The Effect of Directed Movement on the Strong Allee Effect

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Abstract

It is well known that movement strategies in ecology and in economics can make the difference between extinction and persistence. We present a unifying model for the dynamics of ecological populations and street vendors, which are an important part of many informal economies. We analyze this model to study the effects of directed movement of populations subject to strong Allee effect. We begin with the study of the existence of equilibrium solutions subject to homogeneous Dirichlet or no-flux boundary conditions. Next, we study the evolution problem and show that if the directed movement effect is small, the solutions behave like those of the classical reaction-diffusion equation with bistable growth pattern. We present numerical simulations, which show that directed movement can help overcome a strong Allee effect and provide some partial analytical results in this directions. We conclude by making a connection to the ideal free distribution and analyze what happens under competition, finding that an ideal free distribution strategy is a *local neighborhood invader*.

1 Introduction

This article is devoted to the study of movement of groups subject to a strong Allee effect [41]. In particular, we study the equation:

$$\begin{cases} u_t = \mu \nabla \cdot (\nabla u - \chi u \nabla A) + g(x,u)u, \ x \in D, \ t > 0, \\ \mathcal{B}[u] = 0, \ x \in \partial D, t > 0, \\ u(x,0) = u_0(x), \ x \in D, \end{cases} \tag{1}$$

with g a bistable-type growth function, *e.g.* $g(u) = (1-u)(u-\theta)$ with $0 < \theta < 1$, $\mathcal{B}[u] = 0$ are the boundary conditions (homogeneous Dirichlet or no-flux). In equation (1), the *signal* A provides a biased movement of a population $u : D \times [0,\infty) \to [0,\infty)$ for some bounded domain $D \subset \mathbb{R}^n$. In the language of McPeek and Holt [33], we consider *conditional dispersal*, for which a population incorporates environmental information in their dispersal strategy. It has been shown that conditional dispersal can be beneficial for the persistence of species in some cases [5].

Classically, equation (1) models the combination of biased and unbiased dispersal of a population subject to an Allee effect. However, in the section 1.1 we argue that this model is also relevant in economics, *e.g.* for the dynamics of street vendors. Equation (1) with $\chi = 0$ has been well-studied and it is understood that the Allee threshold, θ, plays a critical role in the long-term dynamics of solutions; see for example [4, 25, 37, 46] and references with in. For example, for initial data below θ (under no-flux boundary conditions) the population becomes extinct. On the other hand, if the initial population is above θ then the population persists, modeling precisely the strong Allee effect. For the homogeneous Dirichlet problem with $\chi = 0$, under a mass condition of $g(x,u)u$, it is known that there exists two positive equilibrium solutions for μ small. On the other hand, the Neumann problem with $\chi = 0$ and $g(u) = (1-u)(u-\theta)$, always has two positive equilibrium solutions $u \equiv 1$ and $u \equiv \theta$. Note that χ measures the strength of the biased dispersal. In this work, our interests lies in the case when $\chi > 0$, so the population moves up gradients of the signal A.

We first address the existence and non-existence of equilibrium solutions to (1) subject to homogeneous Dirichlet and no-flux boundary conditions using a variational approach. For the Dirichlet problem we show that there are two positive steady-state solutions, provided the diffusivity coefficient μ is sufficiently small (under the same suitable mass condition of $f(x,u) = g(x,u)u$ required for the case $\chi = 0$; see (6) below). We obtain the existence of at least one equilibrium solution for the no-flux problem independent of μ and at least two equilibrium solutions for μ sufficiently small. For the evolution problem, under mild assumptions on m and θ, we show that the solution to (1), with no-flux boundary conditions and initial data u_0 satisfying $0 < u_0 < e^{\chi A}\min_{x\in\overline{D}}\left(\theta e^{-\chi A}\right)$, converges to zero for all $x \in D$ as $t \to \infty$. On the other hand, a solution to the same problem with initial data satisfying $e^{\chi A}\max_{x\in\overline{D}}\left(\theta e^{-\chi A}\right) < u_0 < e^{\chi A}\min_{x\in\overline{D}}\left(me^{-\chi A}\right)$ will converge to a positive equilibrium solution in the long term. One can then obtain the dynamic behavior dichotomy of the classical reaction-diffusion equation (without directed movement) that was discussed earlier by taking the limit as $\chi \to 0$. On a more interesting note, numerical results presented here indicate that for certain signals A the Allee effect can be overcome, meaning that solutions with initial data below θ can persist if χ is sufficiently large. We present some partial analytical results in this direction.

Finally, we make a connection to the notion of an ideal free distribution. We show that a small population using a movement strategy that leads to an ideal free distribution can invade any resident population whose equilibrium density is larger than the Allee threshold θ, but which uses a movement strategy that does not lead to an ideal free distribution. In the terminology of adaptive dynamics, this shows that strategies that can produce an ideal free distribution are local neighborhood invaders relative to those that cannot produce an ideal free distribution. Thus, being able to produce an ideal free distribution is a necessary condition for evolutionary stability for movement strategies that can produce a large equilibrium density.

If we consider competition between two species that use the same resource or two businesses that seek the same customers, and the competitors are similar in everything, except their dispersal or relocation strategies, we are led to consider models of the form:

$$\begin{cases} u_t = \mathcal{M}_u u + g(x, u+v)u, \\ v_t = \mathcal{M}_v v + g(x, u+v)v, \end{cases}$$

where $\mathcal{M}_u$ and $\mathcal{M}_v$ are dispersal operators of the form shown in equation (1). This system must be equipped with specific boundary and conditions, but for the purpose of this discussion it is not necessary to be specific. Because g is increasing for u small and decreasing for u large, this system is cooperative at low densities and competitive at high densities. Thus, the presence of "competitors" is actually beneficial at low densities, as has been observed in some natural systems; see [29]. A key takeaway from our analysis is that competition can be helpful in overcoming an Allee effect, but once that effect is overcome the dispersal or relocation strategy is key in determining which population or business will dominate.

To place this work in context, recall that classical spatially explicit population models typically used simple diffusion to describe dispersal; see [3]. More recently there has been considerable interest in models that include some sort of biased movement. Two different phenomena that naturally give rise to biased movements have motivated that interest. One is movement by physical advection, specifically in rivers, which typically is unidirectional, constant, affects all populations in a similar way, and often does not involve behavior. The second is taxis on environmental gradients in heterogeneous environments, for example directed movement toward regions with more resources, fewer predators, or other favorable features. That sort of biased movement may be in any direction and may differ qualitatively between populations because it depends on behavioral considerations and the perceptual and cognitive abilities that enable people or organisms to sense and respond to their environment. An early paper on population dynamics in the presence of physical advection is [40]; some representative results on that topic are given in [18, 30, 31, 32]. More references and discussion on models with physical advection can be found in [44]. Early papers on taxis on environmental gradients include [2, 9] and further discussion and references for that class of models are given in [8]. A related class of models involves movement biased on the density of the population itself or another population with which it interacts; see for example [16, 38, 14, 10]. A discussion of models with physical advection versus models for directed movement and additional references is given in [28].

In this work we are specifically interested in the effects of taxis on environmental gradients combined with strong Allee effects. The most popular form of population dynamics in reaction-advection-diffusion models is logistic growth, but there has been interest in models with Allee effects for some time; see [4, 23], and the references in [44]. The discussion in [44] provides a good background on strong Allee effects and reaction-diffusion-advection models for populations that have them, especially in the context of physical advection. The technical aspects of showing the well-posedness of the models treated in this work are similar to those introduced in [26] and extended in [44]. Our results on well-posedness and the general structure of the set of equilibria overlap with those, but allow more general types of advective movement and extend to higher space dimensions. We obtain results on the short term dynamics of the models as well as their asymptotic behavior. We also consider the question of optimal movement from a viewpoint motivated by adaptive dynamics, where we consider patterns of movement as strategies. In various types of models with logistic dynamics, the strategies that are optimal from that viewpoint are known to be those that produce an ideal free distribution, which corresponds to moving in such a way as to exactly match the spatial distribution of resources; see [8] for details. There also has been work on optimal choices of constant diffusion and advection rates for populations with logistic dynamics in river environments; see [21, 28, 45], but that context is quite different from the ones we consider here. There have been a few studies on the ideal free distribution in models with a weak Allee effects; see [22, 36]. We find that a population using a strategy that produces an ideal free distribution for a single species can invade an established population that uses a strategy that does not produce an ideal free distribution.

Outline: We present a motivation for the study of (1) in section 1.1 and discuss some preliminary results in 1.2. Our first main results are presented in section 2 where we discuss the existence and non-existence of equilibrium solutions to (1) subject to homogeneous Dirichlet and no-flux boundary conditions. We address the evolution problem in section 3 and make a connection to the ideal free distribution in section 4. Finally, we conclude with a discussion in section 5.

1.1 Motivation

The manner in which organisms move and arrange themselves is key to their survival and has been a rich area of research in ecology. Analogously, the approach that a company takes to strategically place its stores, factories, or distribution centers can also make or break the company. The study of these placement strategies is also abundant in the economics literature; see for example [34]. The critical role of movement and placement strategies have been brought to light in many contexts, but for the purpose of this work we focus on two: the ideal free distribution (IFD) [15] and the Allee effect [41]. These concepts originated in ecology, but we make the case that they are also suitable in economics. In ecology, IFD is the way in which animals distribute in an environment according to a particular theory proposed by Fretwell and Lucas [15]: if a population has ideal knowledge of their environment and is free to move as desired, then the population distribution should match the resources. Much work has gone into testing the hypothesis of an IFD in ecology and sociology; see for example [35, 42, 43]. Moreover, an extensive mathematical theory of IFD has been developed in the case when species are subject to logistic growth – see for example [6, 7, 10].

Less is known about the effect of different types of movement strategies in the context of the Allee effect, which was first observed by Warder Clyde Allee when he noticed that goldfish grew to be bigger when they were in larger groups [1]. This effect characterizes the correlation between an individuals fitness and the population size. A strong Allee effect presents itself in the decay of a species below a critical threshold. There are a variety of reasons for this, for example some organisms have a social structure that allows for them to communicate about predators at high densities, but this communication network breaks down at lower densities [13]. It is then believed that organisms tend to aggregate in order to overcome this effect [41]. We see that in this context the way organisms move can be a matter of persistence versus extinction.

Interestingly, the phenomena characterized by the IFD and the Allee effect are also wide spread in economics as well. For example, clusters, or geographic concentrations of interconnected companies, are a marked feature of virtually every economy [34]. Particularly, it has been observed that industrial clusters in China provide benefits, such as lowering capital entrance barriers [39]. There are also benefits to competing department store clustering, *e.g.* in malls [19]. In fact, many competing stores, dealerships, or factories actually benefit from clustering [27, 34, 39]. In this context, the question of where to place the next store and how soon to do it is very relevant. Ideal free distributions have also been observed in social systems, for example children selling water in Istanbul have been observed to place themselves in locations in numbers which are proportional to the number of cars passing by that location [12]. Pastoralists in Africa also have been observed to follow an ideal free distribution [35]. It is important to remark that while the relocation of most retail stores is not modeled by the system considered here, the relocation mechanism in (1) can be relevant for food trucks and other street food vendors, which are a huge part of the (many times informal) economy in Latin America and Asia [11, 17].

1.2 Notation and Preliminaries

We now discuss some notation, assumptions and preliminary results needed for the remainder of the paper. First, let us define an *admissible signal*, A, to be a spatially heterogeneous function with properties:

(A1) $A \in C^2(\overline{D})$;

(A2) $\|\Delta A\|_{L^\infty(D)} \leq M, \quad \text{for} \quad M > 0$;

(A3) $\nabla A \cdot \vec{n} = 0$ on ∂D.

Condition (A3) is not necessary for most of the results presented here, in what follows we will point out when it is needed. Note also that signals that are time dependent are beyond the scope of this paper. Let us denote *admissible growth patterns* by $f(x,u) := g(x,u)u$ with g satisfying:

$$\begin{aligned} g(x,\theta(x)) = g(x,m(x)) \; = 0, \; g(x,z) < 0 \text{ for } z \in (-\infty, \theta(x)) \cup (m(x), \infty), \\ g(x,z) > 0 \text{ for } z \in (\theta(x), m(x)), \quad \text{for all } x \in \mathbb{R}. \end{aligned} \tag{2}$$

such that

(G1) $g \in C^2(\overline{D} \times [0,\infty))$;

(G2) $m(x) > \theta(x)$ for all $x \in D$.

As an example, keep in mind the classical growth pattern modeling the Allee effect:

$$g(x,z) = (m(x) - z)(z - \theta(x)), \tag{3}$$

where m represents the resources and θ the Allee effect threshold. The anti-derivative of f is denoted by F:

$$F = \int_0^z f(x,s)\, ds, \tag{4}$$

We assume that there exist functions, a and b such that for all $x \in \overline{D}$ then $\theta(x) < a(x) < m(x) < b(x)$ such that $F(x,u) > 0$ for $a(x) < u < b(x)$. Figure 1 illustrates f and its antiderivative F at a fixed point $x_0 \in D$. Moreover, there exists a positive constant v_0 such that:

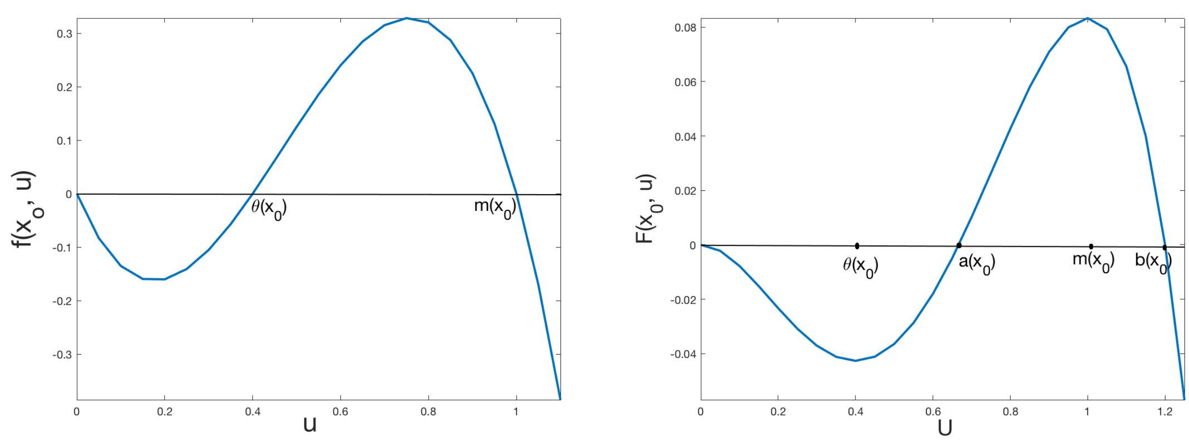
$$e^{-\chi A} a(x) < v_0 < e^{-\chi A} b(x), \quad \text{for all } x \in D. \tag{5}$$

Note that the existence of a, b is guaranteed under the following condition on f:

$$\int_0^{m(x)} f(x,u)\, dx > \delta > 0, \quad \text{for all } x \in D. \tag{6}$$

For future use, we denote the minimum and maximum of A by A_{min} and A_{max}, respectively, and

$$\overline{A} := \max_{x \in D} F(x, m(x)). \tag{7}$$



(a) Growth pattern f for fixed x_0.

(b) Anti-derivative of growth pattern F for fixed x_0.

Figure 1: Example reaction-function and anti-derivative for fixed $x_0 \in D$.

For the remaining of this section we consider no-flux boundary conditions. Our focus is then on the system:

$$\begin{cases} u_t = \mu \nabla \cdot (\nabla u - \chi u \nabla A) + g(x,u)u, \ x \in D, \ t > 0, \\ (\nabla u - \chi u \nabla A) \cdot \vec{n} = 0, \ x \in \partial D, t > 0, \\ u(x,0) = u_0(x), \ x \in D, \end{cases} \tag{8}$$

1.2.1 Maximum Principles and Uniform Bounds

The change of variables $v = e^{-\chi A} u$ is useful in understanding maximum and comparison principles for system (8). Under the proposed change of variables we have the new system for v:

$$\begin{cases} v_t = \mu(\Delta v + \chi \nabla A \cdot \nabla v) + g(x, e^{\chi A} v)v, \ x \in D, \ t > 0, \\ \nabla v \cdot \vec{n} = 0, \quad x \in \partial D, \ t > 0, \\ v(x,0) = e^{-\chi A} u_0(x), \ x \in D. \end{cases} \tag{9}$$

Since system (9) has a comparison principle for all admissible signals A, see for example [6], then the original problem (8) does as well. This means that we can use the method of super and subsolutions, whose definitions are provided below for the reader's convenience.

Definition 1 (Supersolutions and Subsolutions)**.** A function $w \in C^{2,1}(\overline{D} \times (0,\infty))$ is a **supersolution** to system (9) if it satisfies:

$$\begin{cases} w_t \geq \mu(\Delta w + \chi \nabla A \cdot \nabla w) + g(x, e^{\chi A} w)w, \ \text{for } x \in D, \ t > 0, \\ \nabla w \cdot \vec{n} \geq 0, \ \text{for } x \in \partial D, \ t > 0. \end{cases} \tag{10}$$

A function $w \in C^{2,1}(\overline{D} \times (0,\infty))$ is a **subsolution** to system (9) if it satisfies (10) with the signs reversed.

Remark 1. Note that condition (A3) is not needed for the maximum principle to hold; rather, it guarantees that the boundary conditions found in Definition 1 are satisfied by constant functions.

From the maximum principle we obtain a uniform bound on the equilibrium solutions of equation (8), which we state in the following lemma.

Lemma 1 (Uniform Bound on Equilibrium Solutions)**.** *Let A, f be admissible. Then any non-negative equilibrium solution, u^*, to* (8) *has the upper-bound:*

$$u^*(x) \leq \max_{x \in D} \left\{ e^{\chi A(x)} \right\} \max_{x \in D} \left\{ e^{-\chi A(x)} m(x) \right\} := M_1, \quad \textit{for all } x \in D. \tag{11}$$

Proof. After performing the change of variable $v = e^{-\chi A} u$ we work with equation (9). Note that any positive constant v_0 will be a strict subsolution to (9) if $g(x, e^{\chi A} v) > 0$ and a strict supersolution if $g(x, e^{\chi A} v) < 0$. Choose $v_0 > \max_{x \in D} \left\{ e^{-\chi A(x)} m(x) \right\}$ so that $e^{\chi A(x)} v_0 > m(x)$ for all $x \in D$. Hence, $g(x, e^{\chi A} v_0) < 0$ implying that v_0 is a supersolution. From this, we conclude that any equilibrium solution $v^*(x)$ to (9) must be bounded by $\max_{x \in D} \left\{ e^{-\chi A(x)} m(x) \right\}$. Indeed, if not the case, then it must hold that:

$$\max_{x \in D} v^*(x) > \max_{x \in D} \left\{ e^{-\chi A(x)} m(x) \right\}.$$

Let $\max_{x \in D} v^*(x) = v_0$ and consider the solution $v(x,t)$ with initial data v_0, since v_0 is not an equilibrium then $v(x,t)$ will decrease in time. Then, for some $t > 0$ we have that $\max_{x \in D} v^*(x) \leq v(x,t) < v_0 = \max_{x \in D} v^*(x)$, giving a contradiction. Correspondingly, $u^*(x) := e^{\chi A} v^*(x)$ must satisfy the bound given in (11). $\square$

Note that Lemma 1 holds for more general A that do not satisfy (A3). Given that equilibrium solutions are bounded by M_1, from now on we work with a modified growth-pattern:

$$\tilde{f}(x,u) = \begin{cases} f(x,u), & |u| \le M_1, \\ f_1 u, & |u| > M_2, \end{cases} \tag{12}$$

where $M_1 < M_2$, f_1 is a constant, and $\tilde{f}$ is defined for $M_1 < u < M_2$ so that it interpolates between $f(x,u)$ and $f_1 u$ such that it is twice differentiable in u. Dropping the tilde notation above, from (12) we see that there exists a constant $f_2 > 0$ such that:

$$|f(x,u)| \le f_2 |u|, \quad \text{for all} \quad x \in D, u \ge 0. \tag{13}$$

The uniform bound on f_u gives Lipschitz continuity:

$$|f(x,u) - f(x,v)| \le f_3 |u - v|, \quad \text{for all } x \in D \text{ and } u, v \ge 0, \tag{14}$$

for some constant $f_3 > 0$.

1.2.2 Global Existence of Solutions

As equation (9) is uniformly elliptic, classical theory provides a local-in-time $C^{2,1}(D \times (0,T))$ solution for non-negative initial data $v_0 \in L^\infty(D)$ for some $T > 0$ [20, 24]. To extend the solution globally-in-time we need the following L^∞-bound.

Lemma 2 (L^∞-bound of v)**.** *Let A, f be admissible and v be the classical solution to (9) on $D \times (0,T)$, for any $T > 0$, with non-negative initial data $v_0 \in L^\infty(D)$. Then, v is non-negative and globally bounded. Moreover, there exists a sufficiently large $T^* > 0$ such that v satisfies the bound:*

$$\|v(\cdot,t)\|_\infty \le \max_{x \in \overline{D}} \left(e^{-\chi A(x)} m(x) \right), \quad \textit{for all } x \in D, t \in (T^*, \infty).$$

Proof. First, note that $k = \max_{x\in\overline{D}} \left(e^{-\chi A} m\right) + \epsilon$, for any $\epsilon > 0$, is a supersolution to (9). This is seen from the fact that $g(x, e^{\chi A} k) < 0$ for any constant k that satisfies $e^{\chi A} k > m$ in $\overline{D}$. Moreover, zero is a subsolution. These are also respective super and subsolutions to the corresponding equilibrium solution to (9). In fact, for initial data $v(x,0)$ it holds that any

$$k > \max \left\{ \max_{x\in\overline{D}} \left(e^{-\chi A} m\right), \max_{x\in\overline{D}} v(x,0) \right\}$$

will be a supersolution. Thus, the solution v to (9) with initial data $v_0(x) = v(x,0)$ is globally bounded. Furthermore, from the proof of Lemma 1 any equilibrium solution, v^*, must satisfy the bound $v^* \le \max_{x\in\overline{D}} \left(e^{-\chi A} m\right)$. Now, consider the solution to (9), denoted by v_1, with initial data satisfying $v_1(x,0) = k > \max_{x\in\overline{D}} \left(e^{-\chi A} m\right)$. Then, v_1 will decrease pointwise to the maximal equilibrium solution of (9) as $t \to \infty$. Since v_1 is uniformly bounded, pointwise convergence implies L^p convergence. In turn, this implies convergence, for example, in fractional power-spaces that can be defined from the analytic semi-group for the operator $\Delta + \chi \nabla A \cdot \nabla$ and which embeds compactly in $C(\overline{D})$. Thus, we conclude that the convergence of v_1 to the maximal equilibrium solution is uniform. It follows that the solution v must eventually be bounded by $\max_{x\in\overline{D}} \left(e^{-\chi A} m\right) + \epsilon$, for any $\epsilon > 0$.

□

Equation (9) is uniformly parabolic, with smooth and bounded coefficients then by classical theory we can extend the solution to a global-in-time solution – see for example [20, 24]. Since equations (8) and (9) are connected through a change of variables we also get a global-in-time solution $u = e^{\chi A} v$ to equation (8).

1.2.3 Variational Formulation

Note that equation (9) has a variational formulation that will be useful in the following section. The energy functional is the following:

$$\mathcal{F}[v] := \int_D \frac{\mu}{2} e^{\chi A} |\nabla v|^2 - e^{-\chi A} F(x, e^{\chi A} v)\, dx, \tag{15}$$

where F is defined in (4) and $f(x,s) = g(x,s)s$. Indeed, for classical solutions $v(x,t)$ of (9) we have the following:

$$\begin{aligned}
\partial_t \mathcal{F} &= \int_D \mu e^{\chi A} \nabla v \cdot \nabla v_t - f(x, e^{\chi A} v) v_t\, dx \\
&= -\int_D [\mu \nabla \cdot (e^{\chi A} \nabla v) + f(x, e^{\chi A} v)] v_t\, dx \\
&= -\int_D e^{\chi A} [v_t]^2\, dx \leq 0.
\end{aligned}$$

Note with this variational formulation and the global bounds provided by Lemma 2 one can prove that solutions to (8) with non-negative and bounded initial data must converge to an equilibrium solution.

2 Existence of Equilibrium Solutions

We take advantage of the variational formulation (15) of equation (9) to study the existence of equilibrium solutions with both the homogenous Dirichlet and no-flux boundary conditions. In the former case we prove existence of at least two positive equilibrium solutions for μ sufficiently small. The results obtained here are generalizations of those obtained in [25], where they consider the case $\chi = 0$, and overlap with some results from [44]. First, we consider the Dirichlet problem:

$$\begin{cases} u_t = \mu \nabla \cdot (\nabla u - \chi u \nabla A) + g(x,u)u, \ x \in D, \ t > 0, \\ u = 0, \quad x \in \partial D, \ t > 0, \\ u(x,0) = u_0(x), \ x \in D. \end{cases} \tag{16}$$

Theorem 1 (Existence of Positive Equilibriums for the Dirichlet Problem)**.** *Let A, f be admissible. For $\mu > 0$ sufficiently small there exists two positive steady state solutions to* (16)*.*

The proof of Theorem 1 relies on the change of variables $v = e^{-\chi A} u$; thus, v solves:

$$\begin{cases} v_t = \mu(\Delta v + \chi \nabla A \cdot \nabla v) + g(x, e^{\chi A} v)v, \ x \in D, \ t > 0 \\ v = 0, \quad x \in \partial D, \ t > 0, \\ v(x,0) = e^{-\chi A} u_0(x), \ x \in D. \end{cases} \tag{17}$$

We work in the Hilbert Space $H_0^1(D)$ with weighted inner-product:

$$\langle u, v \rangle := \int_D e^{\chi A} \nabla u \cdot \nabla v\, dx$$

and denote the weighted H_0^1 norm by $\|\cdot\|$:

$$\|u\| = \sqrt{\int_D e^{\chi A} |\nabla u|^2\, dx}.$$

Before proving Theorem 1 we state and prove an auxiliary lemma.

Lemma 3. *Let $w \in H_0^1(D)$ be fixed. The map $J'[v](w) : H_0^1(D) \to \mathbb{R}$ defined by $J'[v](w) = \int_D f(x, e^{\chi A(x)}v)w\ dx$ is compact.*

Proof. Let $X \equiv H_0^1(D)$, defined above, and $\{v_k\}_{k\geq 0} \subset X$ be bounded, *i.e* there exists a $K_1 > 0$ such that $\|v_k\| \leq K_1$ for all $k \in \mathbb{N}$. We prove that $J'[v_k]$ has a converging subsequence. Note that $v_k \rightharpoonup v$ (up to a subsequence) for some $v \in X$. Also, for $w \in X$ we have, using (13) and Cauchy-Schwarz inequality , that:

$$\begin{aligned} J'[v_k](w) &= \int_D f(x, e^{\chi A}v)w\ dx \\ &\overset{(13)}{\leq} \int_D f_2 e^{\chi A} |v|\,|w|\ dx \\ &\overset{C.S}{\leq} f_2 \|v_k\| \|w\| \leq f_2 K_1 \|w\|. \end{aligned}$$

Thus, the sequence $\{J'[v_k]\}_{k\geq 0}$ is uniformly bounded on $\mathbb{R}$ and has a strongly convergent subsequence $J'[v_k] \to g$. Moreover, we see that $J'[v](w)$ is continuous from the following estimate, using (14) and Cauchy-Schwarz:

$$\begin{aligned} \left|J'[v_1]w - J'[v_2]w\right| &= \left|\int_D f(x, e^{\chi A}v_1)w\ dx - \int_D f(x, e^{\chi A}v_2)w\ dx\right| \\ &\leq \int_D \left|f(x, e^{\chi A}v_1) - f(x, e^{\chi A}v_2)\right| |w|\ dx \\ &\overset{(14)}{\leq} \int_D e^{\chi A} f_3 \,|v_1 - v_2|\,|w|\ dx \\ &\leq f_3 \|w\| \|v_1 - v_2\|. \end{aligned}$$

By continuity then $g = J'[v]$ and we conclude that $J'[v](w)$ is compact.

□

We are now ready to prove Theorem 1.

Proof. (Theorem 1) We prove the existence of steady-state solutions to (16) in four steps. First, we note that if v is a steady-state solution to (17) then $u = e^{\chi A}v$ is a steady-state solution to (16).

Step 1. (Palais-Smale Condition) We first prove that the energy functional (15) satisfies the Palais-Smale Condition. For this purpose, note that $\mathcal{F}$ is a continuously differentiable function on $H \equiv H_0^1(D)$. Take a sequence $\{v_k\} \subset H$ such that $|\mathcal{F}[v_k]| \leq C$ for $C > 0$ and $\mathcal{F}'[v_k] \to 0$ in H. We see that:

$$\begin{aligned} \mathcal{F}[v_k] &= \int_D \frac{\mu}{2} e^{\chi A} |\nabla v_k|^2 - e^{-\chi A} F(x, e^{\chi A}v_k)\ dx \\ &\overset{(7)}{\geq} \frac{\mu}{2}\|v_k\| - \overline{A}\,|D|\, e^{-\chi A_{min}}, \end{aligned}$$

where $\overline{A}$ is defined in (7) and A_{min} defined in section 1.2. Thus, obtaining the bound:

$$\|v_k\| \leq \frac{2C}{\mu} + \frac{2\overline{A}}{\mu}\,|D|\, e^{-\chi A_{min}}$$

and thus the sequence $\{v_k\}$ is uniformly bounded in H. Next, consider the first variation of $\mathcal{F}$:

$$\mathcal{F}'[v] = \int_D \mu e^{\chi A} \nabla v \cdot \nabla w - f(x, e^{\chi A}v)w\ dx$$

Define $I : H \to H^*$ by

$$I[v](w) = \int_D e^{\chi A} \nabla v \cdot \nabla w \, dx$$

and $J[v] := \int_D e^{-\chi A} F(x, e^{\chi A} v_k) \, dx$, so that

$$\mathcal{F}'[v_k] = \mu I[v_k] - J'[v_k].$$

Note that since I is the dual pairing, the inverse exists and we can solve for v_k to get that:

$$\mu v_k = I^{-1} \mathcal{F}'[v_k] + I^{-1} J'[v_k].$$

By the boundedness of $\{v_k\}_{k \geq 0}$ we know that there exists a $v \in H$ such that $v_k \rightharpoonup v$ (up to a subsequence). By Lemma 3 we know that J' is compact and thus we have that $J'[v_k] \to J'[v]$. Moreover, by assumption we have that $\mathcal{F}'[v_k] \to 0$ in H, thus $I^{-1}\mathcal{F}'[v_k] \to 0$ as $k \to \infty$. Therefore, we have

$$\mu v_k = I^{-1} \mathcal{F}'[v_k] + I^{-1} J'[v_k] \to 0 + I^{-1} J'[v] = \mu v,$$

as $k \to \infty$. Thus, we have found a subsequence that converges in $H_0^1(D)$ and the Palais-Smale Condition holds.

Step 2. (Function with negative energy) Note that $\mathcal{F}[v] \geq -\overline{A} \, |D| \, e^{-\chi A_{min}}$ and thus $\inf_{u \in H} \mathcal{F}[u]$ will be a critical point. Let us now show that there exists a positive v_0 with $\mathcal{F}[v_0] < 0$ and thus the infimum must be negative. Let us define the following disjoint domains for $\varepsilon > 0$:

$$D_0 := \{x \in D : d(x, \partial D) < \varepsilon\}, D_1 := \{x \in D : \varepsilon < d(x, \partial D) < 2\varepsilon\}, \text{ and } D_2 = D \backslash (D_0 \cup D_1).$$

See Figure 2 for an illustration of these subdomains.

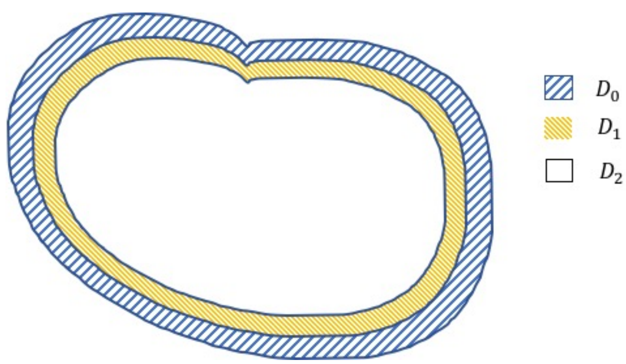


Figure 2: Illustration of disjoint domains D_0, D_1, D_2.

Define,

$$v_0(x) = \begin{cases} m(x) e^{-\chi A(x)}, & x \in D_2, \\ 0, & x \in D_0, \end{cases}$$

such that v_0 is smooth with $\max_{x \in D_1} \{v_0(x)\} \leq \max_{x \in D_2} \left\{ m(x) e^{-\chi A} \right\}$. We compute an energy bound for v_0:

$$\begin{aligned}
\mathcal{F}[v_0] &= \frac{\mu}{2} \int_D e^{\chi A} |\nabla v_0|^2 - \int_D e^{-\chi A} F(x, e^{\chi A} v_0) \, dx \\
&= \frac{\mu}{2} \int_D e^{\chi A} |\nabla v_0|^2 - \int_{D_2} e^{-\chi A} F(x, e^{\chi A} v_0) \, dx - \int_{D_1} e^{-\chi A} F(x, e^{\chi A} v_0) \, dx \\
&\overset{(6),(7)}{\leq} \frac{\mu}{2} \int_D e^{\chi A} |\nabla v_0|^2 - |D_2| \, \delta \inf_{x \in D_2} e^{-\chi A(x)} + |D_1| \sup_{x \in D_1} e^{-\chi A(x)} \overline{A}.
\end{aligned}$$

Choose $\varepsilon > 0$ sufficiently small so that $|D_1|$ is sufficiently small to guarantee that

$$-|D_2|\,\delta \inf_{x\in D_2} e^{-\chi A(x)} + |D_1| \sup_{x\in D_2} e^{-\chi A(x)}\overline{A} > \gamma > 0.$$

We may then choose μ sufficiently small so that $\gamma > \frac{\mu}{2}\|v_0\|$ so that $\mathcal{F}[v_0] < 0$. Therefore, there exists a $v_1 \in H_0^1(D)$ with $\mathcal{F}[u_1] = \inf_{u\in H}\mathcal{F}[u] < 0$.

Step 3. (Mountain Pass Theorem) First we compute the second variation:

$$\mathcal{F}''(0)[w,w] = \int_D \mu e^{\chi A}|\nabla w|^2\,dx - \int_D e^{\chi A} f_u(x,0)w^2\,dx.$$

Note that since $\mathcal{F}[0] = 0$ and $\mathcal{F}'[0] = 0$ and $\mathcal{F}$ is $C^2(H_0^1(D),\mathbb{R})$, then for all $\varepsilon > 0$ there exists a $\delta_\varepsilon > 0$ such that if $\|w\| < \delta_\varepsilon$ the following bound holds:

$$\left|\mathcal{F}[w] - \mathcal{F}''(0)[w,w]\right| \le \varepsilon\|w\|^2.$$

Given that $f_u(x,0) < 0$ we have that

$$\mathcal{F}''(0)[w,w] \ge \mu\|w\|^2.$$

Choose $\varepsilon = \mu/2$ and $\|w\| = r \le \delta_{\frac{\mu}{2}}$ with $r < \|v_0\|$. In this case we have that $\mathcal{F}[w] \ge \frac{\mu}{2}\|w\|^2 = \frac{\mu}{2}r^2 := a$. We then have the existence of $a, r > 0$ such that $\mathcal{F}[w] \ge a$ if $\|w\| = r$ and a function v_0 with $\mathcal{F}[v_0] < 0$ and $\|v_0\| > r$. By the Mountain Pass Theorem there exists a second critical point v_2. Finally, we have our two equilibrium solutions $u_1 = e^{\chi A}v_1$ and $u_1 = e^{\chi A}v_2$. $\square$

Theorem 2 (Existence of Positive Equilibrium for the No-flux Problem)**.** *Let A and f be admissible. There always exists at least one positive steady state solution u to* (1) *and at least two for μ sufficiently small.*

Proof. The proof of Theorem 2 follows the first three steps of the proof of Theorem 1 with the exception that we now work with a different Hilbert Space $H^1(D)$ with weighted inner-product:

$$\langle u, v\rangle := \int_D e^{\chi A}[\nabla u\cdot\nabla v + uv]\,dx,$$

which defines the norm:

$$\|w\| = \sqrt{\int_D e^{\chi A}[w^2 + |\nabla w|^2\,dx]}.$$

Step 1. (Palais-Smale Condition) The steps to show that (15) satisfies the Palais-Smale Condition are very similar to those in *Step 1* in the proof of Theorem 1. Again, take $\{v_k\} \subset H$ such that $|\mathcal{F}[v_k]| \le C$ for $C > 0$ and $\mathcal{F}'[v_k] \to 0$ in $H^1(D)$. Computing as before we obtain the bound

$$\|v_k\| \le \frac{2C}{\mu} + \frac{2\overline{A}}{\mu}e^{-\chi A_{min}}|D| + \int_D e^{\chi A}v_k^2\,dx.$$

Note that since $|\mathcal{F}[v_k]| \le C$ then we have that

$$\left|\int_D e^{-\chi A}F(x,v_k)\,dx\right| \le M,$$

which allows us to conclude that $\{v_k\}$ are uniformly bounded in $L^\infty(D)$ by a constant K and thus we have that:

$$\|v_k\| \leq \frac{2C}{\mu} + \frac{2\overline{A}}{\mu} e^{-\chi A_{min}} |D| + e^{\chi A_{max}} K^2 |D| .$$

Thus, $\{v_k\}$ is bounded in $H^1(D)$. The first variation of $\mathcal{F}$ remains the same, but the dual paring $I : H^1(D) \to (H^1(D))^*$ is now defined by

$$I[v](w) = \int_D e^{\chi A} \nabla v \cdot \nabla w \, dx + \int_D e^{\chi A} v w \, dx.$$

Therefore, we can now rewrite our first variation as follows:

$$\mathcal{F}'[v_k] = \mu I[v_k] - \mu G[v_k] - J'[v_k],$$

where G is a linear functional with

$$G[v_k](w) = \int_D e^{\chi A} v_k w \, dx.$$

Solving for v_k gives:

$$\mu v_k = I^{-1}\mathcal{F}'[v_k] + I^{-1}J'[v_k] + \mu I^{-1}G[v_k].$$

Again, $v \in H^1(D)$ such that $v_k \rightharpoonup v$ (up to a subsequence) and J' being a compact operator implies that $J'[v_k] \to J'[v]$. Moreover, by assumption we have that $\mathcal{F}'[v_k] \to 0$ in $H^1(D)$, thus $I^{-1}\mathcal{F}'[v_k] \to 0$ as $k \to \infty$. Finally, since v_k converges weakly to v then we know that $G[v_k] \to G[v]$ and thus

$$\mu v_k = I^{-1}\mathcal{F}'[v_k] + I^{-1}J'[v_k] \to 0 + I^{-1}(J'[v] + \mu G[v]) = \mu v,$$

as $k \to \infty$. Thus, we have found a subsequence that converges in $H^1(D)$ and the Palais-Smale Condition holds.

Step 2. (Function with negative energy) As before $\mathcal{F}[v] \geq -\overline{A}e^{-\chi A_{min}} |D|$ and thus $\inf_{u \in H} \mathcal{F}[u]$ will be a critical point. Again, we now find a v_0 with $\mathcal{F}[v_0] < 0$. Under condition (5), there is a constant v_0 such that

$$a(x) < e^{\chi A} v_0 < b(x).$$

Therefore, we have that

$$\mathcal{F}[v_0] = -\int_D e^{-\chi A} F(x, e^{\chi A} v_0) \, dx < 0.$$

Thus, we have a minimizer $v_1 \in H^1(D)$. Since v_1 is a critical point we have that $\mathcal{F}'[u_1] = 0$, which after integrating by parts gives that:

$$\mathcal{F}'[v_1] = -\int_D [\nabla \cdot (e^{\chi A} \nabla v_1) + f(x, e^{\chi A} u_1)] w \, dx + \int_{\partial D} \frac{\partial v_1}{\partial n} w \, dx = 0,$$

for all $w \in H^1(D)$. Taking $w \in H_0^1$ implies that v must satisfy:

$$\nabla \cdot (e^{\chi A} \nabla v_1) + f(x, e^{\chi A} v_1) = 0. \tag{18}$$

Now, for all $w \in H^1(D)$ non-zero on ∂D it holds by (18) that

$$-\int_D [\nabla \cdot (e^{\chi A} \nabla v_1) + f(x, e^{\chi A} v_1)] w \, dx = 0.$$

This implies that that
$$\int_{\partial D} \frac{\partial v_1}{\partial n} w \, dx = 0$$
implying that $\frac{\partial v_1}{\partial n} = 0$.

Step 3. (Mountain Pass Theorem) The Mountain Pass theorem can be applied in this case as it was done in the previous theorem with the additional assumption that
$$\mu < -2 f_u(x, 0).$$
Thus, we obtain a second equilibrium solution if μ is sufficiently small. □

Remark 2. Note that the results in this section did not need the condition $(A3)$.

3 The Time Evolution for the No-Flux Problem

In this section we discuss the time evolution dynamics of solutions to (8). Our main interest lies in comparing the long-term behavior between the solutions to the classical reaction-diffusion equation and to equation (8) as a function of χ, which can be seen as the strength of the directed movement of the population. For ease we give our results in terms of the dynamics of a population v satisfying (9) and then interpret them in terms of a population u satisfying (8). Our first result provides a dichotomy between the extinction and the persistence of a population.

Theorem 3 (Extinction versus persistence)**.** *Let A be an admissible signal and g satisfy* (3) *with the additional assumption that:*
$$\max_{x \in \overline{D}} \left(e^{\chi A} \theta \right) < \min_{x \in \overline{D}} \left(e^{\chi A} m \right). \tag{19}$$

- *(i) If v is the solution to system* (9) *with initial data $0 < v_0 < \min_{x \in \overline{D}} (\theta e^{-\chi A})$, then $v(x,t) \to 0$ as $t \to \infty$ for all $x \in D$.*
- *(ii) If v is the solution to system* (9) *with initial data $\max_{x \in \overline{D}} (\theta e^{-\chi A}) < v_0 < \min_{x \in \overline{D}} (m e^{-\chi A})$, then $v(x,t) \to v^*(x)$ as $t \to \infty$ for all $x \in D$, where v^* is the minimal equilibrium solution to* (9) *that is larger than $\max_{x \in \overline{D}} (\theta e^{-\chi A})$. Furthermore,*
$$\min_{x \in \overline{D}} \left[m e^{-\chi A} \right] \leq \min_{x \in \overline{D}} \left[v^*(x) \right]. \tag{20}$$

Proof. Case (i) is proved in two steps. *Step 1:* We first show that there are no positive equilibrium solutions to (9) with maximum less than $\min_{x \in \overline{D}} (\theta e^{-\chi A})$. For contradiction, let v^* be a nontrivial equilibrium solution to (9) such that:
$$v^* < \min_{x \in \overline{D}} \left(\theta e^{-\chi A} \right). \tag{21}$$

Then, for all $x \in \overline{D}$ we have that $e^{\chi A} v^* < \theta$. If v^* is a constant equilibrium then $g(x, e^{\chi A} v^*) v^* = 0$. Thus, if $v^* \neq 0$, either $e^{\chi A} v^* = \theta$ or $e^{\chi A} v^* = m$, which contradicts assumption (21). If v^* is non-constant then it cannot achieve its maximum on the boundary, ∂D, by the strong maximum principle and the Neumann boundary condition imposed. Thus, suppose that the maximum were to occur at the point $x_0 \in D$, then at $x = x_0$ the following holds:

$$\begin{aligned}0 &= \mu[\Delta v^* + \chi \nabla A \cdot \nabla v^*]_{x=x_0} + g(x_0, e^{\chi A(x_0)} v^*(x_0)) v^*(x_0) \\ &\leq g(x_0, e^{\chi A(x_0)} v^*(x_0)) v^*(x_0) \\ &< 0,\end{aligned}$$

by (21). This contradiction shows that there are no positive equilibrium solutions with maximum less than $\min_{x \in \overline{D}}(\theta e^{-\chi A})$. *Step 2:* Now, consider a constant $\overline{v} < \min_{x \in \overline{D}}(\theta e^{-\chi A})$. Note that since g satisfies (3) we obtain that:

$$\begin{aligned}\mu[\Delta \overline{v} + \chi \nabla A \cdot \nabla \overline{v}] + g(x, e^{\chi A} \overline{v}) \overline{v} &= g(x, e^{\chi A} \overline{v}) \overline{v} \\ &= (m - e^{\chi A} \overline{v})(e^{\chi A} \overline{v} - \theta) \overline{v} \\ &< 0,\end{aligned}$$

since $e^{\chi A} \overline{v} < \theta$. Thus, any constant $\overline{v}$ that satisfies the bound $\overline{v} < \min_{x \in D}(\theta e^{-\chi A})$ is a strict supersolution to the equilibrium equation corresponding to (9). Then, initial data $\tilde{v}(x, 0) = \overline{v}$ yields a solution $\tilde{v}$ that decreases towards the maximal equilibrium that is less than $\overline{v}$, which is zero by *Step 1.* We conclude that any solution to (9) with initial data $v_0 \leq \min_{x \in \overline{D}}(\theta e^{-\chi A})$ must approach zero as $t \to \infty$ for all $x \in D$.

To prove case (*ii*) we proceed as in part (*i*) in two steps. *Step 1:* We first show that an equilibrium v^* to (9) that satisfies $v^* > \max_{x \in \overline{D}}(\theta e^{-\chi A})$ must satisfy (20). Suppose that v^* has a minimum at $x_0 \in \overline{D}$. Since $\nabla v \cdot \vec{n} = 0$ on ∂D, the strong maximum principle implies that if $x_0 \in \partial D$ then v^* must be constant. Then $g(x, e^{\chi A} v^*) = 0$. Because of the condition on the initial data, this is possible only if $e^{\chi A} v^* = m$ and thus we have that $v^* = e^{-\chi A} m \geq \min_{x \in \overline{D}}(m e^{-\chi A})$. If $x_0 \in D$, assume for contradiction that:

$$v^*(x_0) = \min_{x \in \overline{D}} v^*(x) < \min_{x \in \overline{D}} \left(m e^{-\chi A} \right).$$

Then at x_0 the following holds:

$$\begin{aligned}0 &= \mu[\Delta v^* + \chi \nabla A \cdot \nabla v^*]_{x=x_0} + g(x_0, e^{\chi A(x_0)} v^*(x_0)) v^*(x_0) \\ &\geq g(x_0, e^{\chi A(x_0)} v^*(x_0)) v^*(x_0) \\ &> 0.\end{aligned}$$

The last inequality follows by combining the assumptions:

$$\max_{x \in \overline{D}} \left(\theta e^{-\chi A} \right) < v^* < \min_{x \in \overline{D}} \left(m e^{-\chi A} \right).$$

To avoid the contradiction (20) must hold. *Step 2:* Consider a constant $\underline{v}$ with

$$\max_{x \in \overline{D}} \left(\theta e^{-\chi A} \right) < \underline{v} < \min_{x \in \overline{D}} \left(m e^{-\chi A} \right),$$

then

$$\begin{aligned}0 &= \mu[\Delta \underline{v} + \chi \nabla A \cdot \nabla \underline{v}] + g(x, e^{\chi A} \underline{v}) \underline{v} \\ &= g(x, e^{\chi A} \underline{v}) \underline{v} \\ &> 0.\end{aligned}$$

Thus, $\underline{v}$ is a strict subsolution to the equilibrium problem for (9). Thus, any solution to (9) with initial data satisfying $v_0(x) > \max_{x \in \overline{D}}(\theta e^{-\chi A})$ will increase towards the minimal equilibrium of (9) that satisfies (20). $\square$

Remark 3. The condition imposed in Theorem 3 case (i), expressed in terms of the original population u, is $e^{-\chi A}u(x,0) = v_0 \le \min_{x\in\overline{D}}(\theta e^{-\chi A})$. Thus, $u \to 0$ as $t \to \infty$ uniformly in x, if

$$u(x,0) \le e^{\chi A} \min_{x\in\overline{D}} \left(\theta e^{-\chi A}\right).$$

Note that condition (21), which suffices for *Step 1* in the proof of case (i) in Theorem 3, is equivalent to $u^* < \theta$. This shows that there are no non-trivial equilibrium solutions to (8) such that $u^* < \theta$. The lower bound condition imposed in case (ii) in terms of u is given by $e^{-\chi A}u(x,0) = v_0 > \max_{x\in\overline{D}}(\theta e^{-\chi A})$, equivalently:

$$u(x,0) > e^{\chi A} \max_{x\in\overline{D}} \left(\theta e^{-\chi A}\right).$$

From this we can conclude that $u(x,t) \to u^* = e^{-\chi A}v^* > e^{\chi A} \min_{x\in\overline{D}} \left(m e^{-\chi A}\right)$. Thus, $u^* > \theta$ if:

$$\min_{x\in\overline{D}} \left(e^{\chi A}\right) \min_{x\in\overline{D}} \left(m e^{-\chi A}\right) > \max_{x\in\overline{D}} \theta,$$

which holds by assumption (19) when χ is sufficiently small.

A consequence of Theorem 3 case (ii) is the existence of a equilibrium solution to (8) such that $u^* > \theta$, under the conditions discussed in Remark 3. The proof actually shows that u^* is at least a semi-stable equilibrium solution. However, under mild additional assumptions we can prove that the equilibrium solution is stable. For this purpose, note that there exists a function $\hat{u}$ with $\theta(x) < \hat{u}(x) < m(x)$ such that:

$$\frac{\partial f}{\partial v}(x, u(x)) < 0 \text{ if } u(x) > \hat{u}(x) \text{ for all } x \in \overline{D}. \tag{22}$$

Proposition 1 (Stability of equilibrium solution)**.** *Let v^* be an equilibrium solution to* (9) *satisfying $v^* > e^{-\chi A}\hat{u}$, where $\hat{u}$ is defined in* (22)*. Then v^* is stable.*

Proof. Let v^* be an equilibrium solution to equation (9). The corresponding linearized equation about v^* and corresponding boundary conditions are given by:

$$\begin{cases} \mu[\Delta\phi + \chi\nabla A \cdot \nabla\phi] + \frac{\partial f}{\partial v}(x, e^{\chi A}v^*)e^{\chi A}\phi = \lambda\phi, \ x \in D, \\ \frac{\partial \phi}{\partial n} = 0, \ x \in \partial D. \end{cases}$$

We multiply the above linearized equation with $e^{\chi A}$ to obtain:

$$\mu\nabla \cdot [e^{\chi A}\nabla\phi] + \frac{\partial f}{\partial v}\left(x, e^{\chi A}v^*\right) e^{2\chi A}\phi = \lambda\phi e^{\chi A},$$

after some algebraic manipulations on the left-hand-side of the equation. Now, integrating over D gives:

$$\int_D \mu\nabla \cdot [e^{\chi A}\nabla\phi] + \frac{\partial f}{\partial v}\left(x, e^{\chi A}v^*\right) e^{2\chi A}\phi \, dx = \lambda \int_D \phi e^{\chi A} \, dx.$$

An application of the Divergence Theorem gives that:

$$\int_D \frac{\partial f}{\partial v}\left(x, e^{\chi A}v^*\right) e^{2\chi A}\phi \, dx = \lambda \int_D \phi e^{\chi A} \, dx.$$

Note that the left-hand-side of the equation above is negative when

$$\frac{\partial f}{\partial v}\left(x, e^{\chi A}v^*\right) < 0.$$

Now, as stated above, there exists a $\theta < \hat{u} < m$ such that $\frac{\partial f}{\partial v}(x,u) < 0$ if $u > \hat{u}$. Thus, if $e^{\chi A}v^* > \hat{u}$ we see that $\lambda < 0$. Thus, v^* is a linearly stable equilibrium.

□

Remark 4. In the case when $f(u) = u(m-u)(u-\theta)$ with positive $\theta < m$, then $\hat{u} = \hat{u}(m,\theta)$ where

$$\hat{u}(m,\theta) = \frac{m+\theta+\sqrt{m^2-m\theta+\theta^2}}{3} < \frac{2(m+\theta)}{3}.$$

Let $\gamma m > \theta$ for some constant γ, then

$$2(m+\theta) < 2(1+\gamma)\max_{x\in\overline{D}} m.$$

Let v^* be the positive equilibrium solution satisfying $v^* > min_{x\in\overline{D}}\left(e^{-\chi A}m\right)$ obtained in case (ii) of Theorem 3. Note that, $e^{\chi A}v^* > \hat{u}$ if

$$2(1+\gamma)\max_{x\in\overline{D}} m < 3\min_{x\in\overline{D}}\left(e^{\chi A}\right)\min_{x\in\overline{D}}\left(e^{-\chi A}m\right),$$

which is satisfied if

$$2\max_{x\in\overline{D}}(m) < 3\min_{x\in\overline{D}}(m),$$

provided γ, χ are sufficiently small.

Remark 4 provides a sufficient condition for the stability of the equilibrium solution v^* to (9) obtained in case (ii) of Theorem 3. We now state a corollary of Theorem 3 that helps us relate the result in Theorem 3 to the classical reaction diffusion equation without directed movement.

Corollary 1 (χ small)**.** *Let the conditions in Theorem 3 hold and $0 < \theta < m$ be constants. The following hold:*

(i) There exists a nonnegative function $C(\chi, A) \leq 1$ with $\lim_{\chi\to 0} C(\chi, A) = 1$ such that if u is the solution to system (8) with initial data $0 < u_0 < \theta C(\chi, A)$, then $u(x,t) \to 0$ as $t \to \infty$ for all $x \in D$.

(ii) There exist nonnegative functions $C_1(\chi, A) \geq 1$ and $C_2(\chi, A) \leq 1$ with

$$\lim_{\chi\to 0} C_1(\chi, A) = 1 \quad \text{and} \quad \lim_{\chi\to 0} C_2(\chi, A) = 1$$

such that if u is the solution to system (8) with initial data $C_1\theta < u_0 < C_2 m$, then $u(x,t) \to u^*(x)$ as $t \to \infty$ for all $x \in D$, where u^* is an equilibrium solution to (8) with $u^*(x) > C_2\theta$ for all $x \in D$.

Proof. We only consider case (i) as case (ii) is proved similarly. Note that as θ is constant then the condition on the initial data for case (i) in Theorem 3 can be written as:

$$0 < u_0 < \theta e^{\chi A}\min_{x\in\overline{D}}\left(e^{-\chi A}\right),$$

since θ is constant. Let $C(\chi, A) = e^{\chi A}\min_{x\in\overline{D}}\left(e^{-\chi A}\right)$ and note that $0 \leq C(\chi, A) \leq 1$ and that $\lim_{\chi\to 0} C(\chi, A) = 1$. □

For general χ, we also prove that for initial data below, but close to, θ the solution u to (8) is such that $u(x,t^*) > \theta$ for some values of $x \in D$ and some $t^* > 0$. For the following result we consider $D = (0,1)$. More or less, the concentration happens in regions where the non-constant signal A is larger than its average. To make this precise, consider a non-constant signal A and for $\eta > 0$, but small, define $\Omega_\eta \subset (0,1)$ as follows:

$$\Omega_\eta = \left\{x \in (0,1) : e^{\chi A(x)} > (1+\eta)\int_0^1 e^{\chi A(x)}\,dx\right\}. \tag{23}$$

Note that Ω_η has positive measure if η is small enough.

Proposition 2. *Let A be admissible and $\theta < 1/2$. There exists an $\varepsilon > 0$ sufficiently small, μ sufficiently large and $t^* > 0$ such that if $u_0 = (1-\varepsilon)\theta$ then the solution u to (8) is such that $u(x,t^*) > \theta$ for $x \in \Omega_\eta$.*

Proof. Again, we perform the change variables $v = e^{-\chi A}u$. Note that $g(x,z) \geq -g_0$, where g_0 is strictly positive and consider the auxiliary problem:

$$\begin{cases} w_t = \mu(w_{xx} + \chi A_x w_x) - g_0 w, \ x \in (0,1), \ t > 0, \\ w_x(0,t) = w_x(1,t) = 0, \\ w(x,0) = v_0(x), \ x \in D. \end{cases} \tag{24}$$

The solution to (24) can be written as $w = e^{-g_0 t}\tilde{w}$, where $\tilde{w}$ is the solution to

$$\begin{cases} \tilde{w}_t = \mu(\tilde{w}_{xx} + \chi A_x \tilde{w}_x), \ x \in (0,1), \ t > 0, \\ \tilde{w}_x(0,t) = \tilde{w}_x(1,t) = 0, \\ \tilde{w}(x,0) = v_0(x), \ x \in D. \end{cases} \tag{25}$$

We rescale (26), with respect to time, with $\tilde{t} = t/\mu$ and $z(x,t) = \tilde{w}(x,\tilde{t})$ then gives:

$$\begin{cases} z_t = z_{xx} + \chi A_x z_x, \ x \in (0,1), \\ z_x(0,t) = z_x(1,t) = 0, \\ z(x,0) = v_0(x). \end{cases} \tag{26}$$

The operator $\partial_x^2 + \chi A_x \partial_x$ appearing in (26) with no-flux boundary conditions has a principal eigenvalue zero with eigenfunction $z \equiv 1$. Thus, $z \to z_0$ as $t \to \infty$, uniformly in x, where z_0 is a constant. To get more information about the actual value of z_0, we multiply (26) by $e^{\chi A}$ to get:

$$[e^{\chi A} z]_t = [e^{\chi A} z_x]_x,$$

and then integrate on $(0,1)$:

$$\frac{d}{dt}\int_0^1 e^{\chi A} z \, dx = \int_0^1 [e^{\chi A} z_x]_x \, dx = 0.$$

Above, we integrated by parts and used the no-flux boundary conditions to obtain the last equality. From this we conclude that z_0 should satisfy:

$$\int_0^1 e^{\chi A} z(x,0) \, dx = z_0 \int_0^1 e^{\chi A} \, dx.$$

Solving for z_0 we get:

$$z_0 = \frac{\int_0^1 e^{\chi A} z(x,0) \, dx}{\int_0^1 e^{\chi A} \, dx}.$$

Now, consider initial data $u_0(x) = (1-\varepsilon)\theta$ (for $\varepsilon > 0$ to be specified later) so $z(x,0) = (1-\varepsilon)\theta e^{-\chi A}$. We then observe that

$$z_0 = \frac{(1-\varepsilon)\theta}{\int_0^1 e^{\chi A} \, dx}.$$

Since $z(x,t) \to z_0$ uniformly in $x \in (0,1)$ as $t \to \infty$, there exist a t^* (depending on ε) such that

$$z(x,t) \geq (1-\varepsilon) z_0 = \frac{(1-\varepsilon)^2\theta}{\int_0^1 e^{\chi A} \, dx},$$

for all $t \geq t^*$. For $\tilde{w}$ this implies that:

$$\tilde{w}(x, t^*/\mu) \geq \frac{(1-\varepsilon)^2\theta}{\int_0^1 e^{\chi A}\, dx},$$

and so

$$w(x, t^*/\mu) \geq \frac{(1-\varepsilon)^2\theta}{\int_0^1 e^{\chi A}\, dx} e^{-g_0 t^*/\mu}.$$

Note that choosing μ large enough ($\mu > \frac{g_0 t^*}{-\ln(1-\varepsilon)}$) we get that $e^{-g_0 t^*/\mu} > (1-\varepsilon)$ and thus

$$v(x, t^*/\mu) \geq w(x, t^*/\mu) \geq \frac{(1-\varepsilon)^3\theta}{\int_0^1 e^{\chi A}\, dx}.$$

Finally, we arrive at the following inequality:

$$u(x, t^*/\mu) \geq \frac{(1-\varepsilon)^3\theta e^{\chi A}}{\int_0^1 e^{\chi A}\, dx}.$$

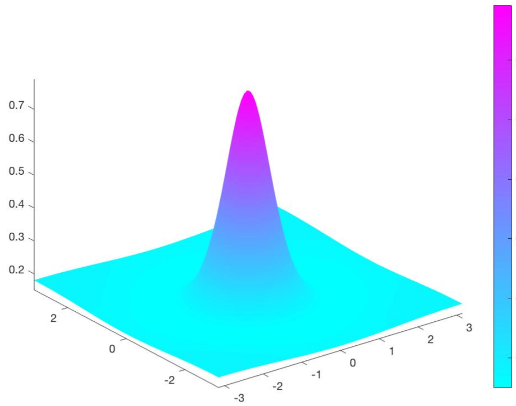
Note that for $x \in \Omega_\eta$ we have that

$$u(x, t^*/\mu) \geq (1-\varepsilon)^3\theta(1+\eta) > \theta,$$

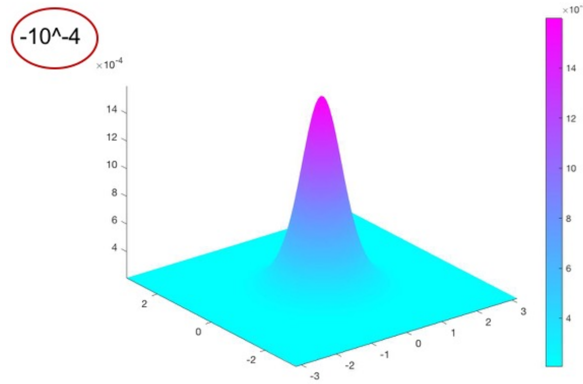
if ε is chosen sufficiently small and with this we conclude. □

Note that Proposition 2 does not imply that the solution u to (8) will always remain above θ, in some regions of our domain, as $t \to \infty$, because t^* depends on μ. In fact, if χ is sufficiently small, we know that the solution will converge to zero uniformly. Therefore, any results related to the persistence of a species must depend directly on χ or the signal A and Proposition 2 does not. However, it does imply that there is always some initial growth in this case, contrary to the case when $\chi = 0$. Figure 3 illustrates the initial growth of the solution with constant initial data $u(x, 0) = .2$, growth-pattern $f(u) = u(1-u)(u-.3)$ (here $\theta = .3, m = 1$) and a Gaussian signal centered at the origin. For $\chi = 1$ we see that at time $t^* = 10$ there are regions that are above θ (as predicted by Proposition 2), but by time $t = 500$ the solution is essentially zero – see Figure 3a-3b. On the other hand, for $\chi = 5$ under the same conditions the solution continues to persist and reaches a nontrivial equilibrium – see Figure 3c-3d.

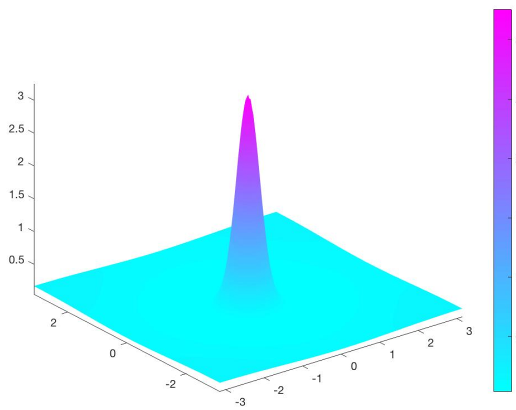
There is an interesting implication of this result: if a population is able to detect that it is above the Allee threshold in some areas, it can choose to stop moving and the population will then survive. This is certainly a viable option in economics, for example, street vendors may realize that they have found a good location where they are profiting and may choose to stay there permanently.



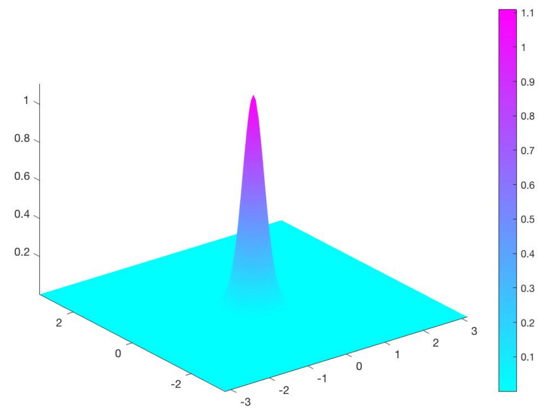
(a) $\chi = 1$ and $t = 10$



(b) $\chi = 1$ and $t = 500$



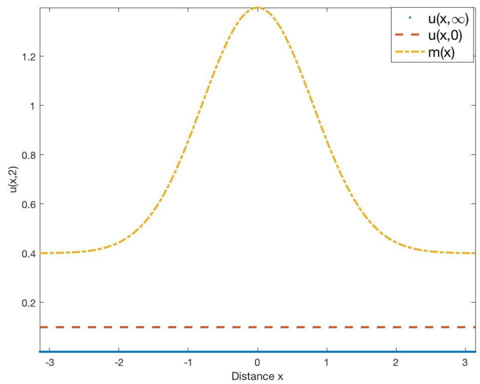
(c) $\chi = 5$ and $t = 10$



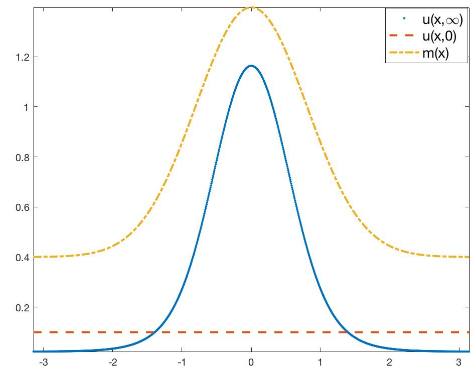
(d) $\chi = 5$ and $t = 500$

Figure 3: The solutions to (8) with $\chi = 1$ for the first row and $\chi = 5$ for the second row. The first column illustrates the initial growth of the solution ($t = 10$) and the second column illustrates the equilibrium solution. For both simulations we consider constant initial data $u_0 = .2$ and a Gaussian signal that is centered at the origin.

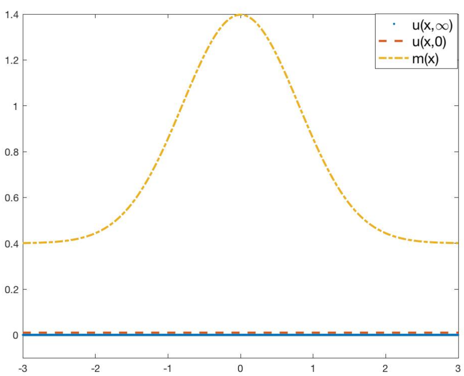
Our numerical simulations support the *conjecture* that u converges to a positive equilibrium if χ is sufficiently large. Specifically, given any initial data $0 < u_0(x) < \theta(x)$ we conjecture the existence of a sufficiently large χ, which depends on $u_0(x)$, such that the solution to (9) converges to a non-trivial equilibrium solution as $t \to \infty$. In order words, the population is conjectured to persist in such case, in contrast to it becoming extinct if $\chi = 0$. Figure 4 provides an illustration of long-term solutions with different values of χ and initial data u_0 in one-dimension. For all simulations we take $\theta = .2$ and the signal A is a Gaussian centered at the origin. Figure 4a ($\chi = 2$) and Figure 4b ($\chi = 3$) illustrate the solution with $u_0 = .1$ with the two different values of χ. In the former case, when χ is small, the solution converges to zero in the long-term. On the other hand, the solution converges to a positive steady-state in the long-term when χ is large. Notice that the smaller the initial data the larger the value of χ that is necessary to overcome the Allee effect. Indeed, Figure 4c ($\chi = 50$) and Figure 4d ($\chi = 100$) illustrate the solution with $u_0 = 0.1$. In that case, $\chi = 50$ leads to the extinction of the species. Moreover, the larger the value of χ the more the species aggregates, as illustrated in Figure 4d.



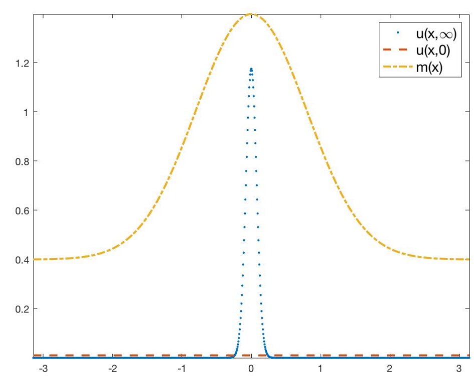
(a) Initial data $u_0(x) \equiv .1$ with $\chi = 2$



(b) Initial data $u_0(x) \equiv .1$ with $\chi = 3$



(c) Initial data $u_0(x) \equiv .01$ with $\chi = 50$



(d) Initial data $u_0(x) \equiv .01$ with $\chi = 150$

Figure 4: Illustration of numerical solutions to (8) with various constant initial data, u_0, directed movement parameter χ, and growth-pattern $f(u) = u(1-u)(u-.2)$. The signal $A = \frac{\ln m}{m}$.

4 Ideal Free Distribution and the Allee Effect

An important concept in spatial ecology is the ideal free distribution (IFD). It refers to a situation where each member of a population can tell its fitness and will move to a location where its fitness is the highest. In the context of reaction-diffusion models and related models in discrete space, a movement strategy produces an ideal free distribution if it allows a population to exactly match the distribution of resources. In the present setting, that means the movement strategy $\mathcal{M}$ by itself without dynamics has $\mathcal{M}[m(x)] = 0$ so that density $u = m$ is an equilibrium for the full model. In many cases, populations using such strategies are predicted to be able to successfully invade and also resist invasion by populations that use strategies that do not produce an ideal free distribution; for additional discussion see [7, 8, 10, 15].

In this section, we discuss some possible relocation strategies that can lead a population to obtain an IFD even if it is subject to the Allee effect. While, the relocation strategy is similar to that observed for populations that follow a logistic growth-pattern, the evolution problem is significantly more complicated for population subject to an Allee effect, as we will see below.

It turn out that if $A = \ln(m)$ where m is the heterogeneous carrying capacity a population, given appropriate initial distributions, can achieve an IFD. In this case system (8) take the following form:

$$\begin{cases} u_t = \mu\nabla \cdot (\nabla u - \chi u \nabla \ln m) + f(x,u), x \in D,\ t > 0, \\ (\nabla u - \chi u \nabla \ln m) \cdot \vec{n} = 0,\ x \in \partial D, t > 0, \\ u(x,0) = u_0(x),\ x \in D, \end{cases} \tag{27}$$

with no-flux boundary conditions and $f(x,u) = u(m(x)-u)(u-\theta(x))$. Note that the population is moving with a velocity field that is prescribed by the resources. Specifically, the log of the resources. By inspection we can see that $u = m$ is in fact an equilibrium solution to (27) when $\chi = 1$. We refer to the movement strategy modeled by:

$$\mathcal{M}[u] = \mu\nabla \cdot (\nabla u - u\nabla \ln m),$$

as the IFD strategy, because $u = m$ is an equilibrium solution to $u_t = \mathcal{M}[u] + g(x,u)u$. To see that (27) has a maximum principle we again use the change of variable, $v = um^{-\chi}$, to obtain the following system for v:

$$\begin{cases} v_t = \mu m^{-\chi}\nabla \cdot (m^{\chi}\nabla v) + m^{-\chi} f(x, vm^{\chi}), x \in D,\ t > 0 \\ \nabla v \cdot \vec{n} = 0,\ x \in \partial D. \\ v(x,0) = u_0(x)m^{-\chi},\ x \in D, \end{cases} \tag{28}$$

This is seen form the fact that $m^{-\chi}\nabla \cdot (m^{\chi}\nabla v) = \Delta v - m^{-\chi}\nabla(m^{\chi}) \cdot \nabla v$. Moreover, equation (28) also has an energy:

$$E_1[v] := \int_D \frac{\mu}{2} m^{\chi} |\nabla v|^2 - m^{-\chi} F(x, m^{\chi} v)\, dx, \tag{29}$$

where F is defined as before. This can also be seen from our discussion in section 1.2.1 by noting that $A = \ln(m)$. Note that the results in this section to not require that A satisfy (A3).

4.1 The IFD Strategy as a Neighborhood Invader Strategy

It is of interest to understand what happens under competition between populations who are using different relocation strategies. There are many ways to assess whether a movement strategy is "good." For example, a strategy is said to be *evolutionarily stable* if a population using that strategy can withstand invasion by another species employing a different movement strategy, if that invading species is initially small. A different but similar concept is that of a *neighborhood invader strategy* which, in our context, is a movement strategy that can invade, even if small, an established population. The main result of this section is that the IFD strategy is a local neighborhood invader. This means that if there is an established population v, so v is at an equilibrium, not employing an IFD movement strategy but close (this will be made precise below), then a population using the IFD movement strategy can invade, even if initially small.

We will only address the case when the movement strategies are sufficiently close. For us, what this means is that the established species has an equilibrium that is larger than the Allee effect threshold, *i.e.* $v \geq \theta$. To make this result precise, consider the system of equations:

$$\begin{cases} u_t = \mathcal{M}_u u + g(x, u+v)u, & x \in D,\ t > 0, \\ v_t = \mathcal{M}_v v + g(x, u+v)v, & x \in D,\ t > 0, \\ u(x,0) = u_0(x), v(x,0) = v_0(x), \end{cases} \tag{30}$$

equipped with no-flux boundary conditions. Here, $\mathcal{M}_u$ and $\mathcal{M}_v$ are used denote the movement strategy operators for u and v, respectively. For example, consider $g(z) = (z - \theta(x))(m(x) - z)$ and fix $\mathcal{M}_u$ to be the IFD strategy.

Because of the Allee effect built into $g(x, u+v)$, the system (30) is cooperative at low densities, but competitive at high densities. Thus, it is not monotone in general, which presents challenges in its analysis. Because it is cooperative at low densities, the presence of "competitors" can actually be beneficial at low densities, but would be detrimental at high densities. This phenomenon has been noted in certain ecological situations, see for example [29].

If we consider the system of ordinary differential equations

$$\begin{aligned} \frac{du}{dt} &= g(u+v)u, \\ \frac{dv}{dt} &= g(u+v)v \end{aligned} \tag{31}$$

where $g(z) = (m - z)(z - \theta)$ for constants $m > \theta > 0$, it is easy to see that it is cooperative when $u+v$ is small but competitive when $u+v$ is large. In fact, we can add the equations to see that for $w = u + v$ we have $dw/dt = g(w)w$. In a situation where $u(0) < \theta$, but $u(0) + v(0) = w(0) > \theta$, if only individuals of one type, say u, are present initially then $u \to 0$ as $t \to \infty$, but if both types u and v are present then $u + v \to m$ as $t \to \infty$, so each benefits the other at low densities. However, at equilibrium the size of the population of each type will generally be less than m, which is what it would be for either type on its own if its initial density were greater than θ and the other type were not present. Thus, it is advantageous to each population for the other to be present if both are present initially at low densities, but it is not advantageous to a population with initial data larger than θ. Something similar happens if both populations simply diffuse at the same rate and have Neumann boundary conditions. However, if the populations have different dispersal patterns, or even just different diffusion rates, it seems difficult to verify similar behavior analytically.

Theorem 4 (IFD Strategy as a Neighborhood Invader)**.** *Let $\mathcal{M}_v = \mu\nabla\cdot(\nabla v - \chi v\nabla A)$, where A is an admissible signal and with $\chi > 0$ chosen to guarantee that the problem:*

$$\mathcal{M}_v + g(x, v)v = 0,\ x \in D, \tag{32}$$

with no-flux boundary conditions has a positive stable equilibrium $v^*(x) > \theta(x)$ for all $x \in D$. Then IFD movement strategy, $\mathcal{M}_u = \mu\nabla\cdot(\nabla u - u\nabla \ln m)$, is a local neighborhood invader strategy, in the sense that it can invade an established population at equilibrium if their movement strategy is given by (32)*.*

The key to studying if a population employing a certain movement strategy is a neighborhood invader is to understand the stability of the equilibrium $(0, v^*)$ to system (30). If it is unstable then we see that even a small perturbation of the equilibrium will lead to the population u being able to establish itself.

Proof. Let v^* be the equilibrium solution to (32) with the property that $v^* > \theta$. Linearizing the first equation of (30) about the equilibrium $(0, v^*)$ gives the following eigenvalue problem:

$$\mathcal{M}_u\phi + g(x, v^*)\phi = \sigma\phi, \quad x \in D,$$

with no-flux boundary conditions. Performing the change of variables $\varphi = \frac{\phi}{m}$ we see that

$$\mathcal{M}_u[\phi] = \mu\nabla\cdot(\nabla\phi + \phi\nabla \ln m) = \mu\nabla\cdot(m\nabla\varphi)$$

and $\nabla\varphi \cdot \vec{n} = 0$ on ∂D. Thus, the eigenvalue problem for φ is

$$\mu\nabla \cdot (m\nabla\varphi) + g(x, v^*)m\varphi = \sigma m\varphi.$$

Dividing by φ, integrating over D, and then integrating the first term by parts (note we apply the no-flux boundary conditions) we obtain that:

$$\int_D \mu \frac{m\,|\nabla\varphi|^2}{\varphi^2} + g(x, v^*)m\; dx = \sigma \int_D m\; dx. \tag{33}$$

Moreover, integrating (32) and using the no-flux boundary conditions we obtain that:

$$\int_D g(x, v^*)v^*\; dx = 0$$

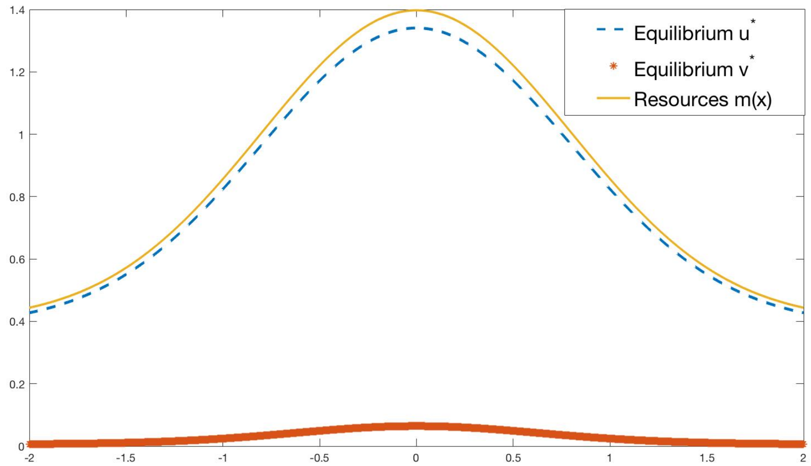
and thus we can rewrite (33) and obtain a lower bound:

$$\begin{aligned} \sigma \int_D m\; dx &= \int_D \mu \frac{m\,|\nabla\varphi|^2}{\varphi^2} + g(x, v^*)(m - v^*)\; dx \\ &\geq \int_D g(x, v^*)(m - v^*)\; dx \\ &= \int_D (v^* - \theta)(m - v^*)^2\; dx, \end{aligned} \tag{34}$$

where the last term in the above series of inequalities is positive since $v^* > \theta$. Thus, $(0, v^*)$ is unstable. $\square$

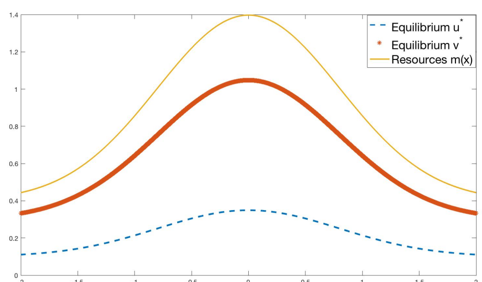
Remark 5. Theorem 4 requires that the established group, here denoted by v, is at a stable equilibrium $v^* \geq \theta$. See Theorem 3, Remark 3, and Proposition 1 for sufficient conditions that guarantee that $v^* \geq \theta$ is stable.

An interesting numerical observation is that movement strategies are more important than initial density or investment. For example, in Figure 5 we observe that if u follows the IFD strategy and v follows the strategy $\mathcal{M}_v[v] = \nabla \cdot [\nabla v - 2v\nabla \ln(m)]$, that is more aggressively pursuing resources, then u is much better of in long run, even if initially it started with significantly less resources. Naturally, if both species use the same movement strategy then the initial distributions makes a difference. This can be observed in Figure 6. In Figure 6 (a) we have that the population v is much better off because it started with more resources initially. However, neither would have survived in the absence of the competitor, as is observed in Figure 6 (b), which illustrates the dynamics of the population v, but in the absence of the competitor u. In this case you see that v becomes extinct as $t \to \infty$.

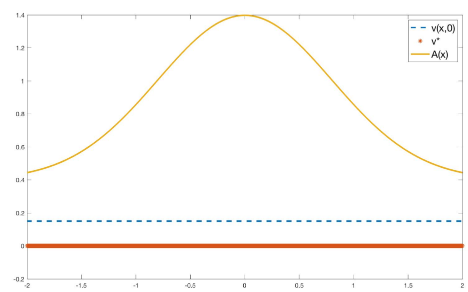


(a) Equilibrium solutions (u^*, v^*) to (30)

Figure 5: Equilibrium solutions for the competitive system (30) with the population u pursuing an IFD movement strategy $\mathcal{M}_u = [u_x - u\partial_x \ln(m)]_x$ and the population v pursuing the movement strategy given by $\mathcal{M}_v = [v_x - 2v\partial_x \ln(m)]_x$. Here the resources is given by a Gaussian and the initial data considered are $u_0(x) \equiv .05$ and $v_0(x) \equiv .2$



(a) Competition with $u_0(x) \equiv .05$ and $v_0(x) \equiv .15$

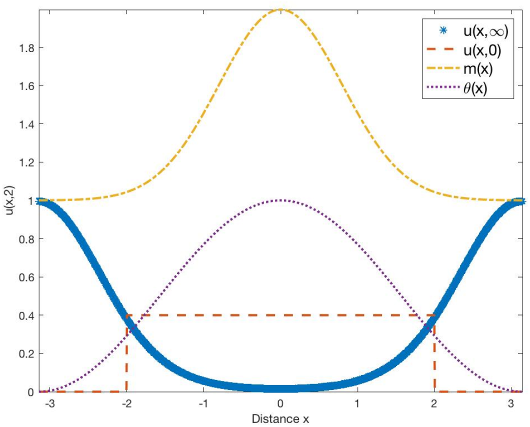


(b) Dynamics of v under no competition: $v_0(x) \equiv .15$

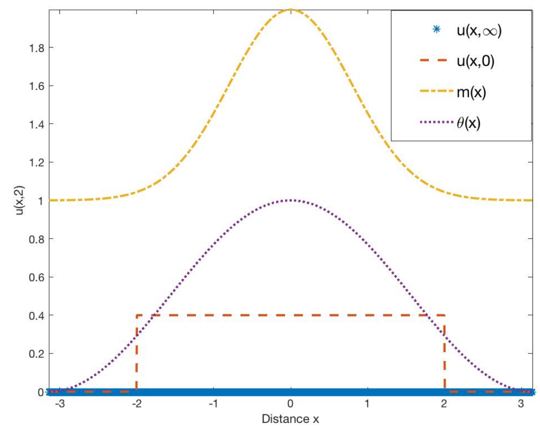
Figure 6: The left panel illustrates the solutions u and v to the competitive system (30), with both populations using an IFD movement strategy, once they have reached an equilibrium. The right panel illustrates the solution v, under no competition, once it reaches an equilibrium.

4.2 Comparing Movement Strategies: Numerical Results and Intuition

In the logistic growth-pattern case, it is clear that an IFD strategy is optimal. However, when an Allee effect is present, this is not so evident as using the resources as a signal may not be the most beneficial. Another reasonable movement strategy is moving down gradients of the Allee effect, assuming it is spatially heterogeneous. There are certain environments where, depending on the distribution of the initial population, it might be more beneficial for the species to use the Allee threshold as a signal rather than using the resources as a signal. Figure 7 illustrates such an example. You can observe the large time behavior of two populations with same initial data (dashed red line) but different movement strategies. Figure 7a illustrates movement down gradients of the Allee threshold and Figure 7b an IFD strategy. We can see that the population using the Allee threshold survives, but the population following the resources does not. Thus, when the Allee effect is present we need to differentiate with movement strategies that can help a population persist versus a movement strategy that are neighborhood invaders or evolutionarily stable.



(a) $\mathcal{M}(u) = (u_x + 3u\theta_x)_x$



(b) $\mathcal{M}(u) = (u_x - u\frac{m_x}{m})_x$

Figure 7: Large time behavior of populations with the same initial data (dashed orange line) but different movement strategies. Figure 7a illustrates results from the population moving down gradients of the Allee threshold and Figure 7b results from the population following an IFD strategy. Here, $\theta = \frac{1}{2}\cos(x) + \frac{1}{2}$ and a Gaussian resource function.

5 Discussion

We have analyzed the effect that movement strategies have on the persistence and/or extinction of a species subject to a strong Allee effect and competition. With regards to the first point, our main interest is to compare the effect of conditional dispersal, a combination of classical diffusion and a directed movement term where the species moves up gradients of some known signal, to that of the classical diffusion. We have shown that when the contribution of the biased movement is small then the population dynamics do not differ from that of the classical reaction-diffusion equation in the long-term. However, in the short term one does observe a concentration of the population in areas where the signal reaches a local maximum. If the biased diffusion effect is small, this is only a short lived effect. In order for the unbiased diffusion to help overcome the Allee effect, the effect has to be strong enough. We have numerically verified that this in fact does happen. In a current work in preparation we can show that in unbounded domains there are signals that do in fact help overcome the Allee effect.

We have also studied the effect of competition. In fact, we can see that, much like the logistic growth case, advecting up the log of the resources in addition to some dispersal can lead to an exact match of population and the resources. However, unlike the logistic growth case, the time evolution problem is more intricate. In addition, it is not always clear that a movement strategy leading to an IFD is always the best strategy. This highly depends on the resources and Allee effect threshold distributions as well as the initial distribution of the population. It would be interesting to explore the conditions under which a movement strategy leading to an IFD is suitable versus when moving down gradients of the Allee threshold is suitable. The difficulty here arises from the fact that the system is cooperative at low densities and competitive at high densities. A possible optimal strategy is one where populations cooperate with their competitors at low densities and, once the population density is sufficiently high, follow an IFD strategy.

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