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Optimal intermittent search strategies: *smelling the prey*

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Abstract

We study the kinetics of the search of a single fixed target by a searcher/walker that performs an intermittent random walk, characterized by different states of motion. In addition, we assume that the walker has the ability to detect the scent left by the prey/target in its surroundings. Our results, in agreement with intuition, indicate that the prey's survival probability could be strongly reduced (increased) if the predator is attracted (or repelled) by the trace left by the prey. We have also found that, for a positive trace (the predator is guided towards the prey), increasing the inhomogeneity's size reduces the prey's survival probability, while the optimal value of α (the parameter that regulates intermittency) ceases to exist. The agreement between theory and numerical simulations is excellent.

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1. Introduction

The study of different approaches to obtain optimal strategies for the search of specific targets has recently experienced a rapid growth and motivated a great deal of work [1]. On one hand, the determination of an efficient search strategy emerged as a crucial problem in behavioral ecology, inspiring a wealth of experimental and theoretical work [2–4]. On the other hand, it is also relevant to broader domains such as stochastic processes theory, applied mathematics as well as of great interest for molecular biology, social sciences and ecology [1, 5–11].

Among the different forms of optimal search strategies, an intermittent one has been recently proposed [1, 5, 8]. Intermittent motion occurs in a wide array of organisms from protozoans to mammals. It has been observed that numerous animal species switch between two distinct type of behavior (and motion) while foraging. In fact, many foragers such as planktivorous fish, ground foraging birds and lizards, adopt an intermittent searching behavior [2–4]. These intermittent search strategies combine phases of relocation (in which the searcher may or may not capture the target), and a thorough search phase, which allow for the target detection.

In [6] a theoretical model for the search kinetics of a hidden target, assuming that each searcher can be in either of two propagation states, was presented. In one of them, the displacement of the searcher is a random walk with symmetric jumps to nearest neighbors sites while in the other state, the searcher also performs a symmetrical random walk, but jumping to next-nearest neighbors. It was shown that intermittent strategies always improve target detection in comparison with the single-state displacement. Recently [12], and in order to include a dynamic bias, the previous results were generalized, finding situations where more than one minimum or maximum could arise in the survival probability or other relevant quantities.

In its simplest form, one assumes that the search is performed at random (i.e. without taking into account the possible signals from the prey), but in general predators often search for prey using chemical cues, particularly where visual or mechanical stimuli are obscured or unavailable. For instance, in [13] the sighting range of predators was also considered as a sort of additional searching ability. This fact may be interpreted as a deterministic motion of predators after the prey gets into their sighting range giving rise a finite step-wise problem between the prey and the predators. The perception of chemical clues acts to bias the locomotion, and feedback of odorant stimulus distributions appears directly to regulate subsequent movement to the route toward the prey [14]. Despite its importance, how olfactory-guided search strategies operate over a distance has not been rigorously studied yet [15]. However, this is an interdisciplinary field of research that is in an early growing stage, particularly in relation to the presence for ‘odor plumes’ [16, 17].

In this work, we make a step forward toward the consideration of prey signals introducing inhomogeneities in the field that may be associated with the trace left by the prey on its surroundings. In order to perform our study, we exploit the theory of *multi-state* random walk (RW) [18] as well as the *local inhomogeneity technique* developed in [20–22]. We use the concepts of the *survival probability* for the target and establish the connection to the *first passage time* of the searcher.

The outline of this paper is as follows. The following section presents the basic definitions, equations and functions to be used later. In section 3, we describe our model, focusing on the one-dimensional analytical solvable case and made the connection with Monte Carlo simulations. In section 4, we present some results for the survival probability and related functions, while in the last section we draw some conclusions.

2. Theory

2.1. The composite process

We assume that at time t each walker can be at site \vec{s} on a lattice, in one of the two internal states. We associate the *internal state 2* with a thorough search phase motion (compact exploration state), whereas *internal state 1* models the relocation phase. There is a transition rate between the two internal states which will be explained later. We follow the walker evolution through the system considering the conditional probability $P_{i,i_0}(\vec{s}, t|\vec{s}_0, t=0)$ of being at site \vec{s} in the internal state i at time t given that it was at site \vec{s}_0 in the internal state i_0 at $t=0$.

The coupled master equations for the two internal state composite processes are

$$\frac{\partial P_{1,i_0}(\vec{s}, t|\vec{s}_0, 0)}{\partial t} = \mathbb{A}_1 P_{1,i_0}(\vec{s}, t|\vec{s}_0, 0) + \gamma_2 P_{2,i_0}(\vec{s}, t|\vec{s}_0, 0) - \gamma_1 P_{1,i_0}(\vec{s}, t|\vec{s}_0, 0) \quad (1)$$

$$\frac{\partial P_{2,i_0}(\vec{s}, t|\vec{s}_0, 0)}{\partial t} = \mathbb{A}_2 P_{2,i_0}(\vec{s}, t|\vec{s}_0, 0) + \gamma_1 P_{1,i_0}(\vec{s}, t|\vec{s}_0, 0) - \gamma_2 P_{2,i_0}(\vec{s}, t|\vec{s}_0, 0), \quad (2)$$

where the γ_i are the transition rates between internal states and the \mathbb{A}_i are the operators that describe the evolution/propagation of the walker within each state. It should be noted here that

- while the walker is switching its internal state no spatial displacement occurs;
- the conditional probabilities $P_{i,i_0}(\vec{s}, t|\vec{s}_0, t=0)$ do not satisfy the normalization condition, i.e., $\sum_{\vec{s}} P_{i,i_0}(\vec{s}, t|\vec{s}_0, t=0) \neq 1$. This is due to the fact that each $P_{i,i_0}(\vec{s}, t|\vec{s}_0, t=0)$ has a ‘leakage’ (controlled by the transition rate γ_i) to the other inner state;
- however, the marginal probability, that is the sum $\hat{P}_{\text{Mar},i_0}(\vec{s}, u|\vec{s}_0, 0) = \hat{P}_{1,i_0}(\vec{s}, u|\vec{s}_0, 0) + \hat{P}_{2,i_0}(\vec{s}, u|\vec{s}_0, 0)$, is well defined and normalized, i.e. $\hat{P}_{\text{Mar},i_0}(\vec{s}, u|\vec{s}_0, 0) = 1$;
- for the sake of simplicity, we have considered only two internal states (however, the theory may be extended to consider an arbitrary number of internal states).

In what follows, we will denote the Laplace transform on t by a caret over the corresponding function; for example,

$$\hat{P}_{i,i_0}(\vec{s}, u|\vec{s}_0, 0) = \int_0^\infty e^{-ut} P_{i,i_0}(\vec{s}, t|\vec{s}_0, 0) dt.$$

2.2. The trapping process

We will focus on the survival probability for the target/prey. A typical walk ends when the walker reaches the target for the first time, i.e. the trapping is assumed to be ‘perfect’. A closely related quantity (for the case of perfect trapping) is the walker’s *first-passage time density* (FPTD).

We define $F_{1,i_0}^I(\vec{0}, t|\vec{s}_0, 0)$ ($F_{2,i_0}^I(\vec{0}, t|\vec{s}_0, 0)$) to be the FPTD through the site $\vec{0}$ at time t given that it was at \vec{s}_0 with the internal state i_0 at time $t=0$ given that adsorption/capture is possible while the walker is only on the *internal state 1* (2). Following [23] we introduce the notion of the *generalized state* which takes into account the position and the internal state of the walker, (\vec{s}, i) .

The connection between the probability density of first arrival at $(\vec{0}, 1)$ at time t from (\vec{s}_0, i_0) , $F_{1,i_0}^I(\vec{0}, t|\vec{s}_0, 0)$, and the conditional probability $P_{i,i_0}(\vec{s}, t|\vec{s}_0, t=0)$ is established as

$$\hat{F}_{1,i_0}^I(\vec{0}, u|\vec{s}_0, 0) = \frac{\hat{P}_{1,i_0}(\vec{0}, u|\vec{s}_0, 0)}{\hat{P}_{1,1}(\vec{0}, u|\vec{0}, 0)}. \tag{3}$$

A similar expression is obtained when the ‘defective state’ (‘trapping state’) is $(\vec{0}, 2)$:

$$\hat{F}_{2,i_0}^I(\vec{0}, u|\vec{s}_0, 0) = \frac{\hat{P}_{2,i_0}(\vec{0}, u|\vec{s}_0, 0)}{\hat{P}_{2,2}(\vec{0}, u|\vec{0}, 0)}. \tag{4}$$

In this way we reobtain the Siegert formula [24], generalized to internal states [25].

When capture/adsorption occurs in any of the two internal states of the walker we define $F_{1,i_0}^{II}(\vec{0}, t|\vec{s}_0, 0)$ ($F_{2,i_0}^{II}(\vec{0}, t|\vec{s}_0, 0)$) as the FPTD through the site $\vec{0}$ at time t given that it was at \vec{s}_0 with the internal state i_0 at time $t=0$ when adsorption/capture occurs on the *internal state 1* (2). An interesting relationship between F^I and F^{II} can be established by noting that

$$F_{1,i_0}^{II}(\vec{0}, t|\vec{s}_0, 0) = F_{1,i_0}^I(\vec{0}, t|\vec{s}_0, 0) - \int_0^t F_{1,2}^I(\vec{0}, t|\vec{0}, \tau) F_{2,i_0}^{II}(\vec{0}, \tau|\vec{s}_0, 0) d\tau \tag{5}$$

$$F_{2,i_0}^{II}(\vec{0}, t|\vec{s}_0, 0) = F_{2,i_0}^I(\vec{0}, t|\vec{s}_0, 0) - \int_0^t F_{2,1}^I(\vec{0}, t|\vec{0}, \tau) F_{1,i_0}^{II}(\vec{0}, \tau|\vec{s}_0, 0) d\tau. \tag{6}$$

The above equations have a simple statistical interpretation: the left-hand sides in both equations represent the FPTD when the absorption takes place in any of the two internal states, while on the right-hand side the first term takes into account absorption only when one internal state captures and the second one discounts the contributions of the paths that go through the absorption ‘state’ $(\vec{0}, 1)$ in equation (5) or $(\vec{0}, 2)$ in equation (6).

These pairs of equations may be expressed in Laplace space as

$$\hat{F}_{1,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0) + \hat{F}_{2,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0)\hat{F}_{1,2}^I(\vec{0}, u|\vec{0}, 0) = \hat{F}_{1,i_0}^I(\vec{0}, u|\vec{s}_0, 0) \quad (7)$$

$$\hat{F}_{2,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0) + \hat{F}_{1,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0)\hat{F}_{2,1}^I(\vec{0}, u|\vec{0}, 0) = \hat{F}_{2,i_0}^I(\vec{0}, u|\vec{s}_0, 0). \quad (8)$$

A similar expression (although in a different context) was established in [26].

When trapping occurs in any of the two states the survival probability (that is, the probability that the prey is not found before a fixed time) is (if $\vec{s}_0 \neq \vec{0}$):

$$\Phi_{i_0}^{II}(\vec{0}, t|\vec{s}_0, 0) = 1 - \int_0^t [F_{1,i_0}^{II}(\vec{0}, \tau|\vec{s}_0, 0) + F_{2,i_0}^{II}(\vec{0}, \tau|\vec{s}_0, 0)] d\tau. \quad (9)$$

Adding equations (7) and (8) and using the results of equations (3) and (4), we find

$$\hat{F}_{1,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0)\hat{P}_{\text{Mar},1}(\vec{0}, u|\vec{0}, 0) + \hat{F}_{2,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0)\hat{P}_{\text{Mar},2}(\vec{0}, u|\vec{0}, 0) = \hat{P}_{\text{Mar},i_0}(\vec{0}, u|\vec{s}_0, 0), \quad (10)$$

where $P_{\text{Mar},i_0}(\vec{s}, t|\vec{s}_0, 0)$ is the *marginal* probability distribution, i.e.

$$P_{\text{Mar},i_0}(\vec{s}, t|\vec{s}_0, 0) = P_{1,i_0}(\vec{s}, t|\vec{s}_0, 0) + P_{2,i_0}(\vec{s}, t|\vec{s}_0, 0). \quad (11)$$

2.3. Long time and high transition rate limit

Following [27] and using equations (1) and (2) it can be shown that in the high transition long time limit the distribution over the internal states becomes stationary and the common spatial distribution is governed by the averaged transport equation

$$\frac{\partial P_{\text{Mar}}(\vec{s}, t|\vec{s}_0, 0)}{\partial t} = \tilde{\mathbb{A}} P_{\text{Mar}}(\vec{s}, t|\vec{s}_0, 0), \quad (12)$$

where

$$\tilde{\mathbb{A}} = \alpha \mathbb{A}_1 + (1 - \alpha) \mathbb{A}_2 \quad (13)$$

with

$$\alpha = \frac{\gamma_2}{\gamma_1 + \gamma_2} \quad (14)$$

and $P_{\text{Mar}}(\vec{s}, t|\vec{s}_0, 0)$ is the *marginal* probability distribution in the stationary case, i.e.

$$P_{\text{Mar}}(\vec{s}, t|\vec{s}_0, 0) = P_{1,i_0}(\vec{s}, t|\vec{s}_0, 0) + P_{2,i_0}(\vec{s}, t|\vec{s}_0, 0). \quad (15)$$

From these equations, it is easy to see that $\alpha = 0$ implies that the walker cannot jump to state 1, while for $\alpha = 1$, it cannot jump to state 2.

It is important to note that in the considered limit, the initial condition on the internal state disappears, i.e., the evaluation of any statistical property becomes independent of the initial internal state of the walker. Taking into account this fact and equation (10),

$$\hat{F}_{1,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0) + \hat{F}_{2,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0) = \frac{\hat{P}_{\text{Mar}}(\vec{0}, u|\vec{s}_0, 0)}{\hat{P}_{\text{Mar}}(\vec{0}, u|\vec{0}, 0)}. \quad (16)$$

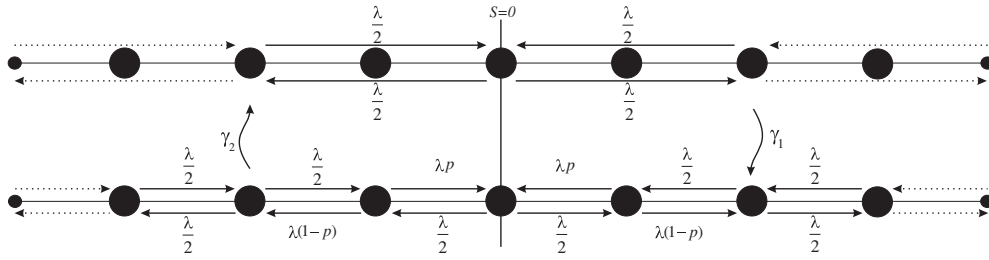


Figure 1. Schematic transitions between sites and between internal states of the chain: state 1 corresponds to the relocation phase, while state 2 corresponds to the compact searching phase.

Then the survival probability (equation (9)) adopts the form

$$\begin{aligned} \hat{\Phi}^{II}(\vec{0}, u|\vec{s}_0, 0) &= \frac{1}{u} \left(1 - [\hat{F}_{1,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0) + \hat{F}_{2,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0)] \right) \\ &= \frac{1}{u} \left(1 - \frac{\hat{P}_{\text{Mar}}(\vec{0}, u|\vec{s}_0, 0)}{\hat{P}_{\text{Mar}}(\vec{0}, u|\vec{0}, 0)} \right). \end{aligned} \tag{17}$$

3. The model: ‘smelling the prey’

As in [6] we restrict ourselves to work on an infinite discrete chain and assume that the fixed target/prey is located at the origin of the lattice. At $t = 0$, a searcher/predator originally at s_0 on the chain, starts the ‘search’, and when it finds the target/prey, catches it with probability one, i.e. perfect trapping. We will assume that the searcher ‘captures’ the prey only upon landing directly on the target site at the end of the re-localization state (next-nearest neighbors walk-internal state 1), or via a one-step walk (compact exploration state-internal state 2) on to that site. Moreover, near the origin (where the prey is located), the prey/target has left a trace/odor which either increases the detection by a predator or confuses the searcher depending on the trace being below or above than a critical (indifferent) value p . While it is possible that the prey is detected in any of the two states or phases of the searcher, the trace left by the prey is only perceptible to the searcher in the compact exploration state. This scheme emphasizes the fact that re-localization phase is at the expense of a coarse-grained sampling, i.e. the predator’s sensory skills are diminished. Conversely, searchers in the compact exploration phase might benefit by detecting the odor more successfully in the spatial domain and could allow subsequent movement toward its source (prey) [28].

Within each internal state, the displacement of the predator on the lattice is described (in the case of $N = 2$ symmetric inhomogeneities) by the following \mathbb{A}_i operators (see figure 1, while figure 2 shows the case of the high transition and long time limit scheme):

$$[\mathbb{A}_2]_{s,s'} = \frac{\lambda}{2} [\delta_{s,s'-1} + \delta_{s,s'+1} - 2\delta_{s,s'}] \quad \forall \quad s' \neq -1, 1, \tag{18}$$

and

$$[\mathbb{A}_2]_{1,0} = [\mathbb{A}_1]_{-1,0} = [\mathbb{A}_1]_{1,2} = [\mathbb{A}_2]_{-1,-2} = \frac{\lambda}{2} \tag{19}$$

$$[\mathbb{A}_2]_{1,1} = [\mathbb{A}_2]_{-1,-1} = [\mathbb{A}_2]_{0,0} = -\lambda \tag{20}$$

$$[\mathbb{A}_2]_{2,1} = [\mathbb{A}_2]_{-2,-1} = (1-p)\lambda \tag{21}$$

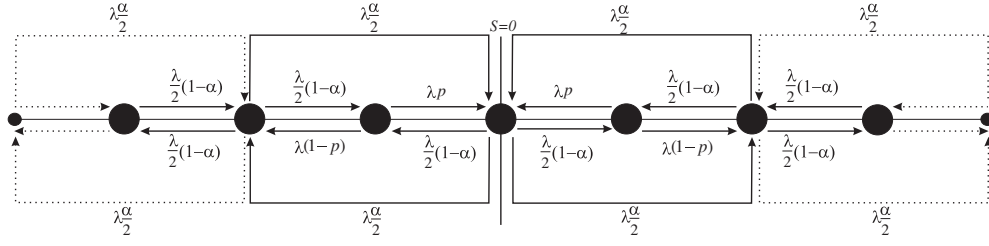


Figure 2. Schematic transitions for the marginal probability distribution in the high transition limit.

$$[\mathbb{A}_2]_{0,1} = [\mathbb{A}_2]_{0,-1} = p\lambda. \quad (22)$$

For the internal state 1 we have

$$[\mathbb{A}_1]_{s,s'} = \frac{\lambda}{2} [\delta_{s,s'-2} + \delta_{s,s'+2} - 2\delta_{s,s'}] \quad \forall \quad s, s'. \quad (23)$$

The γ_j parameters are scaled in terms of the transition rate between chain sites λ , and the olfactory capability is ‘tuned’ with the parameter p . The above schemes can be straightforwardly generalized to include the case $N \geq 2$ (symmetric or asymmetric) inhomogeneities.

In the problem of intermittent search strategies, optimization consists of finding the values of γ_j , the transition rates between internal states (equations (1) and (2)), or the α values (equation (12)) such that the prey’s survival probability at a time t be minimal. In order to perform our study, we exploit the theory of multi-state random walk (RW) [18] in the high transition and long time regime as well as the local inhomogeneity technique developed by Montroll [20–22].

For completeness, we indicate here the Laplace result for the survival probability (equation (17)) that early shows the complexity of these expressions:

$$\hat{\Phi}^{II}(\vec{0}, u | \vec{s}_0, 0) = \frac{1}{u} \left(1 - \frac{\hat{P}_{\text{Mar}}(0, u | s_0, 0)}{\hat{P}_{\text{Mar}}(0, u | 0, 0)} \right) \quad (24)$$

$$= \left(1 - \frac{\hat{P}_{\text{Mar}}(s_0, u)\Delta_1 + [\hat{P}_{\text{Mar}}(s_0 + 1, u) + \hat{P}_{\text{Mar}}(s_0 - 1, u)]\Delta_2}{\hat{P}_{\text{Mar}}(0, u)\Delta_1 + 2\hat{P}_{\text{Mar}}(1, u)\Delta_2} \right) \quad (25)$$

$$\begin{aligned} \Delta_1 &= \hat{P}_{\text{Mar}}(0, u) + \hat{P}_{\text{Mar}}(2, u) - \frac{1}{u+1} [\alpha \hat{P}_{\text{Mar}}(2, u) + (1-\alpha) \hat{P}_{\text{Mar}}(1, u)] - \frac{1}{u+1} \\ &\quad \times \{ \alpha [\hat{P}_{\text{Mar}}(0, u) + \hat{P}_{\text{Mar}}(4, u)] + (1-\alpha) [p \hat{P}_{\text{Mar}}(1, u) + (1-p) \hat{P}_{\text{Mar}}(3, u)] \} \\ \Delta_2 &= \frac{1}{u+1} \left\{ \frac{\alpha}{2} [\hat{P}_{\text{Mar}}(1, u) + \hat{P}_{\text{Mar}}(3, u)] \right. \\ &\quad \left. + (1-\alpha) [p \hat{P}_{\text{Mar}}(0, u) + (1-p) \hat{P}_{\text{Mar}}(2, u)] \right\} - \hat{P}_{\text{Mar}}(1, u), \end{aligned} \quad (26)$$

where $\hat{P}_{\text{Mar}}(s, u | 0, 0) \equiv \hat{P}_{\text{Mar}}(s, u)$ is obtained from

$$\hat{P}_{\text{Mar}}(s, u) = \frac{1}{2\pi} \int_{-\pi}^{\pi} \frac{\cos sk}{1 + u - [(1-\alpha) \cos k + \alpha \cos 2k]} dk. \quad (27)$$

As its analytical inversion is beyond our scope, we have chosen to make the Laplace numerical inversion, exploiting an algorithm that has proven to be adequate in other works [6, 19].

4. Numerical and Monte Carlo results

Here we illustrate and give some general ideas to interpret the results. We have numerically solved our model by making the inverse Laplace transformation of the expressions indicated above. In order to check the numerical results, we have also performed Monte Carlo simulations. An ensemble of independent walkers started their searches in a given lattice position ($s_0 = 5$). The predators chose the way to search the prey randomly, changing between states 1 and 2 according to the ratio α (which has already been defined in equation (14)). The prey was immobile at $s = 0$. We have averaged over 10^5 realizations. All times are given in units of the diffusion constant λ .

It is worth commenting that the high transition rate limit requires that the mean sojourn time in any of the two internal states (γ_1^{-1} and γ_2^{-1}) be short on the timescale determined by the propagators \mathbb{A}_1 and \mathbb{A}_2 (λ^{-1}) [27]. So we have, $\gamma_i^{-1} \ll \lambda^{-1}$ with $i = 1, 2$, or $\frac{\lambda}{\gamma_i} \ll 1$. As time is given in unit of the diffusion constant λ , we have, e.g., if $t = 10 \implies t = 10(\frac{1}{\lambda})$, but this time is much larger than $\frac{1}{\gamma_i}$ (mean sojourn time in internal state i) as suggested above.

In figure 3, we draw the survival probability curves $\Phi^{II}(\alpha; t)$ as a function of α . On the upper panel and for different times ($t = 10, 20, 50, 100$), we analyze the case of a ‘detection (olfactory) skill’ of $p = 0.9$, that is an excellent olfactory skill, or a strongly attractive situation. On the lower panel, we have considered the case of a fixed time ($t = 20$) and analyzed different ‘olfactory skills’: $p = 0.1, 0.4$, corresponding to cases when the prey left a trace which sidetracks the searcher, or a negative trace that repels the searcher from the vicinity of the target, i.e. the ‘skunk’ case; and for $p = 0.9$, that corresponds to the case where a positive trace exists, guiding the searcher toward the prey (the prey’s odor increases the probability of detection by the predator). The results show a clear trend that is in agreement with everyone’s expectation for these situations. That is, when the searcher has developed good olfactory skills ($p > 0.5$) increases its ‘chances’ of catching the prey, while if its olfactory ability is degraded ($p < 0.5$) the prey survival probability rises.

It is apparent how the intermittent search can improve the detection probability, i.e., minimize the survival probability of the target, compared with the *single-state search* ($\gamma_1 = 0$, i.e., $\alpha = 0$ and $\gamma_2 = 0$, i.e., $\alpha = 1$), even for reduced olfactory capabilities ($p < 0.5$). This confirms the robustness of the intermittent search approach [29]. As can be seen from both figures, we always found a minimum in $\Phi^{II}(\alpha; t)$ (for a fixed t) as a function of α . We want to stress that the value of α minimizing $\Phi^{II}(\alpha; t)$ defines the optimal relation between γ_1 and γ_2 for improving the search strategy. From the figures, it is apparent that there is excellent agreement between the numerical solutions of our equations and Monte Carlo simulations.

Figure 4 shows the dependence of curve $\Phi^{II}(\alpha; t)$ versus α , on the inhomogeneity’s size dependence. The upper panel corresponds to $p = 0.1$, again the ‘skunk’ case, and for different inhomogeneity sizes: inhomogeneity in the intervals $[-1,1]$, $[-2,2]$, $[-4,4]$ and $[-9,9]$, while on the lower panel we have the case $p = 0.9$, that is the good olfactory skills case, for the same inhomogeneity sizes as before; in both cases for a $t_{\max} = 10$. For a fixed number of inhomogeneities, the advantage of switching back and forth to the relocation phase is larger in the repelling than in the attracting case; an explanation of this interesting behavior is given in the analysis of figure 5. It is worth remarking here that the minimum in the survival probability disappears for large inhomogeneities and the importance of the initial condition for this problem.

In figure 5, we depict the optimal value of α as a function of the olfactory skill p for different inhomogeneity sizes and for an evolution time $t = 20$. All predators started their searches from the same initial site ($s_0 = 5$). Even though all curves present a monotonous behavior, it is apparent that the inhomogeneity size plays an important role. For low p (that

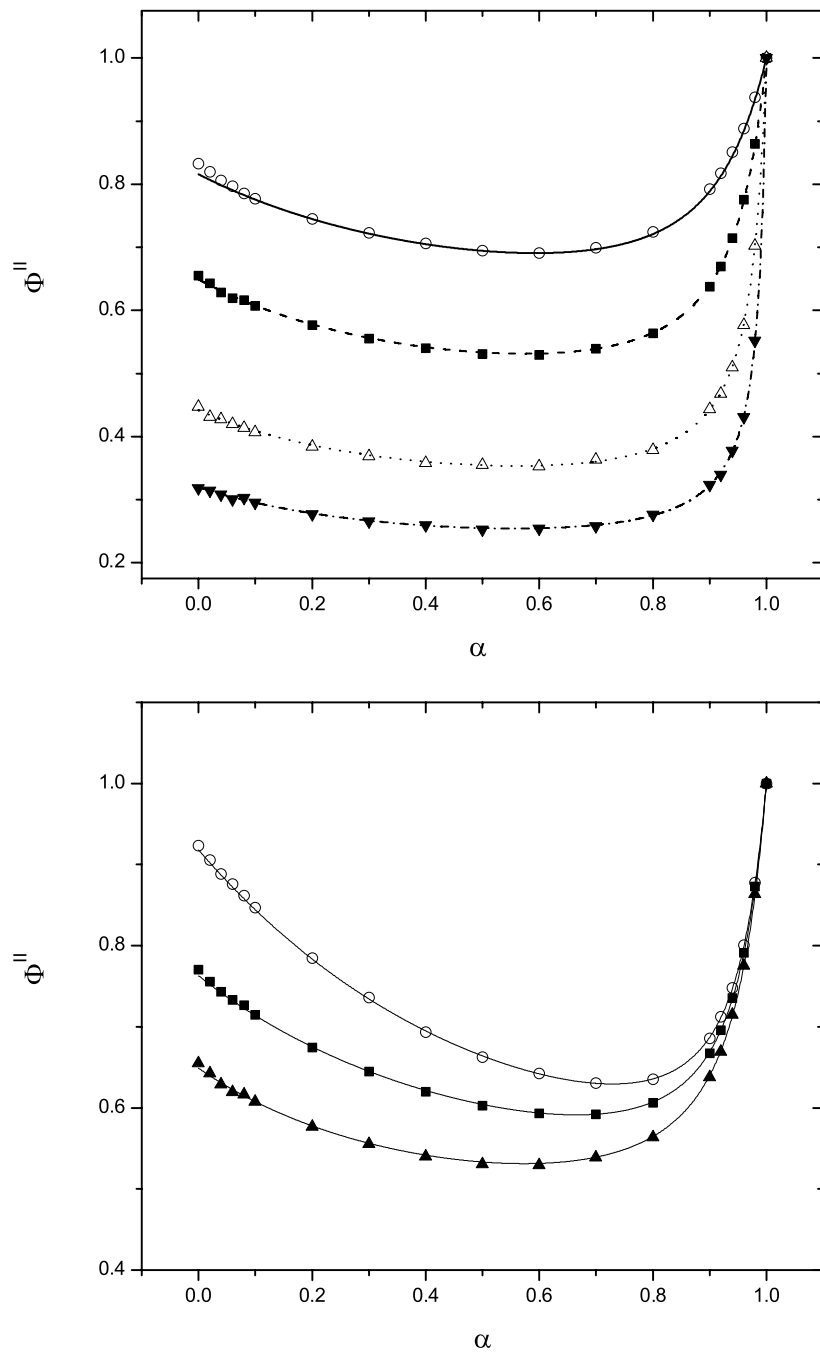


Figure 3. Survival probability curves $\Phi^{II}(\alpha; t)$ versus α . On the upper panel for different times (\circ for $t = 10$; \blacksquare for $t = 20$, \triangle for $t = 50$, and \blacktriangledown for $t = 100$) and for a ‘detection (olfactory) skills’ $p = 0.9$. On the lower panel, we have the case of a fixed time ($t = 20$), and different ‘detection (olfactory) skills’: \circ for $p = 0.1$; \blacksquare for $p = 0.4$, and \blacktriangledown for $p = 0.9$. In both panels lines represent the numerical Laplace anti-transform curves and points represent the corresponding Monte Carlo simulations.

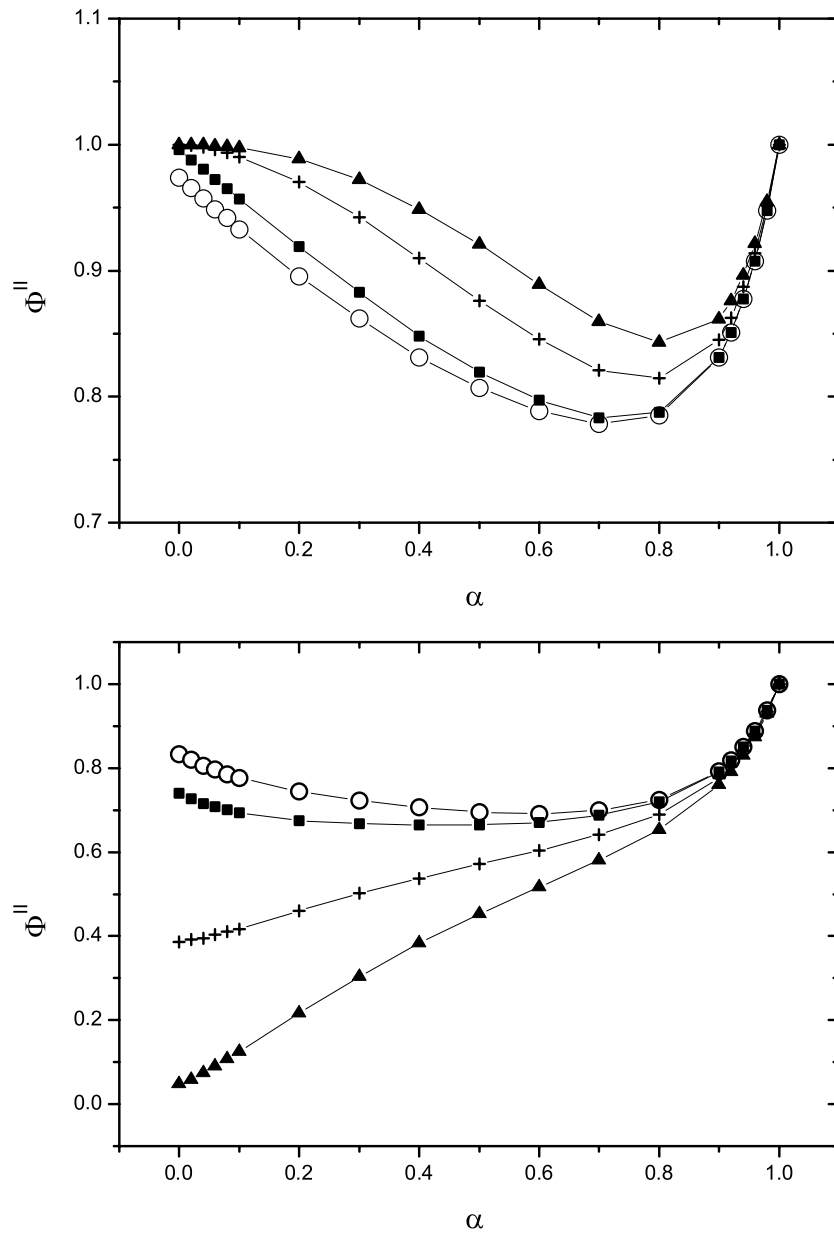


Figure 4. Inhomogeneity size dependence of the survival probability versus α . On top, the case of $p = 0.1$ for: \circ for the interval $[-1, 1]$, \blacksquare for $[-2, 2]$; crosses for $[-4, 4]$, and \blacktriangle for $[-9, 9]$. Below, the case $p = 0.9$ for the same sizes as before. All curves only correspond to Monte Carlo simulations.

is in the skunk region) as the inhomogeneity grows, the optimal α tends to be higher. It is an expected result because in order to capture the prey, predators have to avoid the repulsive skunk effect which is achieved moving essentially in the state 1. For high p , it is observed that when the inhomogeneity is small there still exists an optimal value of α , while for large inhomogeneity such an optimal value of α disappears.

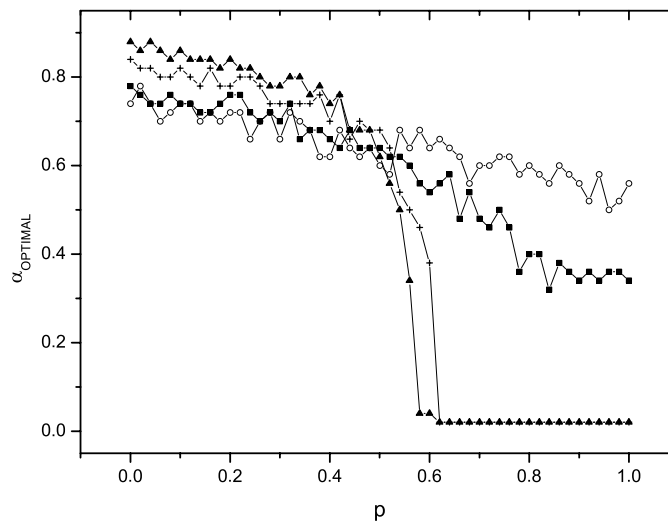


Figure 5. Inhomogeneity size dependence of optimal α versus the olfactory skill p , \circ for the interval $[-1, 1]$, \blacksquare for $[-2, 2]$; crosses for $[-4, 4]$, and \blacktriangle for $[-9, 9]$. All curves only correspond to Monte Carlo simulations.

5. Conclusions

We have presented a model for the searching dynamics of a hidden target performed by a searcher which carries out an intermittent motion, with a short range thorough search and a relocation phase. This model takes into account the traces/signals left by the prey. This was done by introducing field inhomogeneities that may be associated with the signals (trace) left by the prey in its surroundings. The intermittency has been characterized by the probability density functions for jumps between the different states of motion. For simplicity, we have restricted our analysis of intermittency to first-order transitions with parameters γ_1 and γ_2 . In order to perform our study, we exploited the theory of *multi-state* random walk (RW) in the high transition rate regime as well as the local inhomogeneity technique and made the connection between the target's survival probability and the first passage time density of the searcher. We believe that the present scheme is both simple enough to be studied analytically and rich enough to be able to mimic the influence of the 'smell' in the capture process.

In complete agreement with intuition, the results clearly indicate that the prey's survival probability could be strongly reduced (increased) if the predator is attracted (or repelled) by the positive (negative) trace left by it. We have also found that, for a positive trace, increasing the inhomogeneity's size reduces the prey's survival probability, while the optimal value of α ceases to exist. The agreement between theory and numerical simulations is excellent. It is important to remark that this model is a first attempt to describe the smelling phenomenon. We will consider more sophisticated smelling models in future works.

The present model not only takes into account the predator's ability to move in the foraging space, but also the possible attractive or repulsive (trying to avoid trapping) traces left by the prey. In this way, we have made a step forward in the complexity of a searching process by including in its description, both theoretically and through simulations, different situations, for instance the ability of predators in searching the prey and the fact of the distortion left by the prey in its surroundings.

It is worth remarking here that we have considered a ‘short-range’ inhomogeneity because of the simplicity of analytically solving the problem. The present model of intermittent search can be straightforwardly generalized to higher dimensions, finite size domain systems, continuous systems, *imperfect* detection, *dynamical* behavior of the target, non-Markovian transitions between internal states, etc. It is worth indicating here a recent paper [16] that describes an alternative form of finding odor plumes in turbulent environments. The possibility of including such a strategy within our scheme, as well as the analysis of all the above indicated aspects, will be the subject of further work.

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