

# Starvation driven diffusion as a survival strategy of biological organisms<sup>\*</sup>

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**Abstract.** The purpose of this article is to introduce a diffusion model for biological organisms that increase their motility when food or other resource is insufficient. It is shown in this paper that Fick's diffusion law does not explain such a starvation driven diffusion correctly. The diffusion model for non-uniform Brownian motion in [16] is employed in this paper and a Fokker-Planck type diffusion law is obtained. Lotka-Volterra type competition systems with spatial heterogeneity are tested, where one species follows the starvation driven diffusion and the other follows the linear diffusion. In heterogeneous environments the starvation driven diffusion turns out to be a better survival strategy than the linear one. Various issues such as the global asymptotic stability, convergence to an ideal free distribution, the extinction and coexistence of competing species are discussed.

**Key words.** cross-diffusion, fitness, Lotka-Volterra competition systems, non-uniform random walk, random dispersal, spatial heterogeneity, thermal diffusion

## Introduction

In nature, species exist in heterogeneous environments and migrate to adjust to such environments. From bacteria to animals all organisms tend to move toward and aggregate around food. Even the stationary

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organisms like plants change their habitat of the next generation by the dispersal of their pollens or seeds. There is no doubt that dispersal played a critical role in the evolution of species since the search for food and a mate is the reason of the dispersal which are the key determinants for survival of species.

How should we model the migration behavior of animals? If a species does not know the direction where food is, then a possible dispersal strategy will be a random movement. Diffusion is widely used for such a random animal dispersal (see [28] for examples of other diffusion models). In many cases, diffusivity is assumed to be constant so that a simple diffusion model for two competing species with a population growth term can be written as

$$u_t = d\Delta u + u(m - u - v), \quad x \in \Omega, t > 0, \quad (1)$$

where  $\Delta = \sum_{i=1}^n \frac{\partial^2}{\partial x_i^2}$  is the Laplace operator,  $\Omega \subset \mathbf{R}^n$  is the domain of habitat,  $m = m(x) \geq 0$  is a resource distribution and  $u = u(x, t)$  is the population density of a biological species that has a constant diffusivity  $d > 0$ . The last unknown  $v = v(x, t)$  is the population density of a competing species and its model equation will be developed throughout the rest of the paper. It is hard to imagine that animals migrate at a constant rate. Animals slow down their migration when food resources are abundant and start to move diligently again when food is consumed. In other words, even if the species moves randomly, enthusiasm for migration is not uniform and such a non-uniformity produces a certain directed movement. The purpose of this paper is to develop a diffusion model for such a random but non-uniform behavior derived from the need for food or other resources. Such non-uniform biological behavior is very closely related to the thermal diffusion of non-biological particles. Brownian particles move more actively when temperature is high and will slow down if temperature decreases. This is the same dispersal situation of biological organisms we want to model.

Fick's law is a widely accepted diffusion model for a nonconstant diffusivity case:

$$v_t = \nabla \cdot (d\nabla v), \quad (2)$$

where  $\nabla = (\frac{\partial}{\partial x_1}, \dots, \frac{\partial}{\partial x_n})$  is the gradient operator and the population dynamics is dropped for now. However, such a diffusion law does not explain a separation behavior of the Ludwig-Soret effect in thermal diffusion. Some would consider a separation phenomenon as a directed movement by including an advection term. In chemotaxis, advection is used to model bacterial movement toward the attractant (see [34, 35]). However, the movement of bacteria is more like a random walk than going straight to the attractant (see [2, 20, 33]). Therefore, it is often very confusing whether the directed movement

that we observe is really a result of pure advection or a result of a random walk process with spatial heterogeneity. In this paper, we will consider diffusion as the only migration strategy in the model. The goal is to develop a diffusion process that is based on the physics of heterogeneous dispersal phenomena of biological species.

The macroscopic scale diffusion phenomenon is decided by two microscopic scale quantities, which are the mean free path  $\Delta x$  and the mean collision time  $\Delta t$  (the notation  $\Delta$  in these two is to denote the smallness of the quantities and is not the Laplace operator). If temperature is not constant, then neither  $\Delta x$  nor  $\Delta t$  is expected to be constant. In the appendix section, a diffusion equation for non-constant  $\Delta x$  and  $\Delta t$  is derived:

$$v_t = \nabla \cdot \left( \frac{D}{S} \nabla (Sv) \right), \quad D = \frac{|\Delta x|^2}{2n\Delta t}, \quad S = \frac{\Delta x}{\Delta t}. \quad (3)$$

A detailed discussion on the model and its comparison with Monte-Carlo simulations can be found from [16].

The role of the particle speed  $S$  is particularly important since it decides steady states. In biological diffusion models, this particle speed can be easily interpreted as the speed of a species. However, the other coefficient  $\frac{D}{S}$  ( $= \frac{\Delta x}{2n}$ ) does not change the steady states but controls the speed of evolution. In our model we will focus only on the effect of the walk speed and a motility function  $\gamma$  basically represents the walk speed, i.e.,  $\gamma \cong S$ . It is assumed that the motility  $\gamma$  increases if food is insufficient. The corresponding diffusion model is written as

$$v_t = \Delta(\gamma v), \quad (4)$$

where other coefficients are forgotten or scaled out.

This Fokker-Plank type diffusion law has been used by many authors in various contexts. Chapman [4,5] suggested a diffusion law  $v_t = \Delta(Dv)$  with a nonconstant diffusivity  $D$  to explain the thermal diffusion phenomenon. However, this law fails to explain non-uniform random walks (see [16]). In competition models with two species, a diffusion model with  $\gamma = c_1 + c_2u + c_3v$  has been used, where  $c_i$ 's are constants (see [18,23,24,26,32] for related studies). If the probability of a random walk depends on the departure point, then the diffusion is given by (4) with the probability distribution in the place of the motility  $\gamma$  (see §5 of [28]).

Experimental measurements of the motility variation of a species is hard to obtain in many cases. Our plan at this stage is to construct the basic hypothesis required for the motility function  $\gamma$  and study the basic feature of the nonlinear diffusion model. First we assume that the motility is a function of a satisfaction measure to the environment,  $\gamma = \gamma(s)$ , where the satisfaction measure

$$s := \frac{\text{food supply}}{\text{food demand}} = \frac{m}{u + v}$$

is used for the competition situation in (1). Second, we assume that  $\gamma$  is a decreasing function as in (25). Then, the motility increases with starvation and hence we will call it a starvation driven diffusion (or simply SDD). These two basic hypotheses for a motility function are key ingredients of starvation driven diffusion and give key estimates such as uniform parabolicity. We will consider two examples of motility functions,

$$\gamma_0(s) := \begin{cases} h, & 0 \leq s < 1, \\ l, & 1 \leq s < \infty, \end{cases} \quad \gamma_1(s) := \begin{cases} sl + (1-s)h, & 0 \leq s < 1, \\ l, & 1 \leq s < \infty, \end{cases}$$

throughout this paper. For the regularity of the problem we consider a smooth motility function  $\gamma_i^\varepsilon$ ,  $i = 0, 1$ , such that  $\gamma_i^\varepsilon \rightarrow \gamma_i$  as  $\varepsilon \rightarrow 0$ .

It is natural to expect that the chance of survival of a species would increase if the species increases its motility to move to other places when food is consumed. We model the situation using the above motility functions and consider

$$v_t = \Delta(\gamma_i v) + v(m - u - v), \quad i = 0, 1, \quad x \in \Omega, \quad t > 0. \quad (5)$$

The competition model (1) versus (5) has been numerically tested for several cases. For fixed  $l < h$  it is observed that there exist  $0 \leq d_1 < d_2$  such that  $u$  prevails if  $0 < d < d_1$ ,  $u$  and  $v$  may coexist if  $d_1 < d < d_2$  and  $v$  prevails if  $d_2 < d$  (see Figures 3 and 6). For a case  $d = l < h$  the linear diffuser  $u$  always becomes extinct, Figures 7 and 8, and it is conjectured that  $d_2 \leq l$ . If  $\frac{h}{l} > \frac{\max_x m(x)}{\min_x m(x)}$  and the motility function is given by  $\gamma_0$ , then it is shown that  $d_1 = 0$  and hence  $v$  always survives (see [17, Theorem 1]). Related conjectures are given in Section 12. Analysis techniques for linear diffusion models has been extended to prove this numerically observed behavior in two companion papers [17, 18] under additional technical assumptions.

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## Part I: Slower diffuser prevails

We will start this article by reviewing the population modeling theory from fundamentals. In this way we may rediscover the meaning of the model. Then, we will develop a starvation driven diffusion.

### 1. Logistic equation

The logistic equation is commonly used to model population dynamics. Let  $P(t)$  be the total population at time  $t$  and  $r$  be the natural growth rate. However, the resource is usually limited and there exists a maximum population  $K > 0$  that can be supported by the environment, which is called the carrying capacity. Then the total population is modeled by the logistic equation

$$\frac{d}{dt}P = rP\left(1 - \frac{P}{K}\right) = rP - \frac{r}{K}P^2, \quad P(0) = C_0, \quad (6)$$

where  $C_0$  is the initial population. The first term  $rP$  is the natural growth and the second term  $-rP^2/K$  is the negative effect caused by the intra-species competition with limited resources. Using non-dimensional quantities,

$$u = P/K \quad \text{and} \quad c_0 = C_0/K, \quad (7)$$

one may obtain a normalized logistic equation,

$$\frac{d}{dt}u = ru(1 - u), \quad u(0) = c_0. \quad (8)$$

This logistic equation has two steady states. The trivial one  $u = 0$  is unstable and the other one  $u = 1$  is stable. Therefore, for any initial value  $c_0 > 0$ , the solution  $u(t)$  converges to  $u = 1$  as  $t \rightarrow \infty$ , i.e., the stable steady state  $u = 1$  is globally asymptotically stable among all nontrivial and nonnegative solutions.

### 2. Spatial heterogeneity and migration

The ordinary differential equation (8) models the dynamics of the total population in the absence of spatial heterogeneity. The environment and the initial population distribution are two main sources of spatial heterogeneity. Consider a reaction equation,

$$\begin{aligned} u_t &= ru(m - u), & x \in \Omega, \quad t > 0, \\ u(x, 0) &= u_0(x), & x \in \Omega, \end{aligned} \quad (9)$$

where  $u = u(x, t) \geq 0$  is the population density,  $u_0(x) \geq 0$  is the initial distribution,  $m = m(x)$  is the resource (or food supply) distribution and  $u_t := \frac{\partial}{\partial t}u$ . Here, we consider a case where the resource distribution is time independent, i.e.,  $m = m(x)$ . Then, for each fixed  $x \in \Omega$ , the system becomes an ODE and one can easily see that,

$$u(x, t) \rightarrow \begin{cases} 0, & \text{if } 0 = u_0(x), \\ m(x), & \text{if } 0 < u_0(x), \end{cases} \quad \text{as } t \rightarrow \infty.$$

In other words, population grows monotonically in time to the local carrying capacity if the initial population is not zero at that place. However, the population remains zero if it is so initially and hence it is clear that the migration of species is an *essential ingredient* to obtain an ecology model with a spatial heterogeneity. Notice that the above reaction equation is not exactly in the form of the logistic equation (6). The natural growth rate in the logistic equation is independent of a change of carrying capacity  $K$ . However, the resource function  $m$  in (9) plays both roles. A reaction model closer to the logistic equation is  $u_t = ru(1 - \frac{u}{m})$ , which depends on a satisfaction measure.

Two kinds of migration strategies are widely used. Advection is one with directional information. In some cases organisms sense the gradient of food or other signals and move to that direction. Such a dynamics is sometimes modeled by a flux  $\mathbf{f} = cu\nabla m$  with a scaling coefficient  $c > 0$ . If this flux is added to the system, the equation becomes

$$u_t = -\nabla \cdot (cu\nabla m) + ru(m - u). \quad (10)$$

The other migration strategy is diffusion which has no directional information. The migration by diffusion is characterized by the randomness of a Brownian motion like behavior. In this case the migration flux is usually given by  $\mathbf{f} = -d\nabla u$  with a diffusivity constant  $d > 0$ . In many cases diffusion and advection may coexist. The Keller-Segel model in chemotaxis [15] is a typical example. However, we will focus on diffusion in this article and develop a diffusion model that even explains advection phenomena.

If the diffusion flux is added to the system with constant diffusivity  $d > 0$ , then the population model (9) turns into a second order parabolic PDE,

$$\begin{aligned} u_t &= d\Delta u + u(m - u), & t > 0, \quad x \in \Omega, \\ 0 &\leq u(x, 0) = u_0(x), & x \in \Omega, \\ 0 &= \mathbf{n} \cdot \nabla u, & x \in \partial\Omega, \quad t > 0, \end{aligned} \quad (11)$$

where  $\mathbf{n}$  is the unit normal vector to the boundary  $\partial\Omega$ . Notice that we have set the growth rate  $r = 1$ , which is possible after a re-scaling of the time variable and the diffusivity coefficient. Hence the diffusivity  $d$  above is actually the ratio of original diffusivity over the growth rate. The Neumann boundary condition is assumed, which indicates

that there is no diffusion flux across the boundary. We always use this boundary condition in this paper without mentioning it again.

It is well known that there exists a unique globally asymptotically stable steady state and we will denote it by  $\theta_{d,m}$ . In other words, no matter what the initial value  $0 \leq u_0 \neq 0$  is, the solution  $u(x, t)$  converges to  $\theta_{d,m}(x)$  as  $t \rightarrow \infty$ . Furthermore, it is also well known that

$$\theta_{d,m}(x) \rightarrow m(x) \text{ as } d \rightarrow 0, \quad \theta_{d,m}(x) \rightarrow \bar{m} \text{ as } d \rightarrow \infty, \quad (12)$$

where  $\bar{m} = \frac{1}{|\Omega|} \int_{\Omega} m(x) dx$  (see [22]).

### 3. Dispersal is essential but not selected (a paradox)

Consider a Lotka-Volterra competition model of two species with identical population dynamics:

$$\begin{cases} u_t = d_1 \Delta u + u(m - u - v), \\ v_t = d_2 \Delta v + v(m - u - v), \end{cases} \quad d_1 < d_2, \quad x \in \Omega, \quad t > 0. \quad (13)$$

The initial values are nontrivial and nonnegative:

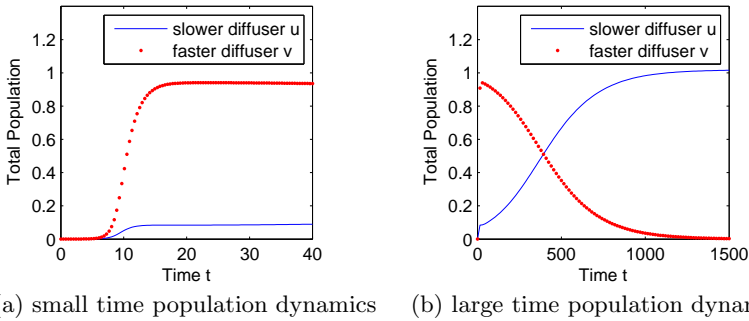
$$0 \leq u(x, 0) = u_0(x) \neq 0, \quad 0 \leq v(x, 0) = v_0(x) \neq 0, \quad x \in \Omega. \quad (14)$$

We will call the solution  $u$  a slower diffuser since it has a smaller diffusivity. It will be denoted by lines in the figures of numerical simulations. The other one  $v$  will be denoted by dots in figures.

Now we are ready to ask an interesting question. Is having a bigger diffusion rate advantageous in this competition? The answer for this question is rather surprising.

**Theorem 1 (Slower diffuser prevails, Dockery *et al.* [9]).** *Suppose that  $d_1 < d_2$  and  $m$  is nonnegative and nonconstant. There are two nontrivial steady states of the competition system (13–14). One is  $(0, \theta_{d_2, m})$ , which is unstable, and the other is  $(\theta_{d_1, m}, 0)$ , which is globally asymptotically stable among positive solutions.*

This theorem implies that, for any initial value, the faster diffuser becomes extinct and the solution  $(u(t), v(t))$  converges to  $(\theta_{d_1, m}, 0)$  as  $t \rightarrow \infty$ . In fact it is well accepted that the spatial variation of resources reduces dispersal rates of linear models (see [8, 12, 14, 25] for more examples). This result is paradoxical. We have seen in the previous section that the dispersal is an essential ingredient in the ecological evolution and, however, this theorem implies that the dispersal should be as small as possible for the survival. This paradox is an indication that the dispersal for biological organisms should be more than a diffusion with a constant diffusivity.



**Fig. 1.** Numerical simulation for (13–14). Faster diffuser has an advantage for a while. However, the slower one prevails eventually. (Here,  $m = \sin(\pi x)\pi/2$ ,  $u(x, 0) = v(x, 0) = 0$  for  $0.02 < x$ ,  $u(x, 0) = v(x, 0) = 0.5m(x)$  for  $x < 0.02$ ,  $d_1 = 0.001$  and  $d_2 = 0.002$ .)

A numerical simulation is given in Figure 1 with the following specifications. The domain is the unit interval,  $\Omega = (0, 1)$ , the resource function is  $m(x) = \sin(\pi x)\pi/2$ , and the diffusivity constants are  $d_1 = 0.001$  and  $d_2 = 0.002$ . The initial values are  $u(x, 0) = v(x, 0) = 0$  for  $x > 0.02$  and  $u(x, 0) = v(x, 0) = 0.5m(x)$  for  $x < 0.02$ . In this situation the total capacity of the habitat is  $\int_{\Omega} m(x)dx = 1$  and the initial total population is small. The evolution of the total population of the two species  $u$  and  $v$  is given in Figure 1(a). In this first stage of a population growth, the faster diffuser looks like to prevail. This is a stage that the diffusion plays a positive role and helps species to arrive a new place earlier and gives a chance to grow without competition. This state looks stable for a while. However, this is only a meta-stable state that holds only in a short time scale. In fact, in a longer time scale, the slower diffuser eventually prevails as in Figure 1(b). In this second stage the diffusion plays a negative role. This is an example of a meta-stable phenomenon and one may find recent studies on meta-stable phenomena from [1, 19] and references therein.

The constant diffusivity in (11) models *uniform* random movements of species. However, biological organisms in a place with abundant food may decrease their motility to stay at the favorable place. On the other hand, organisms in an environment with insufficient food may increase their motility to find food even if they do not know where food is. The constant dispersal rate of biological organisms seems too restrictive to study the role of dispersal as a survival strategy, which is one of the reasons for the paradox. The essence of biological diffusion as a survival strategy can be its adaptability to the change of environmental conditions.



#### 4. Dispersal increase with starvation (biological examples)

Is a migration with a constant motility realistic in nature? In most cases, lack of food resource causes a change of migration speed and such phenomena can be found from all level of animals. *Dictyostelium*, social ameobae, is a classical example that shows a very distinct life cycle depending on food availability (see [3]). This free-moving single-celled organisms undergo a dramatic change when food is limited. They aggregate to form a fruiting body that is a stalk-like structure. The organisms on the top of this fruiting body become spores that can be easily dispersed. The organisms that consist the stalk are there only to help the spores to disperse and are destined to die.

It is clear that motility is beneficial to find food. A similar behavior of motility increase is also observed in much more complex multicellular organisms such as *Caenorhabditis elegans*. *Caenorhabditis elegans* is a small nematode with body length of 1 millimeter. When food is depleted, this species undergoes an extreme transition and enter the stage called *dauer* instead of a normal development. These dauer larvae halt the normal development state and can survive about 10 times longer without food. If these daure larvae encounter favorable environment, they would reenter the normal development and become a normal animal. These dauer larvae show a very interesting behavior called *nictation*, which is only recently understood as a dispersal behavior (see [21]). It has been shown that the nictation behavior is a method that helps the dauer larvae to ride on vehicles such as flies. Flies may carry these nematodes to a new environment where they may have a chance to meet food and therefore, to survive. This behavior produces a huge leap on the rate of diffusion and this dramatic change of diffusion is their survival strategy in a harsh environment.

The desert locust is another example. When locust numbers increase and food sources dwindle, solitary locusts are forced to come together, be social and rub against each other. This behavior gives a signal to locust and makes them molt. After such a series of procedures the solitary desert locusts become social and obtain a body which is appropriate for a long distance travel. Finally, they migrate together through out the continent consuming all the grasses on their path. Such a locust swarming happens during years of drought and gives a better chance to find food (see [6]). In particular, it was recently announced that the molecular signals that trigger such a transition are related to metabolism (see [29]) which supports that such a dramatic change is really to find food.

The migration of human race out of Africa is another example. Historically, famine or war was one of main reasons of a migration of human race. The recent famine of North Korea is making millions of people leave their country. Seasonal drought in Africa makes herds

of animals migrate for water and food. Some of the migrations are guided by experiences or instincts, which are not exactly a diffusion. However, in many cases, although there is a clear intension for the migration, animals and even human beings do not know which way to go until they find something. This is very similar to the diffusion process and the order of dispersal rate is decided by the intention of movement which may depend on the environmental condition.

A dramatic jump of motility is not limited to a case with limited food resources. There are many other reasons such as temperature, weather and mating. However, even though the reasons are different, the non-uniformity in motility is the common physics of the behavior. It is the motility change to adapt the environmental conditions that plays the key role in the survival of species but not simply the motility itself.

## 5. Starvation driven diffusivity? (by Fick's law)

The linear diffusion in (11) models a random walk like migration strategy. Therefore, the predominance of the slower diffuser seems not that wrong since the faster diffuser is being so just randomly. In fact such a triumph by the slower diffuser is related to the time independence of its environment, i.e.,  $m = m(x)$ . The maximum point of  $m$  is the place with most population. Hence the faster diffuser is more willing to leave this better place and this is why the slower diffuser can prevail. However, a life form usually changes its migration strategy for various reasons and we will develop a diffusion model that counts such a non-uniform behavior. In many cases, even if life forms do not know where food is, they at least feel hungry when food is insufficient and, if so, it is natural to expect that they will increase their motility to find food. Such a starvation induced increase of locomotor activity is experimentally confirmed in common model organisms such as fruit fly, mouse and rat (see [11,30,31]). On the other hand, life forms may stay in their place if they are satisfied with the environment.

We define a *satisfaction* measure 's' by

$$s := \frac{\text{food supply}}{\text{food demand}}. \quad (15)$$

In the system (13), the function  $m(x)$  is interpreted as the food supply and sum of populations  $u + v$  as the food demand. Hence the satisfaction measure becomes  $s = m/(u + v)$ . If a single species model (11) is considered, then the satisfaction measure is  $s = m/u$ . This ratio is a simple way to measure the satisfaction on the environment. If  $1 < s$ , then the food supply bigger than the food demand and the reaction term becomes positive. Hence everybody is happy and the population

grows. If  $s = 0.5$ , then the reaction term becomes negative and the population decreases. In this situation only the half of the population are fed or the whole population take only the half of the amount they need. Hence the species will increase their motility.

The first example of a motility function in this paper is a discontinuous one defined by

$$\gamma_0(s) := \begin{cases} h & \text{for } 0 \leq s < 1, \\ l & \text{for } 1 < s < \infty, \end{cases} \quad (16)$$

where  $0 < l < h < \infty$ . If the satisfaction is smaller than 1, then the species increases its motility to the highest level, 'h'. If the satisfaction is bigger than 1, then the motility is decreased to the lowest level, 'l'. Since this motility function is discontinuous, one might want to consider a convolution

$$\gamma_0^\varepsilon := \gamma_0 * \eta^\varepsilon \quad (17)$$

as its smooth approximation, where  $\eta^\varepsilon$  is a typical smooth mollifier with its support in a ball of radius  $\varepsilon > 0$  centered at the origin.

Then what is the correct diffusion model for this situation? We will first consider a model based on Fick's diffusion law. The diffusion flux of Fick's law is given by  $\mathbf{f} = -\gamma_0 \nabla v$ , where the  $\gamma_0$  is considered as a nonconstant diffusivity. Then, the corresponding diffusion equation is  $v_t = \nabla \cdot (\gamma_0 \nabla v)$ . Therefore, the competition system obtained using this diffusion law is

$$\begin{cases} u_t = d \Delta u + u(m - (u + v)), \\ v_t = \nabla \cdot (\gamma_0 \nabla v) + v(m - (u + v)), \end{cases} \quad x \in \Omega, t > 0, \quad (18)$$

where the satisfaction measure  $s$  is

$$s(x, t) = \frac{m(x)}{u(x, t) + v(x, t)}.$$

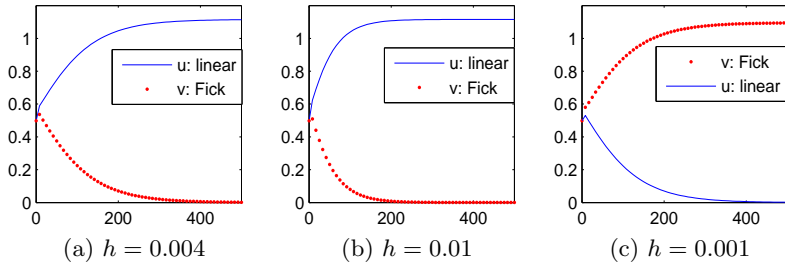
A numerical simulation for the system (18) is given in Figure 2 with the following specifications. First  $d$  and  $l$  are fixed with  $d = l = 0.002$ . The domain is  $\Omega = (0, 1)$  and the resource function is

$$m(x) = \begin{cases} A, & \frac{1}{4} < x < \frac{3}{4}, \\ 2 - A, & \text{otherwise,} \end{cases} \quad (19)$$

where we set  $A = 0$  for this example and then will change it in the following examples. We consider the phenomenon that corresponds to the second stage in Figure 1(b) by starting with an initial value

$$u(x, 0) = v(x, 0) = 0.5 \times m(x).$$

In Figures 2(a,b), two cases of  $d = l < h$  are given. Hence, the linear diffuser  $u$  is a slower one and the nonlinear diffuser  $v$  is a faster one



**Fig. 2.** [ $x$ -axis: competition time,  $y$ -axis: total population]. Numerical simulations for the system (18–19) with  $A = 0$  and  $d = l = 0.002$  fixed. The slower diffuser prevails even if the nonlinear diffuser increases its diffusivity only if the food is not enough.

in these two cases. In the case with  $h = 0.004$ , the nonlinear diffuser  $v$  becomes extinct as in Figures 2(a). If  $h$  is even more increased to  $h = 0.01$ , the nonlinear diffuser  $v$  becomes extinct even earlier. In these example, the advantage of changing diffusivity is not observed. In the last example, Figure 2(c), we set  $h = 0.001$ . In this case the nonlinear diffuser  $v$  reduces its motility and stays in the region where food is insufficient and hence  $v$  is now the slower diffuser. It seems that such a behavior will risk the survival of the species. However, the numerical simulation shows that  $v$  prevails and  $u$  becomes extinct. In the above examples slower diffuser still prevails. Indeed these results are predicted by a corollary of the theorem, where the same arguments of the proof of the theorem are applicable.

**Corollary 1.** *Let  $d = l < h$ . Then the competition system (18–19) has two critical solutions and  $(\theta_{d,m}, 0)$  is globally asymptotically stable among positive solutions.*

These observations violate our common sense that one should look for food for survival. There are two possibilities: (i) our common sense is incorrect or (ii) the diffusion model based on Fick’s law does not explain the situation that biological organisms increase their motility to find food when food is insufficient. We will see that it is the second case and find a corrected diffusion model.

## 6. Diffusion in a heterogeneous environment

The diffusion in the second equation of (18) is by Fick’s diffusion law. The original Fick’s law is for a homogeneous case that the diffusivity is constant. Its application to a heterogeneous case is widely used without a justification. Einstein’s random walk theory says that if the mean free path  $\Delta x$  and mean collision time  $\Delta t$  of a Brownian motion are constant, the diffusivity is given by  $D := \frac{|\Delta x|^2}{2n|\Delta t|}$ .

A dispersal strategy that a species migrates with a different motility can be modeled using a non-uniform Brownian motion or equivalently a random walk system. In the appendix section, the diffusion model in (3) is derived using a non-uniform random walk system. However, in biological situations, there can be other delicate issues depending on the character of species. Let  $\zeta$  be the emigration rate of species from a habitat that depends on the satisfaction to the environment. The emigration rate plays the same role as the departure point depending probability in a random walk model (see §5 of Okubo and Levin [28]), which gives a diffusion model “ $v_t = \Delta(\zeta v)$ ”. Combining it with (3) gives

$$v_t = \nabla \cdot \left( \frac{D}{S} \nabla(\zeta S v) \right), \quad D := \frac{|\Delta x|^2}{2n \Delta t}, \quad S := \frac{\Delta x}{\Delta t}, \quad (20)$$

where  $S$  and  $D$  are called the walk speed and diffusivity, respectively. Notice that the steady state of the equation (20) is reversely proportional to  $\zeta S$ , i.e.,  $v \propto (\zeta S)^{-1}$  as  $t \rightarrow \infty$ . On the other hand, the coefficient  $\frac{D}{S}$  ( $\equiv \frac{\Delta x}{2n}$ ) has no influence in deciding steady states. Biological interpretation of  $\Delta x$  is controversial. For example, it has been observed that a ladybug changes direction less frequently if it is hungry (see [13]) and hence the walk length  $\Delta x$  increases when food is insufficient. On the other hand, *Escherichia coli* increases its tumbling frequency if the density of attractant is low (see [27]), i.e.,  $\Delta x$  decreases when attractant density is low. In other words, the two species show an opposite behavior in terms of walk length when food is insufficient. It seems that the physical interpretation of the walk length requires a more detailed study which is beyond the scope of this paper.

We will focus on the role of  $\zeta S$  that decides the steady state and is more important in our context. However, the role of  $\frac{D}{S}$  can be more crucial for temporally fluctuating environments. Consider

$$v_t = \Delta(\gamma v), \quad (21)$$

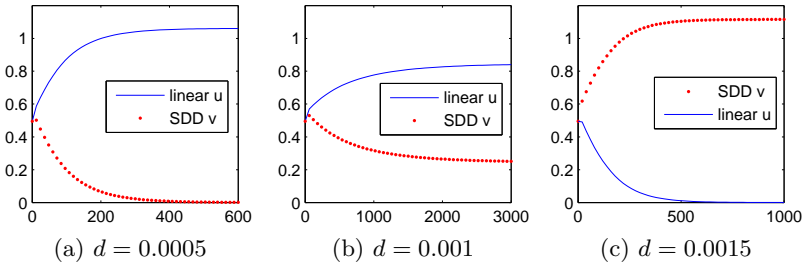
where the motility function  $\gamma$  models  $\zeta S$ . This diffusion model is the one we are going to use later on and the property of  $\gamma$  will be specified in Section 8.

## 7. Linear dispersal versus starvation driven dispersal

Consider a competition between a linear diffuser and a starvation driven diffuser with a Neumann boundary condition:

$$\begin{cases} u_t = d\Delta u + u(m - (u + v)), & x \in \Omega, t > 0, \\ v_t = \Delta(\gamma v) + v(m - (u + v)), & x \in \Omega, t > 0, \end{cases} \quad (22)$$

$$0 = \mathbf{n} \cdot \nabla u = \mathbf{n} \cdot \nabla(\gamma v), \quad x \in \partial\Omega, t > 0. \quad (23)$$



**Fig. 3.** [ $x$ -axis: competition time,  $y$ -axis: total population]. Numerical simulations for the system (22). The resource function is given by (19) with  $A = 0$ . The motility function is  $\gamma_0$  in (16) with  $h = 0.004$  and  $l = 0.002$ .

This competition model is used in the rest of this paper to compare the linear diffusion and the starvation driven diffusion. Since the population dynamics of the two species are identical, such comparisons will clarify the difference of the two diffusions.

Numerical simulations for the system (22)-(23) are given in Figure 3 with the following specifications. The domain is  $\Omega = (0, 1)$ , the resource function is in (19) with  $A = 0$ , and the initial value is

$$u(x, 0) = v(x, 0) = 0.5 \times m(x). \quad (24)$$

The motility function is  $\gamma = \gamma_0$  in (16) with  $h = 0.004$  and  $l = 0.002$ . In Figure 3(a) an evolution of total population is given with  $d = 0.0005$ , where the linear diffuser still prevails. In this case the diffusivity  $d$  is too small for the other species to overcome. In Figure 3(b) the diffusivity is increased to  $d = 0.001$  and the two species coexist. In Figure 3(c) the diffusivity is  $d = 0.0015$  and the species with a motility change prevails. These numerical simulations indicate that there are constants,  $0 < d_1 < d_2$ , such that, the linear diffuser prevails if  $d < d_1$ , the two species may coexist if  $d_1 < d < d_2$ , and the starvation driven diffuser prevails if  $d > d_2$ . According to the numerical simulations in Figure 3 it is expected that  $0.0005 < d_1 < 0.001$  and  $0.001 < d_2 < 0.0015$  (see [17, Theorem 2]). Since  $d_2 < l$ , the starvation driven diffuser is still a faster diffuser everywhere and, however, it may prevail due to the motility increase when there is not enough food. We may conclude that a motility increase on starvation is beneficial for survival of species and the diffusion model in (21) explains such a behavior (see Section 8).

## Part II: Starvation driven diffuser prevails

The transition from a linear diffuser predominance regime to a motility changing diffuser predominance one and the existence of a coexistence regime in Figure 3 leave us many questions. In the rest of

the paper we formulate the starvation driven diffusion and investigate its property.

## 8. Hypothesis for a motility function

Biological organisms may change their motility for several reasons. For example, it is well known that German cockroaches (*Blattella germanica*) change their motility depending on the density of the aggregation pheromone. If the pheromone concentration is low, their motility increases, whereas they become less active if the concentration is high (see [10]). Therefore, the motility measure  $\gamma$  can be modeled accordingly in such a case and the pheromone density can play the role of the satisfaction measure. In this paper we focus on the diffusion related to food.

There are two kinds of responses of biological organisms when almost all the food is consumed. The first one is changing the metabolism so that it can reduce the use of energy and wait for a better environment. The second response is increasing the motility in order to find a place with food. We are going to consider the second case. In the followings we will develop the minimum requirements that a motility function should satisfy in a general situation. First, the speed  $S = \Delta x / \Delta t$  of individuals is a decreasing function of the satisfaction measure,  $s := \frac{m}{v}$ . The emigration rate  $\zeta$  also decreases if the satisfaction increases. Hence it is natural to assume that the motility function  $\gamma(s) := \zeta(s)S(s)$  is a decreasing function of the satisfaction measure  $s$ . For the boundedness and the parabolicity, we also assume that there exist positive values  $l$  and  $h$  such that

$$\gamma(s) \uparrow h \text{ as } s \downarrow 0, \quad \gamma(s) \downarrow l \text{ as } s \uparrow \infty. \quad (25)$$

This hypothesis makes the diffusion equation (21) parabolic and hence the solution  $v$  with nonnegative initial value  $0 \leq v(x, 0) \neq 0$  becomes strictly positive for all  $t > 0$  and hence the satisfaction measure  $s = m/v$  is well defined for all  $t > 0$ . Notice that the meaning of the diffusion could be clearer if a *starvation measure*, say  $\tilde{s} = v/m$ , is used instead of the satisfaction measure. However, in that case, if  $m = 0$  or  $m$  has a sign change, then  $v/m$  is not defined. That is why we are using the satisfaction measure  $s$  with a decreasing motility function  $\gamma$  for  $0 \leq s$ .

## 9. Fitness by starvation driven diffusion without reaction

In nature the population density of species is higher in richer regions and such a phenomenon is called *fitness*. One may ask if the fitness is an effect of the migration or of the population growth. The answer could be both. In the section we study the fitness property of

the starvation driven diffusion. Since the migration by Fick's diffusion law does not produce any advection, this fitness phenomenon in the diffusion reaction equation (11) is purely from the population dynamics. Therefore, one might add an advection term and obtain

$$v_t = \nabla \cdot (d\nabla v - cv\nabla m). \quad (26)$$

Then, one may obtain such a phenomenon without population dynamics. However, it is still a mystery if the added advection has a physical meaning and if it is in a correct form. It is well known that adding such an advection term is not always beneficial in competition models (see [7]). On the other hand, the starvation driven diffusion in (21) gives a separation behavior without adding an advection term. First, the product and the quotient rule for the gradient  $\nabla(\gamma(s)v)$  gives

$$\nabla(\gamma v) = \gamma\nabla v + v\gamma'\nabla s = \gamma\nabla v + v\gamma'\frac{v\nabla m - m\nabla v}{v^2}.$$

Therefore, the new diffusion equation is written as

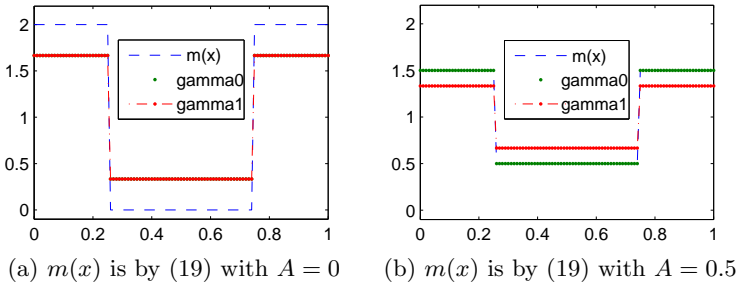
$$v_t = \Delta(\gamma v) = \nabla \cdot \left( (\gamma - s\gamma')\nabla v + \gamma'\nabla m \right), \quad (27)$$

which contains an advection term toward richer regions. This diffusion will be called a starvation driven diffusion or simply SDD when the motility function  $\gamma$  satisfies the hypothesis (25). Let us compare (27) with the advection-diffusion equation (26). The nonconstant diffusivity  $d$  corresponds to  $\gamma(s) - \gamma'(s)s$  which is positive since  $\gamma$  is a decreasing function. Therefore, this diffusion equation is uniformly parabolic. The coefficient of the advection term is  $\gamma'(s)$  which is non-positive and hence the coefficient  $c$  in (26) corresponds to  $-\frac{\gamma'(s)}{v}$ . This advection disappears in regions  $\gamma'(s) = 0$  and, otherwise, the advection is heading to the regions where the resource distribution  $m$  increases. For example, if the motility function  $\gamma_0^\varepsilon$  in (17) is applied, a strong advection exists in the region  $|s - 1| \leq \varepsilon$ . This advection is produced as a result of a nonuniform motility without the assumption that the individuals can sense the resource gradient.

The function  $\gamma_0$  in (16) and its regularization  $\gamma_0^\varepsilon$  in (17) satisfy (25). These motility functions are extreme cases where the whole population increase their motility to the highest level simultaneously even if the resource  $m$  is slightly smaller than the demand  $v$ . It is more realistic in many cases to assume that only 10% of the population increase their motility when  $s = 0.9$ . If so, the corresponding motility is a continuous function

$$\gamma_1(s) := \begin{cases} sl + (1-s)h, & 0 \leq s < 1, \\ l, & 1 \leq s < \infty. \end{cases} \quad (28)$$





**Fig. 4.** [ $x$ -axis: space,  $y$ -axis: concentration density]. Numerical simulations for (29). (a) If  $A = 0$ , two motility functions  $\gamma_0$  and  $\gamma_1$  provide identical steady states. (b) If  $A = 0.5$ , they are different. In this example, the steady state given by  $\gamma_0$  is same as the resource function  $m$ . Here,  $h = 0.05$  and  $l = 0.01$

The first step to study the starvation driven diffusion is to consider steady states. Consider a positive steady state of

$$\begin{aligned} 0 &= \Delta(\gamma(s)v), & x \in \Omega, & \quad t > 0, \\ 0 &= \mathbf{n} \cdot \nabla(\gamma(s)v), & x \in \partial\Omega, & \quad t > 0. \end{aligned} \quad (29)$$

Let the domain be  $\Omega = (0, 1)$  and the resource distribution  $m$  be defined by (19). A steady state or an equilibrium solution  $v^e$  of (29) is not unique and we are looking for the one that has the same total population as the total carrying capacity, i.e.,

$$\int_{\Omega} v^e(x) dx = \int_{\Omega} m(x) dx = 1. \quad (30)$$

The steady state solution has constant *diffusion pressure*,  $\gamma(m/v)v = \text{constant}$ , which is proved in [18, Theorem 1]. One can easily find steady states of (29) explicitly by solving the relation thanks to the simplicity in  $m$ . For example, let  $A = 0, h = 0.05, l = 0.01$  and

$$v^e(x) = \begin{cases} 1/3, & \frac{1}{4} < x < \frac{3}{4}, \\ 5/3, & \text{otherwise.} \end{cases}$$

Then,  $s = 0$  if  $\frac{1}{4} < x < \frac{3}{4}$  and  $s = \frac{6}{5}$  if  $x < \frac{1}{4}$  or  $\frac{3}{4} < x$ . Therefore,  $\gamma_0(s)v^e = \gamma_1(s)v^e = \frac{0.05}{3}$  for all  $0 < x < 1$  and hence  $v^e$  is a steady state for both motility functions,  $\gamma_0$  and  $\gamma_1$ . These steady states are given in Figure 4(a) with resource distribution  $m$ . In this example, the population density in the region with food is 5 times bigger than the one in the region without food, which is the same ratio as  $h/l$ . Remember that the steady state under Fick's diffusion is a constant state.

The next example is the case with  $A = 0.5$ ,  $h = 0.05$  and  $l = 0.01$ .  
Let

$$v^e(x) = \begin{cases} 0.7, & \frac{1}{4} < x < \frac{3}{4}, \\ 1.3, & \text{otherwise.} \end{cases}$$

Then, one can similarly check that  $v^e$  is the steady state when the motility function is  $\gamma_1$ . However, if the motility function is  $\gamma_0$ , we may show that the resource distribution  $m$  itself is a steady state. Of course, if  $v = m$ , then  $s = 1$  and, due to the discontinuity of  $\gamma_0$  at  $s = 1$ , one should clarify the meaning of the steady state. In the following proposition we will see that  $v = m$  is the steady state in the limiting sense of a regularly perturbed problem. Notice that the following proof is possible since the motility ratio is bigger than the resource ratio, i.e.,

$$\frac{\max_x m(x)}{\min_x m(x)} = \frac{1.5}{0.5} = 3 < \frac{h}{l} = \frac{0.05}{0.01} = 5. \quad (31)$$

**Proposition 1.** *Let the motility function be  $\gamma = \gamma_0^\varepsilon$  given by (17) with  $h = 0.05$ ,  $l = 0.01$  and the resource function  $m$  be by (19) with  $A = 0.5$ . If  $v^\varepsilon$  is the steady state of (29) with the unit total population in (30), then  $v^\varepsilon(x) \rightarrow m(x)$  as  $\varepsilon \rightarrow 0$  except the discontinuity points of  $m$ .*

*Proof.* Let  $\varepsilon > 0$  be small,  $0 < a < 2$ , and

$$v(x) = \begin{cases} a, & \frac{1}{4} < x < \frac{3}{4}, \\ 2 - a, & \text{otherwise.} \end{cases}$$

Then, the diffusion pressure in the region  $\frac{1}{4} < x < \frac{3}{4}$  is  $\gamma(0.5/a)a$  and is an increasing function of  $a$ , i.e.,

$$\frac{d}{da} \left[ \gamma\left(\frac{0.5}{a}\right)a \right] = \gamma\left(\frac{0.5}{a}\right)a - 0.5\gamma'\left(\frac{0.5}{a}\right)a^{-1} > 0.$$

Similarly, the diffusion pressure in the other region is  $\gamma\left(\frac{1.5}{2-a}\right)(2-a)$  and is a decreasing function of  $a$ .

If  $1 + \varepsilon < \frac{0.5}{a}$ , then it is easy to check that the diffusion pressure in the region  $\frac{1}{4} < x < \frac{3}{4}$  is lower than the one in the other region. Suppose that  $\frac{0.5}{a} < 1 - 3\varepsilon$ . Then, a series of computations give

$$\begin{aligned} 0.5 < (1 - 3\varepsilon)a &\Rightarrow -0.5 > -a + 3\varepsilon a \\ &\Rightarrow 1.5 > 2 - a + 3a\varepsilon \Rightarrow \frac{1.5}{2-a} > 1 + \frac{3a}{2-a}\varepsilon. \end{aligned}$$

Since  $3a > 2 - a$ , we have  $\frac{1.5}{2-a} > 1 + \varepsilon$  and hence

$$\gamma(0.5/a)a = ha = l5a > l(2-a) > \gamma(1.5/(2-a))(2-a).$$

In other words, the diffusion pressure in the region  $\frac{1}{4} < x < \frac{3}{4}$  is higher than the other region. Therefore, by the monotonicity of the diffusion pressure on  $a$ , there should exist  $a^\varepsilon$  such that  $1 - 3\varepsilon < \frac{0.5}{a^\varepsilon} < 1 + \varepsilon$  and

$$v^\varepsilon(x) = \begin{cases} a^\varepsilon, & \frac{1}{4} < x < \frac{3}{4}, \\ 2 - a^\varepsilon, & \text{otherwise} \end{cases}$$

is the steady state with the unit mass. One can easily see that  $v^\varepsilon \rightarrow m$  as  $\varepsilon \rightarrow 0$  except the discontinuity points of  $m$ .  $\square$

Notice that this proposition holds because of the relation (31). For example a relation ‘ $5a > 2 - a$ ’ has been used in the proof which is related to this relation. A general case is proved in [18, Theorem 5] that  $v = m(x)$  is a steady state of (29) if the motility function is  $\gamma_0$  and  $\frac{\max_x m(x)}{\min_x m(x)} \leq \frac{h}{l}$  is satisfied. More or less, the proof of the proposition shows the dynamics behind an optimal selection phenomenon.

*Remark 1.* The Turing instability explains a pattern formation when there is a big diffusivity difference between two species. The example in Figure 4 shows that a pattern formation can be obtained even in a single species case if there is a motility jump spatially.

## 10. Starvation driven diffusion with population dynamics

Now we consider the starvation driven diffusion with the population reaction term for a single species model,

$$\begin{aligned} v_t &= \Delta(\gamma v) + v(m - v), & t > 0, \quad x \in \Omega, \\ v(x, 0) &= v_0(x) \geq 0, & x \in \Omega. \end{aligned} \quad (32)$$

In this case, the satisfaction measure is given by  $s = \frac{m}{v}$  and the equation can be rewritten as

$$v_t = \nabla \cdot \left( (\gamma(s) - \gamma'(s)s)\nabla v + \gamma'(s)\nabla m \right) + v(m - v). \quad (33)$$

Since the motility function  $\gamma = \gamma_0$  has a discontinuity at  $s = 1$ , its derivative contains a delta measure. One may consider a regularized problem by replacing  $\gamma_0$  with  $\gamma_0^\varepsilon$  to avoid such a situation. In this equation we have all the three different dynamics, advection, diffusion and reaction.

The problem (32) has been studied in [18]. It is shown that, if the motility function  $\gamma$  satisfies (25) and an extra condition

$$\gamma(s) - s(s - 1)\gamma'(s) > 0 \quad \text{for } 0 < s < 1, \quad (34)$$

then a unique steady state  $\theta_{\gamma,m}(x)$  exists and is globally asymptotically stable [18, Theorem 2]. This steady state depends on the motility

function  $\gamma$  and the resource distribution  $m$ . The motility functions in this paper satisfy this extra condition. However, it seems that the global asymptotic stability should hold true without this technical hypothesis.

If the steady state is identical to the resource function, i.e.,  $\theta_{\gamma,m} = m$ , then the phenomenon is called an optimal habitat selection. Under an assumption

$$\frac{\max_x m(x)}{\min_x m(x)} < \frac{h}{l}, \quad (35)$$

it has been shown that  $\theta = m(x)$  is a steady state of the problem (32) without the reaction term if the motility function is  $\gamma = \gamma_0$  in (16) (see Proposition 1 and [18, Theorem 5]). Furthermore, since the population reaction term forces the solution to fit the resource distribution  $m$ , it is natural to expect that the resource distribution  $m$  itself is the globally asymptotically stable solution even with the reaction term and hence

$$\theta_{\gamma_0,m}(x) = m(x).$$

In fact such a global stability has been shown [18, Theorem 6] under an extra condition

$$l \max_{\Omega} m(x) < \frac{h+l}{2} \min_{\Omega} m(x) < \frac{h+l}{2} \max_{\Omega} m(x) < h \min_{\Omega} m(x). \quad (36)$$

It is expected that the optimal habitat selection phenomenon should hold true only with (35) but without the technical condition (36).

In Figure 5 four examples of steady states are given. In these figures  $l$  is fixed at  $l = 0.002$  and four different cases are tested with  $h = 0.002, 0.004, 0.01$  and  $h = 0.04$ . One can clearly see that the steady states becomes steeper if the diffusivity  $h$  increases. This is an example that a diffusion may make edges even in a single equation case if a heterogeneity is allowed. One can also observe that the steady states converges to the resource function  $m$  as the motility ratio  $h/l$  increases.

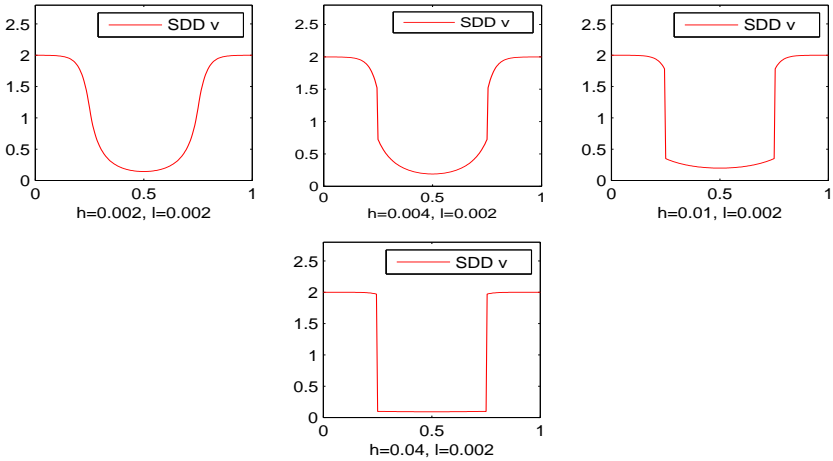
## 11. Starvation driven diffusion in a competition

Now we return to the competition system (22–24). A natural satisfaction measure of this model is

$$s = \frac{m}{u+v}.$$

Then, the equation for  $v$  in (22) can be rewritten as

$$v_t = \nabla \cdot \left( \gamma \nabla v - \frac{s\gamma'}{u+v} v \nabla v - \frac{s\gamma'}{u+v} v \nabla u + \frac{\gamma'}{u+v} v \nabla m \right) + v(m - u - v). \quad (37)$$



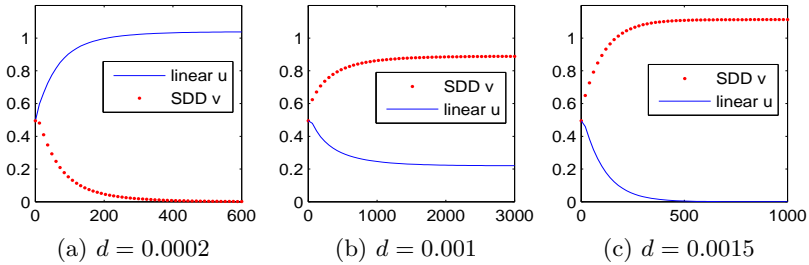
**Fig. 5.** [ $x$ -axis: space,  $y$ -axis: concentration]. Steady states of (32) with  $\gamma_0$  in (16) are given with a resource  $m$  in (19) with  $A = 0$ . If  $h$  is increased with a fixed  $l$ , the steady state converges to  $m$  and the edges become sharper.

There are three kinds of dynamics in this diffusion. The first term  $\gamma(s)\nabla v$  is Fick's diffusion and the second term  $-\frac{s\gamma'(s)}{u+v}v\nabla v$  is *self-diffusion*. These two are trivialization processes that produce a flux in the direction that  $v$  decreases and hence make the distribution of  $v$  flat. The third term  $-\frac{s\gamma'(s)}{u+v}v\nabla u$  is *cross-diffusion* that produces a flux in the direction that  $u$  decreases. Therefore, this cross diffusion guides  $v$  to a region with less  $u$  and hence  $u$  and  $v$  are separated. The fourth term  $\frac{\gamma'(s)}{u+v}v\nabla m$  is advection in the direction that  $m$  increases. Hence this last term makes the species fit to the resource distribution. All these dispersal dynamics disappear in the region that  $\gamma'(s) = 0$  except Fick's law type diffusion. Hence the effect of starvation driven diffusion appears across the region of satisfaction that motility  $\gamma$  changes.

Let  $\gamma = c_1 + c_2u + c_3v$ , where  $c_i$ 's are coefficients to control the weight of each term (see [23, 24, 26, 32]). This case was designed to obtain a separation phenomenon. If one adds an extra advection term  $-c_4v\nabla m$ , the second equation of (22) turns into

$$v_t = \nabla \cdot ((c_1 + c_2u)\nabla v + 2c_3v\nabla v + c_2v\nabla u - c_4v\nabla m) + v(m - u - v). \quad (38)$$

The first term  $(c_1 + c_2u)\nabla v$  is Fick's diffusion and the second term  $2c_3v\nabla v$  is self-diffusion. The third term  $c_2v\nabla u$  is cross diffusion and one may compare the coefficient " $c_2$ " with " $-\frac{s\gamma'(s)}{u+v}$ " in (37). The fourth term is advection that may give  $v$  a fitness to the resource distribution and the coefficient " $-c_4$ " corresponds to " $\frac{\gamma'(s)}{u+v}$ ".



**Fig. 6.** [ $x$ -axis: competition time,  $y$ -axis: total population]. Numerical simulations for the system (22). The resource function is given by (19) with  $A = 0$ . The motility function is  $\gamma_0$  in (16) with  $h = 0.004$  and  $l = 0.002$ .

## 12. Regimes for coexistence and extinction (conjectures)

The numerical simulations in Figure 3 are repeated in Figure 6 using the continuous motility function  $\gamma_1$  in (28). One can find the exactly same behavior as the discontinuous motility function case. As one increases the diffusivity  $d$  starting from zero, one may observe an extinction of  $v$ , coexistence of  $u$  and  $v$  and extinction of  $u$  in that order. The diffusivity regimes for each case can be different if a different motility function  $\gamma$  is chosen. However, one may expect the following:

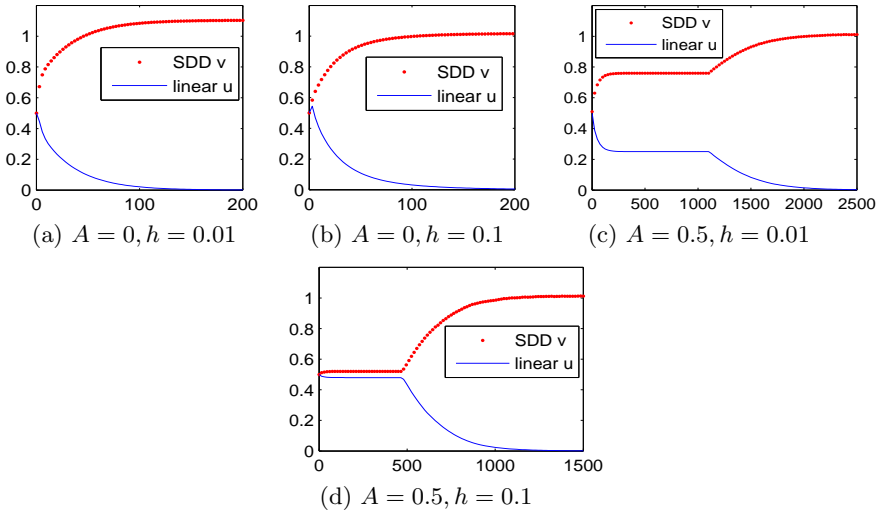
*Conjecture 1.* Let the motility function  $\gamma$  satisfy (25) with  $l < h$  and let  $m \geq 0$  be nonconstant. Then there exist  $0 \leq d_1 < d_2$  such that  $(0, \theta_{\gamma, m})$  is the globally asymptotically stable steady state of (22)-(23) if  $d > d_2$ . The other semi-trivial solution  $(\theta_{d, m}, 0)$  is globally asymptotically stable if  $0 < d < d_1$ . If  $d_1 < d < d_2$ , then  $u$  and  $v$  may coexist.

Remember that  $d_1$  and  $d_2$  in the conjecture depend on the choice of  $m$  and  $\gamma$ . There are two more questions motivated by the conjecture and computational observations:

1. Is it possible to have  $d_1 = 0$ ? If so, the starvation driven diffuser  $v$  is guaranteed to survive even if the slower diffuser is extremely slow.
2. Can we guarantee  $d_2 < l$  for all choices of  $h$  and  $l$  within a class of motility functions? If so, by choosing  $l = d$ , the starvation driven diffusion may drive out the linear diffuser to extinction.

## 13. Resource variation versus motility variation

In this section we will consider the effect of resource variation  $\frac{\max_x m(x)}{\min_x m(x)}$  and motility variation  $\frac{h}{l}$  in the competition of two species. We will



**Fig. 7.** [ $x$ -axis: competition time,  $y$ -axis: total population]. Numerical simulations for (22–24) with the discontinuous motility function  $\gamma_0$  in (16) and  $l = d = 0.002$  fixed.

consider the two motility functions given in (16) and (28) and the resource function given in (19). In the numerical simulations of Figures 7 and 8, we fix

$$d = l = 0.002,$$

and then test several cases of  $A$  and  $h$  to observe the effect of the resource and the motility variations.

### 13.1. Discontinuous motility function

We first consider the discontinuous motility function  $\gamma_0$  given in (16). A numerical simulation for the system (22–24) with  $h = 0.01$  and  $A = 0$  is given in Figure 7(a). In this example the linear diffuser  $u$  becomes extinct. In this case the motility variation  $\frac{h}{l} = 5$  is less than the resource variation  $\frac{\max_x m(x)}{\min_x m(x)} = \frac{2}{0} = \infty$ . In Figure 7(b) the motility variation has been increased by using  $h = 0.1$  and hence the ratio is  $\frac{h}{l} = 50$ . The extinction time and the evolution profile are similar as the ones of Figure 7(a). However, 50 is still less than  $\infty$  and  $u$  similarly becomes extinct. The total population of  $v$  at the final time is less than the one of Figure 7(a). One can see that the case of Figure 7(b) gives a better fitness than the case Figure 7(a) does (see Figure 5) and hence the total population of Figure 7(b) should be closer to the total resource, which is one. Remember that these two cases do not satisfy the relation (35).

In Figures 7(c,d), we consider two cases that (35) is satisfied. In these two cases the total population approaches to a state that both species survive for a while. However, after a certain amount of time, the solution suddenly converges to a semi-trivial solution. Figure 7(c) is for the case with  $A = 0.5$  and  $h = 0.01$ , where  $\frac{h}{l} = 5$  and  $\frac{\max_x m(x)}{\min_x m(x)} = \frac{1.5}{0.5} = 3$ . The intermediate state for the time interval  $200 < t < 1100$  is the following steady state of (22):

$$u^e(x) = 0.25, \quad v^e(x) = m(x) - u^e(x) = \begin{cases} 0.25, & \frac{1}{4} < x < \frac{3}{4}, \\ 1.25, & \text{otherwise.} \end{cases} \quad (39)$$

One may easily check that this is a steady state. Clearly, the population dynamics becomes zero and  $\Delta u^e = 0$ . We have already shown in Proposition 1 that  $\Delta(\gamma_0 v^e) = 0$ . Hence  $(u^e, v^e)$  in (39) is a steady state. In the numerical simulation, the solution  $u(x, t)$  converges to  $u^e$  from the above as  $t \rightarrow 1100$ . However, as soon as  $u(x, t) < u^e$  it suddenly converges to zero. This behavior of numerical solution is a mystery to authors. In fact, there are many more steady states of this type. For example, for any constant state  $0 \leq u^e < 0.25$ , a pair  $(u^e, v^e)$  with  $v^e := m - u^e$  is a steady state. A special feature of the one in (39) is that the variation of  $v^e$  is same as the motility variation, i.e.,

$$\frac{\max_x v^e(x)}{\min_x v^e(x)} = \frac{h}{l}. \quad (40)$$

Since  $v^e = m - u^e$  is two valued piecewise constant function, this situation is very similar to the evolutionary stable strategy of a two-patches problem that the migration ratio is exactly the reverse of the carrying capacity ratio. It seems that this numerical simulation shows a possible appearance of the evolutionary stable strategy and its connection to the starvation driven diffusion somehow. The hidden structure of the phenomenon requires a further survey.

The fourth case is  $A = 0.5$  and  $h = 0.1$ . In this case the relation (35) still holds true and allows a similar steady state that satisfies (40), which is

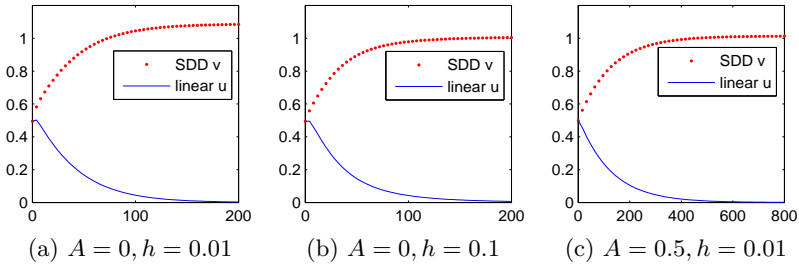
$$u^e(x) = 47/98, \quad v^e(x) = m(x) - u^e(x).$$

A numerical simulation for this case is given in Figure 7(d). We can observe the same phenomenon as in the previous case.

### 13.2. Continuous motility function

We now consider numerical simulations for (22)–(24) with the continuous motility  $\gamma_1$  given in (28). The simulation specifications are exactly same as the case of Figure 7. In Figure 8(a) a simulation is





**Fig. 8.** [ $x$ -axis: competition time,  $y$ -axis: total population]. Numerical simulations for (22–24) with the continuous motility function  $\gamma_1$  in (28).  $l = d = 0.002$  are fixed.

given with  $h = 0.01$ ,  $l = d = 0.002$  and  $A = 0$ . This simulation result is similar as the discontinuous motility case, Figure 7(a), and the linear diffuser with constant diffusivity  $d(=l)$  becomes extinct in a similar time scale. The second simulation, Figure 8(b), is with  $A = 0$  and  $h = 0.1$ . In this case the increase of motility ratio to  $h/l = 50$  does not make a difference in the extinction time. However, the final total population is less than the one of (a), which indicates a better fitness as the discontinuous motility function case. A notable difference in compare with the discontinuous motility function case is the case with  $A = 0.5$ . In Figure 8(c) the linear diffuser becomes extinct without an intermediate steady state. In this case the extinction time is longer than case (a), but shorter than the case in Figure 7(c).

In the previous two examples, Figures 7 and 8, we considered cases with  $d = l$  and  $u$  always becomes extinct. This indicates that  $d_2$  in Conjecture 1 is less than or equal to  $l$  and it has been shown in [17, Theorem 2]) for the case with  $\gamma_0$ . We have seen that the relation between  $\frac{h}{l}$  and  $\frac{\max_x m(x)}{\min_x m(x)}$  plays a key role in the evolution. It is shown in [17, Theorem 1] that the steady state solution  $(\theta_{d,m}, 0)$  is not stable for any  $d > 0$  if (35) is satisfied and  $\gamma = \gamma_0$ . Hence we may conclude  $d_1 = 0$  in the case.

## 14. Conclusions

Inter-species and intra-species competitions take place constantly. Then, how does the dispersal strategy influence the survival of the individuals or species in a competing environment? Only limited experimental methods exist. Modeling the competition among individuals with different diffusion rates is important to understand how diffusion affects the selection. In biological models linear diffusions have been mostly used (see [28] for examples). The linear diffusion is a useful tool to study the ecological evolution as a migration strategy.

However, it is a simplified model and, if we want to conclude something more subtle, the model may lead us to wrong impressions. For example, it is well known that a slower diffuser prevails over a faster one when the diffusivity coefficients are constant. One may conclude from this theory that the evolutionary selection favors slower diffuser, which violates very basic evolutionary observations. To answer such a subtle question, one should consider a more realistic diffusion and the starvation driven diffusion of this paper is designed for that purpose.

The main contribution of this article is to add a nonuniform structure to the random dispersal that species increase their motility when food is not enough. To obtain such a starvation driven diffusion the authors have employed the thermal diffusion developed in [16] and the corresponding diffusion model obtained is (21), where the motility function  $\gamma$  is a decreasing function on the satisfaction measure  $s := (\text{food supply})/(\text{food demand})$ . From numerical computations we observed that the species that increases its motility when food is insufficient has an advantage in the competition.

A model based on Fick's diffusion law has been compared with the one based on starvation driven diffusion in this paper. This comparison shows that Fick's diffusion law does not explain a heterogeneous dispersal behavior. The starvation driven diffusion introduced in this paper seems the preferable choice. Some mathematical analysis of this model has been done in [17,18], which shows that classical theoretical tools for linear diffusion models can be applied to these nonlinear models.

## 15. Appendix: Derivation of non-isothermal diffusion

Let  $\{x^i : i \in \mathbb{Z}\}$  be mesh grids and  $x^{i+1/2} := (x^i + x^{i+1})/2$  be the middle point between two adjacent grids. Let  $V(x^i)$  be the number of particles at  $x^i$ , which jump randomly to one of two adjacent grids every time interval  $\Delta t(x^i)$ . Define the walk length by  $\Delta x(x^{i+1/2}) := x^{i+1} - x^i$  and let  $\Delta x(x^i) := x^{i+1/2} - x^{i-1/2}$ .

Then, the particle flux that crosses the a mid point  $x^{i+1/2}$  from left to right is  $\frac{V}{2\Delta t}|_{x=x^i}$  and the one from right to left is  $\frac{V}{2\Delta t}|_{x=x^{i+1}}$ . Notice that the particle density is given by  $v = \frac{V}{\Delta x}$  and hence the net flux is

$$\mathbf{f}(x^{i+\frac{1}{2}}) = \frac{\Delta x v}{2\Delta t}|_{x^i} - \frac{\Delta x v}{2\Delta t}|_{x^{i+1}} = -\frac{\Delta x|_{x^{i+\frac{1}{2}}}}{2} \left( \frac{\frac{\Delta x}{\Delta t} v|_{x^i} - \frac{\Delta x}{\Delta t} v|_{x^{i+1}}}{x^i - x^{i+1}} \right). \quad (41)$$

If the Brownian motion or the random walk is in a homogeneous environment, we may assume the mean free path  $\Delta x$  and the collision time  $\Delta t$  are constant and hence  $\frac{\Delta x}{\Delta t}$  in the parenthesis of (41) can be

taken out. However, if the temperature is not spatially constant, for example, they depend on the space variable and should stay inside. In conclusion, the diffusion flux for a non-isothermal case in  $n$  space dimension is given by

$$\mathbf{f} = -\frac{D}{S}\nabla(Sv), \quad D := \frac{|\Delta x|^2}{2n\Delta t}, \quad S := \frac{\Delta x}{\Delta t}, \quad (42)$$

where  $S$  and  $D$  are called walk speed and diffusivity, respectively. Notice that the walk length is given by  $|\Delta x| = 2nD/S$ . Therefore, the corresponding non-isothermal diffusion equation is

$$v_t = \nabla \cdot \left( \frac{D}{S} \nabla(Sv) \right). \quad (3)$$

One might numerically check that this diffusion model gives the correct behavior of non-uniform random walks with nonconstant  $\Delta x$  and  $\Delta t$ . The numerical solutions of this diffusion model have been compared with Monte-Carlo simulations in [16].

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## References

1. Margaret Beck and C. Eugene Wayne, *Using global invariant manifolds to understand metastability in the Burgers equation with small viscosity*, SIAM Rev. **53** (2011), no. 1, 129–153. MR 2785882
2. H.C. Berg and D.A. Brown, *Chemotaxis in escherichia coli analysed by three-dimensional tracking*, Nature **239(5374)** (1972), 500–4.
3. G. Burnstock and A. Verkhratsky, *Evolutionary origins of the purinergic signalling system*, Acta Physiol (Oxf) **195(4)** (2009), 415–47.
4. Sydney Chapman, *On the Brownian displacements and thermal diffusion of grains suspended in a non-uniform fluid*, Proc. Roy. Soc. Lond. A **119** (1928), 34–54.
5. Sydney Chapman and T. G. Cowling, *The mathematical theory of nonuniform gases*, third ed., Cambridge Mathematical Library, Cambridge University Press, Cambridge, 1990, An account of the kinetic theory of viscosity, thermal conduction and diffusion in gases, In co-operation with D. Burnett, With a foreword by Carlo Cercignani. MR 1148892 (92k:82001)
6. M. Collett, E. Despland, S.J. Simpson, and Krakauer D.C., *Spatial scales of desert locust gregarization*, Proc Natl Acad Sci **95(22)** (1998), 13052–5.

7. Chris Cosner and Yuan Lou, *Does movement toward better environments always benefit a population?*, J. Math. Anal. Appl. **277** (2003), no. 2, 489–503. MR 1961241 (2004d:35125)
8. U. Dieckman, B. OHara, and W. Weisser, *The evolutionary ecology of dispersal*, Trends Ecol. Evol. **14** (1999), no. 3, 88–90.
9. Jack Dockery, Vivian Hutson, Konstantin Mischaikow, and Mark Pernarowski, *The evolution of slow dispersal rates: a reaction diffusion model*, J. Math. Biol. **37** (1998), no. 1, 61–83. MR 1636644 (99j:92006)
10. S. Ishii and Y. Kuwahara, *An aggregation pheromone of the German cockroach blattella germanica l. (Orthoptera: Blattelidae)*, Appl. Ent. Zool. **2** (1967), 203–217.
11. E.C. Johnson, N. Kazgan, C.A. Bretz, L.J. Forsberg, C.E. Hector, R.J. Worthen, R. Onyenwoke, and J.E. Brenman, *Altered metabolism and persistent starvation behaviors caused by reduced ampk function in drosophila*, PLoS One **5(9)** (2010), e12799.
12. M. Johnson and M. Gaines, *Evolution of dispersal: Theoretical models and empirical tests using birds and mammals*, Ann. Rev. Ecol. Syst. **21** (1990), 449–480.
13. P. Kareiva and G. Odell, *Swarms of predators exhibit “preytaxis” if individual predators use area-restricted search*, Amer. Nat. **130** (1987), 233–270.
14. M. Keeling, *Spatial models of interacting populations, advanced ecological theory: Principles and applications*, J. McGlade, ed. Blackwell Science, Oxford (1999).
15. E.F. Keller and L.A. Segel, *Model for chemotaxis*, J. Theor. Biol. **30** (1971), 225–234.
16. Yong-Jung Kim, *Einstein’s random walk and thermal diffusion*, preprint.
17. Yong-Jung Kim, Ohsang Kwon, and Fang Li, *Evolution of dispersal toward fitness with starvation driven diffusion*, preprint.
18. ———, *Global asymptotic stability and the ideal free distribution in a starvation driven diffusion*, J. Math. Biol. (2013), to appear.
19. Yong-Jung Kim and Athanasios E. Tzavaras, *Diffusive N-waves and metastability in the Burgers equation*, SIAM J. Math. Anal. **33** (2001), no. 3, 607–633 (electronic). MR 1871412 (2002i:35121)
20. S.H. Larsen, R.W. Reader, E.N. Kort, W.W. Tso, and J. Adler, *Change in direction of flagellar rotation is the basis of the chemotactic response in escherichia coli.*, Nature **249(452)** (1974), 74–7.
21. H. Lee, M.K. Choi, D. Lee, H.S. Kim, H. Hwang, H. Kim, S. Park, Y.K. Paik, and J. Lee, *Nictation, a dispersal behavior of the nematode caenorhabditis elegans, is regulated by il2 neurons*, Nat Neurosci **15(1)** (2011), 107–12.
22. Yuan Lou, *On the effects of migration and spatial heterogeneity on single and multiple species*, J. Differential Equations **223** (2006), no. 2, 400–426. MR 2214941 (2006k:92111)
23. Yuan Lou and Wei-Ming Ni, *Diffusion vs cross-diffusion: an elliptic approach*, J. Differential Equations **154** (1999), no. 1, 157–190. MR 1685622 (2000c:35042)
24. Yuan Lou, Wei-Ming Ni, and Yaping Wu, *On the global existence of a cross-diffusion system*, Discrete Contin. Dynam. Systems **4** (1998), no. 2, 193–203. MR 1616969 (99f:35089)
25. M. McPeck and R. Holt, *The evolution of dispersal in spatially and temporally varying environments*, The American Naturalist **140** (1992), 1010–1027.
26. Masayasu Mimura and Kohkichi Kawasaki, *Spatial segregation in competitive interaction-diffusion equations*, J. Math. Biol. **9** (1980), no. 1, 49–64. MR 648845 (83h:92058)
27. N Mittal, EO Budrene, MP Brenner, and A van Oudenaarden, *Motility of escherichia coli cells in clusters formed by chemotactic aggregation*, P. NATL. ACAD. SCI. USA **100** (2003), no. 23, 13259–13263.

28. Akira Okubo and Simon A. Levin, *Diffusion and ecological problems: modern perspectives*, second ed., Interdisciplinary Applied Mathematics, vol. 14, Springer-Verlag, New York, 2001. MR 1895041 (2003a:92025)
29. S.R. Ott, H. Verlinden, S.M. Rogers, C.H. Brighton, P.S. Quah, R.K. Vleugels, R. Verdonck, and J. Vanden Broeck, *Critical role for protein kinase a in the acquisition of gregarious behavior in the desert locust*, Proc Natl Acad Sci **109(7)** (2012), E381–7.
30. J.M. Overton and T.D. Williams, *Behavioral and physiologic responses to caloric restriction in mice*, Physiol Behav **81** (2004), 749–754.
31. S. Sakurada, O. Shido, N. Sugimoto, Y. Hiratsuka, T. Yoda, and K. Kanosue, *Autonomic and behavioural thermoregulation in starved rats*, J Physiol **526** (2000), 417–424.
32. N. Shigesada, K. Kawasaki, and E. Teramoto, *Spatial segregation of interacting species*, Journal of Theoretical Biology **79** (1979), 83–99.
33. M. Silverman and M. Simon, *Flagellar rotation and the mechanism of bacterial motility*, Nature **249(452)** (1974), 73–4.
34. M.J. Tindall, P.K. Maini, S.L. Porter, and J.P. Armitage, *Overview of mathematical approaches used to model bacterial chemotaxis. II. Bacterial populations*, Bull. Math. Biol. **70** (2008), no. 6, 1570–1607. MR 2430318 (2009i:92012b)
35. M.J. Tindall, S.L. Porter, P.K. Maini, G. Gaglia, and J.P. Armitage, *Overview of mathematical approaches used to model bacterial chemotaxis. I. The single cell*, Bull. Math. Biol. **70** (2008), no. 6, 1525–1569. MR 2430317 (2009i:92012a)