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Optimizing the Encounter Rate in Biological Interactions: Lévy versus Brownian Strategies

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An important application involving two-species reaction-diffusion systems relates to the problem of finding the best statistical strategy for optimizing the encounter rate between organisms. We investigate the general problem of how the encounter rate depends on whether organisms move in Lévy or Brownian random walks. By simulating a limiting generalized searcher-target model (e.g., predator-prey, mating partner, pollinator-flower), we find that Lévy walks confer a significant advantage for increasing encounter rates when the searcher is larger or moves rapidly relative to the target, and when the target density is low.

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The interest in systems undergoing a reaction-diffusion process has recently experienced a rapid growth due to their intrinsic relevance in many physical, chemical, and biological phenomena, as well as in the social sciences and ecology [1]. Several models have been proposed to describe their main features by employing a suitable Markovian process together with a set of local transition rules. Usually, these interacting many-particle systems develop long-range correlations as a consequence of the microscopic mechanisms governing their temporal evolution. At high dimensions, the collective behavior can be well described by mean field rate equations. However, for low dimensions, local density fluctuations have to be taken into account. Field theoretical methods [2] as well as Monte Carlo and cellular automata simulations [1], among other techniques, have shown that local fluctuations can dramatically modify the mean field predictions. In particular, the nature of the diffusion mechanism (Brownian or anomalous Lévy motion) is known to be a relevant aspect at low dimensions [3]. Within this context, the particles' encounter rate is an important quantity that deserves systematic study, since it ultimately governs the global reaction rate.

Two-species reaction-diffusion processes are particularly finding applications in quantitatively modeling biological phenomena [4–7]. One important application relates to the general problem of what is the best statistical strategy to adopt when searching for randomly located "targets" [6]. Indeed, 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 interspecific, 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. Hence, factors conditioning encounter rates between organisms conceivably play a crucial role in the ecological constraints important in the evolution of life. To some extent, similar issues may potentially arise at the molecular level in a cell, where molecules may undergo Brownian motion or be themselves motors wandering around or actively transporting other molecules in search of their targets [8,9]. The number of potential factors involved in any kind of interaction is very large and the ecologically possible adaptive pathways are multiple. However, among them, search strategies occupy an important place, since energy expenditure in displacement impinges directly in the energy balance of the individual and, therefore, probably also in its fitness.

Here, we report the results of our simulation studies on how population density and differences in size and velocity between interacting organisms influence the effectiveness of search strategies based on Lévy (superdiffusive) vs Brownian (diffusive) random walks. We show, using numerical simulations, that a Lévy search strategy is the best option in some, but not all, cases for a random search process. In our general approach to the 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 look for the optimal search strategy to maximize encounter rates. Recently, it was 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 [6,7]. It was also shown analytically and numerically that the benefits of Lévy searching for fixed targets [6] are mainly independent of the number d of spatial dimensions [10], for reasons that are analogous to how quantities such as the mean square displacement of Brownian and Lévy random walks are d independent. Hence, we focus here on the theoretically important case of one dimensional (1D) systems, in which diffusion induced density fluctuations away from the mean field behavior are more relevant than in the (computationally more expensive) 2D and 3D cases. Based on the similarities between the fixed targets and moving targets cases, we expect that (i) any observed relative advantage of Lévy searches over Brownian searches will gently decrease with increasing d for organisms with finite lifetimes, and (ii) such decreases in the relative advantages of Lévy searches will represent only quantitative changes, but not qualitative changes that alter the choice of the best search strategy (Lévy vs Brownian) in 2D and 3D. Furthermore, many organisms perform searches over nearly 1D space, e.g., fish species that search in coastal or river ecosystems, and species that search in grassland-forest interfaces.

Specifically, we perform 1D simulations of a single searcher and a single moving target in an interval of size L, under periodic boundary conditions. By varying the system size, we can effectively vary the target densities. 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 $\mu \geq 3$ 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 1D 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 [6]. Model variables are all dimensionless. We study different combinations of target to searcher velocity ratios v and size ratios r for Lévy ($\mu_{\mathrm{t}} = 2$) and Brownian ($\mu_{\mathrm{t}} = 3$) targets. For each of these scenarios, we study the encounter rate for the cases in which the searcher performs Lévy ($\mu_{\mathrm{s}} = 2$) and Brownian ($\mu_{\mathrm{s}} = 3$) random walks. To evaluate the best search behavior, we define γ as the ratio between the encounter rates for the Lévy and the Brownian searchers moving in identical environments and traversing identical total distances $\mathcal{L}$. A value $\gamma > 1$ represents a benefit for the searcher adopting a Lévy strategy.

We now briefly describe the essential features of the simulation method used. For given values of r, v, μ_{s}, and μ_{t}, we simulate a distance $\mathcal{L}$ of searcher motion in a system with size L with periodic boundary conditions. We generate the power-law distributions $P(\ell_j) \sim \ell_j^{-\mu}$ of the step lengths through the transformation $\ell_j \sim x_j^{1/(1-\mu)}$ of random numbers x_j distributed uniformly in the interval $(0, 1)$. Upon completely traveling a distance of step length ℓ_j, the "organisms" change direction randomly with a probability $p = 0.5$. Whenever the searcher and target come within a distance equal to the sum of the radii of the two organisms, an "encounter" is registered and the searcher moves towards the target (a distance equivalent to their added radii). The found target is destroyed and a new one is created in a viable random location. To decrease the computational cost of the simulation algorithms, we analytically solve the equations of motion of the organisms for given values of their step lengths to find whether or not an encounter takes place, starting from the initial conditions of the organisms at the beginning of each step length. We then simulate enough such step lengths for the searcher to travel a total distance $\mathcal{L}$, to obtain good statistics.

We find that the larger the system size L, the better the Lévy search strategy becomes compared to Brownian searches (Fig. 1), consistent with earlier findings [6]. For Brownian target motion, a Lévy searcher is, in general, more efficient than a Brownian searcher. Only for the extreme cases of targets almost an order of magnitude larger [Fig. 1(a)] and faster [Fig. 1(c)] than searchers, is Brownian search as efficient as are Lévy searches. When the targets perform Lévy random walks, the result differs. Lévy motion of targets implies a wider range of ratios r and v for which Brownian searchers are at least as efficient or better than Lévy searchers [Figs. 1(b),1(d)]. Specifically, for high target densities (e.g., for $L = 25$), Brownian motion is as efficient or even better than Lévy motion for $r > 1$, $v > 1$. For fixed size and velocity ratios r and v, Lévy target motion diminishes the efficiency of Lévy searchers [Figs. 1(b),1(d)] in comparison to Brownian targets [Figs. 1(a),1(c)] except when searchers move much faster (×10) than targets [Fig. 1(d)].

Figure 2 is a gray-scale plot of the value of γ against r and v for Lévy and Brownian targets. White corresponds

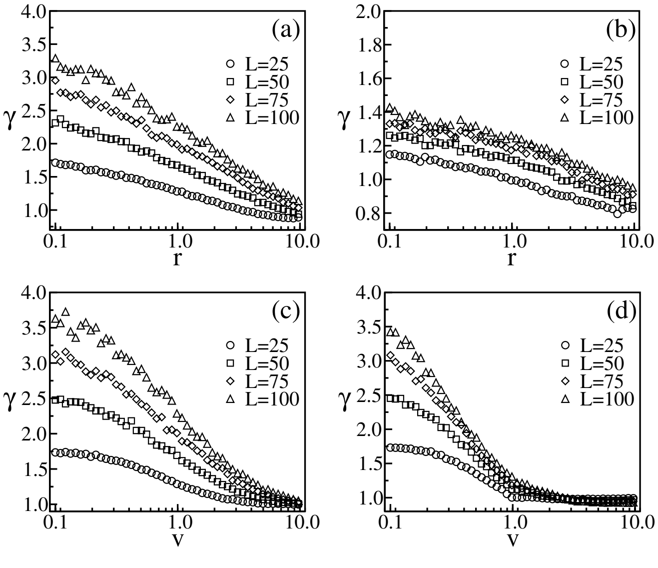

FIG. 1. The ratio γ between encounter rates with targets of Lévy vs Brownian searchers, plotted against the target to searcher size ratio r for the cases where the targets perform (a) Brownian random walks ($\mu_t = 3$) and (b) Lévy random walks ($\mu_t = 2$). For $\gamma > 1$ Lévy searchers have larger encounter rates than Brownian searchers and vice versa. (c) γ vs the target to searcher velocity ratio v for $\mu_t = 3$ and (d) $\mu_t = 2$. In all cases the searchers traversed a distance of $\mathcal{L} = 10^6$ units. Note that Lévy searching is not always beneficial, but only in specific circumstances: (i) low density (large L), (ii) small r (a),(b), and (iii) small v (c),(d).

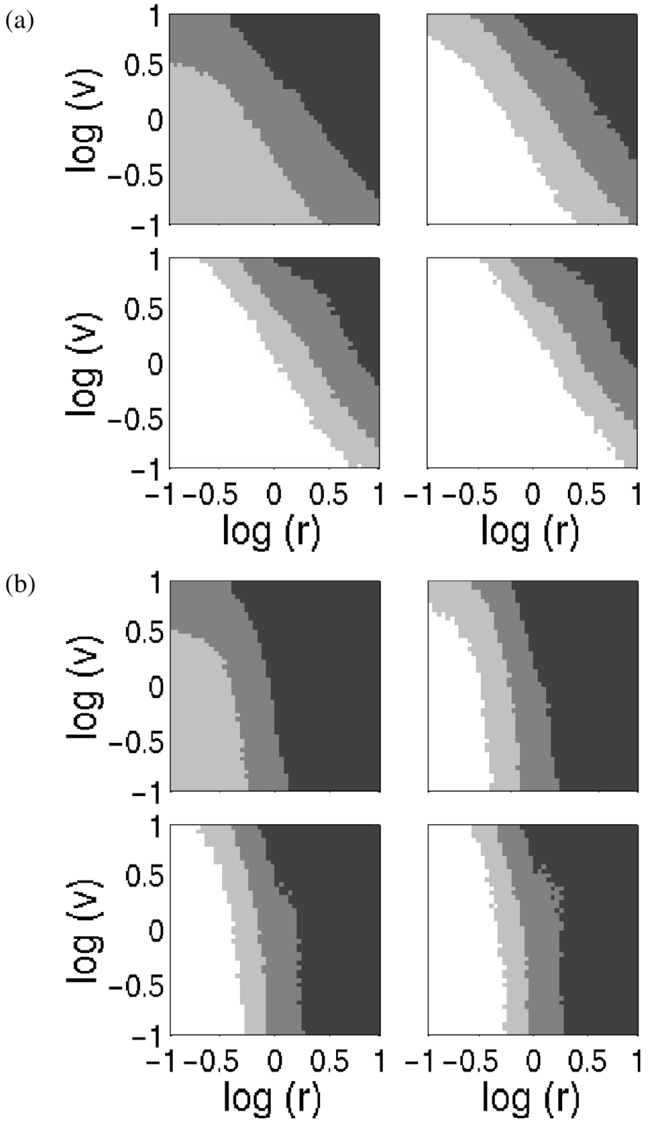

FIG. 2. Gray-scale graph showing γ as a function of r and v for (a) Browning targets and (b) Lévy targets. Each set of 4 graphs corresponds to increasing system size $L = 25$, $L = 50$, $L = 75$, and $L = 100$ from top-left to bottom-right. The areas in white correspond to the case in which Lévy searching is significantly advantageous ($\gamma > 2.5$), while black indicates no advantage.

to large $\gamma > 2.5$ while black to $\gamma \leq 1$. For larger L (i.e., lower target densities), Lévy searching becomes better than Brownian for a wider range of size and velocity ratio combinations. High target densities recover Brownian searcher strategies as optimal. For Brownian target motion [Fig. 2(a)], the white area expands diagonally from left-bottom (small r, v) to right-top (large r, v) as size system increases (following the set of four graphs). In Lévy target motion scenarios [Fig. 2(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, when searching for Lévy targets, size becomes more important than velocity.

Hence, we uncover a new result with biological implications: 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" velocity ratio effects, and, in this case, the best type of searching motion depends only on size ratios: for searchers larger than their targets, Lévy searching is optimal; while for searchers smaller than their targets, Brownian searching is better.

According to optimal foraging theory [11], evolution through natural selection has led over time to highly efficient strategies. Since environmental and biological situations in nature are highly variable, it is therefore conceivable that different optimal foraging strategies should naturally evolve. From Figs. 1 and 2 it is clearly seen that Lévy motion does not lead to significantly higher encounter rates always, but 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 motion 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). Next, we discuss how these variables contribute to optimize Lévy or Brownian search strategies, and how empirical data support our findings:

Target density.—As expected, we find that 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 [6] showing that Lévy searching confers no advantages unless the target density is low. We find that for a wide range of proposed scenarios (r and v ratios, Fig. 1), low target densities enhance the benefits of Lévy searching. This general result is consistent with findings of similar search behaviors observed in many organisms—wide-ranging in size and ecological strategies—which increase turning and tumbling frequencies due to increases in prey density [12].

Brownian vs Lévy targets.—Given a target density, the type of target motion is important in order to choose the best search strategy (Fig. 2). 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. Hence, once a target density is fixed, we can define a target-availability kernel which will depend on both velocity and size relationships between targets and searchers. As targets become less available (i.e., faster or smaller targets), a Lévy search strategy becomes better and vice versa. Nevertheless, it seems that the kind of target motion can modify this target-availability kernel. Lévy targets make velocity relationships between targets and searchers less important, therefore the optimal search strategy will be determined only by size relationships and target-availability kernels might be better defined exclusively by size relationships, since velocities will not matter (i.e., the smaller target sites, the better the Lévy search strategy and vice versa).

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 [Fig. 2(b), following the set of four graphs]. In low density and Lévy target scenarios, Brownian searchers still have acceptable efficiencies [Fig. 2(b)]. The nonrelevance of velocity 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 smaller than their targets even for low target densities, irrespective of velocity [Fig. 2(b)]. Some examples could be *diptera* or other parasitic insects looking for large herbivores while pasturing and, in aquatic systems, planktonic searchers looking for cyanobacteria colonies, or cyclopoid copepodites looking for *Daphnia* incubation-egg chambers.

Relative size.—Prey to predator size ratios are far from being unity in nature (e.g., in planktonic organisms [13]). The "effective size" of the searcher or target could even be larger than the actual geometrical diameter or maximum body length. For the searcher case 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. Our simulations studies, with no other energetic considerations other than the distance traveled by the searcher, show that increasing the target to searcher size ratio r implies a change from Lévy to Brownian search strategies. From known energetic arguments [4,14], it is reasonable to conclude that nonselective grazing should involve Lévy motion while ambushing and parasitelike behavior should involve Brownian motion (observed in viruses and bacteria [15,16]).

Velocity ratios.—The assumption of a more or less constant cruising velocity for real searchers is realistic and reasonable. In any aprioristic approximation, any v ratio can be plausible. Our main finding is that the faster and the more superdiffusive 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.

In summary, we have shown under which conditions a maximum encounter rate (and consequent global reaction rate) is achieved, using data presented for the encounter rate of a two-species diffusion-reaction system in which particles describe either Brownian or Lévy random walk motions. Moreover, we are able to quantitatively and qualitatively model ecological strategies from an evolutionary perspective by analyzing the general ecological searcher-target problem in terms of Lévy or Brownian scaled motions. Within this context, a changing tumbling frequency, which will lead to Brownian or Lévy searching behaviors, is the more direct mechanism for optimizing the search for many different target types and density scenarios, once a scale is defined. Changing the effective size or velocity while keeping the tumbling frequency control may indeed create adaptive pathways to new diets or reproductive behaviors. Most importantly, our findings point to a complex dependence of the optimal encounter strategy on population density, the type of target movement and the size and velocity ratios between searchers and targets, and reveal relevant aspects regarding the optimization of such strategies, such as the actual effectiveness of Lévy walks for slow, low density targets.

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