Original Research Article

Composite random search strategies based on non-directional sensory cues

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A B S T R A C T

Many foraging animals find food using composite random search strategies, which consist of intensive and extensive search modes. Models of composite search can generate predictions about how optimal foragers should behave in each search mode, and how they should determine when to switch between search modes. Most of these models assume that foragers use resource encounters to decide when to switch between search modes. Empirical observations indicate that a variety of organisms use non-directional sensory cues to identify areas that warrant intensive search. These cues are not precise enough to allow a forager to directly orient itself to a resource, but can be used as a criterion to determine the appropriate search mode. As a potential example, a forager might use olfactory information as a non-directional cue. Even if scent is too imprecise for the forager to immediately locate a specific food item, it might inform the forager that the area is worth searching carefully. We developed a model of composite search based on non-directional sensory cues. With simulations, we compared the search efficiencies of composite foragers that use resource encounters as their mode-switching criterion with those that use non-directional sensory cues. We identified optimal search patterns and mode-switching criteria on a variety of resource distributions, characterized by different levels of resource aggregation and density. On all resource distributions, foraging strategies based on the non-directional sensory criterion were more efficient than those based on the resource encounter criterion. Strategies based on the non-directional sensory criterion were also more robust to changes in resource distribution. Our results suggest that current assumptions about the role of resource encounters in models of optimal composite search should be re-examined. The search strategies predicted by our model can help bridge the gap between random search theory and traditional patch-use foraging theory.

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1. Introduction

For many organisms, the ability to efficiently find food resources is a key determinant of fitness (Bell, 1991). It is advantageous for foraging animals to focus search effort on resource rich areas and minimize energy spent searching resource poor areas (Viswanathan et al., 2011). This search tactic has been termed composite search (Plank and James, 2008), area-restricted search (Weimerskirch et al., 2007), or area-concentrated search (Benhamou, 1992). A forager using a composite search strategy alternates between intensive and extensive search modes. In intensive mode, a forager thoroughly searches resource rich areas by making short moves and reorienting frequently; in extensive mode, it moves directly across resource poor areas by making long, relatively straight moves with minimal turning.

Composite search behavior is widespread, observed in taxa as diverse as slime moulds (Latty and Beekman, 2009), beetles (Ferran et al., 1994), honeybees (Tyson et al., 2011), fish (Hill et al., 2003), birds (Nolet and Mooij, 2002), ungulates (Tyson et al., 2011), turtles (Tyson et al., 2011), weasels (Haskell, 1997), and humans (Hills et al., 2013). Given the ubiquity of composite search, an important question arises: how should a forager determine when to switch from intensive to extensive mode, and vice versa? Questions about optimal foraging have traditionally been addressed with patch models that envision intensive search taking place within patches and extensive search as movement between patches (Charnov, 1976; Oaten, 1977). These models are not directly applicable to

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cases where resources do not occur in well-defined patches, and instead take on more general spatial distributions (Arditi and Dacorogna, 1988). Optimal foraging on such landscapes is more properly addressed using random search theory (Viswanathan et al., 2011; James et al., 2010; Reynolds and Rhodes, 2009). In random search models, resources are represented as points, and animal movement is modeled with stochastic processes. Unlike patch models, random search models are spatially explicit; resource locations in these models can be specified according to any spatial point pattern and are not limited to the case of clearly defined patches.

Recently, many studies have compared the efficiencies of different random search movement patterns (James et al., 2008, 2011; Reynolds and Bartumeus, 2009), and composite searches have been a particular focus (Reynolds, 2010a, 2009; Plank and James, 2008; Benhamou, 2007). The criteria that foragers use to switch between modes have received far less attention. Most analyses of optimal composite search presume that foragers use a "giving-up time" (GUT) as their mode-switching criterion (Reynolds, 2010a, 2009; Plank and James, 2008; Scharf et al., 2007). A forager using this criterion switches from extensive to intensive mode upon encountering a resource. It then stays in intensive mode until a fixed amount of time (the GUT) has elapsed without a subsequent resource encounter. GUT models accurately describe some foraging situations, such as ladybird beetle larvae (*Coccinella septempunctata*) feeding on aphids (Carter and Dixon, 1982) and houseflies (*Musca domestica*) feeding on sucrose drops (Bell, 1990).

Rather than keeping track of time, many animals use sensory cues to modulate their search behavior. Parasitoids like *Nermeritis canecens* (Waage, 1979), *Venturia canescens* (Bell, 1990), and *Cardiochiles nigriceps* (Strand and Vinson, 1982) use chemical cues to determine when to search intensively for hosts. When deciding when to leave a foraging site, wolf spiders rely more heavily on visual and vibratory cues than elapsed time since their last prey encounter (Persons and Uetz, 1997). Procellariiform seabirds use chemicals like dimethyl sulfide to identify when to switch to intensive search behavior (in this case, intensive search consists of upwind zig-zag movement) (Nevitt et al., 2008). These seabirds "use changes in the olfactory landscape to recognize potentially productive foraging opportunities as they fly over them" (Nevitt, 2008). Further examples of animals that use sensory cues to determine search mode include ciliates like *Paramecium* and *Tetrahymena* (Levandowsky and Klafter, 1988; Leick and Hellung Larsen, 1992), bacteria, like *Escherichia coli* and *Salmonella typhimurium* (Adler, 1975; Moore and Crimaldi, 2004; Dusenbery, 1998), cod larvae (Døving et al., 1994), and fruit flies (Dalby-Ball and Meats, 2000). It is important to note that identifying discrete behavioral states (e.g., search modes) from empirical movement data is a difficult problem; fortunately, significant progress has been made in this area (Nams, 2014; Postlethwaite et al., 2013; Knell and Codling, 2011; Barraquand and Benhamou, 2008).

There are two primary ways that organisms use sensory cues to find resources: taxis and kinesis (Codling et al., 2008; Dusenbery, 1989). In taxis, an organism uses sensory cues (e.g., the gradient of a stimulus field) to orient itself and move toward the resource. In kinesis, an organism uses sensory cues to determine its speed (orthokinesis) or turning frequency (klinokinesis). Unlike taxis, kinesis does not use directional information. Taxis is an efficient strategy used by many organisms (Seymour et al., 2010), but in some situations limitations on sensory information make it impractical; Hein and McKinley (2012) note that such limitations occur when sensory signals are infrequent, noisy, or contain limited directional information. When organisms are unable to extract directional information from sensory cues, they may still be able to use kinesis. In this paper, we refer to the cues used in kinesis as *non-directional sensory cues*. We use this term to contrast with *directional sensory cues*, which allow foragers to orient their motion toward resources. Most foragers likely use a combination of non-directional and directional sensory cues. For example, a forager might use odor as a non-directional cue to determine where to search intensively; when it comes close to a resource, it might switch to using visual information as a directional cue and move directly to the resource. A forager that uses odor as a non-directional cue when the signal is dilute and the odor gradient is imperceptible might switch to taxis (using odor as a directional cue) when it is close to a resource and the odor gradient is more pronounced. Two specific examples illustrate how foragers use non-directional sensory cues. Williams (1994) proposes that tsetse flies search for targets using kinesis, with carbon dioxide concentration serving as a non-directional sensory cue. Williams hypothesizes that winds in typical tsetse fly habitats are too light and variable to allow for taxis based on wind direction. Juvenile flatfish use kinesis to find bivalves (Hill et al., 2000, 2002); respiratory currents generated by the bivalves are likely the non-directional sensory cue in this system.

In this study, we model two classes of composite search strategies: those with mode transitions triggered by resource encounters and elapsed time (the GUT criterion), and those with mode transitions triggered by non-directional sensory cues. Our modeling framework allows for a full spectrum of random movement patterns for both intensive and extensive mode. We used simulations to compare the efficiencies of different search strategies. Searching efficiency depends in part on the spatial distribution of resources (Cianelli et al., 2009), so we compared search strategies on a variety of landscape types, characterized by different levels of resource aggregation and density. Further, we examined the performance of the search strategies in response to changes in resource aggregation to test the robustness of the search strategies to environmental change. We found that the search strategy based on non-directional sensory cues outperformed the search strategy based on resource encounters across all landscape types, and was more robust to changes in resource aggregation.

2. Methods

2.1. Overview

In our modeling framework, resources are represented as points distributed across a two-dimensional landscape, and a forager is represented as a moving point with a small fixed detection radius. The forager moves at a constant speed, and when a resource falls within its detection radius, the forager moves in a straight line to the resource and consumes it; otherwise, the forager implements a random search strategy. Random search strategies consist of a set of probabilistic movement rules. Although the resulting movement patterns are stochastic, the probability distributions that generate the movement provide a structure for the search.

In accordance with many theoretical studies on optimal random search behavior (e.g., Viswanathan et al., 1999; Reynolds, 2010a; James et al., 2008), our model is very general, and parameters are not fit to any particular species. The distance and time units in our simulation set the characteristic distance and time scales of the system. These units could be quantified in terms of meters and seconds to represent a specific system. Our simulations use a square landscape 101 units in length and width, and foragers have a detection radius of 0.5 units. Coordinates are floating point numbers, and are not restricted to discrete values. Like many random search simulations (e.g., Reynolds, 2009), we focus on a case where the detection radius is less than 0.01 of the landscape scale.