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Persistent search in single and multiple confined domains: a velocity-jump process model

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Abstract. We analyze velocity-jump process models of persistent search for a single target on a bounded domain. The searcher proceeds along ballistic trajectories and is absorbed upon collision with the target boundary. When reaching the domain boundary, the searcher chooses a random direction for its new trajectory. For circular domains and targets, we can approximate the mean first passage time (MFPT) using a Markov chain approximation of the search process. Our analysis and numerical simulations reveal that the time to find the target decreases for targets closer to the domain boundary. When there is a small probability of direction-switching within the domain, we find the time to find the target decreases slightly with the turning probability. We also extend our exit time analysis to the case of partitioned domains, where there is a single target within one of multiple disjoint subdomains. Given an average time of transition between domains T , we find that the optimal rate of transition that minimizes the time to find the target obeys $\min 1/\sqrt{T}$.

Keywords: computational biology, dynamics (theory), self-propelled particles

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1. Introduction

Organisms frequently search to find targets whose position is unknown to them. For example, animals search for food or mates in ways that balance both speed and low energy expenditure [1–3]. In addition, the dynamics of biomolecules can be modeled as a search process. Recently, experiments and modeling studies have identified biochemical processes whose kinetics involve the search for a reaction partner, due to the small number of reactive molecules [4–6]. Regardless of the context of searches, it is often desirable to minimize the amount of time needed to find the target, and this is the most common measure of search efficiency [7].

There are two particularly well studied models of random search processes: passive diffusion and intermittent search. Passive diffusion to a small target in a confined domain is a common model of molecular transport at the biomolecular scale [8, 9]. A distinct advantage of this framework is that the average time to find the target can be formulated as the solution to a mean first passage time (MFPT) problem [10–12]. However, this model is not appropriate in all situations. In particular, foraging organisms and biomolecules that move ballistically often employ an intermittent search strategy, wherein diffusive search periods are punctuated by rapid displacement phases during which no search occurs [13]. Such intermittent strategies can be optimized to obtain a minimal MFPT by balancing time spent in the moving and searching phases [14].

In contrast to such previous work, one could also consider strategies wherein search is persistent and ballistic. The searcher then proceeds according to a velocity-jump

process, moving ballistically and then switching direction at random times 15, 16 . The diffusion limits of velocity-jump processes are described by linear transport systems, specific cases of the Boltzmann equation 17, 18 . Recently, this model has been used to analyze the statistics of foraging insect movement 19, 20 . Presuming an animal can detect targets while moving ballistically 21 , search and travel can be modeled as a single process. One well studied experimental paradigm wherein an animal searches persistently is the Morris water navigation task, in which a rodent must locate a platform in a circular pool 22 . Visual search in psychophysics tasks is another example of persistent search, where the focal point of gaze moves ballistically in search of a visual target 23, 24 . Thus, concrete quantitative models are needed to understand the dynamics of persistent search and identify optimal strategies.

We analyze an idealized model of persistent search, which considers movements of the searcher to be ballistic trajectories with constant speed. For simplicity, we consider two-dimensional circular domains with reflecting boundaries along with circular targets with absorbing boundaries. Initially, we develop an asymptotic theory for approximating the time to find the target when the searcher only turns when encountering the domain boundary. This allows us to understand how the placement of the target impacts the average time to locate it. We extend our analysis to the case where the searcher turns on the domain interior with finite probability, showing this decreases the MFPT for low-probability of turning. Lastly, we introduce a model of persistent search on multiple disjoint domains. When the transit time between subdomains is nonzero, there is an optimal rate of transition between domains that balances domain coverage with the time penalty for traveling between domains. In all cases, we identify how search and domain parameters impact the MFPT.

2. Velocity-jump process model of persistent search

Consider the following model for the stochastically evolving position (x, y) of a persistent searcher. We construct a model of a particle searching for a hidden target in a bounded, circular domain of radius R , i.e. $\mathbb{D} := \{(x, y) \in \mathbb{R}^2 : \sqrt{x^2 + y^2} \leq R\}$. The hidden target is also defined by a circular region with radius r :

$$\mathbb{T} := \{(x, y) \in \mathbb{D} : \sqrt{(x - x_0)^2 + (y - y_0)^2} \leq r\},$$

where (x_0, y_0) denotes the centroid of the target domain. Note, we will restrict $\sqrt{x_0^2 + y_0^2} \leq R - r$, so the entire target is contained in the domain \mathbb{D} . Furthermore, due to the rotation symmetry of the circular domain, we exclusively consider targets with coordinates along the right horizontal radius, $(x_0, y_0) = (\epsilon R, 0)$. All other cases can be reduced to this form by an axial rotation.

The searcher's position evolves according to a velocity-jump process 15 . On the interior of the domain \mathbb{D} , the searcher moves ballistically with velocity v

that as

Persistent search in single and multiple confined domains: a velocity-jump process model along straight trajectories, unless it encounters the target domain Γ . For a trajectory from the domain location \mathbf{x} to \mathbf{y} , there is probability $a(\mathbf{x}, \mathbf{y})$

Note, we have assumed $r \ll R$ small, and this equation is exact in the limit $r \rightarrow 0$. To exactly compute the MFPT for any value of r , we could marginalize over all path lengths from a point on the boundary of the domain to the boundary of the tar-

$$\mathcal{T}_c = \frac{4R \sin(\theta/2)}{2 \sin^{-1}(r/R) - 1} + R, \quad (5)$$

which matches well with numerical simulations of the velocity-jump process (figure 2(B)). For a smaller search arclength θ , the MFPT decreases, since there is a higher probability of heading toward the target τ_T from the boundary.

We also demonstrate that equation (5) is monotone in each parameter by tak-

Applying equation (3) for the MFPT, we have

$$\mathcal{T}_c = \frac{R}{2} \left(\frac{R}{r} - 1 \right) + R. \quad (6)$$

As before, equation (6) is monotone decreasing in r since $\frac{\partial \mathcal{T}_c}{\partial r} = -\frac{R^2}{2r^2}$, whereas it is increasing in R since $\frac{\partial \mathcal{T}_c}{\partial R} = \frac{R}{r} + 1 - \frac{1}{2}$.

For infinitesimal timesteps dt , the probability of a velocity-direction change between t and $t + dt$ is νdt . Velocity changes are sampled from a uniform distribution so that the probability of selecting a new velocity with angle $\theta \in [0, 2\pi)$ is $\Pr(\theta) = \frac{1}{2\pi}$. For an unbounded domain ($R \rightarrow \infty$), this would lead to trajectories made of ballistic step-lengths x over the distribution $p(x) = \nu e^{-\nu x}$ for normalized velocity $v = 1$.

For low turning probability $\nu \ll 1$, we asymptotically approximate the hitting probability for a single path between boundary points a and b . Such paths are no longer necessarily comprised of a single straight segment; paths can be made up of two or more straight segments. However, we only focus on the change in hitting probability arising due to incorporating paths made of two straight segments. To begin, note the probability of not turning (number of turns $n = 0$) along a segment of length l is given

$$\Pr(n = 0|l) = 1 - \int_0^l \nu e^{-\nu x} dx = e^{-\nu l}, \tag{10}$$

so a searcher heading towards the target will not turn with approximate probability $e^{-\nu(R-r)}$. Thus, the likelihood that the searcher is absorbed into the target by following a single segment from the boundary is

$$\Pr(\text{hit}|n = 0)\Pr(n = 0|R - r) = e^{-\nu(R-r)} \frac{2 \sin^{-1}(r/R)}{\pi}, \tag{11}$$

where we assume $f(z) = \text{uni}$

where $\theta = \sin^{-1}(r/R)$ and the total normalization is given by integrating over the probability density e^{-x} : $\mathcal{N} = \left(\int_0^{R/2} 2 \cos \theta e^{-x} dx + \int_0^{R-r} e^{-x} dx \right)$. Note that the angle of trajectories that will hit the target is larger for turns that occur closer to the target (figure 4(A)). This may account for the slight increase in hitting probability due to turning (figure 4(C)).

Therefore, the total likelihood of hitting the target along a single path between boundary points can be linearly approximated by (a) subtracting the probability due to turning away from the target given by equations (10) and (11) and (b) adding the probability due to turning towards the target as computed in equations (12) and (13):

$$a(\theta) = e^{-(R-r)} \frac{2 \sin^{-1}(r/R)}{\mathcal{N}} + (1 - e^{-\bar{c}\theta}) \mathcal{H}(r, R). \tag{14}$$

This provides a new estimate for the probability of hitting in a single path, which we plot in figure 4(C).

Furthermore, we can compute the average length of a single path between boundary points. This will no longer be given by the average chord length $\bar{c}\theta$. Rather, our approximation will average in the paths consisting of two segments. Utilizing the probabilities of turning and not turning computed in equation (10) and (12), we can then appropriately weight the average lengths of one and two segment paths. First, note that paths with no turns will have a new average length given by

$$l_0 = \frac{1}{\mathcal{N}_0} \int_0^{R/2} (2 \cos \theta) e^{-2 \cos \theta} d \tag{15}$$

with normalization constant $\mathcal{N}_0 = \int_0^{R/2} e^{-2 \cos \theta} d$. Paths with a single turn will have length specified by their initial search angle θ , first segment length x , and new angle θ' following a turn. Given paths that start at $(x, y) = (R, 0)$, the turning point will be $(x_0, y_0) = (R - x \cos \theta, x \sin \theta)$ and the new intersection point with the boundary will be

$$(x_c, y_c) = \left(\sin \theta (R \sin \theta' - x \sin \theta) \cos \sqrt{R^2 - (x \sin \theta - R \sin \theta')^2}, \right. \\ \left. \cos \theta (x \sin \theta' - R \sin \theta) \sin \sqrt{R^2 - (x \sin \theta - R \sin \theta')^2} \right).$$



Figure 4. MFPT decreases as the searcher turns in the domain ($\alpha > 0$). (A) To approximate the hitting probability $l(\alpha)$ over a single path, we account for the new probability of hitting after turning $a(\alpha)$. (B) MFPT $\mathcal{T}_c(\alpha)$ as a function of α , as demonstrated both by the analytical solution (14) and numerical simulations (circles).

$$l(\alpha) = e^{-\bar{c}h} l_0 + (1 - e^{-\bar{c}h}) l_1, \tag{17}$$

shown in figure 4(D).

Incorporating equations (14) and (17) into equation (3), the formula for the MFPT, we can account for the effects of interior turning:

$$\mathcal{T}_c(\alpha) = l(\alpha) \left(\frac{1}{a(\alpha)} - 1 \right) + R. \tag{18}$$

The main contribution to the reduction of the MFPT is due to a slight increase in the hitting probability $a(\alpha)$ as shown in figure 4(C). However, increasing turning α does not significantly impact the time to find the target (figure 4(B)). Even for larger values of α , the MFPT remains relatively unchanged as opposed to the case $\alpha = 0$.

4.2. Spiral searches

We now turn our attention to an alternate strategy for locating a hidden target—spiral searches. Both insects and mammals may utilize spiral patterned trajectories as search

paths to locate a target [25](#), [26](#) . This can be more efficient and even optimal, since it can reduce the time spent in previously visited patches of the environment [27](#) . However, spiral search may lead to unnecessarily long times needed to find the target if the spacing between rotations is too large or too small [28](#) .

We consider search trajectories described by an Archimedean spiral $(r) = \frac{b}{2}$ within the circular domain

we aim to identify the optimal strategy for searching the disconnected domain for the single target, especially as it relates to the domain-switching rate λ .

We now compute the MFPT to find the target of radius r in a multiple subdomain environment

Figure 6. Domain with $N = 3$ disconnected subdomains with a single target in subdomain 3

$$\begin{aligned} \mathcal{T}_t &= \sum_{j=0}^{\infty} (1-a)^j [j\mathcal{T}_{na} + j\mathcal{T}_{tl} + \mathcal{T}_{tf}] = \frac{1-a}{a} [\mathcal{T}_{na} + \mathcal{T}_{tl}] + \mathcal{T}_{tf} \\ &= \frac{(1-a)}{a} \left[\frac{(N-1)\bar{c}h}{a + (1-a)} + \frac{\bar{c}h}{a + (1-a)} \right] + \frac{\bar{c}h(1-a)(1-a)}{a + (1-a)} + R - r \\ &= N\bar{c}h \left(\frac{1}{a} - 1 \right) + R - r. \end{aligned}$$

When the searcher begins in a non-target subdomain, the time to find the target is

$$\begin{aligned} \mathcal{T}_o &= \sum_{j=0}^{\infty} (1-a)^j [(j+1)\mathcal{T}_{na} + j\mathcal{T}_{tl} + \mathcal{T}_{tf}] = \frac{1-a}{a} [\mathcal{T}_{na} + \mathcal{T}_{tl}] + \mathcal{T}_{na} + \mathcal{T}_{tf} \\ &= \frac{(1-a)}{a} \left[\frac{(N-1)\bar{c}h}{a + (1-a)} + \frac{\bar{c}h}{a + (1-a)} \right] + \frac{(N-1)\bar{c}h}{a + (1-a)} + \frac{\bar{c}h(1-a)(1-a)}{a + (1-a)} + R - r \\ &= N\bar{c}h \left(\frac{1}{a} - 1 \right) + \frac{(N-1)\bar{c}h}{a + (1-a)} + R - r. \end{aligned}$$

If initial conditions are uniformly distributed across subdomains, the probability of starting in the target subdomain is $1/N$, so the generalized MFPT is

$$\mathcal{T}_c = \frac{1}{N}\mathcal{T}_t + \frac{N-1}{N}\mathcal{T}_o = N\bar{c}h \left[\left(\frac{1}{a} - 1 \right) + \frac{(N-1)^2}{N^2} \right] + R - r. \quad (26)$$

In the case of instantaneous transits between subdomains $T = 0$, the best strategy is to transition at every boundary encounter, $\alpha = 1$

To identify the optimal switching rate $a = a_{\min}$ that minimizes the MFPT $\mathcal{T}_c(a)$, we differentiate

$$\frac{d\mathcal{T}_c(a)}{da} = N T \left(\frac{1}{a} - 1 \right) - \frac{\overline{ch}(N-1)^2}{N^2},$$

and note $\mathcal{T}_c(a) = 2\overline{ch}(N-1)^2/(N^3) > 0$ for $a > 0$. Thus, any critical points occurring when $a > 0$ are minima. To identify the minimum, we set $\mathcal{T}_c'(a_{\min}) = 0$ and solve for

$$a_{\min} = \frac{N-1}{N} \sqrt{\frac{\overline{ch} a}{T(1-a)}}. \tag{28}$$

Thus, the optimal switching rate a_{\min} is inversely proportional to \sqrt{T} , so the switching rate should decrease as the transit time increases (figure 7(A)). This allows for a more thorough search of a single subdomain before transitioning. Interestingly, equation (28) is roughly constant in the variable N as it is increased (figure 7(B)). Thus, for a very large number of sub domains $N \gg 1$, the parameters that determine the best switching rate are the chord length \overline{ch} , probability of hitting the target a , and the transition time T .

6. Discussion

We have studied a velocity-jump process model of persistent search in bounded domains. Initially, we considered a searcher that only turned on the boundary of a single connected domain. Paths of the searcher are partitioned into segments that link points on the boundary. To derive the average MFPT to find the target, we approximated the average probability of hitting the target in a single segment a . Pairing this with our approximation of an average segment-length \overline{ch} , we then marginalized over all possible search path lengths. Importantly, we modeled the search process as memoryless, so each search segment was assumed to have been drawn from the same distribution. Applying this to single domains, we found the time to find the target decreases for targets closer to the boundary. When searchers had a small probability of turning on the interior of the domain, the time to find the target decreases slightly, due to an increase in the hitting probability of a single segment. Lastly, in domains comprised of multiple disconnected subdomains, a key parameter in determining the optimal search strategy is the time it takes the searcher to move between subdomains. Ultimately, we found the searcher should move between domains less often when subdomain transitions take longer.

Our study provides an idealized model of an organism's search for a target in a confined domain. This model could apply to animals foraging in a patchy environment [30](#) or looking for shelter in controlled experiments [31](#) as well as their natural habitat [28](#). Furthermore, the velocity-jump process can produce long spatial correlations [15, 16](#), similar to those often observed in statistical analyses of organismal motion [32, 33](#). Our analysis revealed that low-probability ($\ll 1$) turning on the interior of

