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Optimizing the encounter rate in biological interactions: Ballistic versus Lévy versus Brownian strategies

A. James,[*] M. J. Plank, and R. Brown
Biomathematics Research Centre, University of Canterbury, Christchurch, New Zealand

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Bartumeus *et al.* [Phys. Rev. Lett. **88**, 097901 (2002)] compared the efficiency of a Lévy random walk predator strategy with a Brownian random walk strategy in a periodic one-dimensional domain with nonrevisitable moving targets. Their findings from numerical simulations conclude that "a Lévy search strategy is the best option in some, but not all, cases for a random search process." Using the same methodology, we show that the simplest random search strategy of all, ballistic motion in a random direction, outperforms a Lévy strategy in almost every case. We further show that, in the small set of cases where the ballistic strategy is not optimal, the periodic model does not capture the more realistic nonperiodic case. In the nonperiodic case, the ballistic strategy again outperforms the Lévy strategy.

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Interest in optimal foraging is high. The performance of Lévy random walks [i.e., walks with step lengths x_j drawn from a power-law distribution $P(x_j)\sim x_j^{-\mu}$ with $1<\mu\leqslant 3$] relative to that of other movement strategies has received a large amount of interest [1–10]. Some observational evidence that points to the existence of Lévy walks in nature [11] has been overturned [12], while other evidence remains compelling [13,14]. There is a large body of theoretical work that points to Lévy walks with an exponent of 2 as being the solution to certain optimal foraging problems [1–4,15,16]. In particular, it has been shown that, under certain conditions, the optimal Lévy random walk exponent for scenarios with revisitable stationary targets is approximately 2 [4]. For scenarios with nonrevisitable stationary targets, decreasing the exponent always increases search efficiency, and hence the optimal strategy, as the exponent tends to 1, is ballistic motion [3,4,15–17].

There have also been some studies of scenarios with moving targets [1,2,18]. Bartumeus *et al.* [1] showed that, for nonrevisitable moving targets, a Lévy search strategy (with an exponent of $\mu=2$) outperforms a Brownian search strategy (with an exponent of $\mu=3$). While this is true, Bartumeus *et al.* [1] did not consider any other values of the exponent other that $\mu=2$ and $\mu=3$. In this study, we show that, similar to the scenario with nonrevisitable stationary targets (see Ref. [15]), decreasing the exponent μ always increases search efficiency, and hence the optimal strategy is ballistic motion. Our findings complement those of Faustino *et al.* [18], although they considered a different type of movement strategy that did not include true ballistic motion (this is discussed in more detail later).

To model the scenario of a single predator searching for many targets moving in one dimension, Bartumeus *et al.* [1,2] construct a limiting generalized predator-target simulation model of a single searcher and a single moving target in a one-dimensional periodic interval of length L. The predator and target move with constant speeds v_p and v_t, respectively, and the ratio of speeds is denoted by $v=v_t/v_p$. Step lengths x_j are chosen from a power-law distribution $P(x_j)\sim x_j^{-\mu}$, with $x_j\in(x_{\min},\infty)$, and each step is in a random direction, either left or right. If $\mu>3$ the movement process is a Brownian random walk. If $\mu\leqslant 3$, the distribution of step lengths is heavy tailed and this is termed a Lévy random walk [15,19]. The limiting case of the random walk process as $\mu\to 1$ ($\mu=1$ is not a probability distribution) is ballistic motion, whereby the individual moves in a straight line in a randomly chosen direction [15]. Note that the ballistic motion process still contains a stochastic element as the direction is chosen at random. The efficiency of the predator's walk is defined as the mean number of encounters per unit distance moved. The predator and target are each given a size (i.e., radius) r_p and r_t, respectively, and an encounter is registered whenever the predator and target come within a distance equal to the sum of their two radii. When an encounter occurs, the predator moves toward the target (a distance of their combined radii) and the target is destroyed. A new target is then created at a random location (with the constraint that the initial distance between target and predator must be greater than r_p+r_t), and the search process restarts. In each simulation, the predator travels a total distance $\mathcal{L}$, which is sufficiently large in comparison to L to provide good statistics. As the searcher has no knowledge of the target's position or velocity (i.e., it cannot "see") the immediate search strategy is not obvious. The special case where the searcher always starts very close to a nonmoving target is similar to that analyzed by Viswanathan *et al.* [4] for which it was found that a Lévy strategy was more efficient than both Brownian and ballistic strategies.

Bartumeus *et al.* [1] compare the efficiency of a Lévy predator (defined as having $\mu_p=2$) with that of a Brownian predator (defined as having $\mu_p=3$), searching for either a Lévy target ($\mu_t=2$) or a Brownian target ($\mu_t=3$). In nearly all cases, the efficiency of the Lévy predator is greater than or equal to that of the Brownian predator. The increased efficiency of the Lévy predator is more marked for large system size L, small speed ratio v, and small size ratio r_t/r_p. Their results do not show the actual efficiencies, only the ratio of the two efficiencies when $\mu_p=2$ and $\mu_p=3$.

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[*] a.james@math.canterbury.ac.nz

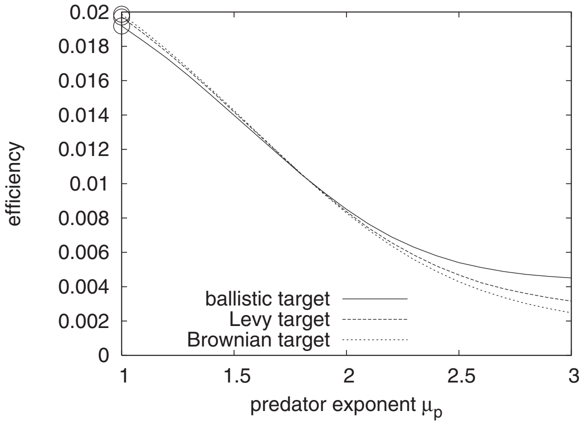

FIG. 1. The mean efficiency for a range of predator exponents μ_p, and for three different target strategies (ballistic, Lévy, Brownian). Random walks with $\mu > 1$ were carried out by drawing step lengths x_j from a power-law distribution; random walks with $\mu = 1$ were carried out by assuming the step length is infinite, so movement is in a straight line. As expected, as $\mu_p \to 1$, the mean efficiency tends toward the value predicted by simulating ballistic motion (open circles). Other parameter values are $L=100$, $v_p=100$, $v_t=20$, $r_p=r_t=0$, $x_{\min}=1$, $\mathcal{L}=10^6$.

We replicate these results and also look at movement strategies, for both the predator and the target, with other values of μ in the range $1 < \mu \leqslant 3$. The predator and target radii are here assumed to be zero (the effect of introducing nonzero radii is discussed below). Figure 1 shows the predator's efficiency against μ_p for a speed ratio of $v=0.2$, i.e., a fast predator, and three different types of target: Brownian ($\mu_t=3$), Lévy ($\mu_t=2$), and ballistic ($\mu_t \to 1$). It is clear that, although a predator strategy of $\mu_p=2$ has higher efficiency than $\mu_p=3$, these are just two arbitrary points in a continuum, and decreasing μ_p toward 1 further increases efficiency. This agrees with the results of Refs. [3,15], which show that a ballistic strategy is optimal in the case of destructive foraging and stationary targets.

We now compare the performance of the ballistic predator strategy to that of the Lévy and Brownian strategies studied by Ref. [1] for a range of speed ratios v. Figure 2 shows the efficiencies of the three predator strategies for (a) ballistic targets ($\mu_t \to 1$), (b) Lévy targets ($\mu_t=2$), and (c) Brownian targets ($\mu_p=3$). In the case where both predator and target are ballistic, the mean efficiency η predicted by the model can be found analytically using a simple geometrical approach:

$$\eta = \begin{cases} 2(1-v^2)/L, & v \leqslant 1, \\ [2(v^2-1)]/(Lv), & v \geqslant 1. \end{cases}$$

The results in Figs. 2(b) and 2(c) agree with those of Ref. [1]: the Lévy predator outperforms the Brownian predator, and its relative advantage is greater for smaller values of v. However, it is clear that, in almost all cases, the ballistic strategy (not considered by Ref. [1]) outperforms both the Lévy and Brownian strategies. The only case where the ballistic strategy is less efficient than either of the other two is when the targets are ballistic and $v \approx 1$ (i.e., the predator and target have approximately the same speed). In this case, there is a 50% chance that the two individuals will set off in the same direction and never encounter one another. Hence the efficiency is very low. However, the conclusion that, in this case, a Brownian or Lévy strategy is more efficient is only applicable to the one-dimensional periodic model.

Figure 3 shows the results of two extended models with many targets moving independently on the real line. These extended models are a more realistic approximation of a higher-dimensional scenario. In Fig. 3(a), the targets are initially evenly spaced at $x=(2n-1)L/2$ for integer values of n. In Fig. 3(b), the targets are placed randomly [i.e., $x \sim \text{uniform}(-kL, kL)$], and the average density of targets is the same as in case (a). In both cases, the predator is initially at $x=0$ and all targets move ballistically, with speed v_t, in a direction (left or right) chosen randomly and independently of the other targets. In case (a), the predicted mean efficiency η of a ballistic predator is

$$\eta = \begin{cases} \dfrac{2(v+1)}{L(3-2\alpha)}, & v < 1, \\ \dfrac{2(v+1)(\alpha^2-1)}{L(3\alpha^2-2\alpha-3)}, & v > 1, \end{cases}$$

with $\alpha = 2^{v/(v-1)}$. In case (b), following the methodology developed for the analogous problem in two dimensions by Koopman [20] and in three dimensions by Gerritsen and Strickler [21], the predicted mean efficiency of a ballistic predator is simply

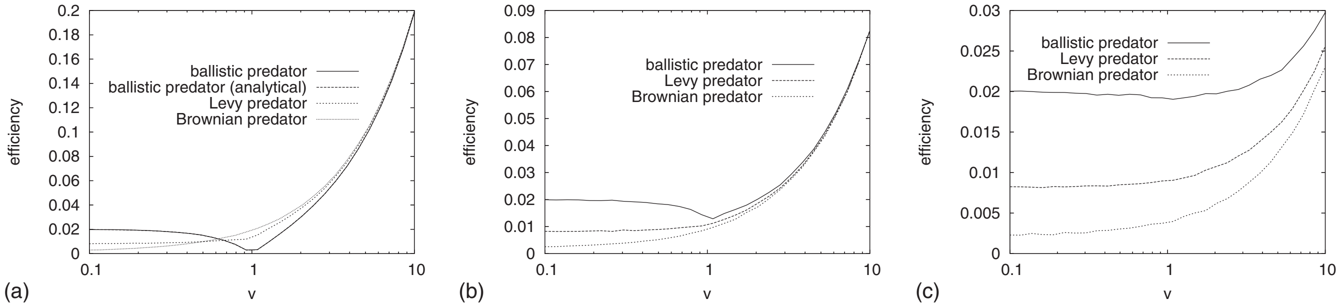

FIG. 2. The mean efficiency of the three different predator strategies (ballistic, Lévy, Brownian) for three different target strategies (ballistic, Lévy, Brownian) for a range of speed ratios. Each step is randomly chosen to be left or right. Other parameter values: $L=100$, $v_p=100$, $r_p=r_t=0$, $x_{\min}=1$, $\mathcal{L}=10^6$. (a) Ballistic target, $\mu_t \to 1$, (b) Lévy target, $\mu_t=2$, (c) Brownian target, $\mu_t=3$.

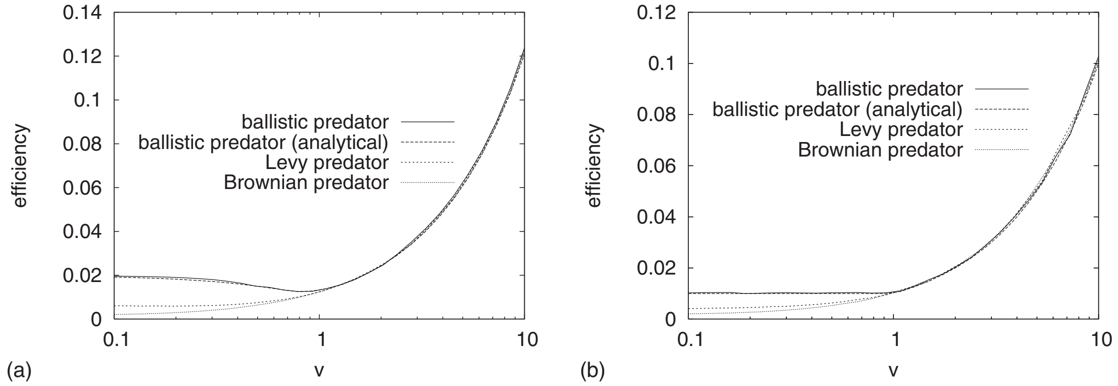

FIG. 3. The mean efficiency of three different predator strategies (ballistic, Lévy, Brownian) with many independent ballistic targets: (a) targets are initially evenly spaced; (b) targets are initially randomly distributed. Other parameter values $L=100$, $v_p=100$, $r_p=r_t=0$, $x_{\min}=1$, $\mathcal{L}=10^6$.

$$\eta=\begin{cases}1/L, & v\leqslant 1,\\ v/L, & v\geqslant 1.\end{cases}$$

Figure 3 shows that, again, the ballistic predator is more efficient than either a Lévy or Brownian predator, and the advantage of the Lévy strategy shown in Fig. 2(a) is an artifact of choosing a periodic model.

It should be noted that Faustino *et al.* [18] conducted a similar study, comparing the encounter rate of predators and targets undergoing random walks with a range of values of μ, in a similar one-dimensional, periodic domain. The critical difference between the two models is that the random walks considered by Ref. [18] do not have step lengths drawn from a pure power-law distribution, but rather from a truncated power law distribution with a maximum step length of $L/2$. As such, the step length distribution used is not heavy tailed and random walks with $\mu=1$ do not correspond to ballistic motion. The model of Ref. [18] therefore differs from that considered here and in Ref. [1]. In particular, Faustino *et al.* [18] restrict their study to the case $v=1$, and find that $\mu_p=1$ from the truncated power-law distribution is optimal for all values of μ_t. In our model, the case $v=1$ leads to a breakdown of the periodic model, particularly when the predator and target are moving ballistically. (The model of Ref. [18] does not break down in this way because neither predator nor target is moving ballistically.) Nevertheless, in our extended nonperiodic model, the ballistic strategy has the same efficiency as the optimal truncated Lévy strategy of Ref. [18] when $v\geqslant 1$, and outperforms this strategy when $v<1$.

The reason for the superior efficiency of the simple ballistic strategy is that, in this type of scenario, where the predator has no knowledge of the target's position, the optimal strategy is usually to cover as much ground as possible. Any strategy, such as a Lévy, truncated Lévy, or Brownian random walk, that involves revisiting previously searched ground is likely to be less efficient [16]. The improved efficiency of the Lévy strategy at $\mu_p=2$ is not a property of the Lévy walk *per se*, but simply a consequence of more frequent long steps and hence less backtracking than Brownian motion. Reducing μ_p toward the ballistic case ($\mu_p\to 1$) gives further improvements in efficiency (as seen in Fig. 1). These results have been explored numerically for a range of values of L, $\mathcal{L}$, and $x_{\min}$ and hold for all parameter values tested.

Bartumeus *et al.* [1,2] also investigate the dependence of the efficiencies on the sizes of the predator and target. Bartumeus *et al.* [2] concludes that size and velocity ratios are equally important to define the optimal search strategy for Brownian targets and when searching for Lévy targets velocity ratios become more important. However, the work only discusses the ratio r_t/r_p of the target radius to the predator radius, rather than their absolute values r_t and r_p. This approach is flawed because it is their combined value r_p+r_t relative to the system size L that determines the effective target density, and hence the efficiency. Figure 4 illustrates this point by showing the efficiency of a Lévy predator with a Lévy target for a range of values of r_p and r_t (the efficiencies of the other predator-target combinations follow the same pattern). It is clear that varying the ratio of the radii while keeping the sum fixed does not change the efficiency. From this, we deduce that the simulations of Ref. [1] not only varied the ratio of the radii, but also another parameter, possibly the sum of the radii, and it is the effect of the latter

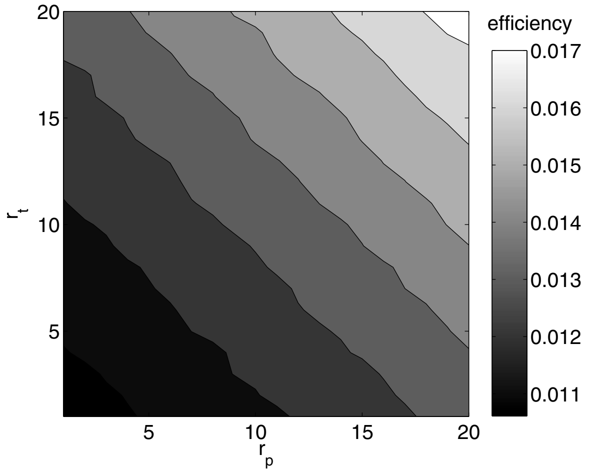

FIG. 4. The mean efficiency of the Lévy search strategy ($\mu_p=2$) for a range of both predator r_p and target r_t radii. Other parameter values were $L=100$, $\mu_t=2$, $v_p=v_t=100$, $\mathcal{L}=10^6$.

that is being observed. A simple geometrical approach shows that, in a system of size L and with predator and target radii of r_p and r_t, respectively, the mean efficiency $\eta(L,r_p,r_t)$ is given by

$$\eta(L,r_p,r_t) = \frac{\eta(L(1-R),0,0)}{1+R/2},$$

where $R=2(r_p+r_t)/L$ is the fraction of the system that is occupied by either predator or target (this relationship has been checked numerically for a range of values of r_p and r_t). Hence, a nonzero value of R simply reduces the effective system size (and reduces the corresponding efficiency slightly due to the jump of r_p+r_t that the predator makes on finding a target). The only parameters which have nontrivial effects on the model results are the exponents μ_p and μ_t and the speed ratio v. It should also be noted that including predator and target radii is unnecessary in a one-dimensional system: it is only necessary in higher dimensions, where the probability of two points exactly colliding is zero.

Although there are some theoretical scenarios, notably the nondestructive foraging scenario of Ref. [15], where a Lévy random walk with exponent $\mu_p \approx 2$ may be a solution to the optimal foraging problem, the case described here (which is destructive foraging) is not one of them. Generally, foraging efficiency increases as the predator's power-law exponent μ_p decreases. This statement is true in the periodic model of Bartumeus *et al.* [1,2], except in the special case where the targets move ballistically and at approximately the same speed as the predator. The statement is always true in the (more realistic) nonperiodic model with many targets. Hence a Lévy strategy with $\mu_p=2$ is more efficient that a Brownian strategy with $\mu_p=3$, but the optimal strategy is ballistic, i.e., to choose a direction at random and continue in that direction until an encounter occurs.

The one-dimensional periodic model presented here can be a good approximation to a more realistic higher-dimensional model. We assert that the optimum predator search strategy, in an unknown environment, is to cover the most ground, minimizing backtracking. Hence a ballistic strategy is the most effective. It is reasonable to expect this principle to extend to higher-dimensional models. There are some cases, notably when the predator and target velocities are similar, for which the one-dimensional periodic model fails to capture the higher-dimensional world. Extensions such as those presented in this paper can give more realistic results in this case.

Finally, it should be remembered that, when a predator is searching for a moving target and efficiency is defined as the number of encounters per unit distance traveled by the predator, the most efficient predator search strategy in this simple model is to remain stationary, so that the targets will come to the predator.

APPENDIX: CALCULATION OF EFFICIENCY IN THE CASE OF MANY EVENLY SPACED BALLISTIC TARGETS

There are targets initially located at $x=(2n-1)L/2$ (for integer values of n). The targets move ballistically and the direction of each target is chosen randomly, and independently of the other targets. The predator begins at $x=0$ and moves ballistically. The direction of the predator is chosen randomly and independently of the targets, though it can be assumed, without loss of generality, that the predator always travels to the right (i.e., in the direction of increasing x). Let L_n and R_n denote the distance traveled by the predator before encountering target n if the target is moving left or moving right, respectively.

The first case is where the targets are moving more slowly than the predator ($v<1$). In this case, the first target encountered will always be to the right (i.e., have a positive value of n), and will either be the first left-moving target (L_n) or, if the first k targets are all moving right, the $n=1$ target (R_1). The value of k is the largest integer such that $L_k<R_1$. Hence, the expected distance $E(D)$ traveled by the predator before encountering a target is

$$E(D) = \sum_{n=1}^{k} P_n L_n + \sum_{n=k+1}^{\infty} P_n R_1, \tag{A1}$$

where $P_n=2^{-n}$ is the probability that the first left-moving target is target n. Simple geometric arguments give the following expressions for L_n, R_n, and k:

$$L_n = \frac{(2n-1)L}{2(1+v)},$$

$$R_n = \frac{(2n-1)L}{2(1-v)},$$

$$k = \text{floor}\left(\frac{1}{1-v}\right).$$

Substituting these expressions into Eq. (A1) and summing the series gives

$$E(D) = \frac{(3-2^{(2v-1)/(v-1)})}{2(v+1)}L,$$

which leads to the expression for efficiency $\eta=1/E(D)$ given in the paper.

The second case is where the targets are faster than the predator ($v>1$). Here, the first target encountered is either the first target that is initially to the right of the predator ($n>0$) and is moving left (L_n), or the first target that is initially to the left of the predator ($n\leq 0$) and is moving right (R_n). The expected distance traveled is therefore

$$E(D) = \sum_{m=0}^{\infty} Q_{-m}\left(\sum_{n=1}^{k(m)} P_n L_n + \sum_{n=k(m)+1}^{\infty} P_n R_{-m}\right), \tag{A2}$$

where $P_n=2^{-n}$ and $Q_{-m}=2^{-m-1}$ are, respectively, the probabilities that the first positive left-moving target is target n and that the first negative right-moving target is target $-m$. Here $k(m)$ is the largest integer such that $L_{k(m)}<R_m$, and is given by

$$k(m) = \mathrm{floor}\left(\frac{m(v+1)+v}{v-1}\right).$$

The expressions for L_n and R_n are as above. Substituting these into Eq. (A2) and summing the series gives

$$E(D) = \frac{3(2^{2v/(v-1)}-1)-2^{(2v-1)/(v-1)}}{2(v+1)(2^{2v/(v-1)}-1)}L,$$

which leads to the expression for efficiency $\eta = 1/E(D)$ given in the paper.

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