Optimal Search Strategies for Hidden Targets

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What is the fastest way of finding a randomly hidden target? Experimental observations reveal that the search behavior of foraging animals is generally intermittent: active search phases randomly alternate with phases of fast ballistic motion. Here, we study the efficiency of this two state search strategy by calculating analytically the mean first passage time at the target. We model the perception mechanism involved in the active search phase by a diffusive process. We show that the search strategy is optimal when the average duration of "motion phases" varies like the power either $3/5$ or $2/3$ of the average duration of "search phases," depending on the regime. This scaling accounts for experimental data over a wide range of species, which suggests that the kinetics of search trajectories is a determining factor optimized by foragers and that the perception activity is adequately described by a diffusion process.

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Searching for a randomly located object is one of the most frequent tasks of living organisms, be it for obtaining food, a sexual partner, or a shelter [1]. In these examples, the search time is generally a limiting factor which has to be optimized for the survival of the species. The question of determining the efficiency of a search behavior is thus a crucial problem of behavioral ecology, which has inspired numerous experimental [1–5] and theoretical [6–10] works. It is also relevant to broader domains such as stochastic processes theory [11,12], applied mathematics [13], and molecular biology [14,15].

Anyone who has ever lost his keys knows that instinctively we adopt an intermittent behavior combining local scanning phases and relocating phases. Indeed, numerous studies of foraging behavior of a broad range of animal species show that such an intermittent behavior is commonly observed and that the durations of search and displacement phases vary widely [1–3]. The spectrum, which goes from cruise strategy (e.g., for large fishes that swim continuously such as tuna) to ambush or sit-and-wait search, where the forager remains stationary for long periods (such as a rattlesnake), has never been interpreted quantitatively. The intermittent strategy, often referred to as "saltatory" [2,3], can be understood intuitively when the targets are "difficult" to detect and sparsely distributed, as is the case for many foragers (such as ground foraging birds, lizards, planktivorous fish, etc.): since a fast movement is known to significantly degrade perception abilities [2,3], the forager must search slowly. Then, it has to relocate as fast as possible in order to explore a previously unscanned space and search slowly again.

Even though numerous models based on optimization of the net energy gain [4–6] predict an optimal strategy for foragers, the large number of unknown parameters used to model the complexity of the energetic constraint renders a quantitative comparison with experimental data difficult. Here, as has already been suggested [8,9], we assume that the search time is the relevant quantity optimized by the forager in order to obtain a sufficient daily amount of food and to precede other competing foragers. We treat the energy cost only as an external constraint that sets the maximal speed of the animal. We develop a general purely kinetic model of target search, which captures the essential features of saltatory search behavior observed for foragers in experiments [2], when the predator has no information about the prey location.

The central point of our schematic model (see Fig. 1) is that it relies on the explicit description of searching trajectories. In particular, as we show, it permits us to elucidate the nature of the search phase. In the following we assume that the searcher displays alternatively two distinct attitudes:

(1) a search phase, hereafter referred to as phase 1, during which the searcher explores its immediate vicinity using its sensory organs. As justified below, this local scanning is modeled as a "slow" diffusive movement (a continuous random walk with diffusion coefficient D). The target is found when this movement reaches the target location for the first time.

(2) a motion phase, referred to as phase 2, during which the searcher moves "fast" and is unable to detect a target.

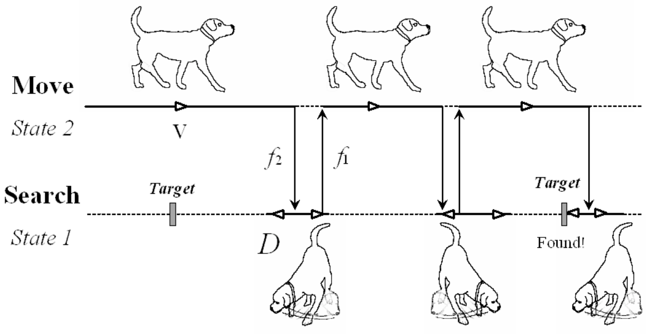

FIG. 1. A two state model of saltatory search behavior.

These repositioning moves are characterized by a ballistic motion (at constant velocity v).

Next, we assume that the searcher randomly switches from phase 1 (respectively, 2) to phase 2 (respectively, 1) with a rate per unit time f_1 (respectively, f_2) and that the preys are immobile and randomly distributed with uniform density. Note that the average durations of phases 1 and 2 are then $1/f_1$ and $1/f_2$. The stochastic nature of the model is justified in the case of foragers by the observation of large fluctuations of the duration of search and motion phases for each animal [3]. Indeed, exponential laws are widely observed for animal behaviors [16]. Our goal is to study the optimal search strategy with respect to its kinetic mechanism only, i.e., to determine the rates f_1, f_2 which minimize the first passage time of the searcher at a target location.

Let us justify briefly our modeling of each phase. It is clearly beyond the scope of our model to describe the sensory search phase in detail, as it involves very complex biological mechanisms. Our goal here is to capture the main features of this activity which are relevant from a kinetic point of view. For hidden targets, the stimuli emitted are very weak and the predator is very likely not to detect them. Then it may have to scan many times the same location before finding the target: we model this mechanism by a diffusion process. Note that in this description, the successive positions of the diffusive trajectory are not necessarily the very positions of the animal, but the focus points of the sense involved. This idea of a diffusion process (or more generally of random walk process) for sensory perception has already been suggested, in particular, for vision [17], tactile sense, or olfaction [1]. As focusing and processing the information received by sensory organs require a minimum time, the search phase cannot be to short, which implies an upper bound $f_{1\,\mathrm{max}}$ for the rate f_1. Since the objective of phase 2 moves is to explore unscanned space, the most efficient solution, which is indeed observed generally, is a straight ballistic motion. Precisely, it has been observed that the turning angle after each pause is usually small [2,18–20]. Since the direction of successive ballistic motions is strongly correlated for most species (enjoying minimal memory skills), the small angles allow us to consider an effective 1-dimensional problem for both phases.

We now evaluate the average time needed to find a target. Following the "closed cell approach" [14,21], our problem of an infinite space with uniform target density $1/L$ can be reduced to the problem of a single target centered on a segment of size L with reflexive boundary conditions. Then, the instantaneous state of the searcher can be described by its position x on the segment and an index μ which specifies its motion: $\mu = \alpha$ (respectively, β) corresponds to a ballistic motion of velocity $+v$ (respectively, $-v$); $\mu = \gamma$ (respectively, δ) corresponds to a diffusive motion, switching only to a ballistic motion of velocity $+v$ (respectively, $-v$). The mean first passage time at the target, starting from state (x, μ), is denoted $t(x, \mu)$. Using the backward Chapman-Kolmogorov differential equation for the conditionnal densities [22,23], we obtain the following system satisfied by the $t(x, \mu)$:

$$\begin{aligned}
v\frac{\partial t(x,\alpha)}{\partial x} + f_2[t(x,\gamma) - t(x,\alpha)] &= -1,\\
-v\frac{\partial t(x,\beta)}{\partial x} + f_2[t(x,\delta) - t(x,\beta)] &= -1,\\
D\frac{\partial^2 t(x,\gamma)}{\partial x^2} + f_1[t(x,\alpha) - t(x,\gamma)] &= -1,\\
D\frac{\partial^2 t(x,\delta)}{\partial x^2} + f_1[t(x,\beta) - t(x,\delta)] &= -1.
\end{aligned} \tag{1}$$

Henceforth, we consider the average search time $\langle t \rangle$ defined as the average of $t(x, \mu)$ over the initial position x of the searcher, which is assumed to be uniformly distributed over the segment $[-L, L]$, and over the nature of the initial motion, equally distributed over α and β (ballistic motions with velocities $\pm v$).

In the low density limit defined by $L \gg \frac{v}{f_2}, \sqrt{\frac{D}{f_1}}, \sqrt{\frac{f_2 D}{f_1 v}}$ the system (1) leads, after some calculation, to

$$\langle t \rangle = \frac{L}{2\sqrt{D}}\left(\frac{1}{f_1} + \frac{1}{f_2}\right)\frac{\tau f_2^2 + 2f_1}{\sqrt{\tau f_2^2 + 4f_1}}, \tag{2}$$

where $\tau = D/v^2$ and $1/L$ is the target density. The linear dependence on L (the typical intertarget distance) ensures that this combined strategy is much more efficient than a purely diffusive strategy [15] which would scale like L^2. The average search time $\langle t \rangle$ presents a single minimum with respect to f_1 and f_2, defined by the following equations:

$$f_1 = f_{1\,\mathrm{max}}, \qquad f_2^5 + \frac{6}{\tau}f_2^3 f_1 - \frac{8}{\tau^2}f_1^3 = 0. \tag{3}$$

This minimum takes a simple form in two different regimes which lead to similar asymptotic:

First, if $f_{1\,\mathrm{max}} \ll 1/\tau$, the optimal frequencies are such that $f_1 = f_{1\,\mathrm{max}}$ and

$$f_2 = \left(\frac{4}{3\tau}\right)^{1/3} f_1^{2/3}. \tag{4}$$

In this regime, denoted S (for search), one has $f_1 < f_2$: the predator spends more time searching than moving.

Second, if $f_{1\,\mathrm{max}} \gg 1/\tau$ the optimal frequencies are such that $f_1 = f_{1\,\mathrm{max}}$ and

$$f_2 = \left(\frac{2\sqrt{2}}{\tau}\right)^{1/3} f_1^{3/5}. \tag{5}$$

In this regime, denoted by $\mathcal{M}$ (for move), one has $f_1 > f_2$ and the predator spends more time moving. Note that the exponents $2/3$ and $3/5$ are numerically very close, and we do not expect to distinguish them experimentally.

We now briefly comment on the structure of optimal trajectories. The threshold value $1/\tau$ has the meaning of an overlap limit: τ is the duration for which the typical

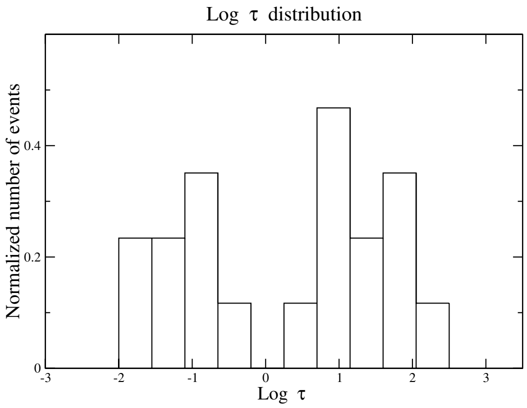

FIG. 2. Log(τ) distribution for saltatory search behaviors. The first peak (around $t = 0.1$ s) corresponds to foragers in the regime S, the second one (around $t = 25$ s) corresponds to foragers in regime M.

distance covered is the same in both states 1 and 2. In order to study the connexity of these trajectories, we introduce the ratio R of the length scanned in phase 1 over the distance covered during a phase 2 move $R = \sqrt{D/f_1} \times f_2/v$. As for the $\mathcal{S}$, one has $R \approx (f_1\tau)^{1/6} < 1$ so that there is no overlap. It is noteworthy that in this regime, R can be small, which means that the overall scanned space is not connex but displays holes of unvisited space. Conversely, in regime $\mathcal{M}$, one has $R \approx (f_1\tau)^{1/10} > 1$ and overlap may occur; nevertheless, the power $1/10$ ensures that R is never much larger than 1 and the optimal trajectory always explores unscanned spaces of significant size.

We now compare our model with experimental data extracted from O'Brien *et al.* [2] and Kramer *et al.* [3] which provide the average duration (and therefore its inverse, the rate) of search and motion phases for 18 different species (as various as planktivorous fish [18], ground foraging birds [19,24], or lizards [25]) performing a saltatory search behavior. The corresponding rates f_1 range from 0.1 to 100 Hz, with no systematic correlation with the animal size. Note that the prefactor involving τ in Eqs. (4) and (5) depends *a priori* on the species, and it seems difficult to evaluate it directly from observations, as D was defined in a phenomenological manner. Nevertheless, as we proceed to show, this characteristic time roughly assumes only two values.

Using the exact relation (3) between f_1, f_2 and τ at the minimum, we compute the value of τ for each species. The distribution of Log(τ), given in Fig. 2, is quite unexpectedly bimodal. Remarkably, we observed that the first peak (around $t = 0.1$ s) corresponds to foragers in the regime S and that the second one (around $t = 25$ s) corresponds to foragers in regime M. Therefore the characteristic time τ defined in our model appears as a tool characterizing distinctly two subclasses of foragers: a set S of animals in the regime $\mathcal{S}$ and a set M in the regime $\mathcal{M}$. Since fluctuations of τ are small within each set [the fluctuations of Log(τ) are of order 1], we can perform a comparative analysis of these data within each set.

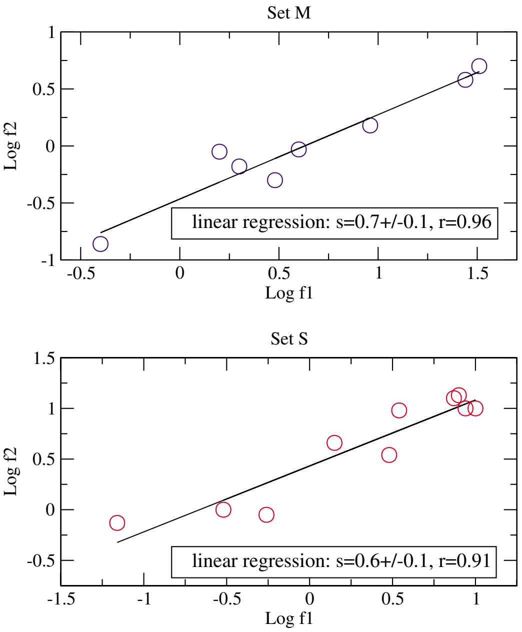

FIG. 3 (color online). Log-Log plot of experimental data [2,3] of saltatory search behaviors and their linear regression.

The Log-Log plots of the f_1 and f_2 data of sets S and M are shown in Fig. 3. Their linear regression shows that both sets are strongly correlated (with a coefficient $r > 0.9$) and that their slopes are in agreement with our theoretical prediction, namely, $3/5$ for M (experimental slope: 0.7 ± 0.1) and $2/3$ for S (experimental slope: 0.6 ± 0.1), taking account of the uncontrolled accuracy of experimental measurements. These results suggest that a wide variety of species indeed minimize their search time for preys according to a strategy described by our model, indicating that our diffusive modeling of the search phase is appropriate. This analysis also puts forward the hypothesis that the kinetics of the trajectories is a prevailing factor which is optimized by natural selection.

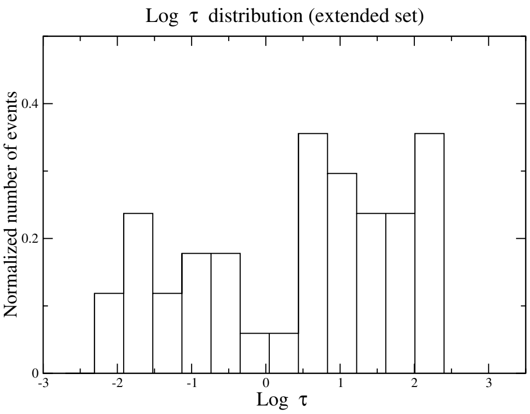

FIG. 4. Log(τ) distribution for nonspecific saltatory behaviors.

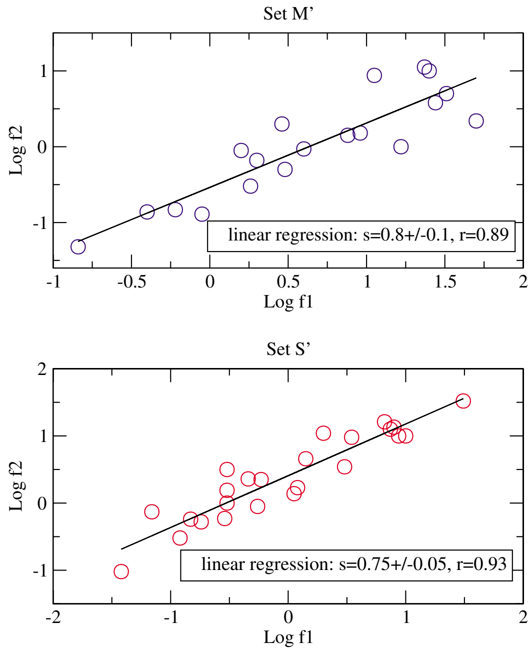

FIG. 5 (color online). Log-Log plot of experimental data [2,3] of nonspecific saltatory behaviors and their linear regression.

Furthermore, using the extensive data of O'Brien *et al.* [2] and Kramer and McLaughlin [3], we have extended this analysis to the case of animals performing a saltatory behavior observed in nonspecific search behaviors, such as fleeing, food carrying, or simple displacement. The distribution of Log(τ) over these species is still bimodal (see Fig. 4) and highly similar to the case of Fig. 2 and leads to the definition of extended sets S$'$ and M$'$ as before. The corresponding Log-Log plots, presented in Fig. 5, show that the correlations between frequencies are maintained and that the agreement with Eqs. (4) and (5) is still significant: we find an experimental slope of 0.8 for both sets S$'$ and M$'$. This suggests that all displacements of these species are conditioned by a searchlike mechanism which could be either the search for a prey, or for a potential threat, as, for example, a hint of a nearby predator. Such an attitude could also be interpreted as a "behavioral economylike" argument, which would allow the animals to minimize the number of behaviors to learn.

In summary, in this Letter we have raised the question of determining the fastest strategy for finding a hidden target. This question of general scope has been tackled through the example of animals searching for food, for which numerous experimental data are available. We have proposed and solved analytically a two state stochastic model of target search, based on a diffusive modeling of the perception mechanism. This model provides a power law relationship between the characteristic times spent in each state, which satisfactorily fits experimental foraging data. Our findings suggest that in various behavioral contexts, saltatory animals adopt the intermittent motion which optimizes the search time of randomly hidden targets. We believe that this kind of search behavior modeling could be extended to other situations, including human behaviors.

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