Part I: Lévy walks and encounter rates

3

Optimizing encounter rates: Lévy *vs.* Brownian strategies

3.1 Abstract

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.

3.2 Introduction

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 (Marro & Dickman, 1999). 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 evolu-

tion. 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 (Cardy & Täuber, 1996) as well as Monte Carlo and cellular automata simulations (Marro & Dickman, 1999), 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 (Albano, 1996a,b). 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 of biological phenomena (Viswanathan et al., 1996, 1999; Catalan, 1999; Fulco et al., 2001; Buldyrev et al., 2001). One important application relates to the general problem of what is the best statistical strategy to adopt when searching for randomly located "targets" (Viswanathan et al., 1999; Buldyrev et al., 2001). 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 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. 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 (Vale & Milligan, 2000; Porto et al., 2000). 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 (Viswanathan et al., 1996; Buldyrev et al., 2001). It was also shown analytically and numerically that the benefits of Lévy searching for fixed targets (Viswanathan et al., 1999; Buldyrev et al., 2001) are mainly independent of the number d of spatial dimensions (Viswanathan et al., 2000), 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 (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. 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 2-D and 3-D. Furthermore, many organisms 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.

3.3 Methods

Specifically, we perform 1-D 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 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 Viswanathan et al. (1999); Buldyrev et al. (2001).

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.

3.4 Results

We find that the larger the system size L, the better the Lévy search strategy becomes compared to Brownian searches (Fig. 3.1), consistent with earlier findings (Viswanathan et al., 1999; Buldyrev et al., 2001). 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. 3.1 a) and faster (Fig. 3.1 c) than searchers, is Brownian search as efficient as are Lévy searches. When the targets per-

form 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. 3.1 b,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, and in comparison to Brownian targets, Lévy target motion diminishes the efficiency of Lévy searches (Figs. 3.1 b,d) in relation to Brownian searches (Figs. 3.1 a,c) except when searchers move much faster than targets (Fig. 3.1 d).

Fig. 3.2 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 $\gamma \leq 1$. 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. 3.2, left), 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. 3.2, right), 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, velocity becomes more important than size.

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" size ratio effects, and, in this case, the best type of searching motion only 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.

3.5 Discussion

According to optimal foraging theory (Stephens & Krebs, 1986), evolution through natural selection has led over time to highly efficient strategies. Since environmental and biological situations in nature are highly variable, therefore it is conceivable that different optimal foraging strategies should naturally evolve. From Fig. 3.1 and Fig. 3.2, it is clearly seen that Lévy motion does not lead to significantly higher encounter rates always, but only

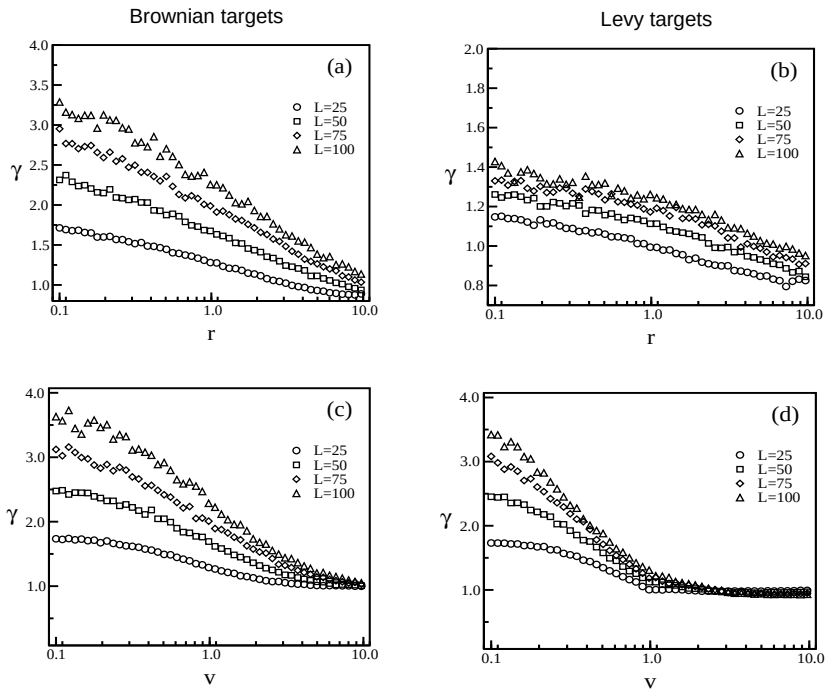

Figure 3.1: The ratio γ between encounter rates with targets of Lévy *vs.* Brownian searchers, plotted against the target to searcher size ratio r for the cases where the targets perform (a) Brownian random walks ($\mu_t = 3$) and (b) Lévy random walks ($\mu_t = 2$). For $\gamma > 1$ Lévy searchers have 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).

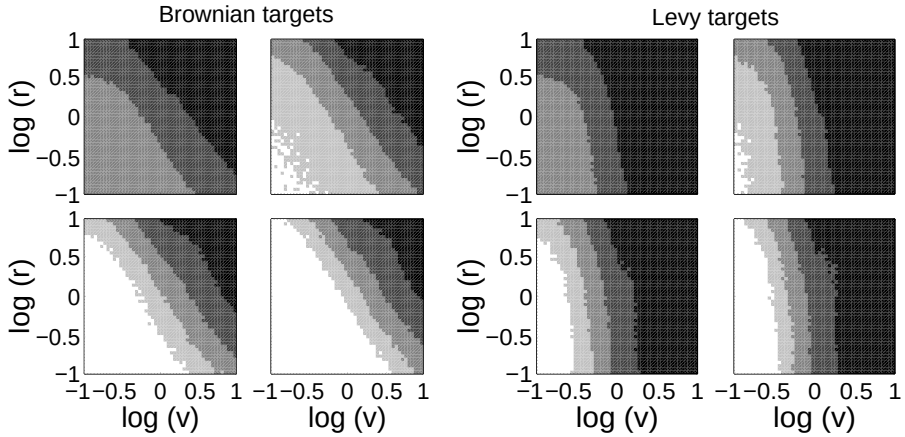

Figure 3.2: Grey-scale graph showing γ as a function of $log(r)$ and $log(v)$ for Brownian targets (left) and Lévy targets (right). Each set of 4 graphs corresponds to increasing system size $L = 25$, $L = 50$, $L = 75$, and $L = 100$ from top-left to bottom-right. The areas in white correspond to the case in which Lévy searching is significantly advantageous ($\gamma > 2.5$) while black indicates no advantage.

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.

3.5.1 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 (Viswanathan et al., 1999; Buldyrev et al., 2001) 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. 3.1), 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 (resembling more a brownian motion) due to increases in prey density (Bell, 1991).

3.5.2 Brownian *vs.* Lévy targets

Given a target density, the type of target motion is important in order to choose the best search strategy (Fig. 3.2). 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 size relationships between targets and searchers less important, therefore the optimal search strategy will be determined only by velocity relationships and target-availability kernels might be better defined exclusively by velocity relationships, since sizes will not matter (i.e., the slower targets, 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. 3.2, right, following the set of four graphs). In low density and Lévy target scenarios, Brownian searchers still have acceptable efficiencies (Fig. 3.2, right). The nonrelevance 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. 3.2, right). This is true even for small searchers (e.g., small detection radius). Some examples could be *diptera* or other parasitic insects looking for large herbivores and, in aquatic systems, small planktonic searchers looking for large cyanobacteria colonies.

3.5.3 Relative size

Prey to predator size ratios are far from being unity in Nature (e.g., in planktonic organisms (Hansen, 1994)). 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 (e.g., increasing target sizes while keeping searcher's size) implies a change from Lévy to Brownian search strategies. From known energetic arguments (Catalan, 1999; Peters, 1983), it is reasonable to determine the sort of interaction on the basis of searcher-target size relationships (due to the frequency at which they need to encounter to compensate metabolic rates). With an increasing target to searcher size ratio it is likely that searchers switch from non-selective grazing to ambush predation, and finally, to a parasite-like behavior (Catalan, 1999). Thus, non-selective grazing should be more related to Lévy motion (although the size-based benefit of Lévy over Brownian searches is decreased if targets are on a Lévy type of motion), while ambushing and parasite-like behavior should be more related to Brownian motion (Brownian motion has been observed in viruses and bacteria (Berg, 1983a; Murray & Jackson, 1992)).

3.5.4 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 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.

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.

Acknowledgements

We thank the Brazilian agencies CNPq and FAPEAL, and CIRIT grant 1997FI 00296 UB APMARN (FB) from the Catalan autonomous government for support, and M. G. E. da Luz, E. P. Raposo and Maurizio Serva for discussions.

4

Super-diffusion phenomena and encounter dynamics

4.1 Abstract

Rate limitation due to encounters is fundamental to many ecological interactions. Since encounter rate governs reaction rates, and thus, dynamics of systems, it deserves systematic study. In classical population biology, ecological dynamics relay on the assumption of perfectly mixed interacting entities (e.g., individuals, populations, etc.) in a spaceless'world. The so-called mean field assumption, involves that encounter rates are driven exclusively by changes in the density of the interacting entities and not on how they are distributed or move in space. Encounter rate equations quantify, by means of geometrical representations of the encounter, the role of other factors affecting random encounters such as size and velocity of particles (organisms). However, such equations do not consider the space explicitly, and thus do not give any insight on relevant spatiotemporal statistical properties produced by the trajectories of the movement through space. In the present study, we develop spatially explicit simulations of random walking particles (i.e., Lévy walkers) to evaluate encounter rate constraints beyond the assumptions of mean field and of encounter rate equations. We show that in certain scenarios encounter rate fluctuations are shaped by some spatiotemporal statistical properties produced by the type of motion rather than by physical aspects such as size or velocity. In particular, super-diffusion phenomena related to movement is relevant at low densities and/or low spatial dimensionality. Finally, we discuss poten-

tial adaptive responses of living organisms that may allow individuals to control how they diffuse through space and/or the spatial dimensionality employed in the exploration process.

4.2 Introduction

Encounter rates play a central role in population and community dynamics by determining which and how many individuals, populations, and species can interact strongly with each other or with abiotic variables at a specific location. A food item that is not encountered cannot be eaten. Hence the dynamics of encounter hold a central position in foraging theory (Jumars, 1993a).

Indeed, physical encounters, that is, the meeting of interacting entities in a space, is the first step of *any* ecological interaction (i.e., predator-prey, male-female, pollinization, habitat selection, etc.). The encounter is preceded by movements of one or the two interacting entities in one, two, or three dimensions (i.e., 1D, 2D, and 3D). However, too often in ecology, the existence of rate limitation due to encounter constrains is not considered, and the possible role of encounter rates in the government of ecological dynamics is underestimated. Most inferences on ecological dynamics are based on the assumption of the perfect mixing of populations and no rate limitation due to spatially explicit constraints (the so-called *mean field assumption*). Thus, encounter rates are assumed to be driven exclusively by the relative density of interacting entities (e.g., number of organisms per unit area, volume, etc.) and its changes through time. The traditional modeling of population dynamics (i.e., Lotka-Volterra models, SIR epidemic models, Levins-like metapopulation models, etc.) is founded on the mean field assumption (Levin & Durret, 1996). In spite of its extreme simplicity, *mean field* models provides a successful framework for population biology studies. In part, this is due to the fact that in mean field models potential deviations from mean field assumptions can be incorpored by means of *interaction coefficients*. Aside from post-encounter inefficiencies (e.g., pursuit, capture, handling, or digestive processing), interaction coefficients may also synthesize potential pre-encounter constrains beyond density-based encounter rates.

Explicit geometrical representations of the encounter scenario (e.g., morphology of the interacting particles, morphology and positioning of the perception regions, etc.) together with some physical insights into the process of encounter (e.g., size and velocity of the interacting particles) allow the development of *encounter rate equations*. Gerritsen & Strickler (1977)

developed the first encounter rate equation to analyze predator-prey interaction in zooplankton. After Gerritsen & Strickler (1977), encounter rate equations have been extended and improved conceptually (Rothschild & Osborn, 1988; Evans, 1989; Jumars, 1993b; MacKenzie & Kiorboe, 1995; Kiorboe, 1997; Catalan, 1999). The estimation of encounter rates $[NT^{-1}]$ by means of encounter rate equations is based on the identification of four elements: i) a boundary length $[L]$ or area $[L^2]$ over which encounter occurs (i.e., detection length, area, or volume), ii) an effective density of items that can be encountered $[NL^{-2}$ or $NL^{-3}]$, iii) a mean encounter speed $[LT^{-1}]$ measured as the relative velocity vector of the body doing the encountering with respect to the body encountered, and iv) the identification of the geometry of the encounter situation (i.e., dimensionality, morphology of the particles, allocation of absorption or perception sites, etc.) (Jumars, 1993a; Catalan, 1999). In this manner, aside from estimating encounter rates, one can evaluate how density, relative velocities, detection radius, and specific geometries of the encounter situation, can alter encounter rates.

The explicit formulation of encounter rate equations depends on the kind of motion behavior considered in the prey (targets) and the predators (searchers): Brownian motion, settling, swimming, or motion due to laminar or turbulent shear (for planktonic organisms). Simplifying, there are basically two main forms: diffusion-like behavior or advection-like behaviors (Catalan, 1999). Kiorboe (1997) summarizes particular expressions for each behavior. Naturally, the movement of the interacting organisms can include several of the above-mentioned mechanisms at the same time, so the effective encounter rate will result from combinations of these simplified behaviors (Rothschild & Osborn, 1988; Evans, 1989; Hill, 1992; Shimeta, 1993). At certain scales, any diffusive process becomes an advection, and independently from the cause forcing the movement, it should be taken into account that there are important statistical spatiotemporal properties emerging from particle's trajectories (e.g., the chances of covering different regions of space, the probability of revisiting a site, etc.) which affect encounter dynamics and rates. Spatial explicit simulations of random walking particles can account for such statistical properties.

Typically, the diffusion of particles through space has been addressed by means of random walk models (Okubo, 1980; Berg, 1983a). Random walks constitute probabilistic discrete step models that involve strong simplifications of organisms' movement behavior. They are aimed to characterize the statistical properties of the movement rather than describing organisms' movement from mechanistic principles (as it is pursuit in other type of models). Different types of diffusion emerge as a function of different classes of random walk models (Mandelbrot, 1977; Shlesinger et al., 1995). The

type of diffusion is characterized by the parameter α. For enough large times, t^{α} quantifies how the random walk root mean square displacement increases with t (Okubo, 1980; Berg, 1983a; Shlesinger et al., 1995). Brownian motion, whose steps increments have finite variance and no correlations, lead to normal diffusion ($\alpha = 1/2$). Super-diffusion corresponds to $\alpha > 1/2$ and sub-diffusion to $\alpha < 1/2$.

The purpose of the present study was to elucidate how changes in the type of motion of particles (organisms) affect the statistical spatiotemporal properties of the trajectories resulting in variations of encounter rates. We must emphasize that this goal can not be addressed by encounter rate equations. Our approximation is based on spatially explicit numerical simulations of interacting particles (named searchers and targets) that perform different types of random walks in a continuous space (i.e., 1D, 2D, and 3D). We employed, a class of random walk models, named Lévy walks, that can give rise to genuine super-diffusive behavior spanning a whole range of values for $\alpha \geq 1/2$: from Brownian to ballistic (i.e., straight-line) motion. We evaluated how super-diffusive phenomena provided by different types of motion affected encounter rates for different densities and dimensions. In addition, the effect of the type of motion (i.e., super-diffusivity) on encounter rates was compared to the one obtained when modifying size and cruising velocity of particles (organisms). We show that the super-diffusive phenomena in organisms' trajectories generated strong fluctuations on encounter rates in 1D, 2D, and 3D. These fluctuations were specially relevant at low resource densities and/or low spatial dimensionality. Changes of several folds in size and velocity of particles were needed to obtain encounter rates equivalent to the ones obtained by different types of motion. Finally, we discuss potential adaptive responses of living organisms that may allow individuals to control how they diffuse through space and/or the spatial dimensionality employed in the exploration process.

4.3 Methods

4.3.1 The model

Lévy walk models are random walks (i.e., probabilistic discrete step models) based on the sampling of a uniform distribution for the turning angles and a power-law distribution for the move lengths (i.e., the so-called Lévy flights). More precisely, Lévy walk models exploit a broad class of move or flight length (ℓ) distributions named Lévy-stable distributions (Mandelbrot, 1977; Shlesinger et al., 1995). These distributions have relevant statistical

properties related to the Generalized Central Limit Theorem (see Technical Appendix C). Let us assume some variables with distributions that follow the power law $P(\ell) = \ell^{-\mu}$. Sums of such variables converge to the Lévy stable distribution, with Lévy stable index $\alpha_{\mathrm{L}} = \mu - 1$. If the power law exponent μ lies in the interval $1 \leq \mu < 3$, then the Lévy stable distribution of the sums of such variables also has a power-law form. For $\mu > 3$ the form of the Lévy stable distribution of the sums converges to a Gaussian distribution due to the Central Limit Theorem. Thus we recover Brownian motion for $\mu \geq 3$. The case of $\mu \leq 1$ does not correspond to normalizable distributions.

In practice, we generate Lévy flights by sampling a power-law distribution (representing the tail of the Lévy-stable distributions) in the following way (inversion method, see Technical Appendix A):

$$\ell = \ell_0 \cdot u^{(1-\mu)^{-1}}. \tag{4.1}$$

Where u is a uniformly distributed random variable ($u \in (0,1)$), ℓ denotes the length of the flights (i.e., move lengths), ℓ_0 the minimum flight length and μ the power-law exponent (i.e., Lévy index). Lévy walk models comprise a rich variety of paths ranging from Brownian motion ($\mu \geq 3$) to straight-line paths or ballistic motion ($\mu \to 1$).

4.3.2 The simulations

We devised a set of simulations in order to explore changes on encounter rates of Lévy walkers (with varying Lévy indexes $1 < \mu < 3$) due to: (i) spatial dimensionality, (ii) target density, (iii) target size and (iv) target cruising velocity. We defined the encounter or search efficiency η as the ratio of the number of target sites encountered to the total distance traversed by the searcher $[NL^{-}1]$. Encounter efficiency times cruising velocity directly provides the encounter rate $[NL^{-}1]$. If velocity is set to one, search efficiency and encounter rates are exactly the same. In the Lévy framework η is a function of the Lévy index μ (i.e., $\eta = \eta(\mu)$). Targets could be either still and randomly distributed, or mobile. Two types of encounter dynamics were considered: non-destructive and destructive. In the case of non-destructive searches, the searcher could visit the same target site many times. This dynamic accounted for those cases in which target sites became only temporarily depleted or searchers became satiated and leaved the area. In the case of destructive searches, the target site found by the searcher became undetectable in subsequent displacements. The target site "disappeared" but to keep a constant target density during the search

a new target site reappeared at random in the searching space. The non-destructive and destructive encounter scenarios represent the limit cases of a continuum of possible target regeneration dynamics (Raposo et al., 2003). In addition, the non-destructive case with uniformly distributed targets bears a similarity to a destructive case with patchy or fractal target-site distributions (Viswanathan et al., 1999). Thus, the statistics computed in these simulations represented a wide range of natural searching scenarios.

The behavior of the searchers was defined as follows:

(1) The searcher walked by successively choosing a direction and a move length at random from a given probability distribution for the turning angles and for the displacement lengths respectively. The displacement during a move length occurred non-instantaneously. Instead the searcher displaced at a constant speed (i.e., cruising velocity), modelled as fixed discrete displacement steps during a move length. The largest move lengths involved many move steps while the minimum move length was equivalent to a displacement step.

(2) If a punctuated target site lied within a direct perceptual range or detection radius of the searcher $R = R_s + R_t$, then an encounter was registered. R_t and R_s were meant to represent any "effective" size for targets and searchers respectively (e.g., body size, perceptual range, maximum detection radius, etc.), The walking displacement became truncated immediately after the encounter (approximately at a distance R from the target site) and the searcher selected a new direction and move length according to (1).

To avoid finite scale artifacts, we represented an effectively infinite landscape by means of periodic space boundaries (i.e., particles leaving the landscape on one side emerge from the opposite side).

4.3.3 The scaling of the simulations

To make comparable the encounter rates of diffusive-like searching processes at distinct dimensional spaces (i.e., 1D, 2D and 3D) the mean free path value (i.e., λ) was fixed at a constant value. The mean free path has been identified as a relevant microscopical parameter of particle and quantum physics (Feynman et al., 1963), being defined as the mean Euclidiane distance between target sites.

For any dimensional system the mean free path was set by the size of the system L, the target density ρ, and the size of the particles R. The relationships between these parameters was given by the equation: