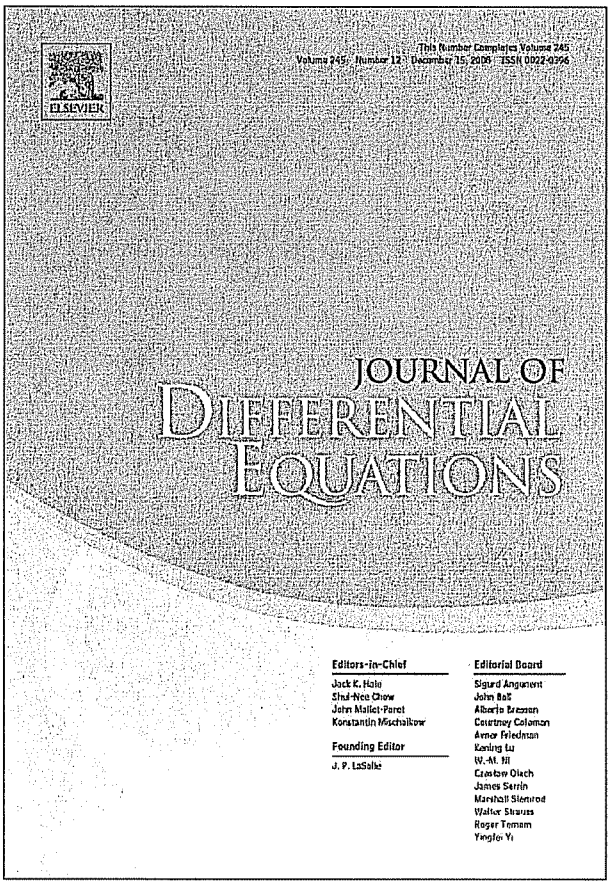
Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Author's personal copy

J. Differential Equations 245 (2008) 3687–3703

Contents lists available at ScienceDirect

Journal of Differential Equations

www.elsevier.com/locate/jde

Approximating the ideal free distribution via reaction–diffusion–advection equations

Robert Stephen Cantrell [a,1], Chris Cosner [a,1], Yuan Lou [b,*,2]

[a] Department of Mathematics, University of Miami, Coral Gables, FL 33124, USA
[b] Department of Mathematics, Ohio State University, Columbus, OH 43210, USA

ARTICLE INFO

Article history:
Received 7 December 2007
Revised 9 July 2008
Available online 6 August 2008

MSC:
35K57
92D25

Keywords:
Ideal free distribution
Reaction–diffusion–advection

ABSTRACT

We consider reaction–diffusion–advection models for spatially distributed populations that have a tendency to disperse up the gradient of fitness, where fitness is defined as a logistic local population growth rate. We show that in temporally constant but spatially varying environments such populations have equilibrium distributions that can approximate those that would be predicted by a version of the ideal free distribution incorporating population dynamics. The modeling approach shows that a dispersal mechanism based on local information about the environment and population density can approximate the ideal free distribution. The analysis suggests that such a dispersal mechanism may sometimes be advantageous because it allows populations to approximately track resource availability. The models are quasilinear parabolic equations with nonlinear boundary conditions.

© 2008 Elsevier Inc. All rights reserved.

1. Introduction

An obvious feature of most biological populations is that they are distributed in space. It is natural to ask how the dispersal processes of those populations lead to patterns of spatial distributions, what sorts of patterns arise from various processes, and why organisms might evolve to disperse in certain ways. Considerable efforts have been made to use spatial models to address those questions. In the present article we will examine some spatially explicit population models that are related to a particular pattern, the ideal free distribution. In its original form the ideal free distribution is simply

* Corresponding author.
E-mail addresses: rsc@math.miami.edu (R.S. Cantrell), gcc@math.miami.edu (C. Cosner), lou@math.ohio-state.edu (Y. Lou).

[1] Partially supported by the NSF grant DMS-0514839.
[2] Partially supported by the NSF grant DMS-0615845.

0022-0396/$ – see front matter © 2008 Elsevier Inc. All rights reserved.
doi:10.1016/j.jde.2008.07.024

Author's personal copy

a description of how organisms would locate themselves if they could move freely to optimize their fitness [17]. A version of the ideal free distribution in continuous space can be derived from a type of advection–diffusion equation that is based on the assumptions that organisms move upward along the local gradient of fitness and that fitness varies spatially and is reduced by crowding [14]. We will consider a variation on that model which also includes random diffusion as part of the dispersal process. We will show that as the rate of movement up fitness gradients becomes large and/or the rate of diffusion becomes small, the distribution of organisms predicted by our models approximates that which would be expected from ideal free habitat selection. Other models where organisms were assumed to disperse upward along fitness gradients have been studied in [3,4,19]. In [3,4] two-patch models were used instead of reaction–advection–diffusion models. In [19] the analytic approach and the questions addressed by the modeling and analysis were different from those in the present paper.

Our analysis is partially motivated by an interest in understanding the evolution of dispersal in spatially varying but temporally constant environments. In that context it is useful to follow McPeek and Holt [28] and distinguish between unconditional and conditional dispersal. Unconditional dispersal refers to dispersal without regard to the environment or the presence of other organisms. Pure diffusion and diffusion with physical advection (e.g. due to winds or currents) are examples of unconditional dispersal. Conditional dispersal refers to dispersal that is influenced by the environment or the presence of other organisms. It has been shown that in the framework of spatially explicit population models on spatially varying but temporally constant environments with only unconditional dispersal that evolution favors slow dispersal [16,21,28]. A reason why unconditional dispersal is not favored is that it leads to a mismatch between the distribution of population and the distribution of resources. However, for certain types of conditional dispersal, evolution can sometimes favor faster dispersal if that allows the population to track resources more efficiently [11,12,28]. These conclusions were obtained by considering models for two competitors that use different dispersal strategies but otherwise are ecologically identical, and examining the evolutionary stability of the strategies in terms of invasibility. (A strategy is considered evolutionarily stable if a population using that strategy cannot be invaded by a small population using a different strategy.) We plan to consider ideal free dispersal from that viewpoint in future work. To do that, we need to understand well the behavior of a single species using ideal free dispersal; developing that understanding is the goal of this paper. Further it is worth noting that dispersal processes that result in patterns embodying certain features of the ideal free distribution have been shown to be evolutionarily stable in discrete diffusion models; see [10,26]. However, it should also be noted that in models with temporal variation in the coefficients or complex dynamics, faster unconditional dispersal may sometimes be favored; see [23,24,28]. Some of these phenomena and other aspects of the ecological effects of directed versus random movement and the evolution of dispersal are studied in the context of two-patch models in [3,4].

A key idea underlying the ideal free distribution is that individuals will locate themselves in such a way as to optimize their fitness. Thus, at equilibrium, all organisms in the occupied part of the habitat will have equal fitness and there will be no net movement of individuals if the population is constant. A continuum model that captures those features was introduced in [25]. Suppose that a population has an intrinsic per capita growth rate $m(x)$ that varies in space but experiences increased mortality and/or decreased reproductive success due to crowding uniformly throughout its environment. If the population density is scaled appropriately the local reproductive fitness of an individual at location x in the presence of conspecifics at density $u(x)$ is given by

$$f(x,u) = m(x) - u(x).$$

Let F denote the fitness of organisms in the occupied part of the habitat Ω. For a fixed total population U the distribution of the population will be given by

$$u = \begin{cases} m(x) - F & \text{if } m(x) > F; \\ 0 & \text{otherwise,} \end{cases}$$

where F is made as large as possible subject to the conditions

Author's personal copy

$$\int_\Omega u(x)\,dx = U;$$

$$\big|\{x \in \Omega:\ u(x) > 0\}\big| \cdot F = \int_{\{x\in\Omega:\ u(x)>0\}} m(x)\,dx - U.$$

The first of these conditions simply requires the total population to be conserved. The second condition is obtained by integrating the previous formula for the density $u(x)$. It can be used to determine F and the region where $u(x) > 0$ by viewing it as a constraint and maximizing F subject to that constraint. In simple cases it is possible to find explicit formulas for F and the region where $u(x) > 0$ in terms of U; see [25]. A dynamic model which supports equilibrium solutions corresponding to this formulation was introduced in [14]. That model has the form

$$u_t = -\alpha\nabla\cdot\big[u\nabla f(x,u)\big] \quad \text{on } \Omega\times(0,\infty),$$

with the no-flux boundary condition

$$u\frac{\partial f(x,u)}{\partial n} = 0 \quad \text{on } \partial\Omega\times(0,\infty),$$

where the habitat Ω is a bounded domain in R^N with smooth boundary $\partial\Omega$, n is the outward unit normal vector on $\partial\Omega$, and α is a positive constant that measures the strength of dispersal up the fitness gradient.

In the present paper we will consider a variation on the model of [14] that incorporates population growth and diffusion along with directed motion up the fitness gradient. It is natural to ask how population growth interacts with dispersal. It is reasonable to assume that the process of assessing the fitness gradient, imperfect tracking of that gradient, and responses to other aspects of the environment could lead to some amount of random movement. Also, by incorporating diffusion and population dynamics into the model, we can put it into a framework that allows us to compare it with other models that have been studied in the context of the evolution of dispersal [11–13,16,24]. In the presence of population dynamics, pure ideal free dispersal would be expected to result in an equilibrium distribution of the population in which the fitness of each individual will be zero, so that there will be no further population growth. That would correspond to a population density $u(x) = m_+(x)$, where $m_+(x)$ denotes the positive part of $m(x)$. If $m(x)$ is interpreted as describing the distribution of resources, having $u = m_+(x)$ would mean that the population perfectly matches the resource density. We will see that as the tendency of the organisms to move upward along fitness gradients becomes large such a distribution is approximated by the equilibria of the corresponding model with diffusion. This is in contrast with the behavior of models that incorporate movement up the gradient of $m(x)$ but no response to crowding. In those models the distribution of organisms tends to become concentrated near local maxima of $m(x)$ as the rate of movement up the gradient becomes large; see [12,13].

The model we will consider has the form

$$u_t = \nabla\cdot\big[\mu\nabla u - \alpha u\nabla f(x,u)\big] + uf(x,u) \quad \text{in } \Omega\times(0,\infty), \tag{1.1}$$

with no-flux boundary conditions

$$\mu\frac{\partial u}{\partial n} - \alpha u\frac{\partial f(x,u)}{\partial n} = 0 \quad \text{on } \partial\Omega\times(0,\infty), \tag{1.2}$$

where

$$f(x,u) = m(x) - u. \tag{1.3}$$

Author's personal copy

Throughout this paper we assume that $m \in C^{2,\tau}(\overline{\Omega})$ for some $\tau \in (0,1)$ and m is positive somewhere in Ω. The dispersal terms in (1.1) can be written in two different forms, corresponding to two distinct ways of thinking about their interpretation in the model, namely

$$\mu\nabla^2 u - \alpha\nabla\cdot u\nabla\big(m(x)-u\big)$$

and

$$\nabla^2\left(\mu u + \frac{\alpha u^2}{2}\right) - \alpha\nabla\cdot u\nabla m(x).$$

In the first form, the first term represents ordinary diffusion while the second term represents directed movement up the gradient of fitness. In the second form, the first term represents a version of nonlinear diffusion where organisms avoid crowding by diffusing more rapidly in the presence of conspecifics, and the second term represents movement up the gradient of underlying environmental quality without reference to the presence of conspecifics or their influence on fitness. Models with nonlinear diffusion terms similar to those occurring in the second form have been used to describe the distribution of populations that avoid crowding; see [20,30]. Models with ordinary diffusion but incorporating a tendency to move up the gradient of underlying environmental quality were considered in [6,11–13,15]. Some related models were considered in [7,19] but the methods and results in those papers are quite different from ours.

Ultimately we plan to study the evolutionary stability of ideal free dispersal relative to other dispersal strategies. To do that, we would consider models of two populations that are ecologically identical but use different dispersal strategies. Such an approach has been used in [11,12,16,24]. Using this modeling approach in the context of ideal free dispersal would lead to a system of the form of

$$\begin{aligned} u_t &= \nabla\cdot\big[\mu\nabla u - \alpha u\nabla f(x,u+v)\big] + uf(x,u+v) \quad \text{in } \Omega\times(0,\infty),\\ v_t &= \nabla\cdot\big[\nu\nabla v - \beta v\nabla g(x,u+v)\big] + vf(x,u+v) \quad \text{in } \Omega\times(0,\infty), \end{aligned} \tag{1.4}$$

with no-flux boundary conditions

$$\mu\frac{\partial u}{\partial n} - \alpha u\frac{\partial f(x,u+v)}{\partial n} = \nu\frac{\partial v}{\partial n} - \beta v\frac{\partial g(x,u+v)}{\partial n} = 0 \quad \text{on } \partial\Omega\times(0,\infty), \tag{1.5}$$

where f is as in (1.3), and g represents part of an alternate dispersal strategy. For example, $g=0$ would correspond to unconditional dispersal by simple diffusion, $g=m$ would correspond to advection up resource gradient without consideration of crowding, while $g=-(u+v)$ would correspond to avoidance of crowding without reference to resource distribution. To analyze such a model from the view point of evolutionary stability, one needs to study the stability of semi-trivial equilibria of (1.4)–(1.5). To do that requires a detailed knowledge of those equilibria. Understanding the semi-trivial equilibrium $(\tilde{u},0)$ where $\tilde{u}$ satisfies (1.1)–(1.2) is essential to this process and it is the subject of this paper.

In the analysis of (1.1)–(1.2) we will use a number of changes of variables. It is not immediately clear that (1.1)–(1.2) or its equilibrium equation will satisfy a comparison principle. We will want to use comparison principles, sub- and super-solutions, and related ideas in our analysis. To that end we will introduce the new variable

$$w = ue^{-(\alpha/\mu)(m-u)}.$$

In other contexts we will also use $\ln(w)$ as a new variable. For purposes of deriving *a priori* estimates we will use the change of variables

$$z = \frac{u^2}{2} + \frac{\mu}{\alpha}u.$$

Author's personal copy

If we set $\mu = 0$ in (1.1) and (1.2), we obtain

$$u_t = -\alpha\nabla\cdot\big[u\nabla f(x,u)\big] + uf(x,u) \quad \text{in } \Omega\times(0,\infty), \tag{1.6}$$

with no-flux boundary conditions

$$u\frac{\partial f(x,u)}{\partial n} = 0 \quad \text{on } \partial\Omega\times(0,\infty). \tag{1.7}$$

Eqs. (1.6), (1.7) can be viewed as the model for the ideal free distribution in [14] with an additional term describing population dynamics, or as a limiting case of (1.1), (1.2) as $\mu\to 0$. The model (1.1), (1.2) can thus be viewed as an approximation of dispersal according to the ideal free distribution in the presence of population dynamics.

Our first major result is an existence theorem for (1.1), (1.2):

Theorem 1. *Suppose that $\mu > 0$ and $\alpha \geqslant 0$. Then (1.1)–(1.2) has a unique solution $u \in C^{2,1}(\overline{\Omega}\times(0,\infty)) \cap C(\overline{\Omega}\times[0,\infty))$.*

For the next result, we need to assume that $u = 0$ is linearly unstable. For that to be the case the principal eigenvalue of the associated eigenvalue problem

$$\nabla\cdot[\mu\nabla\phi - \alpha\phi\nabla m] + m\phi = -\lambda\phi \quad \text{in } \Omega, \qquad \mu\frac{\partial\phi}{\partial n} - \alpha\phi\frac{\partial m}{\partial n} = 0 \quad \text{on } \partial\Omega \tag{1.8}$$

must be negative. The existence of a principal eigenvalue for (1.8) can be shown by making a change of variables. It turns out that if $\int_\Omega m\cdot e^{(\alpha/\mu)m}\,dx > 0$, then $u = 0$ is always unstable, but that condition is not necessary for instability. We discuss linear eigenvalue problems in more detail in Appendix A. If $u = 0$ is unstable then (1.1), (1.2) will have at least one positive equilibrium:

Theorem 2. *If $u = 0$ is linearly unstable, then (1.1)–(1.2) has at least one positive steady state. In particular, there exist maximal and minimal positive steady states of (1.1)–(1.2), denoted by u^* and u_*, such that for any positive steady state u of (1.1)–(1.2), $u_* \leqslant u \leqslant u^*$ in $\overline{\Omega}$.*

Theorems 1 and 2 are proved in Section 2.

Our next two results describe the behavior of equilibria of (1.1) and (1.2) as $\alpha/\mu\to\infty$. Specifically, they describe how those equilibria approximate those that would be expected for the model (1.6), (1.7) for the ideal free distribution in the presence of population dynamics.

Theorem 3. *For any positive steady state u of (1.1)–(1.2), $u\to m_+$ weakly in H^1 and strongly in L^2 as $\alpha/\mu\to\infty$. For any given $\eta > 0$, if $\alpha\geqslant\eta$ and $\alpha/\mu\to\infty$, $u\to m_+$ in $C^\gamma(\overline{\Omega})$ for some $\gamma\in(0,1)$.*

Theorem 4. *Suppose that $m > 0$ in $\overline{\Omega}$. For any given $\eta > 0$, if $\alpha\geqslant\eta$ and $\alpha/\mu\to\infty$, then $u\to m$ in $C^2(\overline{\Omega})$. Moreover,*

(i) *if $\alpha/\mu\to\infty$ and $\alpha\to\infty$, we have*

$$\frac{\alpha}{\mu}(u-m)\to\frac{\int_\Omega m\ln m}{\int_\Omega m} - \ln m \tag{1.9}$$

uniformly in $\overline{\Omega}$;

Author's personal copy

(ii) *if* $\alpha/\mu \to \infty$ *and* $\alpha \to \tilde{\alpha}$ *for some* $\tilde{\alpha} \in (0, \infty)$, *then*

$$\frac{\alpha}{\mu}(u - m) \to \tilde{w} - \ln m \tag{1.10}$$

uniformly in $\overline{\Omega}$, *where* $\tilde{w}$ *is the unique solution of*

$$\tilde{\alpha}\nabla \cdot [m\nabla \tilde{w}] - m\tilde{w} = -m \ln m \quad \text{in } \Omega, \qquad \frac{\partial \tilde{w}}{\partial n} = 0 \quad \text{on } \partial\Omega. \tag{1.11}$$

Theorems 3 and 4 are proved in Section 3.

Once we have characterized the asymptotic behavior of equilibria of (1.1), (1.2) as $\alpha/\mu \to \infty$ we can use that information to conclude that for α/μ large and $m > 0$ the model has a unique positive steady state which is globally asymptotically stable among positive solutions:

Theorem 5. *If* $m > 0$ *in* $\overline{\Omega}$, *then for large* α/μ, (1.1)–(1.2) *has a unique positive steady state which is also globally asymptotically stable.*

Theorem 5 is proved in Section 4.

In Section 5 we discuss the implications of our results and describe how they fit into the more general context of the evolution of dispersal.

2. Global smooth solutions and steady states

This section is devoted to the proofs of Theorems 1 and 2. The local existence of smooth solutions follows from Amann's results [1] for quasilinear parabolic equations with general boundary conditions. Moreover, by Theorem 3 of [2], in order to ensure the global existence of smooth solutions, it suffices to establish uniform bounds on solutions in L^∞ norm.

2.1. A priori estimates and global existence

Given any $m(x)$ and $u \geqslant 0$, set

$$w = u \cdot e^{-(\alpha/\mu)[m(x)-u]}. \tag{2.1}$$

By the inverse function theorem, we can express u as

$$u = h(x, w).$$

Then w satisfies the zero Neumann boundary condition and

$$w_t = \big[h_w(x, w)\big]^{-1}\big[\mu e^{(\alpha/\mu)(m-h)}\Delta w + \alpha e^{(\alpha/\mu)(m-h)}\nabla(m-h)\cdot\nabla w + h(m-h)\big]. \tag{2.2}$$

Lemma 2.1. *For any positive smooth solution* w *of* (2.2) *in* $\Omega \times [0, T]$, *we have*

$$\max_{\overline{\Omega}\times[0,T]} w \leqslant \max\Big\{\max_{\overline{\Omega}} w(\cdot, 0), \max_{\overline{\Omega}} m\Big\}. \tag{2.3}$$

Proof. Choose any $\epsilon > 0$. Let $(x_\epsilon^*, t_\epsilon^*)$ denote a point where $w(x_\epsilon^*, t_\epsilon^*) = \max_{\overline{\Omega}\times[0,T-\epsilon]} w$. If $t_\epsilon^* = 0$, the estimate $w(x_\epsilon^*, t_\epsilon^*) \leqslant \max_{\overline{\Omega}} w(\cdot, 0)$ automatically holds. Suppose $0 < t_\epsilon^* \leqslant T - \epsilon$. We claim that

$$h\big(x_\epsilon^*, w(x_\epsilon^*, t_\epsilon^*)\big) \leqslant m(x_\epsilon^*). \tag{2.4}$$

Author's personal copy

To establish our assertion, we consider two cases: (i) $x_\epsilon^* \in \Omega$. For this case, our assertion follows from (2.2), $\Delta w(x_\epsilon^*, t_\epsilon^*) \leqslant 0$, $\nabla w(x_\epsilon^*, t_\epsilon^*) = 0$, and $w_t(x_\epsilon^*, t_\epsilon^*) \geqslant 0$. (ii) $x_\epsilon^* \in \partial\Omega$. For this case, we argue by contradiction and assume that $h(x_\epsilon^*, w(x_\epsilon^*, t_\epsilon^*)) > m(x_\epsilon^*)$. Therefore, there exists an open ball, denoted by B, with $B \subset \Omega \times (0, T)$ and $\overline{B} \cap \partial\Omega \times (0, T) = \{(x_\epsilon^*, t_\epsilon^*)\}$, such that $h(x, w(x, t)) > m(x)$ in $\overline{B}$. By (2.2),

$$w_t < \big[h_w(x, w)\big]^{-1}\big[\mu e^{(\alpha/\mu)(m-h)}\Delta w + \alpha e^{(\alpha/\mu)(m-h)}\nabla(m-h)\cdot\nabla w\big]$$

in B. Let $(x_\epsilon^{**}, t_\epsilon^{**})$ denote a point where $w(x_\epsilon^{**}, t_\epsilon^{**}) = \max_{\overline{B}} w$. If $(x_\epsilon^{**}, t_\epsilon^{**}) \in \overline{B} \cap \Omega \times (0, T]$ then we obtain a contradiction as in case (i). If $x_\epsilon^{**} \in \partial\Omega$ then by the Hopf boundary lemma [29], $\nabla w \cdot n > 0$ at $(x_\epsilon^{**}, t_\epsilon^{**})$, which is a contradiction. Thus, (2.4) must be satisfied.

By (2.4), $u(x_\epsilon^*, t_\epsilon^*) = h(x_\epsilon^*, w(x_\epsilon^*, t_\epsilon^*)) \leqslant m(x_\epsilon^*)$. Hence,

$$w\big(x_\epsilon^*, t_\epsilon^*\big) = u\big(x_\epsilon^*, t_\epsilon^*\big)e^{(\alpha/\mu)[u(x_\epsilon^*)-m(x_\epsilon^*)]} \leqslant u\big(x_\epsilon^*, t_\epsilon^*\big) \leqslant m\big(x_\epsilon^*\big) \leqslant \max_{\overline{\Omega}} m.$$

Thus,

$$\max_{\overline{\Omega}\times[0,T-\epsilon]} w \leqslant \max\Big\{\max_{\overline{\Omega}} w(\cdot, 0), \max_{\overline{\Omega}} m\Big\}.$$

Since $\epsilon > 0$ was arbitrary, it follows that (2.3) must be satisfied. □

Corollary 2.2. *For any positive smooth solution u of (1.1)–(1.2) in $\Omega \times [0, T]$, we have*

$$\max_{\overline{\Omega}\times[0,T]} u \leqslant \max\Big\{e^{(\alpha/\mu)[\max_{\overline{\Omega}} m - \min_{\overline{\Omega}} m]} \max_{\overline{\Omega}} u(\cdot, 0), \max_{\overline{\Omega}} m\Big\}. \tag{2.5}$$

Proof. If $\max_{\overline{\Omega}\times[0,T]} w \leqslant \max_{\overline{\Omega}} w(\cdot, 0)$, then

$$u(x, t)e^{(\alpha/\mu)u(x,t)} \leqslant e^{(\alpha/\mu)[\max_{\overline{\Omega}} m - \min_{\overline{\Omega}} m]} \max_{\overline{\Omega}}\big[u(x, 0)e^{(\alpha/\mu)u(x,0)}\big],$$

which implies that

$$u(x, t) \leqslant e^{(\alpha/\mu)[\max_{\overline{\Omega}} m - \min_{\overline{\Omega}} m]} \max_{\overline{\Omega}} u(x, 0)$$

for every $(x, t) \in \overline{\Omega} \times [0, T]$. If $\max_{\overline{\Omega}\times[0,T]} w \leqslant \max_{\overline{\Omega}} m$, we claim that $\max_{\overline{\Omega}\times[0,T]} u \leqslant \max_{\overline{\Omega}} m$. Suppose not, i.e., there exists $(x^*, t^*) \in \overline{\Omega} \times [0, T]$ such that $u(x^*, t^*) > \max_{\overline{\Omega}} m$. Then $m(x^*) < u(x^*, t^*)$. Hence,

$$u(x^*, t^*) \leqslant u(x^*, t^*)e^{(\alpha/\mu)[u(x^*,t^*)-m(x^*)]} \leqslant \max_{\overline{\Omega}\times[0,T]} w \leqslant \max_{\overline{\Omega}} m,$$

which is a contradiction. This completes the proof of (2.5). □

2.2. Monotonicity and steady states

Due to the nonlinear boundary condition, it is not clear whether (1.1)–(1.2) is a monotone system as the comparison principle may not apply directly. In this connection we first show:

Lemma 2.3. *Suppose that u_1 and u_2 are two smooth solutions of (1.1)–(1.2). If $u_1(x, 0) \geqslant u_2(x, 0)$ in $\overline{\Omega}$, then $u_1(x, t) \geqslant u_2(x, t)$ in $\overline{\Omega} \times (0, \infty)$. If we further assume that $u_1 \not\equiv u_2$, then $u_1(x, t) > u_2(x, t)$ in $\overline{\Omega} \times (0, \infty)$.*

Author's personal copy

Proof. Set $w_i = u_i \cdot e^{-(\alpha/\mu)(m-u_i)}$, $i = 1, 2$, respectively. Then the functions w_i satisfy zero Neumann boundary conditions and (2.2). By the comparison principle [29] (which applies under the zero Neumann boundary condition) we see that $w_1(x,t) \geqslant w_2(x,t)$ in $\overline{\Omega} \times [0,\infty)$. Since h_w is positive, we have $u_1(x,t) \geqslant u_2(x,t)$ in $\overline{\Omega} \times [0,\infty)$. The rest of the proof is similar and is thus omitted. □

Proof of Theorem 2. We first construct some families of supersolutions and subsolutions for the steady state problem of (1.1)–(1.2). For the construction of supersolutions, choose any positive constant $\overline{C}$ such that $h(x,\overline{C}) > m(x)$ in $\overline{\Omega}$. Set $\bar{w} = C$. It is easy to see that for every $C \geqslant \overline{C}$,

$$e^{(\alpha/\mu)[m-h(x,\bar{w})]}\big[\mu\Delta\bar{w} + \alpha\nabla\big[m - h(x,\bar{w})\big]\cdot\nabla\bar{w}\big] + h\big[m - h(x,\bar{w})\big] < 0 \tag{2.6}$$

in $\overline{\Omega}$. This in turn implies that for every $C \geqslant \overline{C}$, $\bar{u}(x;C) := h(x,\bar{w})$ satisfies

$$\nabla\cdot\big[\mu\nabla\bar{u} - \alpha\bar{u}\nabla f(x,\bar{u})\big] + \bar{u}f(x,\bar{u}) < 0 \quad \text{in } \overline{\Omega} \tag{2.7}$$

and

$$\mu\frac{\partial\bar{u}}{\partial n} - \alpha\bar{u}\frac{\partial f(x,\bar{u})}{\partial n} = 0 \quad \text{on } \partial\Omega. \tag{2.8}$$

To construct subsolutions, we apply the assumption that $u = 0$ is linearly unstable, i.e., the principal eigenvalue (denoted by λ_1) of the eigenvalue problem (1.8) is negative. We denote the corresponding positive eigenfunction by ϕ_1, which is uniquely determined by $\max_{\overline{\Omega}}\phi_1 = 1$. For any $\epsilon > 0$, set $\underline{w} = \epsilon e^{-(\alpha/\mu)m}\phi_1$. One may check that $\underline{w}$ satisfies the zero Neumann boundary condition and there exists some positive constant $\bar{\epsilon}$ such that for every $\epsilon \in (0,\bar{\epsilon})$,

$$e^{(\alpha/\mu)[m-h(x,\underline{w})]}\big[\mu\Delta\underline{w} + \alpha\nabla\big[m - h(x,\underline{w})\big]\cdot\nabla\underline{w}\big] + h\big[m - h(x,\underline{w})\big] > 0 \tag{2.9}$$

in $\overline{\Omega}$. Set $\underline{u}(x;\epsilon) = h(x,\underline{w})$. Then, for every $\epsilon < \bar{\epsilon}$, $\underline{u}$ satisfies

$$\nabla\cdot\big[\mu\nabla\underline{u} - \alpha\underline{u}\nabla f(x,\underline{u})\big] + \underline{u}f(x,\underline{u}) > 0 \quad \text{in } \overline{\Omega} \tag{2.10}$$

and

$$\mu\frac{\partial\underline{u}}{\partial n} - \alpha\underline{u}\frac{\partial f(x,\underline{u})}{\partial n} = 0 \quad \text{on } \partial\Omega. \tag{2.11}$$

Choosing $\bar{\epsilon}$ smaller if necessary we may assume that $\underline{u}(x;\bar{\epsilon}) < \bar{u}(x;\overline{C})$ for $x \in \overline{\Omega}$. By the supersolution and subsolution method for elliptic equations we see that (1.1)–(1.2) has at least one positive steady state. Moreover, there exist two positive steady states of (1.1)–(1.2), denoted by u_* and u^*, such that for any positive steady state u of (1.1)–(1.2) which satisfies $\underline{u}(x;\bar{\epsilon}) \leqslant u \leqslant \bar{u}(x;\overline{C})$ in $\overline{\Omega}$, one has $u_* \leqslant u \leqslant u^*$ in $\overline{\Omega}$.

It remains to show that for any positive steady state u of (1.1)–(1.2), we have $\underline{u}(x;\bar{\epsilon}) \leqslant u \leqslant \bar{u}(x;\overline{C})$ in $\overline{\Omega}$. We argue by contradiction: if not, we may suppose that there exists some positive steady state u of (1.1)–(1.2) such that $u(\tilde{x}) > \bar{u}(\tilde{x};\overline{C})$ for some $\tilde{x} \in \overline{\Omega}$. Set

$$S = \big\{C \geqslant \overline{C}:\ \bar{u}(x;C) > u(x)\ \forall x \in \overline{\Omega}\big\}.$$

Note that $\bar{u}(\cdot;C)$ is strictly monotone increasing in C. Since $\lim_{C\to+\infty} h(x,C) = \infty$ uniformly for $x \in \overline{\Omega}$, for sufficiently large C, $\bar{u}(x;C) > u(x)$ $\forall x \in \overline{\Omega}$. Hence S is non-empty. As $u(\tilde{x}) > \bar{u}(\tilde{x};\overline{C})$, $\overline{C}$ is a lower bound of the set S. Therefore, the largest lower bound of S exists, and is denoted as C^*. Moreover, $\bar{u}(x;C^*) \geqslant u(x)$ in $\overline{\Omega}$, and $\bar{u}(x^*;C^*) = u(x^*)$ for some $x^* \in \overline{\Omega}$. Since $\bar{u}(x;C^*)$ satisfies (2.7) and $u(x)$ is a steady state of (1.1)–(1.2), $\bar{u}(x;C^*) \not\equiv u(x)$. Let $u_i(x,t)$, $i = 1, 2$, denote the solutions

Author's personal copy

of (1.1)–(1.2) with $u_1(x,0) = \bar{u}(x;C^*)$ and $u_2(x,0) = u(x)$, respectively. As $u(x)$ is a steady state of (1.1)–(1.2), $u_2(x,t) \equiv u(x)$ for $t \geqslant 0$. Since $u_1(x,0) \geqslant u_2(x,0)$ and $u_1(x,0) \not\equiv u_2(x,0)$, by Lemma 2.3 we have $u_1(x,t) > u_2(x,t) = u(x)$ for $t > 0$. Since $u_1(x,0)$ is a smooth elliptic supersolution for (1.1)–(1.2), similar to the proof of Lemma 2.3 we have $u_1(x,t) \leqslant u_1(x,0)$ in $\overline{\Omega}$ for $t > 0$. This together with $u_1(x,t) > u(x)$ implies that $u_1(x,0) > u(x)$ in $\overline{\Omega}$, i.e., $\bar{u}(x;C^*) > u(x)$ in $\overline{\Omega}$, which contradicts $\bar{u}(x^*;C^*) = u(x^*)$. Hence, for any positive steady state u of (1.1)–(1.2), $u(x) \leqslant \bar{u}(x;\overline{C})$ in $\overline{\Omega}$. Similarly, we can show that $u(x) \geqslant \underline{u}(x;\underline{\epsilon})$ in $\overline{\Omega}$. This completes the proof of Theorem 2. □

3. Asymptotic behavior of steady states

In Section 3.1 we establish some *a priori* estimates for positive steady states of (1.1)–(1.2). These estimates are then applied in Sections 3.2 and 3.3 to prove Theorems 3 and 4, respectively.

3.1. A priori estimates

Lemma 3.1. *For any positive steady state u of* (1.1)–(1.2),

$$\min_{\overline{\Omega}} m \leqslant u(x)e^{(\alpha/\mu)[u(x)-m(x)]} \leqslant \max_{\overline{\Omega}} m \tag{3.1}$$

for every $x \in \overline{\Omega}$.

Proof. Set

$$w = ue^{-(\alpha/\mu)f(x,u)}. \tag{3.2}$$

Then w satisfies the zero Neumann boundary condition and

$$\mu\nabla\cdot\left[e^{(\alpha/\mu)f}\nabla w\right] + uf(x,u) = 0 \quad \text{in } \Omega. \tag{3.3}$$

Let $w(\bar{x}) = \max_{\overline{\Omega}} w$ for some $\bar{x} \in \overline{\Omega}$. Rewrite the equation of w as

$$\mu\Delta w + \alpha\nabla f\cdot\nabla w + wf(x,u) = 0 \quad \text{in } \Omega.$$

We claim that

$$m(\bar{x}) - u(\bar{x}) \geqslant 0. \tag{3.4}$$

To establish (3.4) we argue by contradiction: Suppose that (3.4) is false. The maximum principle yields a contradiction if $\bar{x} \in \Omega$, so we must have $\bar{x} \in \partial\Omega$. Then there exists an open ball, denoted by B, such that $B \subset \Omega$ and $\partial B \cap \partial\Omega = \{\bar{x}\}$ and $m(x) - u(x) < 0$ for every $x \in B$. This implies that $\mu\Delta w + \alpha\nabla f\cdot\nabla w > 0$ in B. Since $w(\bar{x}) = \max_{\overline{B}} w$, by the Hopf boundary lemma we have $\partial w/\partial n(\bar{x}) > 0$, which contradicts the boundary condition of w. This proves our assertion.

By (3.4) we have

$$\begin{aligned}\max_{\overline{\Omega}} w = w(\bar{x}) &= e^{-(\alpha/\mu)[m(\bar{x})-u(\bar{x})]}u(\bar{x})\\ &\leqslant u(\bar{x})\\ &\leqslant m(\bar{x}) \leqslant \max_{\overline{\Omega}} m,\end{aligned} \tag{3.5}$$

which establishes the upper bound in (3.1). Since the proof of the lower bound is similar, we shall only sketch it. Let w be defined as in (3.2). Let $w(\bar{y}) = \min_{\overline{\Omega}} w$. By the maximum principle, $m(\bar{y}) - u(\bar{y}) \leqslant 0$, which implies that $w(\bar{y}) \geqslant u(\bar{y}) \geqslant m(\bar{y}) \geqslant \min_{\overline{\Omega}} m$. □

Author's personal copy

Corollary 3.2. *For any positive steady state u of* (1.1) *and* (1.2),

$$\min_{\overline{\Omega}} m \leqslant u(x) \leqslant \max_{\overline{\Omega}} m \tag{3.6}$$

for every $x \in \overline{\Omega}$.

Proof. If $u(\tilde{x}) > \max_{\overline{\Omega}} m$ for some $\tilde{x}$, then $m(\tilde{x}) < u(\tilde{x})$. This along with (3.1) implies that

$$u(\tilde{x}) \leqslant u(\tilde{x}) e^{-(\alpha/\mu)[m(\tilde{x})-u(\tilde{x})]} \leqslant \max_{\overline{\Omega}} m,$$

which contradicts our assumption $u(\tilde{x}) > \max_{\overline{\Omega}} m$. Hence, $\max_{\overline{\Omega}} u \leqslant \max_{\overline{\Omega}} m$. The proof for $\min_{\overline{\Omega}} u \geqslant \min_{\overline{\Omega}} m$ is similar and is thus omitted. □

Lemma 3.3. *For any positive steady state u of* (1.1)–(1.2), $\|u\|_{H^1} \leqslant C$ *for some positive constant C which is independent of α and μ.*

Proof. Multiplying the equation of u by $f(x,u)$ and integrating in Ω, we have

$$\mu \int_\Omega |\nabla u|^2 + \alpha \int_\Omega u|\nabla f|^2 + \int_\Omega u f^2 = \mu \int_\Omega \nabla u \cdot \nabla m.$$

By the Cauchy–Schwartz inequality we see that

$$\frac{\mu}{2} \int_\Omega |\nabla u|^2 + \alpha \int_\Omega u|\nabla f|^2 + \int_\Omega u f^2 \leqslant \frac{\mu}{2} \int_\Omega |\nabla m|^2. \tag{3.7}$$

In particular,

$$\int_\Omega |\nabla u|^2 \leqslant \int_\Omega |\nabla m|^2.$$

Since u is also uniformly bounded, this proves our assertion. □

Lemma 3.4. *For any $\eta \in (0,1)$, there exist two constants $\gamma \in (0,1)$ and $C > 0$, dependent only upon η and Ω, such that if $\alpha \geqslant \eta$ and $\alpha/\mu \geqslant 1/\eta$, then for any positive steady state u of* (1.1)–(1.2), $\|u\|_{C^\gamma(\overline{\Omega})} \leqslant C$.

Proof. For any positive steady state u of (1.1)–(1.2), set

$$w_1 = \frac{u^2}{2} + \frac{\mu}{\alpha} u.$$

Then we can write $u = h_1(w_1)$, where

$$h_1(w_1) = -\frac{\mu}{\alpha} + \sqrt{\frac{\mu^2}{\alpha^2} + 2w_1}.$$

Hence, w_1 satisfies

Author's personal copy

$$\nabla\cdot\big[\nabla w_1 - h_1(w_1)\nabla m\big] + (1/\alpha)h_1(w_1)\big[m - h_1(w_1)\big] = 0 \quad \text{in } \Omega,$$
$$\big[\nabla w_1 - h_1(w_1)\nabla m\big]\cdot n = 0 \quad \text{on } \partial\Omega. \tag{3.8}$$

Note that w_1 is uniformly bounded above by Corollary 3.2 and bounded below by zero by the hypothesis of the positivity of u. If we define functions $f_i(x) = -h_1(w_1(x))m_{x_i}(x)$ and $g(x) = (1/\alpha)h_1(w_1(x))[m(x) - h_1(w_1(x))]$ we have that $\|f_i\|_\infty$ and g are both uniformly bounded for $\alpha \geqslant \eta$ and $\alpha/\mu \geqslant 1/\eta$. Then the interior *a priori* Hölder estimates for w_1 follow from standard De Giorgi–Nash theory for second order linear elliptic operators with divergence form, see Gilbarg and Trudinger [18, Theorem 8.24]. For Hölder estimates near the boundary and for the proof of such estimates with nonlinear boundary conditions, we refer to Ladyzhenskaya and Ural'tseva [27]. In particular, such estimates follow from the arguments outlined on pp. 466–467 of [27], Theorem 7.2 and the remarks thereafter (pp. 94–95), and the proofs of Theorem 6.1 in Section 6 of Chapter 2. Combining boundary and interior Hölder estimates we see that $\|w_1\|_{C^{\gamma_1}(\overline{\Omega})} \leqslant C_1$ for some positive constants $\gamma_1 \in (0,1)$ and C_1 depending only on η and Ω. By the relation $u = h_1(w_1)$, applying the inequality

$$\big|h_1\big(w_1(x)\big) - h_1\big(w_1(y)\big)\big| \leqslant \sqrt{2}\big|w_1(x) - w_1(y)\big|^{1/2}$$

for any $x, y \in \overline{\Omega}$, we see that $\|u\|_{C^{\gamma_1/2}(\overline{\Omega})} \leqslant C$ for some C depending only on η and Ω. Set $\gamma = \gamma_1/2$, this finishes the proof of Lemma 3.4. □

The following result is crucial and can be viewed as a non-degeneracy lemma.

Lemma 3.5. *For any positive steady state u of* (1.1)–(1.2),

$$\int_\Omega (m-u)_+ \leqslant \frac{\mu}{\alpha}|\Omega|. \tag{3.9}$$

Proof. Let w be defined as in (3.2). Dividing (3.3) by w and integrating in Ω, we find that

$$\int_\Omega e^{(\alpha/\mu)f} f = -\mu\int_\Omega \frac{e^{(\alpha/\mu)f}|\nabla w|^2}{w^2} \leqslant 0.$$

It is easy to check that $ye^{(\alpha/\mu)y} \geqslant (\alpha/\mu)y^2$ for $y \geqslant 0$, and $ye^{(\alpha/\mu)y} \geqslant -\mu/\alpha$ for every $y \in R^1$. Hence,

$$0 \geqslant \int_{\{f\geqslant 0\}} e^{(\alpha/\mu)f} f + \int_{\{f<0\}} e^{(\alpha/\mu)f} f \geqslant \frac{\alpha}{\mu}\int_{\{f\geqslant 0\}} f^2 - \frac{\mu}{\alpha}|\Omega|.$$

Therefore,

$$\int_{\{f\geqslant 0\}} f^2 \leqslant \frac{\mu^2}{\alpha^2}|\Omega|.$$

By Hölder's inequality, we have

$$\int_\Omega f_+ \leqslant \Big(\int_\Omega (f_+)^2\Big)^{1/2}|\Omega|^{1/2} = \Big(\int_{\{f\geqslant 0\}} f^2\Big)^{1/2}|\Omega|^{1/2} \leqslant \frac{\mu}{\alpha}|\Omega|. \qquad \square$$

Author's personal copy

3.2. Proof of Theorem 3

By Lemma 3.3 and the Sobolev embedding theorem we may assume that as $\alpha/\mu \to \infty$, $u \to u^*$ weakly in H^1 and strongly in L^2. By Corollary 3.2, we see that $u^* \in L^\infty(\Omega)$. Passing to the limit in (3.9), we have

$$\int_\Omega (m - u^*)_+ = 0.$$

Hence, $(m - u^*)_+ = 0$ a.e. in Ω, i.e., $u^*(x) \geqslant m(x)$ a.e. in Ω.

Integrating the equation of u in Ω, we find

$$\int_\Omega u(m - u) = 0.$$

Passing to the limit we have

$$\int_\Omega u^*(u^* - m) = 0.$$

Since $u^* \geqslant m_+$ a.e., we see that $u^* = m_+$ a.e. in Ω. This shows that as $\alpha/\mu \to \infty$, $u \to m_+$ weakly in H^1 and strongly in L^2.

Given any $\eta > 0$, if $\alpha \geqslant \eta$ and $\alpha/\mu \to \infty$, by Lemma 3.4 and the compact embedding properties of Hölder spaces, passing to a subsequence if necessary, $u \to \tilde{u}$ in $C^{\gamma_1}(\overline{\Omega})$ for any $\gamma_1 \in (0, \gamma)$. Since $u \to m_+$ in $L^2(\Omega)$, we see that $\tilde{u} = m_+$. Therefore, $u \to m_+$ in $C^{\gamma_1}(\overline{\Omega})$.

3.3. Proof of Theorem 4

Lemma 3.6. *Suppose that $m > 0$ in $\overline{\Omega}$. Then for any positive steady state u of (1.1)–(1.2), we have*

$$\frac{\mu}{\alpha} \ln \frac{\min_{\overline{\Omega}} m}{\max_{\overline{\Omega}} m} \leqslant u(x) - m(x) \leqslant \frac{\mu}{\alpha} \ln \frac{\max_{\overline{\Omega}} m}{\min_{\overline{\Omega}} m} \tag{3.10}$$

for every $x \in \overline{\Omega}$.

Proof. Note that (3.1) can be rewritten as

$$\ln \min_{\overline{\Omega}} m \leqslant \ln u + \frac{\alpha}{\mu}[u - m] \leqslant \ln \max_{\overline{\Omega}} m. \tag{3.11}$$

This together with Corollary 3.2 implies (3.10). □

Lemma 3.7. *Suppose that $m > 0$ in $\overline{\Omega}$. Then for any positive steady state u of (1.1)–(1.2), if $\alpha/\mu \to \infty$ and $\alpha \to \infty$, (1.9) holds, and if $\alpha/\mu \to \infty$ and $\alpha \to \tilde{\alpha}$, then (1.10) holds.*

Proof. Set

$$w = \ln u + \frac{\alpha}{\mu}(u - m).$$

Author's personal copy

Then w satisfies

$$\alpha\nabla\cdot[u\nabla w]+u(\ln u-w)=0 \quad \text{in } \Omega, \qquad \left.\frac{\partial w}{\partial n}\right|_{\partial\Omega}=0. \tag{3.12}$$

By Lemma 3.6, we see that $\|w\|_{L^\infty(\Omega)}$ is uniformly bounded. Multiplying (3.12) by w and integrating in Ω, we have

$$\alpha\int_\Omega u|\nabla w|^2=\int_\Omega uw(\ln u-w).$$

By Corollary 3.2 and Lemma 3.6, we see that $\|\nabla w\|_{L^2(\Omega)}$ is uniformly bounded. Hence, $\|w\|_{H^1}$ is uniformly bounded. Therefore, $w\to\tilde{w}$ weakly in $H^1(\Omega)$ and strongly in L^2. By Lemma 3.6, $u\to m$ uniformly as $\alpha/\mu\to\infty$. There are two cases for us to consider:

Case 1. $\alpha\to\infty$. For this case, $\tilde{w}$ is a weak solution of

$$\nabla\cdot(m\nabla\tilde{w})=0 \quad \text{in } \Omega, \qquad \frac{\partial\tilde{w}}{\partial n}=0 \quad \text{on } \partial\Omega.$$

This implies that $\tilde{w}\equiv C$ for some constant C. Since $\ln u\to\ln m$ uniformly, by the definition of w, we see that $(\alpha/\mu)(u-m)\to C-\ln m$ in L^2. Multiplying the equation of u by α/μ and integrating in Ω, we have

$$\int_\Omega u\cdot\frac{\alpha}{\mu}(u-m)=0. \tag{3.13}$$

Passing to the limit in (3.13) by letting $\alpha/\mu\to\infty$, we find that

$$C=\frac{\int_\Omega m\cdot\ln m}{\int_\Omega m}.$$

Case 2. $\alpha\to\tilde{\alpha}$. For this case, $w\to\tilde{w}$, where $\tilde{w}$ is the unique solution of (1.11).

By Corollary 3.2, Lemma 3.6 and De Giorgi–Nash estimates, there exists some constant $\beta\in(0,1)$ such that $\|w\|_{C^\beta(\overline{\Omega})}$ is uniformly bounded. This implies that $\|u\|_{C^\beta(\overline{\Omega})}$ is uniformly bounded for large α/μ. Therefore, by elliptic regularity and (3.12), w is uniformly bounded in $C^{1,\beta}(\overline{\Omega})$, which ensures that u is uniformly bounded in $C^{1,\beta}(\overline{\Omega})$. It follows from Schauder theory that w is uniformly bounded in $C^{2,\beta}(\overline{\Omega})$, which implies that u is uniformly bounded in $C^{2,\beta}(\overline{\Omega})$. This together with $\|u-m\|_{L^\infty(\Omega)}\to 0$ implies that $u\to m$ in $C^2(\overline{\Omega})$. □

Remark 3.8. For the case $\alpha/\mu\to\infty$ and $\alpha\to 0$, one can use a blow-up argument to show that $w\to\ln m$ uniformly, i.e., $(\alpha/\mu)(u-m)\to 0$ uniformly.

4. Uniqueness and stability of positive steady state

In this section we show that if $m>0$ in $\overline{\Omega}$, then for large α/μ, (1.1)–(1.2) has a unique positive steady state and it is globally asymptotically stable.

Author's personal copy

4.1. Uniqueness of positive steady states

Let u_1 and u_2 be two positive steady states of (1.1)–(1.2) and suppose that $u_1 \not\equiv u_2$. Without loss of generality we may assume that $u_1 \geqslant u_2$; otherwise, we can simply replace u_1 by the maximal solution u^* and u_2 by the minimal solution u_*, respectively. Integrating the equations of u_i $(i = 1, 2)$ we have

$$\int_\Omega u_1(m - u_1) = \int_\Omega u_2(m - u_2) = 0.$$

Subtracting the two integrals we find

$$\int_\Omega (u_1 - u_2)(m - u_1 - u_2) = 0. \tag{4.1}$$

Since $u_1 \to m$ and $u_2 \to m$ uniformly in $\overline{\Omega}$ as $\alpha/\mu \to \infty$ (Lemma 3.6), we see that $m - u_1 - u_2 \to -m$ uniformly in $\overline{\Omega}$. Since m is strictly positive in $\overline{\Omega}$, for large α/μ we have $m - u_1 - u_2 < 0$ in $\overline{\Omega}$. This along with $u_1 \geqslant u_2$ and $u_1 \not\equiv u_2$ contradicts (4.1).

4.2. Stability of the steady state

This subsection is devoted to the proof of linearized stability of the unique steady state. For the linearized stability, it suffices to consider the linear eigenvalue problem

$$\begin{aligned} &\nabla \cdot \big[\mu \nabla \phi - \alpha \phi \nabla(m - u) + \alpha u \nabla \phi\big] + (m - 2u)\phi = -\lambda \phi \quad \text{in } \Omega, \\ &\big[\mu \nabla \phi - \alpha \phi \nabla(m - u) + \alpha u \nabla \phi\big] \cdot n = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{4.2}$$

We first show that (4.2) has a principal eigenvalue and its corresponding eigenfunction can be chosen positive. To this end, let g be the unique solution of

$$\Delta g + 1 = 0 \quad \text{in } \Omega, \qquad \nabla g \cdot n + Kg = 0 \quad \text{on } \partial\Omega,$$

where $K > 0$ is to be determined later.

Let $\rho = g\phi$. Then ρ satisfies

$$\begin{aligned} &\nabla \cdot \big[(\mu + \alpha u)\nabla(\rho/g) - \alpha(\rho/g)\nabla(m - u)\big] + (m - 2u)(\rho/g) = -\lambda(\rho/g) \quad \text{in } \Omega, \\ &\frac{\partial \rho}{\partial n} + \left[K - \frac{\alpha}{\mu + \alpha u}\frac{\partial}{\partial n}(m - u)\right]\rho = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{4.3}$$

Choose K large so that

$$K - \frac{\alpha}{\mu + \alpha u}\frac{\partial}{\partial n}(m - u) \geqslant 0$$

on $\partial\Omega$. It follows that the operator in (4.3), with a term $-C\rho/g$ added if necessary, will satisfy the strong maximum principle. By the Krein–Rutman Theorem (see [9, Section 2.5]) we see that (4.3) has a principal eigenvalue, denoted by λ_1, which is also real; moreover, its corresponding eigenfunction can be chosen positive. Let ρ_1 denote the positive eigenfunction of λ_1 uniquely determined by $\max_{\overline{\Omega}} \rho_1 = 1$. Clearly, λ_1 is also the principal eigenvalue of (4.2) with corresponding eigenfunction $\phi_1 = \rho_1/g > 0$ in $\overline{\Omega}$.

Author's personal copy

Next we show that $\lambda_1 > 0$ if α/μ is sufficiently large. Integrating (4.2) with $\lambda = \lambda_1$ and $\phi = \phi_1$ in Ω, we have

$$\lambda_1 \int_\Omega \phi_1 = \int_\Omega (2u - m)\phi_1.$$

Since $u \to m$ uniformly as $\alpha/\mu \to \infty$ (Lemma 3.6), we see that $2u - m \to m$ uniformly in $\overline{\Omega}$. Hence, for large α/μ, $2u - m$ is positive in Ω. This together with the positivity of ϕ_1 implies that $\lambda_1 > 0$ for large α/μ.

The global asymptotic stability of the steady state now follows from the monotonicity of (1.1)–(1.2), uniqueness of the steady state solution, and supersolution and subsolution methods.

5. Discussion

The results in this paper show that in temporally constant but spatially heterogeneous environments reaction–advection–diffusion models incorporating a tendency of organisms to move up the gradient of fitness have stable equilibria that can approximate the spatial distribution predicted by the ideal free distribution. The approximation improves as the strength of the tendency to move up fitness gradients increases and/or the amount of random diffusion decreases. The dispersal mechanisms in the models require only local information about the environment; in particular, they do not require that organisms have complete global knowledge of the environment to achieve an approximation to the ideal free distribution. The immediate biological significance of approximately ideal free dispersal is that it leads to a population distribution where the population density approximately matches the availability of resources. This differs from both unconditional dispersal by random diffusion and conditional dispersal where organisms tend to move up gradients of resource density without reference to crowding effects. Both of those sorts of dispersal lead to population distributions where the density overmatches resource availability in some locations but undermatches it in others. This fact is the essential reason why there is selection for slow dispersal in models with purely diffusive dispersal, because for such models the only way for the equilibrium population density to approximately match the distribution of resources is for the diffusion rate to go to zero; see [21]. It is also the reason why too strong a tendency to move up resource gradients without regard to crowding effects can sometimes make a population subject to invasion by another population using a different strategy, as in [12,13].

We expect that because approximately ideal free dispersal allows a population to approximately track the distribution of resources it is often likely to be advantageous relative to other sorts of dispersal. Part of the motivation for the analysis in this paper is to derive results that can be used to address that conjecture in the same sort of framework used in [11–13,16,24]. Specifically, we plan to study models for two competitors that are ecologically identical in all respects except for their dispersal strategies and where one competitor uses an approximately ideal free strategy while the other uses some different strategy from the viewpoint of evolutionary stability. A strategy is considered evolutionarily stable if a population using it cannot be invaded by an otherwise similar population using a different strategy, so determining the evolutionary stability of one strategy relative to another requires that we determine the invasibility of a population using that strategy. This is the essential idea behind the modeling in [11–13,16,24]. In the context of spatially discrete models, strategies that have some features of ideal free dispersal have been shown to be evolutionarily stable; see [10,26]. To perform a similar analysis for approximately ideal free dispersal strategies in continuous space we will need the sort of detailed information about the equilibria of approximately ideal free models that we obtain in the present article. Thus, our results give a rigorous mathematical analysis of some of the sorts of mechanistic models for the ideal free distribution developed in [14] and lay a foundation for comparing those models with other sorts of dispersal models from the viewpoint of evolutionary stability.

Author's personal copy

Acknowledgments

The authors thank the anonymous referee for his/her constructive comments that improved the manuscript. We also thank Prof. Xuefeng Wang for helpful discussion on the reference [2].

Appendix A

We discuss the principal eigenvalue, denoted by λ_1, of the linear eigenvalue problem

$$\nabla\cdot[\mu\nabla\phi-\alpha\phi\nabla m]+m\phi=-\lambda\phi \quad \text{in } \Omega, \qquad \mu\frac{\partial\phi}{\partial n}-\alpha\phi\frac{\partial m}{\partial n}=0 \quad \text{on } \partial\Omega. \tag{A.1}$$

Recall that the sign of λ_1 determines the linearized stability of the equilibrium $u=0$ of (1.1), (1.2), with instability occurring if $\lambda_1<0$.

The change of variable

$$\psi=e^{-(\alpha/\mu)m}\phi$$

converts the linearized problem (A.1) into a variational form, i.e., ψ satisfies

$$\mu\nabla\cdot\left[e^{(\alpha/\mu)m}\nabla\psi\right]+me^{(\alpha/\mu)m}\psi=-\lambda e^{(\alpha/\mu)m}\psi \quad \text{in } \Omega, \qquad \frac{\partial\psi}{\partial n}=0 \quad \text{on } \partial\Omega. \tag{A.2}$$

Hence λ_1 can be characterized as

$$\lambda_1=\inf_{\{\psi\in W^{1,2}:\ \psi\not\equiv 0\}}\frac{\int_\Omega \mu e^{(\alpha/\mu)m}|\nabla\psi|^2-\int_\Omega e^{(\alpha/\mu)m}m\psi^2}{\int_\Omega e^{(\alpha/\mu)m}\psi^2}. \tag{A.3}$$

For the case $\int_\Omega me^{(\alpha/\mu)m}\geqslant 0$, it follows from (A.3) that:

Lemma A.1. *If $\int_\Omega me^{(\alpha/\mu)m}\geqslant 0$ and $m\not\equiv 0$, then $\lambda_1<0$.*

For the case $\int_\Omega me^{(\alpha/\mu)m}<0$, the condition for determining the sign of λ_1 is less explicit. It turns out that the sign of λ_1 is connected with the quantity

$$\lambda_*(\alpha/\mu,m):=\inf_{\psi\in S}\frac{\int_\Omega e^{(\alpha/\mu)m}|\nabla\psi|^2}{\int_\Omega e^{(\alpha/\mu)m}m\psi^2}>0,$$

where

$$S:=\left\{\psi\in W^{1,2}(\Omega):\ \int_\Omega e^{(\alpha/\mu)m}m\psi^2>0\right\}.$$

The quantity $\lambda_*(\alpha/\mu,m)$ can be interpreted as the positive principal eigenvalue for the problem

$$\nabla\cdot\left[e^{(\alpha/\mu)m}\nabla\rho\right]+\lambda me^{(\alpha/\mu)m}\rho=0 \quad \text{in } \Omega, \qquad \frac{\partial\rho}{\partial n}=0 \quad \text{on } \partial\Omega. \tag{A.4}$$

The fact that (A.4) has a positive principal eigenvalue provided that $\int_\Omega me^{(\alpha/\mu)m}<0$ follows from the arguments in [8]. The relation between λ_* and the sign of λ_1 in (A.1) and (A.2) can be stated precisely as

Author's personal copy

Lemma A.2. $\lambda_1 < 0$ *if and only if* $\lambda_* < 1/\mu$.

Lemma A.2 and related results are discussed in [22] and in Theorems 2.5 and 2.6 of [9]. Various aspects of eigenvalue problems of the type described in this appendix are treated in considerable generality in [5].

References

[1] H. Amann, Dynamic theory of quasilinear parabolic equations, II: Reaction–diffusion systems, Differential Integral Equations 3 (1990) 13–75.
[2] H. Amann, Dynamic theory of quasilinear parabolic systems, III: Global existence, Math. Z. 202 (1989) 219–250.
[3] P.R. Armsworth, J.E. Roughgarden, The impact of directed versus random movement on population dynamics and biodiversity patterns, Am. Nat. 165 (2005) 449–465.
[4] P.R. Armsworth, J.E. Roughgarden, Disturbance induces the contrasting evolution of reinforcement and dispersiveness in directed and random movers, Evolution 59 (2005) 2083–2096.
[5] F. Belgacem, Elliptic Boundary Value Problems with Indefinite Weights: Variational Formulations of the Principal Eigenvalue and Applications, Pitman Res. Notes Math. Ser., vol. 368, Longman Sci., 1997.
[6] F. Belgacem, C. Cosner, The effects of dispersal along environmental gradients on the dynamics of populations in heterogeneous environment, Can. Appl. Math. Q. 3 (1995) 379–397.
[7] J.S. Brew, Competition and niche dynamics from steady-state dispersal equations, Theor. Pop. Biol. 32 (1987) 240–261.
[8] K.J. Brown, S.S. Lin, On the existence of positive eigenfunctions for an eigenvalue problem with indefinite weight function, J. Math. Anal. Appl. 75 (1980) 112–120.
[9] R.S. Cantrell, C. Cosner, Spatial Ecology via Reaction–Diffusion Equations, Ser. Math. Comput. Biol., John Wiley and Sons, Chichester, UK, 2003.
[10] R.S. Cantrell, C. Cosner, D.L. DeAngelis, V. Padrón, The ideal free distribution as an evolutionarily stable strategy, J. Biol. Dyn. 1 (2007) 249–271.
[11] R.S. Cantrell, C. Cosner, Y. Lou, Movement towards better environments and the evolution of rapid diffusion, Math. Biosci. 204 (2006) 199–214.
[12] R.S. Cantrell, C. Cosner, Y. Lou, Advection mediated coexistence of competing species, Proc. Roy. Soc. Edinburgh Sect. A 137 (2007) 497–518.
[13] X.F. Chen, Y. Lou, Principal eigenvalue and eigenfunction of elliptic operator with large convection and its application to a competition model, Indiana Univ. Math. J. 57 (2008) 627–658.
[14] C. Cosner, A dynamic model for the ideal-free distribution as a partial differential equation, Theor. Pop. Biol. 67 (2005) 101–108.
[15] C. Cosner, Y. Lou, Does movement toward better environments always benefit a population?, J. Math. Anal. Appl. 277 (2003) 489–503.
[16] J. Dockery, V. Hutson, K. Mischaikow, M. Pernarowski, The evolution of slow dispersal rates: A reaction–diffusion model, J. Math. Biol. 37 (1998) 61–83.
[17] S.D. Fretwell, H.L. Lucas, On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development, Acta Biotheor. 19 (1970) 16–36.
[18] D. Gilbarg, N. Trudinger, Elliptic Partial Differential Equation of Second Order, second ed., Springer-Verlag, Berlin, 1983.
[19] P. Grindrod, Models of individual aggregation or clustering in single and multi-species communities, J. Math. Biol. 26 (1988) 651–660.
[20] W.S.C. Gurney, R.M. Nisbet, The regulation of inhomogeneous populations, J. Theor. Biol. 52 (1975) 441–458.
[21] A. Hastings, Can spatial variation alone lead to selection for dispersal?, Theor. Pop. Biol. 33 (1983) 311–314.
[22] P. Hess, Periodic-Parabolic Boundary Value Problems and Positivity, Pitman Res. Notes Math. Ser., vol. 247, Longman Sci., 1991.
[23] R.D. Holt, M.A. McPeek, Chaotic population dynamics favors the evolution of dispersal, Am. Nat. 148 (1996) 709–718.
[24] V. Hutson, K. Mischaikow, P. Poláčik, The evolution of dispersal rates in a heterogeneous time-periodic environment, J. Math. Biol. 43 (2001) 501–533.
[25] M. Kshatriya, C. Cosner, A continuum formulation of the ideal free distribution and its applications for population dynamics, Theor. Pop. Biol. 61 (2002) 277–284.
[26] S. Kirkland, C.-K. Li, S.J. Schreiber, On the evolution of dispersal in patchy environments, SIAM J. Appl. Math. 66 (2006) 1366–1382.
[27] O.A. Ladyzhenskaya, N.N. Ural'tseva, Linear and Quasilinear Elliptic Equations, Academic Press, New York, 1968.
[28] M.A. McPeek, R.D. Holt, The evolution of dispersal in spatially and temporally varying environments, Am. Nat. 140 (1992) 1010–1027.
[29] M.H. Protter, H.F. Weinberger, Maximum Principles in Differential Equations, second ed., Springer-Verlag, Berlin, 1984.
[30] N. Shigesada, Spatial distribution of dispersing animals, J. Math. Biol. 9 (1980) 85–96.