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# Travelling Waves in a Model of Species Migration

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**Abstract**—A model of species migration is presented which takes the form of a reaction-diffusion system. We consider special limits of this model in which we demonstrate the existence of travelling wave solutions. These solutions can be used to describe the migration of cells, bacteria, and some organisms. © 2000 Elsevier Science Ltd. All rights reserved.

**Keywords**—Travelling waves, Migration, Asymptotics, Exact solution.

## 1. INTRODUCTION

Travelling waves arising in reaction-diffusion systems are a well-documented and striking phenomenon. A particularly good reference is [1] with more biological examples to be found in [2]. In this paper, we present a simple model of how cells, bacteria, and other organisms (hereafter, collectively referred to as 'species') may migrate, based on a reaction-diffusion-chemotaxis system, which is a slight generalisation of the model presented in [3]. We perform some simple asymptotic analysis and demonstrate the existence of both waves that simultaneously diffuse and translate and waves that translate without changing shape. For a particular choice of the chemotactic response function, closed form solutions are obtained. The analysis provides insights into the manner in which a generic species migrates and has many direct applications to the migration of, for example, a population of nematodes moving through soil [4], predator-prey interactions [5], endothelial cell migration during angiogenesis [6,7], and cancer cell invasion of surrounding tissue [8].

## 2. MODEL OF SPECIES MIGRATION

We adopt a simple model of species behaviour: in the absence of any relevant external stimuli, the species move randomly; the presence of an attractant (chemical) gradient provides a directional bias to this motion and the species, on average, move up the attractant gradient. The system we consider is a special case of that determined by Keller and Segel [9] and we work in

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one spatial dimension only. The system we study is

$$\frac{\partial n}{\partial t} = \frac{\partial}{\partial x}\left(D_n \frac{\partial n}{\partial x}\right) - \frac{\partial}{\partial x}\left(\chi(a) n \frac{\partial a}{\partial x}\right), \tag{1}$$

$$\frac{\partial a}{\partial t} = \frac{\partial}{\partial x}\left(D_a \frac{\partial a}{\partial x}\right) - Kn. \tag{2}$$

In these equations, $a$ is the attractant concentration and $n$ is the species population density, both being functions of position $x$ and time $t$. The parameter $D_a$ is the diffusion coefficient of the attractant, $D_n$ is the diffusion coefficient or random motility of the species, $\chi$ is the chemotactic response function, and $K$ is the take-up rate. The chemotactic response (the second term of (1)) describes how the motion of the species becomes directionally biased in the presence of the attractant gradient, i.e., the species preferentially moves up any attractant gradient. The take-up rate $K$ is a measure of how much attractant is consumed or degraded by the species.

These equations are supplemented with the boundary conditions

$$D_n \frac{\partial n}{\partial x} - \chi n \frac{\partial a}{\partial x} = 0, \qquad (x \to \pm\infty), \tag{3}$$

$$D_a \frac{\partial a}{\partial x} = 0, \qquad (x \to \pm\infty), \tag{4}$$

and the initial data

$$n = g(x), \quad a = h(x), \qquad (t = 0). \tag{5}$$

In the next two sections, we consider special limits of our model in which we can make analytical progress in demonstrating the existence of travelling wave solutions.

## 3. STRONG ATTRACTANT DIFFUSION AND NO TAKE-UP

We first consider the implications of strong attractant diffusion ($D_a$ large) and no take-up, $K = 0$. We assume that the attractant has already reached a steady-state profile and all that remains is to determine the response of the species to this profile. The equations that we consider are thus (1), (3), and (5) with

$$\chi(a)\frac{da}{dx} \to \gamma(x). \tag{6}$$

We cannot make analytical progress without making further assumptions. The first situation we consider is that in which $\gamma = \mathcal{O}(1)$ and $D_n = \epsilon D$, where $D = \mathcal{O}(1)$, and $0 < \epsilon \ll 1$, thus, the diffusion of the species is weak relative to the chemotaxis. This allows us to use the asymptotic method of multiple scales. We introduce two separate time-dependencies into the species density $n = n(x, \tau, T)$, where $\tau = t$ is the timescale associated with chemotaxis and $T = \epsilon t$ is the slower timescale of species diffusion. We now pose an asymptotic expansion in terms of the small parameter $\epsilon$,

$$n = n(x, \tau, T; \epsilon) = n_0(x, \tau, T) + \epsilon n_1(x, \tau, T) + \cdots . \tag{7}$$

Working to $\mathcal{O}(1)$, we have

$$\frac{\partial n_0}{\partial \tau} + \frac{\partial}{\partial x}(\gamma n_0) = 0. \tag{8}$$

Using the method of characteristics, we change variables from $\{\tau, x\}$ to $\{\tau, s\}$, where $x = \Theta(\tau - s)$ and $\Theta$ is the solution of $\frac{dx}{d\tau} = \gamma(x)$ (see [10]). The coordinate $s$ is the time since passing $x = 0$. In these coordinates, we rewrite (8) as

$$\left(\frac{\partial}{\partial \tau}\right)_s (\gamma n_0) = 0, \tag{9}$$

whence

$$n_0(x,\tau,T)=\frac{A(s,T)}{\gamma(x)}. \tag{10}$$

Expression (10) tells us that the profile $n_0$ translates on the timescale of $\tau$ with speed $\gamma$ whilst simultaneously changing its shape on the slower timescale $T$.

In order to determine how the profile depends upon $T$, we must work to $\mathcal{O}(\epsilon)$. From (7)–(10) and elementary calculus, we obtain

$$\frac{1}{\gamma}\frac{\partial A}{\partial \tau}+\frac{1}{\gamma}\left(\frac{\partial}{\partial \tau}\right)_s(\gamma n_1)=D\frac{1}{\gamma}\left(\frac{\partial}{\partial s}\right)_\tau\frac{1}{\gamma}\left(\frac{\partial}{\partial s}\right)_\tau\frac{A}{\gamma}. \tag{11}$$

In order to maintain the asymptoticness of the expansion of $n$ to $T=\operatorname{ord}(1)$, the quantity $(\gamma n_1)$ must be kept bounded as $\tau$ increases. This is achieved by setting the right-hand side equal to $(1/\gamma)\frac{\partial A}{\partial T}$. Thus, $A$ must satisfy the differential problem

$$\frac{1}{D}\frac{\partial A}{\partial T}=\frac{1}{\gamma^2}\frac{\partial^2 A}{\partial s^2}+\frac{3}{2}\frac{\partial}{\partial s}\left(\frac{1}{\gamma^2}\right)\frac{\partial A}{\partial s}+\frac{1}{2}\frac{\partial^2}{\partial s^2}\left(\frac{1}{\gamma^2}\right)A, \tag{12}$$

subject to $A\to 0$ as $x\to\pm\infty$, with initial data $A(s,0)=g(\Theta(-s))\gamma(\Theta(-s))$. Unfortunately, further progress along these lines is not possible without a knowledge of the functional form of $\gamma$. It is possible, however, for constant $D$, to determine a condition on $\gamma$ for which the species population will dissipate as it translates; a *sufficient* condition is given by

$$\frac{2}{\gamma}\frac{\partial \gamma}{\partial s}-\frac{9}{8}\left(\frac{\partial\gamma}{\partial s}\right)^2-\frac{\partial^2\gamma}{\partial s^2}\le 0,\qquad \text{for all } s, \tag{13}$$

provided that $\gamma$ is sufficiently continuous. This condition is obtained by Taylor expanding (12) about an arbitrary $s$, transforming the resultant differential problem with constant coefficients into the canonical diffusion problem, and applying the strong maximum and minimum principles, see, for example, [11,12].

If $\gamma$ is, to leading order in $\epsilon$, the constant $\gamma_0$, then (12) reduces to a simple diffusion equation and the solution is given by $n_0=A(x-\gamma_0\tau,T)/\gamma_0$. This profile simultaneously translates with constant speed $\gamma_0$ and diffuses.

We now abandon the case of weak species diffusion and consider the consequences of constant $\gamma$. In this case, we may exploit the following property. The solution to problem (1),(3),(5) is given by

$$n=\phi(x-\gamma t,t), \tag{14}$$

where $\phi(x,t)$ is the solution of the corresponding problem in which $\gamma\to 0$.

If $D_n$ is a constant $D_0$, then $\phi$ may be found in terms of the free-space Green's function, and thus,

$$n(x,t)=\frac{1}{\sqrt{4\pi D_0 t}}\int_{-\infty}^{\infty}\exp\left(-\frac{(x-\gamma t-s)^2}{4D_0 t}\right)g(s)\,\mathrm{d}s, \tag{15}$$

where we have used the well-known solution to the canonical diffusion equation in an unbounded domain (see, for example, [11]).

In the case of porous-media type diffusion $D_n=D_0 n^m$, where $D_0$ and $m$ are positive, real constants. We may exploit a weak similarity solution described in [1] to $u_t=\Delta(u^p)$, $p>0$. Stretching the timescale and using (14), we may write a solution to our problem as

$$n(x,t)=$$

$$\max\left[\left(\frac{m+1}{D_0 t}\right)^{1/(m+2)}\left(\sigma_0-\frac{m}{2(m+1)(m+2)}\left(\frac{m+1}{D_0 t}\right)^{2/(m+2)}(x-\gamma t)^2\right)^{1/m},0\right], \tag{16}$$

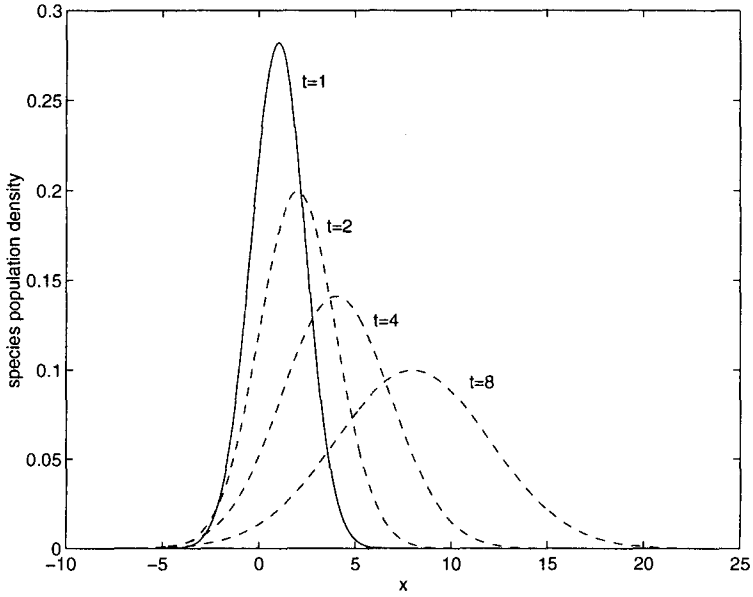

Figure 1. A travelling wave solution to the chemotaxis-diffusion equation with Fickian diffusion.

where $\sigma_0$ is a positive and real constant of integration. Since this solution has compact support, it clearly satisfies our requirements at infinity, though we abandon dependence upon our initial data.

In Figure 1, we plot solution (15) with $D_0 = 1$, $\gamma = 1$, and the initial data chosen to be a Dirac delta function, $g(x) = \delta(x)$. Clearly, the profiles diffuse and translate with speed $\gamma$.

## 4. WEAK ATTRACTANT DIFFUSION

We now turn our attention to the case in which the attractant diffusion is weak or alternatively becomes bound to a substrate, e.g., during angiogenesis, fibronectin secreted by endothelial cells binds to the local extracellular matrix and does not diffuse [13]. In the analysis of weak diffusion of species in the preceding section, we alleviated the singular nature of the $\mathcal{O}(1)$ approximation by determining an evolution equation from the $\mathcal{O}(\epsilon)$ analysis. In this section, however, we shall work only to leading order. The effect of this is to ignore diffusion in the attractant equation (see reasons above). The reaction-diffusion system we consider is (1) and

$$\frac{\partial a}{\partial t} = -Kn, \tag{17}$$

subject to the boundary conditions (3). Our solution will be found to be independent of initial data. We now show that this system exhibits a travelling wave solution in the variable $z = x - \alpha t$, with the solution degenerate in the speed $\alpha$. Looking for the solution $\{n(z), a(z)\}$ reduces the above system to

$$-\alpha\frac{dn}{dz} = \frac{d}{dz}\left(D_n\frac{dn}{dz} - \chi(a)n\frac{da}{dz}\right), \tag{18}$$

$$\alpha\frac{da}{dz} = Kn. \tag{19}$$

In the case in which $D_n = D_0$, a constant, we find, after a number of elementary operations, that

$$-\frac{\alpha}{D_0}z = \log\left|\frac{da}{dz}\right| - \frac{1}{D_0}\int \chi(a)\frac{da}{dz}\,\mathrm{d}z + \sigma_1, \tag{20}$$

where $\sigma_1$ is a constant of integration. We shall assume a chemotactic response function of the form

$$\chi = \frac{\chi_0}{(\beta + a)^r}, \tag{21}$$

where $\chi_0$, $\beta$, and $r$ are real and positive constants. This implies that the strength of the chemotactic response weakens as the concentration of attractant increases. The biological arguments for this form of the chemotactic response function can be found in [14], appropriate values for the parameter $r$ are 1 and 2.

### 4.1. The Case $r \neq 1$

With (21), we may write (20) as

$$-\frac{\alpha}{D_0}z = \log\left|\frac{da}{dz}\right| - \log\left|\exp\left(\frac{1}{D_0}\frac{\chi_0}{-r+1}(\beta + a)^{-r+1}\right)\right| + \sigma_1. \tag{22}$$

After manipulations and integration, we obtain

$$\sigma_1 \exp\left(-\frac{\alpha}{D_0}z\right) = \frac{(\alpha/D_0)}{-1+r}\left(\frac{1}{D_0}\frac{\chi_0}{1-r}\right)^{1/(1-r)} \Gamma\left[\frac{1}{-1+r}, \frac{1}{D_0}\frac{(\beta + a)^{-1+r}\chi_0}{1-r}\right] + \sigma_2, \tag{23}$$

where

$$\Gamma[h, z] = \int_z^\infty t^{h-1} e^{-t}\, dt \tag{24}$$

is the incomplete Gamma function and $\sigma_2$ is a constant of integration. Equation (23) gives an implicit relationship between $a$ and $z$, from which $n(z)$ can be obtained using (19). Further progress requires the use of numerical root-finding techniques to solve the transcendental equation (23). Numerical experiments reveal that noninteger $r$ gives rise to complex solutions $a$ and $n$, which are unrealistic.

### 4.2. The Case $r = 1$

In this case, (20) yields

$$-\frac{\alpha}{D_0}z = \log\left|\frac{da}{dz}\right| - \log\left|(\beta + a)^{\chi_0/D_0}\right| + \sigma_1. \tag{25}$$

If $\chi_0 \neq D_0$, then this equation may be integrated to obtain

$$(\beta + a)^{-\chi_0/D_0+1} = \left(-\frac{\chi_0}{D_0} + 1\right)\left(-\frac{D_0}{\alpha}\sigma_1\right)\exp\left(-\frac{\alpha}{D_0}z\right) + \sigma_2, \tag{26}$$

from which (with redefined constants of integration $\sigma_1, \sigma_2$), we obtain

$$a(z) = \left(\sigma_2 + \sigma_1 \exp\left(-\frac{\alpha}{D_0}z\right)\right)^{1/(-\chi_0/D_0+1)} - \beta, \tag{27}$$

and, from (19),

$$n(z) = \frac{\alpha/K}{-\chi_0/D_0 + 1}\left(-\frac{\alpha}{D_0}\sigma_1 \exp\left(-\frac{\alpha}{D_0}z\right)\right)\left(\sigma_2 + \sigma_1 \exp\left(-\frac{\alpha}{D_0}z\right)\right)^{\chi_0/(D_0-\chi_0)}. \tag{28}$$

If $\chi_0 = D_0$, then (25) can be integrated to obtain

$$a(z) = \exp\left(\sigma_2 + \sigma_1 \exp\left(-\frac{\alpha}{D_0}z\right)\right) - \beta \tag{29}$$

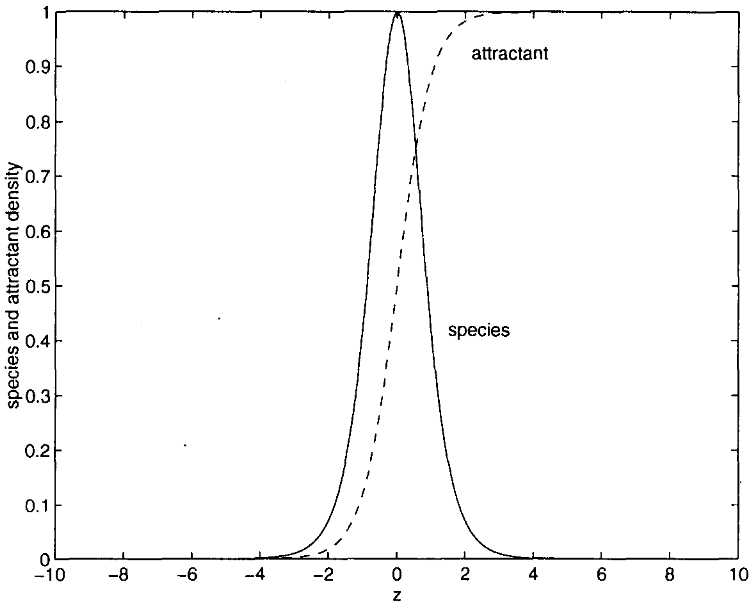

Figure 2. Travelling wave solution to the coupled attractant-species system.

and

$$n(z) = -\frac{\sigma_1}{D_0}\frac{\alpha^2}{K} \exp\left(-\frac{\alpha}{D_0}z\right) \exp\left(\sigma_2 + \sigma_1 \exp\left(-\frac{\alpha}{D_0}z\right)\right). \tag{30}$$

These equations, (27),(28) and (29),(30), describe travelling wave solutions with fixed shape translating in the positive $x$ direction with speed $\alpha$. In Figure 2, we plot the solutions (27) and (28) for the parameter values $\sigma_2 = 1$, $\sigma_1 = 1$, $\alpha = 2$, $D_0 = 1$, $\chi_0 = 2$, $\beta = 0$, and $K = 1$. The shape of the profile is independent of time and clearly shows a propagating pulse of species, which consume or degrade the attractant. Increasing $D_0$ causes the region of appreciable change in the species and attractant density to widen, while increasing $\chi_0$ causes the crest in the species density to move to the right.

## 5. DISCUSSION

We have introduced a model of species migration and examined some of its interesting features. In the case of strong attractant diffusion, we have presented two travelling wave solutions which diffuse as they translate for the case in which the chemotactic response is constant (an analysis which is extended to a bounded domain in [3]). In the case of weak attractant diffusion, we have presented closed-form solutions of travelling waves for a family of chemotactic response functions. The leading order behaviour of these waves is to translate without change of shape; this is a good model of a pulse of species translating whilst degrading an attractant and is particularly appropriate in the context of general invasion theory where one is interested mainly in the activity at the wave-front. This is the case where a population of nematodes is attracted to a root tip and the results obtained in Figure 2 are more realistic and an improvement on previous modelling attempts (cf. [4]). Although the solutions we have presented are directly applicable to the evolution of a population of nematodes, they clearly have more general application.

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