

STEADY-STATES OF INDEFINITE NONLINEAR DIFFUSION PROBLEM IN POPULATION GENETICS,

KIMIE NAKASHIMA

TOKYO UNIVERSITY OF MARINE SCIENCE AND TECHNOLOGY

1. INTRODUCTION

In this article we study the “complete dominant” case of a migration selection model for the solution of gene frequency at a single locus with two alleles A_1, A_2 initiated in [NNS] and [LNS]. This model is due to T.Nagylaki in 1975 [NAG]. We shall give a brief description of this model following the more recent presentation in [LNN] and [NNS].

Let $u(x, t)$ be the frequency of allele A_1 at time t and location x (thus $0 \leq u \leq 1$), and r_{ij} be the fitness (local selection coefficient) of the genotype A_i, A_j for $i, j = 1, 2$ and

$$r_1 = r_{11}u + r_{12}(1 - u)$$

is the marginal selection coefficient of A_1 , and

$$\bar{r} = r_{11}u^2 + r_{12}u(1 - u) + r_{21}(1 - u)u + r_{22}(1 - u)^2.$$

is the mean selection coefficient of the population. Now positing

$$r_{11} = 1, \quad r_{12} = r_{21} = 1 - hg(x), \quad r_{22} = 1 - g(x), \quad (1.1)$$

where $g(x)$ reflects the “environmental variation” and $0 \leq h \leq 1$ specifies the degree of dominance (assumed to be independent of the location). We have the selection term:

$$S_1 = \lambda g(x)u(1 - u)[hu + (1 - h)(1 - u)], \quad (1.2)$$

where $\lambda > 0$ is the ratio of selection intensity to the migration rate. Therefore, under some additional simplification assumptions, the migration-selection model describing the evolution of gene frequencies at a single locus with two alleles takes the following form

$$\begin{cases} u_t = \Delta u + S_1(x, u) & \text{in } \Omega \times (0, \infty), \\ \partial_\nu u = 0 & \text{on } \partial\Omega \times (0, \infty), \end{cases} \quad (1.3)$$

where $\Delta = \sum_{i=1}^n \frac{\partial^2}{\partial x_i^2}$ is the Laplace operator, the habitat Ω is a bounded domain with smooth boundary $\partial\Omega$ in $\mathbf{R}^n$, ν denotes the unit outward normal to $\partial\Omega$ and ∂_ν is the normal derivative on $\partial\Omega$. After scaling t , we have

$$\begin{cases} u_t = d\Delta u + g(x)u(1-u)[hu + (1-h)(1-u)] & \text{in } \Omega \times (0, \infty), \\ \partial_\nu u = 0 & \text{on } \partial\Omega \times (0, \infty), \end{cases} \quad (1.4)$$

It is clear that (1.4) has no nontrivial steady-states if $g(x)$ does not change sign in Ω , i.e. in this case a steady state u is either $u \equiv 0$ or $u \equiv 1$, implying that only one allele survives eventually. Thus, in order to sustain both alleles A_1 and A_2 , the environmental variation has to be so significant that the selection reverses its direction at least once in Ω , i.e. $g(x)$ changes sign at least once in Ω (Note that if $g(x) > 0$, then $r_{11} \geq r_{12} \geq r_{22}$ at location x ; while $r_{11} \leq r_{12} \leq r_{22}$ where $g(x) < 0$). Therefore we shall require in the rest of this paper that $g(x)$ changes sign in Ω .

As was explained in [NNS] that all previous mathematical results in literature deal with the case $0 < h < 1$ and the “complete dominant” case $h = 1$ was left untouched until the publications of the papers [NNS] and [LNS] in 2010. In the case $h = 1$ we have that $r_{12} = r_{22}$, i.e. the heterozygote A_1A_2 has the same fitness as the homozygote A_2A_2 , we say that A_2 is completely dominant to A_1 (The case $h = 0$ is similar). In the “completely” dominant case $h = 1$, (1.4) becomes

$$\begin{cases} u_t = d\Delta u + g(x)u^2(1-u) & \text{in } \Omega \times (0, \infty), \\ \partial_\nu u = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases} \quad (1.5)$$

This “completely dominant” case is not only mathematically challenging but also biologically important. In fact the following conjecture (a) to (c) has existed for a long time (See Lou and Nagylaki [LN]):

- (a) If $\int_\Omega g(x) dx = 0$, then for every $d > 0$, problem (1.5) has unique nontrivial steady state which is globally asymptotically stable.
- (b) If $\int_\Omega g(x) dx > 0$, then there exists $d_0 > 0$ such that for every $d \in (0, d_0)$, problem (1.5) has a unique nontrivial steady state which is globally asymptotically stable.
- (c) If $\int_\Omega g(x) dx < 0$, then there exists $d_0 > 0$ such that for every $d \in (0, d_0)$, problem (1.5) has exactly two nontrivial steady states, one is asymptotically stable and the other is unstable.

Towards the resolution of this important conjecture, we introduce two mathematically rigorous results, [NNS] and [LNS]. In [NNS], the existence of a stable steady

state as well as its limiting behaviors (as d tends to 0 or ∞) are obtained. Furthermore, in [LNS] the existence of at least two steady states, one stable and the other unstable, is established as well. However, the uniqueness part of the conjecture is still left open. Therefore, in [NK1] and [NK2], we consider the uniqueness part of (a) and (b) above, under the condition where the spatial dimension $n = 1$. A steady state solution of (1.5) satisfies

$$\begin{cases} du'' + g(x)u^2(1-u) = 0 & \text{in } (0, 1), \\ u'(0) = u'(1) = 0, \end{cases} \quad (1.6)$$

We set the following “nondegeneracy” condition on g : All zeros on $[0, 1]$ are interior and nondegenerate; i.e.

(H) If $g(x_0) = 0$, then $x_0 \in (0, 1)$ and $g'(x_0) \neq 0$.

The first result is on the stability of nontrivial solution.

Theorem 1.1. *Suppose that g changes sign in $(0, 1)$ and that (H) holds. Then, (1.6) has a linearly stable nontrivial solution u_d for d sufficiently small. Furthermore, u_d has the following properties:*

(i) *On every compact subset S of $[g < 0]$,*

$$C_1 d < u_d < C_2 d. \quad (1.7)$$

(ii) *On every compact subset S of $[g > 0]$,*

$$C_3 \exp\left(-\frac{C_4}{\sqrt{d}}\right) < 1 - u_d < C_5 \exp\left(-\frac{C_6}{\sqrt{d}}\right), \quad (1.8)$$

where the constants $C_1 - C_6$ depend on S .

The facts that $u_d \rightarrow 0$ in $[g < 0]$ and $u_d \rightarrow 1$ in $[g > 0]$ were already established earlier in [NNS] for any dimension n , however, the rates of convergence are not obtained in [NNS]. These rates, (1.7) and (1.8) are essential to prove both stability and uniqueness of u_d (For the proof see [NK1] and [NK2]).

For the uniqueness result, we need some more assumptions on $g(x)$. We first consider the case where g has only one zero. Let $g(x)$ satisfy the following condition:

(G) $g(x) < 0$ in $[0, x_0]$ and $g(x) > 0$ in $(x_0, 1]$.

In [NK1], we have proved that the following two theorems hold:

Theorem 1.2. *Suppose (G) and (H) hold. If $\int_0^1 g(x) dx \geq 0$, then, a solution u_d of (1.6) is a unique nontrivial solution.*

The proof of Theorem 1.2 also shows the next theorem concerning conjecture (c).

Theorem 1.3. *Suppose (G) and (H) hold. If $\int_0^1 g(x) dx < 0$, then, for d sufficiently small, any nontrivial solution v_d of (1.6) satisfies either of the following (i) or (ii):*
 (i) $v_d(x) = u_d(x)$ in $[0, 1]$, where u_d is a linearly stable solution in Theorem 1.1.
 (ii) $v_d(x) \leq C_7 d$ in $[0, 1]$

We next consider the case g has more than two zeros. In this case we need more assumptions on $g(x)$ as follows. We introduce the following auxiliary function $p(x) \in C^1[0, 1]$ satisfying the following (P0) to (P3).

- (P0) z_1 is the only zero of $p(x)$ in $[0, \frac{1}{m}]$, and $p'(z_1) \neq 0$.
- (P1) $p(x)$ is symmetric in $[\frac{k-1}{m}, \frac{k+1}{m}]$ w.r.t. $x = \frac{k}{m}$ ($k = 1, 2, \dots, m-1$).
- (P2) $p(x)$ is monotone in $[\frac{k-1}{m}, \frac{k}{m}]$ ($k = 1, 2, \dots, m$).
- (P3) $\int_0^1 p(x) dx \geq 0$.

Theorem 1.4. *Suppose that $g(x) \geq p(x)$, where $p(x)$ satisfies (P0) – (P3). Then, for every d small, (1.6) has a unique nontrivial solution.*

By the assumption $g(x) \geq p(x)$ and the condition (P3), it holds that $\int_0^1 g(x) dx \geq 0$. (P0) is a condition corresponding to nondegeneracy condition (H). The proof of Theorem 1.4 is in [NK2].

Many results which assure Conjecture (a) - (c) have been obtained. However, we have found a counterexample to Conjecture (c) recently. For simplicity, we consider the case where $g(x)$ has 2 zeros. Let $\ell > 1$ be a constant and $x_1 = x_1(\ell)$, $x_2 = x_2(\ell)$, $(1 - \frac{1}{2\ell} < x_2 < 1)$ be zeros of $g(x)$ such that

- (G1) $g(x)$ is symmetric with respect to $x = \frac{1}{2}$
- (G2) $g(x) > 0$ in $(0, x_1)$, $g(x) < 0$ in $[x_1, x_2]$, $g'(x_1) \neq 0$,
- (G3) $g(x) = -g^*$ in $[\frac{1}{2\ell}, 1 - \frac{1}{2\ell}]$ (g^* is a positive constant)
- (G4) $\int_0^{\frac{1}{2\ell}} g(x) dx < 0$,

As is mentioned in Theorem 1.1, there exists a linearly stable solution of (1.6), $U_d(x; \ell)$ satisfying

$$\begin{aligned} U_d &\rightarrow 1 \text{ uniformly in any compact set in } (0, x_1) \cup (x_2, 1), \text{ as } d \rightarrow 0, \\ U_d &\rightarrow 0 \text{ uniformly in any compact set in } (x_1, x_2), \text{ as } d \rightarrow 0. \end{aligned}$$

This is supposed to be the first solution in Conjecture (c) which is stable. By Theorem 1.3 in [LNS] and [NK1], there exists at least one solution $\omega_d(x)$ of (1.6) satisfying

$$\omega_d \rightarrow 0 \text{ uniformly in any compact set in } (0, 1), \text{ as } d \rightarrow 0.$$

This is supposed to be the second solution in Conjecture (c) which is unstable. In addition to these two solutions, we have proved the existence of the third solution in the following theorem.

Theorem 1.5. *Let $g(x)$ satisfy (G1) - (G4). There exists $\ell > 0$ such that for d sufficiently small, (1.6) has a nontrivial solution w_d satisfying the following property.*

(i) *On every compact subset S of $[0, x_2)$,*

$$C_1 d < w_d < C_2 d. \quad (1.9)$$

(ii) *On every compact subset S of $(x_2, 1]$,*

$$C_3 \exp\left(-\frac{C_4}{\sqrt{d}}\right) < 1 - u_d < C_5 \exp\left(-\frac{C_6}{\sqrt{d}}\right), \quad (1.10)$$

where the constants $C_1 - C_6$ depend on S .

The next result is on the fourth solution.

Theorem 1.6. *Suppose that $g(x)$ satisfy (G1) - (G4). (1.6) has at least two solution satisfying (1.9) and (1.10) for d suff. small. One is stable and another is unstable.*

Clearly, by reflection with respect to $x = \frac{1}{2}$, we obtain two more solutions which are different from the above 4 solutions. The following theorem show that there are also at least 3 solutions in the neighborhood of $u = 0$.

Theorem 1.7. *Suppose that $g(x)$ satisfy (G1) - (G4). (1.6) has at least three solutions $\omega_d^i(x)$ ($i = 1, 2, 3$) satisfying $C_7 d < \omega_d^i(x) < C_8 d$ on every compact subset of $[0, 1]$, for d suff. small. Here the constants C_7, C_8 depend on S .*

The proofs of Theorems 1.5 - 1.7 are given in [NK3].

2. CONSTRUCTION OF UPPER AND LOWER SOLUTIONS

In this section, we will construct, for every $d > 0$ small, a pair of upper solution u^* and lower solution u_* , both exhibit transition layer near the non-degenerate zero x_0 of g and $u^* > u_*$ on $[0, 1]$. This will guarantee the existence of a solution U such that $u^* \geq U \geq u_*$, and thus U also exhibits desired transition layer properties at x_0 . Construction of upper solution and lower solution is a key to prove Theorems 1.1 and 1.5.

We first introduce the correct scaling near x_0 , the zero of g , is $d = \epsilon^3$, and (1.6) takes the following form:

$$\begin{cases} \epsilon^3 u'' + g(x)u^2(1-u) = 0 & \text{in } (0, 1), \\ u'(0) = u'(1) = 0. \end{cases} \quad (2.1)$$

We will first construct a lower solution of (2.1) with a transition layer of width ϵ near x_0 . Letting ϕ be the unique solution of (cf.[NNS]Appendix)

$$\begin{cases} \phi'' + z\phi^2(1-\phi) = 0 & \text{in } (-\infty, \infty), \\ \phi(-\infty) = 0, \quad \phi(\infty) = 1, \end{cases} \quad (2.2)$$

we have the following properties of ϕ , whose proofs are given in Appendix A.

Lemma 2.1. *ϕ is monotone increasing in $(-\infty, \infty)$, and there exist positive constants C_i , $i = 1, \dots, 6$, λ_j , $j = 1, 2, 3$, and R such that the following hold:*

$$1 - C_1 \exp(-\lambda_1 z^{\frac{3}{2}}) < \phi(z) < 1 - C_2 \exp(-\lambda_2 z^{\frac{3}{2}}) \quad \text{for } z > R, \quad (2.3)$$

$$\phi'(z) < C_3 \exp(-\lambda_3 z^{\frac{3}{2}}) \quad \text{for } z > R, \quad (2.4)$$

$$-\frac{C_4}{z^3} < \phi(z) < -\frac{C_5}{z^3} \quad \text{for } z < -R, \quad (2.5)$$

$$\phi'(z) < \frac{C_6}{z^4} \quad \text{for } z < -R. \quad (2.6)$$

Let $L > \max\{R, 1\}$ be a large constant to be chosen later, and we define two C^1 functions as follows:

$$\begin{aligned} \eta(z) &= \frac{|z|^2}{1+|z|}, \\ \theta(z) &= \begin{cases} \exp(-\lambda_2(L+1)^{\frac{3}{2}})\eta(z-L), & z \geq L, \\ 0, & -L \leq z \leq L, \\ \frac{\kappa}{L^4}\eta(z+L), & z \leq -L, \end{cases} \end{aligned}$$

where λ_2 is the constant in (2.3), κ is a constant satisfying $\kappa > C_5$ and C_5 is the constant in (2.5).

We begin our construction of a lower solution near x_0 . Define

$$\underline{u}(x) = \phi\left(\frac{B(x_0)(x-x_0)}{\epsilon} - L^4\right) - \theta\left(\frac{B(x_0)(x-x_0)}{\epsilon} - L^4\right)$$

where $B(x_0) = (g'(x_0))^{\frac{1}{3}}$, and let ξ_1, ξ_2 satisfy

$$\underline{u}(\xi_1) = 0, \quad \xi_1 \leq x_0 + \frac{\epsilon}{B(x_0)}(-L + L^4), \quad (2.7)$$

$$\underline{u}'(\xi_2) = 0, \quad \xi_2 \geq x_0 + \frac{\epsilon}{B(x_0)}(L + L^4). \quad (2.8)$$

We will first show that both ξ_1 and ξ_2 are uniquely determined for all large L . Setting

$$z = \frac{B}{\epsilon}(x - x_0) - L^4, \quad (2.9)$$

we have

$$\underline{u}(x) = \phi(z) - \theta(z). \quad (2.10)$$

Note that

$$\theta'(z) = -\frac{\kappa}{L^4} \left(1 - \frac{1}{(1 + |z + L|)^2} \right) \leq 0 \quad \text{for } z \leq -L.$$

This shows

$$\underline{u}'(x) = \frac{B}{\epsilon}(\phi'(z) - \theta'(z)) \geq 0$$

for $z \leq -L$, which is equiv. to $x \leq x_0 + \frac{\epsilon}{B}(-L + L^4)$. This implies that $\underline{u}'(x)$ is monotone increasing on this interval. Since it holds that

$$\underline{u} \left(x_0 + \frac{\epsilon}{B}(-L + L^4) \right) = \phi(-L) - \theta(-L) = \phi(-L) > 0,$$

and

$$\underline{u} \left(x_0 + \frac{\epsilon}{B}(-2L + L^4) \right) = \phi(-2L) - \theta(-2L) < \frac{C_5}{8L^3} - \frac{\kappa}{L^4} \frac{L^2}{1 + L} < 0,$$

there exists

$$\xi_1 \in \left(x_0 + \frac{\epsilon}{B}(-2L + L^4), x_0 + \frac{\epsilon}{B}(-L + L^4) \right) \quad (2.11)$$

s.t. $\underline{u}(\xi_1) = 0$ and ξ_1 is unique.

For ξ_2 , we remark that

$$\theta''(z) = \exp(-\lambda_2(L + 1)^{\frac{3}{2}}) \frac{2}{(1 + |z + L|)^3} \geq 0.$$

and $\phi''(x) \leq 0$ holds for $z \geq L$. Therefore it holds that

$$\underline{u}''(x) = \frac{B^2}{\epsilon^2}(\phi''(z) - \theta''(z)) \leq 0$$

for $z \geq L$, which is equiv. to $x \geq x_0 + \frac{\epsilon}{B}(L + L^4)$. This shows $\underline{u}'(x)$ is monotone decreasing on this interval. On the other hand, it holds that

$$\underline{u}' \left(x_0 + \frac{\epsilon}{B}(L + L^4) \right) = \frac{B}{\epsilon} \phi'(L) > 0.$$

If we remark that $P = 2 \left(\frac{\lambda_2}{\lambda_3} \right)^{\frac{2}{3}} > 2$, where $\lambda_2 > \lambda_3$ are in Lemma 2.1, we obtain $\lambda_3 P^{\frac{2}{3}} = 2\sqrt{2}\lambda_2$. Therefore,

$$\begin{aligned}
 \underline{u}' \left(x_0 + \frac{\epsilon}{B}(PL + L^4) \right) &= \frac{B}{\epsilon} (\phi'(PL) - \theta'(PL)) \\
 &\leq \frac{B}{\epsilon} \left[C_3 \exp(-\lambda_3(PL)^{\frac{3}{2}}) - \exp(-\lambda_2(L+1)^{\frac{3}{2}}) \left(1 - \frac{1}{((P-1)L+1)^2} \right) \right] \\
 &= \frac{B}{\epsilon} \left[C_3 \exp(-2\sqrt{2}\lambda_2 L^{\frac{3}{2}}) - \exp(-\lambda_2(L+1)^{\frac{3}{2}}) \left(1 - \frac{1}{((P-1)L+1)^2} \right) \right] \\
 &= \frac{B}{\epsilon} \exp(-\lambda_2(L+1)^{\frac{3}{2}}) \left[C_3 \exp(-2\sqrt{2}\lambda_2 L^{\frac{3}{2}} + \lambda_2(L+1)^{\frac{3}{2}}) - 1 + \frac{1}{((P-1)L+1)^2} \right] \\
 &= \frac{B}{\epsilon} \exp(-\lambda_2(L+1)^{\frac{3}{2}}) \left[C_3 \exp(-\lambda_2 L^{\frac{3}{2}} \left(2\sqrt{2} - \left(\frac{L+1}{L} \right)^{\frac{3}{2}} \right)) - 1 + \frac{1}{((P-1)L+1)^2} \right] \\
 &< 0,
 \end{aligned}$$

for L large. We obtain

$$\xi_2 \in \left(x_0 + \frac{\epsilon}{B}(L + L^4), x_0 + \frac{\epsilon}{B}(PL + L^4) \right) \quad (2.12)$$

s.t. $\underline{u}'(\xi_2) = 0$ and ξ_2 is unique.

Moreover, since ϕ is monotone increasing, we have the estimate

$$\begin{aligned}
 \underline{u}(\xi_2) &< \phi(\xi_2) < \phi(PL) < 1 - C_2 \exp(-\lambda_2(PL)^{\frac{3}{2}}) \\
 \underline{u}(\xi_2) &> \underline{u}(x_0 + \frac{\epsilon}{B}(L + L^4)) = \phi(L) > 1 - C_1 \exp(-\lambda_1 L^{\frac{3}{2}}).
 \end{aligned} \quad (2.13)$$

A crucial step in our construction of a lower-solution is the following lemma. Set

$$\Phi(u) \equiv \epsilon^3 u'' + g(x)f(u) \quad \text{and} \quad f(u) = u^2(1-u). \quad (2.14)$$

Lemma 2.2. *There exists $L_0 > 0$ such that for all $L > L_0$, $\Phi(\underline{u}(x)) > 0$ holds on the interval (ξ_1, ξ_2) for ϵ sufficiently small.*

(Proof.) By Taylor's expansion, there exists $\tilde{x}$ between x_0 and $x = x_0 + \frac{\epsilon}{B}(z + L^4)$ and $\tilde{\phi} \in (\phi - \theta, \phi)$ such that

$$g(x) = g'(x_0) \frac{\epsilon}{B}(z + L^4) + \frac{1}{2} g''(\tilde{x}) \frac{\epsilon^2}{B^2}(z + L^4)^2,$$

$$f(\phi - \theta) = f(\phi) - f'(\phi)\theta + \frac{1}{2} f''(\tilde{\phi})\theta^2.$$

Therefore,

$$\begin{aligned}
\Phi(\underline{u}) &= \epsilon^3 \underline{u}_{xx} + g(x)f(\underline{u}) \\
&= \epsilon B^2(\phi_{zz} - \theta_{zz}) + \frac{\epsilon}{B}g'(x_0)z(f(\phi) - f'(\phi)\theta + \frac{1}{2}f''(\tilde{\phi})\theta^2) \\
&\quad + (\frac{\epsilon}{B}g'(x_0)L^4 + \frac{1}{2}\frac{\epsilon^2}{B^2}g''(\tilde{x})(z + L^4)^2)f(\phi - \theta) \\
&= \epsilon B^2(-\theta_{zz} - zf'(\phi)\theta + \frac{1}{2}zf''(\tilde{\phi})\theta^2) + \epsilon B^2L^4f(\phi - \theta) \\
&\quad + \frac{1}{2}\frac{\epsilon^2}{B^2}g''(\tilde{x})(z + L^4)^2f(\phi - \theta)
\end{aligned}$$

Since $z \in (-2L, PL)$ by (2.11) and (2.12), we have

$$B^2L^4 + \frac{1}{2}\frac{\epsilon}{B^2}g''(\tilde{x})(z + L^4)^2 > \frac{1}{2}B^2L^4$$

for $\epsilon > 0$ suff. small. Therefore,

$$\Phi(\underline{u}) \geq \epsilon B^2(-\theta_{zz} - zf'(\phi)\theta + \frac{1}{2}zf''(\tilde{\phi})\theta^2 + \frac{1}{2}L^4f(\phi - \theta)). \quad (2.15)$$

The rest of the proof is divided into three steps.

Step 1. For $x \in [x_0 + \frac{\epsilon}{B}(-L + L^4), x_0 + \frac{\epsilon}{B}(L + L^4)]$, we have $\theta = 0$. Thus (2.15) implies that

$$\Phi(\underline{u}) \geq \frac{1}{2}\epsilon B^2L^4f(\phi) > 0.$$

Step 2. For $x \in [\xi_1, x_0 + \frac{\epsilon}{B}(-L + L^4)]$, we have $\phi - \theta \geq 0$, and $-2L < z < -L$ (by (2.11)). The estimate (2.5) shows

$$\begin{aligned}
f'(\phi) - \frac{1}{2}f''(\tilde{\phi})\theta &= (2\phi - 3\phi^2) - \frac{1}{2}(2 - 6\tilde{\phi})\theta \\
&= (\phi - 3\phi^2) + (\phi - \theta) + 3\tilde{\phi}\theta \\
&\geq \phi - 3\phi^2 \geq \frac{C'_1}{L^3} - \frac{C'_2}{L^6} \geq \frac{C'_1}{2L^3},
\end{aligned} \quad (2.16)$$

if L is large enough s.t. $L > \left(\frac{2C'_2}{C'_1}\right)^{\frac{1}{3}}$. Hereafter, we will denote those constants depending only on the constants in Lemma 2.1 by C'_j , $j = 1, 2, \dots$. Since $-z > L$, (2.15) now gives

$$\begin{aligned}
\Phi(\underline{u}) &\geq \epsilon B^2(-\theta_{zz} - \frac{C'_1}{2L^3}z\theta) \\
&\geq \frac{\epsilon B^2\kappa}{L^4} \left(-\frac{2}{(|z + L| + 1)^3} + \frac{C'_1}{2L^2} \frac{(z + L)^2}{|z + L| + 1} \right) \geq 0
\end{aligned}$$

if

$$(z + L)^2(|z + L| + 1)^2 > \frac{4L^2}{C'_1},$$

which is guaranteed to hold for $x \in \left[\xi_1, x_0 + \frac{\epsilon}{B}(-L^{\frac{2}{3}} - L + L^4) \right)$ and $L > \left(\frac{4}{C'_1} \right)^{\frac{3}{2}}$, as $|z + L| > L^{\frac{2}{3}}$ for all x in this interval.

For the remaining part, i.e. for $x \in \left[x_0 + \frac{\epsilon}{B}(-L^{\frac{2}{3}} - L + L^4), x_0 + \frac{\epsilon}{B}(-L + L^4) \right)$, we have

$$\phi(z) - \theta(z) \geq \frac{C'_3}{L^3} - \frac{C'_4 \kappa}{L^4} \frac{L^{\frac{4}{3}}}{L^{\frac{2}{3}} + 1} > \frac{C'_3}{2L^3} \quad (2.17)$$

if L is sufficiently large. On the other hand,

$$\phi(z) - \theta(z) \leq \phi(z) \leq -\frac{C_5}{z^3} \leq \frac{C_5}{L^3},$$

we choose L large enough so that $\frac{C_5}{L^3} < \frac{2}{3}$. Since f is monotone increasing in $(0, \frac{2}{3})$, we have

$$f(\phi - \theta) > f\left(\frac{C'_3}{2L^3}\right) > \frac{C'_5}{L^6}$$

in view of (2.17). From (2.15) and (2.16) we see that

$$\begin{aligned} \Phi(\underline{u}) &\geq \epsilon B^2(-\theta_{zz} + \frac{1}{2}L^4 f(\phi - \theta)) \\ &\geq \epsilon B^2 \left(-\frac{\kappa}{L^4} \frac{2}{(|z + L| + 1)^3} + \frac{L^4 C'_5}{2 L^6} \right) \geq 0 \end{aligned}$$

if L is sufficiently large.

Step 3. For $x \in (x_0 + \frac{\epsilon}{B}(L + L^4), \xi_2]$: First, we choose L large such that $\exp(-\lambda_2 L^{\frac{3}{2}}) \leq \exp(-\lambda_1 L^{\frac{3}{2}}) \ll 1$, then ϕ is close to 1 and θ is close to 0 by Lemma 2.1, and therefore

$$-f'(\phi) + \frac{1}{2}f''(\tilde{\phi})\theta = -(2\phi - 3\phi^2) + \frac{1}{2}(2 - 6\tilde{\phi})\theta > \frac{1}{2}.$$

From (2.15) it follows that

$$\Phi(\underline{u}) \geq \epsilon B^2(-\theta_{zz} + \frac{1}{2}z\theta + \frac{1}{2}L^4 f(\phi - \theta)). \quad (2.18)$$

For $x \in (x_0 + \frac{\epsilon}{B}(L + L^4), x_0 + \frac{\epsilon}{B}(L + 1 + L^4)]$, we have

$$f(\phi - \theta) \geq f(\phi) \geq C'_6 \exp(-\lambda_2 z^{\frac{3}{2}})$$

since f is decreasing near 1. Note that $z\theta \geq 0$ and

$$-\theta'' = -\exp(-\lambda_2(L + 1)^{\frac{3}{2}}) \frac{2}{(|z - L| + 1)^3} < 0.$$

Substituting these into (2.18) we obtain

$$\Phi(\underline{u}) \geq \epsilon B^2 \left(-2 \exp(-\lambda_2(L + 1)^{\frac{3}{2}}) + \frac{L^4}{2} C'_6 \exp(-\lambda_2 z^{\frac{3}{2}}) \right) > 0.$$

Finally, for $x \in (x_0 + \frac{\epsilon}{B}(L+1+L^4), \xi_2]$, again from (2.18) we deduce

$$\begin{aligned}\Phi(\underline{u}) &\geq \epsilon B^2 \exp(-\lambda_2(L+1)^{\frac{3}{2}}) \left[-\frac{2}{(1+|z-L|)^3} + \frac{z}{2} \frac{(z-L)^2}{(1+|z-L|)} \right] \\ &= \frac{\epsilon B^2 \exp(-\lambda_2(L+1)^{\frac{3}{2}})}{(1+|z-L|)^3} \left[-2 + \frac{z}{2}(z-L)^2(1+|z-L|)^2 \right],\end{aligned}$$

Since $L^4 f(\phi - \theta) > 0$. On this interval $z \geq L+1$, thus

$$z(z-L)^2(1+|z-L|)^2 \geq 4(L+1),$$

which implies that $\Phi(\underline{u}) > 0$ for L large. This completes our proof of Lemma 2.2.

Lemma 2.2 tells us that $\underline{u}$ is a lower solution for (2.1) in the interval (ξ_1, ξ_2) . We now extend it to the entire interval $(0, 1)$. Set $\underline{u}(\xi_2) = 1 - \alpha_1$ and

$$u_*(x) = \begin{cases} 0 & \text{if } 0 \leq x \leq \xi_1, \\ \underline{u}(x) & \text{if } \xi_1 \leq x \leq \xi_2, \\ 1 - \alpha_1 & \text{if } \xi_2 \leq x \leq 1. \end{cases} \quad (2.19)$$

See (2.13). α_1 is close to 0 for L suff. large.

Proposition 2.3. *There exists $L_0 > 0$ such that for all $L > L_0$, u_* is a lower solution for (2.1) for $\epsilon > 0$ sufficiently small.*

(Proof.)First, observe that $u_* \in C^0([0, 1])$ and $\Phi(u_*) > 0$ on $[\xi_1, \xi_2]$. Note that

- (i) $\Phi(0) = 0$, i.e. 0 is a solution for (2.1), and $\underline{u}'(\xi_1) > 0$;
- (ii) $\Phi(1 - \alpha_1) = \Phi(\underline{u}(\xi_2)) > 0$. i.e. the constant $\underline{u}(\xi_2)$ is also a lower solution for (2.1), and $\underline{u}'(\xi_2) = 0$.

By (i) and (ii), it follows from standard arguments that u_* is a lower solution for (2.1) on $[0, 1]$.

An upper solution may be constructed in a similar fashion as the lower solution, thus we shall be brief.

Let

$$\hat{\theta}(z) = \begin{cases} \frac{C_2}{2} \exp(-\lambda_2(L+1)^{\frac{3}{2}}) \eta(z-L), & z \geq L, \\ 0, & -L \leq z \leq L, \\ \frac{\hat{\kappa}}{L^4} \eta(z+L), & z \leq -L, \end{cases} \quad (2.20)$$

and

$$\bar{u}(x) = \phi \left(\frac{B(x-x_0)}{\epsilon} + L^4 \right) + \hat{\theta} \left(\frac{B(x-x_0)}{\epsilon} + L^4 \right). \quad (2.21)$$

Similarly, let ξ_3 and ξ_4 satisfy

$$\bar{u}'(\xi_3) = 0, \quad \xi_3 \leq x_0 + \frac{\epsilon}{B}(-L - L^4), \quad (2.22)$$

$$\bar{u}(\xi_4) = 1 \quad \xi_4 \geq x_0 + \frac{\epsilon}{B}(L - L^4). \quad (2.23)$$

Again, we first show that ξ_3 and ξ_4 are uniquely determined for large L . Setting

$$z = \frac{B}{\epsilon}(x - x_0) + L^4, \quad (2.24)$$

we have

$$\bar{u}(x) = \phi(z) + \hat{\theta}(z). \quad (2.25)$$

Note that z in (2.24) is similar to but different from (2.9). By the fact that $\bar{u}''(x) = \frac{B^2}{\epsilon^2}(\phi''(z) + \hat{\theta}''(z)) \geq 0$ for $z \leq -L$, $\bar{u}'$ is monotone increasing on this interval. Now we compute, by Lemma 2.1,

$$\bar{u}'\left(x_0 + \frac{\epsilon}{B}(-L - L^4)\right) = \frac{B}{\epsilon}(\phi'(-L) + \hat{\theta}'(-L)) = \frac{B}{\epsilon}\phi'(-L) > 0$$

and

$$\begin{aligned} \bar{u}'\left(x_0 + \frac{\epsilon}{B}(-3L - L^4)\right) &= \frac{B}{\epsilon}(\phi'(-3L) + \hat{\theta}'(-3L)) \\ &< \frac{B}{\epsilon}\left(\frac{C_6}{(3L)^4} - \frac{\hat{\kappa}}{L^4}\left[1 - \left(\frac{1}{1+2L}\right)^2\right]\right) < \frac{B}{\epsilon}\left(\frac{C_6}{(3L)^4} - \frac{\hat{\kappa}}{2L^4}\right) < 0 \end{aligned}$$

if $\hat{\kappa} > C_6$ and $L > 1$. Therefore we obtain

$$\xi_3 \in \left(x_0 + \frac{\epsilon}{B}(-3L - L^4), x_0 + \frac{\epsilon}{B}(-L - L^4)\right) \quad (2.26)$$

s.t. $\bar{u}'(\xi_3) = 0$ and ξ_3 is unique. Moreover, by Lemma 2.1 and (2.26) we have

$$\begin{aligned} \bar{u}(\xi_3) &> \phi(\xi_3) > \phi(-3L) > \frac{C_4}{(3L)^3}, \\ \bar{u}(\xi_3) &< \bar{u}\left(\frac{\epsilon}{B}(-L - L^4)\right) = \phi(-L) < \frac{C_5}{L^3}. \end{aligned} \quad (2.27)$$

For ξ_4 , we remark that $\bar{u}'(x) = \frac{B}{\epsilon}(\phi'(z) + \hat{\theta}'(z)) \geq 0$ for $z \geq L$, therefore $\bar{u}$ is monotone increasing on this interval. We set $\hat{P} = 2\left(\frac{\lambda_2}{\lambda_1}\right)^{\frac{2}{3}}$ and observe that $\hat{P} > 2$ by Lemma 2.1. Now,

$$\begin{aligned} \bar{u}\left(x_0 + \frac{\epsilon}{B}(L - L^4)\right) &= \phi(L) + \hat{\theta}(L) = \phi(L) < 1, \\ \bar{u}\left(x_0 + \frac{\epsilon}{B}(\hat{P}L - L^4)\right) &= \phi(\hat{P}L) + \hat{\theta}(\hat{P}L) \\ &> 1 - C_1 \exp(-\lambda_1(\hat{P}L)^{\frac{3}{2}}) + \exp(-\lambda_2(L+1)^{\frac{3}{2}}) \frac{(\hat{P}-1)^2 L^2}{1 + (\hat{P}-1)L} > 1 \end{aligned}$$

if L is sufficiently large. Thus we obtain

$$\xi_4 \in \left(x_0 + \frac{\epsilon}{B}(L - L^4), x_0 + \frac{\epsilon}{B}(\hat{P}L - L^4)\right) \quad (2.28)$$

such that $\hat{u}(\xi_4) = 1$ and ξ_4 is unique.

Next, we will show that $\Phi(\bar{u}) < 0$ on $[\xi_3, \xi_4]$. We proceed in a similar manner as in the lower solution case. There exist $\tilde{x}$ between x_0 and x , and $\tilde{\phi} \in [\phi + \hat{\theta}]$ such that

$$g(x) = g(x_0) + g'(x_0)\frac{\epsilon}{B}(z - L^4) + \frac{1}{2}g''(\tilde{x})\frac{\epsilon^2}{B^2}(z - L^4)^2,$$

$$f(\phi + \hat{\theta}) = f(\phi) + f'(\phi)\hat{\theta} + \frac{1}{2}f''(\tilde{\phi})\hat{\theta}^2.$$

Substituting into $\Phi(\bar{u})$, we obtain

$$\begin{aligned}\Phi(\bar{u}) &= \epsilon B^2(\phi_{zz} + \hat{\theta}_{zz}) + \frac{\epsilon}{B}g'(x_0)z(f(\phi) + f'(\phi)\hat{\theta} + \frac{1}{2}f''(\tilde{\phi})\hat{\theta}^2) \\ &\quad + [-\frac{\epsilon}{B}g'(x_0)L^4 + \frac{1}{2}\frac{\epsilon^2}{B^2}g''(\tilde{x})(z - L^4)^2]f(\phi + \hat{\theta}) \\ &= \epsilon B^2[\hat{\theta}_{zz} + zf'(\phi)\hat{\theta} + \frac{1}{2}zf''(\tilde{\phi})\hat{\theta}^2] + \left[-\epsilon B^2L^4 + \frac{1}{2}\frac{\epsilon^2}{B^2}g''(\tilde{x})(z - L^4)^2\right]f(\phi + \hat{\theta}).\end{aligned}$$

Since $z \in (-3L, \hat{P}L)$, we have

$$-\epsilon B^2L^4 + \frac{1}{2}\frac{\epsilon^2}{B^2}g''(\tilde{x})(z - L^4)^2 < -\frac{1}{2}\epsilon B^2L^4.$$

for ϵ sufficiently small (depending on L). Therefore,

$$\Phi(\bar{u}) \leq \epsilon B^2(\hat{\theta}_{zz} + zf'(\phi)\hat{\theta} + \frac{1}{2}zf''(\tilde{\phi})\hat{\theta}^2 - \frac{L^4}{2}f(\phi + \hat{\theta})). \quad (2.29)$$

Step 1. For $x \in [x_0 + \frac{\epsilon}{B}(-L - L^4), x_0 + \frac{\epsilon}{B}(L - L^4)]$, we have $\hat{\theta} = 0$. Thus

$$\Phi(\bar{u}) \leq -\frac{1}{2}\epsilon B^2L^4f(\phi) \leq 0.$$

Step 2. On the interval $[\xi_3, x_0 + \frac{\epsilon}{B}(-L - L^4))$, we have

$$f'(\phi) + \frac{1}{2}f''(\tilde{\phi})\hat{\theta} = (2\phi - 3\phi^2) + \frac{1}{2}(2 - 6\tilde{\phi})\hat{\theta} > 0$$

by Lemma 2.1. Since $z < 0$ and $f(\phi) < f(\phi + \hat{\theta})$ (as f is increasing near 0), we deduce, from (2.29)

$$\Phi(\bar{u}) \leq \epsilon B^2\left(\hat{\theta}_{zz} - \frac{L^4}{2}f(\phi)\right) \leq \epsilon B^2\left(\frac{\hat{\kappa}}{L^4(1 + |z|)^3} - \frac{L^4}{2}\frac{C'_6}{L^6}\right) \leq 0$$

for L large, as $-3L \leq z \leq -L$ by (2.26).

Step 3. On the interval $x \in (x_0 + \frac{\epsilon}{B}(L - L^4), \xi_4]$, we have $L \leq z \leq \hat{P}L$ and ϕ is close to 1 for L large. Thus,

$$f'(\phi) + \frac{1}{2}f''(\tilde{\phi})\hat{\theta} = (2\phi - 3\phi^2) + \frac{1}{2}(2 - 6\tilde{\phi})\hat{\theta} < -\frac{1}{2}.$$

and it holds that

$$\Phi(\bar{u}) \leq \epsilon B^2(\hat{\theta}_{zz} - \frac{1}{2}z\hat{\theta} - \frac{L^4}{2}f(\phi + \hat{\theta})). \quad (2.30)$$

For x in the interval $(x_0 + \frac{\epsilon}{B}(L - L^4), x_0 + \frac{\epsilon}{B}(L + 1 - L^4))$, we have

$$1 - \phi - \hat{\theta} \geq \frac{C_2}{2} \exp(-\lambda_2(L + 1)^{\frac{3}{2}}).$$

Therefore $f(\phi + \hat{\theta}) \geq C'_7 \exp(-\lambda_2(L + 1)^{\frac{3}{2}})$ holds. This and (2.30) shows

$$\begin{aligned} \Phi(\bar{u}) &\leq \epsilon B^2 \left[\frac{C_2}{2} \exp(-\lambda_2(L + 1)^{\frac{3}{2}}) \frac{2}{(1 + |z|)^3} - \frac{C'_7 L^4}{2} \exp(-\lambda_2(L + 1)^{\frac{3}{2}}) \right] \\ &\leq \epsilon B^2 \left(C_2 - \frac{C'_7 L^4}{2} \right) \exp(-\lambda_2(L + 1)^{\frac{3}{2}}) \leq 0 \end{aligned}$$

for L large. On the interval $(x_0 + \frac{\epsilon}{B}(L + 1 - L^4), \xi_4]$, we have $z \geq 1$ and thus

$$\frac{2}{(1 + z)^3} - \frac{z}{2} \frac{z^2}{(1 + z)} \leq 0$$

i.e. $\hat{\theta}_{zz} - \frac{1}{2}z\hat{\theta} \leq 0$ and $\Phi(\bar{u}) < 0$ follows from (2.30). This establishes our assertion that $\Phi(\bar{u}) < 0$ on $[\xi_3, \xi_4]$.

Set $\bar{u}(\xi_3) = \alpha_2$. (2.27) shows that α_2 is close to 0 for L suff. large. We define our upper solution u^* as follows:

$$u^*(x) = \begin{cases} \alpha_2 & \text{if } 0 \leq x \leq \xi_3, \\ \bar{u}(x) & \text{if } \xi_3 \leq x \leq \xi_4, \\ 1 & \text{if } \xi_4 \leq x \leq 1. \end{cases} \quad (2.31)$$

As in the lower solution case, standard arguments show that u^* is an upper solution in the entire interval $(0, 1)$. From our definitions of u_* and u^* , (2.19) and (2.31), and the estimates for ξ_1 and ξ_4 , (2.11) and (2.28), it follows immediately that $u_* < u^*$ on the entire interval $(0, 1)$.

REFERENCES

- [LN] Y. Lou and T. Nagylaki, A semilinear parabolic system for migration and selection in population genetics, *J. Differential Equations*, **181** (2002), 388–418.
- [LNN] Y. Lou and T. Nagylaki, W.-M. Ni An introduction to migration-selection PDE models, *Discrete and Continuous Dynamical Systems A*, **33** (2013), 4349–4373.
- [LNS] Y. Lou, W.-M. Ni and L. Su, An indefinite nonlinear diffusion problem in population genetics, II: Stability and multiplicity, *Discrete and Continuous Dynamical Systems A*, **27** (2010), 643–655.
- [NAG] T. Nagylaki, Conditions for the existence of clines, *Genetics*, **80** (1975), 595–615.
- [NNS] K. Nakashima, W.-M. Ni and L. Su, An indefinite nonlinear diffusion problem in population genetics, I: Existence, *Discrete and Continuous Dynamical Systems*, **27** (2010), 617–641.
- [NK1] K. Nakashima *The uniqueness of indefinite nonlinear diffusion problem in population genetics, part I*, *J. Differential Equations* **261** (2016), 6233 – 6282.

- [NK2] K. Nakashima *The uniqueness of an indefinite nonlinear diffusion problem in population genetics, part II*, J. Differential Equations **264** (2018), 1946 - 1983.
- [NK3] K. Nakashima *Multiple existence of an indefinite nonlinear diffusion problem in population genetics*, in preparation.

Tokyo University of Marine Science and Technology,
4-5-7 Kounan, Minato-ku, Tokyo,
108-8477, Japan, e-mail adress : nkimie@kaiyodai.ac.jp.

東京海洋大学 中島主恵