

# Perceptual Ranges, Information Gathering, and Foraging Success in Dynamic Landscapes

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**ABSTRACT:** How organisms gather and utilize information about their landscapes is central to understanding land-use patterns and population distributions. When such information originates beyond an individual's immediate vicinity, movement decisions require integrating information out to some perceptual range. Such nonlocal information, whether obtained visually, acoustically, or via chemosensation, provides a field of stimuli that guides movement. Classically, however, models have assumed movement based on purely local information (e.g., chemotaxis, step-selection functions). Here we explore how foragers can exploit nonlocal information to improve their success in dynamic landscapes. Using a continuous time/continuous space model in which we vary both random (diffusive) movement and resource-following (advective) movement, we characterize the optimal perceptual ranges for foragers in dynamic landscapes. Nonlocal information can be highly beneficial, increasing the spatiotemporal concentration of foragers on their resources up to twofold compared with movement based on purely local information. However, nonlocal information is most useful when foragers possess both high advective movement (allowing them to react to transient resources) and low diffusive movement (preventing them from drifting away from resource peaks). Nonlocal information is particularly beneficial in landscapes with sharp (rather than gradual) patch edges and in landscapes with highly transient resources.

**Keywords:** resource matching, advection on nonlocal information, oriented movement, consumer movement, transient resources, viewsheds.

## Introduction

Foraging success provides a critical bridge between consumer behavior and population distributions. At short time-scales, the question of consumer-resource overlap falls within

optimal foraging theory (OFT), which focuses on how movements impact forager success. OFT asks when individual foragers should abandon a focal patch to seek out resources elsewhere and how this decision affects overall distributions of foragers across the landscape (e.g., Charnov 1976; Pyke 1984; Perry and Pianka 1997; Arditi and Dacorogna 1985, 1988; Bracis et al. 2015). At larger timescales, the role of individual decision making is reduced relative to the impact of long-term processes like population dynamics and evolution. For this, OFT is less useful and is often replaced by the theory of evolution of dispersal (TED). TED focuses on population-level success rather than individual success, with the primary questions framed in terms of game theory and evolutionarily stable strategies (Hastings 1983; Johnson and Gaines 1990; McPeck and Holt 1992; Cantrell et al. 2010; Averill et al. 2012). Although OFT and TED differ in context, timescale, and currencies for contrasting movement strategies, the ideal free distribution and related ideas, such as conditional dispersal and density-dependent habitat selection, are relevant in both theories, reflecting broad foundational processes and patterns (Morris 1988; Milinski 1994; Dreisig 1995).

For both OFT and TED, models typically fall within one of three different mathematical formalisms: patch models (Hastings 1983; McPeck and Holt 1992; Cressman and Krivan 2006), integrodifference/integrodifferential equation models (IDEs; Cantrell et al. 2012; Cosner et al. 2012), and partial differential equation models (PDEs; Hastings 1983; Arditi and Dacorogna 1987; Cantrell et al. 2008, 2010). Patch models assume discrete resource regions, whereas IDEs and PDEs allow for continuous variation in resource abundance or quality. A subtler distinction, however, involves what the three formalisms assume about movement. In patch models, movement is tracked only when it occurs between patches—that is, when animals exit one patch and enter another. Movement decisions are thus motivated by patch-level information, which often translates into omniscience about the landscape distribution (e.g., Fretwell and Lucas 1970; Pyke

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1984; Pleasants 1989; Houston and McNamara 1999) or, at the very least, an understanding of the global conditions that could be obtained through sampling or learning (e.g., Charnov 1976; but see Abrahams 1986; Tregenza 1995; Cressman and Křivan 2006). By contrast, in PDE models animals typically follow a resource gradient, with movement deriving from purely local information from the foragers' immediate (infinitesimal) vicinity (Okubo 1980; Cosner 2005; Cantrell et al. 2006, 2008). Finally, in IDE models, although movement is nonlocal (tailed dispersal kernels allow for rapid long-distance movement), the information used to motivate movement decisions is usually purely local or, on occasion, fully omniscient.

In between full omniscience and purely local information lie only a few mathematical biology articles featuring information-limited consumers (e.g., Berec 2000) and movement based on nonlocal information, that is, information derived from well beyond an animal's current location (e.g., Hillen et al. 2007; Barnett and Moorcroft 2008; Martínez-García et al. 2013, 2014). Models that specifically consider nonlocal gradient following are even rarer, appearing in only a handful of ecological scenarios, such as swarming dynamics of animal groups (Grünbaum and Okubo 1994; Mogilner and Edelstein-Keshet 1999) and stochastic models linking nonlocal resource detection, habitat preference, and consumer movement (Barnett and Moorcroft 2008; Moorcroft and Barnett 2008). In general, nonlocal gradient following should be particularly important in dynamic landscapes, where it should be especially beneficial to rapidly dispersing organisms that can reach distant resources before conditions change (Mueller and Fagan 2008; Mueller et al. 2011a). Although extensive research has explored information gathering and resource tracking in static landscapes (e.g., Viswanathan et al. 1999; Edwards et al. 2007; Vergassola et al. 2007; Bartumeus and Levin 2008; Hein and McKinley 2012), corresponding research in dynamic landscapes remains underdeveloped (but see Torney et al. 2011; Berdahl et al. 2013).

Even though few theoretical studies analyze the impacts of nonlocal information on forager success, a large body of animal behavior research deals directly with this issue via species' "perceptual ranges" (e.g., Lima and Zollner 1996; Holdo et al. 2009; Fletcher et al. 2013; Boonman et al. 2013). Perceptual range (i.e., the maximum distance at which landscape elements can be identified) impacts animal dispersal, search strategies, and landscape connectivity (e.g., Lima and Zollner 1996; Zollner and Lima 1999; Gehring and Swihart 2003; Calabrese and Fagan 2004; Fletcher et al. 2013), while movement based on perceptual range can affect dispersal success and survival (Lima and Zollner 1996; Zollner 2000; Olden et al. 2004; Holdo et al. 2009; Prevedello et al. 2011). Indeed, research in landscape ecology, wildlife biology, and related fields that involve specific empirical landscapes of-

ten accounts for perceptual ranges using viewshed analysis—a function of geographic information systems that represents the landscape area that is visually perceptible from a specific location given topographic barriers (e.g., Nassauer 1992; Camp et al. 1997; Etzenhouser et al. 1998).

Perceptual ranges vary tremendously, including variation across species, within a species, and even within individuals (e.g., Zollner 2000). Among species, perceptual ranges vary with both body size and mode of movement: burrowing owls (*Athene cunicularia*), for example, have perceptual ranges of approximately 1.5 km (Todd et al. 2007), whereas garden snails (*Cornu aspersum*) have perceptual ranges of 20–40 cm (Dahirel et al. 2015). Within species, perceptual ranges often vary depending on internal state (e.g., body size, landscape of origin, attention; Downing 1988; Mech and Zollner 2002). For instance, speckled wood butterflies (*Pararge aegeria*) originating from fragmented landscapes have larger perceptual ranges and better habitat-finding ability than those originating from more continuous landscapes (Öckinger and van Dyck 2012). Finally, perceptual range within an individual can change depending on environmental conditions (e.g., vegetation density, illumination, cloud cover, land use; Zollner and Lima 1997; Olden et al. 2004; Flaherty et al. 2008). For example, the Neotropical marsupials *Philander frenatus* and *Didelphis aurita* have perceptual ranges of 100–200 m in mowed pastures and 30–50 m in planted land (Prevedello et al. 2011). Because perceptual ranges vary across and within species and individuals, selection may favor broader or narrower perceptual ranges depending on the stability and predictability of landscape features. For example, longer perceptual ranges may be particularly useful in rough or dynamic landscapes because nonlocal information would offset difficulties arising from weak or transient gradients that would otherwise trap foragers in low-quality areas.

Here we investigate how perceptual range interacts with landscape dynamics to determine how well populations of mobile foragers can concentrate on food resources that are dynamic in space and time. Primarily we seek to determine the types of dynamic resource landscapes that favor large versus small perceptual ranges. Furthermore, we want to understand the contributions that different types of movement (i.e., random diffusion vs. oriented gradient following) make to foraging success. Overall, our modeling approach is much closer to OFT frameworks than to TED frameworks because our approach considers only what is happening on the time-scale of foraging and lacks resource depletion and population dynamics. Specifically, we construct a continuum model in which consumers move through a dynamic landscape of transient patches according to local advection governed by intermediate-scale resource detection functions. Such detection functions fit in between the behavior of foragers that react to purely local gradients and the omniscience of classical optimal foragers.

## Methods

We assume a one-dimensional landscape in which the spatiotemporal variation in resource abundance is defined by a density of resources  $m(x, t)$  at location  $x$  and time  $t$ . On this landscape, we consider a population of foragers that follows what they perceive as a resource gradient. In many models of consumers tracking resource gradients, the gradient in question is a purely local (infinitesimal) one (e.g., Okubo 1980). In contrast, here we base the foragers' perception on the integration of resource abundance over a larger area.

Specifically, we define a forager's resource perception function  $h(x, t)$  as

$$h(x, t) = \int_{-\infty}^{\infty} m(y, t)g(y - x) dy, \quad (1)$$

where  $g(y - x)$  describes modifications in the forager's perception with distance. Because a forager's ability to detect nonlocal resources depends on distance as well as habitat elements between the resources and the forager's location, we explore imperfect, distance-dependent detection by adopting several different forms for  $g(y - x)$ . We develop these functions more fully below, but briefly we consider both finite perceptual ranges and a "decay with distance" approach. Ranta et al. (2000) considered finite perceptual ranges in their individual-based models of nonomniscient foragers, and the decay with distance approach is similar to that which Matsu-mura et al. (2010) used in their studies of foragers inhabiting two-patch and multipatch landscapes. This latter approach captures the same types of complications field ecologists face when they attempt to census organisms located some distance

from a linear transect (e.g., Buckland et al. 2007). To accommodate both types of distance-dependent detection, we mathematize the concept of an animal's perceptual range in terms of the "detection scale" of its perception function, detailed below. At a practical level, equation (1) implies that animals average information about the spatial distribution of their resources; this means that they will effectively lose information if the detection scale is too big. Thus, this kind of perception is functionally quite different from the detection of individual landmarks or prey items. Last, note that differentiating  $h(x, t)$  with respect to  $x$  yields the nonlocal gradient in resources that foragers follow. Table 1 summarizes all mathematical functions and parameters, providing both mathematical definitions and biological interpretations as well as descriptions of what we mean by local versus nonlocal.

Ignoring birth/death processes, we allow the movements of the foragers to include both a random (diffusive) component with diffusion coefficient  $D$  (units: length<sup>2</sup>/time) and a directed (advective) component with advection coefficient  $\alpha$  (units: length/time). Consequently, the dynamics of a population  $u(x, t)$  of foragers at density  $u$ , location  $x$ , and time  $t$  following a perceived nonlocal gradient can be described by the advection-diffusion equation

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} - \alpha \frac{\partial}{\partial x} \left( u \frac{\partial h(x, t)}{\partial x} \right). \quad (2)$$

We refer to equation (2) as an advection-diffusion process on nonlocal information, noting that, because of the integral in  $h(x, t)$ , it is a partial integrodifferential equation. In equation (2), notice that while the extent of gradient following

**Table 1:** Definitions, parameters, and biological interpretations

Symbol or term	Mathematical definition	Additional biological interpretation
Movement based on local information	Advection based on the infinitesimal gradient in the true resource distribution	As a rule of thumb, operates on scales up to 5 or 10 times an organism's body size
Movement based on non-local information	Advection based on the spatially integrated gradient in the perceived resource distribution	Operates on scales greatly exceeding an organism's body size
$D$	Diffusion rate	Random movement
$\alpha$	Advection rate	Gradient-following movement
$\Omega$	See equation (3)	A metric of foraging success quantifying overall forager concentration on resources
$u(x, t)$	Distribution of foragers	...
$m(x, t)$	True distribution of resources	...
$g(y, x, R)$	Detection function	Function characterizing an organism's ability to extract information about its resources from its surroundings
$R$	Detection scale; in the limit $R \rightarrow 0$ , equation (2) collapses to the standard advection-diffusion equation	Standard deviation of the foragers' detection function; when $R = 0$ movement is based on purely local information, whereas when $R > 0$ nonlocal information about the resource influences movement
$h(y, x, R)$	Nonlocal resource-following function	Perceived distribution of resources

is based on nonlocal information (the integral component), movement itself is infinitesimal and thus completely local (the differential component). This distinguishes our model from various IDE formulations that allow for nonlocal (i.e., jump) movement via dispersal kernels. By enforcing local movement, we can focus on nonlocal information and the trade-off between the availability of remote resources and the foragers' ability to capitalize on this information using rapid directed movement toward the distant resources.

To quantify the effectiveness of consumer-resource tracking based on nonlocal information, we introduce a measure of foraging success ( $\Omega$ ).  $\Omega$  parallels OFT's "resource-matching" framework (e.g., Charnov 1976; Ranta et al. 1999; Matsumura et al. 2010). However, because it does not consider mutual interference or depletion of resources by foragers, we have departed from a tenet of OFT. This is a reasonable assumption when population density is low (i.e., sparsely populated regions) and resources are ephemeral (i.e., resources degrade before their density can be reduced much by the foragers). In these systems, the question is more about capitalizing on transient resources as opposed to avoiding competition. Such resource dynamics characterize, for example, the Eastern Steppes of Mongolia that have motivated much of our earlier work on animal movement (Mueller and Fagan 2008; Mueller et al. 2011b; Martínez-García et al. 2013; Fleming et al. 2014).  $\Omega$  is given by

$$\Omega = \int_{t'}^{t_{\max}} \int_{-\infty}^{\infty} u(x, t) m(x, t) dx dt, \quad (3)$$

where the timeframe  $t'$  to  $t_{\max}$  represents some period after transient behaviors have settled down. For static resource distributions, which (with appropriate boundary conditions of mass conservation) always exhibit an equilibrium solution  $u^*(x)$ , the integral is only over space. For dynamic landscapes, such as periodically fluctuating landscapes (which are the focus of the remainder of our article) or stochastically varying landscapes (where there is no single stable distribution), the time integral needs to be taken over a sufficiently long period to discount the transient behaviors and instead capture long-term variation.

#### Example Resource Functions

We consider both static and dynamic resource landscapes. For static landscapes, we use numerical approaches to explore scenarios where resources occur as static uniform or static Gaussian patches. We also obtain analytical results for the special case of infinite, spatially periodic landscapes, where resource availability is driven by one or the sum of two sine curves (app. B; apps. A–C, SA–SD are available online). For dynamic landscapes, we consider two time-

varying resource functions, a pulsed Gaussian resource and a pulsed uniform resource. These resource functions create landscapes that feature either smoothly varying resource variation (Gaussian) or discrete patches with sharp edges (uniform). The pulsed Gaussian resource can be written

$$m_g(x, t) = \frac{1}{\sqrt{2\pi}\sigma} \exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right) \sin^2(\omega t/2), \quad (4)$$

where  $\mu$  and  $\sigma$  are, respectively, the mean and standard deviation of the resource pulse and  $\omega$  is the temporal frequency of the pulse.

The pulsed uniform resource can be written

$$m_s(x, t) = \sin^2(\omega t/2) \times \begin{cases} \frac{1}{2\sqrt{3}\sigma}, & \mu - \sqrt{3}\sigma \leq x \leq \mu + \sqrt{3}\sigma; \\ 0, & \text{else;} \end{cases} \quad (5)$$

where the  $3^{1/2}$  term appears so that the standard deviation of the pulsed uniform function matches that of the pulsed Gaussian. This scale matching facilitates comparisons of results.

#### Example Detection Functions

We consider three detection functions (top hat, Gaussian, and exponential) representing different assumptions about how a forager's ability to detect available resources decays as a function of distance. Because we are interested in a transition from platykurtic (no tails) to leptokurtic (fat tails) detection functions, we choose three detection functions that can all be obtained from the exponential power distribution (Smith and Bain 1975) but that differ in kurtosis.

The top-hat detection function, which is highly platykurtic, is

$$g_u(y, x, R) = \begin{cases} \frac{1}{2R}, & -R\sqrt{3} \leq x - y \leq R\sqrt{3}; \\ 0, & \text{else;} \end{cases} \quad (6)$$

where  $R$  is the standard deviation of the forager's detection function, or "detection scale."

The Gaussian detection function is

$$g_g(y, x, R) = \frac{1}{R\sqrt{2\pi}} \exp(-(y-x)^2/2R^2). \quad (7)$$

The exponential detection function, which is leptokurtic, is

$$g_e(y, x, R) = \frac{1}{2R} \exp(-|y-x|/R). \quad (8)$$



If the detection scale  $R$  is held constant across equations (6)–(8), the exponential detection function provides a forager with the most information about resources located far away from the forager’s current position, while the top-hat detection function provides the least long-distance information and, importantly, sets an absolute bound on how far away a forager can (or chooses to) gather information about resource availability. As with the resource function, these detection functions are parameterized in such a way that, for a given  $R$ , the mean perceptual range is the same for all three functional forms. Appendix A presents and illustrates the exact forms of the nonlocal resource-following function ( $h(x)$ ) and its derivative ( $dh/dx$ ) for each of six scenarios (two resource functions [eqq. (4), (5)]  $\times$  three detection functions [eqq. (6)–(8)]).

### Solutions

Mathematically explicit results are tractable for static resource distributions consisting of one or a sum of sine waves with a top-hat detection function (see app. B). We do not consider these sinusoidal landscapes elsewhere. For dynamic resource distributions, we solve the advection-diffusion process (eq. [2]) numerically, with the goal of quantifying the effect of the detection-length scale ( $R$ ) plus the advection and diffusion constants ( $\alpha$  and  $D$ ) on foraging success ( $\Omega$ ). Specifically, we consider the six scenarios outlined above (two resource functions [eqq. (4), (5)]  $\times$  three detection functions [eqq. (6)–(8)]) and explore 340 parametric cases for forager movement, advancing  $\log_{10}(\alpha)$  from 1 to 5 by 0.25 and  $D$  from 1 to 20 by 1. These ranges span a wide variety of advection strengths and diffusion rates and collectively expose a wide range of model behaviors. For each of the resulting 2,040 cases ( $6 \times 340$ ), we calculate and evaluate the shape of  $\Omega(R)$  for  $R \in [0, 20]$ , recording as  $R_{\max}$  the detection scale at which  $\Omega(R)$  attains a maximum and as  $\Omega_{\max}$  the value of that peak.

Throughout, we solve the initial value equations numerically using a dynamic run discretization on a landscape  $x \in [0, 100]$ . As a baseline, we run  $t \in [0, 100]$  with four pulses, so  $\omega = 8\pi/100$ . To minimize effects from numerical transients, we calculate the foraging success,  $\Omega$ , over the last of the four pulses (i.e.,  $t \in [75, 100]$ ). In subsequent analyses (app. SA), we explore the issue of ephemeral resources to examine how the duration and frequency of resource pulses (which together characterize the “intensity” of resource availability) influence the utility of nonlocal information gathering. Still later (app. SB), we introduce a landscape with two (synchronized) pulsed uniform resource patches to further demonstrate the differential impact of the three detection functions on overall foraging success.

We implement numerical solutions in the R programming environment (R Core Team 2015) using the ReacTran

(Soetaert and Meysman 2012) and deSolve (Soetaert et al. 2010) packages, which in turn implement the FORTRAN LSODE solver (Radhakrishnan and Hindmarsh 1993).

## Results

### Analytical Results for Static Resource Distributions

If the resource distribution  $m$  in equation (1) is constant in time, the perception function is also constant in time, and equation (2) reaches an equilibrium distribution  $u^*$  of foragers over the landscape. To find this equilibrium, we set  $\partial u/\partial t = 0$ , reducing equation (2) to a second-order homogeneous ordinary differential equation:

$$0 = \frac{\partial^2 u}{\partial x^2} - \frac{\alpha}{D} \left( \frac{\partial u}{\partial x} \frac{\partial h}{\partial x} + u \frac{\partial^2 h}{\partial x^2} \right). \quad (9)$$

Solving equation (9) gives

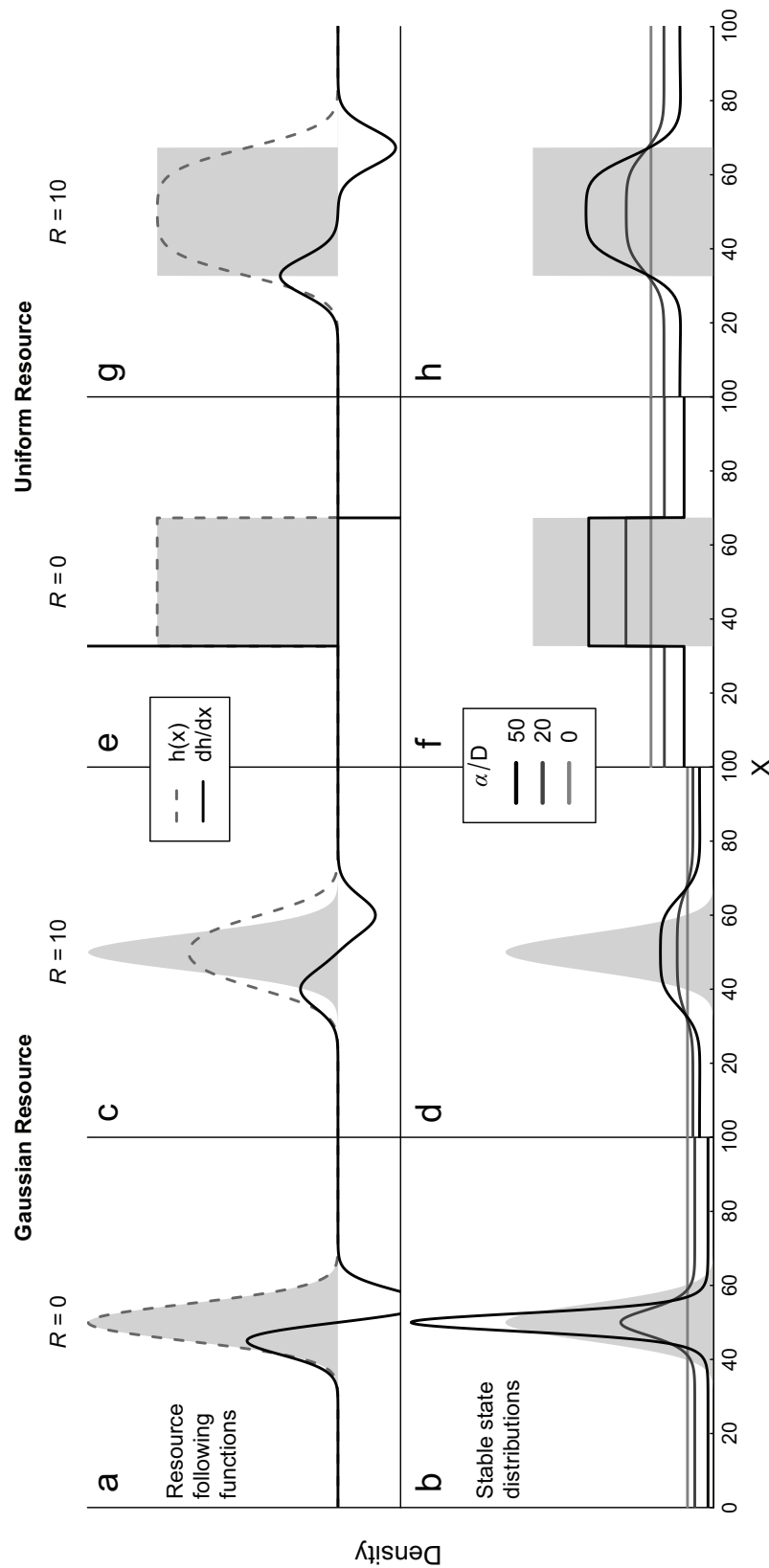
$$u^* = c_2 e^{(\alpha/D)h(x)}, \quad (10)$$

where  $c_2$  is a normalization constant. The foraging success is then given by

$$\Omega = c_2 \int m(x) e^{(\alpha/D)h(x)} dx, \quad (11)$$

where the integral is over the entire landscape or, in the case of an infinite periodic landscape, over a single wavelength of the repeating unit. Appendix B provides analytical results for hypothetical infinite periodic resource landscapes with a top-hat detection function.

**Biological Interpretation.** In static landscapes, the stable forager distribution (fig. 1b, 1d, 1f, 1h) varies from being highly concentrated around the resource peak when minimal random movement accompanies steep gradient-following behavior (i.e., a high  $\alpha/D$  ratio) to being uniformly distributed when the foragers only move randomly (i.e.,  $\alpha/D = 0$ ). When the resource is static, a nonzero detection scale spreads the final forager distribution away from the resource peak (fig. 1; compare results for  $R = 10$  to those for  $R = 0$ ) and thus is detrimental; rather, the optimal solution is to follow the purely local (infinitesimal) resource gradient (for the uniform distribution, this conclusion relies on having at least a small amount of random, exploratory motion,  $D > 0$ ). Interestingly, while purely local information is best, some nonlocal information scales are worse than others, and this depends on the scale of resource distribution itself. For example, in a spatially periodic landscape it is better to use a



**Figure 1:** For the case of static resource distributions, plots illustrate advection (resource-following) functions (upper panels) and their corresponding stable-state distributions (lower panels) for resources ( $m(x)$ , shaded areas) that are Gaussian ( $a-d$ ) or uniform ( $e-h$ ) distributions. In all figures, the  $Y$ -axis is scaled such that the resource distribution (shaded region) has an area of 1. The  $R = 0$  cases correspond to the standard gradient-following kinesis: note that the perceived resource gradient,  $h(x)$ , corresponds exactly to the resource at  $R = 0$  ( $a, e$ ), whereas when  $R > 0$  the perceived resource gradient spreads out spatially relative to the true resource. The vertical black lines in  $e$  occur because  $dh/dx$  for the uniform resource consists of two Dirac delta functions. See appendix A for complete derivations of the nonlocal gradient functions. The lower row of panels illustrates the effect that a higher advection-to-diffusion ratio has on concentrating the equilibrium solution of the process, with a value of 0 corresponding to a uniform distribution under reflecting boundary conditions at 0 and 100.

detection scale equal to the scale of the resource period rather than a scale equal to 1/2 or 3/2 the length of the resource period (app. B).

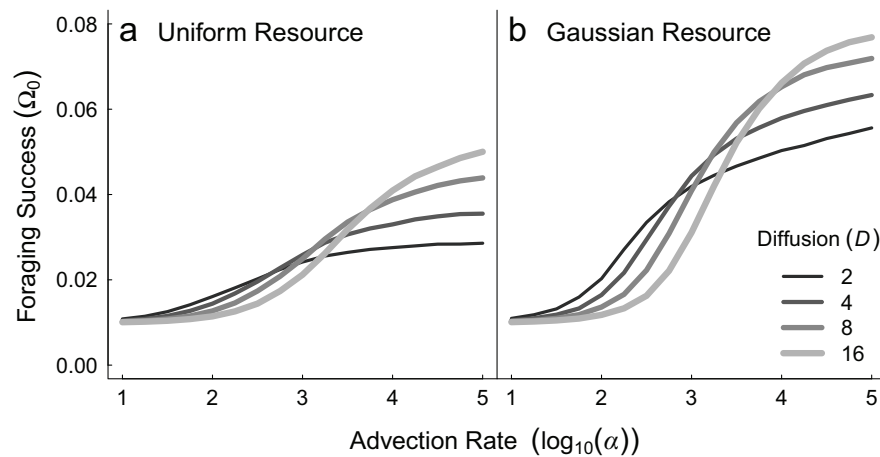
### Numerical Results for Dynamic Resource Distributions

**Limiting Cases  $R = 0$  and  $R = \infty$ .** As benchmarks for our numerical analyses, we obtain results for the limiting cases  $R = 0$  (advection on a purely local gradient) and  $R = \infty$  (advection based on omniscient knowledge about the resource distribution) for the pulsed Gaussian and pulsed uniform resource distributions. For  $R = 0$ , the choice of the detection function is immaterial, and  $\Omega$  (specified as  $\Omega_0$ ) is a sigmoidal function of  $\alpha$  (fig. 2). This is as expected because  $\alpha$  measures the speed with which foragers climb the resource gradient. Overall, higher values of  $\Omega$  occur in the pulsed Gaussian landscape than in the pulsed uniform landscape because it is easier for foragers to advect up the smooth gradient of the Gaussian landscape. Interestingly, for both landscapes plots of foraging success reveal a crossover effect, which represents an interaction between advection and diffusion (fig. 2). Diffusion impedes foraging success when the advection rate is small but enhances foraging success when it is large (fig. 2). At the other extreme, as  $R \rightarrow \infty$ , the perceived resource distribution,  $h(x)$ , is spatially uniform and its gradient is 0. This yields a stable, spatially uniform distribution of foragers.

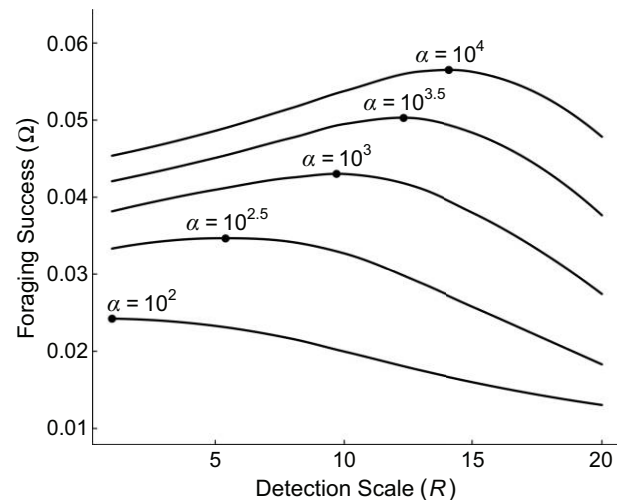
**Biological Interpretation of the Limiting Cases.** The crossover effect (fig. 2) occurs because increased diffusion means

more exploratory movement. When advection is low, exploration weakens foragers' ability to concentrate at resource-rich locations. However, once advection is high enough to compensate, larger diffusion affords the extra advantage of exploratory movement. This in turn inadvertently directs a portion of the forager population toward regions where the spatial gradient is stronger, further facilitating advection. Consequently, concentration of foragers on the resource is higher when both advection and diffusion are high compared with that when only advection is high. Not surprisingly, crossovers occur at smaller values of  $R$  in the pulsed uniform landscape, where gradients are harder to detect, making exploratory movement more important. These results are a fundamental distinction between a dynamic resource landscape and a static one—in the latter, diffusion should inhibit only foraging success (fig. 1b, 1d, 1f, 1h).

**An Optimal Detection Scale for Nonlocal Information Gathering.** In some dynamic landscapes, nonlocal information can distinctly improve foraging success (i.e., it can increase  $\Omega_{\max}$ ; fig. 3). This is particularly true for foragers that can advect quickly on the gradient of their nonlocal information. For a given detection scale,  $R$ , foragers with a greater  $\alpha$  concentrate more readily on their resources. In addition, both the optimal detection scale  $R_{\max}$  and the corresponding maximum foraging success  $\Omega_{\max}$  increase with increasing advection rate  $\alpha$  (fig. 3). Note that the relationship between foraging success and detection scale is asymmetric around  $R_{\max}$ , with too much nonlocal information being worse than not enough. This is especially evident when advection is fast (fig. 3).



**Figure 2:** Foraging success,  $\Omega$  (eq. [3]), for an advection-diffusion equation (eq. [2]) under the special case  $R = 0$ , where advection occurs on a purely local gradient (i.e.,  $\Omega_0$ ). Curves are plotted as functions of the advection coefficient  $\alpha$  for each of four diffusion rates,  $D$ . Foraging success is greater in the pulsed Gaussian resource landscape than in the pulsed uniform resource, but results do not depend on the detection function,  $g(\cdot)$ .



**Figure 3:** Foraging success,  $\Omega$  (eq. [3]), as a function of  $R$ , the detection scale (i.e., standard deviation of the detection function), for different rates of advection,  $\alpha$ , on a nonlocal resource gradient as determined by equation (2). The plot uses a top-hat detection function (eq. [6]) on a Gaussian pulsed resource (eq. [5]) with  $D = 1$ . The curve labels are located at the respective maxima,  $\Omega_{\max}$ . Both  $\Omega_{\max}$  and the optimal detection scale,  $R_{\max}$ , increase with  $\alpha$ , as faster following of the nonlocal gradient allows the foragers to better converge on the resources. Note that for sufficiently large  $\alpha$ , perceptual scales that are either too large or too small relative to optimal (i.e.,  $R > R_{\max}$  or  $R < R_{\max}$ ) reduce  $\Omega$  relative to  $\Omega_{\max}$ . Moreover, the declines are asymmetrical, with overly large detection scales yielding poorer performance.

However, across all scenarios considered results are complex, with advection and diffusion jointly determining  $R_{\max}$  and  $\Omega_{\max}$  (fig. 4). As suggested above,  $R_{\max}$  increases as  $\alpha$  increases because faster advection on the perceived resource gradient facilitates foragers' movement to more remote resources before they disappear. In contrast,  $R_{\max}$  decreases as  $D$  increases because increased random movement dissipates foragers from their resources, weakening the beneficial effects of advection (and thus reducing the importance and usefulness of nonlocal information).

Foragers concentrate more effectively on resources in pulsed Gaussian landscapes (characterized by smooth gradients) than in pulsed uniform landscapes (where patches have sharp edges), and this mechanism affects both  $R_{\max}$  and  $\Omega_{\max}$ . These results hold even though the total amount of resource and the standard deviation of the resource are held constant among scenarios. For example,  $R_{\max}$  is smaller for the pulsed Gaussian resource landscape than for the pulsed uniform resource landscape, and this is particularly pronounced for the top-hat detection function (fig. 4). The reason is that the pulsed Gaussian landscape provides a smoother nonlocal resource gradient for foragers to advect

along. Put differently, the sharp patch edges of the pulsed uniform landscape do not provide as much useful nonlocal information, impeding foragers from concentrating on resources.

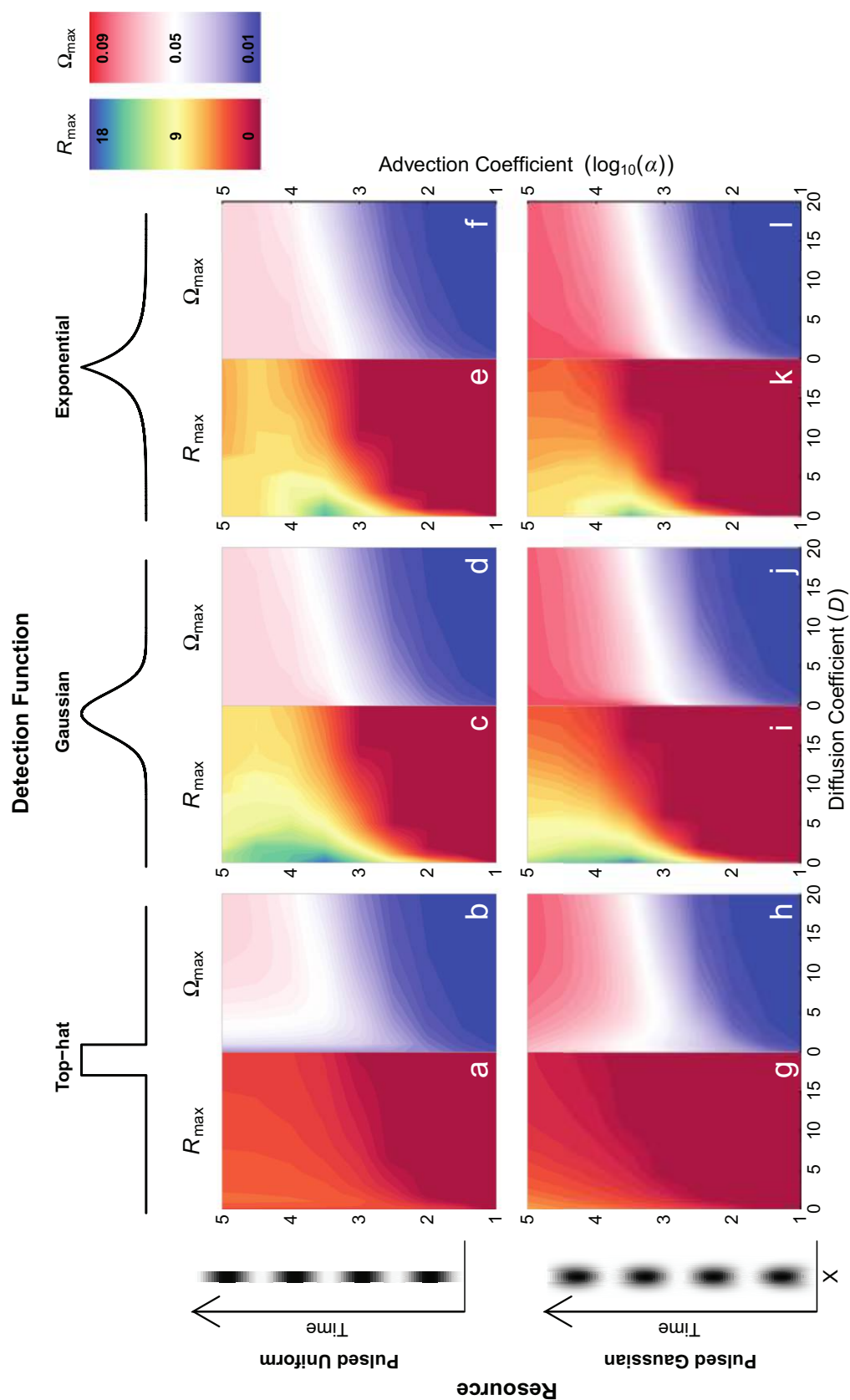
Similarly, switching from the top-hat detection function to the more kurtotic Gaussian and exponential detection functions enhances foraging success because the latter two functions provide substantially more information about remote resources (fig. 4). Having both high advection and high diffusion is especially beneficial for foragers with top-hat detection. This is because diffusion provides some "exploratory movement," compensating for their lack of long-distance information. This is true, however, only when the advection rate is high enough to offset the dissipative effects of diffusion. The overall benefits of a kurtotic detection function are especially clear in landscapes featuring more than one patch (app. SD).

For reference, array plots giving curves of  $\Omega(R)$  as functions of  $(\alpha, D)$  for all six resource distribution  $\times$  resource detection scenarios appear in appendix SA.  $R_{\max}$  and  $\Omega_{\max}$  were extracted from each parametric case in these arrays and then used to construct the contour plots in figure 4. Appendix SB provides additional commentary and figures characterizing how the optimal detection scale and total foraging success depend jointly on advection and diffusion.

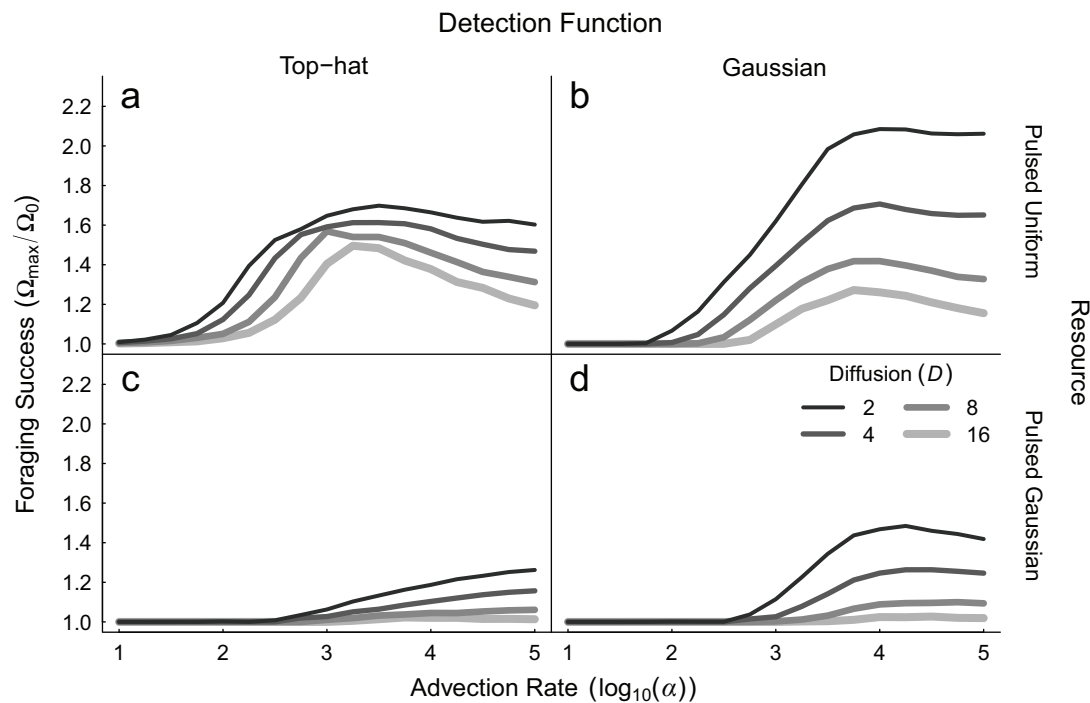
*For What Kinds of Movement and Detection Does Nonlocal Information Provide a Benefit?* Across all landscape types and detection functions considered, a pronounced threshold behavior is evident in foraging success ( $\Omega_{\max}/\Omega_0$ ) as a function of advection rate (fig. 5). Specifically, a sufficiently high rate of gradient-following movement is necessary before nonlocal information provides any benefit. Moreover, increased diffusion pushes this threshold to higher values of  $\alpha$ ; thus, with more random movement, stronger levels of advection are necessary to attain the same level of foraging success. Even small amounts of diffusion are sufficient to create nonmonotone (hump-shaped) curves of relative foraging success as a function of advection rate; this is especially true for pulsed uniform landscapes (fig. 5). Put biologically, for a given level of exploratory movement there is an optimum rate of nonlocal gradient following that provides the greatest foraging success. However, on either side of this optimum too much advection is generally better than not enough.

*For What Kinds of Landscapes Is Nonlocal Information Most Useful?* We observe a strong difference in  $\Omega_{\max}/\Omega_0$  between the pulsed uniform and pulsed Gaussian landscapes, with the pulsed uniform landscape providing greater opportunities for nonlocal information to improve foraging success (fig. 5). This greater potential for improvement hinges on the sharp patch edges in the pulsed uniform landscape.





**Figure 4:** Contour plots for the optimal detection scale,  $R_{\max}$ , and the corresponding maximal concentration of foragers on their resources,  $\Omega_{\max}$ , as functions of forager advection rate,  $\alpha$ , and diffusion rate,  $D$ , for six different resource  $\times$  detection function scenarios. The predominance of higher values of  $\Omega_{\max}$  in the lower panels (denoted by paler grayscale shades) indicates that foragers concentrate more effectively on their resources in landscapes with pulsed Gaussian patches (smooth gradients) than in landscapes with pulsed uniform patches (sharp edges). Similarly, by leveraging increased nonlocal information afforded by the more kurtotic Gaussian and exponential detection functions, foragers concentrate more readily using those detection functions than with the top-hat detection function, which provides substantially less information about remote resources. This manifests as higher  $R_{\max}$  and  $\Omega_{\max}$  values in the center and right sets of panels than in the leftmost ones.



**Figure 5:** Improved foraging success via nonlocal information gathering. Curves of the ratio  $\Omega_{\max}/\Omega_0$  are plotted as functions of the advection coefficient  $\alpha$  for each of four diffusion rates,  $D$ . This ratio quantifies the relative gain in foraging success that is possible with advection on nonlocal information relative to advection on infinitesimal local gradients. In all four panels a threshold effect is easily visible whereby there is no benefit of nonlocal information gathering unless the advection rate is sufficiently high to allow exploitation of that information. Moreover, advection on nonlocal information is more valuable in landscapes with sharp patch edges (comparing the upper panels with the lower ones). However, this benefit depends on the detection function, with Gaussian detection (right panels) providing a greater benefit than top-hat detection (left panels), provided diffusion is not too strong. Note that these dissipative effects are strongest when the advection rate is high.

Sharp edges provide foragers with very limited local information about the resource distribution; however, nonlocal detection functions help to alleviate this limitation, allowing foragers to better track resources (fig. 4).

Advection on nonlocal information is also especially important in landscapes with highly transient resource patches. In particular, using a framework that combines measures of duration and frequency into a “pulse intensity” metric (app. SC) we show that, all else being equal, the relative benefit of nonlocal information (summarized by  $\Omega_{\max}/\Omega_0$ ) as well as the optimal detection distance,  $R_{\max}$ , are greater in more intense landscapes (i.e., landscapes with short-lived, high-abundance resource). However, overall foraging success in intense landscapes is lower than that in less intense systems (i.e., landscapes with long-lived, low-abundance resource). Not surprisingly, increasing rates of advection increases optimal detection distances, overall foraging success, and the benefit of nonlocal information ( $R_{\max}$ ,  $\Omega_{\max}$ , and  $\Omega_{\max}/\Omega_0$ ). As before, though, a threshold-type dependence on advection rate exists wherein no increase in optimal detection scale or payoff from nonlocal information occurs unless the

rate of advection is sufficiently strong (fig. SC2; figs. B1, B2, SB1, SB2, SC1, SC2, SD1 are available online). Interestingly, the advection rate at which nonlocal information becomes beneficial is smaller in more intense landscapes because even a little directed movement is beneficial when resources are very short-lived (app. SC).

### Discussion

We used a continuous space/continuous time movement model to investigate how the acquisition of nonlocal information about resource availability, coupled with local directed movement based on that information, influences foraging success in a dynamic landscape. Nonlocal information, whether attained through an increased scale of detection or via a shift to more kurtotic detection functions, was often highly beneficial, increasing foraging success up to twofold compared with movement using purely local cues (fig. 5). However, nonlocal information was useful only when foragers were sufficiently mobile to reach their transient resources before they disappeared. Nonlocal information was

particularly beneficial in landscapes with sharp (rather than gradual) patch edges and when the rate of random movement was sufficiently low that foragers did not drift away from the transient resource patch.

Broadly speaking, our findings with these continuum models parallel important results from OFT models. This is surprising because the two modeling frameworks are quite different in their assumptions about landscapes, the way individuals move, and even what constitutes foraging success. The convergence of results across modeling frameworks is especially clear when we focus on the consequences of perceptual constraints. In patch-based models, perceptual constraints result in undermatching, such that more foragers occur in resource-poor patches than expected (Abrahams 1986; Tregenza 1995). Likewise, in our models foragers lacking perceptual ranges often have lower overall foraging success. Second, patch-based models also predict that limits on perceptual range are more detrimental in coarse-grained landscapes (Ranta et al. 1999, 2000; Matsumura et al. 2010). Similarly, in our continuum models decreasing  $R$  decreases foraging success, and this effect is especially pronounced in coarse-grained landscapes, where there are only modest nonlocal resource gradients for foragers to advect on. Finally, in patch-based models “blundering foragers” (i.e., foragers that get lost easily from patches) obtain a good, although suboptimal, match to their resources when patch size is unknown (Adler and Kotar 1999). In our model, a similar benefit of wandering appears when increased diffusion increases  $\Omega_{\max}$  (figs. 3, 4).

Beyond broad similarities with patch-based models, however, our continuum approach also offers additional insights. In particular, our framework highlights how different kinds of resource landscapes and resource detection functions interact to provide foragers with either beneficial or detrimental nonlocal information. For example, a clear difference exists in maximum foraging success between the pulsed Gaussian and pulsed uniform resource landscapes (fig. 4). Specifically, the smooth edge of the pulsed Gaussian landscape facilitates consumer convergence on resources, independent of the detailed characteristics of forager behavior. In natural environments, habitat patches may be delimited by hard or soft edges (Stamps et al. 1987), and changes in habitat structure that soften patch edges facilitate movement (Ries et al. 2004). Over the long term, such differences in consumer convergence may be one reason why hard patch edges discourage species dispersal.

Similarly, we observed a clear benefit to Gaussian and exponential detection functions compared with the top-hat function (fig. 4) and, in more complex landscapes, a benefit to the exponential function over the Gaussian (fig. SD1). Kurtotic detection functions facilitate foraging success because the tails of the functions provide tidbits of information about resource conditions at remote locations, which

are essential when trying to navigate through landscapes where conditions change rapidly. Such “tailed” detection functions are especially advantageous when the foragers’ gradient-climbing ability is strong relative to random movement (fig. 4), with the exponential detection function being particularly advantageous in landscapes with more than one patch (fig. SD1).

### *The Utility of Nonlocal Information in Dynamic Landscapes*

Another novel finding of our work is the importance of nonlocal information in highly dynamic resource landscapes (figs. 5, SC2). Not surprisingly, landscapes featuring strongly pulsatile resources hinder absolute foraging success. However, compared with purely local information, advecting on nonlocal information provides a much greater relative gain in foraging success as the pulsatile “intensity” of landscapes increases. In general, nonlocal information appears most useful when it contradicts (or at least augments) local information, identifying the existence of a large-scale resource gradient that may not be detectable from purely local information. This can be seen for the pulsed uniform landscape, where nonlocal information effectively creates a perceived smooth gradient where the true resource distribution has only a sharp edge (fig. 5). There are clear analogies here to other fields, such as finding minima on complex surfaces, evolution on rugged fitness landscapes (where “jumps” avoid entrapment in local minima; Kauffman and Levin 1987), and denoising of images (where nonlocal sampling helps inform what the overall picture looks like; Buades et al. 2005).

We found strong evidence for the existence of optimal detection scales far smaller than the full landscape (figs. 3, 4). Information overload entails real costs in foraging success, even before considering energetic costs (Delgado et al. 2014). Indeed, when foragers have the wrong detection scale for their landscape they are better off having insufficient spatial information than too much (figs. 3, SD1). This is especially true for highly mobile foragers that are able to track resource gradients quickly. In an evolutionary context, such asymmetries would entail differential penalties for being wrong in different ways. In this case, selective pressures to greatly enhance perceptual range would be countered by other factors in all but the most ephemeral of landscapes.

Optimal detection scales exist in our model because global knowledge ( $R \rightarrow x_{\max}$ ) is functionally different from the kinds of omniscience traditionally assumed in OFT (Fretwell and Lucas 1970; Charnov 1976). Our integral approach to perceptual range (eq. [1]) builds in an averaging process that incurs a loss of information relative to moving based on the location of the strongest resource peak. Averaging is det-

rimental any time detection scales exceed the inherent scale of resource distribution across the landscape. This is because it flattens the perceived resource gradient and removes movement cues. In landscapes with multiple resource peaks, this manifests as a kind of spatial confusion in which individuals are simultaneously pulled by the gradients of different peaks (see fig. SD1). Because large detection scales are not always optimal (figs. 3, 4, SB1, SD1), even in static landscapes (app. B), the optimal solution is to select detection scales that minimize information loss due to spatial averaging (see also Martínez-García et al. 2013, 2014).

Different assumptions about how foragers process nonlocal information (e.g., detecting peaks versus averaging) entail losses of different information subsets. This selectivity creates important opportunities for evolutionary trade-offs linking perceptual ranges and mobility. For example, foragers that perceive and quickly move toward resource peaks could be misdirected toward small patches of high-quality resources, when instead they would be better off moving toward larger patches of lower-quality resources, particularly if there is a tendency to wander. Experimental studies of patch choice in which the same total amount of resources is distributed in different ways for animals with different perceptual ranges would facilitate exploration of these ideas.

Evolution likely acts in complex ways on the method by which animals attain the nonlocal information necessary to inform their movement. Our theoretical animals could obtain more nonlocal information about their resources either by increasing their detection scale,  $R$ , or by utilizing a more kurtotic detection function,  $g(y, x, R)$ . The first method increases the total amount of visual or auditory information that an animal would need to process, whereas the second method introduces a measure of selectivity in perception, providing a limited amount of information about remote resources. In our modeling, large values of  $R_{\max}$  together with the more kurtotic Gaussian or exponential detection functions yielded the greatest foraging success, especially in Gaussian landscapes (fig. 4). However, these mechanisms need not covary in nature, as when an animal's ability to discern important details at long distances reduces its perceptual field (Eriksen and James 1986). One prediction here is that increased detection scales should be favored in landscapes where it is actually possible to obtain long-distance information regularly but that kurtotic detection functions should be additionally favored when those landscapes are highly dynamic or spatially complex (figs. SC2, SD1).

Independent of information processing and the inherent information loss that this entails, other disadvantages can also emerge from overreliance on nonlocal information. Most notably, a forager should react to ephemeral resources only if it can reliably reach and exploit them before they disappear. If, instead, an animal is consistently "late to the

party," then it not only fails to acquire distant resources but also misses out on more attainable opportunities nearby. This error becomes even more costly if movement is energetically expensive (Delgado et al. 2014), which is not the case in our current model. Perhaps this is the reason that we see evidence for distant resource discounting in many species (i.e., real resource detection functions may have shapes more like those in eqq. [7] and [8] than in eq. [6]). For example, human and nonhuman primates dramatically discount more remote resources relative to nearby resources (Stevens et al. 2005; Janson 2007; Mühlhoff et al. 2011), and this devaluation occurs even when the costs of locomotion are negligible or nonexistent (Stone 2008; Howard and Fragazy 2014). From these results, we predict such discounting to be less stringent in more dynamic landscapes.

#### *When and Where Is Nonlocal Information Available in the Real World?*

Our model of nonlocal information will be most useful for interpreting animal movement decisions in systems where nonlocal information is readily available. One example is open grassland landscapes, where information about resources in remote areas may be regularly obtainable through visual sensing. For example, Holdo et al. (2009) demonstrated the importance of nonlocal information gathering in their model of Serengeti wildebeest migration. In that system, the model predicted that migration would occur when wildebeest could track the availability of their resources at the ~100-km scale, but there was no migration when the foragers based their movement decision on purely local information (Holdo et al. 2009).

However, even when individuals cannot observe remote resources, nonlocal information gathering may still be possible. In particular, sharing of public information may be a useful surrogate for distant cues (Danchin et al. 2004). Martínez-García et al. (2013) developed a model of animal movement in which pairs of foragers communicate with each other over long distances. Such long-distance communication—which may be achieved, for example, by individuals calling to one another—provides a mechanism for individuals to locate resource patches at distances far beyond their own local wandering. That model yielded a result that parallels predictions from our model: either an excess or a lack of communicated nonlocal information can worsen the spatial match between foragers and their resources (Martínez-García et al. 2013). This is consistent with our findings concerning the benefits of a midrange resource detection scale (figs. 3, 4, SD1).

These ideas concerning a midrange peak in detection ability lend themselves to exploration with empirical data. For example, under the assumption that satellite-derived normalized difference vegetation index (NDVI) data reflect



the availability of food resources for ungulates (e.g., Mueller et al. 2011b), researchers could combine satellite data with GPS movement tracking data to quantify resource availability within the vicinity of real animals moving through real landscapes. Calculations would need to be implemented at the individual level using alternative candidate perceptual ranges, but one expectation would be that key metrics of animals' mobility should correlate positively with the width of the perceptual ranges that provide the optimal overlap with available NDVI values.

#### *Future Directions for Modeling*

Going forward, perceptual range models like the one presented here could be developed to explore a variety of new questions in the spatial ecology of foragers. One immediate extension would focus on what happens when foragers deplete their resources. Such losses are absent from some natural consumer-resource systems (Bewick et al. 2016) but are routinely assumed in models of consumer spatial ecology that invoke the ideal free distribution (Fretwell and Lucas 1970; Lessells 1995). Adding this important piece of realism would require a new metric of foraging success beyond that in equation (3).

Additional challenging but intriguing future opportunities require modifying our movement model (eq. [2]) so that detection distances depend on the foragers' location or rate of movement. These changes would substantially complicate both the model and our numerical analyses, but they would permit exploration of speed versus detection accuracy trade-offs like those identified experimentally in coati-mundis (Hirsch 2010) and capuchins (Janson and Di Bitetti 1997). Additional changes, such as spatially dependent alternatives to our resource detection functions (eqq. [6]–[8]), would provide insights into how local conditions influence detection of remote resources (e.g., Conover 2007). Related opportunities exist for modeling scenarios where movement itself depends on proximity to a detectable resource. For example, Prevedello et al. (2011) report that Brazilian marsupials move in a highly directed fashion when they can perceive a forest patch but move randomly when the nearest patch is located beyond their perceptual range. We discuss additional future directions in appendix C.

#### *Conclusion*

Classical foraging models typically assume either that individuals are omniscient or that they base movement decisions on purely local information. Real biological organisms fall between these extremes: individuals routinely benefit by integrating information from their surroundings before making movement decisions. However, there are strong limits on

their perceptual ranges, in terms of both absolute distance and available detail.

Our model extensively explores this middle ground and suggests that foragers can profitably use nonlocal information to locate and exploit transient resource pulses in dynamic environments. Nonlocal information is especially valuable in highly dynamic landscapes featuring sharp-edged resource patches and in “intense” landscapes where resources are especially fleeting. How organisms detect (or value) nearby versus remote resources determines how well they concentrate on their resources in space and time, and even modest amounts of information about remote resources can lead to profound improvements in foraging success compared with movement based only on local information (fig. 5). However, nonlocal information alone is not enough to improve foraging success. Instead, the foragers must also be sufficiently mobile to react (advent) quickly to exploit transient resources. This link between perceptual range and dispersal traits echoes ideas emerging from evolutionary studies (Delgado et al. 2014) and makes clear that a deeper exploration of nonlocal information use in the context of dispersal will require additional ideas from both OFT and TED. Moreover, our study reveals a strong dose of context dependence as well, suggesting that highly dynamic and edgy landscapes will foster the coevolution of perceptual range and dispersal ability because both kinds of traits are essential to the acquisition of transient resources.

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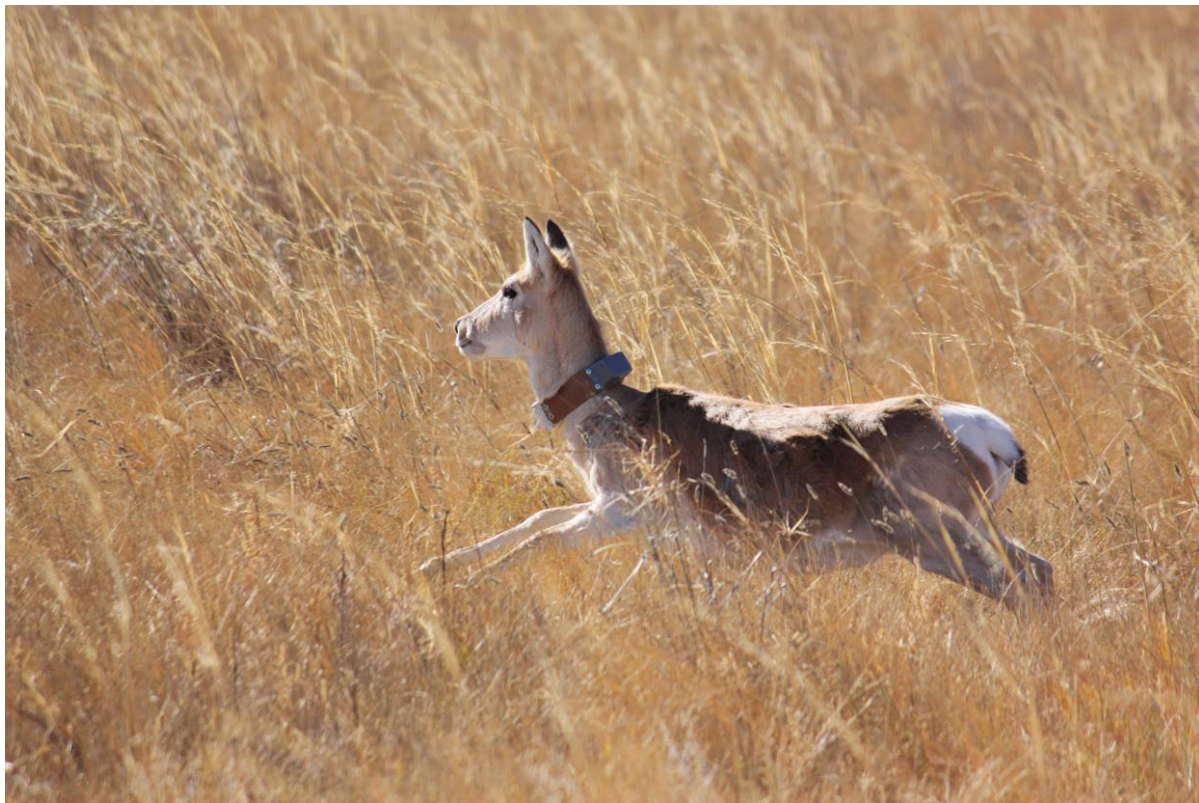


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A Mongolian gazelle (*Procapra gutturosa*) wearing a GPS collar to track its movements over >2 years. The Eastern Steppes of Mongolia, where this species thrives, are some of the most dynamic and spatiotemporally unpredictable landscapes on the planet. Photo credit: William F. Fagan.