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Original Research Article

How spatial resource distribution and memory impact foraging success: A hybrid model and mechanistic index☆

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ABSTRACT

Understanding how animals forage has always been a fundamental issue in Ethology and has become critical more recently in Environmental Conservation. Since the formalization of optimal foraging theory, theoretical models intended to depict the behavior of a generic forager have served as the main tools to analyze and ultimately comprehend the mechanisms of foraging. Due to complexity and technical constraints, these models have traditionally focused on single aspects of foraging, leaving out other concurrent processes that may also interplay. The recent inclusion of several facets inside united models has given rise to interesting results on the importance of interacting factors such as memory and resource heterogeneity.

In this paper, we present a hybrid model integrating metabolism, foraging decisions, memory, as well as spatially explicit movement and resource distribution. We use it to examine the effects of spatial resource distribution – an aspect often neglected in favor of probabilistic resource heterogeneity – on the viability of a generic random-walking forager, and rely on the model to devise an ecological metric that can explain and render the relative profitability of given spatial distributions. Furthermore, we assess the significance of memory properties relatively to the profitability of resource distributions. Most notably, we reveal contrasted effects of memory depending on the aspect of resource varied in space (i.e. prey abundance, or prey body mass).

On the whole, a general comparison of our findings with results obtained with spatially implicit models leads us to stress the complex interaction between memory and spatial resource distribution as well as the criticality of spatial representation in the modeling of foraging. Accordingly, we conclude with a discussion on the ecological implications of these results, as well as the advantages of hybrid modeling for the accurate simulation of foraging.

1. Introduction

Foraging is one of the primary activities supporting life and it is critical for the survival of any animal. Its study has been an active field of research in behavioral ecology since the very beginning of this discipline (MacArthur and Pianka, 1966). With the formalization of increasingly complex foraging theories, mathematic modeling and then computerized dynamic simulations have become important scientific tools to investigate this topic.

Initially, foraging models were limited to finding the strategy optimizing energy intake over short time periods (Stephens and Krebs, 1986), and this trend has survived until nowadays (Bénichou et al., 2005; Moen et al., 1997; Oshanin et al., 2009). Soon, the need for an increased accuracy in the representation of processes became obvious. Among others, it was early recognized that spatially implicit modeling may be insufficient to capture certain aspects of foraging (Pyke, 1983; Roese et al., 1991; Turner et al., 1995). Some traditional models also wrongfully treated metabolism as a mechanism not directly impacting foraging activities (Moen et al., 1997). Furthermore, many studies assumed that the forager is omniscient about its environment, and have thereby neglected the importance of information acquisition and learning (Bernstein et al., 1988; Dall et al., 2005; Eliassen et al., 2007). Within the last two decades, these assumptions have been tackled separately by numerous studies. For instance, some have

☆ *Note*: For demonstration purpose, a simplified version of the model presented in this paper is available online at the following address: http://christian.vincenot.biz/models.html.

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been devoted solely to advanced representations of metabolism (Simoy et al., 2014). A combination of several aspects of foraging inside of single models has on the other hand triggered a diversification of research topics based on the interplay between processes. In this vein, Esposito et al. (2010) studied the coupled effects of memory and metabolism when foraging in a spatially implicit environment. The advent of agent-based modeling has in parallel allowed for the more frequent consideration of foragers inside of an explicit space (Huse et al., 2002; Pettifor et al., 2000; Schwarzkopf and Alford, 2002). This technological progress has given rise to interesting studies on the role of spatial resource distribution on foraging success (Oom et al., 2004; Roese et al., 1991; Turner et al., 1993), whereas another ongoing research axis has emerged on the effect of memory and learning on foraging efficiency (Boyer and Walsh, 2010; Eliassen et al., 2007; Mueller et al., 2011) or population dynamics (Berbert and Fagan, 2012; Dumont and Hill, 2001). Through these works, memory has proven critical to foraging activities, but it remains a very challenging field of study (Fagan et al., 2013). Hudson and White (1985) first observed the importance of digestive kinetics in foraging success. Similarly, Roese et al. (1991) noted that "digestion is of special concern when modeling an animal with time constraint", and stressed again the importance of physiological processes comparatively to physical characteristics. It is noteworthy that modeling exercises on memory in foragers have neglected this aspect, while works on bioenergetics have seldom integrated memory of foraging events.

In this study we intend to contribute to the theoretical understanding of foraging by proposing a spatially explicit model responding to the foregoing concerns. Our solution integrates processes relevant to metabolism, foraging decisions, and memory (similarly to Esposito et al., 2010), while adding a spatial dimension to resource distribution and individual movements. Since Charnov (1976), many models have chosen to picture foraging events inadequately as continuous deterministic processes (McNamara, 1982; Ward et al., 2000), whereas other event-based models have on the other hand strongly simplified the representation of bioenergetics processes. Our solution handles natively purely stochastic events such as prey capture at the same time as continuous processes like metabolism. This integration is technically obtained through the use of a hybrid modeling framework merging System Dynamics (SD) and Individual-Based (IB) models in a spatially explicit environment (Vincenot et al., 2011).

We make use of this model to analyze the effects of different theoretical scenarios of spatial distributions of resources on the foraging success of a generic animal, and first assess the necessity of simulating resource distribution in a spatial way through a comparison between outputs of the model in spatially implicit and spatially explicit mode. In an effort to better understand the spatial properties affecting foraging, we also take advantage of this model to design an ecological index able to measure the relative impact of resource distributions on a forager's viability. Furthermore, we evaluate the importance of memory as mechanism to face resource heterogeneity in space. Finally, as only few hybrid models combining SD and IB components have been published so far in Ecology, and, to the best of the authors' knowledge, none of them related to the study of foraging mechanisms, we also briefly discuss along the way the usefulness of this approach for the modeling of foraging.

2. Method

2.1. Description of the hybrid foraging model

For the sake of standardization, we follow hereafter the 7-points Overview – Design concepts – Details (ODD) model description protocol formulated by Grimm et al. (2006, 2010).

2.1.1. Purpose

The purpose of this model is to reproduce the fluctuations of an animal's body mass when foraging in an environment featuring a fragmented and heterogeneous spatial distribution of resources. Here, we take advantage of this tool to examine the combined effects of spatial variations in resource availability and memory properties, and, incidentally, to assess the importance of representing resource distribution in a spatially explicit manner.

2.1.2. Entities, state variables, and scales

This model includes only a single entity, namely the forager, which can be in four different states: resting, searching, handling, or commuting between patches. The exit of the resting state is synchronized with a basic bimodal circadian clock represented by a state variable with two positions (day, night). The main state variable is the animal's body mass, which is processed based on secondary state variables (food ingested, and food assimilated) as well as state-dependent aggregated energy expenditures. The forager possesses a basic memory represented by two variables – an expected capture time and an expected energy gain – computed based on foraging events experienced previously. Finally, the forager has bidimensional spatial coordinates positioning it in the discrete space with reflecting boundary conditions. Simulations are run with a time step of 1 min and are used to study changes in the forager's body mass over 1–3 years.

2.1.3. Process overview and scheduling

Processes take place in the following order inside of the model: metabolism (ingestion, digestion, assimilation, energy loss), foraging strategy choices (i.e. state changes), and, when necessary, memory adjustment, and movement. The global model runs in hybrid time with metabolism calculated in continuous time, and state changes and their related processes (awakening, prey capture, decision to commute) occurring as discrete asynchronous events. Note that for continuous computations, the Runge–Kutta 4 (RK4) method with an integration step (Δt) of 0.1 min was used to compute the results reported in this study.

2.1.4. Design concepts

2.1.4.1. Basic principles. We follow the same scheme as Esposito et al. (2010), who showed the importance of integrating inside of a single model multiple aspects of foraging. Here, on top of metabolism, foraging activities, and memory, we incorporate a spatially explicit distribution of resources traversed by the forager as well as the notion of individuality of each forager.

Also, another fundamental principle that underlies this work is the fact that the temporal nature of processes is accurately featured. Particularly, unlike in previous works, metabolism is computed in continuous time, while search-capture dynamics take place as stochastic and discrete events.

Finally, the implementation relies on a novel modeling framework to integrate the different aspects inside of an individual-centered spatial foraging model with the concurrent use of discrete and continuous time computation engines. This conceptual framework is referred to as System Dynamics (SD) – Individual-Based (IB) hybrid modeling (Vincenot et al., 2011; Vincenot and Moriya, 2011). It mainly relies on the analysis and breakdown of the ecological system under consideration and on the use of either SD or IB modeling to reproduce each component that interacts within the system. Permissive implementation platforms like AnyLogic, which we used here, allow for the simulation of flexible individual spatial dynamics (e.g. networking)