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ORIGINAL PAPER

Improved foraging by switching between diffusion and advection: benefits from movement that depends on spatial context

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Abstract

Animals use different modes of movement at different times, in different locations, and on different scales. Incorporating such context dependence in mathematical models represents a substantial increase in complexity, but creates an opportunity to more fully integrate key biological features. Here, we consider the spatial dynamics of a population of foragers with two subunits. In one subunit, foragers move via diffusion (random search) whereas in the other, foragers move via advection (gradient-following search). Foragers switch back and forth between the subunits as functions of their spatial context (i.e., depending on whether they are inside or outside of a patch, or depending on whether or not they can detect a gradient in resource density). We consider a one-dimensional binary landscape of resource patches and non-habitat and gauge success in terms of how well the mobile foragers overlap with the distribution of resources. Actively switching between dispersal modes can sometimes greatly enhance this spatial overlap relative to the spatial overlap possible when foragers merely blend advection and diffusion modes at all times. Switching between movement modes is most beneficial when organism's gradient-following abilities are weak compared to its overall capacity for movement, but switching can actually be quite detrimental for organisms that can rapidly follow resource gradients. An organism's perceptual range plays a critical role in determining the conditions under which switching movement modes benefits versus disadvantages foragers as they seek out resources.

Keywords Diffusion · Advection · Context-dependent movement · Oriented movement · Movement behavior · Perception · Perceptual range

Introduction

Movement is critical to the success of animals as they seek out resources, mates, and shelter. However, that success hinges not just on whether or not animals move, but also on how, when, and where they do so. Indeed, the same organism can use multiple modes of movement at different times and at different scales (Ward and Saltz 1994; Skalski and Gilliam 2000; Fryxell et al. 2008; Prevedello et al. 2011; Fleming et al. 2014a, b; Rodríguez et al. 2017). In some cases, particularly those involving acquisition of food resources, certain movement modes can be associated with seeking resources while other modes may be used for obtaining those resources once they have been located (Ward and Saltz 1994; Fortin et al. 2002; Skalski and Gilliam 2003; Morales et al. 2004; Newlands et al. 2004; McClintock et al. 2012; Nabe-Nielsen et al. 2013; Fleming et al. 2014a, b).

This duality of oriented versus non-oriented modes of movement is broadly distributed across species. For example, analyses of the movement trajectories of many terrestrial vertebrates indicate movement patterns that could be characterized as composite correlated random walks, strongly suggesting the existence of multiphasic movement strategies (Morales et al. 2004; Fryxell et al. 2008; Auger-Méthé et al. 2016). In some sharks, transitions between movement modes are a matter of scale, with a form of oriented movement called 'directed walks' occurring at large spatial scales but far more tortuous movements occurring at small scales (Papastamatiou

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et al. 2011). Magellanic woodpeckers switched between area-restricted search and exploratory movement as they foraged in forests of southern Chile, adopting an exploratory movement mode featuring long-distance displacements when located in landscapes with low quality habitat or low levels of heterogeneity (Vergara et al. 2019). These and other empirical studies clearly suggest that animals do indeed switch between different movement modes. In fact, estimating the hidden Markov processes that characterize switching between two states is one of the dominant approaches to analyzing movement data (Patterson et al. 2008; McClintock et al. 2012; Langrock et al. 2012). Exploring the context for such switching remains a key goal (Papastamatiou et al. 2011). Gurarie et al. (2016) provide an overview of statistical techniques for decomposing movement tracks into different movement modes and identifying underlying changes in behavior.

Several studies involving individual based models have explored the consequences of animals' reliance on different modes of movement. For example, in an evolutionary model of foraging movements, Mueller et al. (2011) found that simulated animals evolved to switch among three modes of movement (non-oriented, oriented, and spatial memory) as a function of the spatiotemporal availability of resources. Nabe-Nielsen et al. (2013) found that switching between searching and fine-scale foraging behaviors reproduced observed spatial behavior of porpoises and produced stable home ranges. Bracis et al. (2015) compared foraging efficiency and behavioral allocation in resource-dependent state switching models with and without spatial memory, finding that the benefits of memory (temporally non-local information) depended on the complexity of the resource landscape. Accumulating evidence suggests that such switching may be necessary to capture the complex movement patterns of actual organisms.

In contrast to their utility in individual-based models, switching terms that allow animals to transition between different forms of movement have only rarely been included in mathematical models of animal dispersal. Skalski and Gilliam (2003) developed a model in which animals switch between slow and fast movement states, demonstrating how such switching (which occurred independent of spatial context) influenced the population's spatial distribution. More recently, switching terms (again spatially independent) have appeared in foraging theory such as when Tyson et al. (2011) developed a model in which foragers switch between slow-moving diffusive and fast-moving advective-diffusive states. This switching model provided a stronger fit to data for both honeybees and caribou than did single-movement-mode models in which the forager population was homogeneously diffusive or advective-diffusive. The apparent similarity of animal movement to hyperdiffusive random movements known as Lévy flights can largely be explained by behavioral switching (Reynolds 2008; Bénichou et al. 2011; Petrovskii et al. 2011; Edwards et al. 2007).

Perceptual ranges (i.e., the maximum distance at which landscape elements can be identified) are highly relevant to discussions of behavioral switching. Such ranges provide non-local information that allows an animal to structure or bias its movements in response to landscape features located beyond its immediate position. This non-local information offsets difficulties arising from spatial gradients that are weak, spatially restricted, or hard to detect, any of which could trap dispersers in low-quality areas. Perceptual ranges vary tremendously, with magnitudes that depend on species, individual state, sensory mode, and spatial context (Zollner and Lima 1997; Zollner 2000; Mech and Zollner 2002; Fletcher et al. 2013). Individual-based models of moving animals routinely include some version of a perceptual range, either in the context of attraction–repulsion radii (e.g., Couzin et al. 2002; del Mar Delgado et al. 2018) or in the context of resource detection (e.g., Berec 2000; Mueller et al. 2011; Bläßle and Tyson 2016). In contrast, perceptual ranges are rarely considered explicitly in mathematical models of movement because of the complexity they introduce, but when perceptual ranges are included, they are important elements of the model. For example, information derived from well beyond an animal's current location can shape the spatial distribution of mobile consumers (e.g., Hillen et al. 2007; Barnett and Moorcroft 2008; Martínez-García et al. 2013, 2014), and movement in response to non-local gradients is critical to the swarming dynamics of animal groups (Grünbaum and Okubo 1994; Mogilner and Edelstein-Keshet 1999). Fagan et al. (2017) explored how the size of an organism's perceptual range influenced its foraging success in landscapes featuring transient resource patches, identifying optima in perceptual range under particular resource distributions and dynamics.

Here, we develop and explore a mathematical model that includes context-dependent switching between different modes of movement. The model makes realistic assumptions about movement modes (random search versus gradient-following), introduces the idea that spatial cues may determine the switching between movement modes, and explores the role of non-local information in driving the switches in behavior. We find that switching between movement modes is most useful when a species' gradient-following abilities are weak relative to its capacity for movement. The size of the animal's perceptual range and presence or absence of habitat fragmentation further shape the utility of switching between movement modes. Overall, these results highlight how context-dependent switching between movement modes may benefit resource acquisition and hint at the potential utility of such behavior in evolutionary settings.

Methods

To explore the effects on context-dependent movement on foraging success, we study a perception-based model of animal dispersal in which spatial redistribution is possible but there are no population dynamics. This can be thought of as representing the behavior of foragers in search of resources or dispersers in search of favorable habitat. Following Fagan et al. (2017), we are particularly interested in the role of animals' perceptual range and how this influences decision-making with regard to movement. However, unlike that work, which focused on the interplay between perception and resource dynamics, we focus here on a static landscape to explore the effects of switching between movement behaviors.

We will assume a one dimensional binary landscape of habitat patches and non-habitat such that the resource quality, *m(x)*, at position x can be written

$$m(x) = \begin{cases} 0 & \text{if outside a patch} \\ 1 & \text{if inside a patch} \end{cases} \tag{1}$$

More complex resource functions were considered in Fagan et al. (2017), which explored how the interplay between perception and edge sharpness shapes foraging success.

Building on ideas presented in Tyson et al. (2011), we consider a population in which animals can switch between two distinct modes of dispersal: a random search mode and a resource gradient following mode. However, unlike in Tyson et al. (2011), the gradient following considered in this paper is always directed toward the resource, rather than simply a means of relocating quickly to another area of space that can then be explored via diffusion. The density of the population that is engaged in gradient following at position x and time t is denoted *u(x,t)*, and the density that is engaged in random search is denoted *v(x,t)*. We write

$$\begin{aligned} \frac{\partial u(x,t)}{\partial t} &= \overbrace{\left[\underbrace{\varepsilon \frac{\partial^2}{\partial x^2} u}_{\text{low level random movement}} - \underbrace{\gamma \frac{\partial}{\partial x}\left(u \frac{dh(x)}{dx}\right)}_{\text{advection}}\right]}^{\text{gradient following}} - \overbrace{\alpha[x]u}^{\text{switching to random search}} + \overbrace{\beta[x]v}^{\text{switching from random search}} \\ \frac{\partial v(x,t)}{\partial t} &= \overbrace{D \frac{\partial^2}{\partial x^2} v}^{\text{random search}} + \overbrace{\alpha[x]u}^{\text{switching from gradient following}} - \overbrace{\beta[x]v}^{\text{switching to gradient following}} \end{aligned} \tag{2}$$

where the term

$$\varepsilon \frac{\partial^2}{\partial x^2} u - \frac{\partial}{\partial x} u \frac{dh(x)}{dx} \tag{3}$$

represents the overall movement of the portion of the population engaged in gradient following, with $\varepsilon \ll 1$ representing a small amount of background random movement (necessary for certain theorems about partial differential equations to hold true), γ quantifying the rate of advection (gradient following), and $\frac{dh(x)}{dx}$ representing the perceived spatial gradient in the resource. The parameter D is the rate of diffusion undertaken by the portion of the population that is in the random search mode. The functions $\alpha[x]$ and $\beta[x]$, defined below, are spatially explicit representations of the rates of switching between the two dispersal modes. For simplicity, we kept $\varepsilon = 0.01$ throughout our analyses.

As discussed in Fagan et al. (2017), the available resources *m(x)* are perceived by an animal only when those resources fall within its perceptual range, R, and they are spatially weighted by a detection function, $g(x, y, R)$, which describes modifications in the forager's perception with distance y from position x. We write

$$h(x) = \left[\frac{1}{2R}\int_{x-R}^{x+R}\left[\overbrace{m(y)}^{\text{available resources}}\ \overbrace{g(x,y,R)}^{\text{detection function}}\right]^p dy\right]^{1/p}. \tag{4}$$

Note that (4) is the L^p norm of function $m(y)g(x, y, R)$ on the interval $[x-R,\ \ x+R]$ subject to the probability measure giving the uniform distribution on the interval. The parameter p can be interpreted as a kind of post-perception information processing because it represents the degree of spatial averaging that the animals do, based on the landscape features that they detect. Effectively, p serves to accentuate or de-accentuate resources detected from different parts of the landscape. In one-dimensional models, this parameter merely serves to bias the dispersing animals to the left or the right depending on where the greater habitat signals are coming from within the perceptual radius, R. In two-dimensional models, this parameter serves a similar but even more important role by biasing the movement in the direction of particular habitat patches within the perceptual radius. The larger the value of *p,* the greater the degree to which dispersing animals can 'home in' on the strongest signal within their perceptual radius, ignoring lesser signals. For simplicity, we kept $p = 2$ throughout our analyses. An alternative idea would have $p = \infty$, meaning foragers always move to the absolute best perceived resource. We do not pursue this option here because $p = \infty$ will yield to mathematical discontinuities in *h(x)* and because we feel it important to consider biological and energetic constraints on the detection of and locomotion to optimal resources.

For simplicity, we will consider only the "top-hat" detection function,

$$g(x,y,R) = \begin{cases} \frac{1}{2R} & -R\sqrt{3} \le x-y \le R\sqrt{3} \\ 0 & else \end{cases} \quad (5)$$

where R is the standard deviation of the forager's detection function. The consequences of choosing different functional forms for $g(x, y, R)$ are explored extensively in Fagan et al. (2017).

The remaining terms in the model are the spatially explicit functions that control the rates of behaviorally switching between the two dispersal modes. The term $\alpha[x]$, which controls the rate of switching from gradient following mode to random search mode, is written

$$\alpha[x] = \begin{cases} 0 & if\ m(x) = 1 \\ \tilde{\alpha}\left(\left|\frac{dh}{dx}\right|\right) & if\ m(x) = 0 \end{cases}, \quad (6)$$

which means that no such switching takes place for animals inside a habitat patch. Outside of habitat patches, the rate of switching depends upon the magnitude of the perceived resource gradient, $\left|\frac{dh}{dx}\right|$, according to

$$\tilde{\alpha}\left(\left|\frac{dh}{dx}\right|\right) = \begin{cases} \alpha_0 - \alpha_1 \left|\frac{dh}{dx}\right| & if \quad \left|\frac{dh}{dx}\right| \le \frac{\alpha_0}{\alpha_1} \\ 0 & if \quad \left|\frac{dh}{dx}\right| > \frac{\alpha_0}{\alpha_1} \end{cases} \quad (7)$$

where the rate of switching is α_0 if there is no perceived gradient and then declines in a piecewise linear fashion at rate α_1 as the magnitude of the perceived resource gradient increases, eventually becoming zero for very strong gradients.

Similarly, the term $\beta[x]$, which controls the rate of switching from random search mode to gradient following mode, is written

$$\beta[x] = \begin{cases} \beta_0 & if\ m(x) = 1 \\ \tilde{\beta}(x) & if\ m(x) = 0 \end{cases}, \quad (8)$$

implying that there is a baseline level of switching, β_0, for animals inside a patch. Outside patches, in non-habitat, the switching depends on the perceived resource gradient according to the function $\tilde{\beta}(x)$. Specifically, we write

$$\tilde{\beta}(x) = \begin{cases} 0 & if \quad \left|\frac{dh}{dx}\right| \le h_1 \\ \frac{\beta_0\left(\left|\frac{dh}{dx}\right| - h_1\right)}{\beta_1 + \left(\left|\frac{dh}{dx}\right| - h_1\right)} & if \quad \left|\frac{dh}{dx}\right| > h_1 \end{cases}, \quad (9)$$

where the first condition means that there is no behavioral switching unless the magnitude of the perceived resource gradient is sufficiently strong ($> h_1$) and the second condition means that the rate of switching increases from zero and saturates at a rate β_0 as the gradient continues to increase. Parameter β_1 controls the rate of saturation as a function of $\left|\frac{dh}{dx}\right|$.

Note that the resource thresholds $\frac{\alpha_0}{\alpha_1}$ and h_1 that control the rates of switching between the two dispersal modes may or may not be the same. If they are the same, it means that there is a common criterion for switching between random search and gradient following. In contrast, if the thresholds are different, it implies a kind of behavioral inertia exists. For example, if $\frac{\alpha_0}{\alpha_1} > h_1$, then animals, having switched into gradient following mode, tend to stay in that mode unless the magnitude of the perceived resource gradient drops significantly. One can interpret this kind of behavioral inertia as a kind of hysteresis.

Note further that the switching terms $\alpha[x]$ and $\beta[x]$ depend on the resources available at the foragers' actual positions rather than on the resources detected within their perceptual range (Eqs. 6 and 8). In this way, local information determines whether it is time to leave, but non-local information determines which way to go.

To quantify the effectiveness of switching between movement modes as a foraging strategy, we adopt a measure of foraging success (Ω). This measure quantifies 'resource matching' in the sense that foragers must spatially overlap with resources to be successful. Because our work deals only with animal movement behavior and not population dynamics, we do not consider resource depletion. Here, Ω is given by

$$\Omega = \int_{-\infty}^{\infty} u(x)m(x)dx \quad (10)$$

which simply summarizes the spatial alignment of the foragers and their resources. The entire model is solved numerically, and we calculate this measure at a quasi-equilibrium, after initial transients have faded (see Fagan et al. 2017 for more details on this measure of foraging success).

Throughout, we solved the initial-boundary value equations numerically using the method of lines by discretizing in space over the domain $x = [0,100]$ and solving the system of ordinary differential equations in time. We implemented numerical solutions in the MATLAB environment (MathWorks 2019) using the PDEPE package (Skeel and Berzins 1990), which in turn implements the variable-step, variable-order differential algebraic equation solver ODE15S (Shampine and Reichelt 1997).

We contrasted Switching On scenarios with Switching Off scenarios where the population is permanently subdivided into equal-sized gradient following and random searching subunits. Switching On scenarios followed

Eq. 2, but for the Switching Off scenarios, we used the related form

$$\frac{\delta u(x,t)}{\partial t} = \overbrace{D\frac{\partial^2}{\partial x^2}u}^{\substack{random\\search}} \overbrace{-\gamma\frac{\partial}{\partial x}\left(u\frac{\partial h(x)}{\partial x}\right)}^{advection}, \quad (11)$$

which has an exact analytical solution (see Cantrell et al. 2018 for an example). Note that the diffusion rate is the same as in the second part of Eq. (2). Consequently, the "Switching Off" case includes both diffusion and advection, but performed as a combined motion.

Initial conditions for Switching Off were $u(x, 0) = 0.02$ and for Switching On were $u(x, 0) = v(x, 0) = 0.01$, both of which yield total forager populations $(u + v)$ that integrate to 2 over the domain. We used zero flux boundary conditions on the rectangular domain $(x, t) \in [0, 100] \times [0, 100]$. In most of the numerical solutions, we considered a single, centrally located resource patch of 10 units, i.e., $m(x) = 1$ for $x \in [45, 55]$, but we also considered cases in which the resources were fragmented spatially.

Results

In the Switching On scenarios, foragers actively switched between the gradient-following and random searching movement modes as a function of their spatial context. Integrating the populations spatially, transitions between the two movement modes were clearly evident as equations evolved from their initial conditions towards steady states (Fig. 1a, c). Switching to the gradient-following mode allowed the foragers to concentrate inside the resource patch (Fig. 1b). As that concentration occurred, the forager population became increasingly dominated by the gradient-following mode because the context dependency on $\alpha[x]$ did not permit the foragers to switch back to random search mode once they were inside the resource patch (Eq. 6). As expected, the final transition toward dominance by the gradient-following population (i.e., the dominance by u over v) preceded the spatial concentration inside the resource patch. However, the relative abundance of the subpopulations undertaking gradient-following and random-search modes could shift dramatically as the foragers sought out resources, sometimes undergoing more than one reversal (Fig. 1c). In general, the switching parameters α_0,

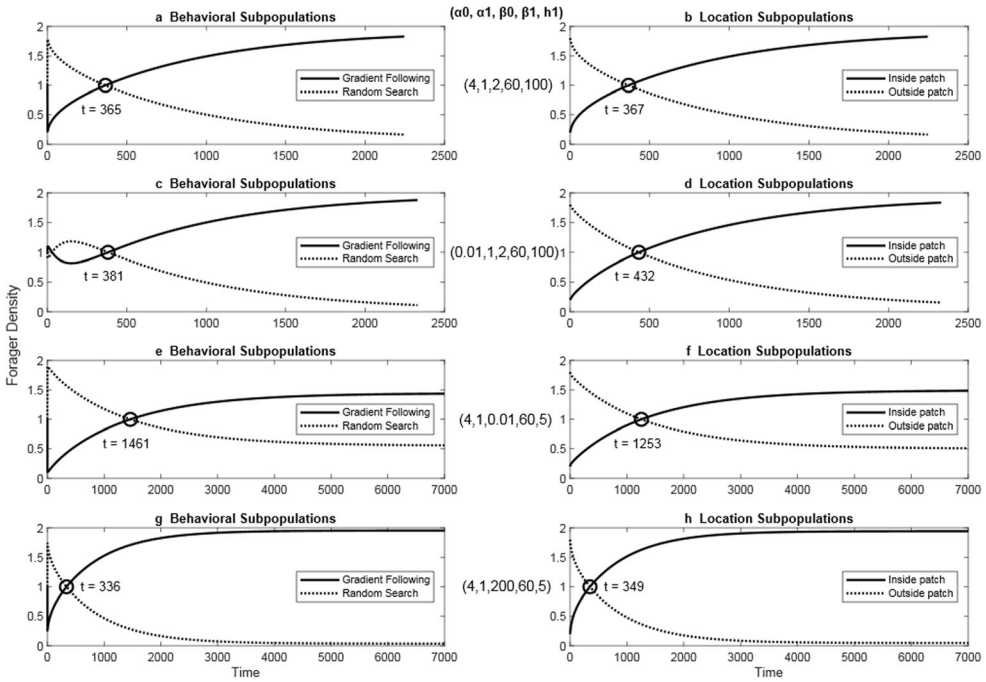

Fig. 1 Forager density as a function of time for a population that can switch between gradient following and random search movement modes (Eq. 2). The left panels (**a**, **c**, **e**, **g**) all show the foragers broken down by behavioral subpopulations (those employing gradient following versus random search), whereas the right panels (**b**, **d**, **f**, **h**) all show the foragers broken down into location subpopulations (inside versus outside the resource patch). Note that the crossover for the curves for the different behavioral modes (left panels) precedes the crossover in spatial position (right panels). The position of these crossover points, and the patterns of transition between gradient-following and random search modes or from outside the patch to inside the patch more generally, varies as a function of the parameters α_0, α_1, β_0, β_1, and h_1 that determine the rates of switching and the spatial contexts under which switching occurs. In all panels, $\gamma = 0.05$, $D = 1$, and $R = 0.9$. In panels **a**, **b** (a case of Fast Switching to Random Search), $\alpha_0 = 4$, $\alpha_1 = 1$, $\beta_0 = 2$, $\beta_1 = 60$, and $h_1 = 100$. In panels **c**, **d** (a case of Slow Switching to Random Search), $\alpha_0 = 0.01$, $\alpha_1 = 1$, $\beta_0 = 2$, $\beta_1 = 60$, and $h_1 = 100$. In panels **e**, **f** (a case of Slow Switching to Gradient-following Search), $\alpha_0 = 4$, $\alpha_1 = 1$, $\beta_0 = 0.01$, $\beta_1 = 60$, and $h_1 = 5$. In panels **g**, **h** (a case of Fast Switching to Gradient-following Search), $\alpha_0 = 4$, $\alpha_1 = 1$, $\beta_0 = 200$, $\beta_1 = 60$, and $h_1 = 5$. Total forager density $(u(x) + v(x))$ always integrates to 2

α_1, β_0, β_1, and h_1 had pronounced influences on the rates at which the subdivision of the forager population by behavioral mode and spatial position occurred (Fig. 1). These parameters tended to have lesser effects on the total success of the foragers in finding and remaining within the resource patch (Supplementary Information).

Plotting forager density as a function of spatial position highlights the ability of the population to concentrate within the resource patch (Fig. 2). Interestingly, we found parameter cases in which the Switching On scenario afforded better matching of foragers to the resource (i.e., higher Ω; Fig. 2a, b) and other parameter cases in which the Switching Off scenario performed better (Fig. 2c).

A little advection consistently improved foraging success relative to the case of diffusion alone. This was true whether the advection rate was a constant or depended on context (Fig. 3). The capacity to switch between random search and gradient search mechanisms (the Switching On scenario) further enhanced foraging success, provided diffusion was strong enough. However, when the diffusion rate was small, the capacity to switch was detrimental to foraging success.

Exploring this result systematically, we plotted forager success as a joint function of γ and D, finding that resource matching was greater for the Switching On scenario when γ was small and D was large (Fig. 4a). For other combinations of movement rates, the Switching Off case yielded greater forager success, reaching the maximum possible level of $\Omega = 2$ for γ large and D small. We found that the transition from Switching On performing better to Switching Off performing better occurred for a fixed ratio of D/γ. The relative (dis)advantage of foragers in the Switching On scenario was often quite substantial compared to the corresponding Switching Off scenario. For example, for foragers with a weak gradient-following ability relative to their overall capacity for movement (i.e., for γ small and D large), the Switching On

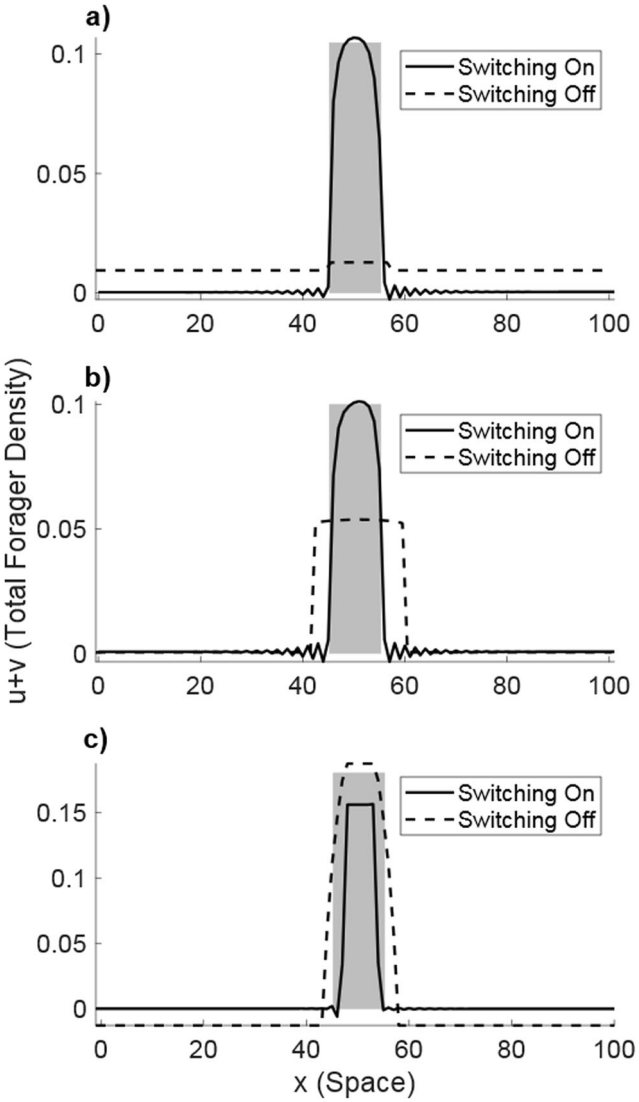

Fig. 2 Total forager density as a function of spatial position illustrating different levels of long-term concentration of foragers in the resource patch (gray rectangle depicting $m(x) = 1$ for $x \in [45, 55]$). Results are plotted for three parameter cases: a) $\gamma = 0.01$, $D = 3$, $R = 1$, b) $\gamma = 0.08$, $D = 1.5$, $R = 4$, and c) $\gamma = 0.2$, $D = 1$, $R = 2$. These additional parameters are constant for all three cases: $\alpha_0 = 5$, $\alpha_1 = 25$, $\beta_0 = 2$, $\beta_1 = 60$, and $h_1 = 5$. Results plotted are steady-state results. Squiggles in the Switching On case are numerical artifacts associated with the transitions between behavioral modes that take place near the sharp edges of the resource patch. These persisted despite our attempts to minimize them using various techniques for numerical analysis of PDEs

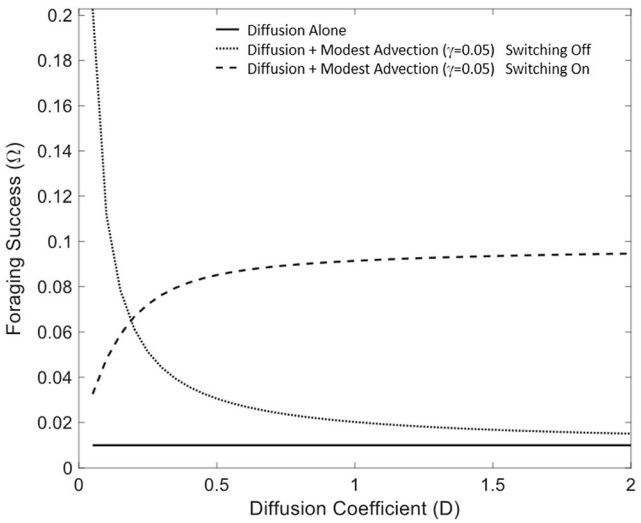

Fig. 3 Comparative foraging success for diffusion, advection, and context-dependent switching. A little advection consistently improves foraging success (Ω) relative to the case of diffusion alone. The capacity to switch between random search and gradient search mechanisms (the Switching On scenario) can further enhance foraging success, provided diffusion is strong enough. However, when the diffusion rate is small, the capacity to switch is detrimental to foraging success. Parameters used were $R = 2$, $\alpha_0 = 1$, $\alpha_1 = 25$, $\beta_0 = 1$, $\beta_1 = 60$, and $h_1 = 5$

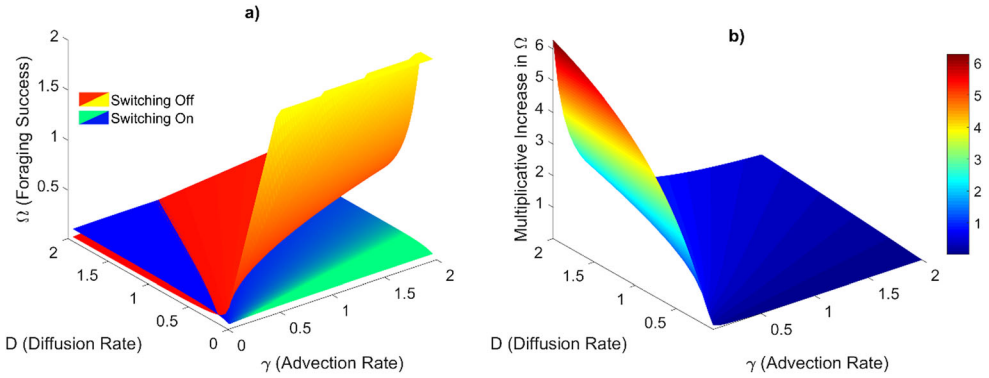

Fig. 4 Forager performance as a function of movement rates for populations with and without the ability to switch between gradient following and random search movement modes. **a** Forager success, quantified using Ω from Eq. 10, is greater for the Switching On case when γ is small and D is large. For other combinations of movement rates, the Switching Off case yields greater forager success, reaching the maximum possible level of $\Omega = 2$ for γ large and D small. Note that the crossover between the Switching On and Switching Off surfaces occurs for a fixed ratio of γ/D. The colors in **a** show the curvatures of the surfaces away from the crossover. Panel **b** plots the relative (dis)advantage of foragers in the Switching On scenario relative to the Switching Off scenario. This exceeds a six-fold advantage for foragers with a weak gradient-following ability relative to their overall capacity for movement (i.e., when γ is small and D is large). Results are plotted for $R = 0.8$, $\alpha_0 = 1$, $\alpha_1 = 25$, $\beta_0 = 1$, $\beta_1 = 60$, $h_1 = 5$

scenarios could improve foraging success by as much as six-fold (Fig. 4b).

The foragers' perceptual range played a critical role in determining when the capability to switch between gradient-following and random search was advantageous versus disadvantageous (Fig. 5). In particular, the ratio of D/γ above which Switching On was advantageous decreased sharply as the perceptual range R increased. This is because a larger perceptual range allowed foragers to detect and respond to gradients in the resource landscape more effectively than if their movement decisions were based purely on immediately local information. For a fixed diffusion rate, either an increase in advection rate or an increase in perceptual range would improve the foragers' access to an existing resource gradient (Fig. 5).

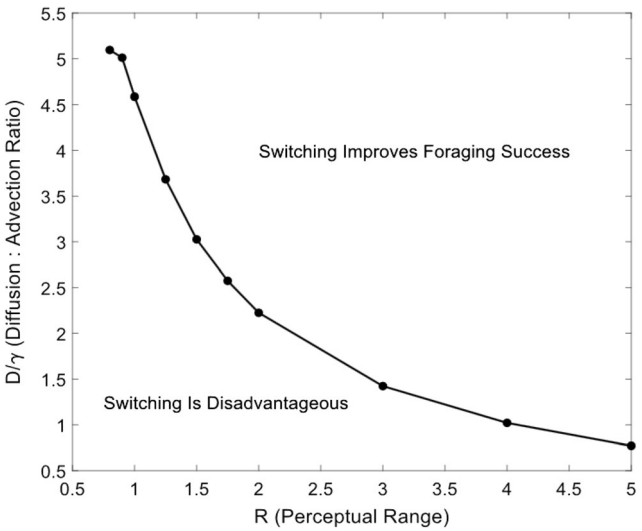

Fig. 5 The interplay between movement rates and perceptual range determines when switching between movement modes is advantageous. The ratio of D/γ that determines when Switching On is advantageous decreases sharply as the perceptual range R increases. Results are plotted for $\alpha_0 = 1$, $\alpha_1 = 25$, $\beta_0 = 1$, $\beta_1 = 60$, $h_1 = 5$

Spatially fragmented resources generally reduced the benefits of switching between movement modes compared to the equivalent cases in which the resources were concentrated in a single patch (Fig. 6). This is because the shortened average distance between foragers and the nearest resource patch made it easier for the foragers to detect and advect up resource gradients even in the Switching Off scenario. Consequently, the reduction in relative foraging success was especially strong for parameter cases involving large perceptual ranges. Note also that the performance of the Switching On scenario improved for γ large and D small when resources were spatially fragmented (Fig. 6b). This occurred because fragmentation of the resource patch decreased the average distance between foragers and the nearest patch. This proximity effect created more opportunities for foragers with strong gradient-following abilities to locate and move into a nearby resource patch when the dissipative effects of diffusion were small.

Discussion

We introduced a mathematical model for animals moving in search of resources that features context-dependent switching between two different modes of movement (diffusive random search and advective gradient-following search). Compared to a situation in which animals merely blended advection and diffusion modes at all times, actively switching between the two different modes of movement greatly enhanced the spatial

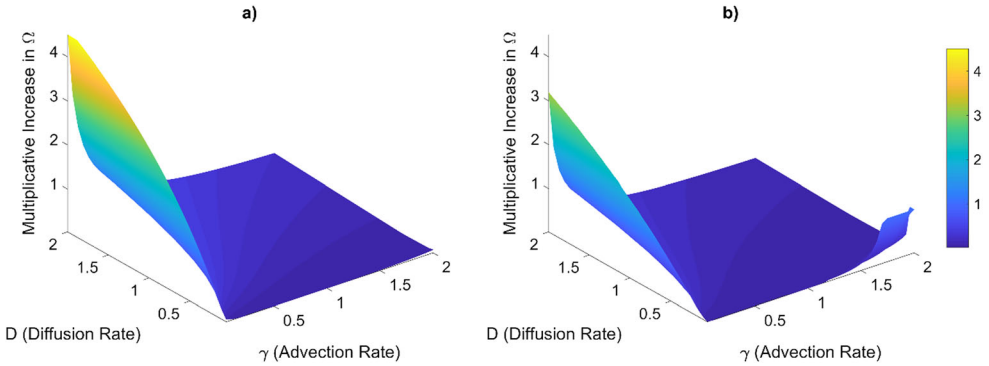

Fig. 6 Compared to a single resource patch (**a**), fragmented resources (**b**) generally reduce the benefits of switching between movement modes. Note, however, that the performance of the Switching On scenario improves for γ large and D small. The relative (dis)advantages for foragers in the Switching On scenario compared to the Switching Off scenario are plotted for **a** a single resource patch of 10 units ($m(x) = 1$ for $x = [45, 55]$) versus **b** five resource patches, each of two units (*i. e.* , $m(x) = 1$ for $x \in [9, 11] \cup [29, 31] \cup [49, 51] \cup [69, 71] \cup [89, 91]$). Results are plotted for $R = 1$, $\alpha_0 = 1$, $\alpha_1 = 5$, $\beta_0 = 1$, $\beta_1 = 60$, $h_1 = 5$

overlap between the animals and their resources in certain circumstances. More specifically, switching between movement modes was most beneficial when an organism's gradient-following abilities were weak compared to its overall capacity for movement. However, switching was actually quite detrimental for organisms that can rapidly follow resource gradients (Figs. 4 and 5).

Multi-state random walk models, hidden Markov models, and other types of models that are routinely fit to animal movement data have included context-dependent switching of behaviors for many years (e.g., Morales et al. 2004; Fryxell et al. 2008; Patterson et al. 2008; McClintock et al. 2012; Langrock et al. 2012; Gurarie et al. 2016). A variety of species appear to switch between movement modes (Papastamatiou et al. 2011; Auger-Méthé et al. 2016) and, at least in some cases, this switching depends explicitly on spatial context (Prevedello et al. 2011; Vergara et al. 2019). Despite such applications, which have a distinct statistical component, context-dependent behavioral switching is not well-investigated from the perspective of mathematical theory, which could help identify the general conditions under which switching is beneficial.

As we have mathematized the problem, our framework assumes that organisms have two 'abilities.' The first is that they can detect and respond to a gradient in the availability of resources. This gradient can range from immediately local to integrated over a large region depending on the perceptual range parameter, but the fundamental ability pertains to gradient detection. The second required ability is that the organisms must be able to tell whether they are currently inside or outside a resource patch. This is clearly related to the detection of a gradient, but it could potentially involve different sensory modalities or information intake for some species.

When interpreting the results, a key point to understand is that once Switching On foragers encounter the resource gradient associated with a resource patch, they will increasingly switch into the gradient-following subpopulation and thereby shut down diffusion. Because foragers cannot switch from gradient-following mode to random search mode when inside a resource patch (Eq. 6), this acted as a concentrating mechanism that kept foragers in resource patches from leaving those patches. Because foragers that are located inside of patches but possess high diffusion rates would quickly leave the patches unless something keeps them there, this concentrating mechanism contributes to the superior performance of the Switching On scenario for those parameter cases involving high diffusion and low advection (Figs. 4 and 5).

Our findings in Fig. 3 are consistent with results from previous work in the mathematics literature. For example, in spatially varying domains that are one dimensional (or in the case of higher dimensions, are convex), movement that blends advection and diffusion (but does not involve switching) always improves resource matching compared to straight diffusion (Cantrell et al. 2007). Likewise, in previous models that blend diffusion and advection to explore alternative evolutionary strategies of movement, some intermediate level of diffusion is favored for any advection rate, but diffusion rates that are too high or too low are not favored (Lam and Lou 2014). The latter type of evolutionary disadvantage may be somewhat analogous to the observation here that if diffusion rates are low, then context-dependent advection is disadvantageous (Figs. 3 and 4) relative to the corresponding No Switching scenario. Roughly speaking, for a single movement mode, having the right balance between advection and diffusion appears advantageous, but having either one too large relative to the other is not.

Our results identified an interesting interplay between perceptual range and the ratio of movement rates separating the advantageous and disadvantageous effects of switching between movement modes (Fig. 5). This linkage is worth thinking about in the context of the evolution of sensory perception.

Operationally, the perceptual range in our model could refer to perception via any number of sensory modalities, such as vision, audition, or chemoreception. However, given pre-existing empirical work on the evolution of vision, particularly pertaining to issues of distance and detectability, it is perhaps easier to discuss the linkage between perception and behavioral switching in a visual context. The evolution of the ability to see is one of the key transitions in life on earth, and sight appears linked to diversification early in evolutionary history (Marcotte 1999; Aberhan et al. 2012; Schoenemann and Clarkson 2013).

Let us consider random search as an evolutionary baseline for movement. Compared to the corresponding No Switching scenario, Switching between movement modes offered the biggest advantage in resource-matching when animals had substantial rates of random search but only low rates of advective gradient following (i.e., D large and γ small) (Fig. 4). Moreover, resource matching for both the Switching and No Switching scenarios would naturally exceed the resource matching achievable using only random searching where dissipative effects would prevent foragers from concentrating on a resource patch (Fig. 3). This sequence of results (Switching outperforming No Switching, which in turn outperformed random search) suggests that an animal that was able to evolve even a rudimentary level of gradient-following in a selective, context-dependent fashion would be advantaged relative to an animal that was always following gradients and relative to an animal that was just moving randomly. This initial advantage could serve as an evolutionary jumping off point for further refinements of a coupled system of detection and movement.

Perceptual range is also highly relevant to this thought problem. Early in evolution, perceptual ranges would likely have been very narrow, as opportunities for visual detection were just developing. In our model, narrow perceptual ranges greatly restricted the region of parameter space in which Switching was advantageous. Importantly, however, that restricted region corresponded to the region of parameter space where the gradient-following ability was weak, which is exactly where the benefits of Switching were most pronounced. A weak gradient-following ability is again a feature that might be expected early in evolution. It is intriguing that this three-part convergence of narrow perceptual ranges, weak gradient-following abilities, and selective, context-dependent use of those gradient-following abilities afforded such dramatically enhanced opportunities for resource matching relative to alternative baseline conditions (Figs. 4 and 5). Clearly, biological systems that improved foragers' abilities to find and remain located in resource patches would be advantageous in an evolutionary setting. We will explore the evolutionary relevance of the convergent benefits of switching, gradient following, and perception in future modeling work.

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