

## Advection–diffusion equations for generalized tactic searching behaviors

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**Abstract.** Many organisms search for limiting resources by using repeated responses to local cues, which cumulatively cause movement towards more favorable parts of their environment. This paper presents a general asymptotic expression, derived under the assumption of shallow environmental gradients, for the population-level flux of organisms moving at a constant speed and reorienting at rates determined by the environmental conditions experienced since the last reorientation. The expression takes the form of an advection-diffusion equation, in which the diffusivity and advection velocity are determined by statistics of the turning algorithm that are directly comparable to empirical observations. This work provides a mechanism with which to systematically evaluate a wide variety of tactic and kinetic strategies for determining turning behaviors.

The model is applied to searchers on spatially-variable, random distributions of discrete resource patches. Such algorithms are functions of the integrated resource density encountered between turns. It is shown that behaviors in which the *turning time distribution* is a function of integrated density cannot result in taxis. In contrast, behaviors in which the *turning rate* is a function of integrated density can result in taxis. These two classes of search algorithm differ in that the latter requires the searcher to “learn” about its local environment, whereas the former requires no such assessment. This suggests neural or physiological mechanisms for remembering previous encounters may be a biological requirement for searchers on discrete resource distributions.

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## 1 Introduction

Many animals confront the problem of using local cues to move from unfavorable parts of their environment to more suitable areas, for example those richer in food or another limiting resource. Movements of this type are widely believed to have important consequences for the population biology of these animals and the dynamics of communities in which they occur. Two largely independent lines of theoretical work have addressed the relative spatial distributions of resources and consumers. Behavioral ecologists have developed an extensive *foraging theory* to give an evolutionary context to the searching strategies of foraging animals. Foraging theory originally addressed animals which have (at least in an evolutionary sense) a relatively complete knowledge of the variable resources distributions in their environment, and must choose only where within those distributions to array themselves (Kacelnik and Houston, 1984; Kacelnik and Krebs, 1985; Kacelnik et al., 1992). More recent models of foraging strategies have focused on various limitations on the information searchers have available to them (e.g., Mangel, 1990; Dukas and Clark, 1995), but have not explicitly incorporated spatial distributions of animals and resources, nor considered the tactic behaviors by which animals may take advantage of spatial correlations in their local environment to lead them to more favorable areas.

A complementary set of mathematical analyses have been developed describing the long-term consequences of tactic gradient-climbing strategies, usually in terms of partial differential equations for fluxes of population or probability density and ordinary differential equations for spatial moments of density (e.g., Patlak, 1953; Nossal and Weiss, 1974; Alt, 1980; Okubo, 1980; Othmer et al., 1988). Examples of gradient-climbing strategies which have been investigated include *area-restricted search* algorithms (Smith, 1974; Kareiva and Odell, 1987; Dukas and Real, 1993; Veit et al., 1993, 1994), in which animals respond to high levels of an environmental attractant by turning more frequently or moving more slowly, and *directional tactic* or *temporally-differential kinetic* algorithms (Keller and Segel, 1971; Segel, 1978, 1982; Murray, 1989; Tranquillo and Alt, 1990), in which animals respond directly to positive attractant gradients by turning less frequently or moving more rapidly. Movements of micro-organisms such as bacteria

and slime molds (Berg and Brown, 1974; Rubinow et al., 1981; Rivera et al., 1989; Tyson et al., 1989; Tranquillo, 1990; Mitchell et al., 1991), cells such as leukocytes (Alt, 1980), and insects such as ladybugs and butterflies (Kareiva and Odell, 1987; Odendaal et al., 1988) have been described in impressive detail. However, such descriptions have for the most part stopped at the population-level flux description, without examining limitations inherent in specific searching strategies on specific resource distributions, and the evolutionary consequences of those constraints. It remains unclear, for example, how to rank resource distributions according to their quality as perceived by a searcher using a particular strategy, or conversely, how to rank searching strategies according to how well they perform on a given set of resource distributions.

One prerequisite for an improved evolutionary understanding of tactic behaviors is a generalized modeling framework which facilitates the systematic study of *variation* in behavior and the *selective consequences* of this variation in different environments. In this paper, I build generalized mathematical tools to study the ecological and evolutionary aspects of animal searching strategies in variable two-dimensional resource distributions. Specifically, the equations analyzed here describe the probability density flux for individuals performing a biased random walk with the following properties (Alt, 1980):

- (1) individuals move at a constant forward speed,  $c$ ;
- (2) changes in orientation angle,  $\theta$ , occur as discrete turning events at random intervals;
- (3) at each turn, orientation changes by an angular displacement chosen randomly according to a reorientation kernel; the reorientation distribution is non-negative and assumed to be symmetrical with respect to right and left turns, and independent of time, space, and pre-turn orientation;
- (4) turning rate is a function of the exposure (since the last turn) to some environmental properties, described in terms of an “attractant” or “resource” distribution,  $\rho(t, x)$ .

The key aspect of non-random taxis in this model is captured by the dependency of turning rate on exposure to some cue – without such a dependency the model would reduce to a simple random walk. The object of the analysis is to determine the *expected* or *population-level* effectiveness of various *individual-level* behavioral responses to environmental heterogeneity, as measured by the resulting rates of taxis to attractant concentrations.

The primary mathematical result of this paper is a Patlak–Keller–Segel-type *advection–diffusion equation* (ADE) giving the population-level

flux of animals, obtained via a regular perturbation expansion (Kevorkian and Cole, 1981) under the assumption of shallow environmental gradients. The analysis follows that of Alt (1980) for leukocyte and bacteria movement. The present derivation generalizes the turning behavior, which can be specified either in terms of the turning time distribution or of turning rates, and the resulting equation can be used to systematically investigate and compare a wide variety of behavioral algorithms. To increase its biological utility, the diffusivity and advection velocity coefficients are specified in terms of statistics of the turning algorithm that are directly comparable to empirical observations. As an example of behaviors that are possible to analyze with the new, generalized model, I examine the effectiveness of two classes of stochastic responses of searching animals to randomly distributed discrete resource patches, as for example in the case of a predator encountering individuals or groups (e.g., schools or swarms) of a prey species. This analysis suggests that some capacity for short-term learning about the environment may be a minimal requirement for effective taxis on discrete resource patches.

## 2 Mathematical derivation

### 2.1 Constitutive equations and non-dimensionalization

Following Alt (1980), turning rates (and therefore searcher density) are specified as functions of time,  $t^*$ , position,  $\mathbf{x}^*$ , orientation angle,  $\theta$ , and time since last turn,  $\tau^*$ ; these variables implicitly determine the environment experienced by an individual since its last turn. The rate of change of searcher probability density,  $\sigma^*(t^*, \mathbf{x}^*, \theta, \tau^*)$ , is given by the material derivative following a cohort moving at speed  $c$  in direction  $\theta$ , which are conserved other than removal by turning,

$$D^{\theta*}\sigma^* + \partial_{\tau^*}\sigma^* = -\beta'^*\sigma^*, \quad (2.1)$$

where  $\beta'^*(t^*, \mathbf{x}^*, \theta, \tau^*)$  is the instantaneous turning rate of individuals at  $t^*$ ,  $\mathbf{x}^*$ , moving in direction  $\theta$  with lag  $\tau^*$  since the last turn (i.e., turns are regarded as Poisson-process events occurring at rate  $\beta'^*$ ).  $D^{\theta*} = (\partial_{t^*} + c\theta \cdot \nabla^*)$ , and  $(^*)$  denotes dimensional quantities. In (2.1), the left hand terms establish a frame of reference that moves with individuals in  $t^*$ ,  $\mathbf{x}^*$ , and  $\tau^*$ , and the right hand side represents “sources” and “sinks” of individuals due to turning behavior. Equation (2.1) is a Boltzmann equation for the probability density of a single animal’s state, in which the animal’s behavior replaces the “collision” term as the mechanism generating changes in particle velocity. However,

since the behavior is density-independent (animals respond to their environment but not to each other directly), (2.1) is a linear equation and we may interpret  $\sigma^*$  as also describing the density distribution of a population.

The system is further described by a boundary condition at  $\tau^* = 0$ , where individuals reappear with zero time lag after they have turned,

$$\sigma^*(\bullet, \eta, 0) = \int_0^\infty \int_S (\beta'^* \sigma^*)(\bullet, \theta, \tau^*) k(\theta - \eta) d\theta d\tau^*. \quad (2.2)$$

In (2.2), the  $(\bullet)$  notation denotes the time and space coordinates,  $t^*$ ,  $\mathbf{x}^*$ , and  $S$  represents the angular domain  $[-\pi, \pi]$ .  $k(\theta)$  is the reorientation kernel, i.e., the probability that a turn results in an angular displacement of  $\theta$ . The reorientation kernel is assumed to be *non-negative* and *symmetric* ( $k(\theta) = k(-\theta)$ ,  $-\pi \leq \theta \leq \pi$ ), i.e., turns to the right and left are equally likely.

The main result of this paper is a regular perturbation expansion of (2.1)–(2.2), under the additional assumption that the searching behavior occurs at much smaller space and time scales than changes in the environment. From the perspective of a searcher, this means that the resource landscape changes in time and space slowly enough that many search steps (or “runs”) are required for the environment to change significantly. The scaling assumption also implies that the behaviors of searchers vary only slightly with orientation angle, as for example may be the case when searchers are limited by their ability to detect and respond to changes in attractant density. The analysis results in an advection–diffusion equation in which the empirically inaccessible variables  $\tau$  and  $\theta$  are removed by integration, i.e., for the *total searcher density*,

$$\bar{\sigma}^*(t^*, \mathbf{x}^*) = \int_0^\infty \int_S \sigma^*(\bullet, \theta, \tau^*) d\theta d\tau^*, \quad (2.3)$$

and in which the spatially varying diffusion and advection are expressed in terms of measurable statistics of the turning rates.

Characteristic variables describing the system are:

$L \equiv$  length scale of attractant change (e.g.,  $\frac{\rho^*}{|\nabla \rho^*|}$ );

$T \equiv \frac{l}{c}$  = time scale of attractant change for searchers;

$l \equiv$  length scale over which attractant density is assessed (e.g., characteristic distance between resource patches,  $\frac{1}{\sqrt{\rho^*}}$ );

$\tau_0 \equiv \frac{l}{c}$  = time scale of decision-making based on attractant density (e.g., patch encounter interval).

Thus, I assume that search run time  $\tau^*$  is appropriately scaled by  $\tau_0$ , and the ratio,  $\varepsilon$ , of the space and time scales of search steps to those of

attractant changes is small,

$$\frac{\tau_0}{T} = \frac{l}{L} = \varepsilon \ll 1.$$

Using the non-dimensionalizations  $\sigma^* = \sigma_0 \sigma$ ,  $\mathbf{x}^* = L\mathbf{x}$ ,  $t^* = Tt$ ,  $\tau^* = \tau_0 \tau$ , and the turning rate scaling

$$\beta^*(t^*, \mathbf{x}^*, \theta, \tau^*) = \frac{1}{\varepsilon T} \beta' \left( \frac{t^*}{T}, \frac{\mathbf{x}^*}{cT}, \theta, \frac{\tau^*}{\varepsilon T} \right),$$

the non-dimensional form of the governing equations is:

$$\begin{aligned} \varepsilon D^\theta \sigma + \partial_\tau \sigma &= -\beta' \sigma, \\ \sigma(\bullet, \eta, 0) &= \int_0^\infty \int_S (\beta' \sigma)(\bullet, \theta, \tau) k(\theta - \eta) d\theta d\tau, \end{aligned} \tag{2.4}$$

where the small parameter  $\varepsilon$  is to be used as the basis of the perturbation expansion. Equation (2.4) reflects the scaling properties that local equilibration of searcher distributions in  $\theta$  and  $\tau$  occurs rapidly, while changes of searcher distributions in space and time occur much more slowly. From a biological perspective, the problem is to explicitly link rapid individual behaviors to population movements at these large space and time scales; thus, the analysis will focus on the long-term or “outer” solution to the regularly perturbed equations.

## 2.2 Turning behaviors

The definition of the turning behavior,  $\beta^*(t^*, \mathbf{x}^*, \theta, \tau^*)$ , in the Boltzmann equation (2.1)–(2.4) projects backwards in space and time, i.e., it specifies turning rate for individuals that are at  $t^*, \mathbf{x}^*$ , but that began their runs at  $t^* - \tau^*, \mathbf{x}^* - c\theta\tau^*$ . This definition has the somewhat confusing consequence that individuals with the same  $t^*, \mathbf{x}^*$  coordinates but different  $\tau^*$ 's began runs at different times and positions. In most cases, it is more intuitive to define turning behavior by projecting forwards in space and time from a fixed starting point, that is, to think of the future turning rates of a cohort of individuals that all began run at  $t^*, \mathbf{x}^*$ . To make use of this more intuitive frame of reference, I give a supplementary definition of turning behavior,

$$\beta^*(t^*, \mathbf{x}^*, \theta, \tau^*) \equiv \beta^*(t^* + \tau^*, \mathbf{x}^* + c\theta\tau^*, \theta, \tau^*). \tag{2.5}$$

Thus,  $\beta^*(t^*, \mathbf{x}^*, \theta, \tau^*)$  is the turning rate of searchers that started a run at  $t^*, \mathbf{x}^*$ , and have been moving in the  $\theta$ -direction for a run time  $\tau^*$ .

Increasing  $\tau^*$  while fixing  $t^*, \mathbf{x}^*$  in the arguments of  $\beta^*$  gives the turning rate for the same cohort of individuals as their runs get longer.

Along its run, each searcher performs an *assessment* of its environment, in which it detects and evaluates some characteristics of the local attractant distribution (concentration, gradient, etc.), and undergoes a *response* to the results of that assessment (i.e., a certain probability of turning). In order to keep the assessment and response behaviors as general as possible, I formalize the searcher's turning rate as a general *response functional*,

$$\beta^*(t^*, \mathbf{x}^*, \theta, \tau^*) = B^*(\rho^*(t^* + \tilde{\tau}^*, \mathbf{x}^* + c\theta\tilde{\tau}^*)|0 \leq \tilde{\tau}^* \leq \tau^*), \quad (2.6i)$$

or, in non-dimensional form,

$$\beta(t, \mathbf{x}, \theta, \tau) = B(\rho(t + \varepsilon\tilde{\tau}, \mathbf{x} + \varepsilon\theta\tilde{\tau})|0 \leq \tilde{\tau} \leq \tau). \quad (2.6ii)$$

This way of specifying behavior allows the turning rate to potentially depend on the attractant distribution at any subset of points along the animal's trajectory,  $t^* + \tilde{\tau}^*, \mathbf{x}^* + c\theta\tilde{\tau}^*$ .

In (2.6), the searcher's assessment of its environment may depend on any features of the attractant distribution, such as derivatives, integrals, etc. For example, the animal might respond to the attractant gradient, either through a *directional* tactic response or by a *temporally differential* kinetic response (Tranquillo and Alt, 1990). It is therefore convenient to rewrite the turning functional as an explicit function of the attractant concentration,  $\rho$ , and its derivative,  $D^\theta\rho$ , both evaluated at the point of departure,

$$\beta(t, \mathbf{x}, \theta, \tau) = B_1(\rho(t, \mathbf{x}), \varepsilon D^\theta\rho(t, \mathbf{x}), \tau) + O(\varepsilon^2). \quad (2.7)$$

The  $\varepsilon$  in the second argument of  $B_1$  reflects the original scaling assumption, i.e., that only small rates of attractant change are perceived within a run, and that behavioral responses are therefore also small.

Now the components of the turning behavior in (2.5) and (2.7) can be summarized in empirically meaningful terms as

$$\begin{aligned} \beta(t, \mathbf{x}, \theta, \tau) &= \gamma_0 + \varepsilon\gamma_1 D^\theta\rho + O(\varepsilon^2), \\ \beta'(t, \mathbf{x}, \theta, \tau) &= \gamma_0 + \varepsilon(\gamma_1 - \tau\gamma_2)D^\theta\rho + O(\varepsilon^2), \\ \gamma_0 &= B_1(\rho(t, \mathbf{x}), 0, \tau), \quad \gamma_1 = \partial_2 B_1(\rho(t, \mathbf{x}), 0, \tau), \\ \gamma_2 &= \partial_1 B_1(\rho(t, \mathbf{x}), 0, \tau). \end{aligned} \quad (2.8)$$

In (2.8),  $\partial_1 B_1, \partial_2 B_1$  are derivatives of the response functional with respect to its first and second arguments. The interpretations of the terms in (2.8) are:  $\gamma_0$  is the *non-directional* component of turning rate

(i.e., averaged over all orientations),  $\gamma_1$  is the *directional sensitivity* of the turning rate to the attractant gradient, and  $\gamma_2$  is the *non-directional sensitivity* of the turning rate.

### 2.3 Regular perturbation expansion

Substituting (2.8) into (2.4), taking the perturbed searcher density as

$$\sigma = s_1 + \varepsilon s_2 + \varepsilon^2 s_3 + \dots,$$

and expanding,

$$\begin{aligned} & \varepsilon(D^\theta s_1 + \varepsilon D^\theta s_2 + \varepsilon^2 D^\theta s_3 + \dots) + \partial_\tau s_1 + \varepsilon \partial_\tau s_2 + \varepsilon^2 \partial_\tau s_3 + \dots \\ & = - [s_1 + \varepsilon s_2 + \varepsilon^2 s_3 + \dots] [\gamma_0 + \varepsilon(\gamma_1 - \tau\gamma_2)D^\theta \rho + \dots]; \\ & s_1(\bullet, \eta, 0) + \varepsilon s_2(\bullet, \eta, 0) + \varepsilon^2 s_3(\bullet, \eta, 0) + \dots \\ & = \int_0^\infty \int_S [s_1 + \varepsilon s_2 + \varepsilon^2 s_3 + \dots] [\gamma_0 + \varepsilon(\gamma_1 - \tau\gamma_2)D^\theta \rho + \dots] \\ & \quad \times (\bullet, \theta, \tau) k(\theta - \eta) d\theta d\tau. \end{aligned} \tag{2.9}$$

Collecting terms of like order, the perturbed equations are:

$O(1)$ :

$$\partial_\tau s_1 + \gamma_0 s_1 = 0, \tag{2.10i}$$

$$s_1(\bullet, \eta, 0) - \int_0^\infty \int_S (s_1 \gamma_0)(\bullet, \theta, \tau) d\theta d\tau = 0; \tag{2.10ii}$$

and

$O(\varepsilon)$ :

$$\partial_\tau s_2 + \gamma_0 s_2 = -D^\theta s_1 - s_1(\gamma_1 - \tau\gamma_2)D^\theta \rho, \tag{2.11i}$$

$$\begin{aligned} & s_2(\bullet, \eta, 0) - \int_0^\infty \int_S (s_2 \gamma_0)(\bullet, \theta, \tau) k(\theta - \eta) d\theta d\tau \\ & = \int_0^\infty \int_S s_1((\gamma_1 - \tau\gamma_2)D^\theta \rho)(\bullet, \theta, \tau) k(\theta - \eta) d\theta d\tau. \end{aligned} \tag{2.11ii}$$

To reiterate, the biologically most interesting features are the relatively slow changes in population distribution in space and time, that correspond to the “outer” solutions of the perturbed equations. Thus, I do not analyze the “inner” solutions to (1.10)–(2.11), corresponding to initial transients in which population distributions in  $\theta$  and  $\tau$  rapidly approach local equilibrium.

Before solving these equations, it is helpful to define some statistics of the searching behavior that will arise in the subsequent analysis.

2.3.7 *Turning statistics*

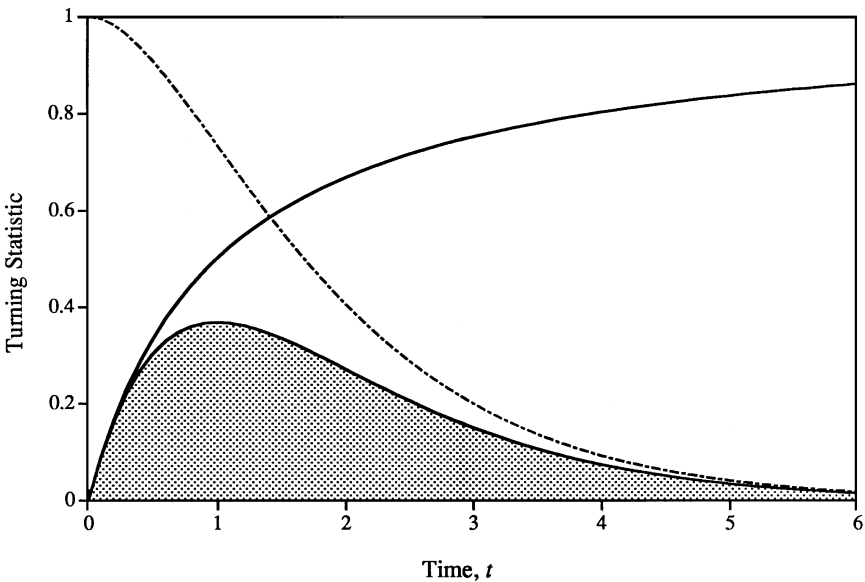
The behavioral property that is in many cases most directly observable and best describes the consequences of a hypothetical turning algorithm is the *turning time distribution* (Alt, 1980),

$q_{t,x,\theta}(\tau) \equiv$  the probability an individual starting at  $t, \mathbf{x}$  in direction  $\theta$  has not turned before time lag  $\tau$ .

Expressions for the turning distribution and statistics derivable from it are given here; these will be used to express the final equation for searcher density flux in empirically meaningful terms (see Fig. 1).

The turning rate and turning distribution are related by

$$q_{t,x,\theta}(\tau) = \exp \left[ - \int_0^\tau \beta(t, \mathbf{x}, \theta, \tau') d\tau' \right], \tag{2.12}$$



**Fig. 1.** Observed turning statistics. A frequently recorded type of movement data is the *probability distribution* of run times,  $\phi(\tau)$ , i.e., the frequency with which steps of duration  $\tau$  are observed. Shown here (shaded area) for illustration is a *gamma*-distribution,  $\phi(\tau) = \lambda^2 \tau e^{-\lambda\tau}$ , for  $\lambda = 1$ . The turning distribution,  $q(\tau) = 1 - \int_0^\tau \phi(\tau') d\tau'$ , is the probability that a given step is *at least of length*  $\tau$ ; for the *gamma*-distribution,  $q(\tau) = (\lambda\tau + 1)e^{-\lambda\tau}$  (dashed curve). The turning rate (see (2.13)) for this distribution is  $\beta(\tau) = \lambda^2\tau/\lambda\tau + 1$  (solid curve). For this distribution the mean step length is  $\bar{\tau}_0 = 2/\lambda$ , the second moment is  $\hat{\tau}_0 = 3/\lambda^2$ .

and

$$\beta(t, \mathbf{x}, \theta, \tau) = -\partial_\tau \ln(q_{t,\mathbf{x},\theta}(\tau)), \tag{2.13}$$

Expanding with the use of (2.8), and dropping terms of  $O(\varepsilon^2)$  for the remainder of this section,

$$q_{t,\mathbf{x},\theta}(\tau) = q_0(\tau)(1 - \varepsilon D^\theta \rho q_1(\tau)), \tag{2.14}$$

where

$$q_0(\tau) = \exp\left[-\int_0^\tau \gamma_0 d\tau'\right], \quad q_1(\tau) = \int_0^\tau \gamma_1 d\tau'$$

are respectively the non-directional and directional components of the turning distribution. The spatial derivative of the non-directional turning distribution is

$$D^\theta q_0(\tau) = -\int_0^\tau \gamma_2 d\tau' q_0(\tau) D^\theta \rho. \tag{2.15}$$

Mean run length of individuals starting at  $t, \mathbf{x}$  in direction  $\theta$  is

$$\bar{\tau} = \int_0^\infty q(\tau) d\tau = \bar{\tau}_0 - \varepsilon D^\theta \rho \bar{\tau}_1 \tag{2.16}$$

where

$$\begin{aligned} \bar{\tau}_0 &= \int_0^\infty q_0(\tau) d\tau, & \bar{\tau}_1 &= \int_0^\infty q_0(\tau) q_1(\tau) d\tau, \\ D^\theta \bar{\tau}_0 &= -\int_0^\infty \int_0^\tau \gamma_2 d\tau' q_0(\tau) d\tau D^\theta \rho \end{aligned}$$

are the non-directional and directional components of mean run length and its derivative. Similarly,

$$\hat{\tau} = \int_0^\infty \tau q(\tau) d\tau = \hat{\tau}_0 - \varepsilon D^\theta \rho \hat{\tau}_1, \tag{2.17}$$

is the second moment of run length, where the non-directional and directional components and the derivative are

$$\begin{aligned} \hat{\tau}_0 &= \int_0^\infty \tau q_0(\tau) d\tau, & \hat{\tau}_1 &= \int_0^\infty \tau q_0(\tau) q_1(\tau) d\tau, \\ D^\theta \hat{\tau}_0 &= -\int_0^\infty \tau \int_0^\tau \gamma_2 d\tau' q_0(\tau) d\tau D^\theta \rho. \end{aligned} \tag{2.18}$$

A further useful statistic of the turning distribution is the *directionality*,  $U_1$ , which is the directional bias of individual run lengths,

$$\varepsilon U_1 = \frac{1}{\pi} \int_S \theta \bar{\tau} d\theta = -\varepsilon \bar{\tau}_1 \nabla \rho. \quad (2.19)$$

### 2.3.2 $O(1)$ solution

From the  $O(1)$  governing equations, (2.10), it follows that

$$s_1(\bullet, \theta, \tau) = s_1(\bullet, \theta, 0) \exp \left[ - \int_0^\tau \gamma_0 d\tau \right] = s_1(\bullet, \theta, 0) q_0(\tau) \quad (2.20)$$

and

$$\begin{aligned} s_1(\bullet, \eta, 0) &= \int_0^\infty \int_S (s_1(\bullet, \theta, 0) \gamma_0(\bullet, \theta, \tau) \exp \left[ - \int_0^\tau \gamma_0 d\tau \right] k(\theta - \eta) d\theta d\tau \\ &= \int_S s_1(\bullet, \theta, 0) k(\theta - \eta) d\theta. \end{aligned} \quad (2.21)$$

In (2.21), use is made of the facts that the factors containing  $\tau$  are explicitly integrable, and that no searcher turns instantly ( $q_0(0) = 1$ ) or runs forever without turning ( $\lim_{\tau \rightarrow \infty} q_0(\tau) = 0$ ). Because there is no preferred direction to  $O(1)$  in the turning distribution, the density of individuals that have just turned is equal for all orientations. Thus, searcher density may be expressed to this order in terms of the average (non-directional) turning distribution.

$$s_1(t, \mathbf{x}, \theta, \tau) = c_1(t, \mathbf{x}) q_0(\tau), \quad (2.22)$$

where  $c_1$  is a scalar function of  $t, \mathbf{x}$ . Integrating over all time lags, the density of searchers heading in any direction is, to  $O(1)$ ,

$$\bar{s}_1(t, \mathbf{x}, \theta) = \int_0^\infty s_1(t, \mathbf{x}, \theta, \tau) d\tau = c_1 \bar{\tau}_0. \quad (2.23)$$

Integrating now over all orientation angles, total searcher density is

$$\bar{\bar{s}}_1(t, \mathbf{x}) = \int_S \bar{s}_1 d\theta = 2\pi c_1 \bar{\tau}_0, \quad (2.24)$$

and the  $O(1)$  density flux,

$$J_1 = \int_S \theta \bar{s}_1 d\theta = 0. \quad (2.25)$$

Thus, to  $O(1)$ , searcher density is constant, and the terms describing the rates of change of searcher density appear first at  $O(\varepsilon)$ .

### 2.3.3 $O(\varepsilon)$ solution

Collecting the unknown  $s_2$  terms, the dynamical equation (2.11i) can be written

$$\partial_\tau s_2 + \gamma_0 s_2 = R_2, \quad R_2 = -D^\theta s_1 - s_1(\gamma_1 - \tau\gamma_2)D^\theta \rho, \quad (2.26)$$

where by use of

$$D^\theta s_1 = D^\theta(c_1(t, \mathbf{x})q_0(\tau)) = q_0(\tau)(D^\theta c_1) - c_1 \int_0^\tau \gamma_2 d\tau' D^\theta \rho q_0(\tau),$$

the inhomogeneous term simplifies to

$$R_2 = q_0 \left\{ -D^\theta c_1 + c_1 D^\theta \rho \left[ \int_0^\tau \gamma_2 d\tau' - (\gamma_1 - \tau\gamma_2) \right] \right\}.$$

With substitution and integration by parts, (2.11ii) becomes

$$s_2(\bullet, \theta, \tau) = q_0(\tau) \left\{ s_2(\bullet, \theta, 0) - \tau D^\theta c_1 - c_1 D^\theta \rho \int_0^\tau (\gamma_1 - \tau'\gamma_2) d\tau' \right\}. \quad (2.27)$$

Eq. (2.27) gives the  $O(\varepsilon)$  searcher density in terms of the unknown  $O(\varepsilon)$  zero time lag boundary condition,  $s_2(\bullet, \theta, 0)$ . This unknown is determined by

$$s_2(\bullet, \eta, 0) - \int_S s_2(\bullet, \theta, 0) k(\theta - \eta) d\theta = Q_2. \quad (2.28i)$$

where again the  $\tau$ -dependent terms are integrable and evaluate to unity. The inhomogeneous part of (2.28i), which contains only known  $O(1)$  terms, is

$$Q_2 = \int_0^\infty \int_S k(\theta - \eta) \left( \gamma_0 \left[ q_0(\tau) \left\{ -\tau D^\theta c_1 - c_1 D^\theta \rho \int_0^\tau (\gamma_1 - \tau'\gamma_2) d\tau' \right\} \right] \right. \\ \left. + c_1 D^\theta \rho (\gamma_1 - \tau\gamma_2) q_0(\tau) \right) d\theta d\tau.$$

Using the identities (from integration by parts)

$$\int_0^\infty \gamma_0 q_0(\tau) d\tau = \bar{\tau}_0$$

and

$$\int_0^\infty \left( \gamma_0 q_0(\tau) \int_0^\tau (\gamma_1 - \tau'\gamma_2) d\tau' \right) d\tau \\ = \int_0^\infty q_0(\tau) \left[ -(\gamma_1 - \tau\gamma_2) + \int_0^\tau (\gamma_1 - \tau'\gamma_2) d\tau' \right] d\tau,$$

$Q_2$  simplifies to

$$Q_2 = \int_S k(\theta - \eta) \left\{ -\bar{\tau}_0 D^\theta c_1 - c_1 D^\theta \bar{\tau}_0 \right\} d\theta = - \int_S k(\theta - \eta) D^\theta \bar{s}_1 d\theta. \tag{2.28ii}$$

As already noted, the time of change of  $\bar{s}_1$  is at most of  $O(\varepsilon)$ ; thus we can take

$$D^\theta \bar{s}_1 = \theta \cdot \nabla \bar{s}_1 + O(\varepsilon)$$

and, retaining highest order terms,

$$s_2(\bullet, \eta, 0) - \int_S s_2(\bullet, \theta, 0) k(\theta - \eta) d\theta = - \int_S k(\theta - \eta) (\theta \cdot \nabla \bar{s}_1) d\theta. \tag{2.29}$$

### 2.3.4 The turning kernel

The symmetric, isotropic turning kernel can be written as an orthogonal expansion,

$$k(\theta) = \frac{1}{2\pi} \left( 1 + \sum_{n=1}^{\infty} k_n \cos(n\theta) \right) \geq 0; \tag{2.30}$$

$$k_n = 2 \int_S \cos(n\theta) k(\theta) d\theta, \quad n = 1, 2, \dots$$

In this expansion, only the first cosine mode will appear in the population flux to  $O(\varepsilon)$ . The coefficient for this mode satisfies  $-2 < k_1 < 2$ ; the limits,  $k_1 = \pm 2$  correspond to  $\delta$ -function reorientation kernels (individuals either do not change direction at all or exactly reverse course at every turn) that are not of interest in the two-dimensional theory.  $k_1$  can be expressed as

$$k_1 = 2\psi, \quad \psi = E\{\theta \cdot \theta'\}, \quad -1 < \psi < 1,$$

where  $\psi$  is the *directional persistence index* (Othmer et al., 1988), i.e., the correlation between pre-turn orientation  $\theta$  and post-turn orientation  $\theta'$ .

Substituting (2.30) into the right-hand side of (2.29),

$$s_2(\bullet, \eta, 0) - \int_S s_2(\bullet, \theta, 0) k(\theta - \eta) d\theta$$

$$= - \int_S \frac{1}{2\pi} \left( 1 + \sum_{n=1}^{\infty} k_n \cos(n(\theta - \eta)) (\theta \cdot \nabla \bar{s}_1) \right) d\theta = - \psi (\eta \cdot \nabla \bar{s}_1). \tag{2.31}$$

Writing an orthogonal expansion for the unknown  $O(\varepsilon)$  zero-lag distribution,

$$s_2(\bullet, \theta, 0) = \mu_0 + \mu_{1,c} \cos(\theta) + \mu_{1,s} \sin(\theta) \\ + \mu_{2,c} \cos(2\theta) + \mu_{2,s} \sin(2\theta) + \dots \quad (2.32)$$

gives

$$\mu_1 \equiv (\mu_{1,c}, \mu_{1,s}) = -\frac{\psi}{1-\psi} \nabla \bar{s}_1 \\ \mu_n \equiv (\mu_{n,c}, \mu_{n,s}) = 0, \quad n \geq 2. \quad (2.33i)$$

The coefficient for the directionally uniform mode,  $\mu_0$ , is undetermined by (2.31). However, being of  $O(\varepsilon)$ , its contribution to the total searcher density is negligible compared to that of the  $O(1)$  solution, and like that solution it has zero contribution to the total density flux. Thus, without loss of generality it can be assumed that the directionally uniform component is entirely represented by the  $O(1)$  solution, and that

$$\mu_0 = 0. \quad (2.33ii)$$

The zero-lag  $O(\varepsilon)$  solution is then

$$s_2(\bullet, \theta, 0) = -\frac{\psi}{1-\psi} (\theta \cdot \nabla \bar{s}_1), \quad (2.34)$$

giving as the complete solution at this order

$$s_2(\bullet, \theta, \tau) = q_0(\tau) \left\{ \frac{-\psi}{1-\psi} (\theta \cdot \nabla \bar{s}_1) - \tau D^\theta c_1 - c_1 D^\theta \rho \int_0^\tau (\gamma_1 - \tau' \gamma_2) d\tau' \right\}. \quad (2.35)$$

Note that the reorientation behavior appears only in the form of the persistence index  $\psi$ .

From (2.35), the density of searchers oriented in direction  $\theta$  is

$$\bar{s}_2(t, \mathbf{x}, \theta) = \int_0^\infty s_2(t, \mathbf{x}, \theta, \tau) d\tau \\ = \left\{ -\frac{\psi}{1-\psi} \bar{\tau}_0 (\theta \cdot \nabla \bar{s}_1) - c_1 D^\theta (\hat{\tau}_0) - \hat{\tau}_0 D^\theta (c_1) - c_1 D^\theta \rho \bar{\tau}_1 \right\}. \quad (2.36)$$

The density flux of searchers in the  $O(\varepsilon)$  solution is

$$J_2 = \int_S \theta \bar{s}_2 d\tau \\ = \pi \left\{ -\frac{\psi}{1-\psi} \bar{\tau}_0 \nabla \bar{s}_1 - \nabla (c_1 \hat{\tau}_0) - c_1 \nabla \rho \bar{\tau}_1 \right\}. \quad (2.37)$$

Writing (2.37) in terms of the  $O(1)$  in terms of the  $O(1)$  searcher density, (2.24),

$$J_2 = \frac{1}{2} \left\{ -\frac{\psi}{1-\psi} \bar{\tau}_0 \nabla \bar{s}_1 - \nabla \left( \bar{s}_1 \frac{\hat{\tau}_0}{\bar{\tau}_0} \right) - \nabla \rho \frac{\bar{\tau}_1}{\bar{\tau}_0} \bar{s}_1 \right\}. \quad (2.38)$$

Equation (2.38) is valid to  $O(1)$ ; to this order,  $\bar{s}_1$  can be replaced by the total searcher density,  $\bar{\sigma}$ , without additional error,

$$J_2 = \frac{1}{2} \left\{ -\frac{\psi}{1-\psi} \bar{\tau}_0 \nabla \bar{\sigma} - \nabla \left( \bar{\sigma} \frac{\hat{\tau}_0}{\bar{\tau}_0} \right) - \nabla \rho \frac{\bar{\tau}_1}{\bar{\tau}_0} \bar{\sigma} \right\} + O(\varepsilon). \quad (2.39)$$

### 2.4 Conservation flux equations

Using the  $O(1)$  and  $O(\varepsilon)$  solutions, and taking advantage of the fact that the density of searchers is conserved, we can write an approximate equation for the evolution in time of the total searcher density distribution,

$$\partial_t \bar{\sigma} = -\nabla J, \quad (2.40)$$

using the first two terms in the expansion for density flux,

$$J = \int_0^\infty \int_S \theta \sigma(\bullet, \theta, \tau) d\theta d\tau = J_1 + \varepsilon J_2 + O(\varepsilon^2).$$

Substituting (2.25) and (2.39) into (2.40) yields the total density flux equation, accurate to  $O(\varepsilon)$ ,

$$\partial_t \bar{\sigma} = \frac{\varepsilon^2}{2} \nabla \left\{ \left( \frac{\psi}{1-\psi} \right) \bar{\tau}_0 \nabla \bar{\sigma} + \nabla \left( \bar{\sigma} \frac{\hat{\tau}_0}{\bar{\tau}_0} \right) + \nabla \rho \left( \frac{\bar{\tau}_1}{\bar{\tau}_0} \right) \bar{\sigma} \right\}. \quad (2.41)$$

Equation (2.41) can also be written in the standard advection–diffusion form

$$\begin{aligned} \partial_t \bar{\sigma} &= \nabla \{ D \nabla \bar{\sigma} - U \bar{\sigma} \}, \\ D &= \frac{\varepsilon^2}{2} \left[ \left( \frac{\psi}{1-\psi} \right) \bar{\tau}_0 + \left( \frac{\hat{\tau}_0}{\bar{\tau}_0} \right) \right], \\ U &= U' \nabla \rho = -\frac{\varepsilon^2}{2} \left[ \partial_\rho \left( \frac{\hat{\tau}_0}{\bar{\tau}_0} \right) + \left( \frac{\bar{\tau}_1}{\bar{\tau}_0} \right) \right] \nabla \rho, \end{aligned} \quad (2.42i)$$

where  $D$  is the searcher *diffusivity* and  $U'$  is the *taxis coefficient*. The dimensional form of this equation is

$$\begin{aligned} \partial_{t^*} \bar{\sigma}^* &= \nabla^* \{ D^* \nabla^* \bar{\sigma}^* - U^* \bar{\sigma}^* \}, & D^* &= \frac{c^2}{2} \left[ \left( \frac{\psi}{1 - \psi} \right) \bar{\tau}_0^* + \left( \frac{\hat{\tau}_0^*}{\bar{\tau}_0^*} \right) \right], \\ U^* &= U'^* \nabla^* \rho^* = - \frac{c^2}{2} \left[ \partial_{\rho^*} \left( \frac{\hat{\tau}_0^*}{\bar{\tau}_0^*} \right) + \left( \frac{\bar{\tau}_1^*}{c \bar{\tau}_0^*} \right) \right] \nabla^* \rho^*, \end{aligned} \tag{2.42ii}$$

Equations (2.41) and (2.42) are the primary mathematical results of this paper: an advection–diffusion equation describing the population-level fluxes resulting from the individual behavior defined by the response functional (2.6), as reflected by the empirically observable turning statistics  $\bar{\tau}_0$ ,  $\hat{\tau}_0$ , and  $U_1$  (2.16)–(2.19). In (2.42), the first diffusion term shows the effect of the reorientation kernel: directional persistence between steps ( $\psi > 0$ ) enhances searcher diffusivity, while tendency to reverse direction upon turning ( $\psi < 0$ ) decreases searcher diffusivity. However, directional persistence has no effect on the advective velocity. The second diffusion term, and the first velocity term, reflect the *area-restricted search*-type dependence of turning rate on attractant concentration. The second velocity term reflects anisotropy in the turning distribution, due to *directional tactic* or *temporally-differential kinetic* responses to the attractant gradient.

Equilibrium searcher distributions in (2.42) are governed by

$$\bar{\sigma}(\mathbf{x}) \propto \exp \left[ \int_{\rho_0}^{\rho(\mathbf{x})} \chi(\rho') d\rho' \right], \tag{2.43}$$

where  $\chi(\rho) = U'/D$  is the *tactic sensitivity* of the search strategy (Alt, 1980). The tactic sensitivity for behaviors described by the response functional (2.6) is then

$$\chi(\rho) = - \left( \frac{\partial_{\rho} \left( \frac{\hat{\tau}_0}{\bar{\tau}_0} \right) + \left( \frac{\bar{\tau}_1}{\bar{\tau}_0} \right)}{\left( \frac{\psi}{1 - \psi} \right) \bar{\tau}_0 + \left( \frac{\hat{\tau}_0}{\bar{\tau}_0} \right)} \right). \tag{2.44}$$

High sensitivity implies effective concentration of searchers in high-resource areas at equilibrium. Thus, a tendency to reverse on turning ( $\psi < 0$ ) leads to more effective localization of resource concentrations at equilibrium.

Note that (2.43)–(2.44) show that for any response functional, total searcher density is a single-valued function of attractant density, to  $O(\epsilon)$ . Thus, there are no behaviors and no landscapes in which

searchers can be “fooled” into concentrating at local maxima in the attractant distribution. However, this property of the steady-state distribution does not exclude the possibility that searchers may *transiently* accumulate at local maxima.

### 2.5 Constant turning-rate behaviors

An especially tractable class of tactic and kinetic behaviors are those in which the statistical properties of search steps are determined exclusively by environmental conditions *at the point of departure* (“repulsive” random walks in the terminology of Skellam (1951); see also Okubo (1986)), and in which turning rate is *constant* throughout a search step. Behaviors of this class have response functionals of the form

$$\beta(t, \mathbf{x}, \theta, \tau) = B_1(\rho(t, \mathbf{x}), \varepsilon D^0 \rho(t, \mathbf{x})) + O(\varepsilon^2). \tag{2.45}$$

Note that, in (2.45), the  $\tau$ -dependence of the response functional is absent. A useful consequence of this simplification is that  $\gamma_0, \gamma_1,$  and  $\gamma_2$  in (2.8) are independent of run time, allowing the integrals which define turning statistics appearing in (2.42) to be evaluated explicitly.

As a general description of how turning rates might vary with attractant density in a repulsive random walk, we may take for (2.8), in dimensional form (but with \*’s dropped),

$$\gamma_0 = F(\rho), \quad \gamma_1 = c G(\rho), \tag{2.46}$$

where  $F(\rho)$  is the dependence of turning rate on local attractant level at the point of departure and  $G(\rho)$  modulates sensitivity to the perceived rate of attractant change. For behaviors of this type, the turning distribution components are

$$q_0(\tau) = \exp[-F(\rho)\tau], \quad q_1(\tau) = cG(\rho)\tau, \tag{2.47}$$

from which the turning statistics are found to be

$$\bar{\tau}_0 = \frac{1}{F(\rho)}, \quad \hat{\tau}_0 = \frac{1}{F(\rho)^2}, \quad \text{and} \quad \bar{\tau}_1 = \frac{cG(\rho)}{F(\rho)^2}. \tag{2.48}$$

The ADE for total population density is then given by

$$\begin{aligned} \partial_t \bar{\sigma} &= \nabla \{ D \nabla \bar{\sigma} - U \bar{\sigma} \}, \\ D &= \frac{c^2}{2(1 - \psi)F(\rho)}, \quad U = \frac{c^2}{2} \left[ \frac{F'(\rho) - G(\rho)F(\rho)}{F(\rho)^2} \right] \nabla \rho, \end{aligned} \tag{2.49}$$

where  $F'(\rho) = \frac{dF}{d\rho}$ . From (2.49), the tactic sensitivity of a constant turn rate, repulsive behavior is

$$\chi(\rho) = (1 - \psi) \left( \frac{F'(\rho)}{F(\rho)} - G(\rho) \right) \quad (2.50)$$

From (2.50), it follows directly that the equilibrium searcher density is

$$\bar{\sigma}(\mathbf{x}) = \sigma_0 [F(\rho(\mathbf{x}))e^{-H(\rho(\mathbf{x}))}]^{1-\psi}, \quad H(\rho) = \int_{\rho_0}^{\rho} G(\rho') d\rho', \quad (2.51)$$

where  $\sigma_0$  is a normalizing constant determining total population density. Equation (2.51) is a remarkably simple and tractable expression of the bases of effective tactic behaviors, showing explicitly the contributions of directional persistence ( $\psi$ ) and sensitivity of turning rates to attractant concentration ( $F$ ) and attractant gradient ( $G$ ).

Equations (2.46)–(2.51) can be used to systematically investigate a variety of searching strategies. For example:

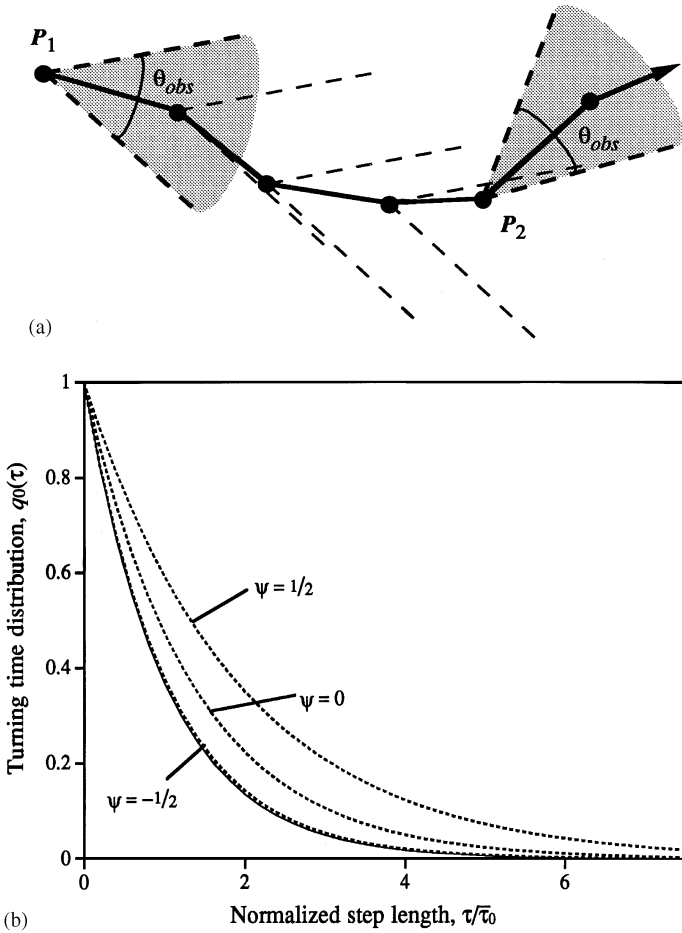
- a simple area-restricted search behavior:  $F(\rho) = \alpha_0 + \alpha_1 \rho$ ,  $G(\rho) = 0$ ;
- a simple taxis algorithm:  $F(\rho) = \alpha_0$ ,  $G(\rho) = -\alpha_2$ ;
- an area-restricted search behavior in which the searcher is sensitive to *relative* increases in attractant density:  $F(\rho) = \alpha_0 + \alpha_1 \ln(\rho)$ ,  $G(\rho) = 0$ ;
- the analogous taxis algorithm, in which the searcher senses relative concentration gradients:  $F(\rho) = \alpha_0$ ,  $G(\rho) = -\frac{\alpha_2}{\rho}$ , etc.

An application of these equations to a particular biological system might begin with determining the environmental response functions  $F(\rho)$  and  $G(\rho)$ , by comparison with observed turning statistics (2.47)–(2.48). This may in many cases be more direct and effective than comparing measured and calculated population fluxes.

Using (2.51), it is also possible to *deduce* attributes of an animal's behavioral sensitivities  $F(\rho)$  and  $G(\rho)$ , from observations of equilibrium searcher distributions. However, it is not possible from the equilibrium distribution alone to distinguish responses to attractant concentration,  $F(\rho)$ , from responses to attractant gradient,  $G(\rho)$  – in fact, the searcher distribution for any concentration response  $F(\rho)$  can be reproduced identically by a gradient response  $G(\rho) = -\frac{d}{d\rho} \ln(F(\rho))$ . Discriminating between these response types requires additional information about turning rates, transient distributions, or searcher density fluxes.

As an example, (2.51) suggests a variety of ways to achieve an *ideal free distribution* of searchers. The ideal free distribution, an important concept in *foraging theory*, is that distribution for which the marginal

“payoff” for each searcher is the same (Kacelnik et al., 1992). For instance, if it is assumed that total payoff in an area is proportional to a power  $n$  of resource concentration, but it must be shared equally between all nearby searchers, the ideal free distribution has  $\bar{\sigma}(\mathbf{x}) \propto \rho^n$ .



**Fig. 2a, b.** Turning time distributions measured by an observer who records a turn only when searcher orientation changes from the initial heading by more than a threshold angular displacement,  $\theta_{obs}$ . Such an observer fails to detect small turns; in this example, an individual initially at  $P_1$  performs several undetected turns before finally exceeding the threshold at  $P_2$  (a). As a result, the turning time is overestimated (b). The “true” behavior in this example is a repulsive random walk with turning kernel  $k(\theta) = 1/2\pi(1 + k_1 \cos(\theta))$ ; the threshold angular displacement is  $\theta_{obs} = \pi/4$ . The true turning distribution is shown (solid line) for comparison with recorded distributions for  $k_1 = -1$  (preferentially reversing reorientation,  $\psi = -1/2$ ),  $k_1 = 0$  (random reorientation,  $\psi = 0$ ), and  $k_1 = 1$  (directionally persistent reorientation,  $\psi = 1/2$ ), shown in dashed lines. Step durations are normalized by mean step length,  $\bar{\tau}_0$

This equilibrium distribution results from any behaviors in which

$$\frac{d}{d\rho} \ln(F(\rho)) - G(\rho) = \frac{n}{(1 - \psi)\rho}. \quad (2.51)$$

As a final comment on repulsive, constant turning rate behaviors, I note that the turning time distribution is defined in some empirical measurements differently from the way it is used in this paper. For example, many observers define a turn as having occurred only when the individual deviates from its original heading by more than a standard angular displacement. Such an observer will not detect a turn if the resulting change in orientation is smaller than this *angular displacement threshold*, and consequently will overestimate step lengths. If the angular detection threshold is  $\theta_{\text{obs}}$ , then the observed turning rate,  $\beta_{\text{obs}}$ , will underestimate the “true” rate  $\beta$  by approximately the factor

$$\beta_{\text{obs}} = \left( 1 - \frac{\theta_{\text{obs}}}{\pi} - \sum_{n=1}^{\infty} \frac{\sin(n\theta_{\text{obs}})k_n}{n\pi} \right) \beta, \quad (2.52)$$

where  $k_n$  are the cosine expansion coefficients of the turning kernel (2.30). Note that the magnitude of this discrepancy depends upon the persistence index of the searcher. If the searcher tends to be directionally persistent ( $k_1 = 2\psi > 0$ ), the number of missed turns is relatively large, while if the searcher tends to reverse upon turning ( $k_1 = 2\psi < 0$ ), the error in the observer’s estimate of  $\beta$  is minimized. An example is shown in Fig. 2.

### 3 Searching on distributions of discrete resource patches

The resources for which many animals forage can be described as having “density” at the board scale, but at the fine scale actually appear in discrete patches. Among the numerous examples are the many species of seabirds that feed on Antarctic krill (Croxall and Prince, 1980; Harrison et al., 1991; Veit et al., 1993, 1994), whales feeding on copepod patches (Wishner et al., 1988), bees collecting nectar from flowers (Dukas and Real, 1993), ladybugs foraging on aphids (Kareiva and Odell, 1987), etc. For animals trying to find areas rich in resource patches, the problem of having only local information may be compounded by the sampling problems inherent in estimating resource abundance and its gradient from a small number of patches which are randomly distributed at local spatial scales. Thus, it is of general interest to investigate the limitations that searchers for discrete

resources face, compared to those faced by searchers for continuously-distributed resources. Of course, if a searcher turns very infrequently, stochasticity in estimates of environmental quality decreases. However, the fact that the environment cannot be assessed at point nonetheless provides major challenge to searching strategies.

To examine this challenge in an explicit manner, I consider an environment in which  $v$  represents the number of randomly distributed resource patches observed within a step of length  $\tau$  by a searcher beginning at  $t, \mathbf{x}$ . I assume  $v$  is a Poisson-distributed random variable (Papoulis, 1984), with probability distribution

$$p(v, \tilde{\rho}) = e^{-\tilde{\rho}} \frac{\tilde{\rho}^v}{v!},$$

$$\tilde{\rho} = \Delta w \int_0^\tau \rho(t + \varepsilon\tau', \mathbf{x} + \varepsilon\theta\tau') d\tau'$$

$$= \Delta w \left( \tau\rho(t, \mathbf{x}) + \varepsilon \frac{\tau^2}{2} D^\theta \rho \right) + O(\varepsilon^2), \quad (3.1)$$

where  $\tilde{\rho}$  is the integrated resource density along the step trajectory, and  $\Delta w$  is the width of the search path within which patches are detected. A simple response to encountering patches, placing minimal demands on the searcher, might be a fixed probability,  $\alpha$ , of turning at every observed patch. In that case, the turning distribution would be

$$q_{t,x,\theta}(\tau) = \sum_{v=0}^{\infty} p(v, \tilde{\rho})(1 - \alpha)^v, \quad (3.2)$$

where  $(1 - \alpha)^v$  is the binomial probability of not turning at any of  $v$  patch encounters.

Another simple strategy would be for the searcher to turn only upon encountering the  $n$ th resource patch; this behavior is defined by

$$q_{t,x,\theta}(\tau) = 1 - \sum_{v=0}^{n-1} p(v, \tilde{\rho}), \quad (3.3)$$

These stochastic behaviors both belong to a more general class of behaviors in which the turning distribution is a function only of  $\tilde{\rho}$ , the integrated density along the step trajectory,

$$q_{t,x,\theta}(\tau) = \exp(-\zeta(\tilde{\rho})), \quad (3.4)$$

where  $\zeta(\tilde{\rho})$  is a monotonically increasing function such that  $\zeta(0) = 0$ ,  $\lim_{\tilde{\rho} \rightarrow \infty} \zeta(\tilde{\rho}) = \infty$ . Using the results of Sect. II, it can be shown that no taxis is possible (to  $O(\varepsilon)$ ) for any behaviors of type (3.4). With (2.8) and

(2.13), the turning rate coefficients are

$$\begin{aligned}\gamma_0 &= \Delta w \zeta'(\Delta w \tau \rho(t, \mathbf{x})) \rho(t, \mathbf{x}), \\ \gamma_1 &= \Delta w \tau (\zeta''(\Delta w \tau \rho(t, \mathbf{x})) + \frac{1}{2} \Delta w \tau \rho(t, \mathbf{x}) \zeta''(\Delta w \tau \rho(t, \mathbf{x}))).\end{aligned}\quad (3.5)$$

In (3.5),  $\zeta'$  and  $\zeta''$  are the first and second derivatives of  $\zeta$ , respectively. With application of (2.14) and (2.17), the diffusion and advection parameters in (2.42) are

$$\begin{aligned}D &= \frac{\varepsilon}{2} \left[ \frac{\psi}{1 - \psi} \int_0^\infty \exp(-\zeta(\Delta w \tau' \rho(t, \mathbf{x}))) d\tau' \right. \\ &\quad \left. + \left( \frac{\int_0^\infty \tau' \exp(-\zeta(\Delta w \tau' \rho(t, \mathbf{x}))) d\tau'}{\int_0^\infty \exp(-\zeta(\Delta w \tau' \rho(t, \mathbf{x}))) d\tau'} \right) \right]\end{aligned}$$

and (after simplification)

$$U \equiv 0. \quad (3.6)$$

Thus, while turning rates vary with resource patch density for searchers employing (3.4)-type algorithms (diffusion varies spatially), they vary in such a way as to result in no net movement relative to the gradient. This result can be understood in terms of the classical searching algorithms, area-restricted search and directional taxis. Suppose, as in (3.3), that a searcher turns at each  $n$ th patch encounter. This is an area-restricted search behavior: it implies increased turning rates where there are many patches, and so should lead to aggregation in dense areas. However, it is also a *negative* taxis algorithm: it implies that searchers moving up-gradient turn faster than those heading down-gradient. These competing effects cancel each other to  $O(\varepsilon)$  for any behavior of class (3.4).

### 3.1 Integral turning rate behaviors

What then is required for taxis on discrete resources? I consider now an algorithm in which turning rate (as opposed to turning distribution) is a function only of  $\tilde{\rho}$ ,

$$\beta(t, \mathbf{x}, \theta, \tau) = b(\tilde{\rho}). \quad (3.7)$$

The turning rate coefficients are now

$$\begin{aligned}\gamma_0 &= b(\Delta w \tau \rho(t, \mathbf{x})), \\ \gamma_1 &= \frac{1}{2} \Delta w \tau^2 b'(\Delta w \tau \rho(t, \mathbf{x})),\end{aligned}\quad (3.8)$$

where  $b'$  is the first derivative of  $b$ . The turning distributions resulting from (3.7) are given by

$$\begin{aligned} q_0(\tau) &= \exp\left[-\int_0^\tau b(\Delta w \tau' \rho(t, \mathbf{x})) d\tau'\right], \\ q_1(\tau) &= \frac{1}{2} \Delta w \int_0^\tau \tau'^2 b'(\Delta w \tau' \rho(t, \mathbf{x})) d\tau'. \end{aligned} \quad (3.9)$$

A key distinction is that the turning rate-based behavior (3.7) results in turning time distributions, (3.9), which are *not* of the same form as (3.4). Thus, an essential difference exists between these two classes of search algorithm.

As an example, suppose turning rate increases with  $\tilde{\rho}$  as

$$b(\tilde{\rho}) = b_1 \tilde{\rho}^n, \quad n > 0. \quad (3.10)$$

in which turning rate increases with  $\tilde{\rho}$  according to a “behavioral” exponent,  $n$ . The diffusion and taxis coefficients can then be solved analytically for  $n > 0$ ,

$$\begin{aligned} D &= \frac{\varepsilon}{2} b_1^{-\varphi} \Delta w^{\varphi-1} \varphi^{-\varphi} \left( \varphi \left( \frac{\psi}{1-\psi} \right) \Gamma(\varphi) + \frac{\Gamma(2\varphi)}{\Gamma(\varphi)} \right) \rho^{\varphi-1}, \\ U' &= \frac{\varepsilon}{2} b_1^{-\varphi} \Delta w^{\varphi-1} \varphi^{-\varphi} \left( \frac{1-\varphi}{1+\varphi} \right) \left( \frac{\Gamma(2\varphi)}{\Gamma(\varphi)} \right) \rho^{\varphi-2}, \end{aligned} \quad (3.11)$$

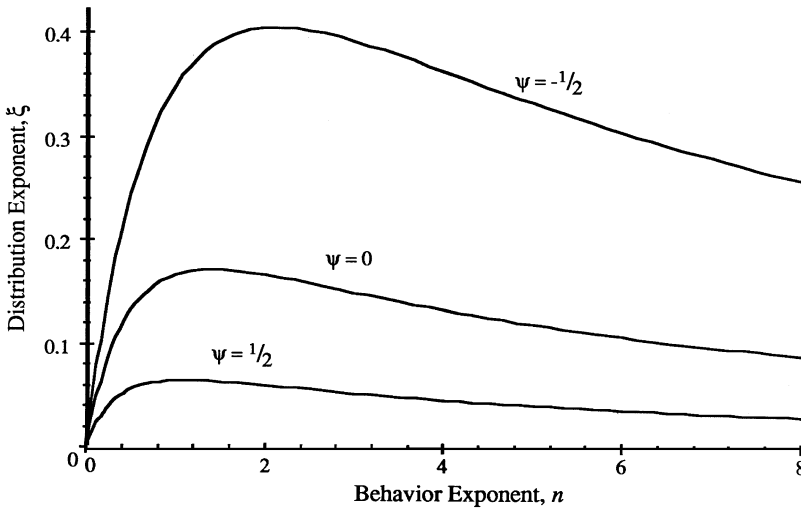
where  $\varphi = \frac{1}{(1+n)}$ . Tactic sensitivity for behaviors of the class (3.10) is given by

$$\chi = \frac{\xi(n)}{\rho(t, \mathbf{x})}, \quad \xi(n) = \left( \frac{\varphi(1-\varphi)}{1+\varphi} \right) \left( 1 + \varphi \left( \frac{\psi}{1-\psi} \right) \left( \frac{\Gamma(2\varphi)}{\Gamma(\varphi)} \right) \right)^{-1}. \quad (3.12)$$

Note that tactic sensitivity is inversely proportional to resource patch density, with a constant of proportionality determined by the behavioral exponent,  $n$ , and the persistence index,  $\psi$ , but independent of the constants  $b_1$  and  $\Delta w$ . From (3.12) and (2.43), it follows that equilibrium searcher distributions resulting from behaviors of type (3.10) take the form

$$\sigma(\mathbf{x}) \propto \rho(\mathbf{x})^{\xi(n)}. \quad (3.13)$$

Clearly, the higher the exponent  $\xi(n)$ , the more effective the behavior is at taxis, at least in the long term. Therefore  $\xi(n)$  may be thought of as a “tactic effectiveness” exponent. Figure 3 shows the variation of the tactic effectiveness exponent with  $n$  for three values of  $\psi$ . The most effective of these strategies, with  $\psi = -0.5$ , reaches a maximally effective value of  $\xi = 0.405$  at  $n = 2$ . It would be interesting to compare this



**Fig. 3.** Variation of the *tactic exponent*,  $\xi$ , as a function of the *behavioral exponent*,  $n$ , for a searching strategy in which turning rate is function of integrated resource density (see (3.12) and (3.13)). Reversing reorientation kernels ( $\psi < 0$ ) yield more effective taxis than random ( $\psi = 0$ ) or directionally persistent ( $\psi > 0$ ) kernels. For each of these kernels, searching effectiveness is maximized by an intermediate choice of  $n$

suggestion of an optimal search behavior,  $\beta(t, \mathbf{x}, \theta, \tau) \propto \tilde{\rho}^2$ ,  $\psi = -0.5$ , with observations of turning rates employed by animals foraging on discrete resource patches.

Equations (3.7)–(3.13) demonstrate that *taxis* is possible for discrete-resource-patch behaviors in which *turning rate* is a function of integrated resource density,  $\tilde{\rho}$ . This is in contrast to behaviors in which *turning time distributions* depend only on  $\tilde{\rho}$ , shown in (3.4)–(3.6) to be incapable of producing taxis. Turning rate-based algorithms such as (3.7)–(3.12) require of the searcher an ability to retain more complete information about patches encountered, either through a cognitive capacity or through a physiological mechanism (as for example the *satiety* attributed to ladybugs: Kareiva and Odell, 1987). The searcher must know not only the number of resource patches encountered, but also the time at which they were seen. These two types of information are sufficient to characterize the local environment (McNamara and Houston, 1987; Mangel, 1990). Thus algorithms of type (3.7) amount to short-term *learning* about the local environmental conditions. In contrast, searchers with (3.4)-type algorithms may accumulate information about the number of patch encounters, but cannot in any way characterize their environment, and so may be thought of as requiring no capacity for learning about environmental conditions. This connection between ability to characterize environment and capacity for climbing

gradients suggests that mechanism for short-term learning may be a biological requirement for searchers on discrete resource distributions.

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