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Research article

On the Allee effect and directed movement on the whole space

Chris Cosner[1] **and Nancy Rodríguez**[2,*]

[1] University of Miami, Department of Mathematics, 1365 Memorial Drive, Ungar 515, Coral Gables, FL 33146, USA

[2] CU Boulder, Department of Applied Mathematics, 11 Engineering Dr, Boulder, CO 80309, USA

* **Correspondence:** Email: rodrign@colorado.edu; Tel: +13034924668; Fax: +13034924066.

Abstract: It is well known that relocation strategies in ecology can make the difference between extinction and persistence. We consider a reaction-advection-diffusion framework to analyze movement strategies in the context of species which are subject to a strong Allee effect. The movement strategies we consider are a combination of random Brownian motion and directed movement through the use of an environmental signal. We prove that a population can overcome the strong Allee effect when the signals are super-harmonic. In other words, an initially small population can survive in the long term if they aggregate sufficiently fast. A sharp result is provided for a specific signal that can be related to the Fokker-Planck equation for the Orstein-Uhlenbeck process. We also explore the case of pure diffusion and pure aggregation and discuss their benefits and drawbacks, making the case for a suitable combination of the two as a better strategy.

Keywords: reaction-advection-diffusion equations; Allee effect; directed movement; evolutionary game theory

1. Introduction

Around 1930 Warder Clyde Allee experimentally showed that the survival rate of goldfish was positively correlated with population density. In [1] Allee documented his finding and concluded that aggregation and cooperation are beneficial for the survival of species. This effect was dubbed the Allee effect, which, informally, is the decreased individual fitness at low population densities [2–4]. Since its discovery, the Allee effect has been documented for many taxa and it is believed that social species are especially prone to it [5]. For example, many species, such as the prairie dogs, communicate via a social network that breaks down when the population density is low [6]. This positive dependence between fitness and population density can put these species at high danger of extinction due to habitat alterations or a decreased population that is, for example, due to hunting. Allee effects that cause the

existence of a critical population density necessary for persistence are called *strong* and those that do not are called *weak*. The critical population density needed in the case of the strong Allee effect is referred to as the *Allee threshold*.

Populations tend to use heterogeneities in the environment and positive influence of the presence of congeners to aggregate and take advantage of social structures [7]. Thus, on the one hand, species develop movement strategies by using environmental cues in order to aggregate and potentially increase their fitness. On the other hand, dispersal, i.e., the spreading of organisms from one location to another, has also been found to help populations establish themselves [8]. For example, dispersal can help populations control their size or expand their territory. While dispersal can be beneficial to species, in some situations it has been found to be detrimental. One example being the case of high dispersal rates, which can prevent the adaptation of a population to a new environment and hinder the survival of small populations [9]. In fact, aggregation and dispersal can be viewed as competing effects, and many works have studied this competition from a mathematical point of view; see [10–12] and the references therein. As mentioned earlier, population aggregation can occur in multiple ways. One way is by individuals moving toward areas where there is a high population density. This type of model has been studied extensively, see, for example [13, 14]. Alternatively, individuals can follow environmental cues [15], such as through taxis on an environmental signal. In [16] the authors considered aggregation in species subject to logistic growth through nonlinear diffusion, meaning that individuals slow down if the population density increases. They showed that this movement strategy, under Dirichlet boundary conditions, allows the population to persist on smaller domains than if they moved using linear diffusion. On the other hand, this movement strategy also produces an Allee effect for some parameter regimes. Naturally, different species will develop different movement strategies to optimize their survival and it is believed that species subject to a strong Allee effect might benefit from aggregation more than species subject to a weak Allee effect or to logistic growth. In [17], Fernandez and collaborators used differential equations and stochastic simulations to compare the survival of species when individuals moved between patches either using individual information or collectively moving though trail setting and following behavior. They found that collective movement was more advantageous than individual movement only when the Allee effect was sufficiently strong.

For this paper we are interested in understanding the benefits of dispersal versus aggregation as movement strategies, in particular for species which are subject to the strong Allee effect. Specifically, we are motivated by the question of whether a population can employ specific movement strategies to overcome a strong Allee effect. The notion of "overcoming the Allee effect" will be made mathematically precise in what follows; but in essence, it means that a population with initial resources that would lead to extinction, if the species were to only employ dispersal as a movement strategy, would otherwise persist if it instead also aggregated. Recall that classical spatially explicit population models typically use simple diffusion to describe dispersal; see [8]. However, in recent years there has been considerable interest in models that include some type of biased movement. There are two natural phenomena that give rise to such biased movement. The first is movement by physical advection, such as movement in rivers. This movement is typically unidirectional, constant, affects all populations in a similar way and often does not involve behavior on the part of the individuals. The second is taxis along environmental gradients in heterogeneous environments, such as 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 be-

havioral considerations and the perceptual and cognitive abilities that allow people or organisms to sense and respond to their environment. An early paper on population dynamics in the presence of physical advection is [18]; some representative results on that topic are given in [19–22]. More references and discussion on models with physical advection can be found in [23]. Early papers on taxis along environmental gradients include [24, 25] and further discussion and references for that class of models are given in [15]. A related class of models involves movement biased by the density of the population itself or another population with which it interacts; see for example [26–29]. A discussion of models with physical advection versus models for directed movement and additional references is given in [30].

Here, we specifically explore the benefits of dispersal and aggregation movement strategies and the benefits of a balance between the two, i.e., when the population occupies the whole space. The aggregation will come from the species following a directed movement strategy. In particular, they will be advected by a spatially heterogeneous environmental signal, which provides the velocity field that advects the population. We are motivated by some numerical experiments presented in [31] that illustrate that directed movement via certain signals can indeed aid a population in overcoming the Allee effect. In other words, there are environmental signals for which a population that is initially below the Allee threshold and moving with a combination of unbiased and directed movement, as defined by the environmental signal, can persist. The numerical experiments presented in [31] are complemented with a partial theoretical result. Specifically, it is proved that for initial data below, but close to the Allee threshold, the population will, at some point in time, be larger than the Allee threshold in certain regions. More or less, the concentration happens in regions where the spatially heterogeneous signal is larger than its average. However, this concentration need only be for a finite amount of time. Indeed, if the directed movement is not sufficiently strong, then the population eventually becomes extinct. The proof required a change in convexity of the environmental signal, which made it challenging for the development of super and sub-solutions at the boundary, to prove a global-in-time result. To make progress on the theoretical side we study the problem in the whole space, which removes the challenge of working with the boundary, but it adds the challenge of finding global-in-time solutions for a model with unbounded coefficients in an unbounded domain.

1.1. Summary of results

The questions motivating us here force us to work with reaction-advection-diffusion models with unbounded coefficients in the whole space. Thus, the first issue we must address is that of the global existence and uniqueness of classical solutions to these models. Note that the global-in-time existence of classical solutions does not follow from classical theory due to the unbounded nature of the coefficients in the equations that we study. Instead, we prove global existence of solutions using ideas from the Krzyżański Method, first introduced in [32] to study the global existence of solutions to the Cauchy problem for a general class of second order linear parabolic equations in non-divergence form with unbounded coefficients.

In terms of the dynamics of the solutions, we observe that when the initial population is bounded at all locations, but has unbounded mass, that is $u_0 \in L^\infty(\mathbb{R}^n)$ but $u_0 \notin L^1(\mathbb{R}^n)$, then species can overcome a strong Allee effect if they aggregate sufficiently fast. This is true even if the initial population is below the Allee threshold at every point. More specifically, we show that super-harmonic signals can help a population overcome the Allee threshold, thus populations with initial data that would not survive with

the simple use of random motion can indeed persist if the directed movement is sufficiently strong. In such cases, the population survives even under a purely aggregative movement strategy through pure taxis. One example of such a signal comes from the Fokker-Planck equation for the Orstein-Uhlenbeck process, where the signal is given by $A = -\frac{1}{2}x^2$. It is important to note that with the same initial conditions, the population would not survive if it employed only dispersal as a movement strategy. We also show that subharmonic signals are detrimental to the population and that directed movement along those signals can cause a population to go extinct, when it would otherwise have persisted under a simple diffusion strategy.

If we require that the initial population have bounded mass, that is $u_0 \in L^\infty(\mathbb{R}^n) \cap L^1(\mathbb{R}^n)$, then the situation is quite different. We show that pure diffusion is more beneficial for a population than pure aggregation. In fact, a population with initial data with compact support will never survive under pure aggregation. Moreover, we use a scaling argument to show that a combination of the two movement strategies is better than employing only one of either of these strategies. This scaling argument is verified through various numerical experiments; see Figure 1 for an illustration of the results. A relevant result in this direction was obtained by Chen *et al.* who studied pairs of competing populations subject to logistic growth in heterogeneous environments and showed in [33] that if the diffusion effect is large, but advection on resource gradients is small, then increasing advection relative to diffusion is beneficial for a population. However, if the diffusion effect is small then the opposite result holds.

We are also interested in understanding the connection between the unbounded domain and the bounded cases, specifically, we study the bounded domain case with Neumann boundary conditions. For the bounded domain case with zero-Neumann boundary conditions we obtain similar results to those obtained on the whole space.

Outline: We present the modeling framework and main results in Section 2. Section 3 considers the case of infinite resources, that is $u_0 \in L^\infty(\mathbb{R})$, as well as the connections to the bounded domain problem. Section 4 considers the case when we have initial data in $L^1(\mathbb{R}^n) \cap L^\infty(\mathbb{R}^n)$.

2. Background and model

In this section we discuss our modeling framework, some previous results that are relevant to this work, and some assumptions. We begin by discussing some aspects of the dynamics of solutions to the classical reaction-diffusion equation that are relevant to our story. In the most general context, without competition, we will work with the following modeling framework:

$$\begin{cases} \partial_t u(x,t) = \mathcal{M}[u] + g(x,u)u, & x \in \mathbb{R}^n,\ t > 0, \\ u(x,0) = u_0(x),\ x \in \mathbb{R}^n, \end{cases} \tag{2.1}$$

where $\mathcal{M}$ is an operator modeling the movement of a population $u : \mathbb{R}^n \times [0,\infty) \to [0,\infty)$ and u_0 is the initial distribution of the population.

2.1. Dynamics of classical reaction-diffusion equations

Classically, dispersal has been represented by linear diffusion, modeling random dispersal of individuals in the population. In such a case, we have $\mathcal{M}[u] = \mu\Delta u$. Specifically, the process of dispersal and growth/decay on the whole space has been traditionally modeled by the now classical reaction-

diffusion equation:

$$\begin{cases} u_t = \mu\Delta u + f(u,x),\ x \in \mathbb{R}^n,\ t > 0, \\ u(x,0) = u_0(x); \end{cases} \tag{2.2}$$

see for example [8, 34] and the references therin. In such a model the species does not take the environment or population density into account when making movement decisions. When the population is subject to logistic growth this equation is known as the Fisher-KPP equation, which has been the subject of much interest; see for example [35–37] and the references therein. For a population that is subject to the Allee effect the prototypical reaction term is given by $f(u) = u(1-u)(u-\theta)$ with $0 < \theta < 1$. Note that at the microscopic level, individuals are simply moving randomly here.

2.1.1. Long-term behavior of solutions on $\mathbb{R}$

The spatio temporal dynamics of populations subject to the Allee effect can be quite complex because the population grows at high densities but decays at low densities. It is, however, beneficial to understand the dynamics of solutions to (2.2) in two specific cases, i.e., in the case of infinite resources, that is $u_0 \in L^\infty(\mathbb{R})$ but not $L^1(\mathbb{R})$ and, in the case of $L^1(\mathbb{R})$ initial data (more specifically when u_0 has compact support).

Consider a population whose density is denoted by u, and whose spatio-temporal dynamics are governed by (2.2) with constant initial data u_0 and $f(u) = u(1-u)(u-\theta)$. If $0 \le u_0 < \theta$, then $u(x,t) \to 0$ uniformly in x as $t \to \infty$ on compact sets. On the other hand, if $\theta < u_0 < 1$, then $u(x,t) \to 1$ uniformly on compact sets as $t \to \infty$ (note that one is carrying capacity here). Of course, in this case, the initial data are not in $L^1(\mathbb{R})$. On the other hand, we can consider now what happens to a population whose initial distribution has compact support; for simplicity take $u_0 = \mathbb{1}_{[-L,L]}$. In [38], Aronson and Weinberger showed that if L is sufficiently large, the population will persist, but it will go extinct if L is too small. Later in [39], Zlatos proved that there exists a critical threshold, L^*, separating persistence versus extinction. More precisely, if $L < L^*$ then $u(x,t) \to 0$ as $t \to \infty$, uniformly on compact sets. On the other hand, if $L > L^*$ then $u(x,t) \to 1$ as $t \to \infty$, uniformly on compact sets. In the critical case, when $L = L^*$, the population approaches a non-constant, positive equilibrium solution. To understand the mechanisms at play we consider a simple scaling argument with the special case when $f(u) = ru(1-u)(u-\theta)$. Let us make the following change of variables:

$$\bar{x} = \frac{x}{x_c},\ \bar{t} = \frac{t}{t_c},\ \bar{u} = \frac{u}{u_c}, \tag{2.3}$$

where x_c, t_c and u_c are the characteristic length, time and solution scales to be determined later. Given the new variables Eq (2.2) becomes

$$\bar{u}_t = \frac{\mu t_c}{x_c^2}\bar{u}_{\bar{x}\bar{x}} + t_c r\bar{u}(1-u_c\bar{u})(u_c\bar{u}-\theta),\ x \in \mathbb{R},\ t > 0.$$

If we consider initial data $u_0(x) = \mathbb{1}_{[-L,L]}$, then the natural characteristic length scale is $x_c = 2L$, which is the size of the support of the initial data. One can consider various time scales, but let us look at the reaction time scale, $t_c = \frac{1}{r}$, and let $u_c = 1$. We then obtain the following equation:

$$\bar{u}_t = \beta u_{\bar{x}\bar{x}} + \bar{u}(1-\bar{u})(\bar{u}-\theta),\ x \in \mathbb{R},\ t > 0, \tag{2.4}$$

where $\beta = \frac{\mu}{4rL^2}$. From this we can observe that for L large, the diffusion term is overpowered by the reaction term; thus, the population grows and can establish itself. On the other hand, when L is small, β is large and the diffusion overpowers the reaction term. Here, we expect the population to disperse and eventually approach zero on compact sets. Apparently the two terms should balance around the following value:

$$L_c = \sqrt{\frac{\mu}{4r}}.$$

This result gives an intuitive understanding of the results proved by Zlatos in [39] which are discussed above. Now, for constant initial data $u_0 \in (0, \theta)$, although the reaction term dominates, the population decays uniformly, as a consequence of the Allee effect.

Remark 1. In the case of constant initial data $u_0 \in (0, \theta)$, the solution to (2.2) approaches zero uniformly in compact sets. Thus, even if we have infinite resources, with this movement strategy the population does not survive.

2.2. *Passive diffusion with directed movement*

Let us now consider a reaction-advection-diffusion equation, which has been used heavily in the study of spatial ecology; see for example [15, 34, 40] and the references therein. Specifically, we study the evolution of a population density:

$$\begin{cases} u_t = \nabla \cdot (\mu \nabla u - \chi u \nabla A) + g(x, u)u, \ x \in \mathbb{R}^n, \ t > 0, \\ u(x, 0) = u_0(x), \ x \in \mathbb{R}^n, \end{cases} \tag{2.5}$$

with g as a bistable-type growth function, modeling the Allee effect. Note that we assume that $0 < \theta(x) < m(x)$ for all $x \in \mathbb{R}$. In Eq (2.5), the function A provides an environmental signal for the biased movement. We work with *admissible signals*, A, which satisfy the following:

(A1) $A \in C^{2+\alpha}(\mathbb{R}^n)$;
(A2) $|\nabla A| \le c_1 \sqrt{\left(1 + |x|^2\right)}$ and $-\Delta A(x) \le c_2$ for some $c_1, c_2 \in \mathbb{R}$ and all $x \in \mathbb{R}^n$;

denote *admissible growth patterns* by $g(x, u)u$ with g satisfying:

$$\begin{aligned} g(\theta(x)) = g(m(x)) \ &= 0, g(z) < 0 \text{ for } z \in (-\infty, \theta(x)) \cup (m(x), \infty), \\ &g(z) > 0 \text{ for } z \in (\theta(x), m(x)) \end{aligned} \tag{2.6}$$

such that m and θ are bounded and sufficiently smooth so that the following is true:

(A3) $g \in C^2(\mathbb{R}^n \times [0, \infty))$;
(A4) $0 < \theta(x) < m(x) \le M$ for all $x \in \mathbb{R}^n$ and $0 < M < \infty$;
(A5) $\lim_{z \to \infty} g(x, z) = -\infty$ for all $x \in \mathbb{R}^n$.

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

$$g(x, z) = (m(x) - z)(z - \theta(x)), \tag{2.7}$$

where m represents the resources and θ represents the Allee effect threshold.

2.3. Global existence and equilibrium solutions

In this section we discuss the fundamental question of the global-in-time existence of solutions to (2.5). We make use of the Krzyżański method [32], which involves constructing an auxiliary function $H(x,t)$, rewriting the equation in terms of $u/H(x,t)$ and solving the new equation in small time steps, which is needed in the construction of H. This affords one more control mechanism for the growth of the coefficients and the solution as $|x| \to \infty$. Here, the type of non linearities that are of interest to us eliminate the need for the functional, H, and we can construct a solution in a more direct way. The main idea is to solve the problem on bounded domains with Dirichlet boundary conditions. We construct a sequence of solutions, each with a larger domain, that is monotonically increasing. Then, using standard interior estimates for parabolic equations, we can construct a diagonal sequence of such solutions that converge to a solution on the entire space.

Theorem 1. Assume that the assumptions (A1)–(A5) hold and $u_0 \in C_b(\mathbb{R}^n)$. Then, for any $T > 0$ there exists a solution $u \in C^{2,1}(\mathbb{R}^n \times (0,T)) \cap C(\mathbb{R}^d \times [0,T])$ to (2.5) with initial data u_0.

Proof. For the proof, it is useful to recast Eq (2.5) as follows:

$$\begin{cases} u_t = \mu\Delta u - \chi\nabla u \cdot \nabla A - \chi u\Delta A + f(x,u)u, \ x \in \mathbb{R}^n, \ t > 0, \\ u(x,0) = u_0(x), \ x \in \mathbb{R}^n, \end{cases} \tag{2.8}$$

where $f(x,u) = -\chi\Delta A + g(x,u)$. Note that, by the conditions $(A2)$ and $(A5)$ there exists a constant $K > 0$ such that $f(x,z) < 0$ if $z \geq K$. We first study an auxiliary problem cast on a bounded domain. For this purpose, consider the parabolic domain $D_T^R = B_R \times (0,T]$ where $B_R = \{x \in \mathbb{R}^n : |x| < R\}$, as defined for any $R, T > 0$. Then, consider the following problem:

$$\begin{cases} u_t = \mu\Delta u - \chi\nabla u \cdot \nabla A - \chi u\Delta A + f(x,u)u, \ x \in D_T^R, & \text{(2.9a)} \\ u(x,0) = u_0(x), \ x \in B_R, & \text{(2.9b)} \\ u(x,t) = 0 \text{ for } (x,t) \in \partial B_R \times (0,T]. & \text{(2.9c)} \end{cases}$$

System (2.9) is a standard reaction-advection-diffusion equation on a bounded domain. Consequently, it has a comparison principle and $u \equiv K + 1$ is a supersolution to System (2.9). Moreover, for non-negative initial data, u_0, which is not identically zero there is a unique positive solution. We denote this solution defined on D_T^R, for $R > 1$, by u_R. Furthermore, note that $\sup_{(x,t)\in D_T^R} u_R(x,t) \leq K + 1$, which is independent of R.

Now, as $B_R \subset B_{R+1}$, it follows that u_R and u_{R+1} both satisfy (2.9a) on D_T^R. Additionally, given that $u_R = 0$ on ∂D_R^T and $u_{R+1} > 0$ on ∂D_R^T, it holds that $u_{R+1}(x,t) \geq u_R(x,t)$ for all $(x,t) \in D_T^R$. Similarly, we conclude that $u_{R+2} \geq u_{R+1}$ on D_T^{R+1} and, consequently on D_T^R. Through this process we obtain a sequence of functions $\{u_{R+n}\}_{n=1}^{\infty}$, that solve (2.9a) on D_T^{R+1}. Moreover, on D_T^R, the sequence of functions are monotonically increasing:

$$u_{R+n} \geq u_{R+n-1} \quad \text{in} \quad D_T^R \quad \text{for all} \quad n \in \mathbb{N}$$

and uniformly bounded by $K + 1$. As a consequence, the sequence of functions converge pointwise to a function, u_R^*, on D_T^R. Moreover, by the Lebesgue dominated convergence theorem we also have that:

$$u_{R+n}^p \to (u_R^*)^p$$

for all $p \geq 1$. Due to the smoothness imposed on the equation coefficients by the conditions $(A1)$–$(A4)$ we obtain standard interior parabolic estimates that guarantee that $u_{R+n} \in W_p^{2,1}(\overline{B_{R-1}} \times (0,T])$ [41].

Thus, by a Sobolev embedding

$$u_{R+n} \in C^{2+\alpha,1+\frac{\alpha}{2}}(\overline{B_{R-1}} \times (0,T])$$

for $0 < \alpha < 1$. Then, there is a subsequence of $\{u_{R+n}\}_{n=1}^{\infty}$ that converges in $C^{2,1}(\overline{B_{R-1}} \times (0,T])$ to a solution of (2.9a) on D_T^{R-1}, which must be u_R^*.

We denote the subsequence of functions of $\{u_{R+n}\}_{n\geq 1}$, defined above on D_T^{R+1} by $\left\{u_{0,k}^R\right\}_{k\geq 1}$. By a similar regularity argument as discussed above, we can extract a subsequence of $\left\{u_{0,k}^R\right\}_{k\geq 1}$ that converges to a function, u_{R+1}^*, on D_T^R, which is a solution to (2.9a) and must equal u_R^* in D_T^{R-1}. Denote such a subsequence by $\left\{u_{1,k}^R\right\}_{k\geq 1}$. We continue with this process, for $m > 2$ the subsequence $\left\{u_{m,k}^R\right\}_{k\geq 1}$ converges to a function u_{R+m}^*, which is a solution to (2.9a) on D_T^{R+m-1}. Moreover, it is equal to u_{R+m-1}^* on D_T^{R+m-2}. We see that the diagonal sequence $\left\{u_{k,k}^*\right\}_{k\geq 1}$ converges to a function, which we can call u^* on D_T^R for any R. Note that the function u^* thus satisfies (2.8).

To prove uniqueness, assume that u and v are two bounded solutions to (2.8). Let $w = u - v$; then, w is bounded and satisfies the following:

$$\begin{cases} w_t = \mu\nabla \cdot (\nabla w - \chi w \nabla A) + h(x,t)w, \ x \in D_T^R, & \text{(2.10a)} \\ w(x,0) = 0, \ x \in \mathbb{R}^n, & \text{(2.10b)} \end{cases}$$

where $h(x,t) = g(u,x)u - g(v,x)v$ is a bounded function. It follows by Theorem 1 in [42] that $w \equiv 0$ and thus $u \equiv v$.

We remark that Theorem 1, follows from Theorem III in [43], which also uses a version of the Krzyżański method. Actually, Theorem III in [43] only gives a local-in-time solution; however, in our case it directly implies global-in-time existence, because the nonlinearity in our system provides a global a priori bound on solutions. We have included the proof of global existence in order to keep this paper self-contained as well as to provide a shorter and more direct proof for our particular problem. Additionally, Theorem 1 in [42] implies that a comparison principle is available for System (2.5), which affords us the use of super- and sub-solutions.

Definition 1 (Super-solutions and sub-solutions)**.** A function $w \in C^2(\mathbb{R}^n)$ is a **super-solution** to (2.5) if it satisfies the following:

$$w_t \geq \mu\nabla \cdot (\nabla w - \chi w \nabla A) + g(x,w)w, \ x \in \mathbb{R}^n, \ t > 0. \tag{2.11}$$

A function $w \in C^2(\mathbb{R}^n)$ is a **sub-solution** to (2.5) if it satisfies (2.11) with the inequality reversed.

As a consequence of Theorem 1 and the comparison principle we obtain the existence of at least one positive equilibrium solution to (2.5). This relies on the now-classical technique that dates back to Aronson and Weinberger [44].

Theorem 2 (Existence of equilibrium solutions). Assume that the conditions for Theorem 1 hold. Additionally, assume that Eq (2.5) admits a strict sub-solution, $u_0(x)$, which is bounded. There exists at least one positive equilibrium solution to Eq (2.5).

Proof. From Theorem 1 we know that System (2.5) has a global classical solution $\tilde{u}$ with initial data $u(x,0) = u_0(x)$, where u_0 is the strict sub-solution. Note that any constant function, u_1, is a super-solution if it satisfies the condition that $u_1 > \sup_{x\in\mathbb{R}^n} u_0(x)$. Since u_0 is a strict sub-solution we see that

$$\mu\nabla\cdot(\nabla u_0 - \chi u_0\nabla A) + g(x,u_0)u_0 > 0;$$

thus, $\tilde{u}_t(x,0) > 0$ for all $x \in \mathbb{R}^n$. Hence, we know that $\tilde{u}(x,t) > \tilde{u}(x,0)$ by the strong maximum principle applied on bounded regions. We define $w(x,t) = \tilde{u}(x,t+\delta)$ for some arbitrary $\delta > 0$ and note that w is a solution to (2.5), as the equation is autonomous in time. Moreover, $w(x,0) = \tilde{u}(x,\delta) > \tilde{u}(x,0)$; thus, by the comparison principle we have that $\tilde{u}(x,t+\delta) = w(x,t) > \tilde{u}(x,t)$.

Since, δ was arbitrary we see that $\tilde{u}(x,t)$ is increasing in time. However, $\tilde{u}(x,t) < u_1$ and thus $\tilde{u}(x,t) \to u^*(x)$ as $t \to \infty$ pointwise in x. Furthermore, classical local parabolic interior estimates on bounded domains imply that u^* has to be smooth and satisfy (2.5).

3. Case of infinite resources: $u_0 \in L^\infty(\mathbb{R})$

The first result in this section states that for general super-harmonic signals, a population can overcome the Allee effect provided that the signal used by the population provides a sufficiently strong pull from infinity. However, if the signal pull is too weak, then the population will approach zero in the long term if the initial population is below the Allee threshold; thus, the population is unable to overcome the Allee effect through aggregation. The strength of pull of the signal is represented in the coefficient χ.

Theorem 3 (Super-harmonic signal). Let A and g respectively represent an admissible signal and growth pattern with

$$-A_0 \le \Delta A(x) \le -A_1 < 0 \quad \text{for all} \quad x \in \mathbb{R}^n. \tag{3.1}$$

Moreover, let u be the $C^{2,1}(\mathbb{R}^n\times[0,\infty))$ solution to (2.5) with constant initial data $0 < u_0 < \inf_{x\in\mathbb{R}^n}\theta(x)$. There exist constants $0 < \underline{\chi}(u_0,A) < \overline{\chi}(u_0,A)$ such that, if

(i) If $\chi < \underline{\chi}$ then $u(x,t) \to 0$ as $t \to \infty$ uniformly for all $x \in \mathbb{R}^n$;
(ii) If $\chi > \overline{\chi}$ then $u(x,t) \to u^*(x)$ as $t \to \infty$ for all $x \in \mathbb{R}^n$, where u^* is a positive equilibrium solution to (2.5).

Remark 2. For more general signals, A, that satisfy $\Delta A(x) \le -A_1 < 0$ for all $x \in \mathbb{R}^n$, such as those in one dimension for $A(x) = -a_4x^4 - a_2x^2 + a_1x + a_0$ with $a_4, a_2 > 0$ and $a_0, a_1 \in \mathbb{R}$, part (ii) of Theorem 3 also holds.

For a specific case, connected to the Fokker-Planck equation for the Orstein-Uhlenbeck process, we obtain the following sharp result. This connection is explained in more detail after the statement of the result.

Theorem 4 (Sharp result). Let g be an admissible growth pattern, u be the solution to (2.5) with $A(x) = -A_0x^2$ with $A_0 > 0$ and initial data u_0 be a positive constant with $0 < u_0 < \inf_{x\in\mathbb{R}^n}\theta(x)$. There exist $0 < \chi^*(u_0,A)$ such that the following is true:

(i) If $\chi < \chi^*$ then $u(x,t) \to 0$ as $t \to \infty$ for all $x \in \mathbb{R}^n$;

(ii) If $\chi > \chi^*$ then $u(x,t) \to u^*(x)$ as $t \to \infty$ for all $x \in \mathbb{R}^n$, where u^* is a positive equilibrium solution to (2.5).

Remark 3. The results of Theorem 4 continue to hold for signals of the form $A(x) = -a_2x^2 + a_1x + a_0$ with $a_2 > 0$ and $a_1, a_0 \in \mathbb{R}$.

The Ornstein-Uhlenbeck process [45] is a stochastic process with applications in financial mathematics, where it is commonly known as the Vasicek model [46]; in the physical sciences, where it models large Brownian particles under the influence of friction [47]; and in evolutionary biology, improving the Brownian motion selection of changes in organism phenotype [48]. This stochastic process is given by the stochastic differential equation:

$$dx_t = -\alpha x_t\, dt + \sigma dW_t,$$

where $\alpha, \sigma > 0$ and W_t represents a Wiener process. We can interpret this stochastic process as a modification of Brownian motion where particles are drawn to the central location at $x = 0$. The pull of the particle towards the origin is strengthened as the particles move further away from the origin. It can be described in terms of the evolution of a probability density function, $u(x,t)$, specifying the probability of finding the process in state x at time t. The evolution equation for u is given by the Fokker-Planck equation:

$$u_t = \frac{\sigma^2}{2}\Delta u + \alpha\nabla\cdot(xu). \tag{3.2}$$

Note that (2.5) corresponds to (3.2) with $\mu = \frac{\sigma^2}{2}$ and $A(x) = -\alpha\mu\frac{x^2}{2}$, for which we obtain the sharp result stated in Theorem 4.

Finally, we obtain that for strictly subharmonic signals, if the directed movement is sufficiently fast, then the population will always become extinct, even if initially it is above the Allee threshold.

Theorem 5 (Sub-harmonic signal). Let A and g respectively represent an admissible signal and growth pattern with

$$\Delta A(x) \geq A_1 > 0 \quad \text{for all} \quad x \in \mathbb{R}^n. \tag{3.3}$$

Moreover, let u be the $C^2(\mathbb{R}^n \times [0,\infty))$ solution to (2.5) with positive constant initial data, u_0. There exist constants $0 < \chi^* = \chi^*(u_0, A_1)$ such that if $\chi > \chi^*$, then $u(x,t) \to 0$ as $t \to \infty$ uniformly for all $x \in \mathbb{R}$.

To prove Theorems 3 and 4 we need the following lemma. First, we show the existence of super- and sub-solutions.

Lemma 1 (Super versus subsolution)**.** *Let A satisfy the conditions of Theorem 3 and $v = u_0 < \theta$. For $\chi > \overline{\chi}$ with*

$$\overline{\chi} := -\frac{g(u_0)}{A_1\mu} \tag{3.4}$$

v is a sub-solution and for $\chi < \underline{\chi}$ with

$$\underline{\chi} = -\frac{g(u_0)}{A_0\mu}, \tag{3.5}$$

v is a super-solution.

Proof. Let $v = u_0 < \theta(x)$ for all x and define the operator $L[w] = \mu\nabla \cdot (\nabla w - \chi w \nabla A) + g(x, w)w$. We show that v is a sub-solution for χ sufficiently large. Note that we simply need to show that $Lv \geq 0$. For this purpose, we compute the following, taking into account that $L[w] = \mu\left(\Delta w - \chi w \Delta A - \chi \nabla w \cdot \nabla A\right)$:

$$Lv \geq (\chi \mu A_1 + g(u_0)) > 0,$$

provided that (3.4) holds, in which case v is a sub-solution However, if χ satisfies (3.5) then we have

$$Lv \leq (\mu\chi A_0 + g(u_0))v < 0,$$

in which case v is a super-solution.

We are now in the position to prove Theorem 3.

Proof. (Theorem 3) Let u_0 be a constant which is below $\theta(x)$ for all x. To prove (ii) consider the case when $\chi > \overline{\chi}$. We have by Lemma 1 that $v = u_0$ is a sub-solution. Moreover, for a fixed χ, take $\overline{u}$ as constant. Then we have

$$L\overline{u} \leq \mu\chi A_0 \overline{u} + g(\overline{u})\overline{u} < 0,$$

provided that $\overline{u}$ is chosen sufficiently large. Note, that $v < \overline{u}$. Thus, if $u(x, 0) = u_0$ then $u(x, t) \nearrow w(x)$ where $w(x)$ is the minimal steady state sandwiched between v and $\overline{u}$. This solution can be constructed by using a standard monotone iteration scheme. Note that $w(x) > \theta(x)$ for all $x \in \mathbb{R}^n$.

To prove (i) consider $\chi < \underline{\chi}$ we have by Lemma 1 that $v = u_0$ is a super-solution. This implies that for $u(x, 0) = u_0$, $u(x, t) \searrow v(x)$ where $v(x)$ is the maximal equilibrium solution satisfying $0 \leq v(x) < u_0$. For contradiction, assume that $v(x)$ is non-zero. Let $v_1 := \max_{x\in D} v(x) < u_0$; thus, if $u(x, t)$ is a solution with initial data $u(x, 0) = v_1$ then we have that $u(x, t)$ decreases, which is a contradiction. We can then conclude that $v(x) \equiv 0$.

We now move on to the proof of Theorem 4.

Proof. (Theorem 4) The proof follows that of Theorem 3 by simply recognizing that

$$\chi^* = \overline{\chi} = \underline{\chi} = \frac{-g(u_0)}{\mu A_0}$$

.

Finally, we consider the proof of Theorem 5.

Proof. (Theorem 5) Let $\chi^* = \frac{1}{\mu A_1} \sup_{0<u} \{g(u)\}$. Then, for any $\chi > \chi^*$ we obtain that $u \equiv u_0 > 0$ is a super-solution and by a similar argument made in Theorem 3 we see that $u(x, t) \to 0$ uniformly as $t \to \infty$.

3.1. Connection to the bounded domain problem

It is more physically relevant to study our equation on a bounded domain, which motivates us to study the connection between our equation posed on a bounded domain with different boundary conditions and the Cauchy problem.

3.1.1. Directed movement on a bounded domain

In this section we explore the relation between the Cauchy problem and Eq (2.5), but now defined on a bounded domain with zero Neumann boundary conditions. Specifically, consider the following system:

$$\begin{cases} u_t = \mu\nabla\cdot(\nabla u - \chi\nabla u\cdot\nabla A) + g(x,u)u, \ x\in\Omega, \ t>0, & \text{(3.6a)}\\ u(x,0) = u_0(x), \ x\in\Omega, & \text{(3.6b)}\\ u(\nabla A\cdot\vec{n}) = 0, \ x\in\partial\Omega, & \text{(3.6c)} \end{cases}$$

where $\Omega\subset\mathbb{R}^n$ is smooth and star-shaped. Recall, that the star-shaped condition means that there exists an $x_0\in\Omega$ such that for all $x\in\Omega$, the line segment from x_0 to x is contained in Ω. Due to the smoothness condition imposed on the signal A, classical theory provides a global-in-time classical solution. Also, in this case, Neumann boundary conditions and no-flux boundary conditions are not the same; see Remark 4. In the case of zero-Neumann boundary conditions we obtain the same results as for the Cauchy problem.

Proposition 1 (Super-harmonic signal)**.** *Let A and g respectively represent an admissible signal and growth pattern with*

$$-A_0\le\Delta A(x)\le -A_1<0 \quad \textit{for all} \quad x\in\Omega. \tag{3.7}$$

Moreover, let u be the $C^{2,1}(\Omega\times[0,\infty))$ solution to (3.6) *with initial data $u_0(x)=u_0$, i.e., a positive constant with $0<u_0<\inf_{x\in\Omega}\theta(x)$. There exist constants $0<\underline{\chi}(u_0,A)<\overline{\chi}(u_0,A)$ such that if*

(i) $\chi<\underline{\chi}$, then $u(x,t)\to 0$ as $t\to\infty$ uniformly for all $x\in\Omega$;
(ii) $\chi>\overline{\chi}^*$, then $u(x,t)\to u^*(x)$ as $t\to\infty$ for all $x\in\Omega$, where u^* is a positive equilibrium solution to (2.5).

Proof. The proof follows exactly that of Theorem 3, as we can use constant super- and sub-solutions.

The sharp result observed in the Cauchy problem also holds, we state the relevant version for convenience.

Proposition 2 (Sharp result)**.** *Let g be an admissible growth pattern, u be the solution to* (2.5) *with $A(x)=-A_0x^2$ with $A_0>0$ and initial data u_0 be a positive constant with $0<u_0<\inf_{x\in\Omega}\theta(x)$. There exist $0<\chi^*(u_0,A)$ such that the following holds:*

(i) If $\chi<\chi^*$ then $u(x,t)\to 0$ as $t\to\infty$ for all $x\in\Omega$;
(ii) If $\chi>\overline{\chi}$ then $u(x,t)\to u^*(x)$ as $t\to\infty$ for all $x\in\Omega$, where u^* is a positive equilibrium solution to (3.6).

Proof. The proof follows exactly that of Theorem 4, as we can use constant super- and sub-solutions.

Remark 4. To gain insight into what is happening in this case, we rewrite the zero Neumann boundary condition as follows:

$$(\nabla u\cdot\vec{n} - \chi u\nabla A\cdot\vec{n}) = -(\chi\nabla A\cdot\vec{n})u,$$

which is the flux into Ω. Thus, if Ω is a star-shaped domain (relative to zero), for the super-harmonic potentials considered in Propositions 1 and 2 we have that $-(\chi\mu\nabla A\cdot\vec{n})>0$. Thus, in effect, there is a positive net-flux into the domain that is proportional to the population density on the boundary,

reflecting an unlimited source of population. This is similar to what is happening in the unbounded domain case where we start with a constant initial population; there, we also have an unlimited source of population. Naturally, this makes it much easier for a population to overcome the Allee effect, because when (3.7) holds there is a net influx on the boundary and the population is gaining. In the more physically relevant case of no-flux boundary conditions, the boundary does not aid the population, and if a population overcomes the Allee effect it will only be due to the aggregation of the population. In the case of zero-Dirichlet boundary conditions, it is unclear that a population would be able to overcome the Allee effect.

3.1.2. Classical diffusion on a bounded domain with an in-flux

If we are trying to compare the benefits of directed movement versus unconditional dispersal on a bounded domain, a fair comparison of System (3.6) is the classical bistable reaction-diffusion equation, but with an influx. Specifically, consider the following system:

$$\begin{cases} u_t = \mu\Delta u + g(x,u)u, \ \ x \in \Omega, \ t > 0, & \text{(3.8a)} \\ u(x,0) = u_0(x), \ \ x \in \Omega, & \text{(3.8b)} \\ \nabla u \cdot \vec{n} = -(\chi \nabla A \cdot \vec{n})u, \ \ x \in \partial\Omega. & \text{(3.8c)} \end{cases}$$

For this system, we have the following result.

Theorem 6 (Overcoming the Allee effect with an influx: Classical case). Let A and g respectively represent an admissible signal and growth pattern, which, additionally, satisfy the following:

$$(\chi^2 |\nabla A|^2 - \chi\Delta A) > \min_{z\in\Omega} g(x,z) \quad \text{for all } x \in \Omega. \tag{3.9}$$

If u is the unique solution to (3.8) with strictly positive initial data, $u_0 > \epsilon$, with some $\epsilon > 0$, then $u(x,t) \to u^*(x)$, which is a positive equilibrium, uniformly in x.

Proof. First, consider that the boundary condition (3.8b) is equivalent to:

$$(\nabla u + \chi u \nabla A) \cdot \vec{n} = 0.$$

Let $w = e^{\chi A}u$ so that $\nabla u = e^{-\chi A}\nabla w - \chi e^{\chi A} w \nabla A$. Thus, in fact we have that

$$[\nabla u + \chi u \nabla A] = e^{-\chi A}\nabla w.$$

Thus, we have that $\nabla w \cdot \vec{n} = 0$ on $\partial\Omega$. Moreover, we have that

$$\Delta u = e^{-\chi A}[\Delta w - 2\chi \nabla w \cdot \nabla A + (\chi^2 |\nabla A|^2 - \chi\Delta A)w].$$

After multiplying (3.8a) by $e^{\chi A}$ we can rewrite the equation as follows:

$$w_t = \Delta w - 2\chi \nabla w \cdot \nabla A + (\chi^2 |\nabla A|^2 - \chi\Delta A)w + g(x, e^{-\chi A}w)w.$$

Now, note that if the condition (3.9) holds, then any $u \equiv \epsilon > 0$ is a sub-solution and will thus increase to a positive equilibrium solution.

Thus, in fact it holds that for super-harmonic signals, if the directed movement is sufficiently large, a population can overcome the Allee effect with any positive initial data. Note that the condition (3.9) actually allows signals that have a change in concavity; this just has to be made up by the gradient of the signal.

4. Case of $L^1(\mathbb{R}^n) \cap L^\infty(\mathbb{R}^n)$ initial data

In this section we explore what happens when a population pursues a movement strategy of pure taxis versus a combination of dispersal and taxis. As a case study we continue to work with the Ornstein-Uhlenbeck signal $A(x) = -\frac{1}{2}x^2$.

4.1. Case of pure directed movement

As it is believed that aggregation is beneficial for a population, in this section we explore what happens when a population only advects following a signal that aggregates the population. The results in this section hold for $x \in \mathbb{R}^n$. Taking into account that $A(x) = -\frac{1}{2}x^2$ we see that the dynamics of the population follow the equation

$$\frac{\partial u}{\partial t} = \chi \nabla(ux) + g(u)u,$$

or, equivalently

$$\frac{\partial u}{\partial t} = \chi x \cdot \nabla u + g(u)u + n\chi u. \tag{4.1}$$

Note that Eq (4.1) can be solved by using the method of characteristics. Here the characteristics satisfy the following equation:

$$\frac{dX^t}{dt}(x_0) = -\chi X^t(x_0),$$

which has the solution $X^t(x_0) = x_0 e^{-\chi t}$. Along the characteristics the solution satisfies the following differential equation:

$$\frac{du(X^t(x_0), t)}{dt} = [n\chi + g(u(X^t(x_0), t)]u(X^t(x_0), t). \tag{4.2}$$

We show that if the initial population has compact support then a movement strategy of taxis along a signal that aggregates is not a good strategy. For example, consider an initial population density of the form $u_0(x) = \gamma \mathbb{1}_{B_r}(x)$ where $r > 0$, $0 < \gamma < 1$ and B_r is the ball of radius r.

Proposition 3. *Let $u_0(x) = \gamma \mathbb{1}_{B_r}(x)$ with $0 < \gamma < 1$; then, the solution to* (4.1) *satisfies*

$$\int_{\mathbb{R}^n} u(x, t)\, dx \to 0$$

as $t \to \infty$.

To prove Proposition 3 we need the following Lemma.

Lemma 2. *For a fixed n and χ there exist non-negative constants $0 \le v_{n,\chi} < \theta$ and $1 < u_{n,\chi}$ such that if $u(X^0(x_0)) = \gamma$ with $v_{n,\chi} < \gamma < u_{n,\chi}$, then the solution to* (4.2) *$u(X^t(x_0))$ is that $\gamma < u(X^t(x_0)) < u_{n,\chi}$ and*

$$\lim_{t\to\infty} u(X^t(x_0)) = u_{n,\chi}.$$

Proof. Define $h(u) = (n\chi + g(u))u$. Note that based on the assumptions on the function g, we have that if χ is small then h has two positive roots $v_{n,\chi}, u_{n,\chi}$ with $v_{n,\chi} < \theta$ and $u_{n,\chi} > \theta$. In particular, we have that $u_{n,\chi}$ is an increasing function of χ and n. Moreover, $h(u) > 0$ for $u \in (v_{n,\chi}, v_{n,\chi})$.

Proof. (Proposition 3) As $u_0(x) = \alpha B_r(x)$ we obtain the following estimate using Lemma 2:

$$\begin{aligned}\int_{\mathbb{R}^n} u(x,t)\,dx &\leq \int_{\mathbb{R}^n} u_0(X^t(x_0)e^{\chi t})u_{n,\chi}\,dx \\ &= \gamma u_{n,\chi}\int_{X^t(x_0)\in B_r e^{-\chi t}} dx = C\gamma r e^{-n\chi t}u_{n,\chi} \to 0,\end{aligned}$$

as $t \to \infty$. Thus, the mass of the population approaches zero as $t \to \infty$ because the characteristics compress exponentially and the solution is bounded.

Remark 5. (Biological interpretation) Proposition 3 is independent of r, which implies that in an unbounded domain if a population has an initial population density with compact support, taxis along an environmental signal, which aggregates the population, will not help a population survive.

To explore how much initial mass is needed for a population to survive under a strategy of pure taxis we consider the initial data $u_0 = \tilde{u}(x)\mathbb{1}_{B_R} + \gamma x^{-\alpha}\mathbb{1}_{\mathbb{R}^n\setminus B_R}$ with $\tilde{u}$ as a bounded function and $R > 0$. From the discussion above we note that if the mass of the population is to remain bounded below away from zero it will be thanks to any mass coming from $|x| \to \infty$. If $0 < \gamma < \theta$ then we can obtain the following crude lower bound:

$$\begin{aligned}\int_{\mathbb{R}^n} u(x,t)\,dx &\geq \int_{\mathbb{R}^n} u_0(X^t(x_0)e^{\chi t})e^{(\chi n+g(0))t}\,dx \\ &\geq \int_J \gamma[X^t(x_0)e^{\chi t}]^{-\alpha}e^{(\chi n+g(0))t}\,dx,\end{aligned}$$

where $J = \{X^t(x_0)e^{\chi t} \in \mathbb{R}^n\setminus B_R\}$. Then, we have that

$$\int_{\mathbb{R}^n} u(x,t)\,dx \geq e^{(-\alpha\chi+\chi n+g(0))t}\int_J \gamma x^{-\alpha}\,dx.$$

We must consider two scenarios here. On the one hand, if $\alpha < n$ then $e^{(-\alpha\chi+\chi n+g(0))t} \to \infty$ as $t \to \infty$ if χ is sufficiently large to guarantee that $(-\alpha\chi + \chi n + g(0)) > 0$. However, in this case $u_0 \notin L^1(\mathbb{R})$. On the other hand, if $\alpha \geq n$, the lower bound will approach zero and in fact we can obtain the upper bound for $\gamma < \theta$

$$\int_{\mathbb{R}^n} u(x,t)\,dx \leq e^{(-\alpha n\chi+\chi n+g(\gamma))t}\int_J x^{-\alpha}\,dx + e^{(-\alpha\chi+\chi+g(\gamma))t}\int_{B_R} x^{-\alpha}\,dx,$$

which approaches zero as $t \to \infty$. Thus, if we begin with initial data in $L^1(\mathbb{R}^n)$, then the population will not survive if it is initially below the Allee threshold outside of a compact set. In order for a strategy of pure taxis along an environmental signal to help a species overcome the Allee effect, it must initially have a mass which is not in $L^1(\mathbb{R}^n)$.

Remark 6. (Biological interpretation) A movement strategy based on a pure taxis movement following the Orstein-Uhlenbeck signal will allow a population to persist only in the case where the initial data is not in $L^1(\mathbb{R}^n)$.

Remark 7. It is of interest to note some related results for the equation $u_t = \nabla\cdot(\nabla u - \chi u\nabla m) + (m(x) - u)u$. In [49], the authors considered the case when $\chi \to \infty$. The authors prove that the equilibrium

concentrates on the maxima of m. In particular, they proved that if m has only finitely many local maxima and the other conditions hold, then, as $\chi \to \infty$, the equilibrium approaches zero in L^2, which led to the conjecture that the solutions are concentrated at maxima. Later, Lam and Ni obtained more detailed results on how the concentration works [50, 51]. We **conjecture** that a similar result holds in our case.

4.2. Combination of dispersal and directed movement

From the above discussion we can conclude that if a population had to choose between a pure dispersal strategy and a pure taxis strategy then it should choose based on the initial population density. Indeed, if a population has initial data with compact support, then it is better off employing the pure diffusive movement strategy, but if it has infinite resources it could be better off employing a pure taxis movement strategy. In this section we explore a movement operator that combines both of these strategies. For simplicity, we consider the following model in one dimension:

$$\begin{cases} u_t = \mu u_{xx} + \chi u_x \cdot x + ru(1-u)(u-\theta) + \chi u, \ x \in \mathbb{R}, \ t > 0, \\ u(x,0) = \mathbb{1}_{[-L,L]}, \ x \in \mathbb{R}. \end{cases} \tag{4.3}$$

Performing the change of variables given by (2.3) with $t_c = \frac{1}{\chi}$ and $x_c = L$ we obtain:

$$\bar{u}_t = \beta \bar{u}_{\bar{x}\bar{x}} + \bar{u}_{\bar{x}} \cdot \bar{x} + \frac{r}{\chi}\bar{u}(1-\bar{u})(\bar{u}-\theta) + \bar{u}, \ x \in \mathbb{R}, \ t > 0, \tag{4.4}$$

where $\beta = \frac{\mu}{\chi L^2}$. One can observe that when χ is large it reduces the effect of the diffusion. In fact, when χL^2 is very large, initially, the dynamics of the solution are dominated by the following equation:

$$\bar{u}_t = u_x \cdot x + u, \ x \in \mathbb{R}, \ t > 0.$$

The solution is initially dominated by taxis and exponential growth. Specifically, the characteristics compress to the origin exponentially fast and the solution grows exponentially so that the mass is initially conserved. Note that the diffusion, growth and advection apparently balance when:

$$L_c = \sqrt{\frac{\mu}{4\chi}}. \tag{4.5}$$

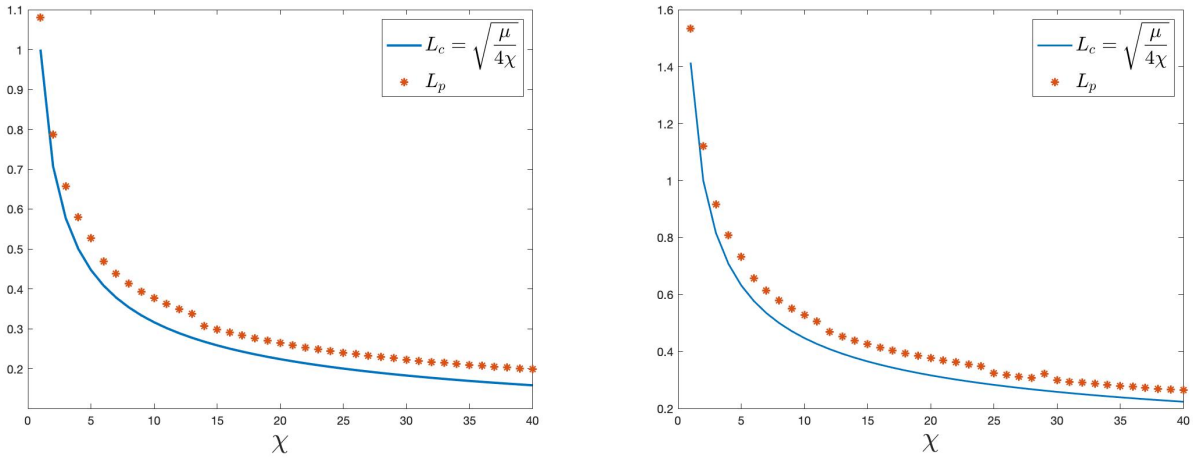
When the characteristics compress enough so that the length scale of the solution is less than L_c, then diffusion begins to dominate and the solution spreads out. This is consistent with what we can conclude from the nonlinear Feynman-Kac representation of (4.3):

$$\begin{cases} dY_t = \chi Y_s + 2\mu \, dW_s, \\ \int_{\mathbb{R}} u(x,t)\varphi(x) \, dx = \mathbb{E}\left[\varphi(Y_t)\exp\left(\int_0^t g(Y_s, u(s, Y_s)) \, ds\right)\right]. \end{cases} \tag{4.6}$$

The Ornstein-Uhlenbeck with the drift coefficient χ and diffusion coefficient μ has an invariant measure which is a Gaussian with variance $\frac{\mu}{\chi}$ as is predicted by (4.5). Thus, we see that a small amount of diffusion is imperative for the population to stabilize and not concentrate at the origin.

We performed some numerical simulations to test our predicted critical value, L_c, which we conjecture separates the extinction versus persistence of a population. Figure 1 illustrates the predicted

value, L_c, as computed by using Eq (4.5), versus the numerically approximated value, denoted by L_p. The numerically approximated critical length, L_p, was found by approximating the transition between extinction and persistence on a large, but bounded domain. We approximated the transition by numerically approximating the time evolution of Eq (4.3) for characteristic initial data with different values of L. We began with a value of L that guarantees that the solution will converge to zero as $t \to \infty$. We then iterated by adding a small increment to L (we increment by .02 in this case). The value L_p was selected to be the first L for which the solution approaches a non-trivial equilibrium as $t \to \infty$. We did not expect this approximation to be exact, but you can see that they follow the same trend. The predicted value given by (4.5) seemed to do a better job when χ is large. To guarantee that the role of the boundary was minimized, we ran the procedure outlined above for various domain sizes until the change was not negligible.



(a) $\mu = 4$ **(b)** $\mu = 8$

Figure 1. Numerically approximated L_p versus the predicted value $L_c = \sqrt{\frac{\mu}{4\chi}}$. The solutions were obtained by using Matlab's *pdepe* on a domain of size 40 with no-flux boundary conditions with initial data $u_0(x) = \mathbb{1}_{[-L,L]}$. The value L_p is the smallest L where the numerical solution is non-trivial.

5. Discussion

In this work we have explored the benefits of different movement strategies including pure diffusion, pure directed movement and a combination of the two, in the context of species who are subject to a strong Allee effect. We have found that some initial population with unbounded mass can lead to a population surviving under the condition of pure directed movement, if the directed movement aggregates the population, but not under pure diffusion. On the other hand, if the initial population has finite mass then it can survive provided that the mass is sufficiently large, but it will not survive under the pure directed movement, even if it aggregates. A balanced combination of the two movement strategies is ideal as proved in the whole space. We expect similar results to hold for the case of bounded domains, but this remains an open problem. It is worth mentioning that the models we studied in this work only include environmental signals with spatial heterogeneities and populations only use local

information. In recent decades there has been increased interest in the study of more general signals and the use of non-local information; see [52–54] and the references therein. Therefore, it would be of interest to study signals that also depend on time and/or the population density. Another extension of interest is the incorporation of non-local signals. In this direction, the authors have provided partial results for a model with non-local aggregation through the use of a non-local velocity field modeled by the convolution of the Newtonian potential and the population density. However, the picture in this situation is much less clear as a big challenge is the lack of maximum/comparison principles.

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Conflict of interest

The authors have not conflict of interest.

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