Optimal search in interacting populations: Gaussian jumps versus Lévy flights

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We investigated the relationships between search efficiency, movement strategy, and nonlocal communication in the biological context of animal foraging. We considered situations where the members of a population of foragers perform either Gaussian jumps or Lévy flights, and show that the search time is minimized when communication among individuals occurs at intermediate ranges, independently of the type of movement. Additionally, while Brownian strategies are more strongly influenced by the communication mechanism, Lévy flights still result in shorter overall search durations.

I. INTRODUCTION

Situations where a single individual or a group of searchers must find an object (target) appear in many different fields including chemistry [1], information theory [2], and animal foraging [3,4]. The study of these searching problems has generated an increasing number of studies in recent years, many of them oriented towards the identification of efficient strategies [1,4–6]. Many remarkable examples can be found in the context of biological encounters, such as proteins searching for targets on DNA [7], or animals searching for a mate, shelter, or food [1,8–16]. In these cases, the search time is generally limiting and minimizing it can increase individual fitness or reaction rates.

The optimality of a search strategy depends strongly on the nature of both the targets and the searchers [17,18]. In the context of animal foraging, which is our focus here, searchers may move randomly, may use memory and experience to locate dispersed targets, or they may also combine random search with memory-based search. In highly social species, groups of searchers may share information when no single individual is sufficiently knowledgeable. This is based on the "many wrongs hypothesis" [19,20] that states that error in sensing of individuals can be reduced by interacting with the rest of the group, where all individuals can act as sensors.

It is well known that individual movement plays a central role in search efficiency, and many studies have focused on the comparative efficiency of Lévy and Brownian movement strategies [1,14,17,18]. Lévy flights are more efficient in some random search scenarios [9,21], but whether or not they are used in real animal search strategies is still an open and contentious topic [11,22]. Much less effort, however, has been spent on trying to understand the long-range (i.e., nonlocal) interaction mechanisms among social searchers. While diverse observations suggest that such interactions occur in many taxa, including bacteria [23], insects, and mammals [24,25], previous studies have focused almost exclusively on how the collective movements of a group of animals can emerge from local interactions among individuals [26–28]. To our knowledge, only two recent studies have explored the effects of long-range communication mechanisms on a searching strategy [12,29]. In particular, [29] showed that when the communication range is intermediate, individuals tend to receive the optimal amount of information on the locations of targets, and search time is consequently minimized. Longer communication ranges overwhelm the searchers as they are simultaneously called from all directions, while shorter ranges do not provide enough information. However, many open questions remain about the relationship between communication and search efficiency, especially concerning the role that the landscape plays in determining the optimal communication range, and on the robustness of the behavior of the model when different random movements are considered. Here we compare the effects of nonlocal communication on the search efficiency of groups of individuals employing either Lévy flight or Brownian random search strategies. We also investigate how the distance between targets influences the optimal communication range for both strategies. For tractability, we consider a simplified, one-dimensional version of the model and compute analytically the search time for both Brownian and Lévy flights as a function of the communication length scale. This simplified model allows us to unveil the dependence of search time on both the parameters governing individual mobility, and on the distance between targets.

The paper is organized as follows. The general model is presented in Sec. II. Sections III and IV present analytical and numerical results for Brownian and Lévy strategies, respectively. In Sec. V, the role of the communication mechanisms in the different searching strategies is discussed, and the paper ends with Sec. VI, where a summary and conclusions are presented.

II. THE MODEL

General. We consider a population of N interacting individuals that move randomly, searching for spatially distributed targets. Every individual is provided with information about the location of the targets coming from two different sources: its own perception (*local information*), and the knowledge on the quality of far away areas coming from a communication mechanism with the rest of the population (*nonlocal information*). The Langevin equation describing this dynamics is

$$\mathbf{r}_i(t) = B_g \nabla g(\mathbf{r}_i) + B_C \nabla S(\mathbf{r}_i) + \eta_i(t), \quad i = 1, \ldots, N,$$

$$(1)$$

where $\eta_i(t)$ is a stochastic function of time, which we specify below, whose statistical properties define the random motion performed by the searchers. The term $B_g \nabla g(\mathbf{r}_i)$ refers to the local search, where $g(\mathbf{r})$ is an environmental quality function (amount of grass, prey, etc.). g takes values between 0 (low quality areas) and 1 (high quality areas), and thus allows us to define the targets of the search as those regions where the environmental quality is higher than a given threshold κ. B_g is the local search bias parameter. $B_C \nabla S(\mathbf{r}_i)$ is the nonlocal search term, where B_C is the nonlocal search bias parameter and $S(\mathbf{r}_i)$ is the *nonlocal information function* of the particle i. It represents the information arriving at the position of the individual i as a result of communication with the rest of the population. The net effect of these two terms is to drift the movement of the searcher towards high quality areas of the environment. The model thus becomes an Ornstein-Uhlenbeck process, with individuals drifting randomly, but with an attraction to the location of the targets [30–32].

Following previous efforts [29,33], the interaction among individuals is given in terms of a nonlocal function defined as the superposition of the pairwise interaction between one individual and each one of the other members of the population,

$$S(\mathbf{r}_i) = \left(\sum_{j=1, j \neq i}^{N} A[g(\mathbf{r}_j)] V(\mathbf{r}_i, \mathbf{r}_j) \right), \qquad (2)$$

where $V(\mathbf{r}_i, \mathbf{r}_j)$ is the two-body interaction between the receptor i at $\mathbf{r}_i$ and the emitting particle fixed at $\mathbf{r}_j$. $A[g(\mathbf{r}_j)]$ is an activation function (typically a Heaviside function) that turns on when the individual at $\mathbf{r}_j$ has found a target and starts communicating.

A study of the behavior of this model in two dimensions (2D) based on Monte Carlo simulations, and using a Gaussian white noise for the function $\eta(t)$, i.e., Brownian motion, has been shown in [29]. To gain clearer insight and provide analytical arguments, we study a minimalistic version of the model.

Specific considerations. Consider a single individual in a one-dimensional (1D) space of length L, so that the highest quality areas are located beyond the limits of the system, i.e., at $x = -1$ and $x = L + 1$ (see Fig. 1). Note that this would correspond to the ideal situation where all the members of the population but one—the searcher—have already reached one of the targets. A landscape quality function $g(x)$ must also be defined. Provided it is a smooth, well-behaved function, its particular shape is not relevant. We therefore assume a Gaussian-like quality landscape,

$$g(x) = e^{-\frac{(x+1)^2}{\sigma_r}} + e^{-\frac{(x-L-1)^2}{\sigma_r}}, \qquad (3)$$

where σ_r gives the characteristic width of a high quality region. Notice that $g(x)$ is defined so that highest quality areas are located, as mentioned, at $x = -1$ and $x = L + 1$. This ensures that the gradient of the function does not vanish at the extremes of the system (Fig. 1), and it is equivalent to setting the value of the threshold κ such that the targets start at $x = 0$ and $x = L$. We assume that a foraging area is good enough when its quality is higher than 80% of the ideal environment, which means $\kappa = 0.8$. As we center the patches of resources at $x = -1$ and $x =$
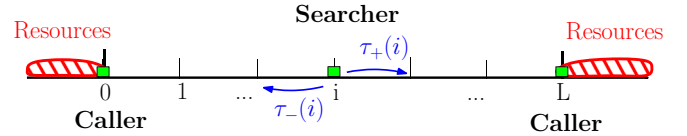

FIG. 1. (Color online) Scheme of the simple version of the model.

$L + 1$, fixing a good quality threshold at $\kappa = 0.8$ is equivalent to fixing the width of the environmental quality function at $\sigma_r = 4.5$, to ensure that $g(0) = g(L) \approx 0.80$. However, the qualitative behavior of the model is independent of this choice.

Finally, the pairwise communication function needs to be specified, and we choose a family of functions given by

$$V(x_i, x_j) = \exp\left(-\frac{|x_i - x_j|^p}{\sigma} \right), \qquad (4)$$

where $\sigma^{1/p}$ gives the typical communication scale. For simplicity, and without loss of generality, we will consider only the case $p = 2$. Indeed, the choice of the function V is not relevant for the behavior of the model, provided that it defines an interaction length scale through the parameter σ. This scale must tend to zero in the limit $\sigma \to 0$ and to infinity in the limit $\sigma \to \infty$. This assures that the gradient of the calling function vanishes in these limits. The combination of local and nonlocal information gives the total available information for the searcher $R(x) = B_g g(x) + B_c S(x)$.

To obtain analytical results, we work in the following on a discrete space. The stochastic particle dynamics equivalent to Eq. (1) considers left and right jumping rates which are defined for every individual using the total information function,

$$\tau_{\pm}(x) = \max\left(\tau_0 + \frac{R(x \pm h) - R(x)}{h}, \alpha \right), \qquad (5)$$

where α is a small positive constant to avoid negative rates that has been given an arbitrary value ($\alpha = 10^{-4}$), and h is the spatial discretization ($h = 1$). Finally, τ_0 is the jumping rate of an individual in absence of information, and it is related to the diffusion component of the dynamics of Eq. (1). Given the transition rates of Eq. (5), the movement with a higher gain of information has a higher rate, and therefore a larger probability of taking place.

The simplest situation, which allows an analytical treatment of the problem, is to consider only $N = 3$ individuals. Two of them are located in the top quality areas just beyond the frontiers of the system limit, $x = -1$ and $x = L + 1$, and the other one is still searching for a target. Under these considerations, using the environmental quality function defined in Eq. (3), and the pairwise potential of Eq. (4), the total available information for the searcher is

$$R(x; \sigma, L) = B_g \left(e^{-\frac{(x+1)^2}{\sigma_r}} + e^{-\frac{(x-L-1)^2}{\sigma_r}} \right)$$
$$+ B_C \left(e^{-\frac{(x-L-1)^2}{\sigma}} + e^{-\frac{(x+1)^2}{\sigma}} \right). \qquad (6)$$

Following [29], the efficiency of the search process is measured in terms of the first arrival time at one of the high quality areas, either at $x = 0$ or $x = L$, starting from $x_0 = L/2$. From the definition of the transition rates in Eq. (5),

$\tau_+(L-1) \gg \tau_-(L)$, and equivalently $\tau_-(1) \gg \tau_+(0)$. This means that at both extremes of the system, the rate at which particles arrive is much higher than the rate at which they leave, so particles do not move when they arrive in the top quality areas. This allows us to consider both extremes $x = 0$ and $x = L$ of the system as absorbing, and the first arrival time may be obtained from the flux of presence probability of the searcher there [34]

$$\langle T(\sigma) \rangle = \int_0^\infty t \left(\frac{\partial P(0,t)}{\partial t} + \frac{\partial P(L,t)}{\partial t} \right) dt. \qquad (7)$$

This definition will be used in the following sections to investigate the influence of sharing information (i.e., of the interaction mechanism) on search times. The results will be compared with those obtained using a deterministic approximation of the movement of the searcher. We study two different random strategies—Brownian and Lévy.

III. BROWNIAN JUMPS

In this case the searcher only jumps—with a given rate—to its nearest neighbors, so the coupling of the set of differential equations describing the occupancy probability of every site of the system is (notice that lattice spacing $h = 1$)

$$\frac{\partial P(0,t)}{\partial t} = -\tau_+(0)P(0,t) + \tau_-(1)P(1,t),$$

$$\frac{\partial P(i,t)}{\partial t} = -[\tau_+(i) + \tau_-(i)]P(i,t) + \tau_+(i-1)P(i-1,t)$$
$$+ \tau_-(i+1)P(i+1,t),$$

$$\frac{\partial P(L,t)}{\partial t} = -\tau_-(L)P(L,t) + \tau_+(L-1)P(L-1,t). \qquad (8)$$

with $i = 1, \dots, L - 1$. If the initial position of the particle is known, it is possible to solve Eq. (8) using the Laplace transform. Once the probability distribution of each point has been obtained, it is possible to obtain the mean first arrival time using Eq. (7). The thick line in Fig. 2 shows this result, indicating that the searching process is optimal (minimal time to arrive to one of the good quality areas) for intermediate values of σ. A particularly simple limit in Eq. (8) appears when $\tau_+ \gg \tau_-$ when $x > L/2$ (and the contrary on the other half of the system). The search time is $T(\sigma) = \frac{L}{2\tau_+}$. This is the expected result since the movement is mainly in one direction and at a constant rate.

In biological terms this means that the optimal situation for the individuals is to deal with intermediate amounts of information. Extreme situations, where too much ($\sigma \to \infty$) or too little ($\sigma \to 0$) information is provided by the population, have the same effect on the mean first arrival time, which tends to the same asymptotic value in both limits. In both cases, the search is driven only by the local perception of the environment [29].

This calculation gives exact results, but it implies fixing the system size, solving a set of equations of dimension L, and finally obtaining the inverse Laplace transform of the solutions. The main disadvantage of this approach is that it is not possible to study the influence of the distance between targets on the optimal communication length. To circumvent this we use a deterministic approach in the continuum limit $h \to 0$ and
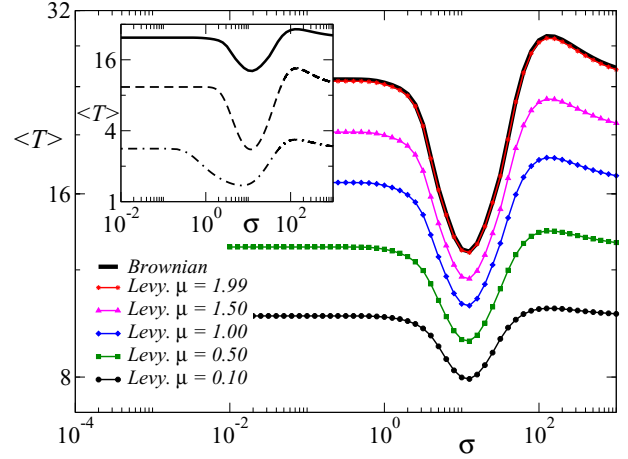

FIG. 2. (Color online) First arrival time solving Eq. (8) for the Brownian jumps and Eq. (17) in the case of Lévy flights for different values of μ. Lines are interpolations. Inset: First arrival time using its definition Eq. (7) (full line) and Eq. (11) with $\epsilon = 2$ (dashed line) and $\epsilon = 0$ (dotted dashed line) for a Brownian searcher. In both panels: $L = 9$, $\sigma_r = 4.5$, $B_g = 1$, and $B_c = 1$.

define, using the symmetry of the system, a mean drift velocity towards one of the high quality areas, $x = L$,

$$\langle v_d(\sigma,L) \rangle = \int_{L/2}^L [\tau_+(x) - \tau_-(x)]dx, \qquad (9)$$

Substituting the definition of the transition rates Eq. (5), the drift velocity is

$$\langle v_d(\sigma,L) \rangle = 2 \left[R(L) - R\left(\frac{L}{2}\right) \right], \qquad (10)$$

and therefore the search time is

$$\langle T(\sigma,L) \rangle = \frac{N/2}{\langle v_d(\sigma,L) \rangle}. \qquad (11)$$

We compute the searching time using Eq. (11) with the same values of the parameters used before ($\sigma_r = 4.5$, $B_g = 1$, and $B_c = 1$, $L = 9$) to compare it with the results given by Eq. (7) (inset of Fig. 2). The approach in Eq. (11) (dotted-dashed line) reproduces the qualitative behavior of the searching time although underestimates the value of the optimal communication range ($\sigma_{\text{opt}} = 7.2$, while Eq. (7) produces $\sigma_{\text{opt}} = 12.5$). This can be fixed excluding from the average in Eq. (9) the boundary of the system introducing a parameter ϵ in the limits of the integration. Results for $\epsilon = 2$ correspond to the dashed line in the inset of Fig. 2 (see Appendix B for details). However, regardless of the value of ϵ used in the average, this approximation underestimates the temporal scale of the problem (the absolute values of the times). This is because it is assumed that the searcher follows a deterministic movement to the target neglecting any fluctuation that may slow the process.

Finally, increasing σ beyond its optimal value, there is a maximum for the search time for any of the approaches. For these values of the communication range, the nonlocal information at the middle of the system coming from both targets is higher than in the extremes and thus there is a bias to
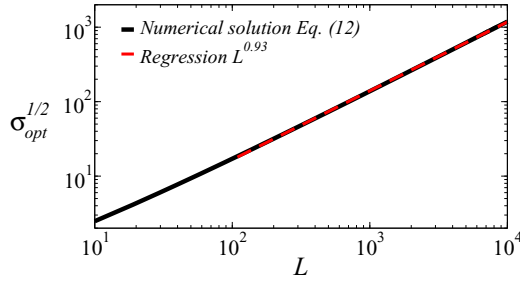
FIG. 3. (Color online) Scaling of the optimal communication range parameter with the distance between targets (system size in the 1D simple model).

the middle in the movement of the searcher. This small effect that vanishes when σ increases and the information tends to be constant in the whole system, seems to be an artifact of the particular arrangement of the simplified 1D system, and does not seem relevant for any real-world consideration of this kind of model. In addition, it does not substantially affect the dynamics because local perception of the environment pushes the individual towards one of the targets.

Finally, within this deterministic approximation, besides studying larger systems with no additional computational cost, it is possible to obtain the optimal value of the interaction range parameter σ_{opt}:

$$\left(\frac{\partial T}{\partial \sigma}\right)_{\sigma=\sigma_{\text{opt}}} = 0, \qquad (12)$$

which has to be solved numerically for different sizes of the system. The typical optimal communication scale defined by $\sigma^{1/p}$ (i.e., by $\sigma^{1/2}$ since $p = 2$) grows approximately linearly with the distance between targets in the asymptotic limit. Using a regression of the results obtained from the integration of Eq. (12) yields an exponent $\sigma_{\text{opt}}^{1/2} \propto L^{0.93}$ for $L \gg 1$ (Fig. 3).

IV. LÉVY FLIGHTS

So far the model has been studied assuming that the searchers employ Brownian motion. Alternatively, Lévy flights have been shown as a good searching strategy that may be used by some species. However, empirical studies have generated controversy, since many of the statistical methods used to support the presence of Lévy flights in nature have been questioned, and the issue remains unresolved [11,22,35]. In this section the case of Lévy searchers is considered. The results will show that neither the behavior of the model, nor the existence of an intermediate optimal communication scale, depend on the characteristics of the motion of the individuals.

Lévy flights do not have a typical length scale and thus the searcher can, in principle, make jumps as large as the size of the system. The lengths of the jumps $l > 0$ are sorted from a probability distribution with a long tail [36,37]

$$P_\mu(l) \approx \tilde{l}^\mu l^{-(\mu+1)}, \qquad l \to \infty, \qquad (13)$$

with $l \gg \tilde{l}$, and $0 < \mu < 2$, where $\tilde{l}$ is a characteristic length scale of the system. This distribution is not defined for $\mu < 0$, its mean and variance are unbounded for $0 < \mu \leqslant 1$, and it has a mean but no variance for $1 < \mu < 2$. Finally, for $\mu \geqslant 2$,

the two first moments exist and thus it obeys the central limit theorem. The Brownian motion limit is recovered in this latter case, while very long jumps are more frequent when $\mu \to 0$. This is usually referred as the ballistic limit, with a high abundance of straight-line long displacements [3,4]:

$$\Psi_\mu(l) \approx \mu^{-1} \left(\frac{l}{\tilde{l}}\right)^{-\mu}, \qquad l \to \infty. \qquad (14)$$

As a simple normalizable cumulative distribution function, with the asymptotic behavior of Eq. (14), we will use [38]

$$\Psi_\mu(l) = \frac{1}{\tilde{l}\left(1 + \frac{l}{\tilde{l}} b^{1/\mu}\right)^\mu}, \qquad (15)$$

whose probability distribution $P_\mu(l) = \Psi'_\mu(l)$ is given by

$$P_\mu(l) = \frac{\mu b^{1/\mu}}{\tilde{l}\left(1 + \frac{l}{\tilde{l}} b^{1/\mu}\right)^{\mu+1}}, \qquad (16)$$

with $0 < \mu < 2$, and $b = [\Gamma(1 - \mu/2)\Gamma(\mu/2)]/\Gamma(\mu)$. We fix $\tilde{l} = h = 1$, and the transition rate as defined in Eq. (5).

Results in one dimension. Proceeding similarly to the previous section, the set of equations for the probability of occupancy is

$$\frac{\partial P(0,t)}{\partial t} = \sum_{j=1}^{L} \tau_-(j) B_j P(j,t) - \tau_+(0) P(0,t)$$
$$\times \left(B_L + \sum_{j=1}^{L-1} A_j\right),$$

$$\frac{\partial P(i,t)}{\partial t} = \sum_{j=0}^{i-1} \tau_+(j) A_{i-j} P(j,t) + \sum_{j=i+1}^{L} \tau_-(j) A_{j-i} P(j,t)$$
$$- \tau_-(i) P(i,t) \left(B_i + \sum_{j=1}^{i-1} A_j\right)$$
$$- \tau_+(i) P(i,t) \left(B_{L-i} + \sum_{j=1}^{L-i-1} A_j\right),$$
$$i = 1, \dots, L-1,$$

$$\frac{\partial P(L,t)}{\partial t} = \sum_{j=0}^{L-1} \tau_+(j) B_{L-j} P(j,t) - \tau_-(L) P(L,t)$$
$$\times \left(B_L + \sum_{j=1}^{L-1} A_j\right). \qquad (17)$$

We assume that if a jump of length in between $j - 1$ and j takes place, the individual gets the position j. To this aim, the coefficients A_j enter in the set of equations (17) and are defined as $A_j = \int_{j-1}^{j} \Psi_\mu(l)dl$. They give the probability of a jump of length between $j - 1$ and j to happen. The coefficients B_j are defined as $B_j = \int_{j-1}^{\infty} \Psi_\mu(l)dl$, to take into account that the searcher stops if it arrives at a target. This introduces a cutoff in the jumping length distribution Eq. (16).

Given the size of the system L, which fixes the dimension of the system of equations (17), it is possible to obtain an
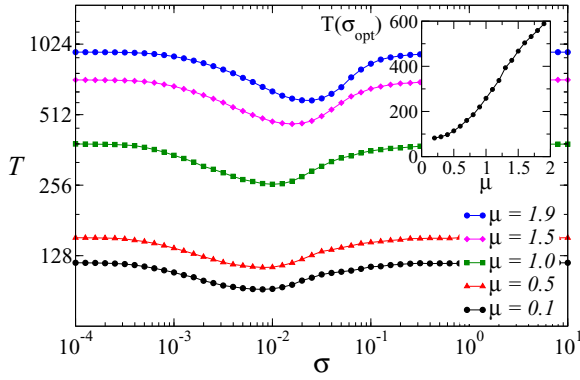
FIG. 4. (Color online) Mean first arrival time for Lévy flights with different exponent μ in the 2D model. $B_g = 1$, $B_c = 1$, $\tau_0 = 50$. Inset: Mean searching time at the optimal communication range as a function of the Lévy exponent μ. Lines are interpolations.
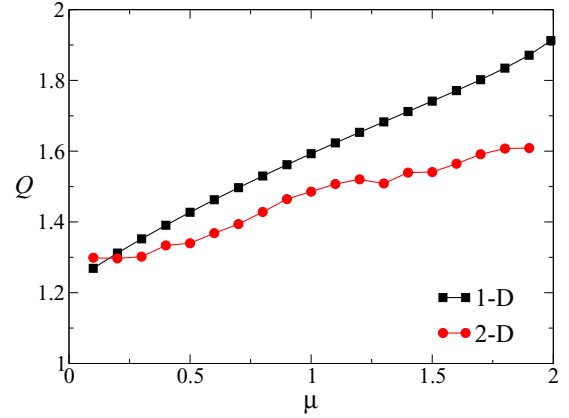

FIG. 5. (Color online) Improvement of the searching process because of the communication mechanism. Circles correspond to the 2D model and squares to 1D. Lines are interpolations.

analytical solution for the occupancy probabilities and the mean arrival time to the targets using Eq. (7). This is shown in Fig. 2, where the Brownian limit is recovered when $\mu \to 2$. It is also observed that when long jumps are frequent the search is much faster, although the gain in search efficiency due to the communication mechanisms is lower close to the ballistic limit (i.e., $\mu \to 0$). This will be explained later in Sec. V.

Similarly to the Brownian case, a particularly simple limit in Eq. (17) appears when $\tau_+ \gg \tau_-$ for $x > L/2$ (and the contrary on the other half of the system). The search time is

$$T(x = L, \sigma) \propto \frac{1}{\tau_+},$$

where the proportionality constant is a combination of the coefficients A_i that depends on the size of the system.

Results in two dimensions. We now present some results in 2D using Monte Carlo simulations, as was done in the case of Brownian particles in [29]. The individuals are moving on a discrete regular square lattice ($L_x = L_y = 1$) of mesh $h = 0.01$, where the targets are randomly distributed. Similarly to the 1D case, the searchers stop if they find a target during a displacement of length l. This naturally introduces a cutoff in the length of the jumps, which becomes more important as target density increases [4]. However, as we will focus on a situation where target density is low, we introduce an exponential cutoff of the order of the system size in the jump length probability distribution to ensure that very long jumps without physical meaning (they imply very high velocities) do not occur:

$$\varphi_\mu(l) = C \frac{\exp(-l/L)\mu b^{1/\mu}}{\tilde{l}\left(1 + \frac{l}{\tilde{l}} b^{1/\mu}\right)^{\mu+1}}, \tag{18}$$

where $C = \int_0^\infty \varphi_\mu(l)\,dl$ is the normalization constant, and $\tilde{l} = h$. We did not need to introduce such a cutoff in the study of the 1D model because the boundaries of the system introduced a natural truncation in the jump length distribution, and jumps longer than the system size never occurred. Generally, the search is faster when long displacements occur more frequently. Figure 4 shows search time for different values of μ and the mean searching time at the optimal communication

range as a function of the Lévy exponent. As the frequency of long displacements decreases (increasing μ) the search is slower. Again, the effect of the communication mechanism is more important when we approach the Brownian limit ($\mu \to 2$), as will be explained next.

V. INFLUENCE OF THE SEARCHING STRATEGY: LÉVY VS BROWNIAN

As a general result of the model, searching is faster when individuals have intermediate amounts of information, regardless of the kind of movement strategy followed by the population (Brownian or Lévy). However, communication has a larger impact on Brownian motion, i.e., the depth of the well at σ_{opt} is larger (Figs. 2 and 4).

A measure of the improvement in search performance at the optimal communication range is given by the ratio between the search time without communication and that at the optimal communication range $Q = T_{\sigma \to 0}/T_{\sigma_{opt}}$. This quantity is plotted in Fig. 5 for different Lévy exponents. As previously mentioned, Brownian searchers that are not able to perform long displacements benefit more from communication than Lévy searchers. This is because introducing an additional source of information increases the directionality of the random motion and prevents the searcher from revisiting the same place many times, which is the key problem with Brownian search strategies [4]. A Brownian walker has no directionality in the movement, so provided with sources of information (communication together with the local quality of the landscape) it can search much more efficiently. This effect is less important for Lévy searchers due to the presence of long, straight-line moves that, by themselves, decrease the number of times that a particular area is revisited. Additionally, the return probability to a given point is much higher in 1D than in 2D. This is because in the 1D case the walker can only move either to the right or to the left at each step. Therefore the directionality introduced by communication has a stronger effect in this simpler scenario.

In summary, the communication mechanism is less important in Lévy strategies, so that its effect is less noticeable as shown in Fig. 5 both in 1D and 2D.
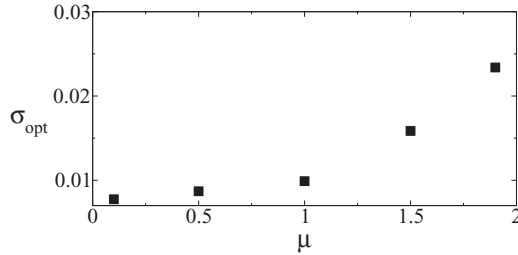
FIG. 6. Optimal communication range as a function of the Lévy exponent.

However, the value of the optimal interaction range changes with the kind of motion. This is shown in the 2D model by the dependence of the mean search time on the communication range for different Lévy exponents (Fig. 4). The value of σ_{opt} increases with the Lévy exponent, so Brownian searchers ($\mu \to 2$) need to spread the information farther (a larger value of σ_{opt}) than Lévy ($\mu = 1$) walkers to obtain the maximum benefit. In Fig. 6 we show this tendency for the 2D model. In Fig. 6 we show the value of the optimal communication range σ_{opt} as a function of the Lévy exponent. Lévy trajectories show clusters of short displacements with frequent turns occasionally broken up by long linear displacements, which account for most of the target encounters. However, because these steps are often much longer than the average distance between targets they are not positively influenced by communication, so any benefit a Lévy strategy gains from communication occurs during the series of short displacements. The time that an individual spends doing short movements is limited by the interarrival time of the large steps, so unless an individual is already relatively close to a target, it will not have time to reach a target before the next big step comes and moves it far away from that original target. Therefore, the optimal communication range decreases with decreasing Lévy exponent μ as longer displacements become more frequent at lower μ values.

In addition, the value of σ_{opt} depends on both the number of targets and their spatial distribution, as was shown at the end of Sec. III for a simple 1D situation where $\sigma_{opt} \sim L$.

VI. SUMMARY AND CONCLUSIONS

In this paper we compared Brownian and Lévy search strategies using a population of individuals that exchange information about the location of spatially distributed targets. Using a simple 1D model we have provided analytical results on both cases, concluding that frequent long jumps ($\mu \to 0$, ballistic limit) minimize the searching times.

However, the effect of a communication mechanism is more pronounced in the limit of short jumps, i.e., Brownian motion. This means that a population of individuals employing Brownian motion gains proportionally more benefit from communicating and sharing information than does a population of Lévy walkers, where long jumps are more or less frequent depending on the value of the Lévy exponent μ. When messages are exchanged in a range that minimizes search duration, communication is the driving force in the Brownian limit, but occasional long jumps are still responsible

for most of the encounters with targets in the case of long-tailed step-length distributions.

The main result of this work is rather general: Independently of the kind of communication performed by the population, and of the spatial distribution of the targets, a population of individuals with the ability to communicate will find the targets in a shorter time if the information is spread at intermediate ranges. Both an excess and a lack of information increase the search time. However, the communication mechanism does not have the same quantitative effect on the different moving strategies (i.e., ballistic, Lévy, or Brownian). Uninformed Brownian individuals perform a random movement revisiting the same position many times, so having an external source of information introduces directionality in the movement, decreasing the number of times that a point in the space is visited. In the case of Lévy and ballistic strategies ($\mu \to 0$), communication is less noticeable because individuals are able to do long jumps. This is already a source of directionality that prevents individuals from revisiting the same points in space many times, and thus weakens the effect of the directionality introduced by communication.

APPENDIX A: VORONOI DIAGRAMS OF THE MODEL

The behavior of the model, resulting in optimal searches at intermediate communication ranges, can be explained in terms of Voronoi diagrams [39]. Consider every target as a seed that has associated a Voronoi cell formed by those points whose distance to that seed is less than or equal to its distance to any other one [see Fig. 7 (top) for a distribution of the space in five Voronoi cells for an initial distribution of particles with five targets (crosses)]. The searching time will be minimized when the information coming from the individuals located on one target covers the full associated Voronoi cell, but only that cell. In this situation, the searchers within that cell will receive information coming only from that target and move towards it. σ_{opt} is the communication range that maximizes the gradient (approximately the smallest value of σ that makes the calling function not vanishing) of the calling function at the frontiers of the Voronoi cells. Increasing the communication range provides individuals with information coming from different targets, and makes them get overwhelmed in the limit $\sigma \to \infty$. This Voronoi construction may also help to explain the improvement of the searching strategies because of sharing information. The difference between Brownian and Lévy strategies can be seen in Fig. 7 (bottom). They show the origin of the individuals that are at each target at the end of a Lévy (left) and a Brownian search (right) (i.e., in which Voronoi cell they were at the beginning). In the case of Brownian individuals most of the particles at every
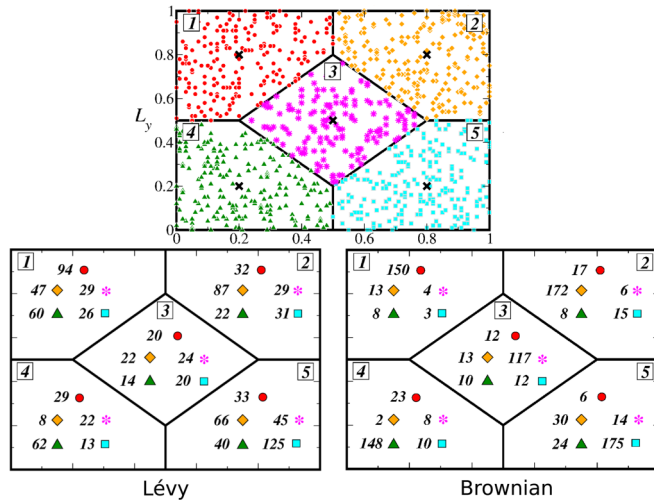
FIG. 7. (Color online) Top: Initial random distribution of individuals, the symbol refers to the Voronoi cell at which every individual belongs initially. Bottom left: Number of individuals coming from each cell at each target at the end of the search using Lévy flights. Right: Number of individuals coming from each cell at each target at the end of the search using Brownian motion. Parameters: $\sigma = 0.01$ (optimal communication range), $B_g = 1$, $B_c = 1$, $\tau_0 = 50$. The black crosses represent the location of the five targets.

target were initially in its Voronoi cell. For Lévy flights the long displacements mix the population in the stationary state (i.e., individuals at a target come from different cells). The communication mechanism is less important in Lévy strategies, so that its effect is less noticeable and the encounters of individuals with targets are caused mainly by the long displacements.

APPENDIX B: DETERMINISTIC APPROACH TO THE SEARCHING TIMES

It is possible to improve the results given by the deterministic approach if the region close to the target, i.e., the boundary of the system, is neglected in the average given by Eq. (9). At that point, one of the rates is much higher than the other and thus would contribute to the drift velocity making its value much higher, mainly in the limit $\sigma \to 0$. To this aim one can include a parameter ϵ, so that the integration limits in Eq. (9) are $L/2$ and $L - \epsilon$.

To estimate the value of ϵ it is useful to plot $\tau_+(x) - \tau_-(x)$ versus x (not shown). The difference between rates, although depending on σ, starts increasing quickly when $x \geqslant L - 2$, so one can estimate $\epsilon = 2$. The inset of Fig. 2 shows the exit time as a function of the communication range computed with this approach (dashed line). Its optimal value is in good agreement with the result obtained using the definition of the search time (thick line), with $\sigma_{\rm opt} \approx 12.5$ for both approaches. However, the temporal scale of the problem (the absolute values of the times), although higher than with $\epsilon = 0$, is still lower in this calculation.

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