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Original Research Article

First capture success in two dimensions: The search for prey by a random walk predator in a comprehensive space of random walks

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ABSTRACT

Random walk models are an important tool used for understanding how complex organisms redistribute themselves through space and time in search of targets such as food, shelter, or mates. These walks are easily studied with agent-based models, which can be used to ask which search strategy is best according to some efficiency metric. Current studies however, generally do not consider the full range of potential random walks, success metrics, and constraints on the walker, and implementation details vary widely. It is therefore difficult to compare results across studies. In this paper, we investigate predator search behaviour in a comprehensive space of key movement variables that allows the predator to select from a continuum of random walks ranging from Brownian walks (BWs) to correlated random walks (CorRWs) which include directional persistence, to composite random walks (ComRWs) which feature intensive and extensive search modes (ISMs and ESMs), and finally to more complex correlated composite random walks (CCRWs). We specifically focus on the search behaviour of a predator between the initiation of a search for a prey item and the first successful acquisition of a prey target: we call this interval the “search-to-capture” event. We measure the predator’s success against three metrics of energetic cost: (1) the time elapsed, (2) the distance travelled, and (3) an equally weighted combination of time and distance. In addition, we explore the effect of three different constraints on the predator: (1) hunting success in the extensive search mode, (2) detection radius when in the extensive search mode, and (3) prey density. Our work confirms the broadly held notion that CCRW movement patterns should always outperform BWs, but find instructive cases where other walks are superior. We also show that, within the CCRW category, there is a wide range of possible walks and rank these according to measures of energetic cost. Our work also offers insights into the evolutionary pressures surrounding the “search-to-capture” event, and suggests that CCRW predators with low hunting success in one movement mode experience higher evolutionary pressures and are thus more likely to adopt a nearly optimal random walk. Our work highlights the need for comprehensive studies that examine several aspects of random walks simultaneously.

1. Introduction

Simulated random walks are an important tool used for understanding how complex organisms redistribute themselves through space and time in search of targets such as food, shelter, or mates (Railsback and Grimm, 2012; Sibly et al., 2013; Wajnberg et al., 2013). A random walk involves an agent (the walker) taking a sequence of spatial steps at discrete times. The rules that dictate the direction and size of each spatial step can be varied to create different types of random walks (Codling et al., 2008). The goal of many random walk studies is to determine the “optimal” random walk, that is, the one that minimises the energetic cost of searching (Pyke, 1984, 2014; Stephens et al., 2007; Reynolds, 2013). This energy expenditure depends crucially on the search context, which is a function of 3 main components: (1) the type of random walk or search strategy (the optimal decision rule), (2) the efficiency metric used to determine cost (the currency), and (3) extrinsic and intrinsic factors or constraints related to properties of the walker and its environment (Pyke, 1984).

Many studies have determined optimal random walks, but it is difficult to generalise across studies as each one considers a different range of search contexts, that is, a different subset of the 3 main components listed above. In order to address this issue, we develop a three-dimensional space of key movement variables that

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allows us to investigate the search efficiency of a walker whose movement pattern exists within a comprehensive space of random walks ranging from simple Brownian walks (BWs) to more complex correlated composite random walks (CCRWs). In addition, we focus on one aspect of foraging: the search process that begins when the predator initiates the search for a prey item, and ends when the predator successfully captures a prey item for the first time. This focus on the ‘‘search-to-capture’’ event is a little different from the traditional paradigms of both optimal foraging and first passage time. Optimal foraging generally involves multiple bouts of searching for prey; the efficiency of a particular search strategy can be given in terms of net energy cost or gain per unit time (Sibly et al., 2013; Sinervo, 1997). First passage time or ‘‘time-to-kill’’ (Knell and Codling, 2012; Travis and Palmer, 2005; McPhee et al., 2012), another common measure of foraging success, focusses on the time elapsed between the initiation of search and the first contact with prey rather than the first successful capture event.

Studies of random walks generally classify random walk movement patterns into one of several categories. We consider here four different random walks. The simplest of these is the Brownian walk (BW), in which the simulated organism moves with no directional preference. By adding directional persistence to the basic BW we obtain the correlated random walk (CorRW). If, instead, we extend the BW with a second movement mode (so that the movement rules are different for local and long-distance searching), we obtain the composite random walk (ComRW) (Owen-Smith et al., 2010). The most complex walk we consider is the correlated composite random walk (CCRW), a combination of the CorRW and ComRW in which the simulated organism exhibits both directional persistence as well intensive and extensive search modes (ISM and ESM, respectively). We do not explicitly consider Lévy walks (LWs), as the relevance of this paradigm is in question (Pyke, 2014; Reynolds, 2009) and CCRWs share many properties with LWs (Reynolds, 2013). We note here that ComRWs and CCRWs are often referred to as ‘‘intermittent random walks’’. Given an efficiency measure and any subset of random walks from the four categories above, the optimal walk from within that subset can be determined. Often, the random walk that is optimal falls in the ComRW or CCRW categories, though there is no clear winner across all studies, as foraging is a complex and multi-faceted process (Codling et al., 2008). Furthermore, comparison across studies is difficult since the details of the random walk implementation vary, most studies do not consider all of the random walk categories listed above, and both the constraints on the walker and the efficiency measures used to evaluate performance differ between studies.

The efficiency metrics we consider are (1) the time taken, (2) the distance travelled, and (3) a linear combination of time and distance. Other studies have considered the first and second metrics (Viswanathan et al., 1999; Bénichou et al., 2008), and the third has been indirectly considered by constraining the disperser's speed of movement (Nolting et al., 2015; Reynolds, 2006). For constraints we consider two intrinsic constraints, predation success and prey detection radius (both hunting handicaps), and one extrinsic constraint, the density of prey.

Comparisons of CCRWs to BWs, and ComRWs to BWs can be found in the literature (Viswanathan et al., 1999; Codling et al., 2008), but there is very little work comparing them all under a common umbrella of movement contexts (constraints and efficiency measures) of the breadth that we consider here (Matsumura et al., 2010; Galanthay and Flaxman, 2012). All four of the random walk categories listed above have been identified in movement data (Berg, 1983; Reynolds, 2012, 2014), though the task of determining which random walk is used by a given biological organism is nontrivial (Reynolds, 2012; Pyke, 2014; Turchin, 1998). Often the emergence of a particular movement pattern is assumed to be the result of evolutionary pressures, so that organisms tend to move according to a walk that is optimal (Stephens et al., 2007; Pyke, 1984), though this is not always the case (Reynolds, 2012; McNamara and Houston, 2009). We show that some insight into the selection pressures acting on the evolution of random walks can be discerned from examination of the relative efficiency of walks from across the full range of possible random walks.

In the following three sections, we present the random walk simulation model. In Section 2 we describe the random walk variables through which we define a continuum of random walks. In Section 3 we describe the movement constraint parameters that we include in the model, and in Section 4 we define the search efficiency metrics that we use to evaluate the random walks. The details of the simulation experiments are given in Section 5. We present our simulation results in Section 6, and close with a discussion of the implications of our work and future research directions in Section 7.

2. The computational movement model

In the following Sections 2.1–2.5, we develop the four movement models (BW, ComRW, CorRW, and CCRW). We begin with a description of our simulation algorithm for the Brownian walk (BW), and then develop the other three movement models. Finally, we show that the four movement models can be interpreted as one main model and three submodels.

2.1. The Brownian walk (BW)

The classical random walk is a Brownian walk (BW). During a BW, at each timestep the walker draws a step length l from an exponential distribution, $l \sim \exp(\lambda)$, and a movement direction θ from a uniform distribution, $\theta \sim U([-\pi, \pi])$. The result is a random walk with mean step length $1/\lambda$ and no directional preference.

2.2. The correlated random walk (CorRW)

Correlated random walks (CorRW), recently reviewed in Fagan and Calabrese (2014), have a long history in biological modelling. Similarly to the BW, a random walker pursuing a CorRW draws each step length from an exponential distribution. The direction between successive steps, however, is correlated, and so directional persistence is added to the BW.

Various movement angle distributions have been used in models with directional persistence. Popular distributions range from wrapped Normal distributions to von Mises distributions and wrapped Cauchy distributions (Codling et al., 2008). In our case, we choose a von Mises distribution with mean θ' and density parameter κ, where θ' is the direction of the last step. Mathematically, $\theta \sim \exp(\kappa \cos(\theta - \theta'))/(2\pi I_0(\kappa))$, where $I_0(\kappa)$ is the modified Bessel function of order 0. The parameter κ controls the shape of the von Mises distribution: if $\kappa \to 0$, the von Mises distribution converges towards a uniform distribution (no directional persistence), while if $\kappa \to \infty$, the distribution converges towards the Dirac-Delta function $\delta(\theta')$ (complete directional persistence). Hence κ can be interpreted as a measure of the degree of correlation between subsequent search steps.

2.3. The composite random walk (ComRW)

The composite random walk (ComRW) is created by combining two BWs with different mean step lengths. Each BW corresponds to a different search mode: small steps correspond to the intensive search mode (ISM) while large steps correspond to the extensive search mode (ESM). The walker switches between these two search modes. Our algorithm is consistent with the design of a ComRW