

# CONCENTRATION PHENOMENA IN AN INTEGRO-PDE MODEL FOR EVOLUTION OF CONDITIONAL DISPERSAL

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**ABSTRACT.** To study the evolution of conditional dispersal we extend the Perthame-Souganidis mutation-selection model and consider an integro-PDE model for a population structured by the spatial variables and one trait variable. We assume that both the diffusion rate and advection rate are functions of the trait variable, which lies within a short interval  $I$ . Competition for resource is local in spatial variables, but nonlocal in the trait variable. Under proper conditions on the invasion fitness gradient, we show that in the limit of small mutation rate, the positive steady state solution will concentrate in the trait variable and forms (i) a Dirac mass supported at one end of  $I$ ; or (ii) a Dirac mass supported at the interior of  $I$ ; or (iii) two Dirac masses supported at both ends of  $I$ , respectively. While Cases (i) and (ii) imply the evolutionary stability of a single strategy, Case (iii) suggests that when no single strategy can be evolutionarily stable, it is possible that two peculiar strategies as a pair can be evolutionarily stable and resist the invasion of any other strategy in our context.

## 1. INTRODUCTION

An important question in ecology and evolutionary biology is how the dispersal of organisms evolves [22, 51, 52]. For the evolution of unconditional dispersal, there is selection for slow dispersal in spatially varying yet temporally constant environments [29, 38, 41], while higher rates of dispersal can be favored when the environments are both spatially and temporally varying [39, 56]. However, the dispersal of organisms often depend upon local biotic and abiotic factors and thus it is often conditional, e.g., a combination of random diffusion and directed movement. Recent studies on the evolution of conditional dispersal suggest that conditional dispersal strategies can be evolutionarily stable; see [3, 4, 14, 15, 16, 19, 20, 23, 33, 37, 46, 47, 42, 53] and references therein.

A common approach to study the evolution of dispersal is the adaptive dynamics approach [26, 27, 34], in which it is assumed that the resident species is at the equilibrium, and a mutant phenotype is introduced to the population. The main questions are: Can the mutant invade when rare? If it can invade, will it coexist with the resident or competitively exclude the resident? Most, if not all, of these mathematical models thus assume that there are only two phenotypes in competition. Very recently, Perthame and Souganidis introduced a novel approach to study the evolution of unconditional dispersal [60]. They considered an integro-PDE model for a population structured by the spatial variables and a (continuous) trait variable which is the random diffusion rate. In a sense, the Perthame-Souganidis model is a

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coupled system of infinitely many PDEs and can be viewed as a competition model for infinitely many phenotypes. By the Hamilton-Jacobi approach, Perthame and Souganidis showed that in the limit of small mutation rate, the steady state solution forms a Dirac mass in the trait variable, supported at the lowest possible diffusion rate. See also [48] for a similar result on the Perthame-Souganidis model.

The goal of this paper is to extend the Perthame-Souganidis model to a case of conditional dispersal. In contrast to the case of unconditional dispersal, the dynamics and structure of evolutionarily stable dispersal strategies seem to be much richer for conditional dispersals. For instance, it was shown in [45] that the steady state found in [48] is supported at a single dispersal strategy and is unique. In the presence of a biased movement, we give sufficient condition for the steady state to be supported at two distinct dispersal strategies, which is connected to the branching phenomena in evolutionary biology. Our methods will be based upon the Hamilton-Jacobi approach, while also drawing on the connections with the adaptive dynamics framework.

The dynamics of a single population with combined random diffusion and directed movement can be described by the following scalar reaction-diffusion equation (see Belgacem and Cosner [5]):

$$(1.1) \quad \begin{cases} u_t = \nabla_x \cdot (\mu \nabla_x u - \alpha u \nabla_x m) + u[r(x) - u] & \text{in } D \times (0, \infty), \\ \mu \partial_n u - \alpha u \partial_n m = 0 & \text{on } \partial D \times (0, \infty), \\ u(x, 0) = u_0(x) & \text{in } D. \end{cases}$$

Here  $u(x, t)$  is the population density at location  $x \in D$  and time  $t > 0$ , where  $D$  represents a bounded domain in  $\mathbb{R}^N$  with smooth boundary  $\partial D$ .  $n$  is the outward unit normal vector on  $\partial D$ , with  $\partial_n := n \cdot \nabla_x$ . Parameters  $\mu > 0$  and  $\alpha \geq 0$  are diffusion and advection coefficients, respectively, and  $r(x)$  is a given function of the environment. Besides random diffusion, the population is also assumed to move upward along the gradient of some function  $m(x)$ . Belgacem and Cosner considered the case  $r(x) = m(x)$  in [5]; see also [24, 43, 44, 49] for further developments.

Throughout this paper, unless otherwise specified, we assume

(M):  $m \in C^2(\overline{D})$  and  $\partial_n m \leq 0$  on  $\partial D$ ;  $r(x)$  is Hölder continuous in  $\overline{D}$ .

Suppose that  $\mu, \alpha$  are both smooth real-valued functions of some phenotypic variable  $\xi$ , such that  $\mu(\xi) > 0$  and  $\alpha(\xi) \geq 0$  for all  $\xi \in \mathbb{R}^+ := (0, \infty)$ . Then the dynamics of the species, consisting of a continuum of phenotypes, as parameterized by the single real variable  $\xi$ , can be described by

$$(1.2) \quad \begin{cases} u_t = \nabla_x \cdot (\mu(\xi) \nabla_x u - \alpha(\xi) u \nabla_x m) + \epsilon^2 \partial_\xi^2 u + u(r(x) - \hat{u}) & \text{in } D \times I \times \mathbb{R}^+, \\ \mu(\xi) \partial_n u - \alpha(\xi) u \partial_n m = 0 & \text{on } \partial D \times I \times \mathbb{R}^+, \\ u = 0 & \text{on } D \times \partial I \times \mathbb{R}^+, \\ u(x, \xi, 0) = u_0(x) & \text{in } D \times I, \end{cases}$$

where  $I$  is a bounded open subinterval of  $\mathbb{R}^+$ , and

$$\hat{u} = \hat{u}(x, t) = \int_I u(x, \xi, t) d\xi$$

is the total population density at a given location  $x \in D$  and time  $t$ .

*Remark 1.1.* Our choice for Dirichlet condition on the boundary of the trait space in (1.2), instead of no-flux condition that was considered in [48, 60], is made so that the boundary condition remains consistent in the corners of our cylindrical domain

$D \times I$ . We also note that due to the vanishing viscosity in the trait variable, the boundary condition has little effect on the dynamics of (1.2). For instance, if  $\partial_n m = 0$  on  $\partial D$ , then the Neumann boundary condition for the trait variable will satisfy the consistency conditions, and all the results in this paper can be similarly established.

For each  $\xi \in \mathbb{R}^+$ , let  $\theta_\xi(x)$  be the unique positive solution of the equation

$$(1.3) \quad \begin{cases} \nabla_x \cdot (\mu(\xi) \nabla_x \theta - \alpha(\xi) \theta \nabla_x m) + \theta(r(x) - \theta) = 0 & \text{in } D, \\ \mu(\xi) \partial_n \theta - \alpha(\xi) \theta \partial_n m = 0 & \text{on } \partial D. \end{cases}$$

We note that (1.3) has a positive solution if and only if the trivial solution is unstable and the positive solution is unique whenever it exists; see, e.g. [13].

The family of phenotypic traits is parameterized by  $\xi > 0$ , where distinct  $\xi$  correspond to different phenotypes, as distinguished by their respective diffusion rates and advection rates. Formally speaking,  $\{\delta_0(\xi - \xi')\theta_{\xi'}(x)\}_{\xi' > 0}$  gives a one-dimensional manifold of steady states of (1.2) when  $\epsilon = 0$ , where  $\delta_0(\xi - \xi')$  is the Dirac measure concentrated at  $\xi'$ . More generally, (1.2) with  $\epsilon = 0$  contains, as subsystems,  $k$ -species competition systems for any  $k \in \mathbb{N}$ . To see this, note that for any  $0 < \xi_1 < \xi_2 < \dots < \xi_k$ ,  $\sum_{i=1}^k \delta_0(\xi - \xi_i)u_i(x)$  gives a steady state of (1.2) with  $\epsilon = 0$ , concentrated at  $\xi_1, \dots, \xi_k$ , if and only if  $(u_1, \dots, u_k)$  satisfies the  $k$ -species system

$$(1.4) \quad \begin{cases} \nabla_x \cdot (\mu(\xi_i) \nabla_x u_i - \alpha(\xi_i) u_i \nabla_x m) + u_i(r(x) - \sum_{j=1}^k u_j) = 0 & \text{in } D, \\ \mu(\xi_i) \partial_n u_i - \alpha(\xi_i) u_i \partial_n m = 0 & \text{on } \partial D. \end{cases}$$

The goal of this paper is to determine which of these concentrated steady state solutions of (1.2) with  $\epsilon = 0$  will persist for small positive mutation rate  $\epsilon$ .

For each  $\xi_1, \xi_2 \in \mathbb{R}^+$ , consider the eigenvalue problem

$$(1.5) \quad \begin{cases} \nabla_x \cdot (\mu(\xi_2) \nabla_x \psi - \alpha(\xi_2) \psi \nabla_x m) + \psi(r(x) - \theta_{\xi_1}) + \lambda \psi = 0 & \text{in } D, \\ \mu(\xi_2) \partial_n \psi - \alpha(\xi_2) \psi \partial_n m = 0 & \text{on } \partial D. \end{cases}$$

For each fixed  $\xi_1, \xi_2$ , it follows from standard variational arguments that eigenvalues of (1.5) are real and ordered. We denote the least eigenvalue of (1.5) by  $\lambda(\xi_1, \xi_2)$ , which in the adaptive dynamics framework is termed the invasion fitness. More precisely, an invader with phenotype  $\xi_2$  can (resp. cannot) invade an established phenotype  $\xi_1$  at equilibrium when rare if  $\lambda(\xi_1, \xi_2) < 0$  (resp.  $\lambda(\xi_1, \xi_2) > 0$ ).

We start the discussion in the most generic case:

**Theorem 1.2** (Evolution of extreme strategies). *Suppose that for some closed interval  $\bar{I}_0 \in \mathbb{R}^+$ ,*

$$(1.6) \quad \inf_{\xi \in \bar{I}_0} \partial_{\xi_2} \lambda(\xi, \xi) > 0.$$

*Then there exists  $\delta > 0$  such that for each interval  $I = (\xi_*, \xi^*) \subset \bar{I}_0$  such that  $|I| = \xi^* - \xi_* < \delta$ , any positive steady state  $u_\epsilon$  of (1.2) satisfies,*

$$u_\epsilon(x, \xi) \rightarrow \delta_0(\xi - \xi_*) \theta_{\xi_*}(x) \quad \text{in distribution sense}$$

*as  $\epsilon \rightarrow 0$ , where  $\delta_0(\xi - \xi_*)$  is the Dirac measure concentrated at  $\xi_* = \inf I$ . Here  $\theta_{\xi_*}$  denotes the unique positive solution of (1.3) with  $\xi = \xi_*$ .*

If the inequality sign in (1.6) is reversed, then a similar conclusion holds with  $\xi_*$  being replaced by  $\xi^* = \sup I$ . This shows that if the selection gradient does not

vanish, it gives rise to a single Dirac-concentration at one of the two most extreme phenotypes, determined by the sign of the selection gradient  $\partial_{\xi_2}\lambda(\xi, \xi)$ .

In adaptive dynamics, the canonical equation is derived to indicate the evolutionary dynamics of monomorphic populations. A consequence of such dynamics is that the phenotypic trait of monomorphic populations evolves towards convergence stable strategies [31], which is characterized by the following relations:

$$(\mathbf{Cv}): \partial_{\xi_2}\lambda(\hat{\xi}, \hat{\xi}) = 0 \quad \text{and} \quad \frac{d}{dt}[\partial_{\xi_2}\lambda(t, t)]_{t=\hat{\xi}} > 0.$$

This leads to two generic cases: (i) Continuously Stable Strategies (CSS) and (ii) Branching Points (BP). Our next two results will show that the first case gives rise to an interior Dirac-concentration, and the second gives rise to two “balanced” boundary Dirac-concentrations. In a sense, CSS gives an evolutionary attractor where a monomorphic population adopting the superior/optimal strategy  $\hat{\xi}$  is able to equilibrate while withstanding the onset of all small and rare mutations. On the other hand, if a trait  $\hat{\xi}$  is a branching point, then although it is capable of invading any resident adopting a different trait  $\xi \neq \hat{\xi}$ , it is prone to invasion by small mutations, and instead a population consisting of a combination of two distinct strategies emerges.

Our next result says that if there is a CSS  $\hat{\xi}$ , then the phenotype in  $I$  that is closest to  $\hat{\xi}$  dominates the competition.

**Theorem 1.3** (Evolution of intermediate strategy). *Suppose that **(Cv)** holds and  $\partial_{\xi_2}^2\lambda(\hat{\xi}, \hat{\xi}) > 0$  for some  $\hat{\xi} \in \mathbb{R}^+$ , then there exists  $\delta > 0$  such that for each fixed interval  $I = (\xi_*, \xi^*) \subset (\hat{\xi} - \delta, \hat{\xi} + \delta)$ , any positive steady state  $u_\epsilon$  of (1.2) satisfies, as  $\epsilon \rightarrow 0$ ,*

*$\hat{u}_\epsilon(x) \rightarrow \theta_{\xi'}(x)$  in  $C(\bar{D})$  and  $u_\epsilon(x, \xi) \rightarrow \delta_0(\xi - \xi')\theta_{\xi'}(x)$  in distribution sense, where the point of concentration  $\xi'$  is the point in  $[\xi_*, \xi^*]$  closest to  $\hat{\xi}$ ; i.e.*

$$\xi' = \begin{cases} \hat{\xi} & \text{if } \hat{\xi} \in [\xi_*, \xi^*], \\ \xi_* & \text{if } \hat{\xi} < \xi_* = \inf I, \\ \xi^* & \text{if } \hat{\xi} > \xi^* = \sup I. \end{cases}$$

The next theorem says that in the neighborhood of a branching point, no single phenotype can dominate. Instead, the two extreme phenotypes form a coalition that together dominates the competition.

**Theorem 1.4** (Evolutionary Branching Point). *Suppose that **(Cv)** holds and  $\partial_{\xi_2}^2\lambda(\hat{\xi}, \hat{\xi}) < 0$  for some  $\hat{\xi} \in \mathbb{R}^+$ . Then there exists  $\delta > 0$  such that for each interval  $I = (\xi_*, \xi^*) \subset (\hat{\xi} - \delta, \hat{\xi} + \delta)$  such that  $\xi_* \leq \hat{\xi} \leq \xi^*$ , there is a sequence  $\epsilon_k \rightarrow 0$ , such that any positive steady state  $u_{\epsilon_k}$  of (1.2) satisfies*

$$u_{\epsilon_k}(x, \xi) \rightarrow \delta_0(\xi - \xi_*)\hat{u}_1(x) + \delta_0(\xi - \xi^*)\hat{u}_2(x) \quad \text{in distribution sense}$$

as  $k \rightarrow \infty$ . Furthermore,  $(\hat{u}_1, \hat{u}_2)$  is a positive steady state of

$$(1.7) \quad \begin{cases} \nabla_x \cdot (\mu_1 \nabla_x \hat{u}_1 - \alpha_1 \hat{u}_1 \nabla_x m) + \hat{u}_1(r(x) - \hat{u}_1 - \hat{u}_2) = 0 & \text{in } D, \\ \nabla_x \cdot (\mu_2 \nabla_x \hat{u}_2 - \alpha_2 \hat{u}_2 \nabla_x m) + \hat{u}_2(r(x) - \hat{u}_1 - \hat{u}_2) = 0 & \text{in } D, \\ \mu_1 \partial_n \hat{u}_1 - \alpha_1 \hat{u}_1 \partial_n m = 0 = \mu_2 \partial_n \hat{u}_2 - \alpha_2 \hat{u}_2 \partial_n m & \text{on } \partial D, \end{cases}$$

such that  $\hat{u}_i(x) \not\equiv 0$  for  $i = 1, 2$ , and that  $\alpha_1 = \alpha(\xi_*)$ ,  $\alpha_2 = \alpha(\xi^*)$ ,  $\mu_1 = \mu(\xi_*)$  and  $\mu_2 = \mu(\xi^*)$ .

We briefly sketch the key ideas in the proofs. Consider the WKB-Ansatz,  $w_\epsilon(x, \xi) = \epsilon \log u_\epsilon(x, \xi)$ . We first establish, in Sects. 2 and 3, appropriate a priori Lipschitz estimates on  $w_\epsilon$ . Our first contribution is to drop the convexity assumption on  $D$ , which was needed in [60] to apply Bernstein's method. Our proof relies on blow-up methods and Liouville theorems of elliptic equations in cylindrical domains. See Appendix A.

The a priori estimates allows the passage to (subsequential) limits of

$$\hat{u}(x) = \lim_{\epsilon \rightarrow 0} \hat{u}_\epsilon(x), \quad \text{and} \quad w(\xi) = \lim_{\epsilon \rightarrow 0} w_\epsilon(x, \xi).$$

An important fact is that the limit function  $w(\xi)$  satisfies, in the viscosity sense, the following constrained Hamilton-Jacobi equation:

$$(1.8) \quad \begin{cases} -|\partial_\xi w|^2 = -H(\xi; \hat{u}) & \text{in } I = (\xi_*, \xi^*), \\ \sup_I w = 0. \end{cases}$$

Here the Hamiltonian  $H(\xi; \hat{u})$  is defined as the principal eigenvalue of

$$(1.9) \quad \begin{cases} \nabla_x \cdot (\mu(\xi) \nabla_x \psi - \alpha(\xi) \psi \nabla_x m) + (r(x) - \hat{u}) \psi + H\psi = 0 & \text{in } D, \\ \mu(\xi) \partial_n \psi - \alpha(\xi) \psi \partial_n m = 0 & \text{on } \partial D, \quad \text{and} \quad \int_D \psi^2 dx = 1. \end{cases}$$

The main difficulty to solve (1.8) is to yield information (and possibly uniqueness) concerning the subsequential limit functions  $\hat{u}(x)$  and  $w(\xi)$ . In [60] the corresponding Hamiltonian  $\tilde{H}(\xi, \hat{u})$  is the principal eigenvalue of

$$(1.10) \quad \begin{cases} \mu(\xi) \Delta_x \psi + (r(x) - \hat{u}) \psi + H\psi = 0 & \text{in } D, \\ \partial_n \psi = 0 & \text{on } \partial D, \quad \text{and} \quad \int_D \psi^2 dx = 1. \end{cases}$$

It is a classical fact in PDE that, provided  $r(x) - \hat{u}(x)$  is non-constant in  $x$ , i.e. the monotonicity properties of  $\tilde{H}$  in  $\xi$  is exactly the same as that of  $\mu(\xi)$  in  $\xi$ . This shows that  $w(\xi)$  attains its maximum at the minimum point of  $\mu(\cdot)$ , at which the concentration of  $u_\epsilon(x, \xi)$  occurs. i.e.  $\hat{u} = \theta_{\xi_*}$ .

In contrast, the dependence of the principal eigenvalue  $H$  of (1.9) on parameters  $\mu$  and  $\alpha$  may not possess monotonicity [17, 18]. In this work, we infer the behavior of  $H(\xi; \hat{u})$  based on the assumptions regarding the invasion fitness function  $\lambda(\xi_1, \xi_2) = H(\xi_2; \theta_{\xi_1})$ , which arises in the study of two-species competition models [46, 47]. For this purpose, we only consider fixed, narrow intervals  $I$  in the trait variable, for which we can quantify how close an arbitrary subsequential limit  $\hat{u}$  is from  $\theta_{\hat{\xi}}$ . This approach partially decouples (1.8) and (1.9), and is done in Appendix B.

In Sects. 4 to 6, we impose three most generic assumptions on the invasion fitness function, namely non-vanishing selection gradient, Continuously Stable Strategies (CSS), and Evolutionary Branching Points (BP). We show that the resulting solutions to the mutation-selection model exhibit one or two Dirac-concentrations at those strategy or strategies that are *evolutionarily stable*. This establishes the connection of (1.2) to the framework of adaptive dynamics. In Sects. 7 and 8 we provide some concrete examples in which those generic assumptions on the invasion fitness function can be verified. To complement Sects. 7 and 8, we present some numerical computations concerning the dynamics of (1.2) in Sect. 9.

This paper serves as an initial exploration of the class of mutation-selection models arising from evolution of conditional dispersal. Our results suggest that, as a consequence of the interplay between ecology and evolution, the dynamics of (1.2) is indeed quite rich. Biologically, our results give a classification of the equilibria

of evolutionary dynamics in generic situations, when the possible mutations is restricted to a small interval  $I$ . We believe, however, that the restriction of the size of the interval  $I$  in our main results is technical.

Finally, we provide some references to background and related works. One of the first works to connect mutation-selection dynamics with adaptive dynamics is [12]. For earlier mathematical works on mutation-selection models, we refer to [11, 55]. For the pioneering Hamilton-Jacobi approach we refer to [28, 59]. For pure selection dynamics, see [1, 25]. The involvement of spatial structure is more recent, see [40, 57] for works on models related to cancer therapy; and [2, 6, 8, 7, 9, 10, 61] for works on unbounded domains concerning spreading front solutions.

## 2. A PRIORI ESTIMATES OF $\hat{u}_\epsilon$

For the rest of this paper, we set

$$I_0 := (\underline{\xi}, \bar{\xi}), \quad I := (\xi_*, \xi^*),$$

where  $\xi_*, \xi^*, \underline{\xi}, \bar{\xi}$  are positive numbers. Furthermore, we always assume that  $I \subset \bar{I}_0$ .

For each bounded open interval  $I \subset \mathbb{R}^+$  and each  $\epsilon > 0$ , let  $u_\epsilon = u_\epsilon(x, \xi)$  be a positive steady state of (1.2), then it satisfies

$$(2.1) \quad \begin{cases} \nabla_x \cdot (\mu(\xi) \nabla_x u_\epsilon - \alpha(\xi) u_\epsilon \nabla_x m) + \epsilon^2 \partial_\xi^2 u_\epsilon + u_\epsilon(r(x) - \hat{u}_\epsilon) = 0 & \text{in } D \times I, \\ \mu(\xi) \partial_n u_\epsilon - \alpha(\xi) u_\epsilon \partial_n m = 0 & \text{on } \partial D \times I, \\ u_\epsilon = 0 & \text{on } D \times \partial I, \end{cases}$$

where

$$(2.2) \quad \hat{u}_\epsilon(x) := \int_I u_\epsilon(x, \xi) d\xi.$$

The following result is the only place where the assumption (M) is needed.

**Lemma 2.1.** *Let  $u_\epsilon$  be any positive solution of (2.1). Then there exists some positive constant  $C$ , which depends on  $I_0$  but is independent of  $I$  and  $\epsilon \in (0, 1]$ , such that*

$$\sup_D \hat{u}_\epsilon \leq C.$$

*Proof.* Let  $u_\epsilon(x, \xi)$  be a positive solution of (2.1). Define

$$(2.3) \quad v_\epsilon(x, \xi) = e^{-\alpha m / (2\mu)} u_\epsilon(x, \xi), \quad \hat{v}_\epsilon(x) = \int_I v_\epsilon(x, \xi) d\xi.$$

Then there exist positive constants  $c_1, c_2$  depending on  $I_0$ , but independent of  $I$  and  $\epsilon$ , such that

$$(2.4) \quad c_1 \hat{u}_\epsilon(x) \leq \hat{v}_\epsilon(x) \leq c_2 \hat{u}_\epsilon(x) \quad \text{for all } x \in D.$$

Moreover,  $v_\epsilon$  satisfies

$$(2.5) \quad \begin{cases} \mu \Delta_x v_\epsilon + \epsilon^2 \left\{ \partial_\xi^2 v_\epsilon + m \partial_\xi \left( \frac{\alpha}{\mu} \right) \partial_\xi v_\epsilon + \frac{m}{2} \partial_\xi^2 \left( \frac{\alpha}{\mu} \right) v_\epsilon + \left[ \frac{m}{2} \partial_\xi \left( \frac{\alpha}{\mu} \right) \right]^2 v_\epsilon \right\} \\ \quad + v_\epsilon \left( -\frac{\alpha}{2} \Delta_x m - \frac{\alpha^2}{4\mu} |\nabla_x m|^2 + r - \hat{u}_\epsilon \right) = 0 \text{ in } D \times I, \\ \partial_n v_\epsilon = \frac{\alpha}{2\mu} v_\epsilon \partial_n m \leq 0 \quad \text{on } \partial D \times I, \\ v_\epsilon = 0 \quad \text{on } D \times \partial I, \end{cases}$$

where we used **(M)** to ensure  $\partial_n m \leq 0$  on  $\partial D$ . Dividing the equation of  $v_\epsilon$  by  $\mu = \mu(\xi)$ , and integrating in the variable  $\xi \in I = (\xi_*, \xi^*)$ , and using the facts that

$$\begin{aligned} \int_I \frac{1}{\mu} \partial_\xi \left( \frac{\alpha}{\mu} \right) \partial_\xi v_\epsilon \, d\xi &= - \int_I \partial_\xi \left[ \frac{1}{\mu} \partial_\xi \left( \frac{\alpha}{\mu} \right) \right] v_\epsilon \, d\xi + \left[ \frac{1}{\mu} \partial_\xi \left( \frac{\alpha}{\mu} \right) v_\epsilon \right]_{\xi=\xi_*}^{\xi^*} \\ &= - \int_I \partial_\xi \left[ \frac{1}{\mu} \partial_\xi \left( \frac{\alpha}{\mu} \right) \right] v_\epsilon \, d\xi, \end{aligned}$$

(since  $v_\epsilon(\cdot, \xi^*) \equiv v_\epsilon(\cdot, \xi_*) \equiv 0$ ) and

$$\int_I \frac{1}{\mu} \partial_\xi^2 v_\epsilon \, d\xi = \int_I \partial_\xi^2 \left( \frac{1}{\mu} \right) v_\epsilon \, d\xi + \left[ \frac{1}{\mu} \partial_\xi v_\epsilon \right]_{\xi=\xi_*}^{\xi^*} \leq \int_I \partial_\xi^2 \left( \frac{1}{\mu} \right) v_\epsilon \, d\xi,$$

(since  $\partial_\xi v_\epsilon(\cdot, \xi^*) \geq 0 \geq \partial_\xi v_\epsilon(\cdot, \xi_*)$  in  $\bar{D}$ ) we have

$$(2.6) \quad \begin{cases} \Delta_x \hat{v}_\epsilon + \hat{v}_\epsilon \left( \epsilon^2 h_0(x) + \frac{r(x)}{\inf_{I_0} \mu} - \frac{\hat{u}_\epsilon(x)}{\sup_{I_0} \mu} \right) \geq 0 & \text{in } D, \\ \partial_n \hat{v}_\epsilon \leq 0 & \text{on } \partial D, \end{cases}$$

where  $h_0$  can be expressed in terms of  $\mu, m, \alpha$  and their derivatives, and is independent of the interval  $I$  and  $\epsilon \in (0, 1]$ :

$$h_0(x) = \sup_{\xi \in I_0} \left\{ \partial_\xi^2 \left( \frac{1}{\mu} \right) - m(x) \partial_\xi \left[ \frac{1}{\mu} \partial_\xi \left( \frac{\alpha}{\mu} \right) \right] + \frac{1}{\mu} \frac{m(x)}{2} \partial_\xi^2 \left( \frac{\alpha}{\mu} \right) + \frac{1}{\mu} \left[ \frac{m(x)}{2} \partial_\xi \left( \frac{\alpha}{\mu} \right) \right]^2 \right\}.$$

Suppose that  $\sup_D \hat{v}_\epsilon = \hat{v}_\epsilon(x_0)$  for some  $x_0 \in \bar{D}$ . Then apply the maximum principle (see [54, Proposition 2.2]) to (2.6), there exists  $C_1 > 0$  independent of  $\epsilon \in (0, 1]$  such that

$$\hat{u}_\epsilon(x_0) \leq C_1 := (\sup_{I_0} \mu) \left( \sup_D h_0 + \frac{\sup_D r}{\inf_{I_0} \mu} \right).$$

Combine this with (2.4), we have

$$c_1 \sup_D \hat{u}_\epsilon(\cdot) \leq \sup_D \hat{v}_\epsilon(\cdot) = \hat{v}_\epsilon(x_0) \leq c_2 \hat{u}_\epsilon(x_0) \leq c_2 C_1.$$

Hence  $\sup_D \hat{u}_\epsilon \leq C'_1$ , where the positive constant  $C'_1$  depends on  $I_0$  but is independent of the open interval  $I \subset I_0$  and  $\epsilon \in (0, 1]$ .  $\square$

**Lemma 2.2.** *Let  $I = (\xi_*, \xi^*)$  and  $\delta_1 := |I| = \xi^* - \xi_*$ .*

(i) *There exists  $C > 0$  independent of  $\delta_1, \epsilon$  such that if  $\epsilon \leq \delta_1/2$ , then*

$$\sup_{x \in D, \xi \in \partial I} |\partial_\xi u_\epsilon| \leq C \epsilon^{-2} \|\hat{u}_\epsilon\|_{L^1(D)} \leq C \epsilon^{-2}.$$

(ii) *For each fixed open interval  $I = (\xi_*, \xi^*) \subset I_0$ , there exists  $\delta_2 > 0$  independent of  $\epsilon$  such that*

$$(2.7) \quad \inf_{D \times (\xi_*, \xi_* + \delta_2 \epsilon)} \partial_\xi u_\epsilon > 0 \quad \text{and} \quad \sup_{D \times (\xi^* - \delta_2 \epsilon, \xi^*)} \partial_\xi u_\epsilon < 0.$$

*In particular,*

$$(2.8) \quad \sup_{D \times (\xi_*, \xi^*)} u_\epsilon = \sup_{D \times (\xi_* + \delta_2 \epsilon, \xi^* - \delta_2 \epsilon)} u_\epsilon.$$

*Proof.* We first show (i). Set  $\tilde{v}_\epsilon(x, \xi) := e^{-\alpha m/\mu} u_\epsilon(x, \xi)$  and  $Q_\epsilon(x, \tau) := \tilde{v}_\epsilon(x, \xi_* + \epsilon \tau)$ . Then  $Q_\epsilon$  satisfies

$$(2.9) \quad \begin{cases} \mu \Delta_x Q_\epsilon + \alpha \nabla_x m \cdot \nabla_x Q_\epsilon + \partial_\tau^2 Q_\epsilon + 2\epsilon m \partial_\xi \left( \frac{\alpha}{\mu} \right) \partial_\tau Q_\epsilon + \epsilon^2 \left[ m \partial_\xi^2 \left( \frac{\alpha}{\mu} \right) + m^2 \left( \partial_\xi \frac{\alpha}{\mu} \right)^2 \right] Q_\epsilon \\ \quad + Q_\epsilon(r - \hat{u}_\epsilon) = 0 & \text{in } D \times (0, \epsilon^{-1}(\xi^* - \xi_*)), \\ \partial_n Q_\epsilon = 0 & \text{on } \partial D \times (0, \epsilon^{-1}(\xi^* - \xi_*)), \quad \text{and} \quad Q_\epsilon = 0 & \text{on } D \times \{0, \epsilon^{-1}(\xi^* - \xi_*)\}, \end{cases}$$

where  $\mu = \mu(\xi_* + \epsilon\tau)$  and  $\alpha = \alpha(\xi_* + \epsilon\tau)$  are uniformly bounded for  $\tau \in (0, \epsilon^{-1}(\xi^* - \xi^*))$ . Then we extend  $Q_\epsilon$  in the direction of  $x$  by reflecting along the boundary  $\partial D \times (0, 2)$ , and apply the boundary elliptic estimate on  $\bar{D} \times \{0\}$  to get

$$(2.10) \quad \epsilon \sup_{x \in D} |\partial_\xi u_\epsilon(x, \xi_*)| \leq \|Q_\epsilon\|_{C^1(\bar{D} \times [0, 1])} \leq C' \|Q_\epsilon\|_{L^\infty(D \times [0, 2])}.$$

On the other hand, by the local maximum principle at the boundary for strong (sub)solutions [36, Theorem 9.26], we have

$$(2.11) \quad \|Q_\epsilon\|_{L^\infty(D \times [0, 2])} \leq C \|Q_\epsilon\|_{L^1(D \times (0, 3))} \leq C \epsilon^{-1} \|u_\epsilon\|_{L^1(D \times (\xi_*, \xi_* + 3\epsilon))}.$$

It follows from (2.10) and (2.11) that

$$\sup_{x \in D} |\partial_\xi u_\epsilon(x, \xi_*)| \leq C \epsilon^{-2} \|u_\epsilon\|_{L^1(D \times (\xi_*, \xi_* + 3\epsilon))} \leq C \epsilon^{-2} \|\hat{u}_\epsilon\|_{L^\infty(D)}.$$

By repeating the same proof for  $\xi = \xi^*$ , we obtain

$$\sup_{x \in D, \xi \in \partial I} |\partial_\xi u_\epsilon| \leq C \epsilon^{-2} \|\hat{u}_\epsilon\|_{L^\infty(D)}.$$

Assertion (i) thus follows from Lemma 2.1.

For the first inequality of (ii), we consider

$$(2.12) \quad \tilde{Q}_\epsilon(x, \tau) := \frac{Q_\epsilon(x, \tau)}{\|Q_\epsilon\|_{L^\infty(D \times (0, 2))}} = \frac{\tilde{v}_\epsilon(x, \xi_* + \epsilon\tau)}{\|\tilde{v}_\epsilon(x, \xi_* + \epsilon\tau)\|_{L^\infty(D \times (0, 2))}}$$

on  $D \times (0, 2)$ , where  $Q_\epsilon$  is defined in the beginning of the proof. Then  $\tilde{Q}_\epsilon$  is a positive solution to the uniformly elliptic equation (2.9) such that  $\|\tilde{Q}_\epsilon\|_{L^\infty(D \times (0, 2))} = 1$ . Moreover, the second inequality of (2.10) and Hopf boundary lemma imply

$$(2.13) \quad \|\tilde{Q}_\epsilon\|_{C^1(\bar{D} \times [0, 1])} \leq C \quad \text{and} \quad \inf_D \partial_\tau \tilde{Q}_\epsilon(x, 0) > 0.$$

This shows that for some  $\delta' > 0$ , independent of  $\epsilon$ , such that

$$(2.14) \quad \epsilon \frac{\inf_{D \times (\xi_*, \xi_* + \delta')} \partial_\xi \tilde{v}_\epsilon(x, \xi)}{\|\tilde{v}_\epsilon(x, \xi_* + \epsilon\tau)\|_{L^\infty(D \times (0, 2))}} = \inf_{D \times (0, \delta')} \partial_\tau \tilde{Q}_\epsilon(x, \tau) \geq \delta'$$

and thus the first inequality of assertion (ii) is proved. The proof for the second inequality of (ii) is analogous and is omitted.  $\square$

**Lemma 2.3.** *Fix a bounded interval  $I_0$ . Then there exist constants  $\gamma \in (0, 1)$  and  $C > 0$  independent of  $I \subset I_0$  and  $0 < \epsilon \ll 1$ , such that*

$$\|\hat{u}_\epsilon\|_{C^\gamma(\bar{D})} \leq C.$$

*Remark 2.4.* Lemma 2.3 asserts the precompactness of  $\hat{u}_\epsilon(\cdot)$  in  $C(\bar{D})$  as  $\epsilon \rightarrow 0$ . One can therefore pass to a sequence  $\epsilon_k \rightarrow 0$  so that  $\hat{u}_{\epsilon_k}$  converges in  $C(\bar{D})$ .

*Proof of Lemma 2.3.* Dividing the equation (2.1) by  $\mu = \mu(\xi)$  and integrating in  $\xi \in I$ , while treating the terms involving derivatives in  $\xi$  in a similar fashion as in the proof of Lemma 2.1, we obtain

$$(2.15) \quad \begin{cases} -\Delta_x \hat{u}_\epsilon = -\nabla_x \cdot (q_1 \nabla_x m) + (r - \hat{u}_\epsilon) q_2 + \epsilon^2 q_3 + \epsilon^2 q_4 & \text{in } D, \\ \partial_n \hat{u}_\epsilon = q_1 \partial_n m & \text{on } \partial D, \end{cases}$$

where

$$(2.16)$$

$$q_1(x) = \int_I \frac{\alpha}{\mu} u_\epsilon d\xi, \quad q_2(x) = \int_I \frac{u_\epsilon}{\mu} d\xi, \quad q_3(x) = \int_I \partial_\xi^2 \left( \frac{1}{\mu} \right) u_\epsilon d\xi, \quad q_4(x) = \left[ \frac{\partial_\xi u_\epsilon}{\mu} \right]_{\xi=\xi_*}^{\xi^*}.$$

By Lemmas 2.1 and 2.2, it is easy to see that

$$(2.17) \quad \|q_i\|_{C(\bar{D})} \leq C \quad \text{for } 1 \leq i \leq 3, \quad \epsilon^2 \|q_4\|_{C(\bar{D})} \leq C, \quad q_4(x) \leq 0 \text{ in } D$$

for some constant  $C$  independent of  $\epsilon$ .

Fix  $p > N$ . By Proposition C.3, there exists a linear (extension) operator  $T : C^\infty(\partial D) \rightarrow C^\infty(\bar{D})$  such that

$$\partial_n(Tg)|_{\partial D} = g, \quad \text{and} \quad \|Tg\|_{W^{1,p}(D)} \leq C\|g\|_{L^p(\partial D)}.$$

Take  $G = T[q_1 \partial_n m]$ , then

$$(2.18) \quad \|G\|_{W^{1,p}(D)} \leq C \|q_1 \partial_n m\|_{L^\infty(\partial D)}$$

and  $U := \hat{u}_\epsilon - G$  satisfies

$$(2.19) \quad \begin{cases} -\Delta_x U = -\nabla_x \cdot (q_1 \nabla_x m - \nabla_x G) + (r - \hat{u}_\epsilon) q_2 + \epsilon^2 q_3 + \epsilon^2 q_4 & \text{in } D, \\ \partial_n U = 0 & \text{on } \partial D. \end{cases}$$

Extending  $U$  by reflection method so that  $U$  satisfies a similar equation in an open set containing  $\bar{D}$ , we may apply De Giorgi-Nash-Moser interior estimates [21, Theorem 2.3] so that for some  $0 < \gamma < 1$  and  $C > 0$ ,

$$(2.20) \quad \begin{aligned} \|U\|_{C^\gamma(\bar{D})} &\leq C [\|U\|_{L^\infty(D)} + \| -q_1 \nabla_x m + \nabla_x G \|_{L^p(D)} \\ &\quad + \|(r - \hat{u}_\epsilon) q_2 + \epsilon^2 q_3 + \epsilon^2 q_4\|_{L^{Np/(N+p)}(D)}]. \end{aligned}$$

Since  $U = \hat{u}_\epsilon - G$ , we can apply Sobolev embedding to get

$$(2.21) \quad \|U\|_{L^\infty(D)} \leq \|\hat{u}_\epsilon\|_{L^\infty(D)} + \|G\|_{L^\infty(D)} \leq \|\hat{u}_\epsilon\|_{L^\infty(D)} + C\|G\|_{W^{1,p}(D)}.$$

Hence, we deduce by (2.20) and (2.21) and also Morrey's inequality [32, Sect. 5.6.2] that

$$\begin{aligned} \|\hat{u}_\epsilon\|_{C^\gamma(\bar{D})} &\leq \|U\|_{C^\gamma(\bar{D})} + \|G\|_{C^\gamma(\bar{D})} \\ &\leq C \left( \|\hat{u}_\epsilon\|_{L^\infty(D)}, \max_{i=1,2} \|q_i\|_{L^\infty(D)}, \epsilon^2 \max_{i=3,4} \|q_i\|_{L^\infty(D)}, \|G\|_{W^{1,p}(D)} \right). \end{aligned}$$

Combining with (2.18), we have (for  $\epsilon \in (0, 1]$ )

$$\|\hat{u}_\epsilon\|_{C^\gamma(\bar{D})} \leq C \left( \|\hat{u}_\epsilon\|_{L^\infty(D)}, \max_{i=1,2} \|q_i\|_{C(\bar{D})}, \epsilon^2 \max_{i=3,4} \|q_i\|_{C(\bar{D})} \right).$$

The right hand side of the last line is bounded independently of  $\epsilon$ , by Lemma 2.1 and (2.17).  $\square$

**Lemma 2.5.** *Let  $I = (\xi_*, \xi^*)$  be given. Suppose for each compact set  $K \subset \subset \bar{D} \times (\xi_*, \xi^*)$ , there exists  $\delta_K > 0$  such that*

$$(2.22) \quad \|u_\epsilon\|_{C(K)} \leq \exp(-\delta_K/\epsilon).$$

*In such event, fix an arbitrary  $\hat{\xi} \in I$ , and define*

$$\hat{u}_{\epsilon,1}(x) = \int_{\xi_*}^{\hat{\xi}} u_\epsilon d\xi, \quad \text{and} \quad \hat{u}_{\epsilon,2}(x) = \int_{\hat{\xi}}^{\xi^*} u_\epsilon d\xi.$$

*Then there exist  $\gamma \in (0, 1)$  and  $C > 0$ , both independent of  $\epsilon$ , such that*

$$\|\hat{u}_{\epsilon,1}\|_{C^\gamma(\bar{D})} + \|\hat{u}_{\epsilon,2}\|_{C^\gamma(\bar{D})} \leq C.$$

*In particular, passing to a subsequence if necessary,  $\hat{u}_{\epsilon,i} \rightarrow \hat{u}_i$  in  $C(\bar{D})$  for  $i = 1, 2$ , and  $u_\epsilon(x, \xi) \rightarrow \delta(\xi - \xi_*) \hat{u}_1(x) + \delta(\xi - \xi^*) \hat{u}_2(x)$  in the distribution sense.*

*Proof.* We first prove the estimate for  $\hat{u}_1$ . First, integrate (1.2) over  $\xi \in (\xi_*, \hat{\xi})$ . We may repeat the proof of Lemma 2.3, provided the following estimate is proved:

$$\epsilon^2 \left[ \sup_{x \in D, \xi=\hat{\xi}} \left( \left| \frac{\partial_\xi u_\epsilon}{\mu} \right| + \left| \partial_\xi \left( \frac{1}{\mu} \right) u_\epsilon \right| \right) \right] \leq C.$$

By (2.22), it therefore suffices to show

$$(2.23) \quad \lim_{\epsilon \rightarrow 0} \left[ \sup_D |\partial_\xi u_\epsilon(x, \hat{\xi})| \right] = 0.$$

To show (2.23), let  $Q_\epsilon(x, \tau) = \tilde{v}_\epsilon(x, \hat{\xi} + \epsilon\tau)$ , where  $\tilde{v}_\epsilon(x, \xi) = e^{-\alpha m/\mu} u_\epsilon(x, \xi)$ , then  $Q_\epsilon$  satisfies a uniformly elliptic equation in  $D \times (-1, 1)$  with  $L^\infty$  bounded coefficients similar to (2.9), hence we may apply the interior  $L^p$  estimate to obtain

$$\begin{aligned} \epsilon \sup_D |\partial_\xi u_\epsilon(x, \hat{\xi})| &\leq C \sup_D |\partial_\tau Q_\epsilon(x, 0)| \\ &\leq C \|Q_\epsilon\|_{L^\infty(D \times (-1, 1))} \leq C \|u_\epsilon\|_{L^\infty(D \times (\hat{\xi} - \epsilon, \hat{\xi} + \epsilon))}. \end{aligned}$$

(2.23) thus follows from (2.22). This enables us to repeat the proof of Lemma 2.3 to show that  $\|\hat{u}_{\epsilon,1}\|_{C^\gamma(\bar{D})} \leq C$ . Since  $\hat{u}_{\epsilon,2} = \hat{u}_\epsilon - \hat{u}_{\epsilon,1}$ , the other inequality  $\|\hat{u}_{\epsilon,2}\|_{C^\gamma(\bar{D})} \leq C$  follows automatically.  $\square$

For later purposes, we will also need the following result.

**Lemma 2.6.** *Let  $I = (\xi_*, \xi^*) \subset \mathbb{R}^+$  be a bounded open interval. Suppose (along a sequence  $(\epsilon, I) = (\epsilon_k, I_k)$ ) that (i)  $\epsilon/|I| \rightarrow 0$  and (ii) for some  $\hat{\xi} > 0$ ,  $I \rightarrow \{\hat{\xi}\}$  in the Hausdorff sense. Then any positive solution  $u_\epsilon$  of (2.1) satisfies*

$$\hat{u}_\epsilon(x) \rightarrow \theta_{\hat{\xi}}(x)$$

*weakly in  $H^1(D)$  and strongly in  $C(\bar{D})$ .*

*Proof.* See Lemma B.1 in Appendix B.  $\square$

### 3. WKB Ansatz and a constrained Hamilton-Jacobi Equation

**Definition 3.1.** Denote, for each  $\xi > 0$  and  $h(\cdot) \in C(\bar{D})$ , by  $H(\xi; h)$  the principal eigenvalue of

$$(3.1) \quad \begin{cases} \nabla_x \cdot (\mu(\xi) \nabla_x \psi - \alpha(\xi) \psi \nabla_x m) + (r(x) - h(x))\psi + H\psi = 0 & \text{in } D, \\ \mu(\xi) \partial_n \psi - \alpha(\xi) \psi \partial_n m = 0 & \text{on } \partial D, \quad \text{and} \quad \int_D \psi^2 dx = 1. \end{cases}$$

Next, set  $h = \hat{u}_\epsilon$  and denote the eigenfunction corresponding to  $H(\xi; \hat{u}_\epsilon)$  by  $\psi_\epsilon(\cdot, \xi)$ .

Recall the Hölder estimate of Lemma 2.3, and the normalization of  $\psi_\epsilon(\cdot, \xi)$ . One can deduce from standard elliptic estimates that for each bounded interval  $I_0 \subset \mathbb{R}^+$ , there exists constant  $C = C(I_0) > 1$  independent of  $\epsilon$  such that (see, e.g. [48, Lemma 4.1])

$$(3.2) \quad \frac{1}{C} \leq \psi_\epsilon(x, \xi) \leq C \quad \text{in } D \times I_0, \quad \sup_{D \times I_0} [|\partial_\xi \psi_\epsilon(x, \xi)| + \partial_\xi^2 \psi_\epsilon(x, \xi)] \leq C.$$

By Remark 2.4, we may pass to a sequence  $\epsilon_k \rightarrow 0$  so that  $\hat{u}_{\epsilon_k}(x) \rightarrow \hat{u}(x)$  for some non-negative function  $\hat{u} \in C(\bar{D})$ . We suppress the subscript  $k$  for convenience. Define

$$(3.3) \quad w_\epsilon(x, \xi) := \epsilon \log u_\epsilon(x, \xi) - \epsilon \log \psi_\epsilon(x, \xi).$$

Then a direct computation shows that

$$(3.4) \quad \begin{aligned} -\frac{\mu}{\epsilon^2} |\nabla_x w_\epsilon|^2 - 2\frac{\mu}{\epsilon} \nabla_x w_\epsilon \cdot \frac{\nabla_x \psi_\epsilon}{\psi_\epsilon} - \frac{\mu}{\epsilon} \Delta_x w_\epsilon + \frac{\alpha}{\epsilon} \nabla_x m \cdot \nabla_x w_\epsilon \\ - |\partial_\xi w_\epsilon|^2 - 2\epsilon \partial_\xi w_\epsilon \frac{\partial_\xi \psi_\epsilon}{\psi_\epsilon} - \epsilon \partial_\xi^2 w_\epsilon - \epsilon^2 \frac{\partial_\xi^2 \psi_\epsilon}{\psi_\epsilon} = -H(\xi; \hat{u}_\epsilon) \end{aligned}$$

in  $D \times I$ , with boundary conditions

$$(3.5) \quad \partial_n w_\epsilon = 0 \quad \text{on } \partial D \times I, \quad \text{and} \quad w_\epsilon = -\infty \quad \text{on } D \times \partial I.$$

We will show that  $w_\epsilon(x, \xi)$  converges locally uniformly in  $\bar{D} \times (\xi_*, \xi^*)$  to a viscosity solution  $w(\xi)$  of a certain constrained Hamilton-Jacobi equation in the variable  $\xi$  only.

**Proposition 3.2.** *Given any fixed interval  $I \subset \mathbb{R}^+$ . Suppose that  $\int_D \hat{u}_\epsilon dx \geq c_0$  for some  $c_0 > 0$  independent of  $\epsilon$ . Then passing to a sequence  $\epsilon_k \rightarrow 0$ , it holds that*

$$\hat{u}_{\epsilon_k}(x) \rightarrow \hat{u}(x) \quad \text{in } C(\bar{D}) \quad \text{and} \quad w_{\epsilon_k}(x, \xi) \rightarrow w(\xi) \quad \text{in } C_{loc}(\bar{D} \times I)$$

where  $w(\xi)$  is a viscosity solution of the constrained Hamilton-Jacobi equation

$$(3.6) \quad \begin{cases} -|\partial_\xi w|^2 = -H(\xi; \hat{u}) & \text{in } I = (\xi_*, \xi^*), \\ \sup_I w = 0. \end{cases}$$

We prepare for the proof of Proposition 3.2 with a series of lemmas.

**Lemma 3.3.** *For each  $\delta > 0$ , there exists  $C > 0$  independent of  $\epsilon$  such that*

$$\sup_{D \times (\xi_* + \delta\epsilon, \xi^* - \delta\epsilon)} \left[ |\partial_\xi w_\epsilon(x, \xi)| + \frac{1}{\epsilon} |\nabla_x w_\epsilon(x, \xi)| \right] \leq C.$$

*Proof.* Let  $\tilde{v}_\epsilon(x, \xi) = e^{-\alpha m/\mu} u_\epsilon(x, \xi)$ , it suffices to show that for each fixed  $\delta > 0$ , there is some  $C > 0$  independent of  $\epsilon > 0$  such that

$$(3.7) \quad |\nabla_x \tilde{v}_\epsilon(x, \xi_0)| + \epsilon |\partial_\xi \tilde{v}_\epsilon(x, \xi_0)| \leq C \tilde{v}_\epsilon(x, \xi_0) \quad \text{for all } (x, \xi_0) \in D \times (\xi_* + \delta\epsilon, \xi^* - \delta\epsilon).$$

Fix  $\delta > 0$  and  $\xi_0 \in [\xi_* + \delta\epsilon, \xi^* - \delta\epsilon]$  and define  $Q_\epsilon(x, \tau) = \tilde{v}_\epsilon(x, \xi_0 + \epsilon\tau)$ . Then  $Q_\epsilon$  is a positive solution of the homogeneous linear elliptic equation (2.9) (with  $\mu(\xi) = \mu(\xi_0 + \epsilon\tau)$  and  $\alpha(\xi) = \alpha(\xi_0 + \epsilon\tau)$ ) in the domain  $D \times (-\delta, \delta)$ , and satisfies the Neumann boundary conditions on  $\partial D \times (-\delta, \delta)$ . By Harnack inequality, we have

$$(3.8) \quad \sup_{D \times (-\delta/2, \delta/2)} Q_\epsilon \leq C \inf_{D \times (-\delta/2, \delta/2)} Q_\epsilon.$$

Also, elliptic  $L^p$  estimates with  $p > N + 1$  ( $N$  being dimension of  $D$ ) implies

$$(3.9) \quad \sup_{x \in D} [|\nabla_x Q_\epsilon(x, 0)| + |\partial_\tau Q_\epsilon(x, 0)|] \leq C \|Q_\epsilon\|_{L^p(D \times (-\delta/2, \delta/2))} \leq C \sup_{D \times (-\delta/2, \delta/2)} Q_\epsilon.$$

Combining equations (3.8) and (3.9), we conclude that for some positive constant  $C = C(\delta)$  independent of  $\epsilon$ ,  $x \in D$  and  $\xi_0 \in [\xi_* + \delta\epsilon, \xi^* - \delta\epsilon]$ ,

$$(3.10) \quad |\nabla_x Q_\epsilon(x, 0)| + |\partial_\tau Q_\epsilon(x, 0)| \leq C \inf_{D \times (-\delta/2, \delta/2)} Q_\epsilon \leq C Q_\epsilon(x, 0).$$

i.e. (3.7) holds. This proves the lemma.  $\square$

We develop a property of  $w$  similar to Lemma 2.2(ii).

**Lemma 3.4.** *Fix an open interval  $I = (\xi_*, \xi^*) \subset \mathbb{R}^+$ . There exists  $\delta_2 > 0$  independent of  $\epsilon$  such that, in addition to the conclusion of Lemma 2.2, we have*

$$(3.11) \quad \inf_{D \times (\xi_*, \xi_* + \delta_2 \epsilon)} \partial_\xi w_\epsilon > 0 \quad \text{and} \quad \sup_{D \times (\xi^* - \delta_2 \epsilon, \xi^*)} \partial_\xi w_\epsilon < 0.$$

*In particular*

$$(3.12) \quad \sup_{D \times (\xi_*, \xi^*)} w_\epsilon = \sup_{D \times (\xi_* + \delta_2 \epsilon, \xi^* - \delta_2 \epsilon)} w_\epsilon.$$

*Proof.* Recall the definition of  $w_\epsilon$  in (3.3), where  $\psi_\epsilon$  is the principal eigenfunction of (3.1). Also recall  $\tilde{v}_\epsilon = e^{-\alpha m/\mu} u_\epsilon$ . Then

$$w_\epsilon(x, \xi) = \epsilon \log \tilde{v}_\epsilon(x, \xi) + \epsilon m(x) \frac{\alpha(\xi)}{\mu(\xi)} - \epsilon \log \psi_\epsilon(x, \xi_* + \epsilon \tau).$$

Differentiating with respect to  $\xi$ , we have

$$\partial_\xi w_\epsilon(x, \xi) = \frac{\epsilon}{\tilde{v}_\epsilon(x, \xi)} \left\{ \partial_\xi \tilde{v}_\epsilon + \tilde{v}_\epsilon \left[ m \partial_\xi \left( \frac{\alpha}{\mu} \right) - \frac{\partial_\xi \psi_\epsilon}{\psi_\epsilon} \right] \right\}.$$

Recall the definition of  $\tilde{Q}_\epsilon(x, \tau)$  in (2.12), we have (setting  $\xi = \xi_* + \epsilon \tau$ )

$$\begin{aligned} \partial_\xi w_\epsilon(x, \xi_* + \epsilon \tau) &= \frac{\epsilon}{\tilde{Q}_\epsilon(x, \xi)} \left\{ \epsilon^{-1} \partial_\tau \tilde{Q}_\epsilon + \tilde{Q}_\epsilon \left[ m \partial_\xi \left( \frac{\alpha}{\mu} \right) - \frac{\partial_\xi \psi_\epsilon}{\psi_\epsilon} \right] \right\} \\ &= \frac{\epsilon}{\tilde{Q}(x, \tau)} \{ \epsilon^{-1} \delta' + O(1) \} > 0, \end{aligned}$$

for  $\tau \in (0, \delta')$  and for  $0 < \epsilon \ll 1$ , where we used (2.12), (2.14) and (3.2). Hence we can deduce that, by taking  $\delta_2$  smaller,  $\partial_\xi w_\epsilon(x, \xi) > 0$  in  $D \times (\xi_*, \xi_* + \delta_2 \epsilon)$ . Similarly,  $\partial_\xi w_\epsilon(x, \xi) < 0$  in  $D \times (\xi^* - \delta_2 \epsilon, \xi^*)$ . Therefore, there exists  $\delta_2 > 0$  such that for  $\epsilon > 0$  small, (3.11) holds and the maximum point of  $w_\epsilon(x, \xi)$  is attained within  $\bar{D} \times [\xi_* + \delta_2 \epsilon, \xi^* - \delta_2 \epsilon]$ , i.e. (3.12) holds.  $\square$

**Lemma 3.5.** *For each constant  $A > 1$ ,*

$$\sup_{D \times (\xi_*, \xi^*)} w_\epsilon \leq A \epsilon |\log \epsilon| \quad \text{for all sufficiently small } \epsilon.$$

*Proof.* Let  $A > 1$  be a given constant. Set  $I(\epsilon) = (\xi_* + \delta_2 \epsilon, \xi^* - \delta_2 \epsilon)$ , where  $\delta_2$  is given in Lemma 3.4. Again by Lemma 3.4, it suffices to show

$$(3.13) \quad \sup_{D \times I(\epsilon)} w_\epsilon \leq A \epsilon |\log \epsilon|.$$

Fix  $x \in D$  and let  $M_\epsilon(x) := \sup_{I(\epsilon)} w_\epsilon(x, \xi)$ . If  $M_\epsilon(x) \leq 0$ , there is nothing to prove.

Suppose  $M_\epsilon(x) > 0$  and choose some  $\xi_\epsilon(x) \in \overline{I(\epsilon)}$  such that  $M_\epsilon(x) = w_\epsilon(x, \xi_\epsilon(x))$ . By Lemma 3.3,  $w_\epsilon$  is Lipschitz continuous in  $D \times I(\epsilon)$ , hence there exists an interval  $I'(x, \epsilon) \subset I(\epsilon)$  such that for some  $c_1 > 0$ ,

$$\xi_\epsilon(x) \in I'(x, \epsilon), \quad \inf_{\xi \in I'(x, \epsilon)} w_\epsilon(x, \xi) \geq \frac{M_\epsilon(x)}{A}, \quad |I'(x, \epsilon)| \geq c_1 M_\epsilon(x).$$

where  $c_1$  depends only on the Lipschitz constant of  $w_\epsilon$  and is independent of  $x$  and  $\epsilon$  (Lemma 3.3). Hence, using Lemma 2.1 and (3.2),

$$c_1 M_\epsilon(x) \exp \left( \frac{M_\epsilon(x)}{A \epsilon} \right) \leq \int_{I'(x, \epsilon)} \exp \left( \frac{w_\epsilon(x, \xi)}{\epsilon} \right) d\xi \leq \hat{u}_\epsilon(x) \leq \sup_D \hat{u}_\epsilon.$$

This implies that for some  $c_1$  and  $C_1$  independent of  $\epsilon$  (but depend on  $\sup_D \hat{u}_\epsilon$  (Lemma 2.1) and the Lipschitz constant of  $w_\epsilon$  in  $D \times (\xi_* + \delta_2 \epsilon, \xi^* - \delta_2 \epsilon)$  (Lemma 3.3)),

$$c_1 \frac{M_\epsilon(x)}{A\epsilon} \exp\left(\frac{M_\epsilon(x)}{A\epsilon}\right) \leq \frac{C_1}{\epsilon},$$

where  $c_1$  and  $C_1$  are independent of  $\epsilon$  and  $x \in D$ . This proves

$$M_\epsilon(x) \leq A\epsilon |\log \epsilon| \quad \text{for all } x \in D$$

and all sufficiently small  $\epsilon > 0$ , i.e. (3.13) holds.  $\square$

**Lemma 3.6.** *If  $\int_D \hat{u}_\epsilon dx \geq c_0$  for some  $c_0 > 0$ , which is independent of  $\epsilon$ , then there exists  $C > 0$  independent of  $\epsilon$  such that*

$$\sup_{D \times I} w_\epsilon \geq -C\epsilon,$$

where  $I = (\xi_*, \xi^*)$ .

*Proof.* By the hypotheses of the lemma,

$$c_0 \leq \int_D \hat{u}_\epsilon dx = \int_{D \times I} \psi_\epsilon \exp\left(\frac{w_\epsilon}{\epsilon}\right) dx d\xi \leq C \exp\left(\frac{\sup_{D \times I} w_\epsilon}{\epsilon}\right),$$

and the assertion follows.  $\square$

*Proof of Proposition 3.2.* In this proof, we omit for the sake of clarity the subscript  $k$  in  $\epsilon_k$ . By Lemmas 3.5 and 3.6, and (2.8), we have

$$(3.14) \quad -C\epsilon \leq \sup_{D \times (\xi_*, \xi^*)} w_\epsilon = \sup_{D \times (\xi_* + \delta_2 \epsilon, \xi^* - \delta_2 \epsilon)} w_\epsilon \leq C\epsilon |\log \epsilon|,$$

where  $\delta_2$  is given in Lemma 3.4. This and the uniform Lipschitz estimate in Lemma 3.3 imply that, up to a sequence,  $w_\epsilon$  converges uniformly to some (Lipchitz) function  $w \in C(\bar{D} \times [\xi_*, \xi^*])$  in compact subsets of  $\bar{D} \times (\xi_*, \xi^*)$ , such that  $\sup_{D \times (\xi_*, \xi^*)} w = 0$ . Furthermore, Lemma 3.3 implies that  $\|\nabla_x w_\epsilon\|_{L^\infty(D \times (\xi_* + \delta_2 \epsilon, \xi^* - \delta_2 \epsilon))} \leq C\epsilon$ . Hence,  $w = w(\xi)$  is a function of  $\xi$  but is independent of  $x$ , and such that

$$(3.15) \quad \sup_{(\xi_*, \xi^*)} w(\xi) = 0.$$

It remains to show that  $w$  satisfies equation (3.6) in the viscosity sense. Let  $\rho(\xi)$  be a  $C^2$  function of  $\xi$  such that  $\xi_0$  is a local maximum of  $w - \rho$ . Then  $w - \rho - (\xi - \xi_0)^4$  has a strict local maximum at some interior point  $\xi_0 \in (\xi_*, \xi^*)$ . We can then deduce that for all  $\epsilon > 0$  small,  $w_\epsilon(x, \xi) - \rho(\xi) - (\xi - \xi_0)^4$  has a local maximum  $(x_\epsilon, \xi_\epsilon) \in \bar{D} \times I$  such that  $\xi_\epsilon \rightarrow \xi_0$  as  $\epsilon \rightarrow 0$ . Hence,

$$(3.16) \quad \begin{aligned} \nabla_x w_\epsilon(x_\epsilon, \xi_\epsilon) &= 0, \quad \Delta_x w_\epsilon(x_\epsilon, \xi_\epsilon) \leq 0; \\ \partial_\xi w_\epsilon(x_\epsilon, \xi_\epsilon) &= \partial_\xi \rho(\xi_\epsilon) + 4(\xi_\epsilon - \xi_0)^3; \\ \partial_\xi^2 w_\epsilon(x_\epsilon, \xi_\epsilon) &\leq \partial_\xi^2 \rho(\xi_\epsilon) + 12(\xi_\epsilon - \xi_0)^2. \end{aligned}$$

Now, we can deduce, by evaluating (3.4) at the point  $(x_\epsilon, \xi_\epsilon)$ , that

$$\begin{aligned} & -|\partial_\xi \rho(\xi_\epsilon) + 4(\xi_\epsilon - \xi_0)^3|^2 - 2\epsilon[\partial_\xi \rho(\xi_\epsilon) + 4(\xi_\epsilon - \xi_0)^3]\partial_\xi(\log \psi_\epsilon)(x_\epsilon, \xi_\epsilon) \\ & - \epsilon \partial_\xi^2 \rho(\xi_\epsilon) - 12\epsilon(\xi_\epsilon - \xi_0)^2 - \epsilon^2 \frac{\partial_\xi^2 \psi_\epsilon}{\psi_\epsilon}(x_\epsilon, \xi_\epsilon) \leq -H(\xi_\epsilon; \hat{u}_\epsilon). \end{aligned}$$

Letting  $\epsilon \rightarrow 0$ , we have  $\xi_\epsilon \rightarrow \xi_0$  and  $\hat{u}_\epsilon \rightarrow \hat{u}$  in  $C(\bar{D})$ , so that

$$-|\partial_\xi \rho(\xi_0)|^2 \leq -H(\xi_0; \hat{u}).$$

Next, if  $w - \rho$  has a local minimum at a point  $\rho_0$ , we can show with a similar argument that

$$-|\partial_\xi \rho(\xi_0)|^2 \geq -H(\xi_0; \hat{u}).$$

Hence,  $w$  is a viscosity solution of (3.6).  $\square$

In general, viscosity solution of the nonstandard, constrained (3.6) may not be unique. The following lemma enumerates two additional properties of those solutions of (3.6) that are realized as the limits of  $w_{\epsilon_k}$ .

**Lemma 3.7.** *Suppose that along a sequence  $\epsilon_k \rightarrow 0$ ,  $\hat{u}_{\epsilon_k} \rightarrow \hat{u}$  uniformly in  $D$ , and  $w_{\epsilon_k} \rightarrow w$  locally uniformly in  $\bar{D} \times (\xi_*, \xi^*)$ . Then*

- (i)  $H(\xi, \hat{u}) \geq 0$  for all  $\xi \in [\xi_*, \xi^*]$  and  $\min_{[\xi_*, \xi^*]} H(\cdot, \hat{u}) = 0$ .
- (ii) If  $(x_k, \xi_k)$  is a local maximum of  $w_{\epsilon_k}$ , then  $\text{dist}(\xi_k, \{\xi : H(\xi, \hat{u}) = 0\}) \rightarrow 0$ .

*Proof.* First, it follows from equation (3.6) that  $H(\xi, \hat{u}) \geq 0$  for all  $\xi$ . Second, notice that at any local maximum point  $(x_\epsilon, \xi_\epsilon)$  of  $w_\epsilon$ , (3.4) implies

$$H(\xi_\epsilon; \hat{u}_\epsilon) \leq \epsilon^2 \frac{\partial_\xi^2 \psi_\epsilon}{\psi_\epsilon} \Big|_{(x, \xi) = (x_\epsilon, \xi_\epsilon)} = O(\epsilon^2).$$

Hence any limit point  $\xi_0$  of  $\{\xi_\epsilon\}$  satisfies  $H(\xi_0; \hat{u}) \leq 0$ , and thus  $H(\xi_0; \hat{u}) = 0$ . This proves (ii). Furthermore, it follows that the set  $\{\xi : H(\xi; \hat{u}) = 0\}$  is non-empty, this proves (i).  $\square$

In some cases, we can determine the limit  $w = \lim_{k \rightarrow \infty} w_{\epsilon_k}$  uniquely, as the following result shows.

**Proposition 3.8.** *Given a sequence  $\epsilon_k \rightarrow 0$ , let  $u_{\epsilon_k}$  be a positive steady state of (1.2), and  $w_{\epsilon_k}$  be defined by (3.3). Suppose that*

$$\hat{u}_{\epsilon_k} \rightarrow \hat{u} \quad \text{in } C(\bar{D}), \text{ and } w_{\epsilon_k} \rightarrow w \quad \text{in } C_{loc}(\bar{D} \times (\xi_*, \xi^*)).$$

If

$$(3.17) \quad \exists \xi' \in [\xi_*, \xi^*] : \quad H(\xi, \hat{u}) = \begin{cases} 0 & \text{when } \xi = \xi'; \\ > 0 & \text{when } \xi \in [\xi_*, \xi^*] \setminus \{\xi'\}, \end{cases}$$

i.e.  $H(\cdot, \hat{u})$  has a unique minimum point  $\xi' \in [\xi_*, \xi^*]$ , then

$$\hat{u}(x) = \theta_{\xi'}(x) \quad \text{and} \quad u_{\epsilon_k}(x, \xi) \rightarrow \delta_0(\xi - \xi')\theta_{\xi'}(x)$$

in distribution sense. In particular,  $\lambda(\xi, \xi') = H(\xi; \hat{u}) \geq 0$  for all  $\xi \in I$ .

*Proof.* First, we claim that  $w(\xi') = 0$ . Let the maximum of  $w_{\epsilon_k}$  in  $\bar{D} \times (\xi_*, \xi^*)$  be attained at some  $(x_k, \xi_k) \in \bar{D} \times (\xi_*, \xi^*)$ , then by Lemmas 3.5 and 3.6,

$$-C\epsilon_k \leq w_{\epsilon_k}(x_k, \xi_k) \leq C\epsilon_k |\log \epsilon_k|.$$

By Lemma 3.4,  $\xi_k \in [\xi_* + \delta_2 \epsilon_k, \xi^* - \delta_2 \epsilon_k]$ , we can then use the equicontinuity of  $w_{\epsilon_k}$  (Lemma 3.3) and the fact that  $\xi_k \rightarrow \xi'$  (Lemma 3.7(ii)) to pass to the limit to obtain  $w(\xi') = 0$ .

**Claim 3.9.**  $w(\xi)$  is strictly increasing (resp. decreasing) for  $\xi < \xi'$  (resp.  $\xi > \xi'$ ).

Suppose not, then  $w(\xi)$  has another local maximum point  $\xi'' \neq \xi'$ . We claim that  $\xi'' \in \{\xi_*, \xi^*\}$ . For if  $\xi''$  is an interior local maximum point of  $w$ , then by property of  $w$  being a viscosity solution of (3.6), we must have  $H(\xi'', \hat{u}) \leq 0$ , i.e.  $H(\xi'', \hat{u}) = 0$  and thus  $\xi'' = \xi'$ , by the hypotheses of the proposition. Hence  $w$  has at least two (and at most three) distinct, strict local maximum points. This implies that for  $k$  large,  $w_{\epsilon_k}$  has another sequence of local maximum points  $(x_k'', \xi_k'')$  such that  $\xi_k'' \not\rightarrow \xi'$ . This contradiction to Lemma 3.7(ii) establishes Claim 3.9.

As a consequence of Claim 3.9,  $w(\xi') = 0$  and  $w < 0$  for  $\xi \neq \xi'$ . Hence

$$(3.18) \quad u_\epsilon(x, \xi) \rightarrow \delta_0(\xi - \xi')\hat{u}(x) \quad \text{in distribution sense.}$$

It remains to show that  $\hat{u} = \theta_{\xi'}$  in  $D$ . First we note that for the  $q_i$ 's defined in (2.16),

$$(3.19) \quad q_1(x) \rightarrow \frac{\alpha(\xi')}{\mu(\xi')}\hat{u}(x), \quad q_2(x) \rightarrow \frac{1}{\mu(\xi')}\hat{u}(x), \quad q_3(x) \rightarrow \partial_\xi^2\left(\frac{1}{\mu}\right)\Big|_{\xi=\xi'}\hat{u}(x)$$

uniformly in  $D$  as  $\epsilon \rightarrow 0$ .

**Claim 3.10.** *If (3.18) holds, then  $\hat{u}(x) \leq \theta_{\xi'}(x)$  in  $D$ .*

Multiply (2.15) by a non-negative test function  $\rho(x)$ , integrate by parts, we have

$$\int_D \{\nabla_x \rho \cdot (\nabla_x \hat{u}_\epsilon - q_1 \nabla_x m) + \rho [-(r - \hat{u}_\epsilon)q_2 - \epsilon^2 q_3]\} dx = \epsilon^2 \int_D \rho q_4 dx \leq 0$$

where we used  $q_4 \leq 0$  (from (2.17)). Passing to the limit and using (3.19), we deduce that  $\hat{u}$  is a weak subsolution of (1.3) with  $\xi = \xi'$ . Hence  $\hat{u} \leq \theta_{\xi'}$ , the latter being the unique positive solution of (1.3). This proves the claim.

On the other hand,

$$0 \leq H(\xi', \hat{u}) \leq H(\xi', \theta_{\xi'}) = 0,$$

where the first inequality follow from Lemma 3.7(i), the second from the eigenvalue comparison principle such that the equality holds if and only if  $\hat{u} \equiv \theta_{\xi'}$ , and the third equality by definition of the principal eigenvalue  $H(\xi'; \theta_{\xi'})$  (as  $\theta_{\xi'}$  clearly gives the positive eigenfunction). In particular the equality holds, and hence  $\hat{u} \equiv \theta_{\xi'}$ . By (3.18), we deduce

$$u_\epsilon(x, \xi) \rightarrow \delta_0(\xi - \xi')\theta_{\xi'}(x) \quad \text{in distribution as } \epsilon \rightarrow 0.$$

Although we have passed to a sequence  $\epsilon = \epsilon_k$  in the above procedure, the fact that the limit  $\hat{u} = \theta_{\xi'}$  is uniquely determined implies that the convergence  $\lim_{\epsilon \rightarrow 0} \hat{u}_\epsilon = \theta_{\xi'}$  is independent of sequences.  $\square$

#### 4. Non-vanishing selection gradient

In this section, we consider the case when the selection gradient do not vanish in a closed bounded interval  $\bar{I}_0 = [\underline{\xi}, \bar{\xi}] \subset \mathbb{R}^+$ . For definiteness, we discuss the case when

$$(4.1) \quad \partial_{\xi_2} \lambda(\xi, \xi) > 0 \quad \text{for all } \underline{\xi} \leq \xi \leq \bar{\xi}.$$

**Theorem 4.1.** *Suppose that (4.1) holds for some closed bounded interval  $\bar{I}_0 = [\underline{\xi}, \bar{\xi}]$ . Then there is  $\delta_1 > 0$  such that for any subinterval  $I = (\xi_*, \xi^*) \subset \bar{I}_0$  such that  $|I| \leq \delta_1$ , any positive steady state  $u_\epsilon$  of (1.2) satisfies  $\hat{u}_\epsilon \rightarrow \theta_{\xi_*}$  uniformly in  $D$  and*

$$u_\epsilon(x, \xi) \rightarrow \delta_0(\xi - \xi_*)\theta_{\xi_*}(x) \quad \text{in distribution sense, as } \epsilon \rightarrow 0.$$

**Lemma 4.2.** *Suppose that (4.1) holds for some closed bounded interval  $\bar{I}_0 = [\underline{\xi}, \bar{\xi}]$ . Then there is  $\delta_1 > 0$  such that for each subinterval  $I = (\xi_*, \xi^*) \subset \bar{I}_0$  with  $|I| \leq \delta_1$ , there exists  $c_0 > 0$  independent of  $0 < \epsilon \ll 1$  and steady state  $u_\epsilon$  of (1.2) so that*

$$(4.2) \quad \inf_{\xi \in I} \partial_\xi H(\xi, \hat{u}_\epsilon(\cdot)) \geq c_0 \quad \text{and} \quad \int_D \hat{u}_\epsilon \, dx \geq c_0,$$

where  $\hat{u}_\epsilon(x) = \int_I u_\epsilon(x, \xi) \, d\xi$ .

*Proof.* Suppose to the contrary that there is a sequence of open intervals  $I_k \subset \bar{I}_0$  such that  $\delta_k = |I_k| \rightarrow 0$  but the associated solution  $\{\hat{u}_{k,\epsilon}\}_{\epsilon>0}$  of (2.1) does not satisfy (4.2). Passing to a further subsequence, we may assume that  $I_k \rightarrow \{\xi_0\}$  in the Hausdorff sense for some  $\xi_0 \in \bar{I}_0$ . Now by (4.1) and the smoothness of  $H(\xi, \theta_{\xi_0}) = \lambda(\xi_0, \xi)$  in  $\xi$ , there exists  $\delta_2 > 0$  such that

$$\min_{\xi \in [\xi_0 - \delta_2, \xi_0 + \delta_2]} \partial_\xi H(\xi, \theta_{\xi_0}(\cdot)) > 0 \quad \text{and} \quad \int_D \theta_{\xi_0} \, dx > 0.$$

Now, by Lemma 2.6 we may choose  $\delta_1 \in (0, \delta_2]$  so that for each open interval  $I \subset (\xi_0 - \delta_1, \xi_0 + \delta_1)$ , then  $\hat{u}_\epsilon$  is close enough to  $\theta_{\xi_0}$  in  $C(\bar{D})$  for all small  $\epsilon$ . This implies that for  $k$  large enough, (4.2) holds for the solution  $\{\hat{u}_{k,\epsilon}\}_{\epsilon>0}$  of (2.1) associated with  $I_k$ . This is a contradiction.  $\square$

*Proof of Theorem 4.1.* Fix  $\delta_1$  small enough as in Lemma 4.2 and choose any open interval  $I \subset \bar{I}_0$  such that  $|I| \leq \delta_1$ . Then for  $\epsilon$  small, (4.2) holds. Pass to a sequence so that  $\hat{u}_\epsilon$  converges uniformly to some  $\hat{u}$  in  $D$ . By Lemma 4.2,  $H(\cdot; \hat{u})$  has a unique minimum point at  $\xi_*$  in the closure  $[\xi_*, \xi^*]$  of  $I$ . By Proposition 3.8,  $\hat{u} = \theta_{\xi_*}$  and

$$u_\epsilon(x, \xi) \rightarrow \delta_0(\xi - \xi_*) \theta_{\xi_*}(x)$$

in distribution sense as  $\epsilon \rightarrow 0$ . This proves the theorem.  $\square$

## 5. Interior CSS $\hat{\xi}$

In this section, we consider the case when the adaptive dynamics has an interior continuously stable strategy (CSS), denoted as  $\hat{\xi}$ .

**Definition 5.1.** We say that  $\hat{\xi} \in I_0$  is a local CSS if **(Cv)** holds and

$$(5.1) \quad \partial_{\xi_2}^2 \lambda(\hat{\xi}, \hat{\xi}) > 0.$$

**Theorem 5.2.** *Suppose that  $\hat{\xi} \in I_0$  is a local CSS in the sense of Definition 5.1. Then there is  $\delta_1 > 0$  such that for each fixed  $I = (\xi_*, \xi^*) \subset (\hat{\xi} - \delta_1, \hat{\xi} + \delta_1)$ , any positive steady state  $u_\epsilon$  of (1.2) satisfies, as  $\epsilon \rightarrow 0$ ,  $u_\epsilon(x) \rightarrow \theta_{\xi'}(x)$  in  $C(\bar{D})$  and*

$$u_\epsilon(x, \xi) \rightarrow \delta_0(\xi - \xi') \theta_{\xi'}(x) \quad \text{in distribution sense,}$$

where the point of concentration  $\xi'$  is the point in  $[\xi_*, \xi^*]$  closest to  $\hat{\xi}$ ; i.e.

$$\xi' = \begin{cases} \hat{\xi} & \text{if } \hat{\xi} \in [\xi_*, \xi^*], \\ \xi_* & \text{if } \hat{\xi} < \xi_* = \inf I, \\ \xi^* & \text{if } \hat{\xi} > \xi^* = \sup I. \end{cases}$$

**Lemma 5.3.** *Suppose that  $\hat{\xi} \in I_0$  is a local CSS in the sense of Definition 5.1. There exists  $\delta_1 > 0$  such that*

$$(5.2) \quad \partial_{\xi_2} \lambda(\xi', \xi') \begin{cases} > 0 & \text{for all } \xi' \in (\hat{\xi}, \hat{\xi} + \delta_1), \\ < 0 & \text{for all } \xi' \in (\hat{\xi} - \delta_1, \hat{\xi}). \end{cases}$$

Moreover, for each fixed interval  $I \subset (\hat{\xi} - \delta_1, \hat{\xi} + \delta_1)$ , there exists  $c_0 > 0$  independent of  $\epsilon \ll 1$  and steady state  $u_\epsilon$  of (1.2), such that

$$(5.3) \quad \inf_{\xi \in I} \partial_\xi^2 H(\xi, \hat{u}_\epsilon(\cdot)) \geq c_0 \quad \text{and} \quad \int_D \hat{u}_\epsilon \, dx \geq c_0,$$

where  $\hat{u}_\epsilon(x) = \int_{\xi_*}^{\xi^*} u_\epsilon(x, \xi) \, d\xi$ .

*Proof.* First, (5.2) follows from **(Cv)**, by choosing  $\delta_1 > 0$  small. Since  $H(\xi, \theta_{\hat{\xi}}(\cdot)) = \lambda(\hat{\xi}, \xi)$  is  $C^2$  in  $\xi$ , (5.1) implies that for some  $\delta_2 > 0$ ,

$$\inf_{\xi \in [\hat{\xi} - \delta_2, \hat{\xi} + \delta_2]} \partial_\xi^2 H(\xi, \theta_{\hat{\xi}}(\cdot)) > 0 \quad \text{and} \quad \int_D \theta_{\hat{\xi}} \, dx > 0.$$

Now, by Lemma 2.6 we may choose  $\delta_1 \in (0, \delta_2]$  smaller if necessary so that for each fixed open interval  $I \subset (\hat{\xi} - \delta_1, \hat{\xi} + \delta_1)$ , and for all  $\epsilon$  small,  $\hat{u}_\epsilon$  is close enough to  $\theta_{\hat{\xi}}$  in  $C(\bar{D})$  so that (5.3) holds.  $\square$

*Proof of Theorem 5.2.* Fix  $\delta_1$  small enough as in Lemma 5.3 and choose any open interval  $I \subset (\hat{\xi} - \delta_1, \hat{\xi} + \delta_1)$ . Then for  $\epsilon$  small, (5.3) holds. Next, use Remark 2.4 to pass to a sequence so that  $\hat{u}_\epsilon \rightarrow \hat{u}$  in  $C(\bar{D})$ .

By Lemma 5.3,  $H(\cdot; \hat{u})$  has a unique minimum point  $\xi' \in [\xi_*, \xi^*]$ . By Proposition 3.8,  $u_\epsilon(x, \xi) \rightarrow \delta_0(\xi - \xi')\theta_{\xi'}(x)$  in distribution sense, and  $\hat{u} = \theta_{\xi'}$ .

**Claim 5.4.** (a) If  $\xi' > \hat{\xi}$ , then  $\xi' = \xi_*$ ; (b) If  $\xi' < \hat{\xi}$ , then  $\xi' = \xi^*$ .

Suppose that  $\xi' > \hat{\xi}$ , then by (5.2),

$$\partial_{\xi_2} \lambda(\xi', \xi') > 0 \quad \text{and} \quad \lambda(\xi', \xi') = 0$$

so that  $\lambda(\xi', \xi) < 0$  for all  $\xi$  less than but close to  $\xi'$ . As  $\lambda(\xi', \xi) = H(\xi, \theta_{\xi'}) \geq 0$  in  $I$  (by Lemma 3.7(i)), this shows  $(\hat{\xi}, \xi') \cap I = \emptyset$ . Since  $\xi' \in [\xi_*, \xi^*]$ , we deduce that  $\xi' = \xi_*$  and thus  $\hat{\xi} < \xi_*$ . This proves part (a) of the claim. Part (b) can be similarly handled and we omit the details.

To finish the proof of the theorem, suppose first  $\xi' \neq \hat{\xi}$ , then by the above claim, we deduce that  $\hat{\xi} \notin [\xi_*, \xi^*]$ . This says that if  $\hat{\xi} \in [\xi_*, \xi^*]$ , then  $\xi' = \hat{\xi}$ .

Next, let  $\hat{\xi} < \xi_*$ , then  $\xi' > \hat{\xi}$  (as  $\xi' \in [\xi_*, \xi^*]$ ). Then Claim 5.4(a) implies that  $\xi' = \xi_*$ . Similarly,  $\hat{\xi} > \xi^*$  implies  $\xi' = \xi^*$ . This completes the proof.  $\square$

## 6. Evolutionary Branching

In this section, we consider the case when the adaptive dynamics has a branching point, denoted as  $\hat{\xi}$ .

**Definition 6.1.** We say that  $\hat{\xi} \in I_0$  is a branching point if **(Cv)** holds and

$$(6.1) \quad \partial_{\xi_2}^2 \lambda(\hat{\xi}, \hat{\xi}) < 0.$$

The following theorem is the main result of this section.

**Theorem 6.2.** Suppose that  $\hat{\xi}$  is a branching point in the sense of Definition 6.1, and there is some  $\delta_1 > 0$  such that if the endpoints of  $I = (\xi_*, \xi^*)$  are chosen such that

$$(6.2) \quad I \subset (\hat{\xi} - \delta_1, \hat{\xi} + \delta_1), \quad \lambda(\xi_*, \xi^*) < 0 \quad \text{and} \quad \lambda(\xi^*, \xi_*) < 0.$$

Then there is  $\epsilon_k \rightarrow 0$  such that any positive steady state  $u_{\epsilon_k}$  of (1.2) satisfies

$$(6.3) \quad u_{\epsilon_k}(x, \xi) \rightarrow \delta_0(\xi - \xi_*)\hat{u}_1(x) + \delta_0(\xi - \xi^*)\hat{u}_2(x)$$

in distribution sense. Furthermore,  $(\hat{u}_1, \hat{u}_2)$  is a positive solution of (1.7).

**Remark 6.3.** In fact, one can show that for  $\delta_1$  small and  $\xi_* < \xi^*$  chosen as above, (1.7) has a unique positive steady state. In that case, the conclusion of Theorem 6.2 can be strengthened to be independent of sequences  $\epsilon_k \rightarrow 0$ . We leave this issue for future studies.

**Lemma 6.4.** *Suppose that  $\hat{\xi}$  is a branching point in the sense of Definition 6.1. Then there is some  $\delta_1 > 0$  such that for each subinterval  $I = (\xi_*, \xi^*) \subset (\hat{\xi} - \delta_1, \hat{\xi} + \delta_1)$ , for all  $\epsilon$  sufficiently small,*

$$\sup_{\xi \in (\xi_*, \xi^*)} \partial_\xi^2 H(\xi, \hat{u}_\epsilon) \leq -c_0 \quad \text{and} \quad \int_D \hat{u}_\epsilon \, dx \geq c_0,$$

for some  $c_0 > 0$  independent of  $\epsilon$ .

*Proof.* The proof is analogous to that of Lemma 5.3 and is omitted.  $\square$

*Proof of Theorem 6.2.* Let  $\delta_1$  be chosen as in Lemma 6.4 and the interval  $I$  chosen satisfying (6.2).

**Claim 6.5.** *There is a sequence  $\epsilon_k \rightarrow 0$  such that  $w_{\epsilon_k} \rightarrow w$  locally uniformly in  $\bar{D} \times (\xi_*, \xi^*)$  and (6.3) holds in distribution sense, for some non-trivial non-negative functions  $\hat{u}_i \in C(\bar{D})$ ,  $i = 1, 2$ .*

Recall that, as shown in the proof of Lemma 3.7, if a viscosity solution  $w$  of (3.6) has an interior maximum point  $\xi_0$ , then necessarily  $H(\xi_0; \hat{u}) \leq 0$ . Since  $H(\cdot; \hat{u})$  is nonnegative (Lemma 3.7(i)) and strictly concave (Lemma 6.4), we deduce that  $H(\xi; \hat{u}) > 0$  in  $(\xi_*, \xi^*)$  and thus  $w$  cannot have any interior local maximum point. Therefore, we conclude that exactly one of the following alternatives holds:

- (i)  $w(\xi_*) = 0$  and  $w(\xi) < 0$  in  $(\xi_*, \xi^*)$ ;
- (ii)  $w(\xi^*) = 0$  and  $w(\xi) < 0$  in  $[\xi_*, \xi^*)$ ;
- (iii)  $w(\xi_*) = w(\xi^*) = 0$  and  $w(\xi) < 0$  in  $(\xi_*, \xi^*)$ .

In each case,  $w(\xi) < 0$  in  $(\xi_*, \xi^*)$  and hence for each  $K_1 \subset \subset (\xi_*, \xi^*)$ ,

$$u_\epsilon(x, \xi) = \psi_\epsilon(x, \xi) \exp\left(\frac{w(\xi) + o(1)}{\epsilon}\right) = O\left(\exp\left(-\frac{\delta_K}{\epsilon}\right)\right)$$

holds for  $(x, \xi) \in D \times K_1$ , where we have used (3.2). Thus Lemma 2.5 is applicable and implies that (6.3) holds in distribution sense, for some non-negative functions  $\hat{u}_i$  ( $i = 1, 2$ ). It remains to show that neither of the  $\hat{u}_i$ 's is identically zero. Suppose  $\hat{u}_2 \equiv 0$ , then, by arguing as in the proof of Proposition 3.8, one deduces that  $\hat{u}_1 = \theta_{\xi_*}$  and hence by Lemma 3.7(i)

$$\lambda(\xi_*, \xi) = H(\xi; \theta_{\xi_*}) = H(\xi; \hat{u}) \geq 0 \quad \text{for all } \xi_* \leq \xi \leq \xi^*,$$

but then we have  $\lambda(\xi_*, \xi^*) \geq 0$ , contradicting (6.2). Similarly,  $\hat{u}_1$  cannot be identically zero. This proves Claim 6.5.

**Claim 6.6.**  *$(\hat{u}_1, \hat{u}_2)$  is a positive steady state of (1.7).*

Let  $\hat{u}_{\epsilon,1}(x) = \int_{\xi_*}^{\hat{\xi}} u_\epsilon d\xi$  and  $\hat{u}_{\epsilon,2}(x) = \int_{\hat{\xi}}^{\xi^*} u_\epsilon d\xi$ , we have by Lemma 2.5  $\hat{u}_{\epsilon,i} \rightarrow \hat{u}_i$  uniformly in  $D$  for  $i = 1, 2$ . By arguments similar to Claim 3.10 we have

$$(6.4) \quad \begin{cases} \nabla_x \cdot (\mu_i \nabla_x \hat{u}_i - \alpha_i \hat{u}_i \nabla_x m) + \hat{u}_i(r(x) - \hat{u}) \geq 0 & \text{in } D, \\ \mu_i \partial_n \hat{u}_i - \alpha_i \hat{u}_i \partial_n m = 0 & \text{on } \partial D, \end{cases}$$

where  $i = 1, 2$ ,  $\mu_1 = \mu(\xi_*)$ ,  $\alpha_1 = \alpha(\xi_*)$ ,  $\mu_2 = \mu(\xi^*)$ ,  $\alpha_2 = \alpha(\xi^*)$ . Also, obviously  $\hat{u} = \hat{u}_1 + \hat{u}_2$ . This implies, by properties of the principal eigenvalue, that

$$H(\xi_*; \hat{u}) \leq 0 \quad \text{and} \quad H(\xi^*; \hat{u}) \leq 0.$$

By Lemma 3.7(i),  $H(\xi_*; \hat{u}) \geq 0$  and  $H(\xi^*; \hat{u}) \geq 0$ . Hence,  $H(\xi_*; \hat{u}) = H(\xi^*; \hat{u}) = 0$ . Therefore, by arguments similar to Claim 3.10, the equalities in (6.4) hold. This completes the proof.  $\square$

Next, we derive Theorem 1.4 as a special case of Theorem 6.2.

*Proof of Theorem 1.4.* Suppose that  $\hat{\xi}$  is a branching point in the sense of Definition 6.1. It remains to show that for  $\xi_*, \xi^*$  such that

$$(6.5) \quad \xi_* \leq \hat{\xi} \leq \xi^* \quad \text{and} \quad |\xi_* - \hat{\xi}| + |\xi^* - \hat{\xi}| \ll 1,$$

then  $\lambda(\xi_*, \xi^*) < 0$  and  $\lambda(\xi^*, \xi_*) < 0$ .

Denote for  $i, j = 1, 2$ ,

$$\lambda_{ij} := \frac{\partial^2 \lambda}{\partial \xi_i \partial \xi_j}(\hat{\xi}, \hat{\xi}).$$

From the fact that  $\lambda(\xi, \xi) \equiv 0$  for all  $\xi$ , we differentiate once at  $\hat{\xi}$  and deduce  $\partial_{\xi_1} \lambda + \partial_{\xi_2} \lambda = 0$  at  $(\xi_1, \xi_2) = (\hat{\xi}, \hat{\xi})$ . By (Cv),  $(\hat{\xi}, \hat{\xi})$  is a critical point of  $\lambda$ . Differentiate again, we have  $\lambda_{11} + 2\lambda_{12} + \lambda_{22} = 0$ . Based on these facts, we may Taylor expand  $\lambda$  near  $(\hat{\xi}, \hat{\xi})$  as

$$(6.6) \quad \lambda(\xi_1, \xi_2) = \frac{\xi_1 - \xi_2}{2} [\lambda_{11}(\xi_1 - \hat{\xi}) - \lambda_{22}(\xi_2 - \hat{\xi}) + o(|\xi_1 - \hat{\xi}| + |\xi_2 - \hat{\xi}|)].$$

Also, the second condition in (Cv) says that  $\lambda_{12} + \lambda_{22} > 0$ . Together with Definition 6.1, we deduce that

$$(6.7) \quad \lambda_{22} < 0 \quad \text{and} \quad \lambda_{11} = -2(\lambda_{12} + \lambda_{22}) + \lambda_{22} < \lambda_{22} < 0.$$

So that for  $\xi_*, \xi^*$  satisfying (6.5), we have

$$\begin{aligned} \lambda(\xi^*, \xi_*) &= \frac{\xi^* - \xi_*}{2} [\lambda_{11}(\xi^* - \hat{\xi}) - \lambda_{22}(\xi_* - \hat{\xi}) + o(|\xi^* - \hat{\xi}| + |\xi_* - \hat{\xi}|)] \\ &= -\frac{|\xi^* - \xi_*|}{2} [|\lambda_{11}| |\xi^* - \hat{\xi}| + |\lambda_{22}| |\xi_* - \hat{\xi}| + o(|\xi^* - \hat{\xi}| + |\xi_* - \hat{\xi}|)] < 0. \end{aligned}$$

Similarly, one can show that  $\lambda(\xi_*, \xi^*) < 0$  as well. Thus one can apply Theorem 6.2 to obtain the desired conclusion.  $\square$

Next, we prove that evolutionarily stable dimorphism can occur even if the branching point  $\hat{\xi}$  is not contained in the interval  $I$ .

**Corollary 6.7.** *Under the assumptions of Theorem 6.2, there exist  $\xi^* > \xi_* > \hat{\xi}$ , so that if we choose  $I = (\xi_*, \xi^*)$ , then the conclusion of Theorem 6.2 holds.*

*Proof.* It remains to choose  $\xi^* > \xi_* > \hat{\xi}$  so that (6.2) holds. Note that by (6.7),

$$\frac{\lambda_{11}}{\lambda_{22}} = \frac{2(\lambda_{12} + \lambda_{22}) - \lambda_{22}}{-\lambda_{22}} > 1 \implies \arctan \frac{\lambda_{11}}{\lambda_{22}} \in (\pi/4, \pi/2).$$

So we may choose  $\tau \in \left(\arctan \frac{\lambda_{11}}{\lambda_{22}}, \frac{\pi}{2}\right)$ , and choose

$$(\xi^*, \xi_*) := \left(\hat{\xi} + r \cos \tau, \hat{\xi} + r \sin \tau\right).$$

Then  $\xi^* > \xi_* > \hat{\xi}$ , and by (6.6),

$$\begin{aligned} \lambda(\xi^*, \xi_*) &= \frac{r(\cos \tau - \sin \tau)}{2} \cdot (\lambda_{11}r \cos \tau - \lambda_{22}r \sin \tau + o(r)) \\ &= \frac{-\lambda_{22}r^2(\sin \tau - \cos \tau) \cos \tau}{2} \left(\frac{\lambda_{11}}{\lambda_{22}} - \tan \tau + o(1)\right) < 0 \end{aligned}$$

and

$$\begin{aligned} \lambda(\xi_*, \xi^*) &= \frac{r(\sin \tau - \cos \tau)}{2} \cdot (\lambda_{11}r \sin \tau - \lambda_{22}r \cos \tau + o(r)) \\ &< \frac{r(\sin \tau - \cos \tau)}{2} \cdot (\lambda_{11}r \cos \tau - \lambda_{22}r \cos \tau + o(r)) \\ &= \frac{r^2 \cos \tau (\sin \tau - \cos \tau)}{2} (\lambda_{11} - \lambda_{22} + o(1)) \\ &= \frac{r^2 \cos \tau (\sin \tau - \cos \tau)}{2} [-2(\lambda_{12} + \lambda_{22}) + o(1)] < 0 \end{aligned}$$

for  $r \ll 1$ , where we have used  $\lambda_{11} + 2\lambda_{12} + \lambda_{22} = 0$  for the last equality, and  $\lambda_{12} + \lambda_{22} > 0$  (from **(Cv)**) for the last inequality.  $\square$

## 7. EXAMPLE 1: EVOLUTION OF ADVECTION

In this section, we apply our results to the case  $\mu \equiv \mu_0$  for some positive constant  $\mu_0$ ,  $\alpha(\xi) = \xi$  and  $I_0 = \mathbb{R}^+$ .

$$(7.1) \quad \begin{cases} \nabla_x \cdot (\mu_0 \nabla_x u - \xi u \nabla_x m) + \epsilon^2 u_{\xi\xi} + u(r(x) - \hat{u}) = 0 & \text{in } D \times I, \\ \mu_0 \partial_n u - \xi u \partial_n m = 0 & \text{on } \partial D \times I, \\ u = 0 & \text{on } D \times \partial I. \end{cases}$$

Then the invasion exponent  $\lambda(\xi_1, \xi_2)$  is the principal eigenvalue of

$$(7.2) \quad \begin{cases} \nabla_x \cdot (\mu_0 \nabla_x \phi - \xi_2 \phi \nabla_x m) + (r(x) - \theta_{\mu_0, \xi_1}) + \lambda \phi = 0 & \text{in } D, \\ \mu_0 \partial_n \phi - \xi_2 \phi \partial_n m = 0 & \text{on } \partial D. \end{cases}$$

**Theorem 7.1** ([46]). *Suppose that  $r(x) = m(x)$ , and  $D \subset \mathbb{R}^N$  is convex with diameter  $d$  and  $d \|\nabla_x \log m\|_{L^\infty(D)} \leq \Lambda_1$ , where  $\Lambda_1 \approx 0.814$  is the unique positive root of the function  $t \mapsto 4t + e^{-t} + 2\log t - 1 - 2\log \pi$ . Then for each  $\mu_0 > 0$  sufficiently small, there exists a local CSS  $\hat{\xi} > 0$  with respect to the selection gradient  $\lambda$  given by the principal eigenvalue of (7.2).*

*Proof.* From [46, Theorem 2.2] we verify **(Cv)**. Also, (5.1) follows from [46, Theorem 2.5].  $\square$

### 8. EXAMPLE 2: EVOLUTION OF DIFFUSION RATE

In this section, we apply our results to the case  $\mu(\xi) = \xi$ ,  $\alpha(\xi) = \alpha_0$  for some positive constant  $\alpha_0$ , and  $I_0 = \mathbb{R}^+$ .

$$(8.1) \quad \begin{cases} \nabla_x \cdot (\xi \nabla_x u - \alpha_0 u \nabla_x m) + \epsilon^2 u_{\xi\xi} + u(r(x) - \hat{u}) = 0 & \text{in } D \times I, \\ \xi \partial_n u - \alpha_0 u \partial_n m = 0 & \text{on } \partial D \times I, \\ u = 0 & \text{on } D \times \partial I. \end{cases}$$

The invasion exponent  $\lambda(\xi_1, \xi_2)$  is the principal eigenvalue of

$$(8.2) \quad \begin{cases} \nabla_x \cdot (\xi_2 \nabla_x \phi - \alpha_0 \phi \nabla_x m) + (r(x) - \theta_{\xi_1, \alpha_0}) + \lambda \phi = 0 & \text{in } D, \\ \xi_2 \partial_n \phi - \alpha_0 \phi \partial_n m = 0 & \text{on } \partial D. \end{cases}$$

**Theorem 8.1** ([47]). *Let  $r(x) = m(x)$ ,  $D \subset \mathbb{R}^N$  be convex with diameter  $d$  and  $d\|\nabla_x \log m\|_{L^\infty(D)} \leq \Lambda_2$ , where  $\Lambda_2 \approx 0.615$  is the unique positive root of the function  $t \mapsto \frac{t^2}{\pi^2} - e^{-4t} \left( \frac{2t}{2^t - 1} - 1 \right)$ . Then for each positive small  $\alpha_0$ , there exists a local CSS  $\hat{\xi} > 0$  with respect to the selection gradient  $\lambda$  given by the principal eigenvalue of (8.2).*

**Theorem 8.2** ([42]). *Suppose that  $\Omega = (0, L)$ ,  $m(x) = x$ ,  $r, r_x > 0$  in  $[0, L]$ , and*

$$(\log r)_x(x) < 2(\log r)_x(y) \quad \text{for all } x, y \in [0, L].$$

- (i) *If  $(\log r)_x$  is decreasing and non-constant, then for each small  $\alpha_0 > 0$ , there exists a local ESS  $\hat{\xi} > 0$  with respect to the selection gradient  $\lambda$  given by the principal eigenvalue of (8.2).*
- (ii) *If  $(\log r)_x$  is increasing and non-constant, then for all small  $\alpha_0 > 0$ , there exists a branching point  $\hat{\xi} > 0$  with respect to the selection gradient  $\lambda$  given by the principal eigenvalue of (8.2).*

*Proof.* Assertion (i) follows from [42, Corollary 6.6(i)]. Assertion (ii) follows from the proof of Theorem 6.5: specifically, equation (57) and the sentence that follows.  $\square$

*Remark 8.3.* Although  $m(x) = x$  does not satisfy the requirement **(M)** that  $\partial_n m \leq 0$  on  $\partial D$ , we may approximate  $m(x)$  by  $\tilde{m}(x) \in C^\infty(\bar{D})$  in the  $C(\bar{D})$  topology, and notice that  $\lambda(\xi_1, \xi_2)$  is defined by the variational formula

$$\lambda(\xi_1, \xi_2) = \inf_{\phi \in H^1(D) \setminus \{0\}} \frac{\int_D e^{\alpha_0 m / \xi_2} [\xi_2 |\nabla_x \phi|^2 + (\theta_{\xi_1, \alpha_0} - r(x)) \phi^2] dx}{\int_D e^{\alpha_0 m / \xi_2} \phi^2 dx},$$

which implies that the mapping  $T : C(\bar{D}) \rightarrow C^\infty(\bar{I}_0 \times \bar{I}_0)$  given by  $m(\cdot) \mapsto \lambda(\cdot, \cdot)$  is smooth. Hence, if for some  $\alpha_0$ ,  $m(x) = x$  and  $r(x)$ , we have a branching point  $\hat{\xi}$ , then we may find a smooth  $\tilde{m}(x) \approx x$  in the topology  $C(\bar{D})$  so that  $\frac{\partial \tilde{m}}{\partial n} \leq 0$  on  $\partial D$  for which there is a branching point  $\hat{\xi}' \approx \hat{\xi}$ .

### 9. NUMERICAL RESULTS

In order to illustrate Theorem 8.2, we present some numerical results of the corresponding time-dependent system of (8.1) in one dimensional case with  $m(x) =$

$x$  and  $\alpha_0 = 1$  on  $D \times I = (0, 1) \times (0.5, 1.5)$ , namely, the case related to Theorem 8.2.

$$(9.1) \quad \begin{cases} u_t = (\xi u_x - u)_x + \epsilon^2 u_{\xi\xi} + u(r(x) - \hat{u}) & \text{for } x \in (0, 1), \xi \in (0.5, 1.5), t > 0, \\ \xi u_x - u = 0 & \text{on } x = 0, 1, t > 0, \\ u = 0 & \text{on } \xi = 0.5, 1.5, t > 0. \end{cases}$$

Here we choose  $r(x) = e^{(1-a)x+ax^2}$  and  $\epsilon = 10^{-3}$ . First, we take initial conditions in the form of one Dirac mass on the phenotypic space, and investigate their evolution for  $a = \pm \frac{1}{4}$ . We use the second order finite difference schemes to discretize  $[\xi, x]$  domain and use the adaptive backward Euler method to solve the time-dependent system (9.1) numerically. We take  $50 \times 50$  uniform grids on both  $x$  and  $\xi$  directions, and the final time is  $10^5$ .

By Theorem 8.2, there is an ESS  $\hat{\xi}$  when  $a \in (-1/3, 0)$ , so that Theorem 1.3 predicts the existence of a positive steady state concentrating at  $\xi = \hat{\xi}$ . See the right picture of Fig. 1.

On the other hand, there is a branching point when  $a \in (0, 1/3)$ , so that Theorem 1.4 applies to predict the existence of steady states with two Dirac masses respectively. This is illustrated by the left picture of Fig. 1. Note that the interval  $I = (0.5, 1.5)$  may not need to be small, as seen from the numerical results.

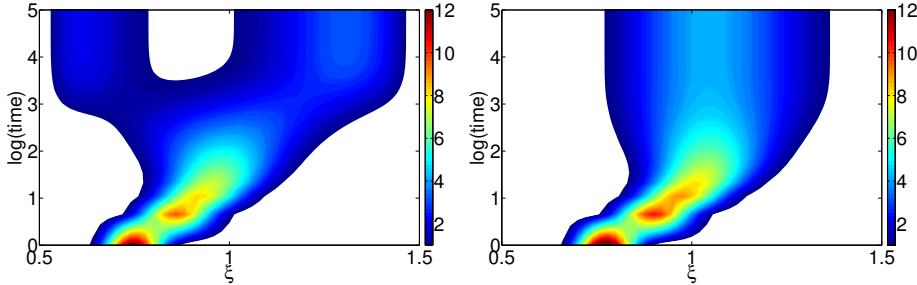


FIGURE 1. Contour plot of  $\int u(x, \xi, t)dx$  as a function of  $\xi$  and time ( $\log(\text{time})$ ) for vertical axis for  $a = \frac{1}{4}$  (left) and  $a = -\frac{1}{4}$  (right), with  $\epsilon = 10^{-3}$ .

Next, we take initial conditions in the form of two Dirac masses on the phenotypic space, and investigate their evolution for  $a = \pm \frac{1}{4}$ . The simulation results are illustrated by Fig. 2.

In addition, we also explore the steady state solution of (9.1) with different values of  $a$ . Fig. 3 shows that the one Dirac mass becomes two Dirac masses, as  $a$  varies from  $-\frac{1}{4}$  to  $\frac{1}{4}$ .

#### APPENDIX A. A Liouville-Type Result

In this chapter we prove a Liouville-Type result in cylinder domains. Our proof is inspired by arguments in [58].

**Proposition A.1.** *Let  $\varphi \in C^2(\bar{D})$  be strictly positive on  $\bar{D}$  and  $h \in C(\bar{D})$ , where  $D$  is a bounded smooth domain in  $\mathbb{R}^N$ . Suppose  $W(x, y) \in C^2(\bar{D} \times \mathbb{R})$  is a non-trivial,*

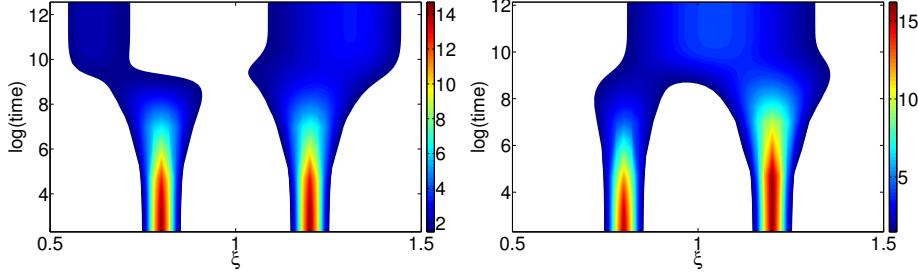


FIGURE 2. Contour plot of  $\int u(x, \xi, t) dx$  as a function of  $\xi$  and time for  $a = \frac{1}{4}$  (left) and  $a = -\frac{1}{4}$  (right), with  $\epsilon = 10^{-3}$ .

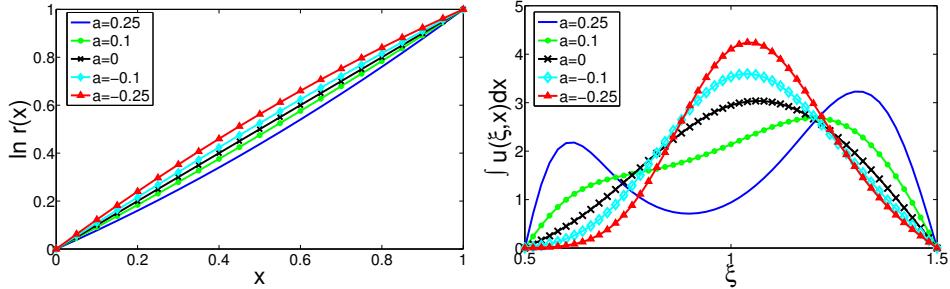


FIGURE 3. **Left:** Profiles of resource distribution  $\ln(r(x))$  with respect to various values of the parameter  $a$ ; **Right:** Phenotypic distributions of the steady state solution  $\int_D u_\epsilon(x, \xi) dx$  with respect to various values of the parameter  $a$ .

non-negative solution of

$$(A.1) \quad \begin{cases} -\varphi^{-2}(x) \nabla_x \cdot (\varphi^2(x) \nabla_x W) - \partial_y^2 W + h(x)W = 0 & \text{for } x \in D, y \in \mathbb{R}, \\ \partial_n W = 0 & \text{for } x \in \partial D, y \in \mathbb{R}. \end{cases}$$

Let  $(\sigma_1, \phi_1)$  be the principal eigenpair of

$$(A.2) \quad -\varphi^{-2}(x) \nabla_x \cdot (\varphi^2(x) \nabla_x \phi) + h(x)\phi = \sigma\phi \quad \text{in } D, \quad \partial_n \phi = 0 \quad \text{on } \partial D.$$

Then  $\sigma_1 \geq 0$  and for some  $C_1, C_2 \geq 0$ ,

$$(A.3) \quad W(x, y) = (C_1 e^{\sqrt{\sigma_1} y} + C_2 e^{-\sqrt{\sigma_1} y}) \phi_1(x).$$

*Remark A.2.* For the convenience of the readers, we supply some basic facts concerning the eigenpairs  $\{(\sigma_k, \phi_k)\}_{k=1}^\infty$  of (A.2): It can be arranged so that

- (i)  $\sigma_k \in \mathbb{R}$  for all  $k$  such that  $\sigma_1 < \sigma_2 \leq \sigma_3 \leq \dots$  and  $\sigma_k \rightarrow \infty$  as  $k \rightarrow \infty$ ;
- (ii)  $\int_D \phi_i \phi_j \varphi^2 dx = \delta_{ij}$ ;
- (iii)  $\sigma_1$  is a simple eigenvalue and the corresponding eigenfunction  $\phi_1$  is strictly positive in  $\bar{D}$ ;
- (iv)  $\sigma_1$  is the unique eigenvalue with a non-negative eigenfunction, i.e.  $\phi_k$  changes sign on  $D$  for all  $k \geq 2$ .

For the proofs of the above facts, see, e.g. [32, Sect. 6.5] or [50, Ch. 28 and 29].

A special case of Proposition A.1 arises when  $\sigma_1 = 0$ .

**Corollary A.3.** *Let  $\varphi \in C^2(\bar{D})$  be strictly positive on  $\bar{D}$ , where  $D$  is a bounded smooth domain in  $\mathbb{R}^N$ . Suppose  $W(x, y) \in C^2(\bar{D} \times \mathbb{R})$  is non-negative solution of*

$$(A.4) \quad \begin{cases} \varphi^{-2}(x) \nabla_x \cdot (\varphi^2(x) \nabla_x W) + \partial_y^2 W = 0 & \text{for } x \in D, y \in \mathbb{R}, \\ \partial_n W = 0 & \text{for } x \in \partial D, y \in \mathbb{R}. \end{cases}$$

*Then  $W(x, y)$  is a constant.*

Before we prove Proposition A.1, we establish the following elementary lemma.

**Lemma A.4.** *Let  $\gamma_k$  ( $1 \leq k \leq k_0$ ) be given positive constants, and  $a_k, b_k$  ( $1 \leq k \leq k_0$ ) be given real numbers, then the function  $f : \mathbb{R} \rightarrow \mathbb{R}$  defined by*

$$f(y) := \sum_{k=1}^{k_0} (a_k \cos(\gamma_k y) + b_k \sin(\gamma_k y))$$

*has at least one real root.*

*Proof.* Let  $F(y) := \sum_{k=1}^{k_0} \left( \frac{a_k}{\gamma_k} \sin(\gamma_k y) - \frac{b_k}{\gamma_k} \cos(\gamma_k y) \right)$ . If  $F$  has at least one critical point, then we are done, since  $f = F'$ . Suppose not, then  $F$  is strictly monotone, and as  $t \rightarrow \infty$ ,

$$t^{-1} \int_0^t F(y) dy \rightarrow F(+\infty) \quad \text{and} \quad t^{-1} \int_{-t}^0 F(y) dy \rightarrow F(-\infty).$$

However, by properties of trigonometric polynomials, we also have

$$t^{-1} \int_0^t F(y) dy \rightarrow 0 \quad \text{and} \quad t^{-1} \int_{-t}^0 F(y) dy \rightarrow 0.$$

Hence  $F(-\infty) = F(+\infty) = 0$  and  $F \equiv 0$ . This contradicts the assumption that  $F$  has no critical points.  $\square$

*Proof of Proposition A.1.* Since  $W$  is non-trivial and non-negative, the strong maximum principle implies that  $W(x, y) > 0$  for all  $x \in D, y \in \mathbb{R}$ .

Let  $(\sigma_k, \phi_k)$  be the  $k$ -th eigenpair of (A.2) counting multiplicities, so that  $\sigma_1 < \sigma_2 \leq \sigma_3 \leq \dots$ . Then by defining

$$c_k(y) := \int_D W(x', y) \phi_k(x') \varphi^2(x') dx',$$

we have  $W(x, y) = \sum_{k=1}^{\infty} c_k(y) \phi_k(x)$  and that  $\frac{\partial^2}{\partial y^2} c_k = \sigma_k c_k$ . Hence for each  $k$ , there exist some  $A_k, B_k$  such that, for  $y \in \mathbb{R}$ ,

$$c_k(y) = \begin{cases} A_k e^{\sqrt{\sigma_k} y} + B_k e^{-\sqrt{\sigma_k} y} & \text{if } \sigma_k > 0, \\ A_k + B_k y & \text{if } \sigma_k = 0, \\ A_k \cos(\sqrt{-\sigma_k} y) + B_k \sin(\sqrt{-\sigma_k} y) & \text{if } \sigma_k < 0. \end{cases}$$

Now, by applying the Harnack inequality to  $W(x, y)$  on  $\bar{D} \times [y_0 - 2, y_0 + 2]$  for any  $y_0 \in \mathbb{R}$ , there exists some constant  $C$  independent of  $y_0 \in \mathbb{R}$  such that

$$\sup_{x \in D, |y - y_0| \leq 1} W \leq C \inf_{x \in D, |y - y_0| \leq 1} W.$$

Hence there exist  $c_1, c_2 > 0$  such that  $0 \leq W(x, y) \leq c_1 e^{c_2 |y|}$  for all  $x \in D$  and  $y \in \mathbb{R}$ . This implies that  $|c_k(y)| = |\int_D W(x, y) \phi_k(x) \varphi^2(x) dx| \leq c'_1 e^{c_2 |y|}$  for  $y \in \mathbb{R}$ . As  $\sigma_k \rightarrow \infty$  when  $k \rightarrow \infty$ , it is necessary the case that  $A_k = B_k = 0$  for all

sufficiently large  $k$ . We may henceforth choose the largest positive integer  $k_0$  such that at least one of  $A_{k_0}, B_{k_0}$  is non-zero. i.e.

$$(A.5) \quad W(x, y) = \sum_{k=1}^{k_0} c_k(y) \phi_k(x).$$

**Claim A.5.** *If  $k_0 > 1$ , then  $\sigma_{k_0} \leq 0$ .*

Suppose not, let  $\sigma_{k_0} > 0$ , then the term with the highest growth in  $y$  is multiplied to  $\phi_k(x)$ , a function of  $x$  that changes sign. This is a contradiction. Hence  $\sigma_{k_0} \leq 0$ .

**Claim A.6.** *If  $k_0 > 1$ , then  $\sigma_{k_0} < 0$ .*

Suppose to the contrary that  $k_0 > 1$ , and there is  $1 < \tilde{k} \leq k_0$  ( $\tilde{k} > 1$  as the principal eigenvalue must be simple) such that  $\sigma_{\tilde{k}} = \sigma_{\tilde{k}+1} = \dots = \sigma_{k_0} = 0$  and  $\sigma_{\tilde{k}-1} < 0$ ; i.e.  $W(y)$  contains the terms  $\sum_{k=\tilde{k}}^{k_0} A_k \phi_k(x) + y \sum_{k=\tilde{k}}^{k_0} B_k \phi_k(x)$ , and at least one of  $A_{k_0}, B_{k_0}$  is non-zero.

We claim that  $B_{\tilde{k}} = \dots = B_{k_0} = 0$ . Now, every term of (A.5) is bounded from below except possibly the term  $y \sum_{k=\tilde{k}}^{k_0} B_k \phi_k(x)$ . Suppose not, then by linear independence of  $\{\phi_k\}_{k=\tilde{k}}^{k_0}$ ,  $\sum_{k=\tilde{k}}^{k_0} B_k \phi_k(x)$  is non-trivial, and changes sign (since it is orthogonal in  $L^2(D)$  to the positive function  $\varphi^2 \phi_1$ ). This implies that for large  $y$ ,  $W(x, y)$  changes sign in  $x$ . This is a contradiction, so we conclude that  $B_{\tilde{k}} = \dots = B_{k_0} = 0$  and  $A_{k_0} \neq 0$ .

Next, observe that  $t^{-1} \int_{-t}^t W(x, y) dy \rightarrow \sum_{k=\tilde{k}}^{k_0} A_k \phi_k(x)$  as  $t \rightarrow \infty$ . Again, we notice that  $\sum_{k=\tilde{k}}^{k_0} A_k \phi_k(x)$  changes sign, which contradicts the non-negativity of  $W$ . This proves Claim A.6.

**Claim A.7.**  $k_0 = 1$ .

Suppose not, then  $k_0 > 1$  and for each  $1 \leq k \leq k_0$ ,  $\sigma_k \leq \sigma_{k_0} < 0$ . For  $x_0 \in D$ ,  $W(x_0, y)$  is a linear combination of trigonometric functions, so we can invoke Lemma A.4 to find some  $y_0$  such that  $W(x_0, y_0) = 0$ . This is impossible as  $W > 0$  for all  $x \in D$  and  $y \in \mathbb{R}$ . Hence, Claim A.7 holds.

As  $k_0 = 1$ , we must have  $\sigma_1 \geq 0$ , since otherwise

$$W(x, y) = (A_1 \cos(\sqrt{-\sigma_1} y) + B_1 \sin(\sqrt{-\sigma_1} y)) \phi_1(x)$$

changes sign. Hence  $W(x, y) = (A_1 e^{\sqrt{-\sigma_1} y} + B_1 e^{-\sqrt{-\sigma_1} y}) \phi_1(x)$  and we must have  $A_1, B_1 \geq 0$ . This completes the proof of Proposition A.1.  $\square$

## APPENDIX B. LOCALIZATION

**Lemma B.1.** *Let  $I = (\xi_*, \xi^*) \subset \mathbb{R}^+$  be a bounded open interval. Suppose (along a sequence  $(\epsilon, I) = (\epsilon_k, I_k)$ ) that (i)  $\epsilon/|I| \rightarrow 0$  and (ii) for some  $\hat{\xi} > 0$ ,  $I \rightarrow \{\hat{\xi}\}$  in the Hausdorff sense. Then any positive solution  $u_\epsilon$  of (2.1) satisfies*

$$\hat{u}_\epsilon(x) \rightharpoonup \theta_{\hat{\xi}}(x)$$

*weakly in  $H^1(D)$  and strongly in  $C(\bar{D})$ .*

*Proof.* Define  $\delta_1 := |I|$ . By the proof of Lemma 2.3,  $\|\hat{u}_\epsilon\|_{C^\gamma(\bar{D})}$  is bounded uniformly for small  $\epsilon$  and  $\delta_1$ . It follows that  $\hat{u}_\epsilon$  is precompact in  $C(\bar{D})$ . Next, we show that it is also bounded, and hence weakly precompact, in  $H^1(D)$ .

**Claim B.2.** *There exists some constant  $C > 0$  independent of  $\epsilon$  and  $I$  such that  $\|\hat{u}_\epsilon\|_{H^1(D)} \leq C$ .*

To see the claim, divide (2.1) by  $\mu = \mu(\xi)$  and integrate in  $\xi \in (\xi_*, \xi^*)$  to obtain (2.15). Multiply (2.15) by  $\hat{u}_\epsilon$ , and integrate by parts, we have

$$\begin{aligned} \int_D |\nabla_x \hat{u}_\epsilon|^2 dx &\leq \int_D [q_1 \nabla_x m \cdot \nabla_x \hat{u}_\epsilon + (r - \hat{u}_\epsilon) q_2 \hat{u}_\epsilon + \epsilon^2 q_3 \hat{u}_\epsilon] dx \\ &\leq \frac{1}{2} \int_D |\nabla_x \hat{u}_\epsilon|^2 dx + \int_D |q_1|^2 |\nabla_x m|^2 dx + C, \end{aligned}$$

where  $q_1, q_2, q_3$  are given in (2.16), such that

$$\|q_i\|_{L^\infty(D)} \leq C \sup_D \hat{u}_\epsilon \leq C' \quad \text{for } i = 1, 2, 3.$$

Note that we have used in the first inequality  $\partial_n \hat{u}_\epsilon = q_1 \partial_n m$  (by (M)) together with the fact that  $[\partial_\xi u_\epsilon / \mu]_{\xi=\xi_*}^{\xi^*} \leq 0$ ; and the uniform boundedness of  $\sup_D \hat{u}_\epsilon$  (Lemma 2.1) throughout. This proves Claim B.2.

Hence, by passing to a sequence, there exists  $\hat{u}_0 \in H^1(D) \cap C^\gamma(\bar{D})$  such that  $\hat{u}_\epsilon \rightarrow \hat{u}_0$  weakly in  $H^1(D)$  and strongly in  $C(\bar{D})$ .

**Claim B.3.**  *$\hat{u}_0$  is a weak lower solution to (1.3) with  $\xi = \hat{\xi}$ . In particular,  $\hat{u}_0 \leq \theta_{\hat{\xi}}$ , where  $\theta_{\hat{\xi}}$  is the unique positive solution to (1.3) when  $\xi = \hat{\xi}$ .*

We pass to the limit by using the weak formulation. Multiply (2.15) by a non-negative test function  $\rho(x) \in C^\infty(\bar{D})$ , and integrate by parts, we have

$$(B.1) \quad \int_D \nabla_x \rho \cdot (\nabla_x \hat{u}_\epsilon - q_1 \nabla_x m) dx - \int_D \rho [(r - \hat{u}_\epsilon) q_2 + \epsilon^2 q_3] dx = \epsilon^2 \int_D \rho q_4 dx \leq 0.$$

Let  $\delta_1, \epsilon/\delta_1 \rightarrow 0$  and use the boundedness of  $\sup_D \hat{u}_\epsilon$ , we have (recall the definition of  $q_i$  in (2.16))

$$q_1(x) \rightarrow \frac{\alpha_0}{\mu_0} \hat{u}_0, \quad q_2 \rightarrow \hat{u}_0 / \mu_0, \quad q_3 \rightarrow \partial_\xi^2 \left( \frac{1}{\mu} \right) \Big|_{\xi=\hat{\xi}} \hat{u}_0,$$

where  $\alpha_0 = \alpha(\hat{\xi})$ ,  $\mu_0 = \mu(\hat{\xi})$ . Thus (B.1) becomes

$$\int_D \left[ \nabla_x \rho \cdot \left( \nabla_x \hat{u}_0 - \frac{\alpha_0}{\mu_0} \hat{u}_0 \nabla_x m \right) - \rho \hat{u}_0 (r - \hat{u}_0) \right] dx \leq 0.$$

Since  $\rho$  is an arbitrary non-negative test function, this implies that  $\hat{u}$  is a weak lower solution of (1.3) (see, e.g. [30]). This proves the claim.

Next, define  $\sigma_1$  to be the principal eigenvalue of

$$(B.2) \quad -\mu_0 \Delta_x \phi - \alpha_0 \nabla_x m \cdot \nabla_x \phi + (\hat{u}_0 - r) \phi = \sigma \phi \quad \text{in } D, \quad \partial_n \phi = 0 \text{ on } \partial D.$$

**Claim B.4.** *Let  $\sigma_1$  be the principal eigenvalue of (B.2), then  $\sigma_1 \leq 0$  and  $\sigma_1 = 0$  if and only if  $\hat{u}_0 = \theta_{\hat{\xi}}$  a.e., where  $\theta_{\hat{\xi}}$  is the unique positive solution of (1.3) with  $(\mu(\xi), \alpha(\xi)) = (\mu_0, \alpha_0)$ .*

To establish the assertion, we observe that the principal eigenvalue of

$$(B.3) \quad -\mu_0 \Delta_x \phi - \alpha_0 \nabla_x m \cdot \nabla_x \phi + (\theta_{\hat{\xi}} - r) \phi = \sigma \phi \quad \text{in } D, \quad \partial_n \phi = 0 \quad \text{on } \partial D$$

is zero, as a positive eigenfunction is given by  $e^{-\alpha_0 m/\mu_0} \theta_{\hat{\xi}}$ . Recall that  $\hat{u}_0 \leq \theta_{\hat{\xi}}$ . It follows by the variational characterization

$$\sigma_1 = \inf_{\phi \in H^1(D) \setminus \{0\}} \frac{\int_D e^{\alpha_0 m/\mu_0} [\mu_0 |\nabla_x \phi|^2 + (\hat{u}_0 - r) \phi^2] dx}{\int_D e^{\alpha_0 m/\mu_0} \phi^2 dx}$$

that  $\sigma_1 \leq 0$  and equality holds if and only if  $\hat{u}_0 = \theta_{\hat{\xi}}$  a.e. The claim is proved.

Next, denote the midpoint of  $I$  by  $\xi'$ , and define

$$\tilde{v}_\epsilon(x, \xi) := e^{-\alpha m/\mu} u_\epsilon(x, \xi), \quad W_\epsilon(x, \tau) := \frac{\tilde{v}_\epsilon(x, \xi' + \epsilon\tau)}{\sup_{x \in D} \tilde{v}_\epsilon(x, \xi')},$$

then  $W_\epsilon(x, \tau)$  is a positive solution of

$$\begin{cases} \mu \Delta_x W_\epsilon + \alpha \nabla_x m \cdot \nabla_x W_\epsilon + \partial_\tau^2 W_\epsilon + 2\epsilon \partial_\xi \left( \frac{\alpha}{\mu} \right) m \partial_\tau W_\epsilon \\ \quad + \epsilon^2 \left[ \partial_\xi^2 \left( \frac{\alpha}{\mu} \right) m + \left( \partial_\xi \frac{\alpha}{\mu} \right)^2 m^2 \right] W_\epsilon + W_\epsilon(r - \hat{u}_\epsilon) = 0 & \text{in } D \times (-\frac{\delta_1}{2\epsilon}, \frac{\delta_1}{2\epsilon}), \\ \partial_n W_\epsilon = 0 & \text{on } \partial D \times (-\delta_1/(2\epsilon), \delta_1/(2\epsilon)), \quad \sup_D W_\epsilon(x, 0) = 1, \end{cases}$$

where  $\mu = \mu(\xi' + \epsilon\tau)$  and  $\alpha = \alpha(\xi' + \epsilon\tau)$  remain bounded.

By applying the Harnack inequality, for each  $M > 1$ , there exists  $C_M$  (independent of small  $\epsilon$ ) such that  $\sup_{D \times [-M, M]} W_\epsilon \leq C_M$ . Hence we may apply  $L^p$  estimates to extract a sequence of  $\delta_1, \epsilon/\delta_1 \rightarrow 0$  so that  $W_\epsilon \rightarrow W$  weakly in  $W_{loc}^{2,p}(\overline{D} \times \mathbb{R})$  and strongly in  $C_{loc}^1(\overline{D} \times \mathbb{R})$ , where  $W(x, \tau)$  is a non-negative, non-trivial solution of

$$\begin{cases} \mu_0 \Delta_x W + \alpha_0 \nabla_x m \cdot \nabla_x W + \partial_\tau^2 W + (r - \hat{u}_0) W = 0 & \text{in } D \times \mathbb{R}, \\ \partial_n W = 0 & \text{on } \partial D \times \mathbb{R}, \quad \text{and} \quad \sup_D W(x, 0) = 1. \end{cases}$$

By Proposition A.1 (taking  $\varphi^2 = \exp(\alpha_0 m/\mu_0)$  and  $h = \hat{u} - r$ ), we deduce that the principal eigenvalue  $\sigma_1$  of (B.2) is non-negative. Hence, by Claim B.4, we must have  $\sigma_1 = 0$ , and that  $\hat{u}_0 = \theta_{\hat{\xi}}$  a.e. By the uniqueness of the limit  $\hat{u}_0$ , we deduce that the convergence actually holds for the full family of  $\hat{u}_\epsilon$  as  $\delta_1, \epsilon/\delta_1 \rightarrow 0$ . This proves Lemma B.1.  $\square$

## APPENDIX C. An Extension Lemma

In this section we prove an extension lemma that is used in the proof of Lemma 2.3. Our arguments are adapted from [35].

**Proposition C.1.** *Let  $R, \epsilon$  be given positive constants,*

$$B' := \{x' \in \mathbb{R}^{n-1} : |x'| < R\},$$

and

$$B_+ := \{(x', x_n) \in \mathbb{R}^n : |x'| < R + 2\epsilon, 0 < x_n < 2\epsilon\}.$$

Then there exists a linear operator  $T : C^\infty(B') \rightarrow C_0^\infty(B_+)$ ,  $Tg = G$  such that

$$G(x', 0) = 0 \quad \text{and} \quad \partial_{x_n} G(x', 0) = g(x') \quad \text{for } x' \in B'.$$

Moreover, for each  $r \geq 1$  and  $1 \leq p < \frac{nr}{n-1}$ , there exists  $C > 0$  such that

$$\|G\|_{W^{1,p}(B_+)} \leq C \|g\|_{L^r(B')}.$$

*Proof.* Fix non-negative test functions  $\psi : C_0^\infty([0, \infty))$  and  $\varphi : C^\infty(\mathbb{R}^{n-1})$  such that  $\psi(0) = 1$ ,  $\psi'(0) = 0$ ,

$$\text{supp } \varphi \subset \{x' \in \mathbb{R}^{n-1} : |x'| < 1\}, \quad \int_{\mathbb{R}^{n-1}} \varphi(y') dy' = 1.$$

Define for  $x' \in \mathbb{R}^{n-1}$ ,  $x_n \geq 0$

$$G(x', x_n) := \psi(x_n) x_n \int_{\mathbb{R}^{n-1}} g(x' - x_n y') \varphi(y') dy'.$$

It is easy to see that  $G$  satisfies the desired boundary conditions when  $x_n = 0$ . By rewriting  $G$  as

$$G(x', x_n) = \psi(x_n) |x_n|^{2-n} \int_{\mathbb{R}^{n-1}} g(y') \varphi\left(\frac{x' - y'}{x_n}\right) dy',$$

we may put the derivatives onto  $\varphi$  and get

$$\begin{aligned} \partial_{x_j} G(x', x_n) &= \psi(x_n) \int_{\mathbb{R}^{n-1}} g(x' - x_n y') \varphi_j(y') dy' \\ &\quad + \delta_{jn} \psi'(x_n) x_n \int_{\mathbb{R}^{n-1}} g(x' - x_n y') \varphi(y') dy', \end{aligned}$$

where

$$\varphi_j(y') = \partial_{y_j} \varphi(y') \quad \text{if } j < n, \text{ and} \quad \varphi_n(y') = (2-n) \varphi(y') + \sum_{j=1}^{n-1} \partial_{y_j} \varphi(y') y_j.$$

The proposition thus follows from the following lemma.

**Lemma C.2.** *Let  $\tilde{\varphi} \in C_0^\infty(\mathbb{R}^{n-1})$  be a test function. For each  $r \geq 1$ , and each  $1 \leq p < \frac{rn}{n-1}$ , there exists  $C > 0$  such that*

$$\tilde{G}(x', x_n) = \int_{\mathbb{R}^{n-1}} \tilde{g}(x' - x_n y') \tilde{\varphi}(y') dy'$$

then

$$\int_{\mathbb{R}^{n-1}} |\tilde{G}(x', x_n)|^p dx' \leq C x_n^{(1-n)(\frac{p}{r}-1)} \|\tilde{g}\|_{L^r(B')}^p.$$

*Proof.* Write

$$\begin{aligned} |\tilde{G}(x', x_n)| &= \left| x_n^{1-n} \int \tilde{\varphi}\left(\frac{x' - y'}{x_n}\right) \tilde{g}(y') dy' \right| \\ &\leq x_n^{1-n} \int \tilde{\varphi}^{1-\frac{1}{r}}\left(\frac{x' - y'}{x_n}\right) \tilde{\varphi}^{\frac{1}{r}}\left(\frac{x' - y'}{x_n}\right) |\tilde{g}(y')| dy' \\ &\leq \left( x_n^{1-n} \int \tilde{\varphi}\left(\frac{x' - y'}{x_n}\right) dy' \right)^{1-\frac{1}{r}} \left( x_n^{1-n} \int \tilde{\varphi}\left(\frac{x' - y'}{x_n}\right) |\tilde{g}(y')|^r dy' \right)^{\frac{1}{r}} \\ &\leq C \left( x_n^{1-n} \int |\tilde{g}(y')|^r dy' \right)^{\frac{1}{r}-\frac{1}{p}} \left( x_n^{1-n} \int \tilde{\varphi}\left(\frac{x' - y'}{x_n}\right) |\tilde{g}(y')|^r dy' \right)^{\frac{1}{p}} \\ &\leq C \left( x_n^{1-n} \int |\tilde{g}(y')|^r dy' \right)^{\frac{1}{r}-\frac{1}{p}} \left( \int \tilde{\varphi}(y') |\tilde{g}(x' - x_n y')|^r dy' \right)^{\frac{1}{p}}, \end{aligned}$$

where we used  $\int \tilde{\varphi}(y') dy' = 1$  for the second inequality, and the  $L^\infty$  boundedness of  $\tilde{\varphi}$  in the third inequality. Note that, by using Fubini's Theorem,

$$\iint \tilde{\varphi}(y') |\tilde{g}(x' - x_n y')|^r dy' dx' = \int \tilde{\varphi}(y') \left[ \int |\tilde{g}(x' - x_n y')|^r dx' \right] dy' \leq C \|\tilde{g}\|_{L^r}^r.$$

Hence, we may raise to the  $p$ -th power, and integrate in  $x'$  to derive the result.  $\square$

By Lemma C.2, we see that for each  $1 \leq j \leq n$ ,

$$\int_{\mathbb{R}^{n-1}} |\partial_{x_j} G(x', x_n)|^p dx' \leq C (|\psi'(x_n) x_n| + \psi(x_n))^p x_n^{(1-n)(\frac{p}{r}-1)} \|g\|_{L^r(B')}^q.$$

By our choice of  $p < \frac{rn}{n-1}$ , the exponent of  $x_n$  is greater than  $-1$ . Integrating with respect to  $x_n$  yields the desired result.  $\square$

The next result follows from Proposition C.1 via a partition of unity argument.

**Proposition C.3.** *There exists a linear operator  $T : C^\infty(\partial\Omega) \rightarrow C^\infty(\bar{\Omega})$ ,  $Tg = G$  such that  $G|_{\partial\Omega} = 0$ ,  $\partial_{\bar{\nu}} G|_{\partial\Omega} = g$  ( $\bar{\nu}$  is the outward unit normal vector on  $\partial\Omega$ ) and for each  $r \geq 1$ ,  $1 \leq p < \frac{nr}{n-1}$ , there exists  $C > 0$  such that*

$$\|G\|_{W^{1,p}(\Omega)} \leq C \|g\|_{L^r(\partial\Omega)}.$$

*Proof.* Now, there exists a locally finite open cover  $\{U_k\}$  of  $\partial\Omega$ , and corresponding  $C^2$ -smooth transformation

$$\Psi_k : B = \{y \in \mathbb{R}^n : |y| < 1\} \rightarrow U_k$$

such that  $U_k \cap \partial\Omega = \Psi_k(B')$  with  $B' = \{y \in B : y_n = 0\}$ , and for each  $x \in \partial\Omega \cap U_k$ , and smooth function  $\varphi$  on  $\bar{\Omega}$ ,

$$\partial_{\bar{\nu}} \varphi(x) = a_{ij} D_i \varphi(x) = [\partial_{x_n}(\varphi \circ \Psi_k)] \circ \Psi^{-1}(x)$$

i.e. we may straighten the boundary so that the boundary condition becomes zero Neumann boundary condition. Take a partition of unity  $\{\eta_k\}$  subordinated to  $\{U_k\}$ , then apply Proposition C.1 to  $(\eta_k \circ \Psi_k)(g \circ \Psi_k)$ . By Proposition C.1, there exists  $\tilde{G}_k \in C_0^\infty(\Psi_k^{-1}[U_k \cap \bar{\Omega}])$  satisfying  $\tilde{G}_k = 0$  and  $\partial_{y_n} \tilde{G}_k = (\eta_k \circ \Psi_k)(g \circ \Psi_k)$  on  $\Psi_k^{-1}[U_k \cap \partial\Omega]$ . Let  $G_k(x) := (\tilde{G}_k \circ \Psi^{-1})(x)$ , we get

$$G_k(x) = 0, \quad \text{and} \quad \partial_{\bar{\nu}} G_k(x) = a_{ij} \partial_{x_i} G(x) = \eta_k(x) g(x) \quad \text{on } U_k \cap \partial\Omega.$$

Finally, we set  $G(x) := \sum_k G_k(x)$ .  $\square$

## REFERENCES

- [1] Azmy S. Ackleh, John Cleveland, and Horst R. Thieme. Population dynamics under selection and mutation: long-time behavior for differential equations in measure spaces. *J. Differential Equations*, 261(2):1472–1505, 2016.
- [2] Matthieu Alfaro, Jérôme Coville, and Gaël Raoul. Travelling waves in a nonlocal reaction-diffusion equation as a model for a population structured by a space variable and a phenotypic trait. *Comm. Partial Differential Equations*, 38(12):2126–2154, 2013.
- [3] Isabel Averill, King-Yeung Lam, and Yuan Lou. The role of advection in a two-species competition model: a bifurcation approach. *Mem. Amer. Math. Soc.*, 245(1161):v+117, 2017.
- [4] Isabel Averill, Yuan Lou, and Daniel Munther. On several conjectures from evolution of dispersal. *Journal of Biological Dynamics*, 6(2):117–130, 2012. PMID: 22873583.
- [5] Fethi Belgacem and Chris Cosner. The effects of dispersal along environmental gradients on the dynamics of populations in heterogeneous environments. *Canad. Appl. Math. Quart.*, 3(4):379–397, 1995.
- [6] Nathanaël Berestycki, Clément Mouhot, and Gaël Raoul. Existence of self-accelerating fronts for a non-local reaction-diffusion equations. *arXiv*, (arXiv:1512.00903v2 [math.AP]), 2015.

- [7] Emeric Bouin and Vincent Calvez. Travelling waves for the cane toads equation with bounded traits. *Nonlinearity*, 27(9):2233–2253, 2014.
- [8] Emeric Bouin, Vincent Calvez, Nicolas Meunier, Sepideh Mirrahimi, Benoît Perthame, Gaël Raoul, and Raphaël Voituriez. Invasion fronts with variable motility: phenotype selection, spatial sorting and wave acceleration. *C. R. Math. Acad. Sci. Paris*, 350(15-16):761–766, 2012.
- [9] Emeric Bouin, Christopher Henderson, and Lenya Ryzhik. Super-linear spreading in local and non-local cane toads equations. *Journal de Mathmatiques Pures et Appliquées*, 2017.
- [10] Emeric Bouin and Sepideh Mirrahimi. A Hamilton-Jacobi approach for a model of population structured by space and trait. *Commun. Math. Sci.*, 13(6):1431–1452, 2015.
- [11] R. Bürger. *The mathematical theory of selection, recombination, and mutation*. Wiley Series in Mathematical and Computational Biology. John Wiley & Sons, Ltd., Chichester, 2000.
- [12] Àngel Calsina and Sí lvia Cuadrado. Small mutation rate and evolutionarily stable strategies in infinite dimensional adaptive dynamics. *J. Math. Biol.*, 48(2):135–159, 2004.
- [13] R. S. Cantrell and C. Cosner. *Spatial ecology via reaction-diffusion equations*. Wiley Series in Mathematical and Computational Biology. John Wiley & Sons Ltd., Chichester, 2003.
- [14] Robert Stephen Cantrell, Chris Cosner, and Yuan Lou. Movement toward better environments and the evolution of rapid diffusion. *Math. Biosci.*, 204(2):199–214, 2006.
- [15] Robert Stephen Cantrell, Chris Cosner, and Yuan Lou. Advection-mediated coexistence of competing species. *Proc. Roy. Soc. Edinburgh Sect. A*, 137(3):497–518, 2007.
- [16] Robert Stephen Cantrell, Chris Cosner, and Yuan Lou. Evolution of dispersal and the ideal free distribution. *Math. Biosci. Eng.*, 7(1):17–36, 2010.
- [17] X.-F. Chen and Y. Lou. Principal eigenvalue and eigenfunctions of an elliptic operator with large advection and its application to a competition model. *Indiana Univ. Math. J.*, 57(2):627–658, 2008.
- [18] X.-F. Chen and Y. Lou. Effects of diffusion and advection on the smallest eigenvalue of an elliptic operator and their applications. *Indiana Univ. Math. J.*, 61(1):45–80, 2012.
- [19] Xinfu Chen, Richard Hambrock, and Yuan Lou. Evolution of conditional dispersal: a reaction-diffusion-advection model. *J. Math. Biol.*, 57(3):361–386, 2008.
- [20] Xinfu Chen, King-Yeung Lam, and Yuan Lou. Dynamics of a reaction-diffusion-advection model for two competing species. *Discrete Contin. Dyn. Syst.*, 32(11):3841–3859, 2012.
- [21] Ya-Zhe Chen and Lan-Cheng Wu. *Second order elliptic equations and elliptic systems*, volume 174 of *Translations of Mathematical Monographs*. American Mathematical Society, Providence, RI, 1998. Translated from the 1991 Chinese original by Bei Hu.
- [22] Jean Clobert, Etienne Danchin, André A. Dhondt, and J. D. Nichols. *Dispersal*. Oxford University Press, 2001.
- [23] Chris Cosner, Juan Dávila, and Salome Martínez. Evolutionary stability of ideal free nonlocal dispersal. *J. Biol. Dyn.*, 6(2):395–405, 2012.
- [24] Chris Cosner and Yuan Lou. Does movement toward better environments always benefit a population? *J. Math. Anal. Appl.*, 277(2):489–503, 2003.
- [25] Laurent Desvillettes, Pierre-Emmanuel Jabin, Stéphane Mischler, and Gaël Raoul. On selection dynamics for continuous structured populations. *Commun. Math. Sci.*, 6(3):729–747, 2008.
- [26] Ulf Dieckmann and Richard Law. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.*, 34(5-6):579–612, 1996.
- [27] Odo Diekmann. A beginner’s guide to adaptive dynamics. In *Mathematical modelling of population dynamics*, volume 63 of *Banach Center Publ.*, pages 47–86. Polish Acad. Sci. Inst. Math., Warsaw, 2004.
- [28] Odo Diekmann, Pierre-Emmanuel Jabin, Stphane Mischler, and Benoît Perthame. The dynamics of adaptation: An illuminating example and a hamiltonjacobi approach. *Theoretical Population Biology*, 67(4):257 – 271, 2005.
- [29] Jack Dockery, Vivian Hutson, Konstantin Mischaikow, and Mark Pernarowski. The evolution of slow dispersal rates: a reaction diffusion model. *J. Math. Biol.*, 37(1):61–83, 1998.
- [30] Yihong Du. *Order structure and topological methods in nonlinear partial differential equations. Vol. 1*, volume 2 of *Series in Partial Differential Equations and Applications*. World Scientific Publishing Co. Pte. Ltd., Hackensack, NJ, 2006. Maximum principles and applications.

- [31] Ilan Eshel and Uzi Motro. Kin selection and strong evolutionary stability of mutual help. *Theoret. Population Biol.*, 19(3):420–433, 1981.
- [32] Lawrence C. Evans. *Partial differential equations*, volume 19 of *Graduate Studies in Mathematics*. American Mathematical Society, Providence, RI, second edition, 2010.
- [33] Richard Gejji, Yuan Lou, Daniel Munther, and Justin Peyton. Evolutionary convergence to ideal free dispersal strategies and coexistence. *Bull. Math. Biol.*, 74(2):257–299, 2012.
- [34] S.A.H. Geritz, E. Kisdi, G. MeszeNA, and J.A.J. Metz. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, 12(1):35–57, 1998.
- [35] David Gilbarg and Lars Hörmander. Intermediate Schauder estimates. *Arch. Rational Mech. Anal.*, 74(4):297–318, 1980.
- [36] David Gilbarg and Neil S. Trudinger. *Elliptic partial differential equations of second order*. Classics in Mathematics. Springer-Verlag, Berlin, 2001. Reprint of the 1998 edition.
- [37] Richard Hambrock and Yuan Lou. The evolution of conditional dispersal strategies in spatially heterogeneous habitats. *Bulletin of Mathematical Biology*, 71(8):1793, 2009.
- [38] Alan Hastings. Can spatial variation alone lead to selection for dispersal? *Theoretical Population Biology*, 24(3):244 – 251, 1983.
- [39] Vivian Hutson, Konstantin Mischaikow, and Peter Poláčik. The evolution of dispersal rates in a heterogeneous time-periodic environment. *J. Math. Biol.*, 43(6):501–533, 2001.
- [40] Pierre-Emmanuel Jabin and Raymond Strother Schram. Selection-mutation dynamics with spatial dependence. *arXiv preprint arXiv:1601.04553*, 2016.
- [41] Stephen Kirkland, Chi-Kwong Li, and Sebastian J. Schreiber. On the evolution of dispersal in patchy landscapes. *SIAM J. Appl. Math.*, 66(4):1366–1382, 2006.
- [42] K.-Y. Lam, Y. Lou, and F. Lutscher. Evolution of dispersal in closed advective environments. *J. Biol. Dyn.*, 9(suppl. 1):188–212, 2015.
- [43] King-Yeung Lam. Concentration phenomena of a semilinear elliptic equation with large advection in an ecological model. *J. Differential Equations*, 250(1):161–181, 2011.
- [44] King-Yeung Lam. Limiting profiles of semilinear elliptic equations with large advection in population dynamics II. *SIAM J. Math. Anal.*, 44(3):1808–1830, 2012.
- [45] King-Yeung Lam. Stability of Dirac concentrations in an integro-PDE model for evolution of dispersal. *Calc. Var. Partial Differential Equations*, 56(3):56:79, 2017.
- [46] King-Yeung Lam and Yuan Lou. Evolution of conditional dispersal: evolutionarily stable strategies in spatial models. *J. Math. Biol.*, 68(4):851–877, 2014.
- [47] King-Yeung Lam and Yuan Lou. Evolutionarily stable and convergent stable strategies in reaction-diffusion models for conditional dispersal. *Bull. Math. Biol.*, 76(2):261–291, 2014.
- [48] King-Yeung Lam and Yuan Lou. An integro-PDE model for evolution of random dispersal. *J. Funct. Anal.*, 272(5):1755–1790, 2017.
- [49] King-Yeung Lam and Wei-Ming Ni. Limiting profiles of semilinear elliptic equations with large advection in population dynamics. *Discrete Contin. Dyn. Syst.*, 28(3):1051–1067, 2010.
- [50] Peter D. Lax. *Functional analysis*. Pure and Applied Mathematics (New York). Wiley-Interscience [John Wiley & Sons], New York, 2002.
- [51] Simon A. Levin. Population dynamic models in heterogeneous environments. *Annual Review of Ecology and Systematics*, 7:287–310, 1976.
- [52] Simon A. Levin, Dan Cohen, and Alan Hastings. Dispersal strategies in patchy environments. *Theoretical Population Biology*, 26(2):165 – 191, 1984.
- [53] Y. Lou and F. Lutscher. Evolution of dispersal in open advective environments. *J. Math. Biol.*, 69(6-7):1319–1342, 2014.
- [54] Yuan Lou and Wei-Ming Ni. Diffusion, self-diffusion and cross-diffusion. *J. Differential Equations*, 131(1):79–131, 1996.
- [55] P. Magal and G. F. Webb. Mutation, selection, and recombination in a model of phenotype evolution. *Discrete Contin. Dynam. Systems*, 6(1):221–236, 2000.
- [56] Mark A McPeek and Robert D Holt. The evolution of dispersal in spatially and temporally varying environments. *The American Naturalist*, 140(6):1010–1027, 1992.
- [57] Sepideh Mirrahimi and Benoît Perthame. Asymptotic analysis of a selection model with space. *J. Math. Pures Appl. (9)*, 104(6):1108–1118, 2015.
- [58] Ikuko Miyamoto and Hidenobu Yoshida. Harmonic functions in a cylinder with normal derivatives vanishing on the boundary. *Ann. Polon. Math.*, 74:229–235, 2000. Dedicated to the memory of Bogdan Ziemian.

- [59] Benoît Perthame and Guy Barles. Dirac concentrations in Lotka-Volterra parabolic PDEs. *Indiana Univ. Math. J.*, 57(7):3275–3301, 2008.
- [60] Benoît Perthame and Panagiotis E. Souganidis. Rare mutations limit of a steady state dispersal evolution model. *Math. Model. Nat. Phenom.*, 11(4):154–166, 2016.
- [61] Olga Turanova. On a model of a population with variable motility. *Math. Models Methods Appl. Sci.*, 25(10):1961–2014, 2015.

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