

Nonlinear Analysis 53 (2003) 683-699



www.elsevier.com/locate/na

An integral equation describing an asexual population in a changing environment

Q. Tang^{a,*}, D. Waxman^b

^aSMS, Pevensey I, University of Sussex, Brighton BN1 9QH, UK ^bSchool of Biological Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK

Received 9 October 1999; accepted 3 April 2002

Abstract

In this paper, we establish the existence of a travelling wave solution to an intrinsically nonlinear differential-integral equation arising from the mathematical modelling of an asexual reproduction process. The techniques used are fixed point theorems and asymptotic analysis. The proofs, although abstract, give a hint on how to obtain the solutions numerically. © 2003 Elsevier Science Ltd. All rights reserved.

1. Introduction

In this paper, we establish the existence of travelling wave solution of a mathematical model describing the population change influenced by a uniformly changing environment. We begin by describing the biological background and the mathematical formulation.

Populations of living organisms generally exist in environments that change with time. These changes may arise for a variety of factors including the presence of other populations, human intervention (agriculture) and geophysical phenomena. It is very important for scientists in evolutionary biology, agriculture and conservation to understand the response of a population to a changing environment. This is a complex matter since population dynamics may be significantly modified by these external factors.

Based on the theory of Kimura [3], Waxman and Peck [5] considered populations consisting of either asexually or sexually reproducing organisms and a number of results were presented for the case where the optimal phenotypic value increases linearly with time. Such a case corresponds to a uniformly changing environment. The regime

^{*} Corresponding author.

E-mail address: q.tang@sussex.ac.uk (Q. Tang).

analysed corresponded to one in which the distribution of genotypic values had settled down to a travelling-wave solution. In such a solution, the shape of the distribution remains fixed, but its position follows the increasing value of the optimal genotype. The results obtained were supported by extensive numerical work.

The present work gives a rigorous proof of the existence of solutions for the differential-integral equation established in [5]. While the model was based on the work of Kimura [3] and a recent extension by Waxman and Peck [5], we include, for completeness, a brief introduction on how we simplify the Kimura's formulation and motivate the equation obeyed by the distribution of genotypic effects.

First, some terminology: (1) *Chromosome*: a string like structure within a cell. (2) *Diploid*: chromosomes are present in pairs. (3) *Locus* (*pl. Loci*): region of a chromosome where a gene resides. (4) *Gene*: part of a chromosome storing hereditary information. It is responsible for the production of an amino acid chain, e.g. a protein. (5) *Alleles*: different possible genes at a locus; different alleles produce different amino acid chains (normally, different proteins).

Consider an effectively infinite population of diploid asexual organisms that evolve in continuous time and have alleles with continuous effects (see [3]). An organism is born, matures instantaneously to adulthood and, before dying, may produce offspring via asexual reproduction. Selection occurs on a single phenotypic trait that is controlled by 2L alleles located at L loci. Mutations in offspring are taken to occur at the time of their birth. The allelic mutation rate is μ and provided $\delta = 2L\mu \ll 1$, an offspring is unlikely to contain more than one mutated allele. If x^* is the parental value of an effect of an allele that is mutated in an offspring, the probability of the allelic effect of the offspring lying in the infinitesimal interval (x, x + dx) is $f(x - x^*) dx$ where

$$f(x - x^*) = \sqrt{\frac{1}{2\pi m^2}} \exp\left[-\frac{(x - x^*)^2}{2m^2}\right].$$
 (1.1)

The phenotypic value of the trait is Z and this decomposes into a genotypic value, G, and an environmental effect E:

$$Z = G + E.$$

G is continuous and runs from $-\infty$ to ∞ and E is a random variable that is independent of G and has a mean expectation of 0 and a variance of V_e .

For each individual, the probability of producing an offspring per unit time, i.e. the birth rate, is taken to be independent of their genotype and given by P(t).

Let $D_{ph}(z)$ be the death rate of individuals in a static environment with phenotypic value Z = z. We assume $D_{ph}(z)$ has a minimum. It thus increases with the deviation of z away from the minimum and this is a form of stabilising selection. We take $D_{ph}(z)=1+z^2/(2V)$ corresponding to an optimal phenotypic value (i.e. the one with the smallest death rate) of z=0. The death rate of individuals with genotypic value G=x, which we denote by D(x), is obtained by averaging $D_{ph}(x+E)$ over all environmental effects E. We obtain

$$D(x) = 1 + \frac{V_{\rm e}}{2V} + \frac{x^2}{2V}.$$

Let us now consider a constantly changing environment, in which the optimum phenotypic value increases uniformly with time. In this case the death rate of individuals with genotypic value G = x at time t is D(x - ct) where c is the constant rate of change of the optimal phenotype. The distribution (probability density) of genotypic values in the population is denoted by $\Phi(x, t)$. From the model specified, it follows, by considering a very small time interval where the non-overlapping events of birth (accompanied by mutation) and death occur, that

$$\frac{\partial \Phi(x,t)}{\partial t} = \left[(1-\delta)P(t) - D(x-ct) \right] \Phi(x,t) + \delta P(t) \int_{-\infty}^{\infty} f(x-y)\Phi(y,t) \, \mathrm{d}y \\ + \Phi(x,t) \left[\int_{-\infty}^{\infty} D(y-ct)\Phi(y,t) \, \mathrm{d}y - P(t) \right].$$

Many natural populations have numbers or densities that remain remarkably close to being constant in time (cf. [1,4]). We incorporate this ecological feature by choosing a birth rate that is equal to the mean death rate of the population, i.e., we choose, for all times,

$$P(t) = \int_{-\infty}^{\infty} D(y - ct)\Phi(y, t) \,\mathrm{d}y.$$
(1.2)

This leads to

$$\frac{\partial \Phi(x,t)}{\partial t} = [(1-\delta)P(t) - D(x-ct)]\Phi(x,t) + \delta P(t) \int_{-\infty}^{\infty} f(x-y)\Phi(y,t) \,\mathrm{d}y.$$
(1.3)

Let us now go to new variables. Define

$$x' = x - ct, \quad t' = t, \quad \Psi(x', t') = \Phi(x, t),$$

then, on omitting the primes for typographical simplicity, $\Psi(x,t)$ obeys

$$\frac{\partial \Psi(x,t)}{\partial t} - c \frac{\partial \Psi(x,t)}{\partial x} = [(1-\delta)P(t) - D(x)]\Psi(x,t) + \delta P(t) \int_{-\infty}^{\infty} f(x-y)\Psi(y,t) \, \mathrm{d}y.$$

On the assumption that $\Psi(x,t)$ settles down in the new coordinate system, after some time, to a time-independent solution (the travelling wave solution in the original coordinates) which we denote by $\psi(x)$, we obtain

$$-c\frac{\partial\psi(x)}{\partial x} = [(1-\delta)P - D(x)]\psi(x) + \delta P \int_{-\infty}^{\infty} f(x-y)\psi(y)\,\mathrm{d}y,\tag{1.4}$$

$$P = \int_{-\infty}^{\infty} D(x)\psi(x) \,\mathrm{d}x. \tag{1.5}$$

Taking into account that ψ is a probability density function, the final form of the equation to be studied mathematically is set as

$$\begin{cases} -\psi'(x) = ((1-\delta)P - \alpha - 3\beta x^2)\psi + \delta P \int_{-\infty}^{\infty} f(x-y)\psi(y) \, \mathrm{d}y, \\ P = \int_{-\infty}^{\infty} (\alpha + 3\beta x^2)\psi(x) \, \mathrm{d}x, \int_{-\infty}^{\infty} \psi(x) \, \mathrm{d}x = 1, \\ \psi(x) \ge 0 \quad \text{for all } x \in \mathbb{R}, \end{cases}$$
(1.6)

where $\alpha = (1 + (V_e/2V))/c$ and $\beta = 1/(6Vc)$ and all constants involved are positive.

Consequently, using an integrating factor, the problem can be re-written as: find a continuous function ψ such that

$$\psi(x) = \delta P \int_{x}^{\infty} \int_{-\infty}^{\infty} e^{((1-\delta)P - \alpha)(z-x) - \beta(z^{3} - x^{3})} f(z-y)\psi(y) \, \mathrm{d}y \, \mathrm{d}z,$$

$$P = \int_{-\infty}^{\infty} (\alpha + 3\beta x^{2})\psi(x) \, \mathrm{d}x,$$

$$\int_{-\infty}^{\infty} \psi(x) \, \mathrm{d}x = 1,$$

$$\psi(x) \ge 0 \quad \text{for all } x \in \mathbb{R}.$$
(1.7)

In this paper, we discuss the existence of a solution for the above problem. In Section 2, we discuss a related linear problem on a finite interval (-M, M), establishing the existence and uniqueness. In Section 3, we discuss the nonlinear problem on (-M, M), using the linear solution to define an operator F, then use a fixed point theorem to establish the existence. It is here that we lose the uniqueness. The method of proof itself suggests a numerical method to obtain a solution but without uniqueness, we cannot control which solution is actually obtained. Finally, in Section 4, the limit in $M \to \infty$ is taken and the solution of the limit problem is obtained. In taking the limit $M \to \infty$, we need a technical assumption that $\delta = 2L\mu < 2/3$. We feel that this assumption could be relaxed but some technical estimates may be needed.

2. A linearized problem

In formulation (1.4) and (1.5), the dependence of P on ϕ makes the problem highly nonlinear, that is causing us technical difficulties. In this section, we assume that P is a given positive constant and investigate the corresponding simplified, linearized problem.

First we make some assumptions on f. Since f is a Gaussian distribution, we know that $f(x) = c_{\gamma} e^{-\gamma x^2}$ for some positive constants γ and c_{γ} . However, our proofs apply to all smooth functions f satisfying

(H1) (1) There exist positive constants
$$\gamma$$
, γ_1 , c and c_1 such that $c_1 e^{-\gamma_1 x^2} < f(x) \leq c e^{\gamma |x|}$.

(2) There exist positive constants γ₂ and c₂ such that |f'(x)| ≤ c₂e^{-γ₂|x|}.
 (3) ∫_{-∞}[∞] f(x) dx = 1.

2.1. Formulation of the problem on the whole real line

Since P is assumed to be a constant, we set $b = \delta P$ and $a = (1 - \delta)P - \alpha$ to reduce the number of constants involved in the discussion. The linear problem is now an eigenvalue problem: find ϕ and λ such that

$$\lambda \phi(x) = b \int_{x}^{\infty} \int_{-\infty}^{\infty} f(z - y) \phi(y) e^{a(z - x) + \beta(x^{3} - z^{3})} dy dz,$$

$$\int_{-\infty}^{\infty} \phi(x) dx = 1,$$

$$\phi(x) \ge 0 \quad \text{for all } x \in \mathbb{R}.$$
 (2.1)

Note that it is necessary to introduce the parameter λ because of the constraint $\int_{-\infty}^{\infty} \phi(x) dx = 1$ need to be dealt with. This turns the problem into a linear eigenvalue problem. We later prove that if the problem has a solution, then $\lambda = 1$.

We can also rewrite Eq. (2.1) as

$$\lambda\phi(x) = \int_{-\infty}^{\infty} H(x, y)\phi(y) \,\mathrm{d}y \tag{2.2}$$

with

$$H(x, y) = b \int_{x}^{\infty} f(z - y) e^{a(z - x) + \beta(x^3 - z^3)} dz.$$
 (2.3)

We have the following results about the kernel H(x, y).

Proposition 2.1. (1) H(x, y) is a uniformly bounded positive function.

(2) $H(x, y) \rightarrow 0$ uniformly with respect to y when $|x| \rightarrow \infty$.

(3) $|H_x(x, y)|$ is a uniformly bounded function in x and y.

The proof of this proposition is fairly straightforward because of the exponential nature of the integrand, we leave the details to interested readers.

2.2. Solution of the eigenvalue problem posed on a bounded domain (-M, M)

Instead of looking at the existence of problem (2.1), Let H be given as in (2.3), we redefine the following operator on a bounded interval (-M, M):

$$F(\phi) = \int_{-M}^{M} H(x, y)\phi(y) \, \mathrm{d}y.$$
 (2.4)

The reason of using this operator on a bounded domain (-M, M) instead of \mathbb{R} is that we can use some existing results on eigenvalues for integral operators to prove the existence of solutions.

Proposition 2.2. For any given M > 0 and any given P, there exists a pair $\{\lambda_M, \phi_M\} \in \mathbb{R}_+ \times C([-M,M])$ satisfying

$$F(\phi) = \int_{-M}^{M} H(x, y)\phi_M(y) \, \mathrm{d}y = \lambda_M \phi_M,$$

$$\int_{-M}^{M} \phi_M \, \mathrm{d}x = 1,$$
 (2.5)

where λ_M is an eigenvalue of the operator F and for any other spectrum point λ of F, we have $|\lambda| > |\lambda_M|$, ϕ_M is the unique eigenfunction associated with λ_M that satisfies (2.5). In addition, ϕ_M has the following property:

$$\phi_M(x) > 0 \quad \forall x \in (-M, M).$$

Proof. The proof of this theorem is a straightforward consequence of the following Jentzsch's theorem (cf. [2]): Let H(x, y) be continuous and > 0 on $[-M, M] \times [-M, M]$ for some positive number M. Denote the spectrum of the operator F as S(F), then the largest point in $\overline{S(F) \cap \mathbb{R}_+}$ is an eigenvalue, denoted by λ_M . All other spectrum points are larger than λ_M in absolute value and λ_M is simple (this means that its associated eigenspace is one dimensional). The eigenfunction ϕ_M associated with λ_M is positive in (-M, M). \Box

The fact that the solution is continuous is obvious from the integral expression. The following is an interesting property of the eigenfunctions of the linear problem:

Proposition 2.3. There exists a constant K depending only on a and b such that for any given continuous function $\phi \ge 0$, $\int_{-M}^{M} \phi(x) dx = 1$, we have

$$\int_{-M}^{M} \int_{-M}^{M} (1+x^2) H(x, y) \phi(y) \, \mathrm{d}y \, \mathrm{d}x \le K.$$

Proof. It is clear that we need only to show that for some constant c depending only on H, we have

$$\int_{-M}^{M}\int_{-M}^{M}(-a+3\beta x^{2})H(x,y)\phi(y)\,\mathrm{d} y\,\mathrm{d} x\leqslant bc.$$

As a matter of fact, when M is sufficiently large, we have

$$\int_{-M}^{M} \int_{-M}^{M} (-a + 3\beta x^{2}) H(x, y) \phi(y) \, \mathrm{d}y \, \mathrm{d}x$$

$$\leq b \int_{-M}^{M} \int_{-M}^{M} \int_{x}^{\infty} (-a + 3\beta x^{2}) f(z - y) \mathrm{e}^{a(z - x) + \beta(x^{3} - z^{3})} \phi(y) \, \mathrm{d}z \, \mathrm{d}y \, \mathrm{d}x$$

Q. Tang, D. Waxman/Nonlinear Analysis 53 (2003) 683-699

$$= b \int_{-M}^{M} \int_{-M}^{M} \int_{x}^{\infty} f(z-y) \frac{\partial}{\partial x} e^{a(z-x)+\beta(x^{3}-z^{3})} \phi(y) dz dx dy$$

$$= b \left(\int_{-M}^{M} \int_{M}^{\infty} \int_{-M}^{M} + \int_{-M}^{M} \int_{-M}^{M} \int_{-M}^{z} \right) f(z-y)$$

$$\times \frac{\partial}{\partial x} e^{a(z-x)+\beta(x^{3}-z^{3})} \phi(y) dx dz dy$$

$$= I_{1} + I_{2}.$$

For I_1 , we have

$$I_{1} = b \int_{-M}^{M} \int_{M}^{\infty} \int_{-M}^{M} f(z - y) \frac{\partial}{\partial x} e^{a(z - x) + \beta(x^{3} - z^{3})} \phi(y) dx dz dy$$

$$= b \int_{-M}^{M} \int_{M}^{\infty} f(z - y) \phi(y) (e^{a(z - M) + \beta(M^{3} - z^{3})} - e^{a(z + M) + \beta(-M^{3} - z^{3})}) dz dy$$

$$\leq bc \int_{-M}^{M} \int_{M}^{\infty} f(z - y) \phi(y) dz dy$$

$$\leq bc,$$

where c is a constant depending on a and β only.

For I_2 , we have

$$I_{2} = b \int_{-M}^{M} \int_{-M}^{M} \int_{-M}^{z} f(z - y) \frac{\partial}{\partial x} e^{a(z - x) + \beta(x^{3} - z^{3})} \phi(y) dx dz dy$$
$$= b \int_{-M}^{M} \int_{M}^{\infty} f(z - y) \phi(y) (1 - e^{a(z + M) + \beta(-M^{3} - z^{3})}) dz dy$$
$$\leq b \int_{-M}^{M} \int_{M}^{\infty} f(z - y) \phi(y) dz dy \leq b. \qquad \Box$$

3. The fully nonlinear problem on a bounded interval

Having established existence and estimates of the solutions of the linearized problem, we study the fully nonlinear problem on the bounded interval (-M, M) in this section. As a result, all our solutions and properties depend on M. However, to simplify notation, we suppress the dependence on M here and defer the detailed study of this dependence to Section 4.

First, we define

$$S_M := \left\{ \phi \in L^1(-M,M), \ \phi \ge 0, \ \int_{-M}^M \phi(x) \, \mathrm{d}x = 1 \right\},$$

Q. Tang, D. Waxman/Nonlinear Analysis 53 (2003) 683-699

$$P_{M}(\phi) := \int_{-M}^{M} (\alpha + 3\beta x^{2})\phi(x) dx,$$

$$b_{\phi} := \delta P_{M},$$

$$a_{\phi} := (1 - \delta)P_{M} - \alpha.$$
(3.1)

Then, for any given $\phi \in S_M$, let $\{\lambda_{\phi}, \hat{\phi}\}$ be the eigenvalue–eigenvector pair defined in Proposition 2.2, it is easy to deduce from Proposition 2.2 that $\lambda_{\phi} > 0$ and moreover, we have

$$\lambda_{\phi}\hat{\phi}(x) = b_{\phi} \int_{x}^{M} \int_{-M}^{M} f(z-y)\hat{\phi}(y) e^{a_{\phi}(z-x) + \beta(x^{3}-z^{3})} \,\mathrm{d}y \,\mathrm{d}z.$$
(3.2)

The full nonlinear problem we want to study is: find $\{\lambda_M, \phi_M\} \in \mathbb{R} \times S_M$ such that

$$b_{\phi_M} \int_x^M \int_{-M}^M f(z-y)\phi_M(y) e^{a_{\phi_M}(z-x) + \beta(x^3 - z^3)} \, \mathrm{d}y \, \mathrm{d}z = \lambda_{\phi_M} \phi_M(x).$$
(3.3)

(3.4)

We then define an operator $F_M : S_M \to S_M$ as follows: for any $\phi \in S_M$,

$$F_M \phi := \hat{\phi},\tag{3.5}$$

where $\hat{\phi} \in S_M$ is a solution of (3.2) and we observe that a solution of (3.3) is a fixed point of the operator F_M . To show the existence of a fixed point for the operator F_M , we use the following.

Theorem 3.1 (Schauder's Fixed Point Theorem). Let S_M be a closed convex subset in a Banach Space, and F_M be a continuous mapping of S_M into itself such that $F_M(S_M)$ is a compact set. Then F_M has at least one fixed point.

To show that the operator F_M defined in (3.4) satisfies the conditions of Schauder's Fixed Point Theorem, we need to show

Theorem 3.2. (1) S_M defined in (3.1) is convex and closed in $L^1(-M, M)$.

- (2) F_M is a continuous mapping and $F_M(S_M) \subset S_M$.
- (3) $F_M(S_M)$ is a compact set in $L^1(-M, M)$.

Proof. The proof of (1) is straightforward.

(2) We need to show that if $\phi \in S_M$, $F_M \phi \in S_M$. This is obvious by definition. Then, we need to show that if $\eta_n = F_M \phi_n$ and if

$$\phi_n \to \phi \in L^1(-M,M),$$

then

$$\eta_n \to \eta \in L^1(-M, M)$$
 and $\eta = F\phi$.

This is equivalent to say that we have two sequences of real numbers b_n and a_n such that

 $b_n \ge c > 0$,

$$b_n \to b,$$

$$a_n \to a,$$

$$b_n \int_x^M \int_{-M}^M f(z - y)\eta_n(y) e^{a_n(z - x) + \beta(x^3 - z^3)} dy dz = \lambda_n \eta_n(x)$$

From

$$\lambda_n = b_n \int_{-M}^{M} \int_{x}^{M} \int_{-M}^{M} f(z - y) \eta_n(y) e^{a_n(z - x) + \beta(x^3 - z^3)} \, \mathrm{d}y \, \mathrm{d}z \, \mathrm{d}x,$$

it is straightforward to conclude that $\{\lambda_n\}$ is a bounded sequence and hence (up to choosing a subsequence) converges to a positive number λ . Following the proof of (3) in the following, subjecting to choosing another sequence, we have $\eta_n \to \eta$ in $L^1(-M, M)$. Up to choosing a further subsequence, we have $\eta_n(x) \to \eta(x)$ almost everywhere. Take the limit $n \to \infty$, we obtain

$$b\int_x^M \int_{-M}^M f(z-y)\eta(y)\mathrm{e}^{a(z-x)+\beta(x^3-z^3)}\,\mathrm{d}y\,\mathrm{d}z = \lambda\eta(x).$$

The above result is for a subsequence. For the full sequence, it is easy to verify that

$$\lim_{n \to \infty} b_n \int_x^M \int_{-M}^M f(z - y) \eta_n(y) e^{a_n(z - x) + \beta(x^3 - z^3)} \, \mathrm{d}y \, \mathrm{d}z$$
$$= b \int_x^M \int_{-M}^M f(z - y) \eta(y) e^{a(z - x) + \beta(x^3 - z^3)} \, \mathrm{d}y \, \mathrm{d}z.$$

The fact that the right-hand side is equal to $\lambda \eta$ guarantees the continuity result (note that we did not prove the convergence of the whole sequence $\lambda_n \phi_n$, it is only a consequence of the conclusion).

(3) For any $\phi \in S_M$, let $F_M \phi = \eta$, we have

$$\delta \alpha \leq b_{\phi} < \delta(\alpha + 3\beta M^2),$$

 $-\delta \alpha < a_{\phi} < (1 - \delta)3\beta M^2 - \delta \alpha$

and

$$\begin{aligned} \lambda_{\phi} &= b_{\phi} \int_{-M}^{M} \int_{x}^{M} \int_{-M}^{M} f(z-y) \eta(y) \mathrm{e}^{a_{\phi}(z-x) + \beta(x^{3}-z^{3})} \,\mathrm{d}y \,\mathrm{d}z \,\mathrm{d}x \\ &\geq \delta \alpha \int_{-M}^{M} \int_{x}^{M} \int_{-M}^{M} f(z-y) \eta(y) \mathrm{e}^{-\delta \alpha(M-x) + \beta(x^{3}-M^{3})} \,\mathrm{d}y \,\mathrm{d}z \,\mathrm{d}x \\ &\geq C > 0, \end{aligned}$$

where C is a positive constant independent of ϕ (but maybe dependent of M). Hence

where B and C_0 are various positive constants independent of ϕ (but could be dependent of M). Consequently,

$$F_M(S_M) \subset \left\{ \phi \in L^1(-M,M), \ \phi \ge 0, \ \int_{-M}^M \phi = 1, \ \|\phi'\|_{L^1(-M,M)} \le C_0 \right\}$$

which is a compact subset of $L^1(-M, M)$. \Box

Finally, we conclude

Theorem 3.3. For any given M > 0, problem (3.3) admits a solution ϕ_M with associated 'eigenvalue' $\lambda_M > 0$.

4. Properties of the solutions of (3.3) when $M \to \infty$

We want to take the limit $M \to \infty$ in (3.3) to obtain a solution for the full nonlinear problem

$$b_{\phi} \int_{x}^{\infty} \int_{-\infty}^{\infty} f(z - y)\phi(y) e^{a_{\phi}(z - x) + \beta(x^{3} - z^{3})} dy dz = \lambda_{\phi}\phi(x),$$

$$b_{\phi} = \delta P,$$

$$a_{\phi} = (1 - \delta)P - \alpha.$$
(4.1)

We now discuss the properties of the solutions (λ_M, ϕ_M) of (3.3) as $M \to \infty$.

Proposition 4.1. λ_M satisfies the following estimate:

$$\lambda_M \leq 1.$$

Proof. Multiplying both sides of the integral equation in (3.3) by $\alpha + 3\beta x^3$ and integrating over (-M, M) yields

$$\lambda_M P_M = b_M \int_{-M}^{M} \int_{-M}^{M} \int_{x}^{M} f(z - y) \phi_M(y) e^{a_M(z - x) + \beta(x^3 - z^3)} (\alpha + 3\beta x^2) dz dx dy$$

= $\delta P_M \int_{-M}^{M} \int_{-M}^{M} \int_{-M}^{z} f(z - y) \phi_M(y) e^{(1 - \delta)P_M(z - x)} \frac{d}{dx}$

$$\times e^{\alpha(x-z)+\beta(x^{3}-z^{3})} dx dz dy = \delta P_{M} \int_{-M}^{M} \int_{-M}^{M} f(z-y)\phi_{M}(y)(1-e^{a_{M}(z+M)-\beta(x^{3}+M^{3})}) dz dy + (1-\delta)P_{M}\delta P_{M} \times \int_{-M}^{M} \int_{-M}^{M} \int_{-M}^{z} f(z-y)\phi_{M}(y)e^{a_{M}(z-x)+\beta(x^{3}-z^{3})} dz dx dy \leq \delta P_{M} + (1-\delta)P_{M}\lambda_{M}.$$

It is easy to deduce then $\lambda_M \leq 1$. The proof is complete.

The next bound is about P_M .

Proposition 4.2. Let $\delta < \frac{2}{3}$, there is a constant C such that for any M sufficiently large,

$$P_M \leq C.$$

Proof. We prove this proposition by contradiction. Assuming that $P_M \to \infty$ as $M \to \infty$ ∞ , we have (defining $Q_M = ((1 - \delta)P_M - \alpha)/\beta)$

$$\lambda_M \phi_M(x) = \delta P_M \int_{-M}^{M} \int_{x}^{M} f(z - y) \phi_M(y) e^{[(1 - \delta)P_M - \alpha - \beta(x^2 + xz + z^2)](z - x)} dz dy$$

$$\geq \delta P_M \int_{-M}^{M} \int_{x^2 + xz + z^2 \leq ((1 - \delta)P_M - \alpha)/\beta} f(z - y) \phi_M(y) dz dy,$$

$$x \leq z \leq M.$$

There are two possibilities: (1) $Q_M < M^2$, we have

$$\lambda_M \ge \delta P_M \int_{-\sqrt{Q_M}}^{\sqrt{Q_M}} \int_{-M}^{M} \int_{x^2 + xz + z^2 \le ((1-\delta)P_M - \alpha)/\beta} f(z-y)\phi_M(y) \, \mathrm{d}z \, \mathrm{d}x \, \mathrm{d}y,$$

$$x \le z \le M.$$

(2) $Q_M \ge M^2$, we have

$$\lambda_M \ge \delta P_M \int_{-M}^M \int_{-M}^M \int_{x^2 + xz + z^2 \le ((1-\delta)P_M - \alpha)/\beta} f(z - y)\phi_M(y) \, \mathrm{d}z \, \mathrm{d}x \, \mathrm{d}y,$$
$$x \le z \le M.$$

In the first case, it is easy to see that

$$\lambda_M \ge \delta P_M R_M \int_{-\sqrt{Q_M}}^{\sqrt{Q_M}} \phi_M(y) \, \mathrm{d} y$$

with $R_M > \gamma$ for some constant $\gamma > 0$ when M is sufficiently large. Also, we have

$$\int_{-\sqrt{Q_M}}^{\sqrt{Q_M}} \phi_M(y) \, \mathrm{d}y = 1 - \int_{-M}^{-\sqrt{Q_M}} \phi_M(y) \, \mathrm{d}y - \int_{\sqrt{Q_M}}^{M} \phi_M(y) \, \mathrm{d}y.$$
(4.2)

From

$$P_M = \int_{-M}^{M} (\alpha + 3\beta x^2) \phi_M \, \mathrm{d}x,$$

we obtain

$$P_{M} \geq \int_{-M}^{-\sqrt{Q_{M}}} (\alpha + 3\beta x^{2})\phi_{M}(y) \,\mathrm{d}y + \int_{\sqrt{Q_{M}}}^{M} (\alpha + 3\beta x^{2})\phi_{M}(y) \,\mathrm{d}y$$
$$\geq 3\beta Q_{M} \left(\int_{-M}^{-\sqrt{Q_{M}}} \phi_{M}(y) \,\mathrm{d}y + \int_{\sqrt{Q_{M}}}^{M} \phi_{M}(y) \,\mathrm{d}y \right).$$

Hence

$$\int_{-M}^{-\sqrt{Q_M}} \phi_M(y) \,\mathrm{d}y + \int_{\sqrt{Q_M}}^{M} \phi_M(y) \,\mathrm{d}y \leqslant \frac{P_M}{3\beta Q_M}.$$

Noting that $Q_M = ((1 - \delta)P_M - \alpha)/\beta$, we have

$$\int_{-M}^{-\sqrt{Q_M}} \phi_M(y) \,\mathrm{d}y + \int_{\sqrt{Q_M}}^{M} \phi_M(y) \,\mathrm{d}y \leq \frac{P_M}{3[(1-\delta)P_M - \alpha]}$$

In order that this is < 1, we simply need, since $P_M \rightarrow \infty$,

$$\frac{1}{3(1-\delta)} < 1$$

or equivalently,

$$\delta < \frac{2}{3}$$

Substitute these into (4.2), we have

$$\int_{-\sqrt{Q_M}}^{\sqrt{Q_M}} \phi_M(y) \, \mathrm{d}y \ge c > 0$$

and consequently

 $1 \ge \lambda_M \ge \delta P_M R_M c$

for some positive constant c independent of M. This implies a contradiction. Hence, $\{P_M\}$ is a bounded set in this case.

In the second case, we have, using previous notation

$$1 \geqslant \lambda_M \geqslant \delta P_M R_M.$$

This also implies a contradiction. So $\{P_M\}$ is a bounded set. \Box

We have obtained

Theorem 4.3. Assume that $\delta < \frac{2}{3}$, the solution pair (λ_M, ϕ_M) of (3.3) satisfy the following estimates:

$$0 \leqslant \lambda_M \leqslant 1, \tag{4.3a}$$

$$\lim_{M \to \infty} \lambda_M \ge C_1, \tag{4.3b}$$

$$\phi_M(x) \ge 0,\tag{4.3c}$$

$$\int_{-M}^{M} \phi_M(x) \,\mathrm{d}x = 1, \tag{4.3d}$$

$$\int_{-M}^{M} (\alpha + 3\beta x^2) \phi_M(x) \,\mathrm{d}x \leqslant C_2, \tag{4.3e}$$

$$\int_{-M}^{M} |\phi'_M(x)| \, \mathrm{d}x \leqslant C_3. \tag{4.3f}$$

Here C_1 , C_2 and C_3 are some positive constants independent of M.

Proof. The first new results in this theorem is $\underline{\lim}_{M\to\infty} \lambda_M \ge C_1$. From

we deduce that

$$\lambda_M = \int_{-M}^{M} \int_{-M}^{M} f(z - y) \phi_M(y) (1 - e^{a_M(z + M) + \beta(-M^3 - z^3)}) \, dz \, dy$$

As a_M is a bounded number, we have, when M is sufficiently large

$$e^{a_M(z+M)+\beta(-M^3-z^3)} \leqslant \begin{cases} 1 & z \in (-M, -M/2), \\ e^{a_MM/2-7\beta M^3/8} & z \in (-M/2, M). \end{cases}$$

Consequently, it is clear that

$$\lambda_M \ge \int_{-M}^{M} \int_{-M/2}^{M} f(z-y)\phi_M(y)(1-e^{a_M M/2-7\beta M^3/8}) \,\mathrm{d}z \,\mathrm{d}y \ge C_1 > 0.$$
(4.4)

Secondly, the proof of $\int_{-M}^{M} |\phi'_{M}(x)| dx \leq C$ follows from (4.4) and Proposition 4.2. Finally, (4.3d) follows from (4.3e) and (4.3f).

All the remaining results in this theorem have already been proved. \Box

Remark 4.4. (1) It is possible to show that the functions ϕ_M are $C^{\infty}([-M,M])$ functions with corresponding norms bounded by numbers independent of M, however, the proof is tedious and the result is not very useful to our subsequent discussions, hence we do not discuss in detail.

(2) It is clear that our functions ϕ_M are defined on [-M, M], so they do not have a common definition domain. In the discussion of convergence, however, we need a common definition domain. We therefore need to discuss the convergence of ϕ_M s on a restricted interval [-L, L] on which all ϕ_M s are defined. From Proposition 4.2, it is easy to see that some constant C independent of M, we have

$$\int_{-M}^{-L} \phi_M(x,t) \,\mathrm{d}x + \int_{L}^{M} \phi_M(x,t) \,\mathrm{d}x \leqslant \frac{C}{L^2}$$

So the contribution of ϕ_M outside [-L, L] can be neglected as the number L is intended to be large.

Choosing a sequence $L_n \to \infty$, using a diagonal argument, it is possible to find a sequence ϕ_{M_n} that converges to ϕ defined on \mathbb{R} .

Corollary 4.5. Assume that $\delta < 2/3$. Let $\phi_M|_{[-L,L]}$ be the restriction of ϕ_M 's defined as in (3.3) to [-L,L], then $\{\phi_M|_{[-L,L]}\}$ is a bounded sequence in $W^{1,1}(-L,L)$.

The convergence on a bounded interval:

Theorem 4.6. Assume that $\delta < 2/3$, for any given L > 0, take a subsequence, if necessary, of $M \to \infty$ (still denoted by M), for any real $p \ge 1$, there exist $\phi \in W^{1,1}_{loc}(-\infty,\infty) \cap L^p_{loc}(-\infty,\infty) \cap L^1(-\infty,\infty)$ and $\lambda > 0$ such that

$$\phi_M \to \phi \ge 0 \quad \text{in } L^p(-L,L) \ \forall p \in [1,\infty) \text{ and } \forall L,$$

$$(4.5a)$$

$$\lambda_M \to \lambda \quad in \ \mathbb{R},$$
 (4.5b)

$$P_M \to P = \int_{-\infty}^{\infty} (\alpha + 3\beta x^2) \phi(x) \, \mathrm{d}x \quad in \ \mathbb{R},$$
(4.5c)

$$a_M \to a = (1 - \delta)P - \alpha \quad in \ \mathbb{R},$$
 (4.5d)

$$\int_{-M}^{M} \phi_M(x) \,\mathrm{d}x \to \int_{-\infty}^{\infty} \phi(x) \,\mathrm{d}x = 1. \tag{4.5e}$$

Moreover, we have

(1)
$$\int_{-\infty}^{\infty} H(x, y)\phi(y) \, \mathrm{d}y = \lambda \phi(x)$$
 with $H = \int_{x}^{\infty} f(z - y) \mathrm{e}^{a(z-x) + \beta(x^3 - z^3)} \, \mathrm{d}z.$
(2) $\lambda = 1.$

Proof. We adopt the diagonal argument outlined in Remark 4.4, as $M \to \infty$, take a subsequence if necessary, the convergence of $\{\phi_M\}$ and $\{\lambda_M\}$ and the fact that $\phi \ge 0$ are obvious. We, of course, still use the same index M to simplify notation. For (4.5c), it is easy to deduce that for any fixed L,

$$\lim_{M\to\infty} P_M \ge \lim_{M\to\infty} \int_{-L}^{L} (\alpha + 3\beta x^2) \phi_M(x) \, \mathrm{d}x = \int_{-L}^{L} (\alpha + 3\beta x^2) \phi(x) \, \mathrm{d}x.$$

Taking the limit $L \to \infty$, we have $\lim_{M\to\infty} P_M \ge P$. To show the inverse inequality, from (*C* is used to denotes various positive constants independent of *M* and ϕ_M , they may have different values in different places)

$$\begin{split} &\int_{-M}^{M} (\alpha + 3\beta x^{2})^{2} \phi_{M}(x) \, dx \\ &= \frac{\delta P_{M}}{\lambda_{M}} \int_{-M}^{M} \int_{x}^{M} \int_{-M}^{M} (\alpha + 3\beta x^{2})^{2} \phi_{M}(y) f(z - y) e^{a_{M}(z - x) + \beta(x^{3} - z^{3})} \, dy \, dz \, dx \\ &= \frac{\delta P_{M}}{\lambda_{M}} \int_{-M}^{M} \int_{-M}^{M} \int_{-M}^{z} \phi_{M}(y) f(z - y) e^{(1 - \delta)P_{M}(z - x)} \\ &\left(\frac{d^{2}}{dx^{2}} e^{\alpha(x - z) + \beta(x^{3} - z^{3})} - 6\beta x e^{\alpha(x - z) + \beta(x^{3} - z^{3})} \right) \, dx \, dz \, dy \\ &\leqslant C + C \int_{-M}^{M} \int_{-M}^{M} \int_{-M}^{z} \phi_{M}(y) f(z - y) e^{(1 - \delta)P_{M}(z - x)} \\ &\frac{d^{2}}{dx^{2}} e^{\alpha(x - z) + \beta(x^{3} - z^{3})} \, dx \, dz \, dy \\ &= C + C \int_{-M}^{M} \int_{-M}^{M} f(z - y) \phi_{M}(y) \\ &\left(\alpha + 3\beta z^{2} - (\alpha + 3\beta M^{2}) e^{\alpha_{M}(z + M) + \beta(-M^{3} - z^{3})} \right) \, dy \, dz \\ &+ C \int_{-M}^{M} \int_{-M}^{M} \int_{-M}^{z} \phi_{M}(y) f(z - y) e^{(1 - \delta)P_{M}(z - x)} \, \frac{d}{dx} e^{\alpha(x - z) + \beta(x^{3} - z^{3})} \, dx \, dz \, dy \\ &\leqslant C + C \int_{-M}^{M} \int_{-M}^{M} f(z - y) \phi_{M}(y) (\alpha + 6\beta(z - y)^{2} + 6\beta y^{2}) \\ &+ C \int_{-M}^{M} \int_{-M}^{z} f(z - y) \phi_{M}(y) (\alpha + 3\beta M^{2}) e^{\alpha_{M}M/2 - 7\beta M^{3}/8}. \end{split}$$

Since

$$P_M \ge \int_{-M}^{-M/2} \phi_M(x)(\alpha + 3\beta x^2) \ge \int_{-M}^{-M/2} \phi_M(x) \left(\alpha + \frac{3}{4}\beta M^2\right) dx,$$

so

$$\int_{-M}^{-M/2} \phi_M(x) M^2 \,\mathrm{d}x \leqslant C.$$

Substituting back into our main estimate, we obtain

$$\int_{-M}^{M} (\alpha + 3\beta x^2)^2 \phi_M(x) \, \mathrm{d}x \leqslant C.$$

Hence, for any given L,

$$P_M = \left(\int_{-L}^{L} + \int_{-M}^{-L} + \int_{L}^{M}\right) (\alpha + 3\beta x^2) \phi_M(x) dx$$

$$\leqslant \int_{-L}^{L} (\alpha + 3\beta x^2) \phi_M(x) dx + \left(\int_{-M}^{-L} + \int_{L}^{M}\right) \frac{(\alpha + 3\beta x^2)^2}{\alpha + 3\beta L^2} \phi_M(x) dx$$

$$\leqslant \int_{-L}^{L} (\alpha + 3\beta x^2) \phi_M(x) dx + \frac{C}{L^2}$$

for some constant C independent of M. Consequently,

$$\lim_{M\to\infty}P_M\leqslant\int_{-L}^{L}(\alpha+3\beta x^2)\phi(x)\,\mathrm{d}x+C/L^2.$$

Letting $L \to \infty$, we obtain (4.5c).

Eq. (4.5d) is now trivial.

For (4.5e), the proof is similar to that of (4.5c). First,

$$\lim_{M \to \infty} \int_{-M}^{M} \phi_M(x) \, \mathrm{d}x \ge \lim_{M \to \infty} \int_{-L}^{L} \phi_M(x) \, \mathrm{d}x = \int_{-L}^{L} \phi(x) \, \mathrm{d}x.$$

Taking the limit $L \to \infty$, we have

$$\lim_{M \to \infty} \int_{-M}^{M} \phi_M(x) \, \mathrm{d}x \ge \int_{-\infty}^{\infty} \phi(x) \, \mathrm{d}x$$

From

$$\int_{-M}^{M} \phi_M(x)(\alpha + 3\beta x^2) \,\mathrm{d}x \leqslant C,$$

we have

$$\int_{L}^{M} \phi_{M}(x) \,\mathrm{d}x + \int_{-M}^{-L} \phi_{M}(x) \,\mathrm{d}x \leqslant \frac{C}{\alpha + 3\beta L^{2}} \leqslant \frac{C}{L^{2}}.$$

Hence

$$\lim_{M\to\infty}\int_{-M}^{M}\phi_M(x)\,\mathrm{d}x\leqslant\lim_{M\to\infty}\int_{-L}^{L}\phi_M(x)\,\mathrm{d}x+\frac{C}{L^2}\leqslant\int_{-L}^{L}\phi(x)\,\mathrm{d}x+\frac{C}{L^2}.$$

Taking the limit $L \to \infty$, we obtain

$$\lim_{M\to\infty}\int_{-M}^{M}\phi_M(x)\,\mathrm{d}x\leqslant\int_{-\infty}^{\infty}\phi(x)\,\mathrm{d}x.$$

Now we prove (1) and (2). Denote

$$H_M(x, y) = \delta P_M \int_x^M f(z - y) e^{a_M(z - x) + \beta(x^3 - z^3)} dz$$

and

$$H(x, y) = \delta P \int_x^\infty f(z - y) \mathrm{e}^{a(z - x) + \beta(x^3 - z^3)} \,\mathrm{d}z,$$

where P is the limit of P_M , a is the limit of a_M .

First, we show (1). For any L > 0 and M > L, taking the limit $M \to \infty$ in

$$\int_{-L}^{L} H_M(x, y) \phi_M(y) \, \mathrm{d} y \leq \lambda_M \phi_M(x),$$

we obtain

$$\int_{-L}^{L} H(x, y)\phi(y) \,\mathrm{d}y \leq \lambda \phi(x).$$

Taking the limit $L \to \infty$, we have

$$\int_{-\infty}^{\infty} H(x, y)\phi(y) \,\mathrm{d}y \leq \lambda \phi(x).$$

We define

$$\tilde{\phi}_M(x) = \begin{cases} \phi_M(x) & |x| < M, \\ 0 & \text{otherwise} \end{cases}$$

then $\tilde{\phi}_M(x) \to \phi(x)$ almost everywhere (subjecting to choosing another subsequence). Using the fact that $\tilde{\phi}_M \ge 0$ and Fatou's Theorem, we have

$$\lambda\phi(x) = \lim_{M \to \infty} \lambda_M \phi_M(x) = \lim_{M \to \infty} \int_{-\infty}^{\infty} H(x, y) \tilde{\phi}_M(y) \, \mathrm{d}y \ge \int_{-\infty}^{\infty} H(x, y) \phi(y) \, \mathrm{d}y.$$

Hence (1) is proved.

For (2), we use (4.3) and take the limit $M \to \infty$. \Box

References

[1] A. Hastings, Population Biology, Springer, Berlin, 1997.

- [2] H. Hochstadt, Integral Equations, Wiley, New York, 1973.
- [3] M. Kimura, A stochastic model concerning the maintenance of genetic variability in quantitative characters, Proc. Nat. Acad. Sci. USA 54 (1965) 731–736.
- [4] M. Ridley, Evolution, Boston: Blackwell, 1996.
- [5] D. Waxman, J.R. Peck, Sex and adaptation in a changing environment, Genetics 153 (1999) 1041–1053.