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A stochastic theory for the intermittent behaviour of foraging animals

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Abstract

The best way of finding a hidden target is a general question which concerns many fields of natural and social sciences. It is of vital importance for foraging animals. It has been observed that many species adopt an intermittent behaviour, alternating phases of intensive search and slow displacement, with phases of fast motion for exploring new regions. Here we present an overview of a simple stochastic model which shows that scaling laws should be valid, relating the average durations of these phases. These laws and other results are in good agreement with available experimental data on a wide class of foraging animals.

Keywords: Foraging animals; Intermittent; Stochastic

1. Introduction

Many problems in natural sciences can be modelled as the search of a target by a mobile particle or predator [1]. The search ends when the particle reaches its target, which can be either destroyed or modified, according to the example treated. Thus, it is often of great importance to minimize the time needed to find a randomly hidden

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target [2,3]. This very general question has been addressed in various articles [2,4–7] in the case of foraging animals, which spend great part of the time looking for small or hidden preys, and must optimize their strategy. In fact, experimental observations show that a great variety of such animals adopt an intermittent behaviour, alternating phases of active search and slow displacement with phases of fast motion. We summarize a recent, stochastic model [7] which shows that such an intermittent strategy allows minimizing the average time needed to find a prey. Its solution leads to scaling laws between the average durations of the two phases, which are in good agreement with available experimental data. Furthermore, it reveals the importance of a characteristic time related to these durations, which can be estimated from the observations.

2. Search strategies of foraging predators

As mentioned previously, studies of foraging behaviour showed that many animals use an intermittent strategy, or saltatory behaviour [8–10], successively displaying phases of intensive search with a slow displacement, focusing attention on prey detection, and phases of fast motion, which degrade the perception abilities but allow to visit unexplored regions. This strategy can be understood when the preys are hidden and sparsely distributed. Examples can be found in very different species, such as birds (ground-foraging species feeding on insects or seeds), fishes (goldfish, bluegill sunfish), lizards or insects (wingless phorid flies). A similar intermittent behaviour can also be observed on humans searching for specific letters sequence in a text. Furthermore, it has been found that (i) no significant displacements occur during the scanning phase; (ii) the velocity is almost constant during the fast displacement; (iii) the angle between the velocities before and after a search phase (turning angle) is usually small: the animal remembers its previous direction; and (iv) the durations of the two phases vary widely, depending on the species. These durations were measured, but the observations received no complete, qualitative interpretation [9].

3. Model

We now incorporate these characteristics in the following simplified model:

Movement: Since the turning angle between different phases is usually small, we assume that the predator follows a one-dimensional motion including two phases:

- The search phase 1 is modelled as a diffusive movement. In fact, the stimuli emitted by hidden targets are very weak; the predator may have to scan the same location several times before detecting the prey: this process may be represented by a Brownian motion. The time needed to discover the prey is in practice identical to the first passage time at this point.

- The motion phase 2 is a ballistic motion at constant absolute velocity v. During this phase, the predator cannot discover a prey because of its reduced censorial abilities.
- The duration of each phase i is an exponential stochastic time T_i: $P(T_i > t) = \exp(-f_i t)$.

Preys: The preys are supposed to be uniformly distributed along the trajectory of the predator.

Representation: the predator is represented by a point P moving on a straight line (Ox) between reflecting points at $-L/2$ and $L/2$. A unique prey is located at $x = 0$: the images of 0 simulate regularly spaced preys with density $1/L$. During phase 1, P performs a diffusive movement with diffusion coefficient D. The predator discovers the prey at its first passage time at 0 during phase 1. During phase 2, P performs a ballistic motion with velocity v or $-v$, which can only change when P reaches the reflecting points $-L/2$ or $L/2$. We consider that the prey P can be in four distinct internal states i:

- State 1 (resp. 2) corresponds to a diffusive motion which can only switch to a ballistic motion with velocity $+v$ (resp. $-v$).
- State 3 (resp. 4) corresponds to a ballistic motion with velocity $+v$ (resp. $-v$).

Let $t(x, i)$ be the time necessary for finding the prey (first arrival time to 0) when P starts from position x and state i. These first passage times satisfy the equations [11]

$$\begin{aligned}
&D\,\frac{\partial^2 t(x,1)}{\partial x^2} + f_1[t(x,3) - t(x,1)] = -1\,,\\
&D\,\frac{\partial^2 t(x,2)}{\partial x^2} + f_1[t(x,4) - t(x,2)] = -1\,,\\
&v\,\frac{\partial t(x,3)}{\partial x} + f_2[t(x,1) - t(x,3)] = -1\,,\\
&-v\,\frac{\partial t(x,4)}{\partial x} + f_2[t(x,2) - t(x,4)] = -1\,. \qquad (1)
\end{aligned}$$

4. Results

These equations can be solved with the relevant boundary conditions. Then, the solutions are averaged on uniform distribution of the initial position and initial diffusive state. In the low target density limit, defined by

$$L \gg \frac{v}{f_2}, \frac{D}{f_1}, \frac{f_2 D}{f_1 v}\,, \qquad (2)$$

it is found that the average search time S (mean first arrival time at 0) is

$$S=\frac{L}{2\sqrt{D}}\left(\frac{1}{f_1}+\frac{1}{f_2}\right)\frac{\tau f_2^2+2f_1}{\sqrt{\tau f_2^2+4f_1}} \tag{3}$$

with $\tau = D/v^2$. The L dependency of S shows that the intermittent behaviour is much more efficient than a mere diffusion, which would imply an L^2 dependence.

Minimization of the search time: We now study the conditions for minimizing the search time. It is easily found that there is no global minimum of the mean search time S for finite values of f_1 and f_2. Nevertheless, as focusing and analysing the information received by sensory organs requires a minimum time, we assume that f_1 has a maximum value $f_{1\,\max}$, depending on the species considered. Then S is minimum when

$$f_1 = f_{1\,\max}\,,$$

$$f_1 f_2^5 + \frac{6}{\tau} f_1^2 f_2^3 - \frac{8}{\tau^2} f_1^4 = 0\,. \tag{4}$$

From these results it can be shown that:

- If $f_{1\,\max} \ll 1/\tau$, the search time is minimal when frequencies are such that $f_1 = f_{1\,\max}$ and

  $$f_2 \approx \left(\frac{4}{3\tau}\right)^{1/3} f_1^{2/3}\,. \tag{5}$$

  In this regime $\mathscr{S}$ (“search”), $f_1 < f_2$: the predator spends more time searching than moving.
- If $f_{1\,\max} \gg 1/\tau$, the minimal frequencies are such that $f_1 = f_{1\,\max}$ and

  $$f_2 \approx \left(\frac{2\sqrt{2}}{\tau}\right)^{1/3} f_1^{3/5}\,. \tag{6}$$

  In this regime $\mathscr{M}$ (“move”), $f_1 > f_2$: the predator spends more time moving than searching.

5. Comparison with experimental data

Experimental data are available [2,3,8] and provide the average durations (and thus frequencies f_1 and f_2) of search and motion phases for various species such as fishes, birds and lizards exhibiting a saltatory search behaviour. Then, the previous minimizing relation allows the calculation of the characteristic time τ from these experimental data. The results are reported as a histogram indicating the proportion of species corresponding to different values of τ (see Fig. 1).

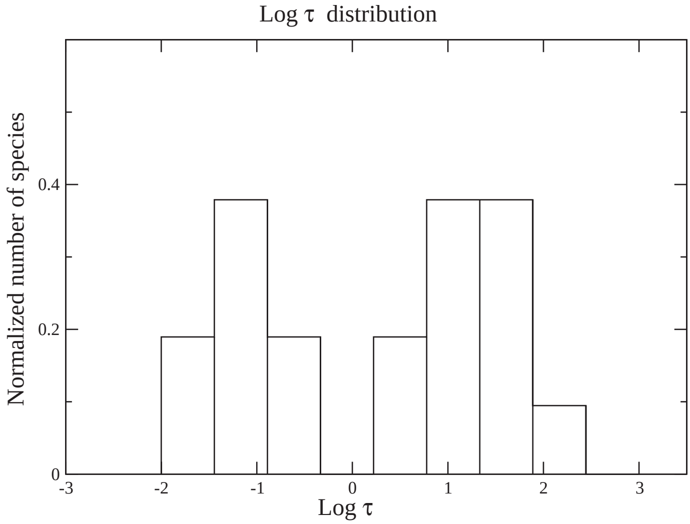

Fig. 1. Histogram of Log(τ): proportions of species corresponding to typical values of τ.

Bimodal distribution: Quite unexpectedly, this distribution is bimodal, with one minimum around 0.1 s and a second one around 25 s, the fluctuations in log(τ) being small (of order 1). The first peak (τ~0.1 s) corresponds to foragers in regime $\mathscr{S}$, which spend more time searching than moving. The second peak (τ~25 s) corresponds to foragers in regime $\mathscr{M}$, which spend more time moving than searching.

Correlation of frequencies: The plot of the frequencies f_1 and f_2 for each of the previous classes $\mathscr{S}$ and $\mathscr{M}$ shows that both sets are strongly correlated. Their linear regression gives slopes in agreement with theoretical predictions: for animals belonging to class $\mathscr{M}$, the experimental slope is 0.7 ± 0.1 (theoretical value: 3/5); for animals belonging to class $\mathscr{S}$, the experimental slope is 0.6 ± 0.1 (theoretical value: 2/3), both with a correlation coefficient r~0.9. Thus, taking into account the limited accuracy of the data, our theoretical results satisfactorily agree with experimental observations.

6. Conclusions

The experimental data seem to confirm the validity of our hypothesis, mainly that the search phase is adequately represented by a diffusion, and that each species tends to optimize its strategy by minimizing its search time. We have seen that this minimization allows defining two classes of foraging animals: animals which spend more time searching than moving, and animals which, more surprisingly, spend more time moving than searching. In each class, scaling laws relate the average durations of each phase, or the corresponding frequencies. These results are in good agreement with the available experimental data.

Our model could be applied to a large variety of search problems in natural sciences, as well as in social sciences and economics, provided that the targets are hidden, and the evolution of the system can be represented as a one-dimensional motion with alternating diffusion and ballistic phases. Then, if minimizing the search time is relevant, scaling laws should relate the phase durations. Clearly, many complex factors are neglected in such oversimplified models, and they can have important roles. In particular, it would be interesting to consider *n*-dimensional examples, as well as extended classes of motion, or non-exponential waiting times. Nevertheless, it appears that such factors do not strongly affect the validity of our conclusions in the prey–predator case studied here.

In this case, minimizing the search time leads to the definition of a characteristic time τ which can be computed as a function of the relaxation frequencies of the phases and is estimated from experimental data. It is remarkable that it is approximately common to all animals in the same class, although they can belong to very different species. No obvious explanation exists for this fact, which seems specific of the search strategy of foraging animals, and could be of importance. Only biologists can discuss it and consider its possible interpretations.

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