

APPROXIMATING THE IDEAL FREE DISTRIBUTION VIA REACTION-DIFFUSION-ADVECTION EQUATIONS

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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.

KEYWORDS: Ideal free distribution, reaction-diffusion-advection.

AMS CLASSIFICATION: 35K57, 92D25.

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 a description of how organisms would locate themselves if they could move freely to optimize their fitness [16]. 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 [13]. 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

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been studied in [2, 3, 18]. In [2, 3] two-patch models were used instead of reaction-advection-diffusion models. In [18] 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 McPeck and Holt [27] 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 [15, 20, 27]. 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 [10, 11, 27]. 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 [9, 25]. 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 [22, 27, 23]. 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 [2, 3].

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 [24]. 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

$$\int_{\Omega} u(x) dx = U$$

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

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 [24]. A dynamic model which supports equilibrium solutions corresponding to this formulation was introduced in [13]. That model has the form

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

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 [13] 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: [10, 11, 12, 15, 23]. 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 [11, 12].

The model we will consider has the form

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

with no-flux boundary conditions

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

where

$$(1.3) \quad f(x, u) = m(x) - u.$$

Throughout this paper we assume that $m \in C^{2,\tau}(\bar{\Omega})$ 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

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

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 [19, 29]. Models with ordinary diffusion but incorporating a tendency to move up the gradient of underlying environmental quality were considered in [5, 10, 11, 12, 14]. Some related models were considered in [6, 18] 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 [15, 23, 10, 11]. Using this modeling approach in the context of ideal free dispersal would lead to a system of the form of

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

with no-flux boundary conditions

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

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

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

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

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

with no-flux boundary conditions

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

Equations (1.6), (1.7) can be viewed as the model for the ideal free distribution in [13] with an additional term describing population dynamics, or as a limiting case of (1.1), (1.2) as $\mu \rightarrow 0$. 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 $\alpha \geq 0$. Then (1.1)-(1.2) has a unique solution $u \in C^{2,1}(\bar{\Omega} \times (0, \infty)) \cap C(\bar{\Omega} \times [0, \infty))$.*

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

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

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 the Appendix. 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. Moreover, there exist two 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), $u_* \leq u \leq u^*$ in $\bar{\Omega}$.*

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 $\alpha/\mu \rightarrow \infty$. 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), $u \rightarrow m_+$ weakly in H^1 and strongly in L^2 as $\alpha/\mu \rightarrow \infty$. For any given $\eta > 0$, if $\alpha \geq \eta$ and $\alpha/\mu \rightarrow \infty$, $u \rightarrow m_+$ in $C^\gamma(\bar{\Omega})$ for some $\gamma \in (0, 1)$.*

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

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

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

uniformly in $\bar{\Omega}$.

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

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

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

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

Theorems 3 and 4 are proved in section 3.

Once we have characterized the asymptotic behavior of equilibria of (1.1), (1.2) as $\alpha/\mu \rightarrow \infty$ 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 $\bar{\Omega}$, 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 Amann's results [1], 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 $u \geq 0$, set

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

By the inverse function theorem, we can express u as

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

Then w satisfies a homogeneous Neumann boundary condition and

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

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

$$(2.3) \quad \max_{\bar{\Omega} \times [0, T]} w \leq \max \left\{ \max_{\bar{\Omega}} w(\cdot, 0), \max_{\bar{\Omega}} m \right\}.$$

Proof. Suppose that $w(x^*, t^*) = \max_{\bar{\Omega} \times [0, T]} w$. If $t^* = 0$, the estimate (2.3) automatically holds. Hence, we may assume that $0 < t^* \leq T$. We claim that

$$(2.4) \quad h(x^*, w(x^*, t^*)) \leq m(x^*).$$

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

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

in B . By the Hopf boundary lemma [28], $\nabla w \cdot n > 0$ at (x^*, t^*) , which is a contradiction.

By (2.4), $u(x^*, t^*) = h(x^*, w(x^*, t^*)) \leq m(x^*)$. Hence,

$$w(x^*, t^*) = u(x^*, t^*) e^{(\alpha/\mu)[u(x^*)-m(x^*)]} \leq u(x^*, t^*) \leq m(x^*) \leq \max_{\bar{\Omega}} m.$$

This completes the proof of (2.3). \square

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

$$(2.5) \quad \max_{\bar{\Omega} \times [0, T]} u \leq \max \left\{ e^{(\alpha/\mu)[\max_{\bar{\Omega}} m - \min_{\bar{\Omega}} m]} \max_{\bar{\Omega}} u(\cdot, 0), \max_{\bar{\Omega}} m \right\}.$$

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

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

which implies that

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

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

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

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

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 $u_1(x, 0) \geq u_2(x, 0)$ in $\bar{\Omega}$, then $u_1(x, t) \geq u_2(x, t)$ in $\bar{\Omega} \times (0, \infty)$. If we further assume that $u_1 \not\equiv u_2$, then $u_1(x, t) > u_2(x, t)$ in $\bar{\Omega} \times (0, \infty)$.*

Proof. Set $w_i = u_i \cdot e^{-(\alpha/\mu)(m - u_i)}$, $i = 1, 2$, respectively. Then the functions w_i satisfy Neumann boundary conditions and (2.2). By the comparison principle [28] (which applies under the Neumann boundary condition) we see that $w_1(x, t) \geq w_2(x, t)$ in $\bar{\Omega} \times [0, \infty)$. Since h_w is positive, we have $u_1(x, t) \geq u_2(x, t)$ in $\bar{\Omega} \times [0, \infty)$. The rest of the proof is similar and is thus omitted. \square

Proof of Theorem 2. Since (1.1)-(1.2) is a monotone system, it suffices to construct suitable supersolutions and subsolutions. To this end, choose any positive constant C such that $h(x, C) \geq m(x)$ in $\bar{\Omega}$. Set $\bar{w} = C$. It is easy to see that

$$(2.6) \quad \bar{w}_t \geq (h_w(x, \bar{w}))^{-1} \left\{ e^{(\alpha/\mu)[m - h(x, \bar{w})]} [\mu \Delta \bar{w} + \alpha \nabla [m - h(x, \bar{w})] \cdot \nabla \bar{w}] + h[m - h(x, \bar{w})] \right\}.$$

This in turn implies that $\bar{u} := h(x, \bar{w})$ satisfies

$$(2.7) \quad \bar{u}_t \geq \nabla \cdot [\mu \nabla \bar{u} - \alpha \bar{u} \nabla f(x, \bar{u})] + \bar{u} f(x, \bar{u}) \quad \text{in } \Omega \times (0, \infty),$$

and

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

If we choose the constant C large enough so that $\bar{u} \geq u(x, 0)$, then \bar{u} is a supersolution of (1.1)-(1.2).

To construct a subsolution, we apply the assumption that $u = 0$ is linearly unstable, i.e., the principal eigenvalue (denoted by λ_1) of the eigenvalue value problem (1.8) is negative. We denote the corresponding positive eigenfunction by ϕ_1 , which is uniquely determined

by $\max_{\bar{\Omega}} \phi_1 = 1$. For any $\epsilon > 0$, set $\underline{w} = \epsilon e^{-(\alpha/\mu)m} \phi_1$. One may check that \underline{w} satisfies a Neumann boundary condition and

$$(2.9) \quad \underline{w}_t \leq (h_w(x, \underline{w}))^{-1} \left\{ e^{(\alpha/\mu)[m-h(x, \underline{w})]} [\mu \Delta \underline{w} + \alpha \nabla [m - h(x, \underline{w})] \cdot \nabla \underline{w}] + h[m - h(x, \underline{w})] \right\}$$

in $\Omega \times (0, \infty)$ for ϵ small enough. Set $\underline{u} = h(x, \underline{w})$. Then, \underline{u} satisfies

$$(2.10) \quad \underline{u}_t \leq \nabla \cdot [\mu \nabla \underline{u} - \alpha \underline{u} \nabla f(x, \underline{u})] + \underline{u} f(x, \underline{u}) \quad \text{in } \Omega \times (0, \infty),$$

and

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

Choosing ϵ smaller if necessary we may assume that $\underline{u} \leq u(x, 0)$. The rest of the proof follows from the standard supersolution and subsolution method for parabolic equations. \square

3. ASYMPTOTIC BEHAVIOR OF STEADY STATES

In subsection 3.1 we establish some *a priori* estimates for steady states of (1.1)-(1.2). These estimates are then applied in subsections 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),*

$$(3.1) \quad \min_{\bar{\Omega}} m \leq u(x) e^{(\alpha/\mu)[u(x)-m(x)]} \leq \max_{\bar{\Omega}} m$$

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

Proof. Set

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

Then w satisfies a Neumann boundary condition and

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

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

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

We claim that

$$(3.4) \quad m(x_\alpha) - u(x_\alpha) \geq 0.$$

To establish (3.4) we argue by contradiction: Suppose that (3.4) is false. The maximum principle yields a contradiction if $x_\alpha \in \Omega$, so we must have $x_\alpha \in \partial \Omega$. Then there exists an open ball, denoted by B , such that $B \subset \Omega$ and $\partial B \cap \partial \Omega = \{x_\alpha\}$ 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 $w(x_\alpha) = \max_{\bar{B}} w$, by the Hopf boundary lemma we have $\partial w / \partial n(x_\alpha) > 0$, which contradicts the boundary condition of w . This proves our assertion.

By (3.4) we have

$$\begin{aligned}
 \max_{\bar{\Omega}} w = w(x_\alpha) &= e^{-(\alpha/\mu)[m(x_\alpha)-u(x_\alpha)]} u(x_\alpha) \\
 (3.5) \qquad \qquad \qquad &\leq u(x_\alpha) \\
 &\leq m(x_\alpha) \leq \max_{\bar{\Omega}} m,
 \end{aligned}$$

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 $w(y_\alpha) = \min_{\bar{\Omega}} w$. By the maximum principle, $m(y_\alpha) - u(y_\alpha) \leq 0$, which implies that $w(y_\alpha) \geq u(y_\alpha) \geq m(y_\alpha) \geq \min_{\bar{\Omega}} m$. \square

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

$$(3.6) \qquad \qquad \qquad \min_{\bar{\Omega}} m \leq u(x) \leq \max_{\bar{\Omega}} m$$

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

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

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

which contradicts our assumption $u(\tilde{x}) > \max_{\bar{\Omega}} m$. Hence, $\max_{\bar{\Omega}} u \leq \max_{\bar{\Omega}} m$. The proof for $\min_{\bar{\Omega}} u \geq \min_{\bar{\Omega}} m$ is similar and is thus omitted. \square

Lemma 3.3. *For any positive steady state u of (1.1)-(1.2), $\|u\|_{H^1} \leq C$ 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

$$(3.7) \qquad \frac{\mu}{2} \int_{\Omega} |\nabla u|^2 + \alpha \int_{\Omega} u |\nabla f|^2 + \int_{\Omega} u f^2 \leq \frac{\mu}{2} \int_{\Omega} |\nabla m|^2.$$

In particular,

$$\int_{\Omega} |\nabla u|^2 \leq \int_{\Omega} |\nabla m|^2.$$

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

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 $\alpha \geq \eta$ and $\alpha/\mu \geq 1/\eta$, then for any positive steady state u of (1.1)-(1.2), $\|u\|_{C^\gamma(\Omega)} \leq C$.*

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

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

By Corollary 3.2, w_1 is uniformly bounded. 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 $\alpha \geq \eta$ and $\alpha/\mu \geq 1/\eta$. 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 [17], 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 [26]. In particular, such estimates follow from the arguments outlined on pages 466-467 of [26], 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 $\|w_1\|_{C^\gamma(\bar{\Omega})} \leq C$ for some positive constants $\gamma \in (0, 1)$ and C depending only on η and Ω . By the relation $u = h_1(x, w_1)$, this establishes the global Hölder estimate for u . \square

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),*

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

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

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

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

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

Therefore,

$$\int_{\{f \geq 0\}} f^2 \leq \frac{\mu^2}{\alpha^2}|\Omega|.$$

By Hölder's inequality, we have

$$\int_{\Omega} f_+ \leq \left(\int_{\Omega} (f_+)^2 \right)^{1/2} |\Omega|^{1/2} = \left(\int_{\{f \geq 0\}} f^2 \right)^{1/2} |\Omega|^{1/2} \leq \frac{\mu}{\alpha} |\Omega|.$$

□

3.2. Proof of Theorem 3. By Lemma 3.3 and the Sobolev embedding theorem we may assume that as $\alpha/\mu \rightarrow \infty$, $u \rightarrow u^*$ 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., $u^*(x) \geq m(x)$ 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 $u^* \geq m_+$ a.e., we see that $u^* = m_+$ a.e. in Ω . This shows that as $\alpha/\mu \rightarrow \infty$, $u \rightarrow m_+$ weakly in H^1 and strongly in L^2 .

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

□

3.3. Proof of Theorem 4.

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

$$(3.10) \quad \frac{\mu}{\alpha} \ln \frac{\min_{\bar{\Omega}} m}{\max_{\bar{\Omega}} m} \leq u(x) - m(x) \leq \frac{\mu}{\alpha} \ln \frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m}$$

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

Proof. Note that (3.1) can be rewritten as

$$(3.11) \quad \ln \min_{\bar{\Omega}} m \leq \ln u + \frac{\alpha}{\mu} [u - m] \leq \ln \max_{\bar{\Omega}} m.$$

This together with Corollary 3.2 implies (3.10). □

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

Proof. Set

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

Then w satisfies

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

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, $w \rightarrow \tilde{w}$ weakly in $H^1(\Omega)$ and strongly in L^2 . By Corollary 3.2 and Lemma 3.6, $u \rightarrow m$ uniformly as $\alpha/\mu \rightarrow \infty$. There are two cases for us to consider:

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

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

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

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

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

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

Case 2. $\alpha \rightarrow \tilde{\alpha}$. For this case, $w \rightarrow \tilde{w}$, 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 $\|w\|_{C^\beta(\bar{\Omega})}$ is uniformly bounded. This implies that $\|u\|_{C^\beta(\bar{\Omega})}$ is uniformly bounded for large α/μ . Therefore, by elliptic regularity and (3.12), w is uniformly bounded in $C^{1,\beta}(\bar{\Omega})$, which ensures that u is uniformly bounded in $C^{1,\beta}(\bar{\Omega})$. It follows from Schauder theory that w is uniformly bounded in $C^{2,\beta}(\bar{\Omega})$, which implies that u is uniformly bounded in $C^{2,\beta}(\bar{\Omega})$. This together with $\|u - m\|_{L^\infty(\Omega)} \rightarrow 0$ implies that $u \rightarrow m$ in $C^2(\bar{\Omega})$. \square

Remark 3.1. For the case $\alpha/\mu \rightarrow \infty$ and $\alpha \rightarrow 0$, one can use a blow-up argument to show that $w \rightarrow \ln m$ uniformly, i.e., $(\alpha/\mu)(u - m) \rightarrow 0$ uniformly.

4. UNIQUENESS AND STABILITY OF POSITIVE STEADY STATE

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

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 $u_1 \geq u_2$; 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

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

Since $u_1 \rightarrow m$ and $u_2 \rightarrow m$ uniformly in $\bar{\Omega}$ as $\alpha/\mu \rightarrow \infty$ (Theorem 4), we see that $m - u_1 - u_2 \rightarrow -m$ uniformly in $\bar{\Omega}$. Since m is strictly positive in $\bar{\Omega}$, for large α/μ we have $m - u_1 - u_2 < 0$ in $\bar{\Omega}$. This along with $u_1 \geq u_2$ and $u_1 \not\equiv u_2$ contradicts (4.1). \square

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

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

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

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

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

Let $\rho = g\phi$. Then ρ satisfies

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

Choose K large so that

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

on $\partial\Omega$. It follows that the operator in (4.3), with a term $-C\rho/g$ added if necessary, will satisfy a maximum principle. By the Krein-Rutman Theorem (See [8], 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 $\max_{\bar{\Omega}} \rho_1 = 1$. Clearly, λ_1 is also the principal eigenvalue of (4.2) with corresponding eigenfunction $\phi_1 = \rho_1 g > 0$ in $\bar{\Omega}$.

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 $u \rightarrow m$ uniformly as $\alpha/\mu \rightarrow \infty$ (Theorem 4), we see that $2u - m \rightarrow m$ uniformly in $\bar{\Omega}$. 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 . \square

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 [20]. 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 [11, 12].

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 [10, 11, 12, 15, 23]. 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 [10, 11, 12, 15, 23]. In the context of spatially discrete models, strategies that have some features of ideal free dispersal have been shown to be evolutionarily stable; see [9, 25]. 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 [13] and lay a foundation for comparing those models with other sorts of dispersal models from the viewpoint of evolutionary stability.

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6. APPENDIX

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

$$(6.1) \quad \nabla \cdot [\mu \nabla \phi - \alpha \phi \nabla m] + m\phi = -\lambda\phi \quad \text{in } \Omega, \quad \mu \frac{\partial \phi}{\partial n} - \alpha \phi \frac{\partial m}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

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 (6.1) into variational form, i.e., ψ satisfies

$$(6.2) \quad \mu \nabla \cdot [e^{(\alpha/\mu)m} \psi] + m e^{(\alpha/\mu)m} \psi = -\lambda e^{(\alpha/\mu)m} \psi \quad \text{in } \Omega, \quad \frac{\partial \psi}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

Hence λ_1 can be characterized as

$$(6.3) \quad \lambda_1 = \inf_{\{\psi \in W^{1,2}; \psi \neq 0\}} \frac{\int_{\Omega} \mu e^{(\alpha/\mu)m} |\nabla \psi|^2 - \int_{\Omega} e^{(\alpha/\mu)m} m \psi^2}{\int_{\Omega} e^{(\alpha/\mu)m} \psi^2}.$$

For the case $\int_{\Omega} m e^{(\alpha/\mu)m} \geq 0$, it follows from (6.3) that

Lemma 6.1. *If $\int_{\Omega} m e^{(\alpha/\mu)m} \geq 0$ and $m \not\equiv 0$, then $\lambda_1 < 0$.*

For the case $\int_{\Omega} m e^{(\alpha/\mu)m} < 0$, 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

$$(6.4) \quad \nabla \cdot [e^{(\alpha/\mu)m} \rho] + \lambda m e^{(\alpha/\mu)m} \rho = 0 \quad \text{in } \Omega, \quad \frac{\partial \rho}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

The fact that (6.4) has a positive principal eigenvalue provided that $\int_{\Omega} m e^{(\alpha/\mu)m} < 0$ follows from the arguments in [7]. The relation between λ_* and the sign of λ_1 in (6.1) and (6.2) can be stated precisely as

Lemma 6.2. *$\lambda_1 > 0$ if and only if $\lambda_* < 1/\mu$.*

Lemma 6.2 and related results are discussed in [21] and in Theorems 2.5 and 2.6 of [8]. Various aspects of eigenvalue problems of the type described in this Appendix are treated in considerable generality in [4].

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