where $\mu_{opt} = 2 - \delta$, $0 \leqslant \delta < 1$. For $\Gamma > \Gamma_{min} = \ln[\lambda/r_v]/(\ln[\lambda/r_v] - 1 + (\lambda/r_v)^{-1})$ and fixed λ/r_v, the solution of Eq. (8) leads to a single peak in η at $1 < \mu_{opt}(\tau) \leqslant 2$, so μ_{opt} decreases with respect to the non-destructive case. For $\Gamma < \Gamma_{min}$, η presents a maximum at $\mu = 1^+$, decreasing monotonically for $\mu > 1$, similarly to the destructive case, where Γ_{min} relates to the revisitability threshold for there to be a peak in $\eta(\mu)$ for a physical value of μ.

All the above analytical results [8,22] have particular significance. They imply that, if the necessary conditions of the theory hold true, then (truncated) Lévy walks with $\mu \approx \mu_{opt}$ optimize random searches in sparse environments for random distribution of target sites. This finding does not depend on the dimension of the search space. Moreover, 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. Hence, learning, predator–prey relationships, and other short-term memory effects may become unimportant in the long-time long-distance limit [13,14]. On the other hand, it has been also found [8] that all advantages related to adopting a Lévy search strategy gradually disappear as the concentration of target sites increases. Indeed, in the extreme limit of abundant food the forager would not need to activate any search mode, so that Lévy and ($\mu \geqslant 3$) Brownian mean efficiencies would not differ greatly in a foraging path [9].

5. Lévy walks as adaptive strategies

Assuming that Lévy strategies indeed optimize random searches, does it necessarily follow that selective pressures systematically force organism adaptation towards this optimal solution? In fact, the adaptive pathway towards the optimal solution may stop half-way, at some sub-optimal point, which can nevertheless sufficiently decrease the selection pressure on this feature to a level below the strength of selective pressures on other issues. Such compromise solutions arise because adaptation (i) includes a stochastic component, (ii) has to build on pre-existing designs, and (iii) occurs in a complex playground where other pressure may be present. As an illustrative example, consider dolphins in the context of mammalian swimming adaptations. Dolphins indeed perform very well, but how can we assure ourselves that this design represents an optimal solution? Moreover, we can even ask why some mammals returned to marine life when selective pressures were pushing for improved terrestrial adaptation. The complex evolutionary history of real organisms contains plenty of contingent situations involving changing selective pressures, genetic drift, low number bottlenecks, etc.

Returning to the issue, the encounter rate *per se* does not constitute a selective pressure, rather the pressure might involve improvements to find food or for mate contact, etc. So, from an evolutionary perspective, the issue is not so much whether Lévy flights are better than other strategies (or similar discussions). Rather, the question is whether a (possibly suboptimal) Lévy-like adaptation to improve stochastic searches could have been selected. In what follows, the reader should interpret any discussion of Lévy walks as adaptive strategies accordingly. (On the other hand, a relevant alternative approach to the question of the origin of Lévy flight foraging relates to possible emergent behavior as result of complex interactions with the environment, as discussed in Section 12.)

5.1. Lévy versus Brownian strategies

With such distinctions in mind, we note that Bartumeus et al. [9] have argued that Lévy walks may confer adaptive advantages in relation to Brownian strategies and investigated the specific scenarios where this advantage may be crucial. In a separate study, Bartumeus et al. [12,24] have observed the fact that the biological mechanisms optimizing the "chances of finding" targets are not necessarily identical to those responsible for allowing and improving the "detection" of the same targets. Indeed, the selective pressures and the triggering stimuli in the two types of processes probably differ. Thus, their combination may provide huge behavioral plasticity for adapting searches to diverse ecological scenarios.

One consequence of this "decoupling" is that random search strategies are not necessarily incompatible with short-range "memory effects" in time or space, such as local scanning mechanisms, systematic "rules of thumb", etc. Overall, the suggestion is that scale-free "punctuations" in animal movement, such as stops and reorientations, could well underpin the stochastic organization of the search at landscape level [12]. Indeed, very recently Bartumeus [25]

goes further and explicitly gives strong arguments maintaining that scale invariant reorientations can form the basis for stochastic organization of the searches whenever perceptual capacities are substantially reduced.

This hypothesis has several consequences. For example, it would imply that not only deterministic but also stochastic processes underly adaptive mechanisms. Moreover, these stochastic effects and relevant adaptive drives could "percolate" upwards in the organization and dynamics of the ecosystem, e.g., at the population level.

Most importantly, this possibility stands in contrast to the view of Lévy motion and scale invariance as epiphenomena—or even as "emergent properties"—that arise solely via interaction with the environment. Instead, it would imply the existence of a genuinely scale-free adaptational property underlying the strategies used by different individuals to enhance biological encounters (see also Sections 9 and 12).

As possible concrete candidates bearing the above discussion, namely, of adaptive advantage of Lévy processes, we cite two thought provoking studies.

5.2. Critical survival states on the edge of extinction

Could Lévy walks have any relation to extinctions—or even to mass extinctions? This question has been tackled in the context of autonomous random walkers whose sole source of energy are search targets that are themselves diffusing random walkers [26]. By analyzing how the energy accumulated by the searcher varies with the target density via numerical simulations and via a simple mean field analytical model, it was found that superdiffusion of either searcher or target confers substantial energetic advantages to the former.

Most importantly, while superdiffusion does not appear to play a crucial role for high target densities, in contrast it confers a vital advantage in the limit of low densities—at the edge of extinction. Specifically, diffusive searchers rapidly die, but superdiffusive searchers can survive for long periods without entering into the extinction state.

It is interesting to apply this reasoning in the context of historical events of mass extinction. It is widely assumed that dinosaurs disappeared due to a single, massive asteroid strike about 65 million years ago, or possibly due to multiple nearly simultaneous impacts, which would necessarily cause huge extinctions. But why did some species survive and not others? Except for primitive birds, all dinosaurs went extinct. In contrast, not all other reptiles or mammals died. Why not the opposite? Why did not the dinosaurs survive and mammals die? An impact may well be the starting (triggering) or proximal cause for the death of the dinosaurs, but what was the long-term, ultimate, cause? It is not inconceivable that the relative diffusiveness of the various species played a role in determining which animals survived and which did not.

Actually, empirical data indicate that some insects [27] and fish [28] near starvation increase their movement intensity and diffusiveness in the search for food when compared to their foraging activity under normal conditions. During scarce environmental conditions, species presenting such behavior can have an adaptive advantage with respect to those which do not. As already observed above, it may determine what species do and do not perish in extreme conditions. This could have relevance to the dinosaur case, and eventually also to the greatest mass extinction on Earth, the Permian–Triassic event.

5.3. Lévy flight foraging in data bases and human memory

As will be discussed in Sections 7 and 8, Lévy flight search patterns can lead to optimal outcomes in computer data bases, networks, etc. The operation of the brain itself has been interpreted as a parallel distributed neural network computer. Could Lévy walks then occur in the human brain?

Rhodes and Turvey [29] conducted an intriguing study in this respect. They studied attempts by people to recall as many words as possible from a specific category, such as animal names. The retrievals occur sporadically over an extended period and decline as recall progresses. However, they found that short retrieval bursts occur even after many minutes of performing the task. They found that for each participant in the experiment the intervals between retrievals conformed to a Lévy distribution. The closer the exponent on the inverse square power-law distribution of retrieval intervals approximated the optimal foraging value of 2, the more efficient was the retrieval.

They point out that "at an abstract dynamical level, foraging for particular foods in one's niche and searching for particular words in one's memory must be similar processes if particular foods and particular words are randomly and sparsely located in their respective spaces at sites that are not known a priori". This raises the possibility that the Lévy flight search dynamics, typically associated with foraging, may also characterize retrieval from human semantic
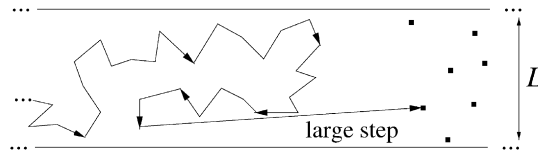
Fig. 3. Deterministic walks in rectangular environments with randomly distributed targets, where the "go-to-the-nearest-site" rule leads to power-law distributions of move lengths for specific critical aspect ratios for L. This surprising result is due to the fact that in the critical condition the walker can "accidentally" back track and end up having to make an ultra-long flight to return to the forward more abundant region of target sites. Consequently, a non-Lévy process can lead to an emergent scale-free behavior—via interaction with a disordered environment.

memory. Thus, again conceivably a Lévy process would result in an adaptive advantage, this time related to the cognitive power of a particular species, the *Homo sapiens*.

6. Emergence of Lévy behavior in deterministic walks

So far we have discussed random walks with inherently stochastic dynamics. In other words, we assume randomness from *a priori* in the rules of motion. A less widely known and studied class of problems concerns deterministic walks [30–32]. As in the usual stochastic case, they describe the movement of a walker in a certain environment, which may or may not have a random character. However, the rules of locomotion are always taken from some purely deterministic model, rather than from a probability distribution [32], i.e., randomness is present only in the disordered media, never in the motion rules.

In this context, Boyer et al. [33] have pioneered a novel approach to Lévy flight patterns by showing that deterministic walks can interact with complex environments in ways that lead to the emergence of a variety of memory effects, angular (i.e., orientational) correlations, and scale-free properties. Subsequently, Santos et al. [34] have studied the probability density function of step lengths taken by a deterministic walker, who always travels to the nearest randomly distributed site in a closed rectangular geometry of fixed area $A = 1 = L_x \times L$. As expected, a characteristic scale of step lengths emerges for the one (L very small) and two ($L \sim L_x$) dimensional limits of the geometry.

Remarkably, however, a scale invariant step length distribution takes place for specific aspect ratios of L and L_x in a strip-like geometry. One might in principle expect the model to lead to a Poisson process, since the initial distribution of target sites (which are destroyed once visited) is random. Indeed, one finds that in both one- and two-dimensional limiting cases the step length distribution has finite variance. Nevertheless, for values of the "order parameter" L/ℓ_0 (with ℓ_0 associated to the average minimum distance between two targets) in the interval $10 < L/\ell_0 < 30$, a non-trivial dynamical process with arbitrarily large variance takes place, combining a great number of relatively small steps with rare long steps. What happens is that although the destruction of previously visited sites makes the walker to tend to move forwards with higher probability, there is also a finite fraction of large turning angles along the walk, allowing the walker to back track. Eventually, the walker is forced to make an ultra-long jump. An illustration of such mechanism is given in Fig. 3.

This result has important implications. Specifically, it shows that a scale-invariant Lévy-like behavior can "emerge" as a consequence of the interaction with the disordered media, even when the dynamics is driven by deterministic rules of movement (in this case, the "go-to-nearest-site" rule). Emergence and adaptation need not preclude each other, in the biological context. We will return to this topic in Sections 9 and 12.

7. Lévy random searches on networks and their biological interest

The interest in the random search problem is not limited to the context of continuous (Euclidean) landscapes. Actually, this subject is also of relevance to discrete spaces [35,36]. In fact, in many potential technological applications, such as the Internet, the search environment is discrete or digital rather than continuous. For instance, this is true in the case of memory search in neural networks [37] or in automated computer searches of registers in high-capacity data bases [38]. In an "actual" world case, to look randomly for a grocery store in the streets of a small or medium size town [39] may also constitute a searching process in a network-like structure. Moreover, as a more biologically oriented example, we also mention that gene networks [40] can form what is called a large-world network (see below).

There are distinct reasons to study random search in networks. First, as pointed above, such analysis is interesting in its own right since it finds applications in many concrete situations in Nature (e.g., neuroscience and genetics in

biology; for a review, see [41]). Nevertheless, there is also another more theoretically oriented aspect, related to the comparison between strategies for optimal searching in continuous and lattices spaces. Indeed, since both types of landscapes share a number of similar properties, we can infer useful results for the continuous scenario (e.g., animal foraging) by analyzing the somewhat less complex situation of discrete lattices.

This motivation leads to the first major question: what are the key features determining the transport characteristics of a lattice, and therefore directly influencing the outcomes and properties of a random search on it? Many studies [42–44] have confirmed the widespread hypothesis that such features are related to the topological characteristics of the lattices, particularly the site connectivity. In this respect one can classify lattice networks into two classes: (i) large-world and (ii) small-world networks. Large-world networks are locally connected and rich in clusters, with only short-range links, typically between first-neighbor sites. In such cases, the distribution of link sizes is a narrow Gaussian, truncated close to the origin, giving rise to a linear increase of the mean distance between two arbitrary sites (lattice diameter) with the total number of sites [43,45]. In contrast, small-world networks are globally connected. They possess power-law link distance distributions. The lattice diameter grows sublinearly (logarithmically) [43,45] with the number of sites due to the existence of rare long-range links—the ultra-long links act as shortcuts that reduce the number of links necessary across which the information must propagate (an example being the World Wide Web [46]).

From the discussion above the second major question follows: how to define a strategy for random search on lattices? As noticed from the continuous case, the advantage of Lévy flights relies both in its superdiffusion aspect and in its self-affinity property, i.e. scale invariance. The structure of small-world lattices has already as a "built-in" feature a power-law distribution of lengths for the bonds, allowing great connectivity along the whole net. So, search optimization on such structures is not too critical an issue. Nevertheless, it does not mean that an increase of the efficiency cannot be obtained from more appropriate searching strategies in small-world lattices. We should mention, however, that in order to implement them using ideas based on Lévy distributions, a number of subtle technicalities arise. For instance, since there is not a characteristic size for the lattice bonds, we cannot think about an average characteristic length on the network. So, when defining step lengths along a small-world lattice from a Lévy distribution, the effective lower cut-offs may not be fixed by the lattice properties alone. Also, the detection mechanism (e.g., vision radius) is not homogeneous in all directions, since the distances between connected nodes have a power-law distribution. It makes the parameter r_v to have a more complex role in optimizing the search in the discrete case, if compared to the continuous one. We finally remark that all these aspects for small-world networks are presently being investigated in detail [47], including several biological implications. The results will be reported in the due course.

On the other hand, large-world lattices, usually associated with more inefficient systems for transport, are much more sensitive to the exact method used for looking for randomly distributed target sites, in total analogy with the continuous case. Furthermore, there is a really important reason to expect that in these networks Lévy flights can result in the best strategies for random search: metric similarity to continuous spaces. Indeed, in both situations, the farther a target site, the larger is the traveled distance to reach it. This is not true, for instance, for non-scaled small-world lattices, in which a single bond may connect two extremely distant nodes.

8. Searches on regular and defective lattices

To illustrate the previous discussion, we review recent findings for regular and defective lattices [35,36]. There are many factors determining the final outcomes of a random search in such systems. Here we explicitly address connectivity, boundary conditions, density of targets, and presence of defects.

For definiteness, let us consider regular and isotropic square and triangular lattices, characterized by the lattice parameter s and the coordination number k. The latter is the number of bonds leaving each node or, equivalently, the number of different directions that the search can follow from a given node. Observe that $k = 4$ (6) for the square (triangular) lattice. Furthermore, their total areas are given by $L \times L$ (square) and $\sqrt{3}L'/2 \times L$ (triangular), where $L = (\mathcal{N} - 1)s$, $L' = \mathcal{N}s$ and $\mathcal{N}$ denotes the number of nodes along the y-direction (see Fig. 4(a)).

One way to create defects, by diluting the network, is to randomly eliminate a certain fraction of nodes from an initially regular lattice. Hence, if n_0 is the initial number of nodes in a perfect lattice, then a *fragmentation coefficient* can be defined by $\chi = n_d/n_0$, where n_d is the total number of nodes removed ($\chi = 1$ implies an empty space—total dilution, complete destruction of the lattice). Examples are given in Fig. 4(b) for the triangular case.
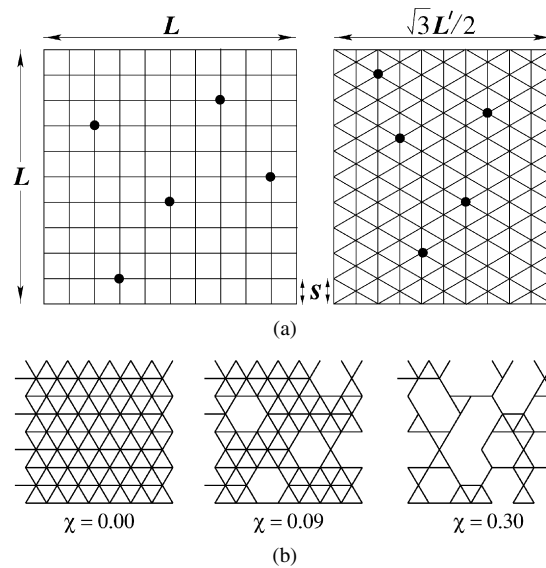
Fig. 4. (a) Examples of square and triangular lattices. The dots at the nodes represent randomly distributed target sites. (b) Different defective lattices.

There are many possible choices for the boundary conditions. Among them we cite three of particular interest: periodic (PBC), helical (HBC) and (not specular) wall (WBC). In Fig. 5 they are depicted, and it is also illustrated how a walker always moving straightforward in a single very long walk can "scan" the lattice. For PBC we see that horizontal paths are closed circles, whereas diagonal paths form solenoid-like curves. Indeed, note that the trajectory $A\,B\,C\,D\,E\dots$ in the figure is not closed until all the nodes are visited. The HBC differs from the PBC because the left (bottom) is connected to the corresponding right (top) border shifted by one node. Therefore, the horizontal paths create a solenoid that is closed after half of the nodes have been visited. The diagonal paths also create a solenoid, which, analogously to the PBC case, closes only after all nodes being visited. Finally, in the WBC any path hitting a border node becomes truncated and a new path, with direction randomly chosen, begins.

The search dynamics is similar to that of the continuous case previously mentioned. The target sites are randomly distributed at the lattices nodes (Fig. 4(a)). At each step j, a certain direction, allowed by the lattice structure, is chosen at random and the movement takes place in a straight line of bonds. The step lengths ℓ_j are sorted from the truncated Lévy distribution, Eq. (1), such that μ determines the specific strategy. The rules for the searcher are equivalent to those described in Section 3. However, in the presence of defects an extra rule is necessary: if a defect exists along the direction of step j (within the distance ℓ_j), and no target site is found before reaching it, then the step is truncated at the node immediately before such defect. In the sequence, new direction and step length are chosen and the process resumes.

As before, a key quantity to analyze the random search problem is the statistical search efficiency $\eta(\mu)$, given by Eq. (4). Furthermore, parameter λ (see Section 4)—which in the lattice case is not exactly a free mean path (in units of s), but is closely related to it—is an appropriate quantity to rescale the efficiency function.

We summarize the main results by first discussing the difference in efficiency for different connectivities, namely, for the cases of square and triangular lattices. Ref. [35] reports the findings for periodic boundary conditions, in three regimes of target densities (low, intermediate, and high), no defects, and destructive and non-destructive searches. The local connectivity affects more drastically the search efficiency only at low densities. At a low density the triangular lattice has higher outcomes than the square one, regardless the values of μ.

Qualitatively differences can also be seen for the same type of lattice with different target densities. For low densities $\eta(\mu) \to 0$ when $\mu \to 1$. Furthermore, one finds that $\mu_{\text{opt}} \approx 2$ is the optimal exponent and that η starts to diminish for larger values of μ. In this regime we expect the continuous limit and the relation between μ_{opt} and λ [8] to remain valid.

Finally, we notice that if the number of defects is too high, all steps are truncated to small displacements—of the order of the free mean path for defects. Thus, in order to choose a particular strategy, setting the value of μ no longer
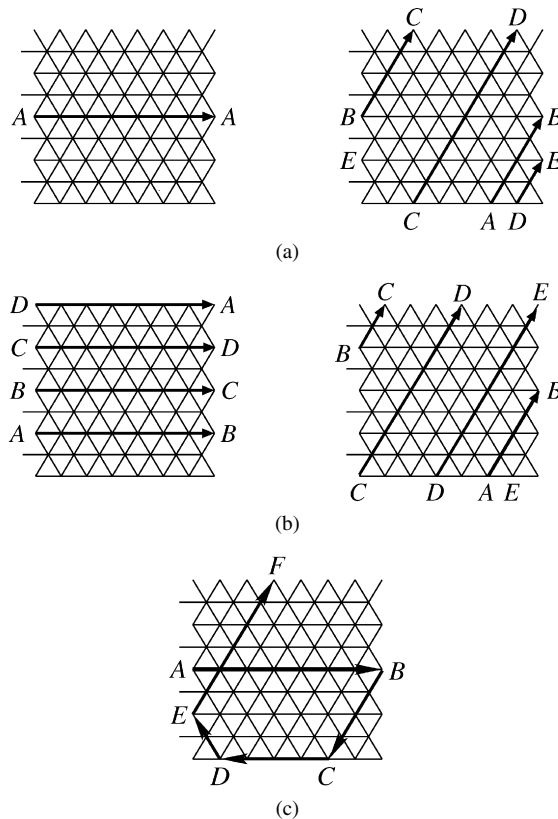
Fig. 5. Three boundary conditions in the case of a triangular lattice: (a) periodic (PBC); (b) helical (WBC); and (c) not specular wall (WBC).

makes any sense for optimization. In this way, we restrict our overview to low density of defects (of course, what is the exact threshold for a "small density" is a very relevant, but still open question). Assuming that the concentration of defects is low enough, the crucial point is that the dynamics of truncation of flights due to defects is similar to that due to normal target sites. Then, the only, but certainly fundamental, difference is that when a flight is truncated by a defect the searcher does not gain any resource (e.g., food). Therefore, such truncation contributes negatively for the global efficiency, the defect acting as a "fake" target site. Thus, we can expect the efficiency function to decrease by a factor just weakly dependent on μ, so that in a first approximation we have only a global diminishing of the η curve, without any important qualitative change of its shape. This prediction is indeed observed when one compares the triangular lattices with periodic boundary conditions at a low density, which present very similar behavior, even though only the latter case has a quantity of defects. An analytical model to quantify the change in $\eta(\mu)$ due to defects has been derived in [36], but its description is beyond the scope of the present review.

9. Empirical evidence of biological Lévy flights and superdiffusion

How much empirical evidence is there for biological Lévy flights? Before going into this, we shall carefully discuss a number of important related points. First of all, Lévy flights comprise instantaneous displacements—hence they involve infinite velocities and so, cannot take place in Euclidean space. A Lévy walk refers to a finite velocity walk in which the "step lengths" are still chosen from $P(\ell)$ in Eq. (1), but which are traversed at a finite, typically constant, velocity. Thus, Lévy walks in principle are physically realizable in Euclidean space.

Also, the power law tails of pure Lévy walks extend to infinity. Unlike exponentially decaying tails, a power law tail cannot simply be ignored because it possesses self-affine properties. Specifically, a "zoom" or renormalization by a factor b leaves power law tails intact: $P(b\ell) \approx b^{-\mu} P(\ell)$. They have no "characteristic scale" and thus have scale-invariant properties. This fractal behavior must be observed when dealing with experimental data.
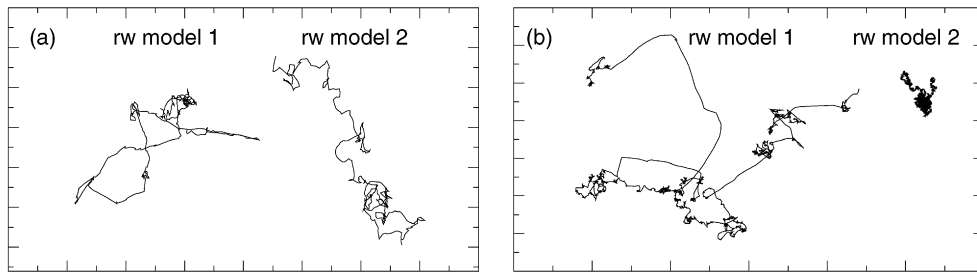
Fig. 6. Two random walks with identical turning angle distributions shown (a) on a scale not much larger than the correlation length; (b) on a very much larger scale. Turning angles refer to the change in angle between successive random walk steps. The difference between the models arises solely due to long-range memory effects equivalent to a Lévy distribution of travel times during which directional persistence is approximately maintained. Distinguishing between different kinds of walks from experimental data can pose challenges [48]. The difficulty acquires practical relevance because real walks always have some curvature. For example, whereas rw model 2 is a Markovian Correlated Random Walk, in contrast rw model 1 corresponds to a kind of "curved" Lévy walk [48]. Only rw model 1 is genuinely superdiffusive at all scales. The fact that it was generated from a power law tailed distribution of travel times shows that—at least in foraging studies—it is not necessarily useful to distinguish between superdiffusion in the general sense and Lévy walks as a special case. Is the difference between a curved Lévy walk and other kinds of superdiffusive walks really important in a biological context?

Furthermore, upper and lower cutoffs should be considered as well. They indicate the scales at which there is a breakdown of the continuous scale invariance symmetry discussed above. For this reason, a pure Lévy walk cannot take place in a finite space (e.g., the animal territory), since its limited size will naturally lead to an upper cutoff. Only *truncated* Lévy walks are biologically plausible. Truncated Lévy walks and flights, nevertheless, retain the most important properties of pure Lévy processes to a considerable extent [20].

We also raise a number of issues related to the experimental methods concerning the observation of foraging patterns in nature. Usually, they involve measuring either (i) the distribution of step sizes and times or (ii) the scaling of the square displacements. Regarding point (i), although we stated above that pure Lévy walks cannot take place in actual foraging, it is also true that even truncated Lévy walks represent an idealization because they typically stipulate straight rectilinear motion during the "steps" or "flights". In contrast, a real "flight" will involve a certain degree of curvature. The question is then: with what tolerance should we decide whether a new flight has started or whether the flight has merely acquired a small but acceptable change of direction? Indeed, the analysis of trajectories typically involve discretization procedures to treat the experimental data, which therefore must be explicitly taken into consideration. Recently, a criterion has been proposed to address some of these questions [48].

What does an evidence of Lévy flights look like? On the one hand, a power law tailed histogram of steps or "flights" could be interpreted as constituting such evidence. A power law distribution for the times of the flights or steps—rather than distances—perhaps may bypass the problems associated with curved trajectories (see Fig. 6). But the problem of how to tell one flight or step from the next still remains. Superlinear scaling of the mean squared displacement, i.e., a Hurst exponent larger than $1/2$, would also lend indirect support to Lévy flights. However, although Lévy flights generate superdiffusion, other mechanisms, such as fractional Brownian motion, can also lead to it. For this reason, hard evidence of superdiffusion does not automatically translate into hard evidence of Lévy flights. Hence, a (truncated) power law tailed distribution of flights or steps conceivably constitutes the best candidate in pointing towards Lévy motion.

Now, turning our attention to certain aspects related to point (ii) above, it has been recently shown by Giuggioli et al. [49] that the finiteness of the probing windows or theaters of observation may have to be taken into account explicitly for an adequate analysis of a given experimental data set. Actually, finite probing windows can lead to spurious conclusions about multifractal anomalous diffusion where each absolute moment of the position variable x scales with its own Hurst exponent $H(q)$:

$$\langle |x|^q \rangle^{1/q} \sim t^{H(q)}. \tag{9}$$

In contrast, monofractal walks have a single Hurst exponent $H(q) = H$, so the scaling of the mean squared displacement $\langle x^2 \rangle \sim t^{2H}$ is sufficient to describe the diffusive properties. In this same work [49], the authors have developed a method to correct for such misleading artifacts for an experimental setup commonly used to study rodents.

Although these specific findings do not bear directly on all experimental methodologies, in general to eliminate spurious detections is not a trivial task. It makes the issue of finite probing windows to be pertinent in many instances. For example, a fundamental question is to determine what is the minimum amount of data needed to reach credible conclusions [48].

In fact, beyond the multifractal analysis method itself, other considerations arise. One is whether or not there is indeed multifractality in foraging patterns. For a sole individual performing random search, conceivably it could be the case only in a very complex landscape (perhaps too complex to be realistically studied with present methodologies). For instance, in a recent theoretical work analyzing a landscape having a mixing of patchy and random homogeneously distributed target sites [12], this type of multifractal structure has not been observed. On the other hand, interesting studies of spider-monkeys foraging in group [19,33,50] reveal that different elements may adopt different Lévy μ exponents (a choice eventually determined by each individual "duties" within the group). So, taken as a whole, i.e., not separating the single search trajectories, the collective pattern of a group random search can present a multitude of Hurst exponents, however the multifractality is here induced by social behavior (of primates in this case) and not by dynamical or environmental processes. A second consideration is how the experimental gathering of data or even its methodological features influence the results. In fact, approximations in the way one records the step lengths (see below) or includes different time scales [48] in an unique large data set may induce erroneous conclusions regarding superdiffusion (and multifractality).

Having discussed the subtleties of Lévy flights and walks, we next review the early [8,18,51–55] studies of Lévy motion of biological organisms. In order not to distract from the main arguments, a chronological review of other studies [19,33,50,56–66] appears separately in Appendix A.

9.1. Early studies: amoebas, fruit flies, albatrosses and bumble bees

The earliest reference to the idea that biological organisms could perform Lévy walks seems to be a 1986 paper by Shlesinger and Klafter [51]. Another early reference is a 1988 paper by Levandowsky et al. [52] about the swimming behavior of microorganisms. The next earliest published experimental studies of Lévy motion appeared in print around 1995–1996 [18,53–55].

Cole [53] studied the episodes of activity and rest of *Drosophila melanogaster* and found fractal (i.e., self-similar or scale-invariant) structure, concluding that the fractality could lead to Lévy flight patterns of movement. Schuster and Levandowsky [54] used time-lapse videomicroscopy to analyze the chemotactic behavior of axenically grown *Acanthamoeba castellanii*. They concluded that the diffusive behavior did not support Brownian motion or Gaussian diffusion and raised the possibility of Lévy walks. A subsequent study, by Levandowsky, White and Schuster [55], confirmed the earlier findings of superdiffusion. Viswanathan et al. [18] conducted the first study of very large scale foraging motion of the wandering albatross *Diomedea exulans* with the aim of looking for Lévy flights. They found that the distribution of flight times followed a power law with $\mu = 2$ (see Eq. (1)) [18]. A second study by Viswanathan et al. [8] suggested that deer and bumble bees might also perform Lévy walks in order to optimize the success of random searching in scenarios of low food densities. However, a recent study by Edwards et al. [56] has questioned the earlier conclusions (see discussion below). Specifically for deer, it is now known that their data did not actually correspond to travel times, but rather to pausing times. Even if a power law were found, this would indicate not a Lévy walk but a continuous time random walk [67]. Appendix A lists other relevant studies.

10. How strong is the evidence?

Power laws in physical systems (e.g., earthquakes) typically scale over at least three orders of magnitude. For biological systems in general and foraging dynamics in particular, two orders of magnitude of scaling can represent a luxury. Over a sufficiently small range of scaling, almost any smooth function will appear as a straight line on a double log plot.

Sims et al. have raised important points about how to minimize errors when trying to identify Lévy flight search patterns of organisms [68]. Actually, this is not a trivial problem and remains the subject of ongoing investigations. We are co-authors of a study by Edwards et al. [56] that has raised concerns about using straight lines on double log plots to infer Lévy walks (and power laws in general). The new study [56] showed the spurious nature of the ultra-long flights reported in the original albatross analysis [18]—some of the data did not correspond to actual flights.

Very recent independent studies by Boyer et al. [69] and by Reynolds [70] have, however, argued that the measured flight distributions for albatrosses do not disagree with the hypothesis of a truncated Lévy walk. Indeed, it is well known that truncation effects are generated by finding targets. For example, consider Eq. (3) expressing the mean flight length $\langle \ell \rangle$ as a function of the pure power law tailed distribution $P(\ell)$, and the "mean free path" λ which depends only on the target density. This calculation, from 1999 [8], already shows that $\ell_j \gg \lambda$ is astronomically (i.e., exponentially) improbable. The scale invariance symmetry associated with the original "bare" distribution becomes broken in the distribution of the actual flights because ultra-long flights are truncated upon finding targets. Thus, a characteristic scale emerges from the interaction with the environment, washing out the scale invariance symmetry, inherent in the underlying Lévy walk process.

Benhamou [71] has leveled a different kind of criticism against the Lévy flight foraging hypothesis. Benhamou argues that even with unambiguous evidence supporting Lévy walks, still this does not necessarily imply an underlying Lévy walk process—the Lévy behavior "may emerge from the way the animal interacted with the environment structure through more classical movement processes" [71]. We leave to Section 12 a more detailed discussion about this possibility.

In summary, there is plenty of evidence for faster than normal (Brownian) diffusion—superdiffusion ($H > 1/2$). The question of whether this superdiffusion arises due to Lévy walks or due some other mechanism still remains partially open. The authors of this article strongly suspect that many biological organisms do in fact perform Lévy walks—for instance, the experimental studies by Reynolds et al. [61,62] and by Bartumeus et al. [59] appear to us to constitute robust results pointing in this direction. Yet, at the present time we cannot affirm for sure that biological Lévy flight search patterns are actually common in Nature. However, we feel optimistic that in the near future new experimental studies will lay the matter to rest one way or another.

In this context, the very recent study by Sims et al. earlier this year [66] analyzing more than one million movement displacements recorded from animal-attached electronic tags was an important contribution. The impressive amount of data convincingly shows that diverse marine predators perform Lévy-like random walks (see also Appendix A). According to Bartumeus, this analysis may well come to be seen as the study that shifted the debate from "whether animals perform Levy walks to when and how often they use this strategy and why" [72].

11. Anthropic Lévy flight foraging

As a last example of Lévy flight foraging, we wish to mention two other intriguing experimental studies. Although the reported power laws do not scale sufficiently convincingly (for understandable reasons), on the other hand they break new ground on a conceptual level. Bertrand et al. [73] found that trajectories of Peruvian purse-seiners might follow a Lévy walk. The scaling does not appear to extend over a range sufficient to draw unambiguous conclusions. Nevertheless, the possibility that fishing boats might adopt a Lévy walk search strategy, analogously to top-predators, suggests that the idea may in fact apply to humans.

In this context, a study by Brown et al. [74] of the distribution of distances between campsites of Ju'hoan hunter-gatherers represents a conceptual advance. The foraging patterns of the Dobe Ju'hoansi may in fact follow a Lévy or Lévy-like walk. It has become clear in the last few decades that humans do not differ fundamentally from other animals in what concerns biological issues—including it seems, migrations and random searches.

12. Alternative theories, final remarks and conclusion

As above mentioned, Benhamou [71] has raised concerns about the Lévy hypothesis, considering the possibility that the underlying process may not represent Lévy walks at all, but rather mere or composite Brownian walks or correlated random walks. Any observed Lévy or similar behavior could "emerge" as a result of interaction with the environment structure. In other words, even if the original dynamics does not possess scale invariance symmetry, the Lévy distribution of step lengths might arise as a byproduct and not as a consequence of *a priori* superdiffusive mechanism.

Indeed, it is not inconceivable that Lévy walks could be generated by a fractal distribution of food [18] or via complex heterogeneous structures in the search scenario [19]. In fact, the results discussed in Section 6 clearly show that a power law can arise even when there is no power law in the system dynamics, exactly in the spirit suggested by Benhamou. However, such a demonstration (i.e., that Lévy-like motion can "emerge" via "external" interactions)

constitutes only a necessary but not a sufficient condition for the thesis of emergent phenomena. One would also have to show that there is no Lévy or similar processes underlying the biological encounter process.

Bartumeus [25] has argued against the view that Lévy flight patterns *always* can be interpreted as resulting from other more fundamental phenomena. The arguments are based on evolutionary advantages of Lévy walks as adaptive strategies (see Section 5). If sophisticated neural tissues are not necessary for such adaptation, thus increasing the chances of being rather general among organisms, then it seems plausible that mechanisms producing departure from Gaussian behavior and Brownian walks (by increasing the probability of long walks) could have been selected and fixed—provided no other selective pressures become more relevant.

Investigation of the molecular and physiological processes that control the movement may bring definitive light on the discussion. In that sense, it is interesting to investigate theoretically how Lévy searches can be physiologically generated. This question can become a major issue in the debate between emergence and adaption.

A Gaussian approach is also favored by Bénichou et al. [4–6], who propose intermittent searches with two phases. The locally static or diffusive search phases alternate with ballistic relocations, during which detection is switched off. Remarkably, intermittent searches appear to work well (e.g., for planktivorous fish and ground foraging birds [65]) and represent an alternative to Lévy searches. Very recently Lomholt et al. [75] have proposed a kind of hybrid model of intermittent searches, where the ballistic relocation distances are Lévy distributed. Finally, and interesting enough, Reynolds [76] has shown that intermittent searches can be understood within the context of an optimal scale-free, Lévy-flight, searching strategy.

In our view, as explained previously, the main issue is not about comparing competing theories, because Nature is replete with suboptimal adaptations. Consider, for instance, Correlated Random Walks (CRW), whose corresponding step lengths distribution $P(\ell)$ has a characteristic scale and whose moments are all finite. They display a degree of directional memory, introduced on the basis of a non-uniform distribution of turning angles [77]. As a Markovian process, for large time scales they present normal diffusion, i.e., $H = 1/2$. Hence, for any random search necessarily demanding superdiffusion (such as the situation in Section 5.2), this type of random walk is not optimal. Yet CRW have been successfully used to describe the movement of many species [78].

One can pose the question: exactly which random walk model leads to the best outcomes given the actual environmental, metabolic and (eventually) social conditions and constraints of the process? Probably the answer could be Lévy walks, intermittent walks, Correlated Random Walks or something else, depending on which model is best (or better) capable of describing a given, specific, search process. Given such considerations, we wish to avoid a Manichaean discussion on whether Lévy flights are a better option compared to composite random plus ballistic intermittent strategies (and other similar discussions). It may happen that many possibilities were explored to improve stochastic searches throughout evolutionary history. Due to the huge variability and diversity of biological systems, we can imagine that natural selection has followed distinct—nonuniversal—pathways, often finding good (but not necessarily optimal) solutions depending on specific circumstances.

As a last comment, we mention that in the face of the complexity of real organisms and their interactions, it is quite remarkable how well Lévy flight patterns account for widely differing scenarios, which have been described in this review. In the historical context, the concept of scale-free Lévy flight foraging constituted a conceptual advance and inspired a number of further studies. However, there is no reason to expect the innovation to stop with "plain" Lévy flights. As a recent example, curved Lévy trajectories have been proposed [48] (e.g., see Fig. 6). There are a number of possibilities for interesting studies, both theoretical and experimental. For instance, recently [79] there has been substantial progress understanding the first passage times for Lévy flights and other walks [80]. Such analyses may reveal in a near future still more profound and unexpected features of the very rich dynamics underlying biological encounters.

Acknowledgements

Appendix A. Chronological review

In addition to the early studies we discuss in the main text, here we briefly review other experimental studies.

A.1. Reindeer

Mårell et al. [57] studied foraging-site selection by the semidomesticated female reindeer (*Rangifer tarandus tarandus L.*) and found discrepancies between the actual reindeer foraging paths and a (non-Lévy) correlated random walk model.

A.2. Jackals

Atkinson et al. [58] used radio-tracking techniques employed by field ecologists to look for fractal behavior in the foraging trajectories of a species of African jackal, the side-striped jackal. They not only reported strong evidence for superdiffusion, but also clearly show the complexity of actual foraging trajectories, which include curvature (or, equivalently, a degree of sinuosity).

A.3. Dinoflagellates

An important study in the context of biological Lévy flight foraging, by Bartumeus et al. [59], concerned the flight times of the dinoflagellate *Oxyrrhis marina*. They found that the distribution of flight times switched from an exponential (diffusively equivalent to $\mu > 3$, $H = 1/2$) to an inverse square power-law distribution ($\mu = 2$, $H > 1/2$) when the prey (*Rhodomonas sp.*) decreased in abundance.

They also studied the amplitude and frequency of the short-term helical path, which increased with decreasing density. They suggested that for a three-dimensional environment, a stronger helical component combines with Lévy search strategy to enhance the relevant encounter rates. They conclude that their results support the idea of a universally applicable statistical "law" of foraging.

A.4. Spider monkeys

Ramos-Fernández et al. [50] and Boyer et al. [33] studied the foraging patterns of free-ranging spider monkeys (*Ateles geoffroyi*) in the forests of the Yucatan Peninsula and found a power law tailed distribution of steps, consistent with a Lévy walk. The study reported, moreover, a power law distribution for waiting times, which would indicate (not explicitly mentioned in Ref. [50]) a continuous time random walk [67]. They also found strong evidence of superlinear scaling of the mean squared displacement ($H > 1/2$)—evidence of superdiffusion. A subsequent study by Boyer et al. [19] interpreted these findings in the context of the interaction of the foragers among them and with complex heterogeneous environments.

A.5. Sharks

Lévy flight search patterns possess structure across multiple scales, as mentioned above. Sims et al. [60] analyzed the relative success of shark searches by comparing prey (zooplankton) biomass encountered by sharks in a dynamic prey landscape (in the north-east Atlantic Ocean) with encounters by random-walk simulations of "model sharks". They found results "consistent with basking sharks using search tactics structured across multiple scales".

A.6. Honey bees and fruit flies

The evidence for honey bees is particularly strong. In contrast with some other studies, Reynolds et al. [61,62] use a variety of techniques, few or none of which have been criticized by the recent study by Edwards et al. [56].

In one study, Reynolds et al. [61] used harmonic radar to record the flight paths of honey bees that were searching for their hives. Analysis of the trajectories indicated scale invariant walks with a $\mu = 2$ (see also Ref. [63]). They argue that these results, combined with the "no preferred direction" characteristic of the segments, demonstrate that the bees were flying an optimal search pattern. In another recent study, Reynolds et al. [62] trained foraging honey bees to an artificial feeder that was then removed. The subsequent bees flight patterns were recorded using harmonic radar. The authors show that the flight patterns have the scale-free characteristic of Lévy walks and argue that this constitutes an optimal searching strategy for the location of the feeder. They also demonstrate that this searching strategy would remain optimal even for imperfect implementation of the walks. Very recently, Reynolds has shown that $\mu = 2$ optimizes central place foraging via a power law distribution of loop-lengths [64].

Reynolds and Frye [65] studied trajectories of fruit flies in still air and found evidence suggesting optimal scale free searching and an inverse square power law distribution of inter-saccade interval lengths. They also find evidence of intermittent searching [4–6] of alternating search and relocation phases. This study may constitute the first reported example of searching behavior that is both scale-free and intermittent.

A.7. Sharks, bony fish, sea turtles and penguins

Very recently, a study by Sims et al. [66] analyzed data sets comprising more than 10^6 data points and found convincing evidence of Lévy-like behavior. Their use of rank-frequency plots and comparison of different models takes into account recent criticisms of the use of double log plots of histograms. We expect that this study will shift the debate about biological Lévy flights.

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