Optimal search strategies for hidden targets

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What is the fastest way of finding a randomly hidden target? This question of general relevance is of vital importance for foraging animals. Experimental observations reveal that the search behaviour of foragers is generally intermittent: active search phases randomly alternate with phases of fast ballistic motion. In this letter, we study the efficiency of this type of two states search strategies, 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. In this framework, 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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during which the searcher explores its immediate vicinity using its sensory organs. As justified below, this local scanning is modelled 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. These repositioning moves are characterized by a ballistic motion (at constant velocity $v$).

Next, We assume that the searcher randomly switches from phase 1 (resp. 2) to phase 2 (resp. 1) with a rate per unit time $f_1$ (resp. $f_2$), 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\[8\]. Indeed, exponential laws are widely observed for animal behaviours\[1\]. 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 modelling of each phase. It is clearly beyond the scope of our model to describe the sensory search phase in details, 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 can not be to short, which implies an upper bound $f_{1\text{max}}$ 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\[19\[20\]. Since the direction of successive ballistic motions is strongly correlated for most of species (enjoying minimal memory skills), the small angles allows 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 $\mu$ which specifies its motion:

- $\mu = \alpha$ (resp. $\beta$) corresponds to a ballistic motion of velocity $+v$ (resp. $-v$)
- $\mu = \gamma$ (resp. $\delta$) corresponds to a diffusive motion, switching only to a ballistic motion of velocity $+v$ (resp. $-v$)

The mean first passage time at the target, starting from state $(x, \mu)$ is denoted $t(x, \mu)$. Using the Backward Chapman-Kolmogorov differential equation for the conditional densities\[22\[23\], we obtain the following system satisfied by the $t(x, \mu)$:

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

Henceforth, we will 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 $\alpha$ and $\beta$ (ballistic motions with velocities $\pm v$).

In the low density limit defined by $L \gg \frac{\sqrt{Dv}}{\sqrt{\pi}}\sqrt{\frac{f_2f_1}{f_1f_2}}$ the system leads, after some calculation, to:

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

(2)

where $\tau = D/v^2$ and $1/L$ is the target density. The linear dependence on $L$ (the typical inter-target distance) ensures that this combined strategy is much more efficient than a purely diffusive strategy\[12\] 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:

$$
\begin{align*}
  &f_1 = f_{1\text{max}} \\
  &f_2 + \frac{6}{\tau} f_2^2 f_1 - \frac{8}{\tau^2} f_1^3 = 0
\end{align*}
$$

(3)

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

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

$$
\begin{align*}
  f_2 = & \left( \frac{4}{3\tau} \right)^{1/3} f_1^{2/3}
\end{align*}
$$

(4)
In this regime, denoted $S$ (for search), one has $f_1 < f_2$: the predator spends more time searching than moving. 

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

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

In this regime, denoted by $M$ (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: $\tau$ is the duration for which the typical 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 $R = \sqrt{D/v_1} \times f_2/v$. As for the $S$, 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 $M$, 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. and Kramer et al. 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, ground foraging birds or lizards) performing a saltatory search behaviour. 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 $\tau$ in equation (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 (5) between $f_1$, $f_2$ and $\tau$ at the minimum, we compute the value of $\tau$ for each species. The distribution of $\log(\tau)$, given in figure 2, is quite unimodal. Remarkably, we observed that the first peak (around $t=0.1s.$) corresponds to foragers in the regime $S$ and that the second one (around $t=25s.$) corresponds to foragers in regime $M$. Therefore the characteristic time $\tau$ defined in our model appears as a tool characterizing distinctly two subclasses of foragers: a set $S$ of animals in the regime $S$, and a set $M$ in the regime $M$. Since fluctuations of $\tau$ are small within each set (the fluctuations of $\log(\tau)$ are of order 1), we can perform a comparative analysis of these data within each set.

The Log-Log plots of the $f_1$ and $f_2$ data of sets $S$ and $M$ are shown in figure 3. Their linear regression shows that both sets are strongly correlated (with a coefficient $\tau > 0.9$) and that their slopes are in agreement with our theoretical prediction, namely $3/5$ for $M$ (experimental slope: $0.7 \pm 0.1$) and $2/3$ for $S$ (experimental slope: $0.6 \pm 0.1$), 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 modelling 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.

Furthermore, using the extensive data of O’Brien et al. and Kramer et al., we have extended this analysis to the case of animals performing a saltatory behaviour observed in non specific search behaviours, such as fleeing, food carrying, or simple displacement. The distribution of $\log(\tau)$ over these species is still bimodal.
FIG. 4: Log(τ) distribution for non specific saltatory behaviours.

FIG. 5: Log-Log plot of experimental data[2, 3] of non specific saltatory behaviours and their linear regression.

(see figure 4) and highly similar to the case of figure 2, and leads to the definition of extended sets S’ and M’ as before. The corresponding Log-Log plots, presented in figure 5, show that the correlations between frequencies are maintained, and that the agreement with equations 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 search-like 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 "behavioural economy" like argument, which would allow the animals to minimize the number of behaviours 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 states 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 behavioural contexts, saltatory animals adopt the intermittent motion which optimizes the search time of randomly hidden targets. We believe that this kind of search behaviour modeling could be extended to other situations, including human behaviours.

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