Global asymptotic stability and the ideal free distribution in a starvation driven diffusion [⋆]

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Abstract. We study a logistic model with a nonlinear random diffusion in a Fokker-Planck type law, but not in Fick's law. In the model individuals are assumed to increase their motility if they starve. Any directional information to resource is not assumed in this starvation driven diffusion and individuals disperse in a random walk style strategy. However, the non-uniformity in the motility produces an advection toward surplus resource. Several basic properties of the model are obtained including the global asymptotic stability and the acquisition of the ideal free distribution.

Key words. ecological diffusion, global asymptotic stability, ideal free distribution, starvation induced motility

1. Introduction

The dispersal strategies of biological organisms are key ingredients in their ecological evolution. In this paper we show the global asymptotic stability and the optimal habitat selection phenomenon of a logistic model with a non-uniform random dispersal in a Fokker-Planck type

law,

$$u_t = \Delta(\gamma(s)u) + \kappa u(m(x) - u), \quad 0 < t, \ x \in \Omega, \quad \quad (1)$$
$$0 = \nabla[\gamma(s)u] \cdot \mathbf{n}, \quad \quad \quad \quad 0 < t, \ x \in \partial\Omega, \quad \quad (2)$$
$$0 < u(x,0) = u_0(x), \quad \quad \quad \quad x \in \Omega, \quad \quad \quad \quad (3)$$

which was introduced by Cho and Kim [9]. Here, $\Omega \subset \mathbf{R}^n$ is a bounded domain of habitat and $\mathbf{n}$ is the outward unit normal vector to the smooth boundary $\partial\Omega$. The unknown function $u(x,t)$ is the population density of a species at time $t > 0$ and position $x \in \Omega$ that satisfies the zero-flux boundary condition (2) and the initial condition (3). The given function $m : \Omega \to \mathbf{R}^+$ could be understood as a time independent resource or food supply distribution and $\kappa > 0$ is the growth rate.

The main feature of this model is in the diffusion, where the *motility* $\gamma = \gamma(s)$ is decided by a measure of the fitness of the population,

$$s := \frac{m}{u}. \quad \quad \quad \quad (4)$$

The study of fitness has been one of main issues in ecology and one can find a discussion related to fitness measure given by differences in [10] and references therein. One may interpret this ratio 's' as a *satisfaction measure* to the habitat from the side of individuals and we will call it so. For example, if the food supply m is bigger than the food demand u, i.e., $s > 1$, then all biological organisms in the habitat will have enough food and be satisfied with the environment. Therefore, the logistic term in the model (1) became positive, i.e., $\kappa u(m(x) - u) > 0$, and the population will grow. Therefore, we may expect that they will decrease their motility to stay in the habitat. However, if the food supply is less than the demand, i.e., $s < 1$, then the organisms starve and hence they will increase their motility to leave their habitat. Therefore, the motility γ is assumed to be a decreasing function on $s > 0$. We assume that there exist $0 < l < h < \infty$ such that

$$\gamma(s) \uparrow h \text{ as } s \downarrow 0, \quad \gamma(s) \downarrow l \text{ as } s \uparrow \infty, \quad \gamma'(s) \leq 0. \quad \quad (5)$$

It is clear that the motility of biological organisms should be bounded even if there is no food at all, i.e., $s = 0$. The lower bound $l > 0$ is necessary to make the system uniformly parabolic.

One might want to model the satisfaction measure as a function of the leftover, $s := m - u$, which is an example of a fitness measure. However, this quantity cannot be used as a satisfaction measure since individuals cannot feel it. For example, individuals should be hungrier in the case of '$m = 1, u = 2$' than in the case of '$m = 9, u = 10$' even though $m - u = -1$ in both cases. In fact, as long as re-scaled

quantities are used in the model, the two cases, '$m = 1, u = 2$' and '$m = 10, u = 20$', can not be distinguished.

The above hypotheses are for an ecological situation and hence the starvation driven diffusion can be considered as an example of ecological diffusion. For the simplicity in our analysis we will assume C^2 smoothness of the motility and the resource distribution, i.e.,

$$\gamma \in C^2(R^+) \quad \text{and} \quad m \in C^2(\overline{\Omega}), \quad m \geq 0. \tag{6}$$

We also assume that there exists $M > 0$ such that

$$|s\,\gamma'(s)| < M, \quad s > 0. \tag{7}$$

Fick [15] found that the concentration diffusion in a homogeneous environment has an analogy with the heat conduction for a homogeneous case and modeled the diffusion flux and the diffusion equation using

$$\mathbf{J} = -d\nabla u, \quad u_t = -\text{div}(\mathbf{J}) = d\Delta u,$$

where the diffusivity d is a constant depending on the property of the material. Such a linear diffusion has been used to model the random dispersal strategy of biological organisms, which leads the logistic model to

$$u_t = \text{div}(d\nabla u) + \kappa u(m(x) - u), \quad t > 0, \ x \in \Omega. \tag{8}$$

This logistic model is well understood and used as a building block for various ecological systems (see [14, 21, 28, 31, 36]).

However, under an external temperature gradient, Fick's law fails and the phenomenon is called thermal diffusion. Recently, the third author [27] explained such a heterogeneous diffusion process using a non-uniform random walk which is given by

$$u_t = \text{div}\left(\frac{d}{S}\nabla\left(Su\right)\right), \tag{9}$$

where S is the instantaneous particle speed[1] (see [32]).

Skellam [46] has emphasized the importance of a realistic biological diffusion model to overcome the limitations that a random walk model has (see [40, §5]). Animal response to environment, interference between individuals and non-uniformity of the use of space and time are examples to be considered. Let $\zeta(x)$ be the rate of individuals who want to leave the habitat. (One might consider it as the departing probability depending on departure location as in [40, §5.4].) Then the diffusion model (9) turns into

$$u_t = \text{div}\left(\frac{d}{S}\nabla\left(\zeta Su\right)\right), \tag{10}$$

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[1] If Δx is the walk length and Δt is the jumping time, then $d = \frac{|\Delta x|^2}{2n\Delta t}$ and $S = \frac{\Delta x}{\Delta t}$. Hence $\frac{d}{S} = \frac{\Delta x}{2n}$, where n is the space dimension.

which has been derived in [9]. Even though the speed of a Brownian particle is hard to be measured (see [32]), the speed S and the diffusivity d of biological organisms can be measured experimentally (see [1]). The probability measure ζ can be decided by comparing the model with actual diffusion phenomenon. The coefficient d/S is a walk length in a random walk model. The motility γ of the diffusion operator in (1) is now viewed as the product of the speed S and the emigration rate ζ, i.e., $\gamma \approx \zeta S$. Therefore, the name of motility for γ is justifiable, which can be also called the emigration rate. In this paper, we will focus on the heterogeneity of the motility and disregard d/S for simplicity. Notice that the motility γ decides the steady state of (10) and the diffusivity d controls the speed to arrive the steady state.

The product rule splits the diffusion operator $\Delta(\gamma(s)u)$ in (1) into three parts,

$$\Delta(\gamma(s)u) = \operatorname{div}\big(\gamma(s)\nabla u - \gamma'(s)s\nabla u + \gamma'(s)\nabla m\big). \qquad (11)$$

The first term, $\gamma(s)\nabla u$, is the diffusion of Fick's law that counts the interference between individuals. Remember that γ is a decreasing function on the satisfaction measure s and hence the diffusivity $\gamma(s) = \gamma(m/u)$ increases as u increases. The second term, $-\gamma'(s)s\nabla u$, behaves similarly. One might consider the two terms as self-diffusion since the diffusivity of a species increases as its own population increases. The last term, $\gamma'(s)\nabla m$, gives an advection toward the resource, which shows the response to environment. These two mechanisms in the starvation driven diffusion produce a flow heading to the place with less population and more resources, respectively.

The Fokker-Planck type diffusion operator $\Delta(\gamma(s)u)$ in (1) has been used in ecology models in several contexts. For example, a diffusion operator derived from a random walk process is written in this form, where $\gamma(x)$ is the probability for a particle to depart the place x (see §5.4 of [40]). It is observed and believed that the individuals do not move around uniformly but show a spatial aggregation around food or separation from other species (see §4.2.3 of [47]). Separation phenomenon has been successfully obtained by using $\gamma(x) = c_1 + c_2 u + c_3 v$ with constant c_i's and the density of the competing species v. Then, the three terms in the operator $\Delta(\gamma(x)u)$ give the linear diffusion, the self-diffusion and the cross-diffusion in that order and it is the cross-diffusion that gives a spatial segregation. Such a system has been intensively studied by many authors (see [33, 34, 37, 45]). However, one cannot add an aggregation effect in this way. On the other hand, the third advection term in (11) gives an aggregation effect toward more food.

One might find a similar idea from *preytaxis* models (see [26, 13]). Kareiva and Odell obtained the Fokker-Planck type diffusion in (1) when predators restrict the area of their search to a place with more

preys and change their direction of movement more often with more food. In that case the corresponding motility was a decreasing function of the density of prey, i.e., $\gamma = \gamma(m)$ with $\frac{\partial \gamma}{\partial m} \leq 0$ in our notation. Another interesting example is the dispersal phenomenon of a species when the species swaps its motility level between the activated state and the deactivated one. Such a case has been modeled using the Fokker-Planck type diffusion by M. Mimura *et al.* [18, 23].

The goal of this paper is to analyze the influence of the starvation driven diffusion in the logistic model (1) and compare it with the linear diffusion case. The study will be on two main issues of analytical ecology models. The first one is the global asymptotic stability, which has been well studied for the linear model (8) and Lotka-Volterra competition models. To do that we will study the long time asymptotics and zero-diffusion and zero-reaction limits. In this analysis the linear diffusion theory is extended to the nonlinear diffusion one with appropriate modifications. (Readers are referred to [39] for an expository presentation with linear diffusion, where proofs of this paper are based on.) However, we could not obtain fully generalized results and a genuine improvement from the linear theory seems needed.

The second issue is obtaining the optimal habitat selection or the ideal free distribution which has been one of main topics in ODE patch models (see [17, 16, 6, 22, 38]). A population distribution is called ideal free if each individual has the same fitness to environment at equilibrium. Therefore, if the total population in each patch is identical to the capacity and there is no net migration between patches, then it is the ideal free distribution, which is also called the optimal habitat selection.

In PDE models, the corresponding equilibrium is $u = m(x)$. Much effort has been devoted in this direction by adding an appropriate advection term. Then, the logistic model (8) became

$$u_t = \operatorname{div}(d\nabla u - cu\nabla P) + \kappa u(m(x) - u), \quad 0 < t, \ x \in \Omega, \qquad (12)$$

where $0 < c$ is a scaling coefficient. The advection term, $-cu\nabla P$, models the migration of the organisms toward food. The case with '$P = m$' has been intensively studied and it is shown that having such an advection is advantageous in a competition if $0 < c$ is small. However, if $0 < c$ is large, the population became concentrated only near the maximum points of m, which may give an disadvantage in a competition (see [3, 4, 12, 29]). A species is always advantageous if the advection is given with '$P = m - u$' and the steady state converges to the ideal free distribution $u = m$ as $c \to \infty$, where the ideal free distribution is obtained only in this limiting sense (see [7, 10]). If the advection term is given with '$P = \ln m$', then the steady state becomes ideal free distribution $u = m$ and this is the evolutionarily stable strategy (see [2, 8, 11]).

A key question related to the convergence to the ideal free distribution is: Is it possible for a local dispersal to produce a global ideal free distribution without knowing the whole distribution m? We will see that the dispersal in (1) has such a property if certain assumptions are imposed on the mobility function $\gamma(s)$. In fact, we will see that $u = m(x)$ is an equilibrium solution of (1) if the motility function is given by

$$\gamma_0(s) = \begin{cases} h & \text{if } 0 \leq s < 1, \\ l & \text{if } 1 \leq s < \infty, \end{cases} \tag{13}$$

and $\frac{\max_x m(x)}{\min_x m(x)} < \frac{h}{l}$, where $0 < l < h < \infty$ are constants. One might interpret this motility as that, if the food supply is not enough to support the population and hence the organisms are not satisfied with the environment, i.e., $s < 1$, then the species increase their motility to the highest level h. On the other hand, if they are satisfied with the environment, i.e., $1 < s$, then they decrease their motility to the lowest level l.

The motility function γ_0 in (13) is an extreme case that the whole population increase their motility to the highest level simultaneously. It is more realistic in a certain case that only 50% of the population increase their motility if the food supply supports only 50% of the population, i.e., if $s = 0.5$. In that situation, the corresponding motility is

$$\gamma_1(s) = \begin{cases} sl + (1 - s)h, & 0 \leq s < 1, \\ l, & 1 \leq s < \infty. \end{cases} \tag{14}$$

Note that this motility has a similarity to the one in Mimura *et al.* [18, 23], which has a motility depending on the density of pheromone. One might design various motility functions depending on the character of species or on field data.

The property (5) is a basic requirement for any motility function. The ones in (6) and (7) are technical requirements for the analysis in this paper. Since the motility in the previous two examples are not smooth, one may consider its regularized perturbation

$$\gamma_i^\epsilon := \gamma_i * \eta^\epsilon,$$

where η^ϵ is a typical smooth mollifier with its support in $(-\epsilon, \epsilon)$.

The rest of this paper is organized as follows. In Section 2, the influence of the starvation driven diffusion is analyzed without the logistic reaction. It is shown in Theorem 1 that it is not the population density but the diffusion pressure, $U = \gamma u$, that tends to a constant asymptotically. The global asymptotic stability of the system (1)–(3) is obtained in Theorem 2, Section 3, under an extra technical assumption (30) on the motility function γ. This assumption is satisfied by the ones in (13) and (14) after a regularization. If

the resource function $m(x)$ satisfies one of the two conditions in Theorem 3, we can also obtain the global asymptotic stability without (30). Both conditions in Theorem 3 indicate that the spatial concentration of resources is not large. In Section 4, the zero-diffusion and the zero-reaction limits of the globally asymptotically stable solution are obtained. The zero-diffusion limit of the population density is the resource distribution $m(x)$, which extends the linear diffusion theory. However, the zero-reaction limit of the density is not a constant, but the one of the diffusion pressure is (see Theorem 4). This is the main difference between the linear diffusion and the starvation driven diffusion.

Finally, in Section 5, we consider the optimal habitat selection property of the starvation driven diffusion. For that purpose we consider the motility function in (13) and its regularized ones under the assumption that the relative variation of motility is bigger than the one of resource distribution, i.e.,

$$\frac{\max_{\bar{\Omega}} m(x)}{\min_{\bar{\Omega}} m(x)} < \frac{h}{l}. \tag{15}$$

The solution of the system (1)-(5) with the discontinuous motility in (13) is viewed as the limit of solutions with regularized motilities. In Theorem 5, it has been shown that $u = m$ is one of the steady states for the problem without the logistic reaction term. In Theorem 6, it is shown that it is the globally asymptotically stable solution under a more restrictive condition in (62).

2. Starvation driven diffusion without reaction

The steady state solution of the reaction-diffusion equation (8) is not a state without any dynamics but a one in a balance of two different ones. The logistic reaction pushes the solution $u(x,t)$ to fit it into the resource distribution $m(x)$ and the linear diffusion flattens the solution into a constant as $t \to \infty$.[1] Such steady state solutions are well understood and we will study similar dynamics when the linear diffusion is replaced with the ecological one.

In this section we first study the dynamics of the diffusion without the logistic reaction term. Consider

$$u_t = \Delta(\gamma(s)u), \quad 0 < t, \ x \in \Omega, \tag{16}$$

where $s = s(x,t) = m(x)/u(x,t)$ and the boundary and the initial conditions in (2) and (3) are imposed. We will call

$$U := \gamma u \tag{17}$$

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[1] Therefore, '$m(x) =$ constant' is the only case that there is no dynamics at all in the steady state solution. If '$m(x) \neq$ constant', such a balance exists in a steady state.

a (biological) diffusion pressure or simply a pressure. We will freely abuse the notation by writing $u = u(x, U)$ or $U = U(x, u)$ throughout this paper. Then, one may write $U(x, u) = \gamma(\frac{m(x)}{u})u$. Then,

$$\frac{\partial U}{\partial u} = \gamma\left(\frac{m}{u}\right) - \gamma'\left(\frac{m}{u}\right)\frac{m}{u^2}u = \gamma(s) - \gamma'(s)s > l, \qquad (18)$$

i.e., the pressure U is monotone increasing on the density u for a fixed point $x \in \Omega$. One can write $\frac{\partial u}{\partial U} = \left(\frac{\partial U}{\partial u}\right)^{-1}$ under the notational convention. Combining this estimate and (7) gives

$$0 < l \le \frac{\partial U}{\partial u} \le L(:= M + h) < \infty. \qquad (19)$$

The equation (16) can be written in terms of pressure,

$$U_t = \frac{\partial U}{\partial u}u_t = (\gamma - \gamma'(s)s)\Delta U.$$

One can easily see that $U = $ constant is a steady state. In the following theorem, we will show that the pressure converges to a constant state for t large.

Theorem 1. *Let the motility γ satisfy (5)–(7) and u be the solution of (16). Then there exists a constant $0 < U_0$ such that*

$$\gamma(s(x,t))u(x,t) \to U_0 \quad \text{weakly in } W^{1,2}(\Omega) \quad \text{as } t \to \infty.$$

Proof. The positivity and local existence of the problem is standard. The equation (16) and the boundary and the initial conditions (2) and (3) can be rewritten in terms of the pressure, $U = \gamma u$, as

$$\begin{cases} \frac{\partial u}{\partial U}U_t = \Delta U & \text{for } x \in \Omega,\ t > 0, \\ \nabla U \cdot \mathbf{n} = 0 & \text{for } x \in \partial\Omega,\ t > 0, \\ U(x,0) = U_0(x), \end{cases} \qquad (20)$$

where $U_0(x) = \gamma(\frac{m(x)}{u_0(x)})u_0(x)$ and $\frac{\partial U}{\partial u}$ satisfies (19).

Integrating the first equation over Ω after a multiplication by U_t gives

$$\frac{1}{2}\frac{d}{dt}\int_\Omega |\nabla U|^2 dx = -\int_\Omega \frac{\partial u}{\partial U}U_t^2 dx \le 0. \qquad (21)$$

This monotonicity of the energy gives

$$\int_\Omega |\nabla U(x,t)|^2 dx \le \int_\Omega |\nabla U_0(x)|^2 dx. \qquad (22)$$

The maximum principle is applicable thanks to the uniform bound for $\frac{\partial U}{\partial u}$ in (19) and we obtain

$$\min_{\overline{\Omega}} U_0(x) \leq U(x,t) \leq \max_{\overline{\Omega}} U_0(x). \tag{23}$$

Next, multiply the equation in (20) by U. Then, integrating both sides over Ω gives

$$\int_{\Omega} |\nabla U|^2 dx = -\int_{\Omega} \frac{\partial u}{\partial U} U U_t dx \leq \frac{1}{l}\left(\int_{\Omega} U^2 dx\right)^{\frac{1}{2}}\left(\int_{\Omega} U_t^2 dx\right)^{\frac{1}{2}}, \tag{24}$$

where $l > 0$ is the lower bound in (19). Thus, (23) and (24) imply that there exists a constant $c > 0$, which is independent of t and

$$c\left(\int_{\Omega} |\nabla U|^2 dx\right)^2 \leq \int_{\Omega} U_t^2 dx.$$

Moreover, (21) implies that, for any $T > 0$, there exists $C > 0$ such that

$$\int_T^\infty \left(\int_{\Omega} U_t^2 dx\right) dt \leq C.$$

It follows that for some constant $C' > 0$,

$$\int_T^\infty \left(\int_{\Omega} |\nabla U|^2 dx\right)^2 dt \leq C'.$$

Therefore, (21) implies that

$$\int_{\Omega} |\nabla U|^2 dx \to 0, \text{ as } t \to \infty. \tag{25}$$

Thus, (22) and (23) together give that

$$\|U(\cdot,t)\|_{W^{1,2}(\Omega)} \leq c_1,$$

where the constant $c_1 > 0$ is independent of t. Therefore, it follows that there exist $\tilde{U} \in W^{1,2}(\Omega)$ and a sequence $t_n \to \infty$ such that

$$U(x,t_n) \rightharpoonup \tilde{U}(x) \text{ weakly in } W^{1,2}(\Omega) \text{ as } t_n \to \infty. \tag{26}$$

For any non-negative function $\phi \in C^1(\Omega)$ with $\nabla\phi \cdot \mathbf{n} = 0$ on $\partial\Omega$, (25) and (26) imply

$$\int_{\Omega} \nabla\tilde{U} \cdot \nabla\phi \, dx = 0.$$

Therefore, $\tilde{U}$ is a *weak* solution of the problem

$$\begin{cases} \Delta\tilde{U} = 0 & \text{for } x \in \Omega, \\ \nabla\tilde{U} \cdot \mathbf{n} = 0 & \text{for } x \in \partial\Omega. \end{cases} \tag{27}$$

It is known that (27) has constant solutions only and hence $\tilde{U} = U_0 > 0$. The conservation of mass of the problem (1)-(3) implies that

$$\int_\Omega u(x, U_0)dx = \lim_{t\to\infty} \int_\Omega u(x, U(x,t))dx = \int_\Omega u_0(x)dx.$$

Therefore, the strict monotonicity of $u(x, U)$ in U for all x implies that U_0 is independent of the choice of the sequence $\{t_n\}$ and hence the proof is complete. □

3. Starvation driven diffusion with logistic reaction

In this section, we return to the full system (1)–(7) that includes the population dynamics. We let the growth rate be fixed by setting $\kappa = 1$. Let us write the equation and boundary and initial conditions again,

$$\begin{cases} u_t = \Delta\left(\gamma(s)u\right) + u[m(x) - u] & \text{for } x \in \Omega,\ 0 < t, \\ 0 = \nabla[\gamma(s)u] \cdot \mathbf{n} & \text{for } x \in \partial\Omega,\ 0 < t, \\ 0 < u(x, 0) = u_0(x) & \text{for } x \in \Omega, \end{cases} \quad (28)$$

where $s = \frac{m}{u}$. We will show the existence, uniqueness and global asymptotic stability of the unique positive stationary solution of (28).

Let $U = \gamma(s)u$ be the pressure. As we did in the previous section, we abuse the notation by writing $u = u(x, U)$ and $U = U(x, u)$. Then, Eq. (28) can be rewritten as

$$\begin{cases} U_t = \frac{\partial U}{\partial u}\left[\Delta U + u(m - u)\right], & x \in \Omega,\ t > 0, \\ \nabla U \cdot \mathbf{n} = 0, & x \in \partial\Omega,\ t > 0, \\ U(x, 0) = U_0(x), & x \in \Omega, \end{cases} \quad (29)$$

where $\frac{\partial U}{\partial u}$ satisfies (18) and (19).

Theorem 2. *Suppose that the motility γ satisfies (5)–(7) and an extra technical assumption*

$$\gamma(s) - s(s - 1)\gamma'(s) > 0 \quad \text{for}\ \ 0 < s < 1. \quad (30)$$

Then, there exists a unique globally asymptotically stable positive steady state solution of (28).

Proof. It suffices to show (29) has a unique positive steady state. To this end, we will generalize the classical upper/lower solution method. Consider an eigenvalue problem

$$\begin{cases} \Delta\varphi + \frac{m}{\gamma(\frac{m}{u_0})}\varphi = \mu\varphi & \text{in } \Omega, \\ \nabla\varphi \cdot \mathbf{n} = 0 & \text{on } \partial\Omega. \end{cases} \quad (31)$$

Let $\mu_1 > 0$ and $\varphi_1 > 0$ be the first eigenvalue and eigenfunction, respectively. Without loss of generality, we can assume $u_0 > 0$ in Ω by the strong maximum principle. Since $\gamma(s)\frac{m}{s}$ is decreasing as s increases, there exists a sufficiently small ε such that $\mu_1 > \frac{\varepsilon\varphi_1}{l^2}$ and $\gamma(\frac{m}{\underline{u}})\underline{u} \le \gamma(\frac{m}{u_0})u_0$, where $\underline{u}(x) := u(x, \varepsilon\varphi_1)$.

Clearly, for $s = m/\underline{u}$,

$$\left[\gamma(s) - \gamma'(s)s\right]\left[\Delta\underline{U} + \underline{u}(m - \underline{u})\right] > 0$$

in Ω. Let $\underline{U}(x,t)$ denote the solution of the initial value problem (29) with initial data $U(x,0) = \varepsilon\varphi_1$. Differentiating (29) with respect to t gives that

$$\underline{U}_{tt} = \frac{\partial U}{\partial u}\left[\Delta\underline{U}_t + (m - 2u)\frac{\partial u}{\partial U}\underline{U}_t\right] + \gamma''s^2u^{-1}\left(\frac{\partial u}{\partial U}\underline{U}_t\right)^2,$$

where $\nabla\underline{U}_t \cdot \mathbf{n} = 0$ for $x \in \partial\Omega, t > 0$. Then, the maximum principle implies that $\underline{U}_t \ge 0$ for $x \in \Omega, t > 0$.

Now choose a constant

$$\bar{U} > h\max_{\bar{\Omega}} m(x). \tag{32}$$

Similarly, this implies that, for all $x \in \Omega$,

$$\bar{u}(x) := u(x, \bar{U}) > \max_{\bar{\Omega}} m(x).$$

Then let $\overline{U}(x,t)$ denote the solution of the initial value problem (29) with initial data $\overline{U}(x,0) = \bar{U}$. Similarly, $\overline{U}_t \le 0$ for $x \in \Omega, t > 0$.

Since $\underline{U}(x,0) < \overline{U}(x,0)$ in $\bar{\Omega}$ and, for $t > 0$,

$$\Delta\underline{U} + u(x,\underline{U})[m(x) - u(x,\underline{U})] \ge 0,$$

$$\Delta\overline{U} + u(x,\overline{U})[m(x) - u(x,\overline{U})] \le 0,$$

$\underline{U}(x,t) < \overline{U}(x,t)$ for $x \in \bar{\Omega}$ and $t > 0$ by the maximum principle and Hopf boundary lemma. Therefore, the pointwise limits

$$\underline{U}(x) = \lim_{t\to\infty} \underline{U}(x,t),$$

$$\overline{U}(x) = \lim_{t\to\infty} \overline{U}(x,t)$$

exist and

$$\underline{U}(x,0) \le \underline{U}(x,t) \le \underline{U}(x) \le \overline{U}(x) \le \overline{U}(x,t) \le \overline{U}(x,0). \tag{33}$$

(Note that we are abusing a notation here but with a consistency. For example, we use the same notation $\overline{U}$ for a solution $\overline{U}(x,t)$, for

its long time limit $\overline{U}(x)$ and for the constant $\overline{U}$ in (32). They should be distinguished from context.)

Next, we show that $\underline{U}(x)$ is the smooth steady state solution of (29). Let $\varphi \in C^2(\overline{\Omega})$ with $\frac{\partial \varphi}{\partial \nu} = 0$ on $\partial \Omega$ be a test function. Multiply $\frac{\varphi}{T}$ to the first equation in (29) for $\underline{U}(x, t)$ and then integrate it over $\Omega \times (0, T)$. Then,

$$\int_\Omega \frac{u(x, \underline{U}(x, T)) - u(x, \underline{U}(x, 0))}{T} \varphi(x) dx$$

$$= \frac{1}{T} \int_0^T \int_\Omega (\Delta U_1 + u(x, \underline{U})[m(x) - u(x, \underline{U})]) \varphi dx dt$$

$$= \int_\Omega \left\{ \Delta \varphi \frac{1}{T} \int_0^T U_1(x, t) dt + \varphi \frac{1}{T} \int_0^T u(x, \underline{U})[m(x) - u(x, \underline{U})] dt \right\} dx.$$

Now, it is easy to see that

$$\lim_{T \to \infty} \int_\Omega \frac{u(x, \underline{U}(x, T)) - u(x, \underline{U}(x, 0))}{T} \varphi(x) dx = 0,$$

$$\lim_{T \to \infty} \frac{1}{T} \int_0^T \underline{U}(x, t) dt = \underline{U}(x),$$

and

$$\lim_{T \to \infty} \frac{1}{T} \int_0^T u(x, \underline{U})[m(x) - u(x, \underline{U})] dt = u(x, \underline{U})[m(x) - \rho(x, \underline{U})].$$

Therefore, by the Lebesgue dominated convergence theorem, we get

$$\int_\Omega \underline{U} \Delta \varphi + u(x, \underline{U})[m(x) - u(x, \underline{U})] \varphi dx = 0.$$

The arguments in [44, Page 989] show that $\underline{U}(x)$ is a classical stationary solution of (29). Similarly, it can be proved that $\overline{U}(x)$ is also a classical stationary solution. Consequently, the existence of unique positive steady state of (28) is proved.

Clearly, $\underline{U}(x)$ and $\overline{U}(x)$ satisfy

$$\begin{cases} -\Delta U = u(m - u), & x \in \Omega, \\ \nabla U \cdot \mathbf{n} = 0, & x \in \partial \Omega. \end{cases} \tag{34}$$

Therefore,

$$\int_\Omega \nabla \underline{U} \cdot \nabla \overline{U} \, dx = -\int_\Omega \underline{U} \Delta \overline{U} \, dx = \int_\Omega \underline{U} \overline{u}(m - \overline{u}) dx$$

$$= \int_\Omega \underline{U} \overline{U} m (1 - \overline{s}^{-1}) \gamma^{-1}(\overline{s}) dx,$$

where $\overline{s} := \frac{m}{\overline{u}}$. Replacing the role of $\overline{U}$ and $\underline{U}$ gives a similar relation and hence we can conclude that

$$\int_\Omega \underline{U}\,\overline{U}m(1 - \underline{s}^{-1})\gamma^{-1}(\underline{s})dx = \int_\Omega \underline{U}\,\overline{U}m(1 - \overline{s}^{-1})\gamma^{-1}(\overline{s})dx.$$

One can easily check that the extra condition (30) gives the monotonicity of the function $s \to (1 - s^{-1})\gamma^{-1}(s)$. Hence if $\underline{u} \neq \overline{u}$, then it gives a contradiction. Therefore, (29) has a unique positive steady state, which is globally asymptotically stable. $\square$

Remark 1. One may see that the theory for the linear diffusion case is extended to our nonlinear diffusion case. However, for the uniqueness part, the motility γ is assumed to satisfy an extra condition (30). This assumption is for technical difficulties and a technical improvement is required to obtain the uniqueness without such an assumption. However, the examples (13) and (14) of our main interest satisfy this assumption after a typical regularization. It is also worth to point out that the proof of the theorem shows that the uniqueness of the steady state solution implies the global asymptotic stability.

The globally asymptotically stable solution in Theorem 2 will be denoted by $\theta(x)$ in the rest of this paper. Notice that the uniqueness has been shown under an assumption (30) on the motility function γ. In the following lemma we will show that steady state solutions should satisfy certain structure without using the assumption. This lemma will be used in proving the uniqueness under extra conditions on the resource distribution $m(x)$, but without the assumption (30) on γ.

Lemma 1. *Let θ be a positive steady state:*

$$\begin{cases} \Delta U + \theta(m(x) - \theta) = 0 & \text{for } x \in \Omega, \\ \nabla U \cdot \mathbf{n} = 0 & \text{for } x \in \partial\Omega, \end{cases} \tag{35}$$

where $U = \gamma(\frac{m}{\theta})\theta$. Then,

(i) $\min_{\overline{\Omega}} m(x) \leq \min_{\overline{\Omega}} \theta(x) \leq \max_{\overline{\Omega}} \theta(x) \leq \max_{\overline{\Omega}} m(x)$.
(ii) $\int_\Omega m(x)dx \leq \int_\Omega \theta(x)dx$.
(iii) Furthermore, if m is not constant, then the inequalities are strict, i.e.,

$$\min_{\overline{\Omega}} \theta(x) < \max_{\overline{\Omega}} \theta(x), \quad \int_\Omega m(x)dx < \int_\Omega \theta(x)dx.$$

Proof. Let $U(x_1) = \max_{\overline{\Omega}} U(x)$. Suppose that θ has a maximum at $x_0 \in \overline{\Omega}$ such that

$$\theta(x_0) = \max_{\overline{\Omega}} \theta(x) > \max_{\overline{\Omega}} m(x).$$

We will show that this assumption derives a contradiction. First, assume that $x_1 \in \Omega$, then

$$\theta(x_1)[m(x_1) - \theta(x_1)] = -\Delta U(x_1) \geq 0.$$

This implies that $m(x_1) - \theta(x_1) \geq 0$ and thus

$$\theta(x_1) \leq m(x_1) \leq \max_{\overline{\Omega}} m(x) < \theta(x_0).$$

Therefore

$$\max_{\overline{\Omega}} U(x) = U(x_1) = \gamma\Big(\frac{m(x_1)}{\theta(x_1)}\Big)\theta(x_1)$$

$$\leq \gamma(1)\theta(x_1) < \gamma(\frac{m(x_0)}{\theta(x_0)})\theta(x_0) = U(x_0),$$

which is a contradiction.

Next, assume that $x_1 \in \partial\Omega$. Note that if $\theta(x_1) \leq m(x_1)$, then a contradiction can be derived by repeating the previous arguments. Now the only possible situation is $x_1 \in \partial\Omega$ and $\theta(x_1) > m(x_1)$. This yields that

$$\Delta U = -\theta(x)[m(x) - \theta(x)] > 0 \ \text{ in } \ B(x_1, r)\bigcap\Omega,$$

where $B(x_1, r)$ denotes a ball centered at x_1 with sufficiently small radius $r > 0$. A contradiction arises due to the Hopf boundary lemma and the boundary condition imposed on U. Therefore the inequality $\max_{\overline{\Omega}} \theta(x) \leq \max_{\overline{\Omega}} m(x)$ in (i) is proved. The inequality $\min_{\overline{\Omega}} m(x) \leq \min_{\overline{\Omega}} \theta(x)$ can be handled similarly.

For the proof of (ii), notice that it follows easily from the problem (34) that

$$\int_{\Omega}\left[\frac{|\nabla U|^2}{U^2} + \frac{m - \theta}{\gamma(\frac{m}{\theta})}\right] dx = 0.$$

Moreover, observe that since γ is decreasing,

$$(s - 1)(\gamma(s) - \gamma(1)) \leq 0,$$

which implies that

$$(m - \theta)\left(1 - \frac{\gamma(1)}{\gamma(m/\theta)}\right) \leq 0.$$

Therefore,

$$\int_{\Omega}(m - \theta)dx \leq \gamma(1)\int_{\Omega}\frac{m - \theta}{\gamma(\frac{m}{\theta})}dx = -\gamma(1)\int_{\Omega}\frac{|\nabla U|^2}{U^2}dx \leq 0. \quad (36)$$

Now we show (iii). Suppose that $m(x)$ is not constant and $\min_{\overline{\Omega}} \theta(x) = \max_{\overline{\Omega}} \theta(x)$, i.e., $\theta(x) \equiv c > 0$, a constant. Then, the part (i) implies that $\min_{\overline{\Omega}} m(x) \leq c \leq \max_{\overline{\Omega}} m(x)$. Since m is not a constant $\min_{\overline{\Omega}} m(x) < c$ or $c < \max_{\overline{\Omega}} m(x)$. We will assume $\min_{\overline{\Omega}} m(x) < c$ and the other case is similar. Let x_2 be the maximum point of the pressure, i.e.,

$$U(x_2) = \max_{\overline{\Omega}} \gamma(\frac{m(x_2)}{c})c.$$

Clearly, due to the monotonicity of γ, $m(x_2) = \min_{\overline{\Omega}} m(x)$. If $x_2 \in \Omega$, then $\Delta U(x_2) = -c(m(x_2) - c) > 0$, which is not possible. If $x_2 \in \partial\Omega$, then we still have $\Delta U(x_2) > 0$ and Hopf's boundary lemma yields that $\nabla U \cdot \mathbf{n} > 0$ at $x = x_2 \in \partial\Omega$. We obtain a contradiction and thus $\min_{\overline{\Omega}} \theta(x) < \max_{\overline{\Omega}} \theta(x)$.

Notice that because of (36), $\int_{\Omega} m(x)dx = \int_{\Omega} \theta(x)dx$ implies that $U \equiv U_0$, a constant pressure. Then according to the problem (34), we easily get $m(x) \equiv \theta(x)$ a.e., which however yields that

$$U = \gamma(\frac{m}{\theta})\theta = \gamma(1)\theta = \gamma(1)m.$$

This is a contradiction since $m(x)$ is not a constant. Therefore $\int_{\Omega} m(x)dx < \int_{\Omega} \theta(x)dx$. $\square$

The relations in the lemma between the resource distribution $m(x)$ and the steady population distribution $\theta(x)$ are classical ones for ODE patch models and PDE models with linear diffusion. This lemma shows that such classical relations are naturally extended to equations with the Fokker-Planck type diffusion considered in this article.

Theorem 3. *Suppose that one of the following two conditions holds:*

(i) $\max_{\overline{\Omega}} m(x) \leq 2\min_{\overline{\Omega}} m(x)$,
(ii) $\nabla m \cdot \mathbf{n} \leq 0$ *on* $\partial\Omega$ *and* $\triangle m + \frac{1}{2\alpha(2)}m^2 \geq 0$ *in* $\bar{\Omega}$.

Then the solution of (35) is unique and hence it is the globally asymptotically stable positive solution of (28).

Proof. Let $\theta_1(x)$ and $\theta_2(x)$ be positive solutions of (35). Thanks to the proof of Theorem 2, we can assume that $\theta_1(x) \leq \theta_2(x)$ in Ω. Recall that $\theta_i(x)$, $i = 1, 2$, satisfy

$$\begin{cases} \Delta U_i + \theta_i[m(x) - \theta_i] = 0 & \text{for } x \in \Omega, \\ \nabla U_i \cdot \mathbf{n} = 0 & \text{for } x \in \partial\Omega, \end{cases}$$

where $U_i = U(x, \theta_i) = \alpha(m/\theta_i)\theta_i$. It is easy to see that

$$\int_{\Omega} \theta_1[m(x) - \theta_1]dx = \int_{\Omega} \theta_2[m(x) - \theta_2]dx = 0,$$

which immediately implies that

$$\int_{\Omega} (\theta_1 - \theta_2)[m(x) - \theta_1 - \theta_2]dx = 0. \qquad (37)$$

We will show that if either (i) or (ii) holds, a solution θ of (34) satisfies

$$\theta(x) \geq \frac{m(x)}{2} \quad \text{in} \quad \Omega. \qquad (38)$$

Then, this claim, $\theta_1(x) \leq \theta_2(x)$ and $\theta_1(x) \neq \theta_2(x)$ immediately imply that

$$\int_{\Omega} (\theta_1 - \theta_2)[m(x) - \theta_1 - \theta_2]dx > 0,$$

which contradicts (37). Hence, the uniqueness of the positive solution of (34) follows. First, if (i) is assumed, then (38) is immediate from Lemma 1(i), i.e.,

$$m(x) \leq \max_{\overline{\Omega}} m(x) \leq 2 \min_{\overline{\Omega}} m(x) \leq 2 \min_{\overline{\Omega}} \theta(x) \leq 2\theta(x).$$

Now we show (38) under the assumption of (ii). Let

$$\beta(s) = \alpha(s)s^{-1}.$$

Then,

$$U = \beta(s)m \quad \text{and} \quad \beta'(s) = \alpha'(s)s^{-1} - \alpha(s)s^{-2} < 0.$$

On the boundary $\partial\Omega$,

$$0 = \nabla[\alpha(s)\theta] \cdot \mathbf{n} = \nabla[\beta(s)m] \cdot \mathbf{n} = \left[\beta'(s)m\nabla s + \beta(s)\nabla m\right] \cdot \mathbf{n}.$$

Therefore, since $\nabla m \cdot \mathbf{n} \leq 0$ and $\beta'(s) < 0$, we have

$$\nabla s \cdot \mathbf{n} \leq 0 \quad \text{on} \quad \partial\Omega. \qquad (39)$$

Hence (34) can be rewritten as

$$\begin{cases} \Delta\left(\beta(s)m\right) + m^2 s^{-1}\left[1 - s^{-1}\right] = 0 & \text{for } x \in \Omega, \\ \nabla s \cdot \mathbf{n} \leq 0 & \text{for } x \in \partial\Omega. \end{cases}$$

This equation can be written as

$$\Delta s + \frac{\beta''}{\beta'}|\nabla s|^2 + \frac{2}{m}\nabla m \cdot \nabla s + \frac{\beta}{\beta'm}\left[\Delta m + \frac{m^2}{\alpha}\left(1 - s^{-1}\right)\right] = 0. \quad (40)$$

Suppose that there exists $x_0 \in \bar{\Omega}$ such that

$$s(x_0) = \max_{\overline{\Omega}} s(x) > 2.$$

Suppose that the critical point is an interior one $x_0 \in \Omega$. Then, since $\alpha(s)$ is a decreasing function,

$$\Delta m(x_0) + \frac{m^2(x_0)}{\alpha(s(x_0))}\left(1 - \frac{1}{s(x_0)}\right) > \Delta m(x_0) + \frac{m^2(x_0)}{2\alpha(2)}.$$

By (40) and (ii), we have $\Delta s(x_0) > 0$, which is impossible since the maximum value of s is achieved at $x_0 \in \Omega$. Let $x_0 \in \partial\Omega$. Obviously, $\nabla s(x_0) \cdot \mathbf{n} \geq 0$ since x_0 is a boundary point with a maximum value. Thus, $\nabla s(x_0) \cdot \mathbf{n} = 0$ because of (39). Moreover, the maximum value of s is obtained at $x_0 \in \partial\Omega$ and $\nabla s(x_0) \cdot \mathbf{n} = 0$ together imply that $|\nabla s(x_0)| = 0$. Similarly, from (ii), we also have

$$\Delta m(x_0) + \frac{m^2(x_0)}{\alpha(s(x_0))}\left(1 - \frac{1}{s(x_0)}\right) > 0.$$

Therefore, from (40) with $|\nabla s(x_0)| = 0$, $\Delta s(x) > 0$ in $B(x_0, r) \bigcap \Omega$ for small $r > 0$. Then $\nabla s(x_0) \cdot \mathbf{n} = 0$ contradicts to the Hopf boundary lemma. Therefore, $\max_{\bar{\Omega}} s(x) \leq 2$, and hence (38) is satisfied.   □

4. Zero-diffusion and zero-reaction limits

Let $\theta_d(x)$ be the positive solution of the stationary problem

$$\begin{cases} d\Delta U + \theta[m - \theta] = 0 & \text{for } x \in \Omega, \\ \nabla U \cdot \mathbf{n} = 0 & \text{for } x \in \partial\Omega, \end{cases} \tag{41}$$

where $U(x) = \gamma(s(x))\theta(x)$ and $s(x) = \frac{m(x)}{\theta(x)}$. We will explore the behavior of the solution $\theta_d(x)$ as $d \to 0$ or $d \to \infty$. This behavior is well known for the linear diffusion case,

$$d\Delta\theta + \theta(m - \theta) = 0.$$

The technique for the linear diffusion case is modified appropriately for the nonlinear case, where the analysis will show their similarities and differences.

In the followings we develop techniques in [19] for our nonlinear diffusion. We will first construct an auxiliary function with a solution of the following problem,

$$\begin{cases} d\Delta v + \frac{v}{\gamma^2(\frac{m}{\theta_d})}(c - v) = 0 & \text{in } B(x_0, r), \\ v = 0 & \text{on } \partial B(x_0, r), \end{cases} \tag{42}$$

where $c > 0$ is a constant and θ_d is the solution of (41). It is standard to verify that $\bar{v} \equiv c + 1$ is a upper solution and $\underline{v} \equiv \frac{c}{\|\varphi\|_\infty}\varphi$ is a lower

solution, where $\varphi \geq 0$ is an eigenfunction corresponding to the first eigenvalue of

$$\begin{cases} \Delta\varphi + \mu\varphi = 0 & \text{in } B(x_0, r), \\ \varphi = 0 & \text{on } \partial B(x_0, r). \end{cases} \tag{43}$$

Thus we have the existence of a positive solution of (42). Moreover, let v_1 and v_2 be two distinct positive solutions. Then we may assume that $v_1 \leq v_2$ and so,

$$\int \left[dv_2 \Delta v_1 + \frac{v_1 v_2}{\gamma^2(\frac{m}{\theta_d})}(c - v_1) \right] = 0 = \int \left[dv_1 \Delta v_2 + \frac{v_1 v_2}{\gamma^2(\frac{m}{\theta_d})}(c - v_2) \right] dx.$$

This implies that

$$\int \left[\frac{v_1 v_2}{\gamma^2(\frac{m}{\theta_d})}(v_1 - v_2) \right] dx = 0.$$

Therefore, $v_1 \equiv v_2$, i.e., the solution of (42) is unique. We will denote this unique solution by v_d^r and omit the dependency on x_0 since the center of the ball is clear in most of cases.

Lemma 2. $\lim_{d \to 0} \left(\inf_{x \in K} v_d^r(x) \right) \geq c$ *on any compact set* $K \subset B(x_0, r)$.

Proof. We show that for any given compact set $K \subset B(x_0, r)$ and $\varepsilon > 0$, there exists $d_0 = d_0(K, \varepsilon) > 0$ such that $v_d(x) \geq c - \varepsilon$, for any $x \in K$ and $0 < d < d_0$.

Let $y_0 \in K$ and fix $\delta > 0$ so that $B(y_0, 2\delta) \subset B(x_0, r)$. Let $\mu_1 = \mu_1(B(y_0, \delta))$, $\varphi_1 > 0$ with $\|\varphi_1\|_{L^\infty} = 1$ be the first eigenvalue and eigenfunction of

$$\begin{cases} \Delta\varphi + \mu\varphi = 0 & \text{in } B(y_0, \delta), \\ \varphi = 0 & \text{on } \partial B(y_0, \delta). \end{cases} \tag{44}$$

We claim that $(c - dh^2\mu_1)\varphi_1(x) \leq v_d^\delta(x) \leq v_d^r(x)$, for all $x \in B(y_0, \delta)$ and sufficiently small $d > 0$, where h is the maximum of the motility γ.

Since v_d^r is the solution of (42), we have $v_d^\delta \leq v_d^r$ on $B(y_0, \delta)$. Assume that $dh^2\mu_1 < c$ otherwise the claim is trivial. Let $U_1 = v_d^\delta$ and $U_2 = (c - dh^2\mu_1)\varphi_1$. Then

$$\begin{cases} \Delta U_1 + \frac{U_1}{d\gamma^2(\frac{m}{\theta_d})}(c - U_1) = 0 & \text{in } B(y_0, \delta), \\ U_1 = 0 & \text{on } \partial B(y_0, \delta) \end{cases} \tag{45}$$

and

$$\begin{cases} \Delta U_2 + \mu_1(B(y_0, \delta))U_2 = 0 & \text{in } B(y_0, \delta), \\ U_2 = 0 & \text{on } \partial B(y_0, \delta). \end{cases} \tag{46}$$

Hence, it follows that

$$\Delta U_2 + \frac{U_2}{d\gamma^2(\frac{m}{\theta_d})}(c - U_2)$$

$$= -\mu_1(B(y_0, \delta))U_2 + \frac{U_2}{d\gamma^2(\frac{m}{\theta_d})}(c - U_2)$$

$$= \left\{ \frac{c}{d\gamma^2(\frac{m}{\theta_d})} - \mu_1(B(y_0, \delta)) - \left(\frac{c}{d\gamma^2(\frac{m}{\theta_d})} - \frac{h^2\mu_1(B(y_0, \delta))}{\gamma^2(\frac{m}{\theta_d})} \right) \varphi_1 \right\} U_2$$

$$\geq \left(\frac{c}{d\gamma^2(\frac{m}{\theta_d})} - \frac{h^2\mu_1(B(y_0, \delta))}{\gamma^2(\frac{m}{\theta_d})} \right) (1 - \varphi_1)U_2 \geq 0.$$

Therefore, U_2 is a lower solution and hence $U_2 \leq U_1$.

Let $d_0(y_0, \varepsilon) = \frac{\varepsilon}{2h^2\mu_1}$. For every $d < d_0(y_0, \varepsilon)$, since $v_d^\delta(x)$ is continuous, we can choose $0 < \tilde{\delta} < \delta$ such that $\tilde{\delta} = \tilde{\delta}(y_0, d, \varepsilon)$ and $v_d^\delta(x) \geq v_d^\delta(y_0) - \frac{\varepsilon}{2}$, for all $x \in B(y_0, \tilde{\delta})$. Then, for every $x \in B(y_0, \tilde{\delta})$,

$$v_d^r(x) \geq v_d^\delta(x) \geq v_d^\delta(y_0) - \frac{\varepsilon}{2}$$

$$\geq [c - dh^2\mu_1)]\varphi_1(y_0) - \frac{\varepsilon}{2} \geq c - \varepsilon.$$

Then the conclusion follows by standard compactness argument. □

Next, we construct two estimates for the positive solutions of (41).

Lemma 3. *Let $\theta_d(x)$ denote a positive solution of (41) and $U = \gamma(m/\theta_d)\theta_d$. Then*

$$\gamma(1) \min_{\bar{\Omega}} m(x) \leq U(x) \leq \gamma(1) \max_{\bar{\Omega}} m(x). \tag{47}$$

Proof. Suppose that $\max_{\bar{\Omega}} U(x) > \gamma(1)\max_{\bar{\Omega}} m(x)$ and that the pressure U attains it maximum at $x_0 \in \Omega$, i.e.,

$$U(x_0) = \max_{\bar{\Omega}} U(x) > \gamma(1) \max_{\bar{\Omega}} m(x). \tag{48}$$

Then, since $\theta_d(x_0)[m(x_0) - \theta_d(x_0)] = -d\Delta U(x_0) \geq 0$, we have

$$s(x_0) = \frac{m(x_0)}{\theta_d(x_0)} \geq 1. \tag{49}$$

Therefore,

$$\gamma(1)\theta_d(x_0) \geq \gamma(s(x_0))\theta_d(x_0) = U(x_0) > \gamma(1)\max_{\bar{\Omega}} m(x) \geq \gamma(1)m(x_0),$$

which contradicts to (49).

Now, suppose that $x_0 \in \partial\Omega$. One may similarly derive a contradiction if $m(x_0) \geq \theta_d(x_0)$. Hence we consider the case $m(x_0) < \theta_d(x_0)$, which implies that

$$\Delta U(x_0) = -\theta_d(x_0)[m(x_0) - \theta_d(x_0)] > 0.$$

Hence,

$$\Delta U > 0 \text{ in } B(x_0, r) \bigcap \Omega,$$

where $B(x_0, r)$ denotes a ball centered at x_0 with sufficiently small radius $r > 0$. Therefore, the Hopf boundary lemma implies that $\nabla U \cdot \mathbf{n} > 0$, which contradicts with the boundary condition of the problem. Consequently,

$$U(x) \leq \gamma(1) \max_{\bar{\Omega}} m(x).$$

The first inequality in (47) is obtained similarly. □

Lemma 4. *Let $\theta_d(x)$ be a positive solution of (41). Then there exist positive constants K_1 and K_2 independent of d such that*

$$K_1 \leq \frac{m(x)}{\theta_d(x)} \leq K_2. \tag{50}$$

Proof. Let $\beta(s) = \gamma(s)s^{-1}$. Since $\beta'(s) < 0$, $\beta(s)$ is invertible. Moreover, by Lemma 3, we have

$$\gamma(1)\frac{\min_{\bar{\Omega}} m(x)}{m(x)} \leq \beta(s) = \frac{U}{m} \leq \gamma(1)\frac{\max_{\bar{\Omega}} m(x)}{m(x)}.$$

Therefore (50) is satisfied with

$$K_1 = \beta^{-1}\left(\gamma(1)\frac{\max_{\bar{\Omega}} m(x)}{\min_{\bar{\Omega}} m(x)}\right) \text{ and } K_2 = \beta^{-1}\left(\gamma(1)\frac{\min_{\bar{\Omega}} m(x)}{\max_{\bar{\Omega}} m(x)}\right).$$

The proof is complete. □

Theorem 4. *Let $\theta_d(x, t)$ be a positive solution of (41) under assumptions in (5)–(7). Then, (i) $\lim_{d\to 0} \theta_d = m$ uniformly on any compact subset of Ω. (ii) $\lim_{d\to\infty} U_d = $ constant in $C^{1,\alpha}$ for any $0 < \alpha < 1$.*

Proof. The proof of the first part (i) consists of two parts. First, we set that $U_d^{r,\tilde{x}_0}$ is the solution of

$$\begin{cases} d\Delta U + \frac{U}{\gamma^2(\frac{m}{\theta_d})}\left(\gamma(\frac{m}{\theta_d})m - U\right) = 0 & \text{in } B(x_0, r), \\ U = 0 & \text{on } \partial B(x_0, r). \end{cases} \tag{51}$$

Let $\Omega_\varepsilon \equiv \{x \in \Omega \mid l \cdot m(x) \geq \varepsilon\}$.

Claim. For a given $\varepsilon > 0$ and $x_0 \in \Omega_\varepsilon$, there exist $\delta > 0$ and $d_0 > 0$ such that $U_d(x) \geq \gamma(\frac{m}{\theta_d})m(x) - \varepsilon$ in $B(x_0, \delta)$ for any $0 < d < d_0(x_0, \varepsilon)$.

Proof of claim: Since m is continuous on $\overline{\Omega}$, there exists a constant $\delta_1 = \delta_1(x_0, \varepsilon) > 0$ such that $B(x_0, \delta_1) \subset \Omega$ and $\min_{B(x_0, \delta_1)} \gamma(\frac{m}{\theta_d})m \geq \gamma(\frac{m}{\theta_d})m - \frac{\varepsilon}{2}$, for all $x \in B(x_0, \delta_1)$. Then, since U_d is an upper solution of (51) in $B(x_0, \delta_1)$, $U_d \geq U_d^{\delta_1, x_0}$. Moreover, since the solution $v_d^{\delta_1}$ of (42) is a lower solution of (51), $U_d^{\delta_1, x_0} \geq v_d^{\delta_1}$, where $c = \min_{B(x_0, \delta_1)} \gamma(\frac{m}{\theta_d})m$. Let $\delta = \min\{\tilde{\delta}(x_0, d, \varepsilon), \delta_1\}$, where $\tilde{\delta}$ is the one in the proof of Lemma 2. Then, the lemma guarantees the existence of $d_0(x_0, \varepsilon)$ such that, for every $d < d_0(x_0, \varepsilon)$ and $x \in B(x_0, \delta)$, $v_d^{\delta_1} \geq \min_{B(x_0, \delta)} \gamma(\frac{m}{\theta_d})m - \frac{\varepsilon}{2}$. Therefore, $U_d \geq v_d^{\delta_1} \geq \min_{B(x_0, \delta)} \gamma(\frac{m}{\theta_d})m - \frac{\varepsilon}{2} \geq \gamma(\frac{m}{\theta_d})m(x) - \varepsilon$ for all $x \in B(x_0, \delta)$.

Claim. For any given $\varepsilon > 0$, there exists $d_0 > 0$ such that $0 \leq U_d(x) \leq \gamma(\frac{m}{\theta_d})m + \varepsilon$ in Ω for any $0 < d < d_0$.

Proof of claim: Let $U \in C^2$ satisfy $\gamma(\frac{m}{\theta_d})m + \frac{\varepsilon}{2} \leq U \leq \gamma(\frac{m}{\theta_d})m + \varepsilon$ for all $x \in \Omega$ and $\frac{\partial U}{\partial \nu}|_{\partial \Omega} \geq 0$. Then, there exists $d_0(\varepsilon) > 0$ s.t. for any $d < d_0(\varepsilon)$

$$d\Delta U + \frac{U}{\gamma^2(\frac{m}{\theta_d})}\left(\gamma(\frac{m}{\theta_d})m - U\right)$$

$$\leq d\Delta U + \frac{U}{\gamma^2(\frac{m}{\theta_d})}\left(\gamma(\frac{m}{\theta_d})m - \gamma(\frac{m}{\theta_d})m - \frac{\varepsilon}{2}\right)$$

$$\leq d\Delta U - \frac{\varepsilon U}{2\gamma^2(\frac{m}{\theta_d})} \leq 0.$$

So U is an upper solution. Therefore $0 \leq U_d(x) \leq U(x) \leq \gamma(\frac{m}{\theta_d})m + \varepsilon$ in Ω for every $0 < d < d_0$.

Now we prove the second part *(ii)*. We denote the solution by $U_d = \bar{U} + \psi$, where $\bar{U} = \frac{1}{|\Omega|}\int_\Omega U_d dx$ and $\int_\Omega \psi dx = 0$. Set

$$C = 2\max_\Omega m(x).$$

Thanks to Lemma 3, we have $\|U_d\|_{L^\infty} \leq C/2$, $\|\bar{U}\|_{L^\infty} \leq \|U_d\|_{L^\infty} \leq C/2$ and $\|\psi\|_{L^\infty} = \|U_d - \bar{U}\|_{L^\infty} \leq C$.

Consider the equation satisfied by ψ,

$$\begin{cases} d\Delta\psi + \frac{\bar{U}+\psi}{\gamma(\frac{m}{\theta_d})}\left(m - \frac{\bar{U}+\psi}{\gamma(\frac{m}{\theta_d})}\right) = 0 & \text{in } \Omega, \\ \frac{\partial\psi}{\partial\nu} = 0 & \text{on } \partial\Omega. \end{cases} \tag{52}$$

Hence,

$$d \int_\Omega |\nabla \psi|^2$$

$$= \int_\Omega \frac{\bar{U} + \psi}{\gamma(\frac{m}{\theta_d})} \left(m - \frac{\bar{U} + \psi}{\gamma(\frac{m}{\theta_d})} \right) \psi$$

$$= \bar{U} \int_\Omega \frac{m\psi}{\gamma(\frac{m}{\theta_d})} - \bar{U}^2 \int_\Omega \frac{\psi}{\gamma^2(\frac{m}{\theta_d})} + \int_\Omega \left(m\gamma(\frac{m}{\theta_d}) - 2\bar{U} - \psi \right) \frac{\psi^2}{\gamma^2(\frac{m}{\theta_d})}.$$

This, combined with Lemma 4, implies that

$$d \int_\Omega |\nabla \psi|^2 \leq \frac{\bar{U}}{l} \|m\|_{L^2} \|\psi\|_{L^2} + \bar{U}^2 \|\gamma^{-2}(\frac{m}{\theta_d})\|_{L^2} \|\psi\|_{L^2}$$

$$+ \frac{\|m\gamma(\frac{m}{\theta_d}) - 2\bar{U} - \psi\|_{L^\infty}}{l^2} \int_\Omega \psi^2,$$

where $l = \gamma(K_2)$.

Since $\mu_1 := \inf \left\{ \frac{\int_\Omega |\nabla v|^2 dx}{\int_\Omega v^2 dx} : \int_\Omega v dx = 0, v \neq 0, \frac{\partial v}{\partial \nu}|_{\partial\Omega} = 0 \right\} > 0$,

$$\mu_1 d \int_\Omega \psi^2 \leq d \int_\Omega |\nabla \psi|^2 \leq c \|\psi\|_{L^2} + c \int_\Omega \psi^2.$$

When $d > 0$ is large such that $c < \frac{1}{2} d\mu_1$, we get $\|\psi\|_{L^2} \leq \frac{c}{d}$. And this implies that $\|\nabla \psi\|_{L^2} \leq \frac{c}{d}$. Therefore, we have $\|\psi\|_{H^1} \leq \frac{c}{d}$ and thus $\|\psi\|_{L^{q_1}} \leq \frac{c}{d}$, where $q_1 = \frac{2n}{n-2}$. Since ψ satisfies that

$$\begin{cases} \Delta \psi - \psi = \frac{1}{d} \frac{\bar{U} + \psi}{\gamma(\frac{m}{\theta_d})} \left(m - \frac{\bar{U} + \psi}{\gamma(\frac{m}{\theta_d})} \right) - \psi & \text{in } \Omega, \\ \frac{\partial \psi}{\partial \nu} = 0 & \text{on } \partial\Omega, \end{cases} \tag{53}$$

and

$$\left\| \frac{1}{d} \frac{\bar{U} + \psi}{\gamma(\frac{m}{\theta_d})} \left(m - \frac{\bar{U} + \psi}{\gamma(\frac{m}{\theta_d})} \right) - \psi \right\|_{L^{q_1}} \leq \frac{c}{d},$$

we obtain that $\|\psi\|_{U^{2,q_1}} \leq \frac{c}{d}$. Moreover, from the embedding theorem, it follows that $\|\psi\|_{L^{q_2}} \leq \frac{c}{d}$, where $q_2 = \frac{nq_1}{n-2q_1}$. By this iteration, we get $\|\psi\|_{U^{2,q}} \leq \frac{c}{d}$, for any $1 < q < \infty$. This implies that $\|\psi\|_{C^{1,\alpha}} \leq \frac{c}{d}$ and so, $\psi \to 0$ in $C^{1,\alpha}$ as $d \to \infty$. Therefore, U_d converges to a constant in $C^{1,\alpha}$ as $d \to \infty$. □

Remark 2. Since $\Delta U_d + u(x, U_d)[m(x) - u(x, U_d)] = 0$, it follow that $\int_\Omega u(x, U_d)[m(x) - u(x, U_d)]dx = 0$. Therefore, as $d \to \infty$, U_d converges to a constant C_1, where $\int_\Omega u(x, C_1)[m(x) - u(x, C_1)]dx = 0$.

5. Ideal free distribution

Suppose that $u_0(x) \geq 0$ for all $x \in \Omega$ and diffusivity $d = 0$. Then, the solution $u(x, t)$ of (8) with the initial condition $u(x, 0) = u_0(x)$ will converge to $m(x)$ as $t \to \infty$ for all $x \in \Omega$. Such a case that the population grows to exactly match the carrying capacity is sometimes called the optimal habitat selection or the ideal free distribution, which has been considered for many ODE models. The linear diffusion allows the population to spread and the solution to be strictly positive, $u(x, t) \geq 0$, for $t > 0$ if $u_0(x) \geq 0$. However, it plays a negative role in achieving the optimal selection eventually for nonconstant resource distribution $m(x)$ since the linear diffusion flattens the solution. In fact, this is the reason why the slower diffuser prevails (see [9,14]). In the rest of this section we will consider an example of starvation driven diffusion that shows the optimal selection phenomenon even in the PDE model.

Consider the two modes motility function introduced in Section 1,

$$\gamma_0(s) = \begin{cases} h, & 0 \leq s < 1, \\ l, & 1 \leq s < \infty. \end{cases} \tag{13}$$

The state $s = 1$ is a critical one that the amount of resource supply m and the demand u are exactly balanced. Therefore, this motility function indicates that the organisms decrease their motility to l if the food is enough. If not, they increase their motility to h to find more resource. Notice that this motility function is discontinuous. We first consider its continuous approximation

$$\beta_\epsilon(s) = \begin{cases} h, & 0 \leq s \leq 1 - \epsilon, \\ l, & 1 + \epsilon \leq s \leq \infty, \\ \frac{1+\epsilon-s}{2\epsilon}h + \frac{s-(1-\epsilon)}{2\epsilon}l, & \text{otherwise,} \end{cases} \tag{54}$$

where $h > l > 0$ and $\epsilon > 0$ is small. Then a smooth approximation of γ_0 is given by

$$\gamma_\epsilon := \beta_\epsilon * \eta^{\epsilon^2}, \tag{55}$$

where η^{ϵ^2} is a symmetric mollifier with its support in $(-\epsilon^2, \epsilon^2)$. Then, the symmetry of η gives γ_ϵ explicitly

$$\gamma_\epsilon(s) = \begin{cases} h, & 0 \leq s \leq 1 - \epsilon - \epsilon^2, \\ l, & 1 + \epsilon + \epsilon^2 \leq s \leq \infty, \\ \frac{1+\epsilon-s}{2\epsilon}h + \frac{s-(1-\epsilon)}{2\epsilon}l, & 1 - \epsilon + \epsilon^2 \leq s \leq 1 + \epsilon - \epsilon^2, \end{cases} \tag{56}$$

where two missing regions $(1-\epsilon-\epsilon^2, 1-\epsilon+\epsilon^2)$ and $(1+\epsilon-\epsilon^2, 1+\epsilon+\epsilon^2)$ are of length $2\epsilon^2$.

We first consider the equation without the logistic reaction, i.e.,

$$u_t = \Delta(\gamma(s)u), \quad t > 0, \ x \in \Omega, \tag{16}$$

and compute steady state solutions. These steady states show the rich structure of the starvation driven diffusion in compare with linear diffusion, which gives only constant steady state without reaction. The stationary problem for (16) with regularized motility γ_ϵ is given by, for $\epsilon > 0$,

$$\begin{cases} \Delta(\gamma_\epsilon(s)u) = 0, & x \in \Omega, \\ \nabla(\gamma_\epsilon(s)u) \cdot \mathbf{n} = 0, & x \in \partial\Omega. \end{cases} \tag{57}$$

Using the pressure, $U = \gamma_\epsilon(\frac{m(x)}{u})u$, the equation simply becomes $\Delta U = 0$ with a boundary condition $(\nabla U) \cdot \mathbf{n} = 0$ and the steady state is $U = \text{constant}$. Therefore, for any given $U_0 > 0$, there exists a positive steady state solution u given by

$$\gamma_\epsilon\left(\frac{m(x)}{u(x)}\right)u(x) = U_0.$$

Note that the steady state solution u is decided by two parameter and we write $u = u(x, U_0; \epsilon)$ to denote the parameters if needed. The computation is straight forward. Fix $x \in \Omega$ and consider the case $s < 1 - \epsilon - \epsilon^2$, which corresponds to the case that $\frac{m(x)}{u(x)} < 1 - \epsilon - \epsilon^2$. Then, the motility is $\gamma_\epsilon(s) = h$ and hence $u = U_0/h$. Therefore,

$$u(x) = \frac{U_0}{h} \quad \text{if} \quad \frac{m(x)}{U_0} < \frac{1 - \epsilon - \epsilon^2}{h}.$$

Similarly,

$$u(x) = \frac{U_0}{l} \quad \text{if} \quad \frac{m(x)}{U_0} > \frac{1 + \epsilon + \epsilon^2}{l}.$$

Suppose that $1 - \epsilon + \epsilon^2 \le \frac{m(x)}{u(x)} \le 1 + \epsilon - \epsilon^2$. Then, $\gamma_\epsilon(\frac{m(x)}{u(x)})u(x) = U_0$ yields that

$$\frac{h}{2\epsilon}\left(1 + \epsilon - \frac{m(x)}{u(x)}\right) + \frac{l}{2\epsilon}\left(\frac{m(x)}{u(x)} - 1 + \epsilon\right) = \frac{U_0}{u(x)}.$$

It follows from a direct calculation that

$$u(x) = \frac{m(x)h - m(x)l + 2\epsilon U_0}{h(1 + \epsilon) - l(1 - \epsilon)}.$$

Summing up, we have

$$u(x, U_0; \epsilon) = \begin{cases} U_0/l, & \frac{m(x)}{U_0} > \frac{1+\epsilon+\epsilon^2}{l}, \\ U_0/h, & \frac{m(x)}{U_0} < \frac{1-\epsilon-\epsilon^2}{h}, \\ \dfrac{m(x)(h-l) + 2\epsilon U_0}{(h-l) + \epsilon(h+l)}, & \frac{1-\epsilon+\epsilon^2}{h} < \frac{m(x)}{U_0} < \frac{1+\epsilon-\epsilon^2}{l}. \end{cases} \tag{58}$$

Taking $\epsilon \to 0$ limit gives

$$\lim_{\epsilon \to 0} u(x, U_0; \epsilon) = \begin{cases} U_0/l, & m(x) > U_0/l, \\ U_0/h, & m(x) < U_0/h, \\ m(x), & \text{otherwise,} \end{cases} \tag{59}$$

which should be understood as the steady state under the discontinuous motility function given in (13). Now we are ready to show the following.

Theorem 5. *Let the motility function $\gamma_\epsilon(s)$, $\epsilon \geq 0$, be given by (13) and (55) and the resource distribution $m(x)$ satisfy*

$$(15) \qquad\qquad \frac{\max_{\bar{\Omega}} m(x)}{\min_{\bar{\Omega}} m(x)} < \frac{h}{l}.$$

Then, there exists a constant $U_0 > 0$ such that the solution $u(x, U_0; \epsilon)$ of (57), which is given by (58), converges to $m(x)$ as $\epsilon \to 0$. In other words, $u = m(x)$ is a steady state solution under the motility function (13).

Proof. Notice that, even if there is no logistic reaction term in the equation (57), the resource distribution $m(x)$ is involved since $\gamma = \gamma(m/u)$. The inequality (15) implies that there exists a small $\epsilon > 0$ such that

$$\frac{\max_{\bar{\Omega}} m(x)}{\min_{\bar{\Omega}} m(x)} \leq \left(\frac{1 + \epsilon - \epsilon^2}{1 - \epsilon + \epsilon^2} \right) \frac{h}{l},$$

Then, there exists $U_0 > 0$ such that

$$\frac{l}{1 + \epsilon - \epsilon^2} \max_{\bar{\Omega}} m(x) \leq U_0 \leq \frac{h}{1 - \epsilon + \epsilon^2} \min_{\bar{\Omega}} m(x), \tag{60}$$

which implies

$$\frac{1 - \epsilon + \epsilon^2}{h} U_0 \leq m(x) \leq \frac{1 + \epsilon - \epsilon^2}{l} U_0.$$

Hence, $u(x)$ should be given by the third case in (58) for all $x \in \Omega$ and a direct computation gives

$$1 - \epsilon \leq \frac{m(x)}{u(x)} \leq 1 + \epsilon. \tag{61}$$

By taking the limit as $\epsilon \to 0$, one obtains the convergence $u(x, U_0; \epsilon) \to m(x)$ as $\epsilon \to 0$. $\square$

Notice that the condition (15) can be satisfied only for strictly positive resource function $m(x) > 0$. The condition implies that the relative variation of motility h/l is bigger than the relative variation of resource distribution. The motility function in (13) shows a dramatic change of motility across the interface that $m(x) = u(x,t)$. For example, (11) is written in one space dimension as

$$(\gamma(s)u)_{xx} = \left(\gamma(s)u_x - (h-l)\delta|_{s=1}(m-u)_x\right)_x,$$

which shows Fick's law type diffusion and an advection with a Dirac-δ type coefficient across the interface $s = 1$. This advection gives a strong migration effect to the region with enough resources $\{x : m > u\}$ and is the reason that the distribution of the population could match the resources distribution.

In the theorem, a boundary condition is not imposed to $m(x)$. Suppose that γ is smooth and consider a necessary condition for $u = m(x)$ to be a steady state solution. Then, $s = 1$ and (57) is written as

$$\mathrm{div}(\gamma(1)\nabla m) = 0, \quad \gamma(1)\nabla m \cdot \mathbf{n} = 0.$$

Therefore, the only case is $m =$ constant. Hence the acquisition of the ideal free distribution (or the optimal selection property) as a steady state solution depends on the discontinuity of motility function γ in (13). This kind of phenomenon related to discontinuous motility has never been reported as far as authors know and requires deeper analytical understanding.

If $u = m(x)$ is a steady state solution of (57), then this indicates that both of the diffusion and the logistic reaction push the solution $u(x,t)$ to match the resource distribution $m(x)$ as $t \to \infty$. Therefore, the starvation driven diffusion is not an obstacle to obtain the ideal free distribution asymptotically. In fact, we will show in the following theorem that the ideal free distribution is globally asymptotically stable under an assumption on $m(x)$ such that

$$l \max_{\bar{\Omega}} m(x) < \frac{h+l}{2} \min_{\bar{\Omega}} m(x) < \frac{h+l}{2} \max_{\bar{\Omega}} m(x) < h \min_{\bar{\Omega}} m(x),$$

$$(62)$$

which is a stronger restriction to $m(x)$ than (15) is.

Theorem 6 (Ideal free distribution). *Let the motility function* $\gamma_\epsilon(s)$, $\epsilon \geq 0$, *be given by (13) and (55), the resource distribution* $m(x)$ *satisfy (62), and* $\theta(x;\epsilon)$ *be the globally asymptotically stable solutions in Theorem 2. Then,* $\theta(x;\epsilon)$ *converges to* $m(x)$ *as* $\epsilon \to 0$. *In this sense,* $u = m(x)$ *is the globally asymptotically stable positive solution of (28) with the discontinuous motility function in (13).*

Proof. The proof uses the classical upper/lower solution method. Let $\epsilon > 0$ be small. First note that, for the case $u = m(x)$, we have

$$U(x, m(x)) = \gamma_\epsilon(1) m(x) = \frac{h+l}{2} m(x).$$

Let $\underline{U} := \frac{h+l}{2} \min_{\bar{\Omega}} m(x)$. Then, $\underline{U} \leq U(x, m(x))$ for all $x \in \Omega$ and hence $u(x, \underline{U}; \epsilon) \leq m(x)$. Therefore, $\Delta(\gamma_\epsilon u(x, \underline{U}; \epsilon)) = \Delta \underline{U} = 0$ and $u(x, \underline{U}; \epsilon)(m - u(x, \underline{U}; \epsilon)) \geq 0$. Hence $u(x, \underline{U}; \epsilon)$ is a lower solution to the problem (28) with the motility function γ_ϵ. Similarly, let $\overline{U} := \frac{h+l}{2} \max_{\bar{\Omega}} m(x)$. Then, $u(x, \overline{U}; \epsilon)$ is an upper solution. Therefore, the unique globally asymptotically stable solution $\theta(x; \epsilon)$ should be placed as

$$u(x, \underline{U}; \epsilon) \leq \theta(x; \epsilon) \leq u(x, \overline{U}; \epsilon).$$

The relation (62) implies that there is a small $\epsilon > 0$ such that $\overline{U}$ and $\underline{U}$ satisfy the relation in (60). Therefore, the proof of Theorem 5 gives that

$$u(x, \underline{U}; \epsilon) \to m(x) \quad \text{and} \quad u(x, \overline{U}; \epsilon) \to m(x) \quad \text{as} \quad \epsilon \to 0.$$

Therefore, $\theta(x; \epsilon) \to m(x)$ as $\epsilon \to 0$. $\square$

Remark 3. The condition in (62) seems unnecessarily restrictive. The condition (15) seems the sufficient and necessary condition for the ideal free distribution.

6. Discussion

Dispersal strategy is a key element for the survival of species and each species has developed its own way. Diffusion models a random dispersal and only the constant diffusivity case has been intensively studied. However, the need of food or mating causes a huge leap in the motility of species and such a change is the key to understand the role of dispersal in the evolution. In this paper such a motility change has been analyzed for the simplest logistic equation case

$$u_t = \Delta(\gamma(s)u) + u(m - u),$$

where u is the population density and m is the resource distribution. Readers are referred to [9] for a detailed discussion about this model including competition cases.

The key feature of this model is that the motility $\gamma(s)$ is a decreasing function on the satisfaction measure $s := \frac{m}{u}$. In other words, if there is enough food and the satisfaction level is high, then organisms will reduce their motility. However, if organisms are starved, they will increase the motility to leave the habitat. For example, *Dictyostelium,*

social ameobae, undergoes a dramatic change when foods are consumed. Then they aggregate to form a stalk-like fruiting body. The organisms on top of it become spores that can be easily dispersed (see [5, 20]). Starvation driven motility is also observed from much more complex organism such as *Caenorhabditis elegans* and desert locust (see [30, 41]). It is experimentally confirmed that locomotor activity is increased under starvation in common model organisms such as *Drosophila*, mice and rats (see [25, 42, 43]).

The starvation driven diffusion is closely related to Ludwig's thermophoresis [35], where salt particles move toward cold regions. Theoretical foundation of the phenomenon has been a long standing debate and, recently, it is shown in [27] that the source of such an advection is the motility change of particles on a temperature change. Similarly, many biological organisms aggregate around food without knowing where the food is until they find the food. Such a phenomenon is due to migration and its time scale is a lot shorter than the effect of the logistic reaction term. A phenomenological way to explain it is to put an appropriate advection term as in (12). However, in many cases, although there is a clear intension for the migration, animals including human beings do not know which way to go until they find something. Hence it should be understood as a random dispersal. In the model of this paper, such an aggregation has been obtained from the motility change that depends on the satisfaction of species to the environment. Furthermore, the ideal free distribution, Theorems 5 and 6, has been obtained from such a motility change without adding a phenomenological advection term in Section 5.

In certain cases biological organisms may sense the gradient of resource or chemical concentration and move toward or against it. However, in other cases, they do sense the concentration only and control the motility depending on it. For example, German cockroaches (*Blattela germanica*) change their motility level depending on the concentration of aggregation pheromone (see [18, 24]). It seems that the limitation of the classical diffusion of Fick's law type forces to introduce a phenomenological advection. However, such an advection should be distinguished from the real advection to understand the dispersal correctly. The diffusion model in this paper is based on the new diffusion law (9) for a heterogeneous motility and gives aggregation phenomenon even without the logistic term as shown in Section 2.

Mathematically, this paper develops its theory much the same way as its linear diffusive counterpart, but the analysis is more sophisticated. The global asymptotic stability has been obtained in Section 3 and the zero-diffusion and the zero-reaction limits are obtained in Section 4. The methods of proofs are also similar to the linear diffusion case. However, it seems needed to develop them to obtain the

full potential of the model without technical hypotheses assumed in this paper.

Acknowledgement

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