A stochastic model for intermittent search strategies

A stochastic model for intermittent search strategies

O Bénichou[1]**, M Coppey**[1]**, M Moreau**[1]**, P H Suet**[1] **and R Voituriez**[2]

[1] Laboratoire de Physique Théorique de la Matière Condensée, Université Paris 6,
4 Place Jussieu, 75252 Paris, France
[2] Physicochimie Curie (CNRS-UMR168), Institut Curie, Section de Recherche,
26 rue d'Ulm 75248, Paris Cedex 05, France

Abstract
It is often necessary, in scientific or everyday life problems, to find a randomly
hidden target. What is then the optimal strategy to reach it as rapidly as possible?
In this article, we develop a stochastic theory for intermittent search behaviours,
which are often observed: the searcher alternates phases of intensive search and
slow motion with fast displacements. The first results of this theory have already
been announced recently. Here we provide a detailed presentation of the theory,
as well as the full derivation of the results. Furthermore, we explicitly discuss
the minimization of the time needed to find the target.

1. Introduction

The search for specific targets plays an important role in many physical, chemical or biological
problems, as well as in social and economical sciences [1–3]. This is for instance the case
when reactants are diffusing in a solvent till they meet and are in condition to react [4], or when
a protein is searching for its specific target site on DNA [5, 6]. One can also mention predators
searching for prey [1–3], prospectors looking for minerals, or rescuers trying to locate victims,
for instance in avalanches. These various and complex situations can obviously be precisely
studied only by specific models. However, there are a few general features that are shared
by many search processes. In particular, when the targets are sparse and hidden, or difficult
to detect, the searcher should adopt a strategy which efficiently explores its environment.
Obviously, any rational search process should first identify the regions where the target presence
probability is the highest; however, this preliminary analysis is usually very uncertain. For
these reasons, the stochastic theory of search processes has become a field of growing interest
during the last few years [7–14].

In many examples, it can be observed that the searcher alternates phases of intensive search
and slow motion with phases of fast displacement non-receptive to the target. Recently, we
proposed [14] a one-dimensional description of such intermittent search strategies, especially
suitable to the case of foraging animals. This method was outlined in [14] and the first results
were presented without complete derivation. It was shown that the available experimental data

support our main hypothesis: many animal species seem to adjust their intermittent behaviour in order to minimize the search time.

Here, we extend this hypothesis to more general systems and present a detailed, new derivation of the results. In particular, we provide a comprehensive analysis of the problem of optimizing the search time for intermittent search processes. First, we define the model, and briefly introduce the stochastic formalism involved. Then, we give a detailed treatment of the specific, one-dimensional model, and we discuss the minimization of the mean search time explicitly. The application to foraging animals is summarized in section 5, showing that our results are validated by experimental data. The complete, somewhat lengthy, calculations are given in the appendix.

2. Model

We present here an idealistic one-dimensional model, which can be justified in many cases as a simple, approximate description for an intermittent search process.

Searcher

The searcher is a point particle moving on a circle of length L. Its position along the circle is denoted by x, $0 \leqslant x \leqslant L$ (note that this geometry is equivalent to an infinite axis Ox with period L). The searcher can adopt two different dynamical regimes, labelled by index $i = 1$ or 2.

- During regime 1, the searcher undergoes a simple diffusion process (or Brownian motion) with diffusion coefficient D, modelling the phase of intensive search and slow displacement. In this regime, the target is discovered at the first passage of the searcher at its position. We call this phase 'search'.
- During regime 2, the searcher undergoes a ballistic motion with constant velocity v. We call this phase 'move'.

The use of a Brownian motion to model the search phase is justified by the difficulty of detecting a hidden target. Indeed in this case multiple passages at the same position are required in order to scan the environment efficiently. The resulting wavering trajectory can be modelled in a simplified way by a Brownian motion. If we assume that at each passage at the target position the searcher has a finite probability to find it, the mathematical properties of Brownian motion ensure that the time of discovery is equal to the first passage time at the target.

Similarly, the ballistic motion is also used for the sake of simplicity to describe the rapid, but not instantaneous displacement during the move regime. More sophisticated models of fast displacement can be introduced, but they should not change significantly our qualitative conclusions. Note that on the contrary permitting instantaneous displacements, which may be justified in some cases, could drastically change our results; this point will be discussed in further publications.

The successive durations of each regime i are assumed to be independent, exponential stochastic variables T_i:

$$\text{Prob}(T_i > t) = \exp(-\lambda_i t) = \exp(-t/\tau_i). \tag{1}$$

λ_i can be seen as a constant transition rate from regime i to regime $i + 1 \bmod [2]$. In particular, $\tau_i = 1/\lambda_i$ is the average duration of regime i. Clearly, these laws are justified if the system has no memory, and can be represented by a Markov process, which we will assume from now on.

In the context of foraging animals, this assumption is valid for species with low memory skills, for which the transition probabilities between search and move phases are constant in time.

Target

The target, assumed to be point-like, is located at $x = 0$ on the circle. This would correspond, on an infinite line Ox, to an infinite number of regularly spaced targets at points $x = kL$, with k integer. In many problems, an irregular or random array of targets would be more realistic, but our model is valid as soon as the fluctuations of the inter-target distance are small compared to L.

We then compute analytically the mean first passage time (MFPT) [15] at the target, claiming that it is the most suitable variable to study quantitatively the efficiency of the search process. Our goal is to find the optimal search strategy, from a kinetic point of view, by determining the frequencies λ_i of each mode that minimize the MPFT.

3. Basic equations

First, it may be useful to recall the general equations satisfied by the MFPT. Let us consider a general Markov process, and let $p(\mathbf{r}, i, t)$ be the probability density to find the system at position $\mathbf{r}$ in state i at time t, and $p(\mathbf{r}, i, t | \mathbf{r}_0, i_0, t_0)$ the transition probability from $(\mathbf{r}_0, i_0)$ at time t_0 to $(\mathbf{r}, i)$ at time t. Both satisfy the forward Chapman–Kolmogorov equation [16], i.e.

$$\frac{\partial}{\partial t} p(\mathbf{r}, i, t) = L_i p(\mathbf{r}, i, t) + \sum_j (\lambda_{ij} p(\mathbf{r}, j, t) - \lambda_{ji} p(\mathbf{r}, i, t)) \tag{2}$$

where L_i is the stochastic evolution operator in regime i, and λ_{ji} is the transition rate from regime i to regime j.

We now assume that a region A (the target) is absorbing in regime α: as soon as the system reaches A in regime α, it is trapped. Let $\langle T | \mathbf{r}_0, i_0 \rangle$ be the mean first arrival time in (A, α), starting from $(\mathbf{r}_0, i_0)$ at time zero. It satisfies the backward (adjoint) equation

$$-1 = L_{i_0}^+ \langle T | \mathbf{r}_0, i_0 \rangle + \sum_i \lambda_{ii_0} (\langle T | \mathbf{r}_0, i_0 \rangle - \langle T | \mathbf{r}_0, i \rangle) \tag{3}$$

where L_i^+ is the adjoint evolution operator in regime i, with the boundary conditions

$$\langle T | \mathbf{r}_0, i_0 \rangle = 0 \qquad \text{if } \mathbf{r}_0 \in A \quad \text{and} \quad i_0 = \alpha. \tag{4}$$

We now rewrite the equations of the previous paragraph in the case of the one-dimensional model described in section 2, where the target A is point-like. Note that here $\alpha = 1$. We call $t(x, i)$ the mean first passage time at the target starting from (x, i).

The backward Chapman–Kolmogorov differential equation (3) reads in this case

$$\begin{aligned} D \frac{\partial^2 t(x, 1)}{\partial x^2} + \lambda_1 [t(x, 2) - t(x, 1)] &= -1 \\ v \frac{\partial t(x, 2)}{\partial x} + \lambda_2 [t(x, 1) - t(x, 2)] &= -1. \end{aligned} \tag{5}$$

The boundary conditions, expressing space periodicity $t(x + L, i) = t(x, i)$, and absorption for $x = 0$ and $i = 1$ are as follows:

$$\begin{aligned} t(0, 1) &= t(L, 1) = 0 \\ t(0, 2) &= t(L, 2). \end{aligned}$$

After some computations (see appendix A), we obtain

$$t(x, 1) = \frac{\lambda_1 + \lambda_2}{\lambda_1 \lambda_2} \frac{L}{\beta - \alpha} \left[\beta^2 \frac{1 - e^{\alpha x}}{1 - e^{\alpha L}} - \alpha^2 \frac{1 - e^{\beta x}}{1 - e^{\beta L}} \right] - \frac{\lambda_1 + \lambda_2}{\lambda_1} \frac{x}{v} \tag{6}$$

$$t(x, 2) = \frac{\lambda_1 + \lambda_2}{\lambda_1 \lambda_2} \frac{L}{\beta - \alpha} \left[\beta^2 \frac{1 - \frac{\lambda_2}{v} \frac{1}{\beta} e^{\alpha x}}{1 - e^{\alpha L}} - \alpha^2 \frac{1 - \frac{\lambda_2}{v} \frac{1}{\alpha} e^{\beta x}}{1 - e^{\beta L}} \right] - \frac{\lambda_1 + \lambda_2}{\lambda_1} \frac{x}{v} - \frac{1}{\lambda_1} \tag{7}$$

with

$$\alpha = \frac{1}{2} \left(\frac{\lambda_2}{v} + \sqrt{\frac{\lambda_2^2}{v^2} + 4\frac{\lambda_1}{D}} \right) \qquad \text{and} \qquad \beta = \frac{1}{2} \left(\frac{\lambda_2}{v} - \sqrt{\frac{\lambda_2^2}{v^2} + 4\frac{\lambda_1}{D}} \right).$$

Let $\langle t \rangle$ be the MFPT averaged over the initial position x of the searcher, assumed to be uniformly distributed over the 'circle' $[0, L]$. This quantity defines what we call the search time.

$$\langle t \rangle = \langle t(x, 1) \rangle = \frac{1}{L} \int_0^L t(x, 1) \, dx = \frac{\lambda_1 + \lambda_2}{\lambda_1 \lambda_2} \frac{L}{\beta - \alpha} \left[\beta^2 \frac{1 - \frac{e^{\alpha L} - 1}{\alpha L}}{1 - e^{\alpha L}} \right.$$

$$\left. - \alpha^2 \frac{1 - \frac{e^{\beta L} - 1}{\beta L}}{1 - e^{\beta L}} \right] - \frac{\lambda_1 + \lambda_2}{\lambda_1} \frac{L}{2v}. \tag{8}$$

In the low density limit defined by $L \gg \frac{v}{\lambda_2}, \sqrt{\frac{D}{\lambda_1}}, \frac{\lambda_2 D}{\lambda_1 v}$, we obtain

$$\langle t \rangle = \frac{L}{2v} \left(\frac{1}{\lambda_1 \tau} + \frac{1}{\lambda_2 \tau} \right) \frac{\tau^2 \lambda_2^2 + 2\lambda_1 \tau}{\sqrt{\tau^2 \lambda_2^2 + 4\tau \lambda_1}} \tag{9}$$

where $\tau = \frac{D}{v^2}$ and $\frac{1}{L}$ is the target density. One can notice that the linear dependence in L (the typical inter-target distance) ensures that this intermittent strategy is much more efficient than a pure diffusive strategy which would scale like L^2.

4. Minimization of the search time

We now study the minimization of $\langle t \rangle$. It can be shown (see appendix B) that $\langle t \rangle$ has no global minimum for finite values of λ_1 and λ_2. However, it is reasonable to assume that λ_1 has an upper bound $\lambda_{1\max}$. Indeed, it is clear that the predator cannot gather its sensorial abilities and its attention instantaneously: thus, we assume that the average duration τ_1 of the search phase has a minimum value $\tau_{1\min}$ or equivalently that λ_1 has a maximum value $\lambda_{1\max}$. This assumption is discussed further on in appendix B. After some computations, it is shown that in this case there is a single minimum when λ_1 and λ_2 are such that

$$\lambda_1 = \lambda_{1\max} \tag{10}$$

$$\lambda_2^5 \lambda_1 + \frac{6}{\tau} \lambda_2^3 \lambda_1 - \frac{8}{\tau^2} \lambda_1^3 = 0. \tag{11}$$

Writing $(\lambda_2 \tau) \approx C(\lambda_1 \tau)^\nu$, a simple scaling analysis shows that equation (11) yields two different regimes.

- If $\lambda_1 \tau \ll 1$ (regime S), one finds

$$\lambda_1 = \lambda_{1\max} \tag{12}$$

$$\lambda_2 \approx \left(\frac{4}{3\tau} \right)^{\frac{1}{3}} \lambda_1^{\frac{2}{3}} \tag{13}$$

and the predator spends more time searching than moving.

- If $\lambda_1 \tau \gg 1$ (regime M), one has

$$\lambda_1 = \lambda_{1\mathrm{max}} \tag{14}$$

$$\lambda_2 \approx \left(\frac{8}{\tau^2}\right)^{\frac{1}{5}} \lambda_1^{\frac{3}{5}} \tag{15}$$

and quite surprisingly the searcher spends more time moving than searching.

We finally end up with two scaling relations involving λ_1 and λ_2 with very close exponents $\frac{2}{3}$ and $\frac{3}{5}$. The threshold value $\frac{1}{\tau}$ has the meaning of an overlap limit: τ is the duration for which the typical distance covered is the same for both states 1 and 2. The non-overlap condition is determined by forming the ratio ρ of the length scanned in phase 1 over the distance covered in a phase 2 move $\rho = \frac{\lambda_2}{v}\sqrt{\frac{D}{\lambda_1}}$. In the regime S, $\rho \approx (\lambda_1 \tau)^{\frac{1}{6}} < 1$ and there is no overlap. It is noteworthy that in this regime ρ 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 $\rho \approx (\lambda_1 \tau)^{\frac{1}{10}} > 1$ and overlap may occur, which seems counterintuitive for an optimal exploration. Nevertheless the power $\frac{1}{10}$ ensures that ρ is never much larger than unity and the optimal trajectory always explores unscanned space of significant size.

5. Application to foraging animals

Numerous studies of foraging behaviour of a broad range of animal species show that intermittent behaviours, such as the one sketched by our model, are commonly observed and that the durations of search and displacement phases vary widely [1–3]. In this section we compare our model with experimental data extracted from O'Brien *et al* [2] and Kramer *et al* [3]. These studies provide the average duration (and therefore its inverse, the rate) of search and motion phases for 18 different species including planktivorous fish [17], ground foraging birds [18, 19] and lizards [20], which perform an intermittent search behaviour. The corresponding rates λ_1 range from 0.1 to 100 Hz, with no systematic correlation with the animal size. Note that the prefactor involving τ in equation (12) and (14) is *a priori* species dependent. Nevertheless, we will show that this characteristic time roughly assumes only two values.

The value of τ for each species can be obtained from equation (11), and leads to the distribution of $\log(\tau)$ given in figure 1. This distribution is quite unexpectedly bimodal. Moreover, it appears 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. Thus the characteristic time τ defined in our model proves to be a tool characterizing distinctly two subclasses of foragers: a set of animals in the regime S, and a set in the regime M. The small amplitude of the fluctuations of τ within each set allows us to perform a comparative analysis of these data within each set.

Figure 2 gives the log–log plots of the λ_1 and λ_2 data of sets S and M. Both sets are strongly correlated (with a coefficient $r > 0.9$), as shown by the linear regressions. Moreover, 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). Note that the theoretical values of these slopes are very close, and we do not expect to distinguish them experimentally due to the error bars of experimental data. However, this agreement suggests that many species minimize their search time for prey according to the intermittent strategy described by our model, and puts forward the idea that the kinetics of the trajectories is a prevailing factor which is optimized by natural selection.
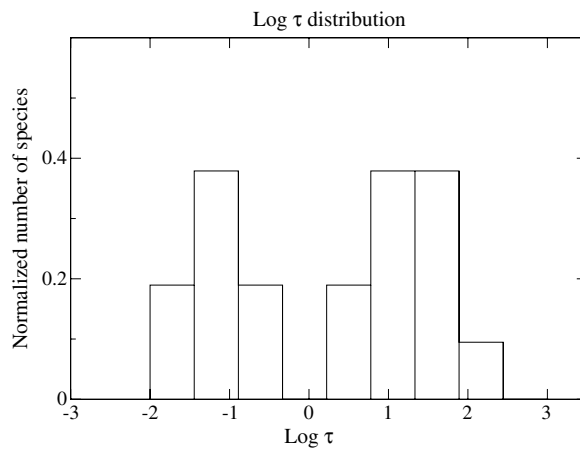
Figure 1. Log (τ) distribution for intermittent search behaviours. The first peak (around $t = 0.1$ s) corresponds to foragers in the regime $\mathcal{S}$, the second one (around $t = 25$ s) corresponds to foragers in the regime $\mathcal{M}$.
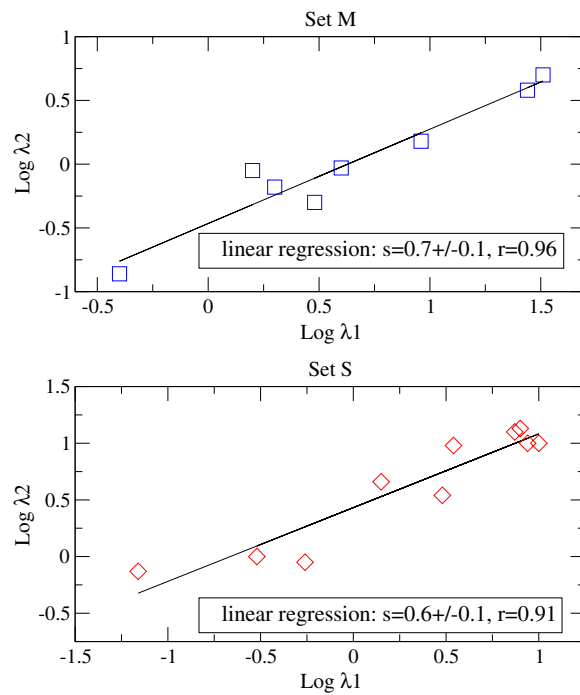

Figure 2. Log–log plot of experimental data [2, 3] of intermittent search behaviours, and their linear regression.

(This figure is in colour only in the electronic version)

6. General analysis of the minimum search time

Section 4 describes the case of a minimum value τ_{1m} of the search regime. It is realistic to consider that the move regime could also have a minimum duration τ_{2m}, corresponding for

instance to an acceleration phase. The analysis of the minimum of the MFPT is in this case different and is explicitly performed in appendix B. It can be summarized as follows:

- in regime M, the limitation on τ_2 does not modify the scaling laws (14)

$$\lambda_2 \tau \sim (\lambda_1 \tau)^{3/5}, \qquad \text{with } \lambda_1 \tau \ll \lambda_2 \tau \ll 1 \qquad (16)$$

- in contrast, in regime S, the scaling laws (12) only apply if τ_{2m} is much smaller than τ_{1m}; then

$$\lambda_2 \tau \sim (\lambda_1 \tau)^{2/3}, \qquad \text{with } \lambda_1 \tau \gg \lambda_2 \tau \gg 1 \qquad (17)$$

- if τ_{2m} is smaller than but of the same order as τ_{1m}, the minimum search time is obtained for $\tau_1 = \tau_{1m}$ and $\tau_2 = \tau_{2m}$.

The fact that the scaling laws agree with experimental observations in the case of foraging animals supports the hypothesis that for these animals τ_{2m} is indeed much smaller than τ_{1m}.

7. Conclusion

In summary, the model discussed in this paper raised the question of determining the fastest strategy for finding a hidden target. In the general framework of intermittent search strategies, we put forward scaling laws which have been validated by comparison with observations in the case of foraging animals, despite the huge simplifications we adopted to describe the complex, actual situation. This indicates that the hypothesis should be at least partially valid, and that the kinetics of the trajectories is a prevailing factor which is optimized by natural selection.

Within a broader scope, similar hypotheses should be applicable to many problems in science and technology. Obviously, it would be necessary to generalize the model by considering more sophisticated motions for each regime, for instance, abnormal diffusion during the search regime, or Levy flights for the move regime. Furthermore, non-exponential lifetimes, corresponding to non-Markovian processes, would be realistic in many cases. On the other hand, using a one-dimensional model can be coarsely justified for certain predator–prey systems, but it is clearly necessary to address the problem in n-dimensional spaces, although it can be very difficult to obtain an analytical result and exact asymptotics. The study of such generalizations is in progress.

Appendix A. Calculation of the search time

One can use a matrix formulation of the differential system:

$$\frac{\mathrm{d}}{\mathrm{d}x} \begin{pmatrix} t(x,1) \\ t(x,2) \\ t'(x,1) \end{pmatrix} = \begin{pmatrix} 0 & 0 & 1 \\ -\frac{\lambda_2}{v} & \frac{\lambda_2}{v} & 0 \\ \frac{\lambda_1}{D} & -\frac{\lambda_1}{D} & 0 \end{pmatrix} \begin{pmatrix} t(x,1) \\ t(x,2) \\ t'(x,1) \end{pmatrix} + \begin{pmatrix} 0 \\ -\frac{1}{v} \\ -\frac{1}{v} \end{pmatrix} \qquad (A.1)$$

which is easily solved and gives

$$t(x,1) = C_1 \mathrm{e}^{\alpha x} + C_2 \mathrm{e}^{\beta x} + C_3 + \frac{\lambda_1 + \lambda_2}{\lambda_1 v} \left(\frac{\lambda_2 D}{\lambda_1 v} - x \right) + \frac{1}{\lambda_1}$$

$$t(x,2) = \frac{\lambda_2}{\beta v} C_1 \mathrm{e}^{\alpha x} + \frac{\lambda_2}{\alpha v} C_2 \mathrm{e}^{\beta x} + C_3 + \frac{\lambda_1 + \lambda_2}{\lambda_1 v} \left(\frac{\lambda_2 D}{\lambda_1 v} - x \right) \qquad (A.2)$$

$$t'(x,1) = \alpha C_1 \mathrm{e}^{\alpha x} + \beta C_2 \mathrm{e}^{\beta x} - \frac{\lambda_1 + \lambda_2}{\lambda_1 v}$$

with

$$\alpha = \frac{1}{2}\left(\frac{\lambda_2}{v} + \sqrt{\frac{\lambda_2^2}{v^2} + 4\frac{\lambda_1}{D}}\right) \qquad \text{and} \qquad \beta = \frac{1}{2}\left(\frac{\lambda_2}{v} - \sqrt{\frac{\lambda_2^2}{v^2} + 4\frac{\lambda_1}{D}}\right).$$

Using the periodic boundary condition, this yields

$$
\begin{aligned}
C_1 &= \left(\frac{1}{\lambda_1} + \frac{1}{\lambda_2}\right) L \frac{\beta^2}{\alpha - \beta} \frac{1}{1 - e^{\alpha L}} \\
C_2 &= \left(\frac{1}{\lambda_1} + \frac{1}{\lambda_2}\right) L \frac{\alpha^2}{\alpha - \beta} \frac{1}{1 - e^{\beta L}} \\
C_3 &= -(C_1 + C_2) - \left(\frac{1}{\lambda_1} + \frac{1}{\lambda_2}\right) \frac{D}{\lambda_1^2} \frac{\lambda_2}{v^2} - \frac{1}{\lambda_1}.
\end{aligned}
\tag{A.3}
$$

Eventually one can write the final solution,

$$t(x, 1) = \frac{\lambda_1 + \lambda_2}{\lambda_1 \lambda_2} \frac{L}{\beta - \alpha} \left[\beta^2 \frac{1 - e^{\alpha x}}{1 - e^{\alpha L}} - \alpha^2 \frac{1 - e^{\beta x}}{1 - e^{\beta L}}\right] - \frac{\lambda_1 + \lambda_2}{\lambda_1} \frac{x}{v} \tag{A.4}$$

$$t(x, 2) = \frac{\lambda_1 + \lambda_2}{\lambda_1 \lambda_2} \frac{L}{\beta - \alpha} \left[\beta^2 \frac{1 - \frac{\lambda_2}{v}\frac{1}{\beta} e^{\alpha x}}{1 - e^{\alpha L}} - \alpha^2 \frac{1 - \frac{\lambda_2}{v}\frac{1}{\alpha} e^{\beta x}}{1 - e^{\beta L}}\right] - \frac{\lambda_1 + \lambda_2}{\lambda_1} \frac{x}{v} - \frac{1}{\lambda_1}. \tag{A.5}$$

Appendix B. Optimization of the search time

Search time

The search time $\langle t \rangle$ given by (9) can be written with adimensional variables as

$$\frac{\langle t \rangle}{\tau} = \frac{L}{2v\tau} \frac{X + Y}{Y} \frac{X + 2Y^2}{\sqrt{X^2 + 4XY}} \equiv \frac{L}{2v\tau} C \tag{B.1}$$

with

$$X = \frac{1}{\lambda_1 \tau} = \frac{\tau_1}{\tau} \qquad \text{and} \qquad Y = \frac{1}{\lambda_2 \tau} = \frac{\tau_2}{\tau} \tag{B.2}$$

τ_i being the average duration of phase i ($i = 1, 2$). Introducing the new variable $u = X/Y$, we have

$$(1 + u)\frac{u + 2Y}{\sqrt{u^2 + 4uY}} = C \geqslant 1 \tag{B.3}$$

which allows expression of Y and X as functions of u and C

$$Y = \frac{u}{2}\sqrt{\theta^2 - 1}\left[\theta + \sqrt{\theta^2 - 1}\right] \qquad \text{and} \qquad X = uY = \frac{u^2}{2}\sqrt{\theta^2 - 1}\left[\theta + \sqrt{\theta^2 - 1}\right] \tag{B.4}$$

with

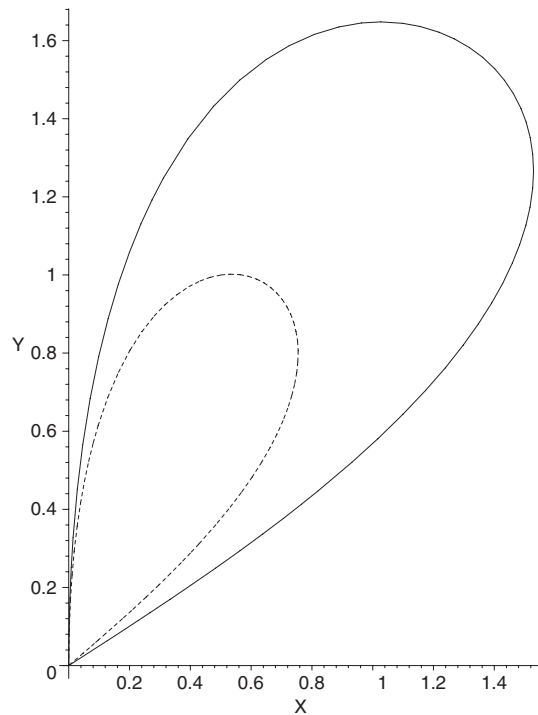$$\theta = \frac{C}{1 + u} \in [1, C]. \tag{B.5}$$

Figure B.1. Contourlines of the average search time. Plain line: $C = 3$. Dashed line $C = 2.5$.

Contourlines (curves of equal C)

It is now easy to obtain the contourlines of the average search time in the plane (X, Y) corresponding to a given value of C: X and Y are given by (B.4) and (B.5) as a function of the parameter u, with $u \in [0, C - 1]$. When $u \to 0$, X and Y tend to 0 and $X/Y \to 0$: the curve is tangent to axis (Ox). When $u \to C - 1$, X and Y tend to 0 and $X/Y \to C - 1$.

It is seen that for a given value of u, X and Y increase with C and the range $[0, C - 1]$ of possible values of u also increases with C, so that the contourline Γ_C corresponding to the value C is contained in the interior of any $\Gamma_{C'}$ with $C' > C$ (see figure B.1).

Maximum values of X and Y

It is clear that for a given value of C, X and Y have maximum values X_m and Y_m respectively. From (B.4), (B.5), we find that

$$\frac{\mathrm{d}Y}{\mathrm{d}u} = \frac{1}{2C}\theta\left[\theta + \sqrt{\theta^2 - 1}\right]\left[\frac{\theta^3 - C}{\theta\sqrt{\theta^2 - 1}} + \theta - C\right]$$

$$\frac{\mathrm{d}X}{\mathrm{d}u} = \frac{1}{2C}\theta\left[\theta + \sqrt{\theta^2 - 1}\right]\left[\frac{\theta^3 + C\theta^2 - 2C}{\theta\sqrt{\theta^2 - 1}} + \theta - C\right]. \tag{B.6}$$

From these expressions, it is easily shown that $\mathrm{d}X/\mathrm{d}u$ and $\mathrm{d}Y/\mathrm{d}u$ respectively vanish for $u = u_1$ and $u = u_2$, respectively, u_1 and u_2 being uniquely determined values of $[0, C - 1]$, corresponding to the maxima of X and Y.

Curves of maximum X

If $dX/du = 0$, we see from (B.6) that

$$C = \frac{\theta^2(\theta + \sqrt{\theta^2 - 1})}{2 - \theta(\theta - \sqrt{\theta^2 - 1})} \qquad \text{and} \qquad u = \frac{C}{\theta} - 1 = \frac{2(\theta^2 - 1)}{2 - \theta(\theta - \sqrt{\theta^2 - 1})}. \tag{B.7}$$

Inserting the expression of u into (B.4), we obtain the equation for the curve of maximum X, parametrized with $\theta \in [1, \infty]$:

$$Y = (\theta^2 - 1)^{3/2} \frac{\theta + \sqrt{\theta^2 - 1}}{2 - \theta(\theta - \sqrt{\theta^2 - 1})}, \qquad X = 2(\theta^2 - 1)^{5/2} \frac{\theta + \sqrt{\theta^2 - 1}}{[2 - \theta(\theta - \sqrt{\theta^2 - 1})]^2}. \tag{B.8}$$

It is seen that if $\theta \to 1$, which corresponds to $u \to 0$, or $X \ll Y$, then

$$Y \sim \left(\frac{X}{2}\right)^{3/5} \tag{B.9}$$

whereas if $\theta \to \infty$, then $u \to \infty$, $X \gg Y$ and

$$Y \sim \left(\tfrac{3}{4}\right)^{1/3} X^{2/3}. \tag{B.10}$$

Thus, we recover the scaling laws given in (14) and (12), but a discussion is necessary.

Optimal search time with minimum τ_1

We have shown that the smallest value of the average search time is $L(2v\tau)^{-1}$, obtained when $C = 1$, corresponding to $X = Y = 0$, or $\tau_1 = \tau_2 = 0$: this is clearly not a realistic condition, since, practically, the researcher cannot perform infinitely fast oscillations between phases 1 and 2! In fact, it is reasonable to assume that, as noticed in section 6, the researcher needs a minimum time τ_{1m}, so that the average duration of phase 1, τ_1, should be at least τ_{1m}. Then, the smallest accessible value of C corresponds to a contourline Γ_C for which the maximum value of X is $X_m = \tau_{1m}/\tau$. Thus, we obtain the optimal condition given previously:

$$X = X_m, \qquad Y \sim C X^\alpha \tag{B.11}$$

C and α being given by (B.9) or (B.10), which agree with experimental data for a broad class of predators searching for a prey.

However, it may be remarked that phase 2, corresponding to a ballistic, fast motion, should also have a minimum duration τ_{2m}, necessary for the researcher to obtain the best physical performances.

Optimal search time with minimum τ_2

To discuss this new situation, we need to consider curves of maximum Y.

If $dY/du = 0$, we see from (B.6) that

$$C = \frac{\theta^2(\theta + \sqrt{\theta^2 - 1})}{1 + \theta\sqrt{\theta^2 - 1}} \qquad \text{and} \qquad u = \frac{\theta^2 - 1}{1 + \theta\sqrt{\theta^2 - 1}}. \tag{B.12}$$

By (B.4) and (B.12), we get the equations for the curve of maximum Y:

$$Y = \frac{1}{2}(\theta^2 - 1)^{3/2} \frac{\theta + \sqrt{\theta^2 - 1}}{1 + \theta\sqrt{\theta^2 - 1}} \qquad \text{and} \qquad X = \frac{1}{2}(\theta^2 - 1)^{5/2} \frac{\theta + \sqrt{\theta^2 - 1}}{[1 + \theta\sqrt{\theta^2 - 1}]^2} \tag{B.13}$$

from which it is seen that if $\theta \to 1$, then $u \to 0$, $X \ll Y$ and

$$Y \sim 2^{-2/5} X^{3/5} \tag{B.14}$$

and if $\theta \to \infty$, then $u \to 1$, and

$$Y \sim X. \tag{B.15}$$

If we want to optimize the search time with the condition that $Y \geqslant Y_{\mathrm{m}} \equiv \tau_{2m}/\tau$ (and no condition on X), we have to choose C in such a way that the maximum value of Y on the corresponding contourline is just τ_{2m}/τ, and we obtain the limiting scaling laws (B.14), (B.15), with $Y = Y_{\mathrm{m}}$.

Optimal search time: general case

In fact, it seems reasonable to optimize the search time with both conditions

$$X \geqslant \frac{\tau_{1m}}{\tau}, \qquad Y \geqslant \frac{\tau_{2m}}{\tau}. \tag{B.16}$$

Then, we have to consider several situations, depending on the respective values of τ_{1m} and τ_{2m}. Obviously, it is very difficult to know these values precisely for animals, but it should be possible if the pursuer is a man-built device. Nevertheless, we can remark that the minimum time τ_{1m} required for the search phase—which needs to process the information contained in the weak or intricate signals provided by receptors of the searcher—should presumably be larger than the minimum time τ_{2m} in the move phase. Thus, we will suppose that

$$\tau_{1m} \geqslant \tau_{2m}. \tag{B.17}$$

Then, the minimum value of C corresponds to a contourline Γ_C which is tangent to the boundary of the permitted region ($X \geqslant \tau_{1m}/\tau, Y \geqslant \tau_{2m}/\tau$) or which passes by point $(X_{\mathrm{m}}, Y_{\mathrm{m}})$. But the contact point cannot be a point of maximum Y, given by (B.13), because for these points, $u = X/Y$ is always smaller than one, by (B.12).

Finally, if the contact point of Γ_{c} with the line $X = \tau_{1m}/\tau$ corresponds to $u = u_1 \geqslant \tau_{1m}/\tau_{2m}$, then the optimal value of the search time occurs for $X = X_{\mathrm{m}} = \tau_{1m}/\tau, Y = Y_{\mathrm{m}} = \tau_{2m}/\tau$: the pursuer should switch from one phase to the other one as frequently as possible. From (B.7), this situation occurs when parameter θ satisfies the inequality

$$\frac{2(\theta^2 - 1)}{2 - \theta(\theta - \sqrt{\theta^2 - 1})} \geqslant \frac{\tau_{1m}}{\tau_{2m}} = \frac{X_{\mathrm{m}}}{Y_{\mathrm{m}}} \equiv u_{\mathrm{m}}. \tag{B.18}$$

Using (B.3) and (B.5), inequality (B.15) can be written

$$4Y_{\mathrm{m}}^2(1 + u_{\mathrm{m}}) - 2Y_{\mathrm{m}}u_{\mathrm{m}}(1 + 2u_{\mathrm{m}}) - u_{\mathrm{m}}^3 \geqslant 0. \tag{B.19}$$

Thus, in the region (A) of the positive quarter of plane $(X_{\mathrm{m}}, Y_{\mathrm{m}})$ where (B.19) holds, the minimal value of the average search time is obtained for $X = X_{\mathrm{m}}$ and $Y = Y_{\mathrm{m}}$, and no scaling law should be available (at least, due to the optimization of search time, since other justification of scaling laws cannot be discarded). On the contrary, in the complementary region (B) of the positive quarter of the plane, the minimal average search time is obtained for $X = X_{\mathrm{m}}$ and Y scaling according to (B.9) and (B.10), depending on whether $Y \gg X$ or $Y \ll X$. It should be noticed that the curve Γ separating regions (A) and (B) satisfies the equations

$$Y = \frac{u}{4(1 + u)}\left[1 + 2u + \sqrt{1 + 8u(1 + u)}\right], \qquad u = X/Y \tag{B.20}$$

so that, when $u \to 0$, X and $Y \to 0$, with $Y \sim (\frac{1+\sqrt{2}}{2}X)^{1/2}$, and when $u \to \infty$, X and $Y \to \infty$, with $Y \sim (\frac{X}{2})^{1/2}$. When $u = 1$, $X = Y = \frac{1}{8}[3 + \sqrt{17}] \approx 0.89$.

Region (B), where the scaling laws hold, lies below Γ. If the heuristic but reasonable condition (B.14) $Y_{\mathrm{m}} \leqslant X_{\mathrm{m}}$ is satisfied, all points $(X_{\mathrm{m}}, Y_{\mathrm{m}})$ are in (B) for $X_{\mathrm{m}} \leqslant 0.89$ and the scaling law (B.9) holds. On the other hand, for $X_{\mathrm{m}} \geqslant 0.89$, the scaling law (B.10) is

only justified if (X_m, Y_m) lies in region (B), i.e. if, for $X_m \gg 1$, $Y_m \leqslant (X_m/2)^{1/2}$, which is considerably stronger than (B.14).

Clearly, one should not expect actual search processes to be in exact agreement with the numerical values given above, but this discussion can shed a new light on many intermittent processes.

References

[1] Bell J W 1991 *Searching Behaviour, The Behavioural Ecology of Finding Resources* (*Animal Behaviour Series*) (London: Chapman and Hall)
[2] O'Brien W J, Browman H I and Evans B I 1990 *Am. Sci.* **78** 152
[3] Kramer L D and McLaughlin R L 2001 *Am. Zool.* **41** 137
[4] Rice S A 1985 *Diffusion-Limited Reactions* (*Compr. Chem. Kinetics* vol 25) ed C H Bamford, C F H Tipper and R G Compton (New York: Elsevier)
[5] Berg O G and Blomberg C 1976 *Biophys. Chem.* **4** 367
[6] Coppey M, Bénichou O, Voituriez R and Moreau M 2004 *Biophys. J.* **87** 1640
[7] Stephens D W and Krebs J R 1986 *Foraging Theory* (Princeton, NJ: Princeton University Press)
[8] Viswanathan G M *et al* 1999 *Nature* **401** 911
[9] Viswanathan G M *et al* 1996 *Nature* **381** 413
[10] Levandowsky M, Klafter J and White B S 1988 *Bull. Marine Sci.* **43** 758
[11] Bartumeus F *et al* 2002 *Phys. Rev. Lett.* **88** 097901
     Bartumeus F *et al* 2002 *Phys. Rev. Lett.* **89** 109902
[12] Raposo E P *et al* 2003 *Phys. Rev. Lett.* **91** 240601
[13] Stone L D 1989 *Theory of Optimal Search* (Arlington, VA: Operations Research of America)
[14] Bénichou O, Coppey M, Moreau M, Suet P H and Voituriez R 2005 *Phys. Rev. Lett.* **94** 98101
[15] Redner S 2001 *A Guide to First Passage Time Processes* (Cambridge: Cambridge University Press)
[16] Gardiner C W 1985 *Handbook of Stochastic Methods for Physics, Chemistry and Natural Science* (Berlin: Springer)
[17] O'Brien W J, Evans B I and Howick G 1986 *Can. J. Fish. Aquat. Sci.* **43** 1894
[18] Pienkowski M W 1983 *Anim. Behav.* **31** 244–64
[19] Cody M 1968 *Am. Nat.* **47** 102
[20] Huey R B and Pianka E R 1981 *Ecology* **62** 991