EVOLUTIONARILY STABLE AND CONVERGENT STABLE STRATEGIES IN REACTION-DIFFUSION MODELS FOR CONDITIONAL DISPERSAL

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ABSTRACT. We consider a mathematical model of two competing species for the evolution of conditional dispersal in a spatially varying but temporally constant environment. Two species are different only in their dispersal strategies, which are a combination of random dispersal and biased movement upward along the resource gradient. In the absence of biased movement or advection, Hastings showed that the mutant can invade when rare if and only if it has smaller random dispersal rate than the resident. When there is a small amount of biased movement or advection, we show that there is a positive random dispersal rate that is both locally evolutionarily stable and convergent stable. Our analysis of the model suggests that a balanced combination of random and biased movement might be a better habitat selection strategy for populations.

KEYWORDS: Conditional dispersal; Evolutionarily stable strategy; Convergent stable strategy; Reaction-diffusion-advection; Competition.

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1. **Introduction**

Biological dispersal refers to the movement of organisms from one location to another within a habitat. Dispersal of organisms has important consequence on population dynamics, disease spread and distribution of species [3, 32, 36, 37]. Unconditional dispersal refers to the movement of organisms in which the probability of movement is independent of the local environment, while conditional dispersal refers to those that are contingent on the local environmental cues. Understanding the evolution of dispersal is an important topic in ecology and evolutionary biology [9, 35]. In the following, we limit our discussion to phenotypic evolution under clonal reproduction, where the importance of genes and sex are ignored.

The evolution of unconditional dispersal is relatively well understood. For instance, Hastings [18] showed that in spatially heterogeneous but temporally constant environment an exotic species can invade when rare if and only if it has a smaller dispersal rate than the resident population; See also [26]. It is shown by Dockery et al. [13] that a slower diffusing population can always replace a faster diffusing one, irrespective of their initial distributions; See also [21]. In contrast, faster unconditional dispersal rate can be selected in spatially and temporally varying environments [19, 30].

Conditional dispersal is prevalent in nature. It is well-accepted that conditional dispersal confers a strong advantage in variable environments, as long as ecological cues give an accurate prediction of the habitat [14]. In recent years there has been growing interest in studying the evolution of conditional dispersal strategies in reaction-diffusion models and more broadly, advective movement of populations across the habitat [1, 2, 4, 5, 10, 20, 27, 28, 31, 34, 38].

In this paper we consider a reaction-diffusion-advection model, which is proposed and studied in [6, 7, 17], for two competing populations. In this model, both populations have the same population dynamics and adopt a combination of random dispersal and directed movement upward along the resource gradient. We

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regard two populations as different phenotypes of the same species, which are varied in two different traits: random dispersal rate and directed movement rate, and inquire into the evolution of these traits in spatially heterogeneous and temporally constant environments. A previous result (Theorem 7.1, [17]) implies that if both traits evolve simultaneously, the selection is against the movement, a prediction similar to the evolution of unconditional dispersal.

As a natural extension of the studies on the evolution of unconditional dispersal rate, in which the directed movement rate is fixed to be zero, we turn to investigate the evolution of random dispersal rate with the directed movement rate, or advection rate, being fixed at a positive value. In this direction, the following results were established (see [7, 17]): For any positive advection rate (equal for both populations),

- if one random dispersal rate is sufficiently small (relative to the advective rate) and the other is sufficiently large, two populations will coexist;
- if both random dispersal rates are sufficiently small, then the population with larger dispersal rate drives the other to extinction. In particular, small dispersal rate is selected against;
- if both random dispersal rates are sufficiently large, then the population with the smaller dispersal rate will drive the other to extinction. In particular, large dispersal rate is selected against.

These results suggest that intermediate random dispersal rates, relative to the advection rate, are favored.

In this paper we focus on the evolution of intermediate random dispersal rates. We closely follow the general approach of Adaptive Dynamics [11, 12, 15, 16]. Roughly speaking, it is an invasion analysis approach across different phenotypes. The first important concept is the invasion exponent. The idea is as follows: Suppose that the resident population is at equilibrium and a rare mutant population is introduced. The invasion exponent corresponds to the initial (exponential) growth rate of the mutant population. If the mutant has identical trait as the resident, the invasion exponent is necessarily zero. The primary focus of Adaptive Dynamics is to determine the sign of the invasion exponent (which corresponds to success or failure of mutant invasions) in the trait space, whose graphical representation is referred to as the Pairwise Invasibility Plot (PIP). A central concept in evolutionary game theory is that of *evolutionarily stable strategies* [29]. A strategy is called evolutionarily stable if "a population using it cannot be invaded by any small population using a different strategy". A closely related concept is that of *convergent stable strategies*. We say that a strategy is convergent stable, loosely speaking, if the mutant is always able to invade a resident population when the mutant strategy is closer to the convergent stable strategy than the resident strategy. We will use the standard abbreviations ESS for "evolutionarily stable strategy" and CSS for "convergent stable strategy." More precise mathematical descriptions of the invasion exponent, ESS and CSS in the reaction-diffusion-advection context will be given in the next section.

The goal of this paper is to show that there is selection for intermediate random dispersal rate, relative to directed movment rate, by rigorously proving the existence of ESS and CSS in the *ratio* of random dispersal rate to directed movement rate. Surprisingly, the multiplicities of ESS and CSS depend on the spatial heterogeneity in a subtle way. More precisely,

- if the spatial variation of the environment is less than a threshold value, there exists a unique ESS, which is also a CSS;
- if the spatial variation of the environment is greater than the threshold value, there might be multiple ESS/CSS.

This paper is a continuation of our recent work [24], where we considered the case when two populations have equal random dispersal rates but different directed movement coefficients.

2. Statement of main results

We shall follow the general approach of Adaptive Dynamics to state and interpret our main results. Let the habitat be given by a bounded domain Ω in $\mathbb{R}^N$ with smooth boundary $\partial\Omega$, and denote by n the outward unit normal vector on $\partial\Omega$, and $\frac{\partial}{\partial n} = n \cdot \nabla$. Let $m(x)$ represent the quality of habitat, or available resource, at location x. Throughout this paper, we assume

(A1) $m \in C^2(\bar{\Omega})$, it is positive and non-constant in $\bar{\Omega}$.

Let us recall the reaction-diffusion-advection model proposed and studied in [6, 7, 17].

$$
(1) \qquad \begin{cases} u_t = \nabla \cdot (d_1 \nabla u - \alpha_1 u \nabla m) + u(m-u-v) & \text{in } \Omega \times (0,\infty), \\ v_t = \nabla \cdot (d_2 \nabla v - \alpha_2 v \nabla m) + v(m-u-v) & \text{in } \Omega \times (0,\infty), \\ d_1 \frac{\partial u}{\partial n} - \alpha_1 u \frac{\partial m}{\partial n} = d_2 \frac{\partial v}{\partial n} - \alpha_2 v \frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega \times (0,\infty), \\ u(x,0) = u_0(x) \quad \text{and} \quad v(x,0) = v_0(x) & \text{in } \Omega. \end{cases}
$$

Here $u(x,t)$, $v(x,t)$ denote the densities of two populations at location x and time t in the habitat Ω; d_1, d_2 are their random dispersal rates, and α_1, α_2 are their rate of directed movement upward along the resource gradient. The boundary conditions is of no-flux type, i.e. there is no net movement across the boundary.

Now, if we fix the directed movement rates to be equal, i.e. assume that $\alpha_1 = \alpha_2 = \alpha$, and set $\mu = d_1/\alpha$ and $\nu = d_2/\alpha$. Then (1) can be rewritten as

$$
(2) \qquad \begin{cases} u_t = \alpha \nabla \cdot (\mu \nabla u - u \nabla m) + u(m-u-v) & \text{in } \Omega \times (0,\infty), \\ v_t = \alpha \nabla \cdot (\nu \nabla v - v \nabla m) + v(m-u-v) & \text{in } \Omega \times (0,\infty), \\ \mu \frac{\partial u}{\partial n} - u \frac{\partial m}{\partial n} = \nu \frac{\partial v}{\partial n} - v \frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega \times (0,\infty), \\ u(x,0) = u_0(x) \quad \text{and} \quad v(x,0) = v_0(x) & \text{in } \Omega. \end{cases}
$$

It is well known that under assumption (A1), any single population persists (so long as $\mu > 0$ and $\alpha \geq 0$) and reaches an equilibrium distribution given by the unique positive solution to the equation (See, e.g. [8])

$$
(3) \qquad \begin{cases} \alpha \nabla \cdot (\mu \nabla u - u \nabla m) + (m-u)u = 0 & \text{in } \Omega, \\ \mu \frac{\partial u}{\partial n} - u \frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega \end{cases}
$$

We denote this unique solution of (3) by $\tilde{u} = \tilde{u}(\mu, \alpha)$. Now we are in position to define, mathematically, the invasion exponent of our reaction-diffusion-advection model. By standard theory, if some rare population v is introduced into the resident population u at equilibrium (i.e. $u \equiv \tilde{u}$), then the initial (exponential) growth rate of the population of v is given by $-\lambda$, where $\lambda = \lambda(\mu, \nu; \alpha)$ is the principal eigenvalue of the problem ([6])

$$
(4) \qquad \begin{cases} \alpha \nabla \cdot (\nu \nabla \varphi - \varphi \nabla m) + \varphi(m - \tilde{u}) + \lambda \varphi = 0 & \text{in } \Omega, \\ \nu \frac{\partial \varphi}{\partial n} - \varphi \frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega, \end{cases}
$$

where the positive principal eigenfunction $\varphi = \varphi(\mu, \nu; \alpha)$ is uniquely determined by the normalization

$$
(5) \qquad \int_\Omega e^{-m/\mu} \varphi^2(\mu, \nu; \alpha) = \int_\Omega e^{-m/\mu} \tilde{u}^2(\mu, \alpha).
$$

In particular, when $\mu = \nu$, we have $\varphi(\mu, \mu; \alpha) \equiv \tilde{u}$ and $\lambda(\mu, \mu; \alpha) \equiv 0$ for any α and μ. This is easy to understand since two species u and v are identical when $\mu = \nu$. Intuitively, (4) gives the exponential growth rate of a population adopting random dispersal rate ν in the "effective environment" as given by $m - \tilde{u}$, after taking the resident population u into account.

Therefore, $-\lambda$ is the invasion exponent in the language of Adaptive Dynamics, and it is the main object of our investigation. Roughly speaking, a rare mutant species v can invade the resident species u at equilibrium if $\lambda < 0$ and fails to invade if $\lambda > 0$. Since an evolutionarily stable strategy must be evolutionarily singular, we first study the existence and multiplicity of *evolutionarily singular strategies*. The latter refers to the class of strategies where the selection pressure is neutral, i.e. there is neither selection for higher nor for lower dispersal rates. For the convenience of readers we recall the definition of evolutionarily singular strategy.

Definition 1. *Fix $\alpha > 0$. We say that $\mu^* > 0$ is an evolutionarily singular strategy if*

$$\frac{\partial \lambda}{\partial \nu}(\mu^*, \mu^*; \alpha) = 0.$$

We abbreviate $\frac{\partial\lambda}{\partial\nu}$ as λ_ν. Our first main result concerns the existence and multiplicity of singular strategies.

Theorem 1. *Suppose that $\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m} \leq 3 + 2\sqrt{2}$. Given any $\delta \in (0, \min\{\min_{\bar\Omega} m, (\max_{\bar\Omega} m)^{-1}\})$, for all small positive α, there is exactly one evolutionarily singular strategy, denoted as $\hat\mu = \hat\mu(\alpha)$, in $[\delta, \delta^{-1}]$. Moreover, $\hat\mu \in (\min_{\bar\Omega} m, \max_{\bar\Omega} m)$ and $\hat\mu \to \mu_0$ as $\alpha \to 0$, where μ_0 is the unique positive root of the function*

$$g_0(\mu) := \int_\Omega \nabla m \cdot \nabla(e^{-m/\mu} m), \quad 0 < \mu < \infty. \tag{6}$$

Furthermore, λ_ν satisfies

$$\lambda_\nu(\mu, \mu; \alpha) = \begin{cases} -, & \mu \in [\delta, \hat\mu); \\ 0, & \mu = \hat\mu; \\ +, & \mu \in (\hat\mu, \delta^{-1}]. \end{cases} \tag{7}$$

The ratio $\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m}$ is a measurement of the spatial variation of function m. Theorem 1 says that if the spatial variation of the inhomogeneous environment is suitably small, then for small advection rate, there is exactly one evolutionarily singular strategy. Interestingly, this singular dispersal strategy is of the same order as the advection rate. Moreover, (7) implies that when the dispersal rate of the resident population is less (or greater) than the evolutionarily singular strategy, then a rare mutant with a slightly greater (resp. smaller) dispersal rate ν can invade the resident population successfully.

When Ω is an interval and m is a monotone function, Theorem 1 can be improved as follows.

Theorem 2. *Suppose that $\Omega = (a, b)$, $m_x > 0$ in $[a, b]$, and $\frac{m(b)}{m(a)} \leq 3 + 2\sqrt{2}$. Then for all small positive α, there is exactly one evolutionarily singular strategy in $[0, \infty)$.*

A bit surprisingly, the constant $3 + 2\sqrt{2}$ in Theorems 1 and 2 is sharp, as shown by the following result.

Theorem 3. *Let $\Omega = (a, b)$. For any $L > 3+2\sqrt{2}$, there exists some function $m \in C^2([a, b])$ with m, $m_x > 0$ and $\frac{m(b)}{m(a)} = L$ such that for all $\alpha > 0$ small, there are three or more evolutionarily singular strategies.*

From the proof of Theorem 3 we know that at least one of the three evolutionarily singular strategies is not an ESS (Remark 5.1). It is natural to inquire whether the unique singular strategy in Theorems 1 and 2 is evolutionarily stable and/or convergent stable. To address these issues, we first recall the definition of a local ESS.

Definition 2. *Fix $\alpha > 0$. A strategy μ^* is a local ESS if there exists $\delta > 0$ such that $\lambda(\mu^*, \nu; \alpha) > 0$ for all $\nu \in (\mu^* - \delta, \mu^* + \delta) \setminus \{\mu^*\}$.*

Under some further restrictions we are able to show that the unique singular strategy $\hat{\mu}$ in Theorem 1 is a local ESS.

Theorem 4. *Suppose that Ω is convex with diameter d and $\|\nabla \ln m\|_{L^\infty(\Omega)} \le \beta_0/d$, where $\beta_0 \approx 0.615$ is the unique positive root of the function $t \mapsto \frac{t^2}{\pi^2} - e^{-4t}\left(\frac{2t}{e^t-1} - 1\right)$. Then for α sufficiently small, $\hat{\mu}$ given in Theorem 1 is a local ESS.*

The assumption of Theorem 4 on m is more restrictive than that of Theorem 1, as can be seen from

$$\frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m} \le e^{d\|\nabla \ln m\|_{L^\infty}} \le e^{\beta_0} \approx 1.849 < 3 + 2\sqrt{2}.$$

We do not know whether an evolutionarily singular strategy, whenever it is unique, is always an ESS. On the other hand, at least one of the singular strategies constructed in Theorem 3 is not an ESS, so in general we do not expect every singular strategy to be evolutionarily stable.

Our next result shows that for our model a local ESS is always a local CSS. Again, for the convenience of readers we recall the definition of a local CSS.

Definition 3. *A strategy μ^* is a local convergence stable strategy if there exists some $\delta > 0$ such that*

$$\lambda(\mu,\nu;\alpha) = \begin{cases} > 0 & \text{if } \mu^* \le \mu < \nu < \mu^* + \delta \text{ or } \mu^* - \delta < \nu < \mu \le \mu^*, \\ < 0 & \text{if } \mu^* \le \nu < \mu < \mu^* + \delta \text{ or } \mu^* - \delta < \mu < \nu \le \mu^*. \end{cases}$$

Our final result is

Theorem 5. *For any small $\delta > 0$, there exists some $\alpha_1 > 0$ such that if $\alpha \in (0, \alpha_1)$, any local ESS in $[\delta, \delta^{-1}]$ is necessarily a local CSS.*

In particular, this excludes the possibility of a "Garden of Eden" type of ESS in the class of random dispersal rates which are of the same order as the advection rate. Figure 1(a) gives an illustration of Theorems 1, 2, 4 and 5, where there is a unique singular strategy which is both locally evolutionarily stable and convergent stable. Figure 1(b) illustrates the possibility of multiple evolutionarily stable strategies, as suggested by Theorem 3.

Our results, especially Theorems 4 and 5, suggest that in spatially varying but temporally constant environment, an evolutionarily stable and convergent stable strategy for random dispersal is proportional to the directed movement rate. In the biological context, while tracking the resource gradient might help a population invade quickly, but if the population overly pursue the resource by excessive advection along the resource gradient, its distribution will only be concentrated near locally most favorable resources; See [8, 22, 23, 25]. Such strategy may not be evolutionarily stable since populations using a better mixture of random movement and resource tracking can utilize all available resource and thus invade when rare. Hence a balanced combination of random and biased movement might be a better habitat selection strategy for populations.

This paper is a continuation of our recent work [24], where we considered the case when two populations have equal diffusion rates but different advection coefficients. While some proofs in current paper rely upon those in [24], there exist some notable differences between these two works:

(1) Convergent stability is an important aspect in the evolution of dispersal. There were no discussions of CSS in our previous work [24], while in this paper we are able to show that a local ESS is always

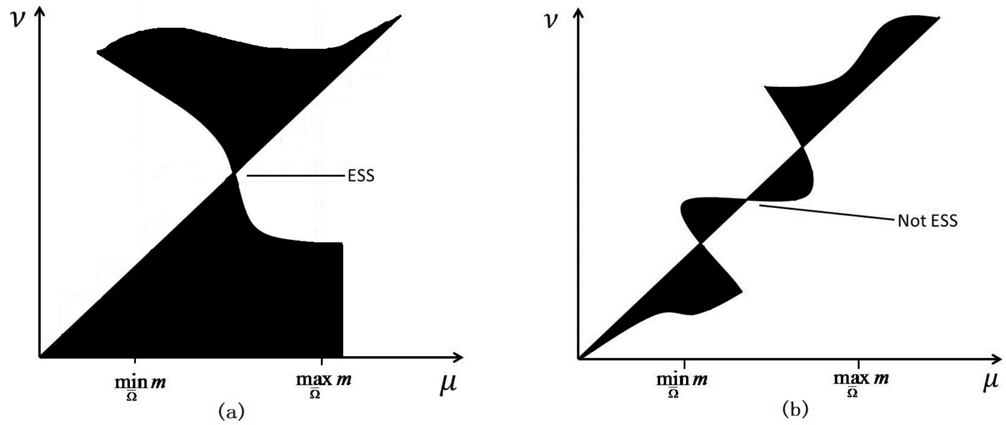

FIGURE 1. Possible pairwise invasibility plots (PIP) illustrating Theorems 1, 2 (Fig. 1(a)) and Theorem 3 (Fig. 1(b)). White coloring indicates the mutant invades, and black that the mutant loses (does not invade). On the horizontal axis the resident random dispersal rate (μ) is represented, and on the vertical axis the mutant random dispersal rate (ν). The evolutionarily singular strategies are given by the intersection of black and white parts of the plane, along the diagonal. In Fig. 1(a), the unique singular strategy is an ESS (since it lies vertically between black regions). It is also a CSS. In Fig. 1(b), there are three singular strategies. The one in the middle is neither an ESS nor a CSS.

a CSS, provided that the advection rate is small and the random dispersal rate is of the same order as the advection rate.

(2) When two populations have same random dispersal rates ($d_1 = d_2 := d$), we proved in [24] that if the random dispersal rate d is small, there is an evolutionarily stable strategy for advection rate. That is, there exists some $\bar{\alpha} = \bar{\alpha}(d)$ such that if $\alpha_1 = \bar{\alpha}$ and α_2 is close to (but not equal to) $\bar{\alpha}$, then population v can not invade when rare. Moreover, as $d \to 0+$, $\bar{\alpha}/d \to \eta^*$, where η^* is the unique positive root of the function

$$g_1(\eta) := \int_\Omega m\nabla m \cdot \nabla(e^{-\eta m} m), \quad 0 < \eta < \infty.$$

On the other hand, Theorem 4 shows that when two populations have same but small advection rates ($\alpha_1 = \alpha_2 := \alpha$), there is an evolutionarily stable strategy for random dispersal rate. That is, there exists some $\bar{d} = \bar{d}(\alpha)$ such that if $d_1 = \bar{d}$ and d_2 is close to (but not equal to) $\bar{d}$, then population v can not invade when rare. Moreover, as $\alpha \to 0+$, $\bar{d}/\alpha \to \xi^*$, where ξ^* is the unique positive root of the function

$$g_0(\xi) := \int_\Omega \nabla m \cdot \nabla(e^{-m/\xi} m), \quad 0 < \xi < \infty.$$

Since $\bar{\alpha}/d$ is the "optimal" ratio of advection rate to random dispersal rate and $\bar{d}/\alpha$ is the "optimal" ratio of random dispersal rate to advection rate, our first thought is that $\bar{\alpha}/d$ might be inverse to $\bar{d}/\alpha$ for small dispersal rates. But apparently this is not the case since their limits are not inverse to each other; i.e., $\eta^* \neq \frac{1}{\xi^*}$. These discussions indicate that understanding the invasion exponent at $(\tilde{u}, 0)$ is quite subtle, even for small d_i, α_i, $i = 1, 2$.

While there are these differences between current paper and our previous work [24], both works suggest that a balanced combination of random and biased movement might be a better habitat selection strategy for populations, provided that the diffusion and advection rates are small. It is interesting to inquire whether similar conclusions can be drawn for large advection rate.

This paper is organized as follows. Section 3 is devoted to the study of evolutionarily singular strategies and we establish Theorems 1 and 2 there. In Section 4 we determine whether the evolutionarily singular strategy from Theorem 1 is evolutionarily stable and prove Theorem 4. In Section 5 we establish Theorem 3. Theorem 5 is proved in Section 6. Finally we end with some biological discussions and interpretations of our results.

3. **Evolutionarily Singular Strategies**

In this section we establish Theorems 1 and 2. We first derive the formula of $\lambda_\nu(\mu,\mu;\alpha)$ in Subsect. 3.1. Subsect. 3.2 is devoted to various estimates of $\tilde{u}$ for sufficiently small α, which in turn enables us to obtain the limit problem for $\lambda_\nu(\mu,\mu;\alpha)$ with sufficiently small α in Subsect. 3.3. The proofs of Theorems 1 and 2 are given in Subsect. 3.4. Materials of this section rely heavily on results from [24], especially those in Subsects. 3.2 and 3.3. Readers who are interested in learning more about the technical details may wish to consult [24].

3.1. **Formula for λ_ν.** We recall that $\tilde{u}$ satisfies

$$\begin{cases} \alpha\nabla\cdot(\mu\nabla\tilde{u}-\tilde{u}\nabla m)+(m-\tilde{u})\tilde{u}=0 & \text{in } \Omega,\\ n\cdot(\mu\nabla\tilde{u}-\tilde{u}\nabla m)=0 & \text{on } \partial\Omega. \end{cases} \tag{8}$$

The stability of $(\tilde{u},0)$ is determined by the sign of the principal eigenvalue $\lambda=\lambda(\mu,\nu;\alpha)$ of (4). Differentiate (4) with respect to ν we get

$$\begin{cases} \alpha\nabla\cdot(\nu\nabla\varphi_\nu-\varphi_\nu\nabla m)+(m-\tilde{u})\varphi_\nu+\lambda\varphi_\nu=-\alpha\Delta\varphi-\lambda_\nu\varphi & \text{in } \Omega,\\ n\cdot(\nu\nabla\varphi_\nu-\varphi_\nu\nabla m)=-\frac{\partial\varphi}{\partial n} \quad \text{on } \partial\Omega \quad \text{and} & \int e^{-m/\mu}\varphi_\nu\varphi=0. \end{cases} \tag{9}$$

Multiplying (9) by $e^{-m/\nu}\varphi$ and (4) by $e^{-m/\nu}\varphi_\nu$, subtracting and integrating the result, we get

$$\frac{\lambda_\nu}{\alpha}\int e^{-\frac{m}{\nu}}\varphi^2=\int\nabla\varphi\cdot\nabla\left(e^{-\frac{m}{\nu}}\varphi\right). \tag{10}$$

Setting $\nu=\mu$ in (10), then by $\varphi(\mu,\mu;\alpha)=\tilde{u}$ and (10) we have the following result:

Lemma 3.1. *For any $\alpha>0$ and $\mu>0$, the following holds:*

$$\frac{\lambda_\nu(\mu,\mu;\alpha)}{\alpha}\int e^{-m/\mu}\tilde{u}^2=\int\nabla\tilde{u}\cdot\nabla(e^{-m/\mu}\tilde{u}). \tag{11}$$

3.2. **Estimates.** We collect some known limiting behaviors of $\tilde{u}$ as $\alpha\to 0$.

Lemma 3.2 (See, e.g. Lemma 3.2 of [24])**.** *For any $\delta>0$, there exists a positive constant C such that for all α and $\mu\geq\delta$,*

$$C^{-1}\leq\tilde{u}\leq C \quad \text{in } \Omega. \tag{12}$$

Moreover, as $\alpha\to 0$, $\|\tilde{u}-m\|_{L^\infty(\Omega)}\to 0$ uniformly for $\delta\leq\mu\leq 1/\delta$.

Lemma 3.3 (Lemma 3.3 of [24])**.** *For each $\delta>0$, there exists $C>0$ such that for any $\phi\in H^1(\Omega)$,*

$$\int|\nabla\tilde{u}-\nabla m|^2\phi^2\leq C\|\tilde{u}-m\|_{L^\infty(\Omega)}\|\phi\|^2_{H^1(\Omega)},$$

where $C=C(\mu)$ is independent of α and bounded uniformly for $\mu\geq\delta$.

For later purposes, we state the following corollary, which follows from Lemmas 3.2 and 3.3.

Corollary 3.4. *For each $\delta > 0$, there exists $C > 0$ such that for all $\phi_i \in H^1(\Omega)$, $i = 1, 2$,*

$$\int |\nabla\tilde{u} - \nabla m|^2 \frac{\phi_1\phi_2}{\tilde{u}^2} \leq C\|\tilde{u} - m\|_{L^\infty(\Omega)} \left(\|\phi_1\|^2_{H^1(\Omega)} + \|\phi_2\|^2_{H^1(\Omega)}\right),$$

where $C = C(\mu)$ is independent of α and bounded uniformly for $\mu \geq \delta$.

Next, we have the following estimate of $\frac{\partial\tilde{u}}{\partial\mu}$.

Lemma 3.5. *For each $\delta > 0$, $\frac{\partial\tilde{u}}{\partial\mu} \to 0$ in $H^1(\Omega)$ as $\alpha \to 0$, uniformly for $\delta \leq \mu \leq 1/\delta$.*

Proof. Denote $\frac{\partial\tilde{u}}{\partial\mu} = \tilde{u}'$ and differentiate (8) with respect to μ, we have

$$\begin{cases} \alpha\nabla\cdot(\mu\nabla\tilde{u}' - \tilde{u}'\nabla m) + (m - 2\tilde{u})\tilde{u}' = -\alpha\Delta\tilde{u} & \text{in } \Omega, \\ \mu\frac{\partial\tilde{u}'}{\partial n} - \tilde{u}'\frac{\partial m}{\partial n} = -\frac{\partial\tilde{u}}{\partial n} & \text{on } \partial\Omega. \end{cases} \tag{13}$$

Multiply (13) by $e^{-m/\mu}\tilde{u}'$ and integrate by parts, we find

$$\alpha\mu\int e^{m/\mu}|\nabla(e^{-m/\mu}\tilde{u}')|^2 + \int e^{m/\mu}(2\tilde{u} - m)(e^{-m/\mu}\tilde{u}')^2 = -\alpha\int\nabla\tilde{u}\cdot\nabla(e^{-m/\mu}\tilde{u}'). \tag{14}$$

By Hölder's inequality,

$$\frac{\alpha\mu}{2}\int e^{m/\mu}|\nabla(e^{-m/\mu}\tilde{u}')|^2 + \int e^{m/\mu}(2\tilde{u} - m)(e^{-m/\mu}\tilde{u}')^2 \leq \frac{\alpha}{2\mu}\int e^{-m/\mu}|\nabla\tilde{u}|^2.$$

By the fact that $2\tilde{u} - m \to m > 0$ uniformly in $\bar{\Omega}$ as $\alpha \to 0$ (Lemma 3.2), we see that uniformly for $\mu \geq \delta$, $\int|\nabla(e^{-m/\mu}\tilde{u}')|^2 = O(1)$ and $\int(e^{-m/\mu}\tilde{u}')^2 = O(\alpha)$ and hence $e^{-m/\mu}\tilde{u}' \rightharpoonup 0$ in $H^1(\Omega)$. Upon considering (14) again, we conclude that $e^{-m/\mu}\tilde{u}' \to 0$ in $H^1(\Omega)$ as $\alpha \to 0$. □

Next, we show the following lemma.

Lemma 3.6. *For each $\delta > 0$,*

$$\frac{d}{d\mu}\left(\int\nabla\tilde{u}\cdot\nabla(e^{-m/\mu}\tilde{u})\right) \to \frac{1}{\mu^2}\int\nabla m\cdot\nabla(e^{-m/\mu}m^2),$$

as $\alpha \to 0$ uniformly, for $\delta \leq \mu \leq 1/\delta$.

Proof. By Lemma 3.5, as $\alpha \to 0$,

$$\begin{aligned} &\frac{d}{d\mu}\left(\int\nabla\tilde{u}\cdot\nabla(e^{-m/\mu}\tilde{u})\right) \\ &= \int\nabla\frac{\partial\tilde{u}}{\partial\mu}\cdot\nabla(e^{-m/\mu}\tilde{u}) + \frac{1}{\mu^2}\int\nabla\tilde{u}\cdot\nabla(e^{-m/\mu}m\tilde{u}) + \int\nabla\tilde{u}\cdot\nabla\left(e^{-m/\mu}\frac{\partial\tilde{u}}{\partial\mu}\right) \\ &\to \frac{1}{\mu^2}\int\nabla m\cdot\nabla(e^{-m/\mu}m^2). \end{aligned}$$

This completes the proof. □

By Lemmas 3.3 and 3.6, we have the following result.

Corollary 3.7. *As $\alpha \to 0$,*

$$\int\nabla\tilde{u}\cdot\nabla(e^{-m/\mu}\tilde{u}) \to g_0(\mu) := \int\nabla m\cdot\nabla(e^{-m/\mu}m) \quad \text{in } C^1_{loc}((0,\infty)). \tag{15}$$

And we see that for α small, the roots of $\lambda_\nu(\mu,\mu;\alpha) = 0$ and the roots of g_0 are in one-to-one correspondence, provided that the latter roots are non-degenerate.

3.3. **Limit Problem for λ_ν.** By Lemma 3.1 and Corollary 3.7, the first step in establishing the existence of evolutionarily singular strategies is to study the roots of $g_0(\mu) = \int \nabla m \cdot \nabla(e^{-m/\mu}m)$. Since $g_0(\mu) = \int e^{-m/\mu}|\nabla m|^2 \left(1 - \frac{m}{\mu}\right)$, we observe that

$$g_0(\mu) < 0 \quad \text{for } \mu \in (0, \min_{\bar\Omega} m] \quad \text{and} \quad g_0(\mu) > 0 \quad \text{for } \mu \in [\max_{\bar\Omega} m, \infty). \tag{16}$$

Proposition 3.8. *Let $\Omega \subset \mathbb{R}^N$. Suppose that $\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m} \leq 3 + 2\sqrt{2}$. Then there exists $\mu_0 > 0$ such that* (i) $g_0(\mu) < 0$ *if* $[0, \mu_0)$*;* (ii) $g_0(\mu) = 0$ *if* $\mu = \mu_0$*;* (iii) $g_0(\mu) > 0$ *if* $\mu > \mu_0$*. Moreover,* $g'(\mu_0) > 0$.

Proof. Let $\tilde g_0(\eta) = g_0(1/\eta)$, then it suffices to show that $\tilde g_0$ has a unique non-degenerate root in $(0, \infty)$, which follows from Proposition 3.8 and Remark 3.11 of [24]. □

3.4. **Proofs of Theorems 1 and 2.**

Proof of Theorem 1. By Proposition 3.8, $g_0(\mu) = \int \nabla m \cdot \nabla(e^{-m/\mu}m)$ has a unique, non-degenerate root in $(0, \infty)$. For each $\delta > 0$,

$$\int \nabla \tilde u \cdot \nabla(e^{-m/\mu}\tilde u) \to \int \nabla m \cdot \nabla(e^{-m/\mu}m)$$

in $C^1([\delta, \delta^{-1}])$ as $\alpha \to 0$. Hence, we see that for any $0 < \delta < \min_{\bar\Omega}[\min\{m(x), m(x)^{-1}\}]$, $\int \nabla \tilde u \cdot \nabla(e^{-m/\mu}\tilde u)$ has a unique positive root in $[\delta, \delta^{-1}]$ for all sufficiently small α. By Lemma 3.1

$$\frac{1}{\alpha}\lambda_\nu(\mu, \mu; \alpha) = \frac{\int \nabla \tilde u \cdot \nabla(e^{-m/\mu}\tilde u)}{\int e^{-m/\mu}\tilde u^2}.$$

Therefore, given any $\delta > 0$, for sufficiently small α, λ_ν also changes sign exactly once in $[\delta, \delta^{-1}]$. Moreover, denoting the unique root by $\hat\mu$, we see that $\hat\mu \to \mu_0$ as $\alpha \to 0$, where μ_0 is the unique positive root of $g_0(\mu)$. □

To show Theorem 2, we first prove a useful lemma.

Lemma 3.9. *Let $\phi \in C^2([0,1])$ be a solution to*

$$\begin{cases} \phi_{xx} + b(x)\phi_x + g(x, c(x) - \phi(x)) = 0 & \text{in } (0,1), \\ \phi_x \geq 0 & \text{at } x = 0, 1, \end{cases} \tag{17}$$

where $\operatorname{sign} g(x,s) = \operatorname{sign} s$ *and $c_x > 0$ in $[0,1]$. Then $\phi_x > 0$ in $(0,1)$.*

Proof of Lemma 3.9.

Claim 3.10. *$\phi_x \geq 0$ in $(0,1)$ if c is strictly increasing in* $[0,1]$.

Suppose to the contrary that there exists $0 \leq x_1 < x_2 \leq 1$ such that $\phi_x < 0$ in (x_1, x_2) and $\phi_x(x_1) = \phi_x(x_2) = 0$. Then x_1, x_2 are one-sided local maxima of ϕ_x in $[x_1, x_2]$. Hence $\phi_{xx}(x_1) \leq 0 \leq \phi_{xx}(x_2)$, which implies (by (17)), that $c(x_1) \geq \phi(x_1)$ and $c(x_2) \leq \phi(x_2)$. Combining with the strict monotonicity of ϕ in $[x_1, x_2]$, we have

$$c(x_1) \geq \phi(x_1) > \phi(x_2) \geq c(x_2),$$

which contradicts the strict monotonicity of c. This proves Claim 3.10.

Next, assume further that $c_x > 0$ in $[0,1]$. Suppose for contradiction that $\phi_x(x_0) = 0$ for some $x_0 \in (0,1)$. Then by the previous claim, x_0 is a local interior minimum of ϕ_x in $(0,1)$. Therefore, $\phi_{xx}(x_0) = 0$ and by (17), we have $c(x_0) = \phi(x_0)$. Together with

$$(c - \phi)_x(x_0) = c_x(x_0) > 0,$$

we derive that $c - \phi > 0$ in $(x_0, x_0 + \delta)$ for some $\delta > 0$. But then

$$\left(e^{\int_0^x b(s)\,ds}\phi_x\right)_x = -e^{\int_0^x b(s)\,ds} g(x, c-\phi) < 0 \quad \text{and} \quad \phi_x(x_0) = 0.$$

Hence $\phi_x < 0$ in $(x_0, x_0 + \delta)$. This contradicts Claim 3.10, and completes the proof. □

Corollary 3.11. *Suppose* $\Omega = (0,1)$, $m, m_x > 0$ *in* $[0,1]$ *and let* $\tilde{u}$ *be the unique positive solution of* (3). *Then*

(i) *for all* $\alpha > 0$ *and* $\mu > 0$, $\tilde{u}_x > 0$ *in* $(0,1)$;
(ii) *if* $\mu > \max_{[0,1]} m$, *then* $(e^{-m/\mu}\tilde{u})_x > 0$ *in* $(0,1)$;
(iii) *if* $\mu < \min_{[0,1]} m$, *then* $(e^{-m/\mu}\tilde{u})_x < 0$ *in* $(0,1)$.

Proof of Corollary 3.11. Firstly, (i) follows as a direct consequence of Lemma 3.9. For (ii), we observe that $v := e^{-m/\mu}\tilde{u}$ satisfies

$$\begin{cases} \alpha\mu v_{xx} + \alpha m_x v_x + e^{m/\mu} v(m e^{-m/\mu} - v) = 0 & \text{in } (0,1), \\ v_x = 0 & \text{at } x = 0, 1. \end{cases}$$

In addition, the assumption $\mu > \max_{[0,1]} m$ implies that $(me^{-m/\mu})_x > 0$ in $[0,1]$. Hence, Lemma 3.9 applies and yields $(e^{-m/\mu}\tilde{u})_x = v_x > 0$ in $(0,1)$. For (iii), set $w(x) = v(1-x)$, then w satisfies

$$\begin{cases} \alpha\mu w_{xx} - \alpha \tilde{m}_x w_x + e^{\tilde{m}/\mu} w(\tilde{m} e^{-\tilde{m}/\mu} - w) = 0 & \text{in } (0,1), \\ w_x = 0 & \text{at } x = 0, 1, \end{cases}$$

where $\tilde{m}(x) = m(1-x)$. In addition, the assumption $\mu < \min_{[0,1]} m$ implies that $(\tilde{m}e^{-\tilde{m}/\mu})_x > 0$ in $[0,1]$. Hence, Lemma 3.9 applies and yields $w_x > 0$, which is equivalent to $(e^{-m/\mu}\tilde{u})_x < 0$ in $[0,1]$. This completes the proof of the corollary. □

Proof of Theorem 2. Without loss of generality, assume $\Omega = (0,1)$. In view of Lemma 3.1 and Theorem 1, it suffices to show that

$$\lambda_\nu \int e^{-m/\mu}\tilde{u}^2 = \int \tilde{u}_x (e^{-m/\mu}\tilde{u})_x \neq 0$$

for all $\mu \in (0, \min_{[0,1]} m) \cup (\max_{[0,1]} m, \infty)$, which follows from Corollary 3.11. □

4. Evolutionarily Stable Strategies

In this section we provide a sufficient condition for the evolutionarily singular strategy identified in Theorem 1 to be evolutionarily stable. The formula of $\lambda_{\nu\nu}(\mu,\mu;\alpha)$ is given in Subsect. 4.1. We establish various estimates of eigenfunctions for sufficiently small α in Subsect. 4.2. We apply these results to find the limit of $\lambda_{\nu\nu}(\hat{\mu},\hat{\mu};\alpha)/\alpha$ as $\alpha \to 0$. The sign of this limit is determined in Subsect. 4.3, which helps us complete the proof of Theorem 4.

4.1. **Formula for $\lambda_{\nu\nu}$.** Differentiate (9) with respect to ν and denote $\frac{\partial^2\varphi}{\partial\nu^2} = \varphi_{\nu\nu}$ and $\frac{\partial^2\lambda}{\partial\nu^2} = \lambda_{\nu\nu}$, we have

$$\begin{cases} \alpha\nabla\cdot(\nu\nabla\varphi_{\nu\nu} - \varphi_{\nu\nu}\nabla m) + (m-\tilde{u})\varphi_{\nu\nu} + \lambda\varphi_{\nu\nu} = -2\alpha\Delta\varphi_\nu - 2\lambda_\nu\varphi_\nu - \lambda_{\nu\nu}\varphi & \text{in } \Omega, \\ \mu\frac{\partial\varphi_{\nu\nu}}{\partial n} - \varphi_{\nu\nu}\frac{\partial m}{\partial n} = -2\frac{\partial\varphi_\nu}{\partial n} & \text{on } \partial\Omega. \end{cases} \tag{18}$$

Set $\nu = \mu$, we have $\lambda = 0$, $\varphi(\mu,\mu;\alpha) = \tilde{u}$ and

$$\begin{cases} \alpha\nabla\cdot(\mu\nabla\varphi_{\nu\nu} - \varphi_{\nu\nu}\nabla m) + (m-\tilde{u})\varphi_{\nu\nu} = -2\alpha\Delta\varphi_\nu - 2\lambda_\nu\varphi_\nu - \lambda_{\nu\nu}\tilde{u} & \text{in } \Omega, \\ \mu\frac{\partial\varphi_{\nu\nu}}{\partial n} - \varphi_{\nu\nu}\frac{\partial m}{\partial n} = -2\frac{\partial\varphi_\nu}{\partial n} & \text{on } \partial\Omega. \end{cases} \tag{19}$$

Multiplying (19) by $e^{-m/\mu}\tilde{u}$, we obtain, via integration by parts,

$$\frac{\lambda_{\nu\nu}(\mu,\mu;\alpha)}{\alpha}\int e^{-m/\mu}\tilde{u}^2 = 2\int \nabla\varphi_\nu\cdot\nabla\left(e^{-m/\mu}\tilde{u}\right) - 2\frac{\lambda_\nu(\mu,\mu;\alpha)}{\alpha}\int \varphi_\nu e^{-m/\mu}\tilde{u} \tag{20}$$

where $\varphi_\nu = \varphi_\nu(\mu,\mu;\alpha)$ is the unique solution to (9). Hence, we have the following formula for $\lambda_{\nu\nu}$:

Lemma 4.1. *Suppose that μ is an evolutionarily singular strategy, i.e., $\lambda_\nu(\mu,\mu;\alpha)=0$. Then*

$$\frac{\lambda_{\nu\nu}(\mu,\mu;\alpha)}{\alpha}\int e^{-m/\mu}\tilde{u}^2 = 2\int \nabla\varphi_\nu\cdot\nabla\left(e^{-m/\mu}\tilde{u}\right), \tag{21}$$

where $\varphi_\nu=\varphi_\nu(\mu,\mu;\alpha)$ is the unique solution to

$$\begin{cases} \alpha\nabla\cdot(\mu\nabla\varphi_\nu - \varphi_\nu\nabla m) + \varphi_\nu(m-\tilde{u}) = -\alpha\Delta\tilde{u} & \text{in } \Omega, \\ \mu\frac{\partial\varphi_\nu}{\partial n} - \varphi_\nu\frac{\partial m}{\partial n} = -\frac{\partial\tilde{u}}{\partial n} \quad \text{on } \partial\Omega, & \int e^{-m/\mu}\varphi_\nu\tilde{u} = 0. \end{cases} \tag{22}$$

4.2. **Estimates.** Let (λ_k,φ_k) be the eigenpairs of (4) (counting multiplicities) with $\nu=\mu$ such that $\lambda_1 < \lambda_2 \le \lambda_3\cdots$. By the transformation $\phi = e^{-m/\mu}\varphi$ and (8), (4) becomes

$$\begin{cases} \mu\nabla\cdot(e^{m/\mu}\nabla\phi) - \frac{\nabla\cdot(\mu\nabla\tilde{u}-\tilde{u}\nabla m)}{\tilde{u}}e^{m/\mu}\phi + \frac{\lambda}{\alpha}e^{m/\mu}\phi = 0 & \text{in } \Omega, \\ \frac{\partial\phi}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{23}$$

Then λ_k/α is the k-th eigenvalue of (23) (counting multiplicities). The following result determines the asymptotic behavior of λ_k as $\alpha\to 0$.

Proposition 4.2. *For each $\delta>0$, $\lambda_k/\alpha\to\sigma_k$ as $\alpha\to 0$ uniformly for $\delta\le\mu\le 1/\delta$, where $\lambda_k=\lambda_k(\mu,\mu;\alpha)$ is the k-th eigenvalue of (4) when $\nu=\mu$, and $\sigma_k=\sigma_k(\mu)$ is the k-th eigenvalue of*

$$\begin{cases} \mu\nabla\cdot(e^{m/\mu}\nabla\phi) - \frac{\nabla\cdot[(\mu-m)\nabla m]}{m}e^{m/\mu}\phi + \sigma e^{m/\mu}\phi = 0 & \text{in } \Omega, \\ \mu\frac{\partial\phi}{\partial n} - \frac{(\mu-m)}{m}\phi\frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{24}$$

Remark 4.1. *One can check that all σ_k are real, $\sigma_1=0$, and $e^{-m/\mu}m$ is an eigenfunction corresponding to σ_1. In particular, $\sigma_k>0$ for $k\ge 2$.*

Proof of Proposition 4.2. It follows from Proposition 4.2 of [24]. ☐

Next, we study the asymptotic behavior of $\varphi_\nu(\mu,\mu;\alpha)$ as $\alpha\to 0$. Recall that $\varphi_\nu(\mu,\mu;\alpha)$ is the unique solution of (22). We shall assume that $\mu=\mu(\alpha)$ is an evolutionarily singular strategy (i.e. $\lambda_\nu(\mu,\mu;\alpha)=0$) and $\mu\to\mu^*$ as $\alpha\to 0$. Note that if $\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m}\le 3+2\sqrt{2}$, then $\mu=\hat\mu(\alpha)$ is the unique evolutionarily singular strategy as determined in Theorem 1, and $\mu^*=\mu_0$ is the unique positive root of $g_0(\mu)=\int\nabla m\cdot\nabla(e^{m/\mu}m)$ as determined in Proposition 3.8.

Lemma 4.3. *Suppose that $\mu=\mu(\alpha)$ is an evolutionarily singular strategy and $\mu\to\mu^*$ as $\alpha\to 0$. By passing to a subsequence, $\varphi_\nu(\mu,\mu;\alpha)\rightharpoonup\varphi'$ in $H^1(\Omega)$ as $\alpha\to 0$, where φ' is the unique solution to*

$$\begin{cases} \nabla\cdot(\mu^*\nabla\varphi' - \varphi'\nabla m) - \frac{\nabla\cdot[(\mu^*-m)\nabla m]}{m}\varphi' = -\Delta m & \text{in } \Omega, \\ \mu^*\frac{\partial\varphi'}{\partial n} - \frac{\mu^*}{m}\varphi'\frac{\partial m}{\partial n} = -\frac{\partial m}{\partial n} \quad \text{on } \partial\Omega, & \int e^{m/\mu^*}\varphi' m = 0. \end{cases} \tag{25}$$

Proof. First we estimate $\|\nabla\varphi_\nu\|_{L^2(\Omega)}$ in terms of $\|\varphi_\nu\|_{L^2(\Omega)}$. To this end, multiply (22) by $e^{-m/\mu}\varphi_\nu$ and integrate by parts,

$$\mu\int e^{m/\mu}|\nabla(e^{-m/\mu}\varphi_\nu)|^2 - \mu\int e^{m/\mu}\nabla(e^{-m/\mu}\tilde{u})\cdot\nabla\left[\frac{(e^{-m/\mu}\varphi_\nu)^2}{e^{-m/\mu}\tilde{u}}\right] = -\int\nabla\tilde{u}\cdot\nabla(e^{-m/\mu}\varphi_\nu), \tag{26}$$

which can be rewritten as

$$
\begin{aligned}
&\textstyle\int e^{m/\mu}|\nabla(e^{-m/\mu}\varphi_\nu)|^2 + \int e^{m/\mu}\frac{|\nabla(e^{-m/\mu}\tilde{u})|^2}{(e^{-m/\mu}\tilde{u})^2}(e^{-m/\mu}\varphi_\nu)^2 \\
&\quad = 2\textstyle\int e^{m/\mu}\frac{\nabla(e^{-m/\mu}\tilde{u})\cdot\nabla(e^{-m/\mu}\varphi_\nu)}{e^{-m/\mu}\tilde{u}}e^{-m/\mu}\varphi_\nu - \frac{1}{\mu}\int\nabla\tilde{u}\cdot\nabla(e^{-m/\mu}\varphi_\nu).
\end{aligned}
\tag{27}
$$

By Hölder's inequality, this yields

$$
\begin{aligned}
&\frac{1}{3}\int e^{m/\mu}|\nabla(e^{-m/\mu}\varphi_\nu)|^2 \\
&\le 2\int e^{m/\mu}\frac{|\nabla(e^{-m/\mu}\tilde{u})|^2}{(e^{-m/\mu}\tilde{u})^2}(e^{-m/\mu}\varphi_\nu)^2 + \frac{3}{4\mu^2}\int e^{-m/\mu}|\nabla\tilde{u}|^2 \\
&\le C\left(\int|\nabla\tilde{u}|^2(e^{-m/\mu}\varphi_\nu)^2 + \int(e^{-m/\mu}\varphi_\nu)^2 + 1\right) \\
&\le C\int\left[|\nabla m|^2 + |\nabla\tilde{u} - \nabla m|^2 + 1\right](e^{-m/\mu}\varphi_\nu)^2 + C \\
&\le C\left(\int(e^{-m/\mu}\varphi_\nu)^2 + \|\tilde{u} - m\|_{L^\infty(\Omega)}\|e^{-m/\mu}\varphi_\nu\|^2_{H^1(\Omega)} + 1\right).
\end{aligned}
$$

The second and last inequalities follow from Lemmas 3.2 and 3.3 respectively. Hence for each $\delta > 0$, there is some constant C independent of α small and $\mu \ge \delta$ such that

$$
\int|\nabla\varphi_\nu|^2 \le C\left(\int(\varphi_\nu)^2 + 1\right). \tag{28}
$$

Next, we show that $\|\varphi_\nu\|_{H^1(\Omega)}$ is bounded uniformly as $\alpha \to 0$. By applying the Poincaré's inequality and (26),

$$
\begin{aligned}
\frac{\lambda_2}{\alpha}\int e^{-m/\mu}(\varphi_\nu)^2 &\le \mu\int e^{m/\mu}|\nabla(e^{-m/\mu}\varphi_\nu)|^2 - \mu\int e^{m/\mu}\nabla(e^{-m/\mu}\tilde{u})\cdot\nabla\left(\frac{e^{-m/\mu}(\varphi_\nu)^2}{\tilde{u}}\right) \\
&= -\int\nabla\tilde{u}\cdot\nabla(e^{-m/\mu}\varphi_\nu) \\
&\le C(\|\varphi_\nu\|^2_{H^1(\Omega)} + 1).
\end{aligned}
$$

By Proposition 4.2, $\frac{\lambda_2}{\alpha} \to \sigma_2$ as $\alpha \to 0$. Observe that $\sigma_1 = 0$ and is simple, one can deduce that $\sigma_2 > 0$ (Remark 4.1). So combining with (28), we deduce that

$$
\|\varphi_\nu\|^2_{H^1(\Omega)} \le C(\|\varphi_\nu\|_{H^1(\Omega)} + 1).
$$

Hence $\|\varphi_\nu\|_{H^1(\Omega)}$ is bounded independent of α small and φ_ν converges weakly in $H^1(\Omega)$ to some $\varphi_0 \in H^1(\Omega)$ satisfying $\int e^{m/\mu^*}\varphi_0 m = 0$. Passing to the limit using the weak formulation of (22), we see that $\varphi_0 = \varphi'$ by uniqueness. This proves the lemma. □

The following result is a direct consequence of Lemmas 4.1 and 4.3.

Corollary 4.4. *Suppose that $\mu = \mu(\alpha)$ is an evolutionarily singular strategy and $\mu \to \mu^*$ as $\alpha \to 0$. Then*

$$
\lim_{\alpha\to 0}\frac{\lambda_{\nu\nu}(\mu,\mu;\alpha)}{\alpha} = \frac{2}{\int e^{-m/\mu^*}m^2}\int\nabla\varphi'\cdot\nabla(e^{-m/\mu^*}m), \tag{29}
$$

where φ' is the unique solution of (25).

4.3. **Limit problem for $\lambda_{\nu\nu}$.** In this subsection we study, for sufficiently small α, the sign of $\lambda_{\nu\nu}(\hat{\mu},\hat{\mu};\alpha)$ where $\hat{\mu}$ is the unique evolutionarily singular strategy determined in Theorem 1. By Corollary 4.4, it suffices to study the sign of $\int \nabla\varphi' \cdot \nabla(e^{-m/\mu_0}m)$, where φ' is the unique solution of (25) with $\mu^* = \mu_0$, and μ_0 is a positive root of $g_0(\mu)$. A sufficient condition for the uniqueness of μ_0 is given in Proposition 3.8. The main result of this subsection is

Proposition 4.5. *Suppose that Ω is convex with diameter d. If m is non-constant and $d\|\nabla \ln m\|_{L^\infty(\Omega)} \le \beta_0$, then*

$$\lim_{\alpha\to 0}\frac{\lambda_{\nu\nu}(\hat{\mu},\hat{\mu};\alpha)}{\alpha} = \frac{2}{\int e^{m/\mu_0}m^2}\int \nabla\varphi'\cdot\nabla(e^{-m/\mu_0}m) > 0,$$

where φ' is the unique solution to (25) (with $\mu^* = \mu_0$), $\beta_0 \approx 0.615$ is the unique positive root of $t \mapsto \frac{t^2}{\pi^2} - e^{-4t}\left(\frac{2t}{e^t-1} - 1\right)$, and μ_0 is given in Proposition 3.8.

That β_0 is well-defined follows from the following lemma.

Lemma 4.6. *Let $f_4(t) = \left(\frac{t}{\pi}\right)^2 - e^{-4t}\left(\frac{2t}{e^t-1} - 1\right)$, then f_4 has a unique root $\beta_0 \approx 0.615$ in $(0,1)$. In fact, we have*

$$f_4(t) = \begin{cases} -, & t\in(0,\beta_0);\\ 0, & t=\beta_0;\\ +, & t\in(\beta_0,\infty).\end{cases}$$

Proof of Lemma 4.6. One can show that (i) $\lim_{t\searrow 0} f_4(t) = -1$, (ii) f_4 is strictly increasing in $[0,0.8]$ and that (iii) $f_4(t) > 0$ for all $t > 0.8$.

$$\begin{aligned}
f_4(t) &= \left(\frac{t}{\pi}\right)^2 - \frac{e^{-4t}}{1-e^{-t}}(2te^{-t} - 1 + e^{-t})\\
\frac{d}{dt}f_4(t) &= \frac{2t}{\pi^2} + \frac{e^{-4t}(4-3e^{-t})}{(1-e^{-t})^2}(2te^{-t} - 1 + e^{-t}) + \frac{e^{-4t}}{1-e^{-t}}e^{-t}(2t-1)\\
&= \frac{2t}{\pi^2} + \frac{e^{-4t}}{1-e^{-t}}\left[(4-3e^{-t})\left(2\frac{t}{1-e^{-t}}e^{-t} - 1\right) + e^{-t}(2t-1)\right]\\
&> \frac{2t}{\pi^2} + \frac{e^{-4t}}{1-e^{-t}}\left[(4-3e^{-t})\left(2e^{-t}-1\right) + e^{-t}(2t-1)\right] \qquad \left(\frac{t}{1-e^{-t}} > 1\right)\\
&= \frac{2t}{\pi^2} + \frac{-2e^{-6t}}{1-e^{-t}}\left[3 - (5+t)e^t + 2e^{2t}\right].
\end{aligned}$$

Since the first term is positive and $t > t_0 := 0$, f_4 is strictly increasing if $t \in (t_0, t_1]$, where $t_1 := \ln\frac{(5+t_0)+\sqrt{(5+t_0)^2-24}}{4}$. Therefore we may assume $t > t_1$. Similarly, f_4 is strictly increasing if $t \in (t_1, t_2]$, where $t_2 := \ln\frac{(5+t_1)+\sqrt{(5+t_1)^2-24}}{4}$. Thus defining an increasing sequence $\{t_i\}_{t=0}^{\infty}$ by induction

$$t_{i+1} = \ln\frac{(5+t_i)+\sqrt{(5+t_i)^2-24}}{4},$$

then we see that f_4 is strictly increasing for $t \in (0, \lim_{i\to\infty} t_i)$, where $\lim_{i\to\infty} t_i \approx 0.8004 > 0.8$. Also, for all $t \ge 0.8$ (by $\frac{t}{e^t-1} < 1$),

$$\left(\frac{t}{\pi}\right)^2 - e^{-4t}\left(\frac{2t}{e^t-1} - 1\right) > \left(\frac{t}{\pi}\right)^2 - e^{-4t} > 0.$$

This completes the proof. $\square$

Let w denote the unique solution to

$$\begin{cases} \nabla\cdot(\mu\nabla w - w\nabla m) - \frac{\nabla\cdot[(\mu-m)\nabla m]}{m} w = -\Delta m & \text{in } \Omega, \\ \mu\frac{\partial w}{\partial n} - \frac{\mu}{m} w \frac{\partial m}{\partial n} = -\frac{\partial m}{\partial n} \quad \text{on } \partial\Omega, & \int m e^{-m/\mu} w = 0. \end{cases} \tag{30}$$

It is clear that Proposition 4.5 follows from the following result:

Proposition 4.7. *Suppose that Ω is convex with diameter d. If m is non-constant, $\mu > 0$ satisfies $g_0(\mu) = 0$ and $d\|\nabla \ln m\|_{L^\infty(\Omega)} \leq \beta_0$, then*

$$\int \nabla w \cdot \nabla (e^{-m/\mu} m) > 0. \tag{31}$$

Proof. First, consider the transformation $w = m\left(z - \frac{\ln m}{\mu}\right)$. After some tedious but direct calculations, z satisfies

$$\begin{cases} \mu \nabla\cdot(m^2 e^{-m/\mu}\nabla z) = \nabla m\cdot\nabla(m e^{-m/\mu}) & \text{in } \Omega, \\ \frac{\partial z}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{32}$$

Integrating over Ω, we have

$$0 = \int \nabla\cdot(m^2 e^{-m/\mu}\nabla z) = \int \nabla m\cdot\nabla(m e^{-m/\mu}) = \int e^{-m/\mu}|\nabla m|^2\left(1 - \frac{m}{\mu}\right). \tag{33}$$

Multiplying by z and integrate by parts, we have

$$-\mu\int m^2 e^{-m/\mu}|\nabla z|^2 = \int z\nabla m\cdot\nabla(m e^{-m/\mu}) = \int z e^{-m/\mu}|\nabla m|^2\left(1 - \frac{m}{\mu}\right). \tag{34}$$

Lemma 4.8. $\displaystyle\int \nabla w\cdot\nabla(e^{-m/\mu} m) = \frac{1}{\mu}\int\left(\frac{2\ln\frac{m}{\mu}}{\frac{m}{\mu} - 1} - 1\right) e^{-m/\mu}|\nabla m|^2\left(1 - \frac{m}{\mu}\right)^2 - \mu\int m^2 e^{-m/\mu}|\nabla z|^2.$

Proof of Lemma 4.8.

$$\begin{aligned}
&\int \nabla w\cdot\nabla(m e^{-m/\mu}) \\
&= \int \nabla\left[m\left(z - \frac{\ln m}{\mu}\right)\right]\cdot\nabla(m e^{-m/\mu}) \\
&= \int \nabla(zm)\cdot\nabla(m e^{-m/\mu}) - \int \frac{\ln m}{\mu}\nabla m\cdot\nabla(m e^{-m/\mu}) \\
&= \int m e^{-m/\mu}\left(1 - \frac{m}{\mu}\right)\nabla m\cdot\nabla z + \int\left(z - \frac{\ln m}{\mu}\right)\nabla m\cdot\nabla(m e^{-m/\mu}) \\
&= \int m^2 e^{-m/\mu}\nabla\left(\ln m - \frac{m}{\mu}\right)\cdot\nabla z + \int\left(z - \frac{\ln m}{\mu}\right)\nabla m\cdot\nabla(m e^{-m/\mu}) \\
&= -\int\left(\ln m - \frac{m}{\mu}\right)\nabla\cdot(m^2 e^{-m/\mu}\nabla z) + \int\left(z - \frac{\ln m}{\mu}\right)\nabla m\cdot\nabla(m e^{-m/\mu}) \\
&= \int\left[\frac{1}{\mu}\left(-2\ln m + \frac{m}{\mu}\right) + z\right]\nabla m\cdot\nabla(m e^{-m/\mu})
\end{aligned}$$

where we used (33) in the second equality, integrated by parts in the second last equality and used (32) in the last line. By (33) and (34),

$$\begin{aligned}\int \nabla w\cdot\nabla(me^{-m/\mu}) &= \int \frac{1}{\mu}\left(-2\ln\frac{m}{\mu}+\frac{m}{\mu}-1\right)\nabla m\cdot\nabla(me^{-m/\mu}) + \int z\nabla m\cdot\nabla(me^{-m/\mu})\\ &= \frac{1}{\mu}\int\left(-2\ln\frac{m}{\mu}+\frac{m}{\mu}-1\right)e^{-m/\mu}|\nabla m|^2\left(1-\frac{m}{\mu}\right) - \mu\int m^2e^{-m/\mu}|\nabla z|^2\\ &= \frac{1}{\mu}\int\left(\frac{2\ln\frac{m}{\mu}}{\frac{m}{\mu}-1}-1\right)e^{-m/\mu}|\nabla m|^2\left(1-\frac{m}{\mu}\right)^2 - \mu\int m^2e^{-m/\mu}|\nabla z|^2.\end{aligned}$$

This completes the proof of Lemma 4.8. □

By Lemma 4.8, (31) is equivalent to

$$\mu\int m^2e^{-m/\mu}|\nabla z|^2 < \frac{1}{\mu}\int\left(\frac{2\ln\frac{m}{\mu}}{\frac{m}{\mu}-1}-1\right)e^{-m/\mu}|\nabla m|^2\left(1-\frac{m}{\mu}\right)^2. \tag{35}$$

In particular we may assume without loss of generality (by replacing z by $z+C$) that z satisfies (32) and

$$\int e^{-m/\mu}|\nabla m|^2 z = 0. \tag{36}$$

Set $L=\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m}$. Since $L^{-1}<\frac{m}{\mu}<L$ (by (16)) and that $f(t)=\frac{\ln t}{(t-1)}$ is strictly decreasing for $t>0$, it is enough to show the following:

$$\mu\int m^2e^{-m/\mu}|\nabla z|^2 \le \frac{1}{\mu}\int\left(\frac{2\ln L}{L-1}-1\right)e^{-m/\mu}|\nabla m|^2\left(1-\frac{m}{\mu}\right)^2. \tag{37}$$

To this end, we prove the following Poincaré-type inequality.

Lemma 4.9.

$$\mu\int m^2e^{-m/\mu}|\nabla z|^2 \le \frac{1}{\mu\hat\gamma_2}\int e^{-m/\mu}|\nabla m|^2\left(1-\frac{m}{\mu}\right)^2,$$

where $\hat\gamma_2$ is the second (or first positive) eigenvalue of

$$\begin{cases}\nabla\cdot\left[\left(\frac{m}{\mu}\right)^2 e^{-m/\mu}\nabla\phi\right]+\hat\gamma e^{-m/\mu}\left|\nabla\frac{m}{\mu}\right|^2\phi=0 & \text{in } \Omega,\\ \frac{\partial\phi}{\partial n}=0 & \text{on } \partial\Omega.\end{cases} \tag{38}$$

Proof of Lemma 4.9. Let $(\hat\gamma_k,\phi_k)$ be the eigenpairs of (38), canceling $\frac{1}{\mu^2}$ on both sides, we have

$$\begin{cases}\nabla\cdot(m^2e^{-m/\mu}\nabla\phi)+\hat\gamma e^{-m/\mu}|\nabla m|^2\phi=0 & \text{in } \Omega,\\ \frac{\partial\phi}{\partial n}=0 & \text{on } \partial\Omega.\end{cases} \tag{39}$$

Observe that $\gamma_1 = 0$ and $\phi_1 = 1$. Now set $z = \sum_{k=2}^{\infty} a_k \phi_k$ ($a_1 = 0$ by (36)) and $1 - \frac{m}{\mu} = \sum_{k=1}^{\infty} b_k \phi_k$, then one can deduce that $a_k = -\frac{b_k}{\mu \hat{\gamma}_k}$ and $b_1 = 0$. Now,

$$
\begin{aligned}
\mu \int m^2 e^{-m/\mu} |\nabla z|^2 &= -\int z \left[\mu \nabla \cdot (m^2 e^{-m/\mu} \nabla z) \right] \\
&= -\int z |\nabla m|^2 e^{-m/\mu} \left(1 - \frac{m}{\mu}\right) \\
&= -\int \left(\sum_{k=2}^{\infty} \frac{-b_k}{\mu \hat{\gamma}_k} \phi_k \right) |\nabla m|^2 e^{-m/\mu} \left(\sum_{k=2}^{\infty} b_k \phi_k \right) \\
&= \frac{1}{\mu} \int |\nabla m|^2 e^{-m/\mu} \sum_{k=2}^{\infty} \frac{b_k^2}{\hat{\gamma}_k} \phi_k^2 \\
&\leq \frac{1}{\mu \hat{\gamma}_2} \int |\nabla m|^2 e^{-m/\mu} \left(1 - \frac{m}{\mu}\right)^2.
\end{aligned}
$$

And the lemma follows. □

Next, we derive a lower estimate of $\hat{\gamma}_2$ in terms of L. Recall that $L = \frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m}$ and set $s = \|\nabla \ln m\|_{L^\infty(\Omega)}$, $d = \operatorname{diam}(\Omega)$. Then by mean value theorem, we have

$$\ln L = \ln \frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m} \leq d \|\nabla \ln m\|_{L^\infty(\Omega)}.$$

Suppose $ds \leq \beta_0$, then

$$L \leq e^{ds} \leq e^{\beta_0} < \frac{13 + \sqrt{105}}{8}. \tag{40}$$

The following claim follows from $0 < ds \leq \beta_0$ and Lemma 4.6.

Claim 4.10. $\left(\frac{ds}{\pi}\right)^2 \leq e^{-4ds} \left[\frac{2ds}{e^{ds} - 1} - 1 \right]$.

Next, we show the following claim.

Claim 4.11. *Suppose that Ω is convex with diameter d, then*

$$\left(\frac{ds}{\pi}\right)^2 \leq L^{-4} \left[\frac{2 \ln L}{L - 1} - 1 \right].$$

By (40), Claim 4.11 is proved if we can show that

$$f_3(t) = t^{-4} \left(\frac{2 \ln t}{t - 1} - 1 \right) = \frac{t^{-4}}{t - 1} (2 \ln t - t + 1)$$

is strictly decreasing in $t \in \left[1, \frac{13+\sqrt{105}}{8}\right]$. Now,

$$\frac{d}{dt} f_3(t) = \frac{t^{-5}(4 - 5t)}{(t - 1)^2} (2 \ln t - t + 1) + \frac{t^{-5}}{(t - 1)^2} (2 - t)(t - 1).$$

For $t \geq 1$, $\ln t = -\ln(t^{-1}) > -(t^{-1}-1) + \frac{(t^{-1}-1)^2}{2}$. Hence,

$$\begin{aligned}
\frac{d}{dt} f_3(t) &< \frac{t^{-5}}{(t-1)^2}\left\{(4-5t)\left[-2(t^{-1}-1)+(t^{-1}-1)^2-t+1\right]+(2-t)(t-1)\right\} \\
&= \frac{t^{-7}}{(t-1)^2}\left\{(4-5t)\left[-2t(1-t)+(1-t)^2-t^2(t-1)\right]+t^2(2-t)(t-1)\right\} \\
&= \frac{t^{-7}}{t-1}\left\{(4-5t)(-t^2+3t-1)+2t^2-t^3\right\} \\
&= t^{-7}(4t^2-13t+4) = 4t^{-7}\left(t-\frac{13-\sqrt{105}}{8}\right)\left(t-\frac{13+\sqrt{105}}{8}\right).
\end{aligned}$$

Therefore $f_3(t)$ is strictly decreasing in $\left[1, \frac{13+\sqrt{105}}{8}\right]$. This proves Claim 4.11.

Recalling that $\hat{\gamma}_2$ is the second (or first positive) eigenvalue of (38), we claim the following:

Claim 4.12. $\hat{\gamma}_2 > \left[\dfrac{2\ln L}{L-1} - 1\right]^{-1}$.

We prove Claim 4.12. Let $f_2(t) := t^2 e^{-t}$. If $L \in [1, 3+2\sqrt{2}]$, then $f(t) \geq f(L^{-1})$ for all $t \in [L^{-1}, L]$. Hence by $L^{-1} < \frac{m}{\mu} < L$ and eigenvalue comparison,

$$\begin{aligned}
\hat{\gamma}_2 &> \mu_2^N(\Omega)\left(\max_{\bar{\Omega}} e^{-m/\mu}\left|\frac{\nabla m}{\mu}\right|^2\right)^{-1}\left(\min_{\bar{\Omega}} f_2\left(\frac{m}{\mu}\right)\right) \\
&\geq \mu_2^N(\Omega)\left(\max_{\bar{\Omega}} e^{-m/\mu}\left|\frac{\nabla m}{m}\right|^2\left(\frac{m}{\mu}\right)^2\right)^{-1} f_2(L^{-1}) \\
&\geq \mu_2^N(\Omega)\left(e^{1/L}\|\nabla \ln m\|^2_{L^\infty(\Omega)} L^2\right)^{-1} f_2(L^{-1}) \\
&= \mu_2^N(\Omega)\|\nabla \ln m\|^{-2}_{L^\infty(\Omega)} L^{-4} \\
&\geq \left(\frac{\pi}{d}\right)^2 s^{-2} L^{-4} \\
&\geq \left[\frac{2\ln L}{L-1} - 1\right]^{-1}
\end{aligned}$$

where the last inequality follows from Claim 4.11, whereas $\mu_2^N(\Omega)$ is the second Neumann eigenvalue of the Laplacian of Ω and the second last inequality follows from the following optimal estimate of $\mu_2^N(\Omega)$ for convex domains due to Payne and Weinberger.

Theorem 6 ([33]). *Suppose that Ω is a convex domain in $\mathbb{R}^N$ with diameter d, then*

$$\mu_2^N(\Omega) \geq \frac{\pi^2}{d^2}.$$

This proves Claim 4.12. Finally, by Lemma 4.9 and Claim 4.12, we have

$$\mu \int m^2 e^{-m/\mu} |\nabla z|^2 < \frac{1}{\mu} \int \left(\frac{2\ln L}{L-1} - 1\right) e^{-m/\mu} |\nabla m|^2 \left(1 - \frac{m}{\mu}\right)^2.$$

This proves (37) and hence Proposition 4.7. □

4.4. **ESS: Theorem** 4.

Proof of Theorem 4. By the assumptions,

$$\ln\left(\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m}\right) \le d\|\nabla \ln m\|_{L^\infty(\Omega)} \le \beta_0 < \ln(3+2\sqrt{2}).$$

Hence (by Theorem 1), for all μ sufficiently small, there exists a unique evolutionarily singular strategy, denoted by $\hat\mu = \hat\mu(\alpha) \in (\min_{\bar\Omega} m, \max_{\bar\Omega} m)$. Moreover, $\hat\mu \to \mu_0$ as $\mu \to 0$, where μ_0 is the unique positive root of $g_0(\mu)$ guaranteed by Proposition 3.8. Then, by Corollary 4.4 and Proposition 4.5, we have

$$\lim_{\alpha\to 0} \frac{\lambda_{\nu\nu}(\hat\mu,\hat\mu;\alpha)}{\alpha} = \frac{2\int \nabla\varphi' \cdot \nabla(me^{-m/\mu_0})}{\int e^{-m/\mu_0} m^2} > 0. \tag{41}$$

As $\lambda(\hat\mu,\hat\mu;\alpha) = \lambda_\nu(\hat\mu,\hat\mu;\alpha) = 0$ for all α small, there exists $\delta_1 = \delta_1(\alpha) > 0$ such that $\lambda(\hat\mu,\nu;\alpha) > 0$ if $\nu \in (\hat\mu - \delta_1, \hat\mu + \delta_1) \setminus \{\hat\mu\}$. Thus, the strategy $\mu = \hat\mu(\alpha)$ is a local ESS. □

The following result will be needed in the next section.

Lemma 4.13. *Let w denote the unique solution of* (30). *If $g_0'(\mu) < 0$, then $\int \nabla w \cdot \nabla(e^{-m/\mu} m) < 0$.*

Proof. Suppose

$$0 > g'(\mu) = \frac{1}{\mu^2}\int e^{-m/\mu}|\nabla m|^2 m\left(2 - \frac{m}{\mu}\right). \tag{42}$$

Define as before z by $w = m\left(z - \frac{\ln m}{\mu}\right)$ such that z satisfies (32). Then z can be characterized as a global minimizer of the functional

$$J(\tilde z) = \frac{\mu}{2}\int e^{-m/\mu} m^2 |\nabla \tilde z|^2 + \int \tilde z e^{-m/\mu}|\nabla m|^2\left(1 - \frac{m}{\mu}\right).$$

By (34), we have $J(z) = -\frac{\mu}{2}\int e^{-m/\mu} m^2|\nabla z|^2$. Hence,

$$\begin{aligned} J(z) &\le J\left(\frac{\ln m}{\mu}\right) \\ -\frac{\mu}{2}\int e^{-m/\mu} m^2 |\nabla z|^2 &\le \frac{1}{2\mu}\int e^{-m/\mu}|\nabla m|^2 + \int e^{-m/\mu}\frac{\ln m}{\mu}|\nabla m|^2\left(1 - \frac{m}{\mu}\right) \\ &= \frac{1}{2\mu}\int e^{-m/\mu}|\nabla m|^2\left[1 + 2\ln m\left(1 - \frac{m}{\mu}\right)\right] \\ &\overset{(33)}{=} \frac{1}{2\mu}\int e^{-m/\mu}|\nabla m|^2\left[1 + 2\ln m\left(1 - \frac{m}{\mu}\right) - 2\ln\mu\left(1 - \frac{m}{\mu}\right)\right] \\ &\overset{(42)}{<} \frac{1}{2\mu}\int e^{-m/\mu}|\nabla m|^2\left[\left(1 - \frac{m}{\mu}\right)^2 + 2\ln\frac{m}{\mu}\left(1 - \frac{m}{\mu}\right)\right] \\ &= -\frac{1}{2\mu}\int\left[\frac{2\ln\frac{m}{\mu}}{\frac{m}{\mu} - 1} - 1\right] e^{-m/\mu}|\nabla m|^2\left(\frac{m}{\mu} - 1\right)^2. \end{aligned}$$

By Lemma 4.8, this is equivalent to $\int \nabla w \cdot \nabla(me^{-m/\mu}) < 0$. □

5. Counterexample for $\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m} > 3 + 2\sqrt{2}$

To study the multiplicity of evolutionarily singular strategies when α is small, by (16) it suffices to consider the number of roots of $g_0(\mu)$ for $\mu \in (\min_{\bar\Omega} m, \max_{\bar\Omega} m)$. Equivalently, let $\eta = \mu^{-1}$, it suffices to consider the number of roots of

$$g_1(\eta) = \int e^{-\eta m}|\nabla m|^2(1-\eta m) \quad \text{ for } \eta \in \left(\frac{1}{\max_{\bar\Omega} m}, \frac{1}{\min_{\bar\Omega} m}\right). \tag{43}$$

Suppose that $\Omega = (0,1)$ and m is non-decreasing (i.e. $m' \geq 0$), then by making the substitution $s = \eta m(x)$,

$$\eta^2 g_1(\eta) = \int_0^1 \eta|m'|^2(\eta m)(1-\eta m)e^{-\eta m}dx = \int_{\eta m(0)}^{\eta m(1)} m'(x)h(s)ds, \tag{44}$$

where $h(s) = e^{-s}(1-s)$.

Proposition 5.1. *If $\Omega = (0,1)$ and $m(x) = a + (b-a)x$ for some $0 < a < b$, then $g_1(\eta)$ has exactly one root in $[0,\infty)$.*

Proof. By (16), it suffices to consider $\eta \in \left[b^{-1}, a^{-1}\right]$. Now $m'(x) = b - a$. By (44),

$$\begin{aligned}\frac{d}{d\eta}\left(\frac{\eta^2}{b-a}g_1(\eta)\right) &= \frac{d}{d\eta}\left(\int_{\eta a}^{\eta b} h(s)ds\right)\\ &= h(\eta b)b - h(\eta a)a\\ &= \left[b(1-\eta b)e^{-\eta b}\right] + \left[-a(1-\eta a)e^{-\eta a}\right]\\ &< 0\end{aligned}$$

for all $\eta \in [b^{-1}, a^{-1}]$, as both terms on the last line are negative. Hence $\eta^2 g_1(\eta)$ is strictly decreasing in $[b^{-1}, a^{-1}]$ and has exactly one root. □

Proposition 5.2. *Let $\Omega = (0,1)$, then for each $L > 3+2\sqrt{2}$, there exists $m \in C^2([0,1])$ satisfying $m, m' > 0$ such that $g_0(\mu)$ has at least three roots in $(\min_{\bar\Omega} m, \max_{\bar\Omega} m)$.*

Proof. Consider again $g_1(\eta) = g_0(1/\eta)$ defined in (43). Fix $L > 3 + 2\sqrt{2}$. Set $\min_{\bar\Omega} m = a = 1$ and $\max_{\bar\Omega} m = b = L$. Choose $\eta_* \in (1/L, 1)$ such that $\eta_* a < 2 - \sqrt{2}$ and $\eta_* b > 2 + \sqrt{2}$. Such η_* exists as $L > 3 + 2\sqrt{2}$. Note that

$$sh'(s) + 2h(s) > 0 \quad \text{ if and only if } \quad s < 2-\sqrt{2} \text{ or } s > 2+\sqrt{2}. \tag{45}$$

Hence, by our choice of η_*, $(\eta_* a)h'(\eta_* a) + 2h(\eta_* a) > 0$ and $(\eta_* b)h'(\eta_* b) + 2h(\eta_* b) > 0$. Furthermore, as $\eta_* a < 1 < \eta_* b$, we also have

$$h(\eta_* a) > 0 > h(\eta_* b). \tag{46}$$

Let $m(x)$ be the piecewise linear function given by $m(0) = a$, $m(1) = b$, and

$$m'(x) = \begin{cases} L_1 & x \in \left[0, \frac{\epsilon}{L_1}\right] \\ L_2 & x \in \left[1 - \frac{\epsilon}{L_2}, 1\right] \\ L_3 := \frac{(b-\epsilon)-(a+\epsilon)}{1-\frac{\epsilon}{L_1}-\frac{\epsilon}{L_2}} & x \in \left(\frac{\epsilon}{L_1}, 1 - \frac{\epsilon}{L_2}\right), \end{cases}$$

where $\epsilon > 0$ is to be chosen small, and L_1, L_2 are to be chosen positive and large. Note that $L_3 \to b - a$ remains uniformly bounded for small ϵ and $L_1, L_2 \geq 1$. By the choices of m and η_*, we see that η_* satisfies $\eta_* \in \left(\frac{1}{\max_{\bar\Omega} m}, \frac{1}{\min_{\bar\Omega} m}\right)$. Then

$$\begin{aligned}\eta^2 g_1(\eta) &= L_1 \int_{\eta a}^{\eta(a+\epsilon)} h(s)\,ds + L_2 \int_{\eta(b-\epsilon)}^{\eta b} h(s)\,ds + L_3 \int_{\eta(a+\epsilon)}^{\eta(b-\epsilon)} h(s)\,ds \\ &:= L_1 I_1 + L_2 I_2 + L_3 I_3.\end{aligned}$$

Both $|I_3|$ and $|\frac{d}{d\eta} I_3|$ are uniformly bounded for $\epsilon > 0$ small:

$$\begin{aligned}I_3 &= H(\eta(b-\epsilon)) - H(\eta(a+\epsilon)), \quad H(s) = e^{-s}s, \\ \frac{d}{d\eta} I_3 &= h(\eta(b-\epsilon))(b-\epsilon) - h(\eta(a+\epsilon))(a+\epsilon).\end{aligned}$$

It is easy to see that for sufficiently small ϵ,

$$I_1 = I_1(\eta_*, \epsilon) \approx \epsilon h(\eta_* a) > 0 \quad \text{and } I_2 = I_2(\eta_*, \epsilon) \approx \epsilon h(\eta_* b) < 0.$$

Therefore, for each small but fixed ϵ, there exists L_1, L_2 arbitrarily large such that

$$\frac{L_1}{L_2} \approx \frac{-h(\eta_* b)}{h(\eta_* a)} \quad \text{and} \quad g_1(\eta_*) = 0. \tag{47}$$

It remains to fix sufficiently small $\epsilon > 0$ such that for L_1, L_2 arbitrarily large, we have

$$L_1 \frac{d}{d\eta} I_1\Big|_{\eta=\eta_*} + L_2 \frac{d}{d\eta} I_2\Big|_{\eta=\eta_*} \to +\infty. \tag{48}$$

Since then $g_1\left(\frac{1}{\max_{\bar\Omega} m}\right) > 0$, $g_1\left(\frac{1}{\min_{\bar\Omega} m}\right) < 0$ and $g_1'(\eta_*) > 0$ and therefore g_1 has at least 3 roots in $\left(\frac{1}{\max_{\bar\Omega} m}, \frac{1}{\min_{\bar\Omega} m}\right)$.

Firstly we compute $\frac{d}{d\eta} I_1$.

$$\begin{aligned}\frac{d}{d\eta} I_1 &= h(\eta(a+\epsilon))(a+\epsilon) - h(\eta(a))a \\ &= a[h(\eta(a+\epsilon)) - h(\eta a)] + \epsilon h(\eta(a+\epsilon)) \\ &= \epsilon[\eta a h'(\theta_1) + h(\eta(a+\epsilon))]\end{aligned}$$

where $\theta_1 \in (\eta a, \eta(a+\epsilon))$, and $\lim_{\epsilon\to 0} [\eta a h'(\theta_1) + h(\eta(a+\epsilon))] = \eta a h'(\eta a) + h(\eta a)$.

Similarly,

$$\frac{d}{d\eta} I_2 = \epsilon[\eta b h'(\theta_2) + h(\eta(b-\epsilon))],$$

where $\theta_2 \in (\eta(b-\epsilon), \eta b)$ and $\lim_{\epsilon\to 0} [\eta b h'(\theta_2) + h(\eta(b-\epsilon))] = \eta b h'(\eta b) + h(\eta b)$. In view of (47), a sufficient condition for (48) is

$$-h(\eta^* b)[(\eta^* a)h'(\eta^* a) + h(\eta^* a)] + h(\eta^* a)[(\eta^* b)h'(\eta^* b) + h(\eta^* b)] > 0$$

which is equivalent to

$$-h(\eta^* b)[(\eta^* a)h'(\eta^* a) + 2h(\eta^* a)] + h(\eta^* a)[(\eta^* b)h'(\eta^* b) + 2h(\eta^* b)] > 0, \tag{49}$$

which holds by (45) and (46). We have proved the proposition.

In conclusion, we have found a piecewise C^1 function m and some $\eta_* > 0$ such that the statement of the proposition holds. Although the m constructed is only piecewise C^1, one can approximate it by $C^2(\bar\Omega)$ functions $\tilde m$ such that $\frac{\max_{\bar\Omega} \tilde m}{\min_{\bar\Omega} \tilde m} = \frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m}$ and $\tilde m \to m$ in $W^{1,\infty}(\Omega)$. □

Remark 5.1. For the singular strategy $\mu = \mu(\alpha)$ such that $\mu \to \mu^* := 1/\eta^*$, by Lemma 4.1 we have

$$\left(\lim_{\alpha \to 0} \frac{\lambda_{\nu\nu}(\mu, \mu; \alpha)}{\alpha} \right) \int e^{-m/\mu^*} m^2 = 2 \int \nabla \varphi' \cdot \nabla (m e^{m/\mu^*}).$$

Since $g_0'(\mu^*) = -\frac{1}{(\mu^*)^2} g_1'(\eta^*) < 0$, the last term above is negative by Lemma 4.13. Hence $\lambda_{\nu\nu} < 0$ for α sufficiently small. That is, the evolutionarily singular strategy $\mu = \mu(\alpha) \to \mu^*$ is not an ESS for all α sufficiently small.

6. **Convergence Stable Strategy**

This section is devoted to the proof of Theorem 5. In fact, we will prove a stronger result.

Theorem 7. *For each $\delta > 0$, there exists $\alpha_1 > 0$ such that for all $\alpha \in (0, \alpha_1)$, if $\hat{\mu}$ is an evolutionarily singular strategy satisfying $\hat{\mu} \in [\delta, \delta^{-1}]$ and*

$$\frac{d}{dt} \lambda_\nu(t, t; \alpha) \bigg|_{t=\hat{\mu}} = (\lambda_{\mu\nu} + \lambda_{\nu\nu})(\hat{\mu}, \hat{\mu}; \alpha) > 0, \tag{50}$$

then $\hat{\mu}$ is a local CSS.

Corollary 6.1. *For all α sufficiently small, the unique evolutionarily singular strategy $\hat{\mu}$ from Theorem* 1 *is a local CSS. In particular, the local ESS from Theorem* 4 *is also a local CSS.*

Proof. By Theorem 1, $\hat{\mu} = \hat{\mu}(\alpha) \to \mu_0$, the latter being the unique positive root of $g_0(\mu)$. By Lemma 3.1, Corollary 3.7 and Proposition 3.8, as $\alpha \to 0$ we have

$$\frac{d}{dt} \lambda_\nu(t, t; \alpha) \bigg|_{t=\hat{\mu}} \to g_0'(\mu_0) > 0.$$

Hence the desired result follows from Theorem 7. □

For the sake of brevity we abbreviate the invasion exponent as $\lambda(\mu, \nu)$; i.e., omitting its dependence on α. Firstly,

$$\lambda(\mu, \mu) = 0 \quad \text{for all } \mu. \tag{51}$$

Secondly, for any evolutionarily singular strategies $\mu = \hat{\mu}$

$$\lambda_\mu(\hat{\mu}, \hat{\mu}) = -\lambda_\nu(\hat{\mu}, \hat{\mu}) = 0 \tag{52}$$

and hence any evolutionarily singular strategy $(\hat{\mu}, \hat{\mu})$ is a critical point of λ on the μ-ν plane. Therefore, the sign of $\lambda(\mu, \nu)$ in a neighborhood of $(\hat{\mu}, \hat{\mu})$ is determined by the Hessian of λ, which satisfies (by (51) again)

$$\lambda_{\mu\mu}(\hat{\mu}, \hat{\mu}) + 2\lambda_{\mu\nu}(\hat{\mu}, \hat{\mu}) + \lambda_{\nu\nu}(\hat{\mu}, \hat{\mu}) = 0. \tag{53}$$

By the proof of Theorem 1, $\lambda_\nu(\hat{\mu}, \hat{\mu}) = 0$ and $\frac{d}{dt} \lambda_\nu(t, t)|_{t=\hat{\mu}} \neq 0$, hence λ changes sign in every neighborhood of $(\hat{\mu}, \hat{\mu})$.

6.1. **Formulae for λ_μ and $\lambda_{\mu\mu}$.** Denote by the subscript μ derivatives with respect to μ. Differentiate (4), the equation of φ with respect to μ, we have

$$\begin{cases} \alpha\nabla\cdot(\nu\nabla\varphi_\mu - \varphi_\mu\nabla m) + (m-\tilde{u})\varphi_\mu + \lambda\varphi_\mu = \tilde{u}_\mu\varphi - \lambda_\mu\varphi & \text{in } \Omega, \\ \nu\frac{\partial\varphi_\mu}{\partial n} - \varphi_\mu\frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{54}$$

Suppose $\mu = \hat{\mu}$ is an evolutionarily singular strategy, and set $\nu = \mu = \hat{\mu}$, then by (52), (54) becomes

$$\begin{cases} \alpha\nabla\cdot(\mu\nabla\varphi_\mu - \varphi_\mu\nabla m) + (m-\tilde{u})\varphi_\mu = \tilde{u}_\mu\varphi & \text{in } \Omega, \\ \mu\frac{\partial\varphi_\mu}{\partial n} - \varphi_\mu\frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{55}$$

Multiplying (54) by $e^{-m/\nu}\varphi$ and integrate by parts, we have

$$\lambda_\mu\int e^{-m/\nu}\varphi^2 = \int e^{-m/\nu}\tilde{u}_\mu\varphi^2. \tag{56}$$

Differentiate (56) and set $\nu = \mu = \hat{\mu}$ and divide by α, we have

$$\frac{\lambda_{\mu\mu}}{\alpha}\int e^{-m/\hat{\mu}}\tilde{u}^2 = \frac{1}{\alpha}\int e^{-m/\hat{\mu}}\tilde{u}_{\mu\mu}\tilde{u}^2 + \frac{2}{\alpha}\int e^{-m/\hat{\mu}}\tilde{u}_\mu\tilde{u}\varphi_\mu \quad \text{when } \mu = \nu = \hat{\mu}, \tag{57}$$

where φ_μ satisfies (55).

6.2. **Asymptotic limit of $\lambda_{\mu\mu}$.**

Proposition 6.2. *Suppose that $\mu = \mu(\alpha)$ is an evolutionarily singular strategy and $\mu \to \mu^*$ as $\alpha \to 0$, then necessarily* $\limsup_{\alpha\to 0}\frac{1}{\alpha}\lambda_{\mu\mu}(\mu,\mu) < 0$.

We prove the proposition with three lemmas.

Lemma 6.3. *Set $\nu = \mu$, then as $\alpha \to 0$, a subsequence $\varphi_\mu \rightharpoonup \bar{\varphi}'$ in $H^1(\Omega)$, where $\bar{\varphi}'$ satisfies*

$$\begin{cases} \nabla\cdot(\mu^*\nabla\bar{\varphi}' - \bar{\varphi}'\nabla m) - \frac{\nabla\cdot[(\mu^*-m)\nabla m]}{m}\bar{\varphi}' = \Delta m & \text{in } \Omega, \\ \mu^*\frac{\partial\bar{\varphi}'}{\partial n} - \frac{\mu^*}{m}\bar{\varphi}'\frac{\partial m}{\partial n} = \frac{\partial m}{\partial n} & \text{on } \partial\Omega. \end{cases} \tag{58}$$

In particular, if we define

$$\varphi_\mu^\perp = \varphi_\mu - \frac{\int e^{-m/\mu^*}\varphi_\mu\tilde{u}}{\int e^{-m/\mu^*}\tilde{u}^2}\tilde{u}$$

then $\varphi_\mu^\perp \rightharpoonup \bar{\varphi}'^\perp$ in $H^1(\Omega)$, where $\bar{\varphi}'^\perp$ is the unique solution to

$$\begin{cases} \nabla\cdot(\mu^*\nabla\bar{\varphi}' - \bar{\varphi}'\nabla m) - \frac{\nabla\cdot[(\mu^*-m)\nabla m]}{m}\bar{\varphi}' = \Delta m & \text{in } \Omega, \\ \mu^*\frac{\partial\bar{\varphi}'}{\partial n} - \frac{\mu^*}{m}\bar{\varphi}'\frac{\partial m}{\partial n} = \frac{\partial m}{\partial n} \quad \text{on } \partial\Omega \quad \text{and} & \int e^{-m/\mu^*}\bar{\varphi}' m = 0. \end{cases} \tag{59}$$

Proof. It follows from the observation that $\varphi_\mu + \varphi_\nu = \tilde{u}_\mu + C\tilde{u}$ for some constant C, where φ_ν is the unique solution to (22) and $\tilde{u}_\mu \to 0$ in $H^1(\Omega)$ (Lemma 3.5). □

Lemma 6.4. $\limsup_{\alpha\to 0}\frac{1}{\alpha}\int e^{-m/\hat{\mu}}\tilde{u}_{\mu\mu}\tilde{u}^2 \leq 0$.

Proof. First, we derive the equations for $\tilde{u}_\mu$ and $\tilde{u}_{\mu\mu}$.

$$\begin{cases} \alpha\nabla\cdot(\mu\nabla\tilde{u}_\mu - \tilde{u}_\mu\nabla m) + (m-2\tilde{u})\tilde{u}_\mu = -\alpha\Delta\tilde{u} & \text{in } \Omega, \\ \mu\frac{\partial\tilde{u}_\mu}{\partial n} - \tilde{u}_\mu\frac{\partial m}{\partial n} = -\frac{\partial\tilde{u}}{\partial n} & \text{on } \partial\Omega. \end{cases} \tag{60}$$

$$\begin{cases} \alpha\nabla\cdot(\mu\nabla\tilde{u}_{\mu\mu} - \tilde{u}_{\mu\mu}\nabla m) + (m-2\tilde{u})\tilde{u}_{\mu\mu} = -2\alpha\Delta\tilde{u}_\mu + 2(\tilde{u}_\mu)^2 & \text{in } \Omega, \\ \mu\frac{\partial\tilde{u}_{\mu\mu}}{\partial n} - \tilde{u}_{\mu\mu}\frac{\partial m}{\partial n} = -2\frac{\partial\tilde{u}_\mu}{\partial n} & \text{on } \partial\Omega. \end{cases} \tag{61}$$

Set $\mu = \hat{\mu}$ in (61), multiply by $-\frac{1}{\alpha}e^{-m/\hat{\mu}}\tilde{u}$ and integrate by parts, we have

$$\frac{1}{\alpha}\int e^{-m/\hat{\mu}}\tilde{u}^2\tilde{u}_{\mu\mu} = -2\int \nabla\tilde{u}_\mu\cdot\nabla(e^{-m/\hat{\mu}}\tilde{u}) - \frac{2}{\alpha}\int e^{-m/\hat{\mu}}\tilde{u}(\tilde{u}_\mu)^2$$
$$\leq -2\int \nabla\tilde{u}_\mu\cdot\nabla(e^{-m/\hat{\mu}}\tilde{u}) \to 0.$$

Here the last quantity is of order $o(1)$ as $\|\tilde{u}_\mu\|_{H^1(\Omega)} \to 0$ as $\alpha \to 0$ by Lemma 3.5. □

Lemma 6.5. $\limsup\limits_{\alpha\to 0}\dfrac{1}{\alpha}\displaystyle\int e^{-m/\mu}\varphi_\mu\tilde{u}_\mu\tilde{u} < 0.$

Proof. Multiply (55) by $e^{-m/\mu}\varphi_\mu$, then

$$\begin{aligned}
&\frac{1}{\alpha}\int e^{-m/\mu}\varphi_\mu\tilde{u}_\mu\tilde{u}\\
&= -\mu\int\left[e^{m/\mu}|\nabla(e^{-m/\mu}\varphi_\mu)|^2 - (m-\tilde{u})e^{-m/\mu}\varphi_\mu^2\right]\\
&\leq -\frac{\lambda_2}{\alpha}\int e^{-m/\mu}\left(\varphi_\mu^\perp\right)^2\\
&\to -\sigma_2\int e^{-m/\mu}\left(\bar{\varphi}'^\perp\right)^2
\end{aligned}$$

where the second last inequality follows from Poincaré's inequality and the last term is negative by the spectrum estimate in Proposition 4.2, Remark 4.1 and Lemma 6.3. □

Proposition 6.2 follows from (57), Lemma 6.4 and $\bar{\varphi}'^\perp \neq 0$ (Lemma 6.5).

Proof of Theorem 7. For any evolutionarily singular strategy $\hat{\mu}$, we have $\lambda_\mu(\hat{\mu},\hat{\mu}) = -\lambda_\nu(\hat{\mu},\hat{\mu}) = 0 = \lambda(\hat{\mu},\hat{\mu})$. Therefore the sign of λ depends on the Hessian of λ. We first claim

Claim 6.6. *Given $\delta > 0$, for all α small, $\lambda_{\mu\mu}(\hat{\mu},\hat{\mu}) < 0$ for any evolutionarily singular strategy $\hat{\mu} \in [\delta, \delta^{-1}]$.*

Suppose to the contrary that for some $\alpha = \alpha_j \to 0$ and evolutionarily singular strategies $\hat{\mu} = \hat{\mu}_j \to \mu_*$,

$$\limsup_{\alpha\to 0}\frac{\lambda_{\mu\mu}}{\alpha} \geq 0. \tag{62}$$

Now let $\alpha = \alpha_j \to 0$ in (57), then by Lemmas 6.4 and 6.5, we have

$$\left(\limsup_{\alpha\to 0}\frac{\lambda_{\mu\mu}}{\alpha}\right)\int e^{-m/\mu_*}m^2 < 0.$$

And we obtained a contradiction to (62). This proves Claim 6.6.

Denote $a = \lambda_{\mu\mu}(\hat{\mu},\hat{\mu}) < 0$, $b = \lambda_{\mu\nu}(\hat{\mu},\hat{\mu})$ and $c = \lambda_{\nu\nu}(\hat{\mu},\hat{\mu})$. We assume in addition that $b+c > 0$. Then by (53) we can write

$$b = -a - (b+c) \quad\text{ and }\quad c = a + 2(b+c).$$

By Taylor's theorem,

$$\begin{aligned}
\lambda(\mu,\nu) &= \frac{a}{2}(\mu-\hat{\mu})^2 + b(\mu-\hat{\mu})(\nu-\hat{\mu}) + \frac{c}{2}(\nu-\hat{\mu})^2 + o(|\mu-\hat{\mu}|+|\nu-\hat{\nu}|)(\mu-\nu)\\
&= \frac{a}{2}(\mu-\hat{\mu})^2 - [a+(b+c)](\mu-\hat{\mu})(\nu-\hat{\mu}) + \frac{a+2(b+c)}{2}(\nu-\hat{\mu})^2 + o(|\mu-\hat{\mu}|+|\nu-\hat{\nu}|)(\mu-\nu)\\
&= (\mu-\nu)\left[\frac{a}{2}(\mu-\nu) - (b+c)(\nu-\hat{\mu}) + o(|\mu-\hat{\mu}|+|\nu-\hat{\nu}|)\right] < 0
\end{aligned}$$

for all $|\mu - \hat{\mu}| + |\nu - \hat{\mu}|$ small and either $\mu > \nu \geq \hat{\mu}$ or $\mu < \nu \leq \hat{\mu}$, by considering the cases (i) $\frac{|\mu-\hat{\mu}|}{\nu-\hat{\mu}} \leq O(1)$ and (ii) $\frac{|\mu-\hat{\mu}|}{\nu-\hat{\mu}} \to \infty$ separately. This completes the proof of Theorem 7. □

Proof of Theorem 5. Suppose that $\hat{\mu} = \hat{\mu}(\alpha)$ is a sequence of local ESS such that $\hat{\mu} \to \mu^* > 0$. By Claim 6.6, $\lambda_{\mu\mu}(\hat{\mu}, \hat{\mu}) < 0$ for all α sufficiently small. Suppose $\hat{\mu}$ is a local ESS, i.e. $\lambda_{\nu\nu}(\hat{\mu}, \hat{\mu}; \alpha) \geq 0$, then by (53),

$$(\lambda_{\mu\nu} + \lambda_{\nu\nu})(\hat{\mu}, \hat{\mu}; \alpha) = \frac{1}{2}(\lambda_{\nu\nu} - \lambda_{\mu\mu})(\hat{\mu}, \hat{\mu}; \alpha) > 0.$$

And Theorem 5 follows from Theorem 7. □

7. Discussions

We considered a mathematical model of two competing species for the evolution of conditional dispersal in a spatially heterogeneous but temporally constant environment. The two species have the same population dynamics but different dispersal strategies, which are a combination of random dispersal and biased movement upward along the resource gradient. If there is no biased movement for both species, Hastings [18] showed that the mutant can invade when rare if only if it has smaller random dispersal rate than the resident. In contrast, we show that positive random dispersal rate can evolve when both species adopt some biased movement. More precisely, if both species have same but small advection rate, a positive random dispersal rate is locally evolutionarily stable and convergent stable. We further determine the asymptotic behavior of this evolutionarily stable dispersal rate for sufficiently small advection rate.

A recurring theme in the study of evolution of dispersal is resource matching. For unconditional dispersal in spatially heterogeneous but temporally constant environments, selection is against dispersal since slower dispersal helps individuals better match resources. However, if the population is able to tract local resouce gradients, thus exhibiting a form of conditional dispersal, then intermediate dispersal rate might be selected. On one hand, small random dispersal is selected against as it will cause the individuals to concentrate at the locally most favorable locations and severely undermatch other available resources so that the mutant can invade when rare. On the other hand, large random dispersal is selected against as well since the population is only using average resource and is therefore also undermatching resources in high quality patches. Our results suggest that a balanced combination of random and directed movement can help the population better match resources and could be a better habitat selection strategy for populations. Furthermore, when the spatial variation of the environment is not large, there may exist a unique random dispersal rate which is evolutionarily and convergent stable. However, multiple evolutionarily stable strategies may appear if the spatial variation of the environment is large.

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