Optimal Intermittent Search Strategies: Smelling a Prey

J. Revelli,¹ F. Rojo,^{2,*} C. E. Budde,² and H. S. Wio¹

¹Instituto de Física de Cantabria, Universidad de Cantabria and CSIC

E-39005 Santander, Spain

²Fa.M.A.F., Universidad Nacional de Córdoba,

Ciudad Universitaria, X5000HUA Córdoba, Argentina

Abstract

We study the kinetics of search of a single fixed target by a large number of searchers performing an intermittent random-walk, jumping between different internal states. Walkers have the ability to detect the scent left by a prey on the environment.

PACS numbers: 05.45.-a, 05.40.Ca, 82.40.Ck

*Fellow of Consejo Nacional de Investigaciones Científicas y Técnicas

I. INTRODUCTION

The study of different forms to obtain optimal strategies for the search of specific targets has recently experienced a rapid growth and motivated a great deal of work. Among other aspects, the determination of an efficient search strategy emerged as a crucial problem in behavioral ecology, inspiring numerous experimental and theoretical works (**REF**). It is also relevant to broader domains such as stochastic processes theory, applied mathematics and molecular biology as well as in social sciences and ecology [1–6].

It has been observed that numerous animal species (**REF**) switch between two distinct type of behavior (and motion) while foraging. In fact, many foragers like planktivorous fish [?], ground foraging birds and lizards (**REF**), adopt an intermittent searching behavior. 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 target detection. In its simplest form one assumes that the search is made at random (i.e. without taking into account the possible signals from the prey) but in general mobile predators often search for prey using chemical cues, particularly where visual or mechanical stimuli are obscured or unavailable. The perception of chemical cues acts to bias locomotion upcurrent, and feedback from odorant stimulus distributions appears directly to regulate subsequent stopping and turning en route to prey [PreyOdor2]. Despite its importance, how olfactory-guided search strategies operate over distance has not been rigorously studied, yet these behaviors stand as some of the most remarkable navigational feats of nature (Nevitt, 1999b-PreyOdor3).

In previous works [NOS, NOS BIAS] we have presented a theoretical model for the search kinetics of a hidden target. In that model we considered searchers that performed an intermittent search strategy with several types of foraging motion. In particular we had assumed that the searcher had “some general clue” (i.e. a preferred direction of motion, which not necessarily pointed to the prey) that depends on its internal state. We had translated that foraging behavior into our model as a biased walk.

In this work we make a step more towards the considerations of prey signals taking into account the introduction of inhomogeneities in the field that may be associated with the “smell” that the prey produces on its surroundings.

We set up our scheme exploiting the *multi-state* random-walk (RW) as well as the Local

inhomogeneity technique developed by Montroll [Montroll, Hughes, Tesis Budde]

The outline of this paper is as follows. The next section presents a brief review of the multi-state RW [? ?] and defines the functions to be used latter. In Section III we describe our model, focusing on the one dimensional analytical solvable case and made the connection with Monte Carlo simulations. In the Section IV we present some results for the survival probability and related functions, while in the last Section we draw some conclusions.

II. THEORY

A. Brief Review

We start the section briefly introducing the basic definitions and equations.

We assume that at time t each walker can be at site s on a lattice, in one of 2 internal states. We follow the walker evolution through the system considering the conditional probability $\mathbf{P}_{i,i_0}(s, t|s_0, t=0)$ corresponding to the walker be at site s with internal state i at time t given that it was at site s_0 with internal state i_0 at $t=0$.

The coupled master equations that describe the composite process proposed are [Nos]:

$$\frac{\partial P_{1,i_0}(s, t|s_0, 0)}{\partial t} = \mathbb{A}_1 P_{1,i_0}(s, t|s_0, 0) + \gamma_2 P_{2,s_0}(s, t|s_0, 0) - \gamma_1 P_{1,i_0}(s, t|s_0, 0) \quad (1)$$

$$\frac{\partial P_{2,i_0}(s, t|s_0, 0)}{\partial t} = \mathbb{A}_2 P_{2,i_0}(s, t|s_0, 0) + \gamma_1 P_{1,s_0}(s, t|s_0, 0) - \gamma_2 P_{2,i_0}(s, t|s_0, 0) \quad (2)$$

Where the γ_i 's are the transition rates between internal states and the $\mathbb{A}_i$'s are the operators that describe the evolution/propagation of the walker within each state. We remark here that while the walker is switching his internal state no spatial displacement occurs.

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

$$\hat{\mathbf{P}}_{i,i_0}(s, u|s_0, 0) = \int_0^\infty e^{-ut} \mathbf{P}_{i,i_0}(s, t|s_0, 0) dt$$

B. The Trapping process

The quantity of our interest is the Survival Probability of the target/prey, which ends when the walker reaches the target for the first time, i.e., the trapping is assumed to be “per-

fect". A closely related quantity to the Survival probability (in the case of perfect trapping) is the first-passage time density of the walker.

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 First Passage time density through the site $\vec{0}$ at time t given that it was at s_0 with internal state i_0 at time $t = 0$ when adsorption/capture is possible while the walker is **only** on *internal state* 1 (2). Following Spouge, Szabo and Weiss [PRE96] we introduce the notion of *generalized state* which takes into account the position and the internal state of the walker, (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 $\mathbf{P}_{i,i_0}(s, t|s_0, t = 0)$ is established as:

$$F_{1,i_0}^I(\vec{0}, u|\vec{s}_0, 0) = \frac{P_{1,i_0}(\vec{0}, u|\vec{s}_0, 0)}{P_{1,1}(\vec{0}, u|\vec{0}, 0)} \quad (3)$$

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

$$F_{2,i_0}^I(0, u|s_0, 0) = \frac{P_{2,i_0}(\vec{0}, u|\vec{s}_0, 0)}{P_{2,2}(\vec{0}, u|\vec{0}, 0)} \quad (4)$$

In this way we reobtain the Siegert formula [REF 141], generalized to internal states [ROERDINK and SHULER].

When capture/adsorption may be in **any** of the two internal state 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 First Passage time density through the site $\vec{0}$ at time t given that it was at s_0 with internal state i_0 at time $t = 0$ when adsorption/capture occurs on *internal state* 1 (2). An interesting relationship between F^I and F^{II} could be established by noting that:

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

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

They may be expressed in Laplace space as:

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

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

A similar expression (although in a different context) was established by Darling and Siegert in [PAPER 53]

The connection between the survival probability and the F^I and F^{II} is set as:

$$\Phi_{1,i_0}^I(0, t|s_0, 0) = 1 - \int_0^t F_{1,i_0}^I(0, \tau|s_0, 0) d\tau \quad (9)$$

$$\Phi_{2,i_0}^I(0, t|s_0, 0) = 1 - \int_0^t F_{2,i_0}^I(0, \tau|s_0, 0) d\tau \quad (10)$$

When trapping occurs in **any** of the two states the corresponding Survival probability is (if $s_0 \neq 0$):

$$\Phi_{i_0}^{II}(0, t|s_0, 0) = 1 - \int_0^t [F_{1,i_0}^{II}(0, \tau|s_0, 0) + F_{2,i_0}^{II}(0, \tau|s_0, 0)] d\tau \quad (11)$$

Replacing in equations (7) and (8) the expressions for F_{1,i_0}^I y F_{2,i_0}^I , Eq. (3) and (4) we obtain:

$$F_{1,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0)P_{1,1}(\vec{0}, u|\vec{0}, 0) + F_{2,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0)P_{1,2}(\vec{0}, u|\vec{0}, 0) = P_{1,i_0}(\vec{0}, u|\vec{s}_0, 0) \quad (12)$$

$$F_{2,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0)P_{2,2}(\vec{0}, u|\vec{0}, 0) + F_{1,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0)P_{2,1}(\vec{0}, u|\vec{0}, 0) = P_{2,i_0}(\vec{0}, u|\vec{s}_0, 0) \quad (13)$$

Adding this pair of equations we obtain:

$$F_{1,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0)P_{Mar,1}(\vec{0}, u|\vec{0}, 0) + F_{2,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0)P_{Mar,2}(\vec{0}, u|\vec{0}, 0) = P_{Mar,i_0}(\vec{0}, u|\vec{s}_0, 0) \quad (14)$$

Where $\mathbf{P}_{Mar,i_0}(s, t|s_0, 0)$ is the *marginal* probability distribution i.e.

$$\mathbf{P}_{Mar,i_0}(s, t|s_0, 0) = \mathbf{P}_{1,i_0}(s, t|s_0, 0) + \mathbf{P}_{2,i_0}(s, t|s_0, 0) \quad (15)$$

C. Long time and High Transition Limit

Following Van Kampen [PONER CITA] and using Eq.(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:

$$\frac{\partial \mathbf{P}_{Mar}(s, t|s_0, 0)}{\partial t} = \tilde{\mathbb{A}} \mathbf{P}_{Mar}(s, t|s_0, 0) \quad (16)$$

Where $\tilde{\mathbb{A}} = \alpha\mathbb{A}_1 + (1-\alpha)\mathbb{A}_2$ with $\alpha = \frac{\gamma_1}{\gamma_1 + \gamma_2}$ and $\mathbf{P}_{Mar}(s, t|s_0, 0)$ is the *marginal* probability distribution in the stationary case, i.e.

$$\mathbf{P}_{Mar}(s, t|s_0, 0) = \mathbf{P}_{1,i_0}(s, t|s_0, 0) + \mathbf{P}_{2,i_0}(s, t|s_0, 0) \quad (17)$$

It is important to note that in the limit considered the initial conditions on the internal state disappear. Taking into account this fact and Eq.(14):

$$F_{1,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0) + F_{2,i_0}^{II}(\vec{0}, u|\vec{s}_0, 0) = \frac{\mathbf{P}_{Mar}(\vec{0}, u|\vec{s}_0, 0)}{\mathbf{P}_{Mar}(\vec{0}, u|\vec{0}, 0)} \quad (18)$$

III. THE MODEL: “SMELLING A PREY”

As in [NOS] we restrict ourselves to work on a infinite discrete chain, and assume that the fixed target/prey is located at the origin of the lattice. We suppose that near the origin (where the prey is located) remains, a smell left by the target/prey which may increase the detection by the searcher or may sidetrack it.

At $t = 0$, a searcher/predator originally at s_0 on the chain, starts the “search”. When he finds the target/prey, catches it with probability one, i.e., perfect trapping. Moreover near the origin (where the prey is located), the prey/target has left a trace/odor/smell which increases the detection by a predator or sidetracks the searcher, depending if it is a positive/negative trace. As before the predator can make two types of motion on the lattice. The $\mathbb{A}_i$ ’s operators that describe the evolution/propagation of the walker within each state are (in the case of two symmetrically inhomogeneities):

$$[\mathbb{A}_1]_{s,s'} = \frac{\lambda}{2}[\delta_{s,s'-2} + \delta_{s,s'+2} - 2\delta_{s,s'}] \quad \forall \quad s, s' \quad (19)$$

$$[\mathbb{A}_2]_{s,s'} = \frac{\lambda}{2}[\delta_{s,s'-1} + \delta_{s,s'+1} - 2\delta_{s,s'}] \quad \forall \quad s' \neq -1, 1 \quad (20)$$

and

$$[\mathbb{A}_2]_{1,0} = [\mathbb{A}_1]_{-1,0} = [\mathbb{A}_1]_{1,2} = [\mathbb{A}_1]_{-1,-2} = \frac{\lambda}{2} \quad (21)$$

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

$$[\mathbb{A}_2]_{0,1} = [\mathbb{A}_2]_{0,-1} = p\lambda \quad (23)$$

FIG. 1:

In the High transition and long time limit the scheme turns into:

FIG. 2:

The optimization problem (independently of the type of foraging motion considered above) is to find the values of γ_j such that the prey's *survival probability* at a time t be *minimal*.

In what follows, we will scale the γ_j in terms of λ , the transition rate between the sites on the chain.

We analyze the behavior of the system in the *high transition rate between internal states* regime (that can be studied almost analytically).

IV. RESULTS

In this section we show the results obtained...

Graficas a poner

Inhomogeneity

Capture in any state

different times

FIG. 3:

different transition probabilities to the trap

FIG. 4:

Capture in only one state

Effect of inhomogeneity size

V. CONCLUSIONS

We have presented a simple model for the search kinetics of a hidden target located at the origin of a chain, by a set of searchers performing intermittent motion. (COMPLETAR)

FIG. 5:

FIG. 6:

Acknowledgments

The authors wish to acknowledge supports by CONICET and SECYT-UNC, Argentina.

-
- [1] Oshanin G., Wio H.S. ,Lindenberg K. and Burlatsky S.F., J.Phys. Cond. Mat. **19**, 065142 (2007).
 - [2] Rojo F., Budde C. E. , Wio H. S., J. Phys. A: Math. Theor. **42**, 125002 (2009)
 - [3] Reynolds A., Europhys. Lett., **75** (4), pp. 517520 (2006)
 - [4] Benichou O. et al, Phys. Rev. Lett.**94**, 198101 (2005); J. Phys.: Condens. Matter **19**, 065141 (2007).
 - [5] Bartumeus F. et al, Ecology, **86** (11), pp. 3078-3087 (2005)
 - [6] Raposo E. et al. , Phys. Rev. Lett. **91**, 240601 (2003)
 - [7] Bartumeus F. et al , Phys. Rev. Lett. **88** 097901; Phys. Rev.Lett. **89** 109902,(2002)

- [8] Viswanathan G. et al, Nature 401 911 (1999)
- [9] OBrien W J, Browman H I and Evans B I Am. Sci. **78** pp.152-160 (1990)
- [10] Kramer D, Mclaughlin R, Amer. Zool., **41** pp. 137153 (2001)
- [11] McAdam A, Kramer D, Anim. Behav., **55**, pp. 109117 (1998)
- [12] A.K. Harrison and R. Zwanzig, Phys. Rev. A, **32**,1072 (1985),
- [13] A. Nitzan and M.A. Ratner, J. Phys. Chem.,**98**,1765 (1994),
- [14] H.L. Friedman and A. Ben-Naim, J. Chem. Phys.,**48**, 120 (1968),
- [15] J.L. Spouge, A. Szabo and G.H. Weis, Phys. Rev.E,**54**, 2248 (1996).
- [16] M.A. Re, C.E. Budde and M.O. Caceres, Phys. Rev. E,**54**, 4427 (1996).
- [17] Weiss G H, *Aspects and Applications of the Random Walk*, in *Random Materials and Processes*, H.E. Stanley and E. Guyon, Eds. (North Holland, 1994) .
- [18] Montroll, E. y West, B.: *On an Enriched Collection of Stochastic Processes, in Fluctuation Phenomena* , Montroll E, Lebowitz J, eds. North-Holland (1979).
- [19] Shlesinger M , Nature **443** pp.281-282 (2006)
- [20] Blumen A, Klafter J, and Zumofen G, in Optical Spectroscopy of Glasses, edited by I . Zschokke (Reidel, New and Berkeley Symposium (University of California Press, York, 1986), pp. 199-265.
- [21] Haus J., Kehr K, Phys. Rep, **150**, 195 (1987).
- [22] Condat C A, Phys. Rev. A **41**, 3365 (1990).
- [23] Kryzhniy V.V. “On regularization of numerical inversion of Laplace transforms” , J. Inv. Ill-Posed probl. , **12**, No.3,279 (2004)
- [24] A. J. F. Siegert, Phys. Rev. **81**, 617 (1951).