

*EVOLUTION IN A CHANGING ENVIRONMENT:
EXISTENCE OF SOLUTIONS*

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Abstract. We establish the existence of solutions of an intrinsically nonlinear differential-integral equation that arises from the mathematical modelling of the evolution of an asexual population in a changing environment. The main objective is to pave the way for a rigorous analysis of the linear stability of travelling wave solutions of the corresponding problem.

1. Introduction. Populations of living organisms generally exist in environments that change with time. Knowledge of the behaviour of populations under conditions of external change is very important for evolutionary biology, agriculture and conservation. In this work we investigate mathematical properties of a model where the response of a population to environmental change has been considered in the biological literature [7]. In this model it was assumed that individuals are characterized by a single quantitative trait, which can take on a continuous range of values; a possible example being a physical length, such as the height of an individual. The phenotypic (i.e. observed) value of this trait determines the death rate, which is the probability of the individual dying per unit time. Different phenotypic values generally lead to different death rates, so the population is under some form of natural selection. The form of the death rate adopted had an optimal phenotypic value, such that individuals with phenotypic values smaller or larger than the optimal value had an enhanced death rate. It was further assumed in [7] that the optimal phenotypic value was not constant in time, as is often assumed, but changed with time. The simplest time variation was considered, namely a linear increase in the optimal phenotypic value. This seems reasonable in an evolutionary context, where the earth's environment has certain features that have changed over long time scales, the amount of oxygen in the atmosphere being one possible example. Another example, on a smaller time scale, is the much discussed possible increase in global temperature (global warming). In [7] the following conjectures were made: (i) The probabilistic density distribution

describing the population admits a travelling wave solution, in the presence of the changing optimal phenotype, (ii) solutions for general initial data, in a neighbourhood of the travelling wave solution, should converge to the travelling wave solution as time $t \rightarrow \infty$. These statements were supported by extensive numerical work and non-rigorous mathematical approximations.

The model of [7] was based on a mathematical model of mutation introduced by Crow and Kimura [1] of a random walk type, which was analysed in [3] and by subsequent authors including Turelli [6]. A first mathematical investigation of the model of [7], for an asexual population, was given in [5], where the authors considered conjecture (i), made in [7] about travelling wave solutions. In [5], it was rigorously established that the travelling wave solution does exist. There are a number of open mathematical questions concerning this model and that is the rationale for the present paper.

In particular, we discuss the existence of solutions in greater detail. First, we show that the fully nonlinear problem has a local solution in time t . Second, we linearize the fully nonlinear equation around the travelling wave solution and prove the global in time existence of the linearized solution. These results indicate the technical difficulties in dealing with the mathematical models of this type and pave the way for the linear stability analysis for the full problem.

In order to describe the biological content of our paper we briefly recall the biological background and terminology. A *chromosome* is a string-like structure within a cell. A *diploid* organism has chromosomes in pairs. A *locus* (pl. loci) is a region of a chromosome where a gene resides. Subsequently by *gene* we mean a part of a chromosome storing hereditary information. It is responsible for the production of an amino acid chain, e.g. a protein. Finally, *alleles* are different possible genes at a locus; different alleles produce different amino acid chains (normally, different proteins).

We shall 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 $U = 2L\mu \ll 1$, an offspring is unlikely to contain more than one mutated allele, thus the distribution of mutant effects is accurately taken to be that of a single 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

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

We could consider more general smooth probability densities having finite higher moments and our analysis would not be changed much. However, we consider only the case of normal probability density, most important for applications.

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 $D_{\text{ph}}(z)$ be the death rate of individuals in a static environment with phenotypic value $Z = z$. We assume $D_{\text{ph}}(z)$ has a minimum. Thus, it increases with the deviation of z away from the minimum and this is a form of stabilizing selection. We take $D_{\text{ph}}(z) = 1 + z^2/(2V)$ 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 $D_{\text{ph}}(x + E)$ over all environmental effects E . Due to our form of D_{ph} we obtain

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

Let us now consider a constantly changing environment, in which the optimum phenotypic value increases uniformly in 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 $\Phi(x, t)$. In our model we assume that birth (accompanied by mutation) and death are nonoverlapping events. Thus,

$$(1.1) \quad \frac{\partial \Phi(x, t)}{\partial t} = [(1 - U)P(t) - D(x - ct)]\Phi(x, t) \\ + UP(t) \int_{-\infty}^{\infty} f(x - y)\Phi(y, t) dy \\ + \Phi(x, t) \left[\int_{-\infty}^{\infty} D(y - ct)\Phi(y, t) dy - P(t) \right].$$

Many natural populations have numbers or densities that remain remarkably close to being constant in time (cf. [2] and [4]). We incorporate this ecological feature into the calculations by choosing a birth rate that is equal to the mean death rate of the population: i.e. we choose, for all times,

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

Moreover, this condition closes the system, otherwise we would need one more equation for $P(t)$.

The above condition leads to a simplification of (1.1). Upon some normalization this system takes the form

$$(1.2) \quad \begin{cases} \frac{\partial \phi}{\partial t} = ((1 - U)\bar{d}(t) - d(x - ct))\phi + U\bar{d}(t)f \star \phi, \\ \phi(x, 0) = \phi_0(x), \\ \phi(x, t) \geq 0 \quad \text{for all } (x, t) \in (-\infty, \infty) \times (0, \infty), \\ \int_{-\infty}^{\infty} \phi(x, t) dx = 1 \quad \text{for all } t \geq 0. \end{cases}$$

where

$$f \star \phi = \int_{-\infty}^{\infty} f(x - y)\phi(y, t) dy,$$

$$d(x) = 1 + x^2, \quad \bar{d}(t) = \int_{-\infty}^{\infty} d(x - ct)\phi(x, t) dx.$$

The last two conditions of (1.2) ensure that ϕ is a probability density distribution.

In this paper, we look first at the fully nonlinear initial value problem (1.2). Interestingly, we seek solutions of (1.2) in function spaces which involve second and fourth statistical moments of solutions. It turns out that this is a convenient technical device.

We are able to show existence of local in time solutions of (1.2) for admissible data. The question of existence of global in time solutions is open. However, for special data this is solved. Indeed, existence of travelling wave solutions was shown in [5]. Now we look at how this effect comes into play. To this end, we introduce new variables

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

Then, on omitting the primes for typographical simplicity, $\phi(x, t)$ obeys

$$\frac{\partial \phi(x, t)}{\partial t} - c \frac{\partial \phi(x, t)}{\partial x} = [(1 - U)P(t) - D(x)]\phi(x, t) + UP(t) \int_{-\infty}^{\infty} f(x - y)\phi(y, t) dy.$$

Assume that $\phi(x, t)$ settles down in the new co-ordinate system, after some time, to a time-independent solution (the travelling wave solution in the original co-ordinates) which we still denote by $\phi(x)$. Then we obtain

$$(1.3) \quad \left\{ \begin{array}{l} -c \frac{d\phi(x)}{dx} = [(1-U)P - D(x)]\phi(x) + UP \int_{-\infty}^{\infty} f(x-y)\phi(y) dy, \\ P = \int_{-\infty}^{\infty} D(x)\phi(x) dx, \\ \int_{-\infty}^{\infty} \phi(x) dx = 1, \\ \phi(x) \geq 0 \quad \text{for all } x \in \mathbb{R}, \\ \phi(x) \rightarrow 0 \quad \text{as } |x| \rightarrow \infty, \end{array} \right.$$

which was discussed in [5].

Denote a solution to the travelling wave problem (1.3) by $\phi_0(x)$. Upon returning to the original co-ordinate frame, $\phi(x, t) = \phi_0(x - ct)$ is a solution of (1.2). Assume that the initial data of the fully nonlinear problem is sufficiently close to $\phi_0(x)$. We postulate that the solution of the fully nonlinear problem can be written as an asymptotic power series of a small parameter ε :

$$\phi = \phi_0 + \varepsilon\phi_1 + \varepsilon^2\phi_2 + \dots$$

If we substitute this into the equation and take the coefficient of ε , then we obtain the linearized problem. This is in fact an equation involving ϕ_1 . Moreover, the linear stability of the travelling wave solutions is equivalent to proving that

$$\|\phi_1\|_X(t) \rightarrow 0 \quad \text{as } t \rightarrow \infty,$$

where X is some appropriate function space with respect to the x variable. In the present paper, we show that the linearized problem is well posed and it has a global in time solution. But the question of stability of the travelling wave remains open and it is postponed to further research.

The layout of this paper is as follows: In Section 2, we establish the local existence of solutions for the fully nonlinear problem. In Section 3, we state the global existence of solutions for the linearized problem. We only sketch the proof, because it is based upon the same idea as Theorem 2.1, which is the main result of Section 2, and the detailed calculations are omitted.

2. Existence of solutions to the fully nonlinear problem. The idea is to convert the equation in (1.2) to an integral-differential type equation to which we can apply the Banach contraction mapping theorem.

First, we introduce the function space

$$X = \left\{ u \in C^0(\mathbb{R}) : \sum_{j=0}^2 p_{2j}(u) < \infty \right\},$$

where

$$p_j(u) = \|x^j u(x)\|_{L^\infty(\mathbb{R})}.$$

It is easy to see that X is a Banach space.

The main result of this section is local in time existence of probability density distributions which are solutions to (1.2). This goal is achieved in two steps. First, local in time solutions to (1.2) (neglecting (1.2_{3,4})) are constructed in Theorem 2.1. Subsequently we show that the solutions are nonnegative provided the initial data are. Finally, we establish that the average of solutions is preserved in time. We begin with the first stated task.

THEOREM 2.1. *Suppose that*

$$\phi(x, 0) = \phi_0(x), \quad \phi_0 \in X.$$

Then there exists a $T = T(\phi_0) > 0$ such that

$$(2.1) \quad \begin{aligned} \frac{\partial \phi}{\partial t} &= ((1 - U)\bar{d}(t) - d(x - ct))\phi + U\bar{d}(t)f \star \phi, \\ \phi(x, 0) &= \phi_0(x), \end{aligned}$$

admits a unique solution $\phi \in C^1([0, T], X)$.

We start with some preparations. Suppose that $\phi \in C^1([0, T], X)$ is a solution to (2.1). Then we can treat \bar{d} as a given function of time. Hence we obtain, using the ODE variation of parameter technique,

$$(2.2) \quad \begin{aligned} \phi(x, t) &= \exp\left(-\int_0^t [d(x - cs) - (1 - U)\bar{d}(s)] ds\right) \phi_0(x) \\ &\quad + \int_0^t \exp\left(-\int_s^t [d(x - c\tau) - (1 - U)\bar{d}(\tau)] d\tau\right) U\bar{d}(s)f \star \phi ds. \end{aligned}$$

In view of the dependence of \bar{d} on ϕ , this equation is highly nonlinear.

Denote the right hand side of (2.2) by $\Psi(\phi)$. Then our problem is to find a fixed point for the mapping $\Psi(\phi) : C([0, T], X) \rightarrow C([0, T], X)$. For this purpose we define

$$Y_T = C([0, T], X), \quad \|\phi\|_{Y_T} = \max_{t \in [0, T]} \|\phi\|_X(t),$$

$$B(\phi_0, R_0) = \{\phi \in Y_T : \phi(0) = \phi_0, \max_{t \in [0, T]} \|\phi(t) - \phi_0\|_X \leq R_0\} \subset Y_T.$$

Thus, Ψ can be regarded as a mapping from Y_T into Y_T . From now on we will tacitly use the convention that a real-valued function of two variables $F(t, x)$ is in fact a function of one variable t with values in an appropriate function space.

Next, we show

PROPOSITION 2.2. *For any $R > 0$ and $\phi_0 \in X$, there exists $T = T(R, \phi_0) > 0$ such that*

- (a) Ψ is a contraction mapping in $B(\phi_0, R)$.
- (b) Ψ maps $B(\phi_0, R)$ into itself.

Proof. For (a), the task is to estimate

$$\max_{t \in [0, T]} p_j(\Psi(\phi_1)(t) - \Psi(\phi_2)(t)), \quad j = 0, 2, 4.$$

In the following, we shall use the following quantities:

$$\bar{d}_j = \int_{\mathbb{R}} d(x - ct)\phi_j(x, t) dx \quad \text{for } j = 1, 2,$$

$$G_j(s, t, x) = \frac{1}{t - s} \int_s^t [d(x - c\tau) - (1 - U)\bar{d}_j(\tau)] d\tau.$$

By the very definition of Y_T we may write

$$(\Psi(\phi_1) - \Psi(\phi_2))(t) = I_1 + I_2$$

with

$$\begin{aligned} I_1(x, t) &= \left(\exp\left(-\int_0^t (d(x - cs) - (1 - U)\bar{d}_1(s)) ds\right) \right. \\ &\quad \left. - \exp\left(-\int_0^t (d(x - cs) - (1 - U)\bar{d}_2(s)) ds\right) \right) \phi_0(x) \\ (2.3) \quad &= \phi_0(x) e^{-t(1+x^2-xtc+c^2t^2/3)} e^{(1-U)\int_0^t \bar{d}_1(\tau) d\tau} \\ &\quad \times (1 - e^{(1-U)\int_0^t (\bar{d}_2(\tau) - \bar{d}_1(\tau)) d\tau}), \\ I_2(x, t) &= \int_0^t \exp((t - s)G_1(t, s, x)) U \bar{d}_1(s) f \star \phi_1(x, s) ds \\ &\quad - \int_0^t \exp((t - s)G_2(t, s, x)) U \bar{d}_2(s) f \star \phi_2(x, s) ds. \end{aligned}$$

Before we start estimating I_1 and I_2 , we make a simple observation regarding the quantity $|e^{-a} - e^{-b}|$ for $a, b \in \mathbb{R}$. Namely, by the mean value theorem we obtain

$$(2.4) \quad |e^{-b} - e^{-a}| \leq |a - b| \max\{e^{-b}, e^{-a}\} \quad \text{for } a, b \in \mathbb{R}.$$

1) *Estimates of $p_0(I_1)$.* In virtue of (2.4) and $d(x) \geq 0$, we obtain

$$p_0(I_1) \leq \|\phi_0(x)\|_{L^\infty(\mathbb{R})} \exp\left((1-U) \int_0^t \bar{d}_2(\tau) d\tau\right) (1-U) \int_0^t |\bar{d}_1(\tau) - \bar{d}_2(\tau)| d\tau.$$

Now, we estimate $\bar{d}_1(\tau) - \bar{d}_2(\tau)$. We have

$$\begin{aligned} (2.5) \quad |\bar{d}_1(\tau) - \bar{d}_2(\tau)| &\leq \int_{\mathbb{R}} d(y - c\tau) |\phi_1 - \phi_2|(\tau) dy \\ &= \left(\int_{\mathbb{R} \setminus [-1,1]} + \int_{-1}^1 \right) d(y - c\tau) |\phi_1 - \phi_2|(\tau) dy \\ &\leq \int_{\mathbb{R} \setminus [-1,1]} (1 + 2c^2\tau^2 + 2y^2) |\phi_1 - \phi_2|(\tau) dy \\ &\quad + 2\|d(\cdot - c\tau)\|_{L^\infty[-1,1]} \|\phi_1(\tau) - \phi_2(\tau)\|_{L^\infty(\mathbb{R})} \\ &\leq \int_{\mathbb{R} \setminus [-1,1]} [(1 + 2c^2\tau^2)y^{-2}p_2(\phi_1 - \phi_2)(\tau) + y^{-2}p_4(\phi_1 - \phi_2)(\tau)] dy \\ &\quad + 2(3 + 2c^2\tau^2) \|\phi_1(\tau) - \phi_2(\tau)\|_{L^\infty(\mathbb{R})} \\ &= 2(1 + 2c^2\tau^2)p_2(\phi_1 - \phi_2)(\tau) + 2p_4(\phi_1 - \phi_2)(\tau) \\ &\quad + 2(3 + 2c^2\tau^2)p_0(\phi_1 - \phi_2)(\tau). \end{aligned}$$

In particular, if $\phi_2 = 0$, then for $\phi_1 \in B(\phi_0, R)$ we obtain

$$(2.6) \quad \begin{aligned} \bar{d}_1(t) &\leq 2(3 + 2c^2t^2) \|\phi_1\|_{Y_T} \\ &\leq 2(3 + 2c^2t^2)(\|\phi_0\|_X + R) =: C_0(t, R). \end{aligned}$$

Hence

$$p_0(I_1) \leq T \|\phi_0\|_{L^\infty(\mathbb{R})} e^{(1-U)C_1(R,T)} (1-U) \left(6 + \frac{4}{3}c^2T^2\right) \|\phi_1 - \phi_2\|_{Y_T},$$

where

$$C_1(R, T) := 2\left(3 + \frac{4}{3}c^2T^2\right)T(\|\phi_0\|_X + R).$$

2) *Estimates of $p_0(I_2)$.* It is obvious that

$$\begin{aligned} p_0(I_2) &\leq U \sup_x \left| \int_0^t (e^{-(t-s)G_1(t,s,x)} - e^{-(t-s)G_2(t,s,x)}) \bar{d}_1(s) f \star \phi_1(s) ds \right| \\ &\quad + U \sup_x \int_0^t e^{-(t-s)G_2(t,s,x)} |\bar{d}_1(s) - \bar{d}_2(s)| f \star \phi_1(s) ds \end{aligned}$$

$$\begin{aligned}
& + U \sup_x \int_0^t e^{-(t-s)G_2(t,s,x)} |\bar{d}_2(s)| |f \star (\phi_1 - \phi_2)|(s) ds \\
& = I_{21} + I_{22} + I_{23}.
\end{aligned}$$

We notice that (2.4) and (2.6) imply that

$$I_{21} = U \int_0^t \int_0^t |\bar{d}_1(\tau) - \bar{d}_2(\tau)| d\tau e^{(1-U)C_1(R,T)} C_1(R,T) \sup_{x \in \mathbb{R}} |f \star \phi_1(s)| ds.$$

Note that

$$(2.7) \quad \|f \star \phi\|_{L^\infty(\mathbb{R})} \leq \|\phi\|_{L^\infty(\mathbb{R})}.$$

Hence,

$$(2.8) \quad \begin{aligned} \|f \star \phi_1\|_{L^\infty(\mathbb{R})} & \leq \|f \star (\phi_1 - \phi_0 + \phi_0)\|_{L^\infty(\mathbb{R})} \\ & \leq \|\phi_1 - \phi_0\|_{L^\infty(\mathbb{R})} + \|\phi_0\|_{L^\infty(\mathbb{R})}. \end{aligned}$$

In virtue of (2.8), estimate (2.5) implies that

$$I_{21} \leq 4UT e^{(1-U)C_1(R,T)} C_1^2(R,T) \|\phi_1 - \phi_2\|_{Y_T}.$$

Now, in a similar way we deal with I_{22} :

$$\begin{aligned}
I_{22} & \leq U \int_0^t e^{(1-U)(t-s)C_1(R,T)} (R + \|\phi_0\|_{L^\infty(\mathbb{R})}) |\bar{d}_1(s) - \bar{d}_2(s)| ds \\
& \leq UTC_2(R,T) \|\phi_1 - \phi_2\|_{Y_T},
\end{aligned}$$

where

$$C_2(R,T) := e^{(1-U)C_1(R,T)} (R + \|\phi_0\|_{L^\infty(\mathbb{R})}) \left(6 + \frac{4}{3}c^2T^2\right).$$

Because of (2.6) and (2.7) we arrive at

$$I_{23} \leq UTC_0(R,T) e^{C_1(R,T)} \|\phi_1 - \phi_2\|_{Y_T}.$$

We may now collect those estimates:

$$\max_{s \in [0, T]} p_0(\Psi(\phi_1)(s) - \Psi(\phi_2)(s)) \leq TC_3(R, T, \phi_0) \|\phi_1 - \phi_2\|_{Y_T},$$

with an obvious definition of $C_3(R, T, \phi_0)$.

Furthermore, we have to estimate $p_i(\Psi(\phi_1)(s) - \Psi(\phi_2)(s))$, $i = 2, 4$, as well. Similarly to what we have done before, we note that

$$p_2(\Psi(\phi_1)(s) - \Psi(\phi_2)(s)) \leq p_2(I_1) + p_2(I_2)$$

and using similar computations to those for $p_0(I_1)$, employing (2.4) we can obtain

$$p_2(I_1) \leq \|x\phi_0(x)\|_{L^\infty(\mathbb{R})} (1-U) e^{C_1(R,T)} \int_0^t |\bar{d}_2(\tau) - \bar{d}_1(\tau)| d\tau.$$

Hence, due to (2.5),

$$p_2(I_1) \leq p_2(\phi_0)(1 - U)e^{C_1(R,T)}\left(6 + \frac{4}{3}c^2T^2\right)\|\phi_1 - \phi_2\|_{Y_T}.$$

Estimating $p_2(I_2)$ requires a bit more care. We need the following simple fact:

$$(2.9) \quad |x^2f(y)\psi(x - y)| \leq 2|f(y)y^2\psi(x - y)| + 2|f(y)\psi(x - y)|(x - y)^2.$$

Hence, if we write $M_2(f) = \int_{\mathbb{R}} f(y)y^2 dy$, we obtain

$$(2.10) \quad p_2(f \star \psi) \leq 2(M_2(f) + 1)p_2(\psi).$$

Thus, by (2.6),

$$\begin{aligned} p_2(I_2) &\leq U \int_0^t \int_0^t |\bar{d}_1(\tau) - \bar{d}_2(\tau)| d\tau e^{C_1(R,T)} |\bar{d}_1(s)| p_2(f \star \phi_1)(s) ds \\ &\quad + U e^{C_1(R,T)} \max_{0 \leq s \leq T} p_2(f \star \phi_1)(s) \int_0^t |\bar{d}_1(\tau) - \bar{d}_2(\tau)| d\tau \\ &\quad + TUC_0(R, T) e^{C_1(R,T)} \max_{0 \leq s \leq T} p_2(f \star (\phi_1(s) - \phi_2(s))) \end{aligned}$$

and because of (2.5), (2.9) and (2.10) we arrive at

$$\max_{0 \leq s \leq T} p_2(\Psi(\phi_1)(s) - \Psi(\phi_2)(s)) \leq TC_4(R, T, \phi_0)\|\phi_1 - \phi_2\|_{Y_T},$$

for some computable $C_4(R, T, \phi_0)$.

To estimate $p_4(\Psi(\phi_1)(s) - \Psi(\phi_2)(s))$ we need

$$\begin{aligned} |x^4f(y)\psi(x - y)| &\leq 4|f(y)y^4\psi(x - y)| + 2|f(y)\psi(x - y)|y^2(x - y)^2 \\ &\quad + f(y)|\psi(x - y)|(x - y)^4, \end{aligned}$$

which is easy to derive from (2.9). Hence,

$$(2.11) \quad p_4(f \star \phi) \leq 4M_4(f)\|\phi\|_{L^\infty} + 2M_2(f)p_2(\phi) + p_4(\phi),$$

where

$$M_4(f) = \int_{\mathbb{R}} x^4 f(x) dx.$$

Thus, re-visiting the estimates for $p_2(\Psi(\phi_1)(s) - \Psi(\phi_2)(s))$ and taking into account (2.11) leads us to

$$\max_{0 \leq s \leq T} p_4(\Psi(\phi_1)(s) - \Psi(\phi_2)(s)) \leq TC_5(R, T, \phi_0)\|\phi_1 - \phi_2\|_{Y_T}$$

for some $C_5(R, T, \phi_0)$. We therefore conclude that

$$(2.12) \quad \|\Psi(\phi_1) - \Psi(\phi_2)\|_{Y_T} \leq TC(R, T, \phi_0)\|\phi_1 - \phi_2\|_{Y_T}.$$

Now for fixed R and ϕ_0 , we can choose $T > 0$ such that

$$(2.13) \quad TC(R, T, \phi_0) = 1/2.$$

Hence we conclude that Ψ is a contraction mapping.

For (b), we notice that (a) implies

$$\begin{aligned} \|\Psi(\phi) - \phi_0\|_{Y_T} &\leq \|\Psi(\phi) - \Psi(\phi_0)\|_{Y_T} + \|\Psi(\phi_0) - \phi_0\|_{Y_T} \\ &\leq \frac{1}{2}\|\phi - \phi_0\| + \|\Psi(\phi_0) - \phi_0\|_{Y_T} \\ &\leq \frac{1}{2}R + \|\Psi(\phi_0) - \phi_0\|_{Y_T}. \end{aligned}$$

When T is sufficiently small, we can easily deduce that

$$(2.14) \quad \|\Psi(\phi_0) - \phi_0\|_{Y_T} \leq \frac{1}{2}R.$$

Indeed, we have

$$\begin{aligned} \Psi(\phi_0) - \phi_0 &= \phi_0(e^{-\int_0^t [d(x-cs) - (1-U)\bar{d}_0] ds} - 1) \\ &\quad + U \int_0^t e^{-\int_s^t [d(x-c\tau) - (1-U)\bar{d}_0] d\tau} \bar{d}_0(s) f \star \phi_0 ds, \end{aligned}$$

and the results of part (a) imply (2.14). Thus (b) is established. ■

Proof of Theorem 2.1. Using the Banach contraction mapping theorem and Proposition 2.2, it is straightforward to establish the existence of a unique solution to (2.1) in the class $C([0, T], X) \cap C^1([0, T], X)$. ■

PROPOSITION 2.3. *The unique solution to (2.1) depends continuously on the initial conditions in the X norm.*

Proof. Let $u(\phi)$ be the unique solution with initial condition ϕ . It is sufficient to show that for any given ϕ_1 and $R > 0$, if $T(R, \phi_1)$ satisfies (2.13), then there is a constant $C(R, \phi_1, T)$ such that

$$(2.15) \quad \|u(\phi_1) - u(\phi_2)\|_{Y_T} \leq C(T, R, \phi_1)\|\phi_1 - \phi_2\|_X$$

for ϕ_2 sufficiently close to ϕ_1 .

We slightly change the notation compared to that of Theorem 2.1, namely we denote by Ψ_ϕ the operator defined by the RHS of (2.2) for initial data ϕ . We shall consider $\phi_2 \in B(\phi_1, R)$ which is sufficiently close to ϕ_1 . It is clear from the definition that (see (2.2) and (2.3))

$$(2.16) \quad \|\Psi_{\phi_1}(\xi) - \Psi_{\phi_2}(\xi)\|_{Y_T} \leq C(T, R)\|\phi_1 - \phi_2\|_X.$$

Let $\phi_2 \in B(\phi_1, R)$ be arbitrary. By (2.13), we can find $\varrho < R$ such that Ψ_{ϕ_2} has a unique fixed point in $B(\phi_2, \varrho) \subset Y_T$ (i.e., we keep T fixed). Thus

$$\begin{aligned} \|u(\phi_1) - u(\phi_2)\|_{Y_T} &= \|\Psi_{\phi_1}(u(\phi_1)) - \Psi_{\phi_2}(u(\phi_2))\|_{Y_T} \\ &\leq \|\Psi_{\phi_1}(u(\phi_1)) - \Psi_{\phi_1}(u(\phi_2))\|_{Y_T} \\ &\quad + \|\Psi_{\phi_1}(u(\phi_2)) - \Psi_{\phi_2}(u(\phi_2))\|_{Y_T}. \end{aligned}$$

By (2.12), (2.13) and (2.16) we obtain

$$\|u(\phi_1) - u(\phi_2)\|_{Y_T} \leq \frac{1}{2}\|u(\phi_1) - u(\phi_2)\|_{Y_T} + C(R, T)\|\phi_1 - \phi_2\|_X,$$

that is, (2.15) follows. ■

THEOREM 2.4. *If $\phi_0 \geq 0$, then the unique solution to (2.1) satisfies $\phi(t, x) \geq 0$ for all $t < T_{\max}$, where T_{\max} is the maximal time of existence. Moreover, if*

$$\int_{\mathbb{R}} \phi(0, x) dx = 1,$$

then

$$(2.17) \quad \int_{\mathbb{R}} \phi(t, x) dx = 1,$$

i.e. we have constructed a unique solution to (1.2).

Proof. We first consider the case $\phi_0 > 0$. We define the set

$$E = \{t : \forall s \in [0, t], \phi(s) > 0\}.$$

Obviously, $0 \in E$. Assume that $t_0 \in \partial E$, i.e., for some x_0 , $\phi(t_0, x_0) = 0$. We must have $\phi(t_0) \not\equiv 0$. For otherwise, $\phi(t) \equiv 0$ for all $t > 0$ due to the uniqueness of solution. Hence $\bar{d}(t_0) > 0$ and $f * \phi(t_0) > 0$. Then the equation of (2.1) evaluated at $x = x_0$ yields

$$\frac{\partial}{\partial x} \phi(t_0, x_0) = U \bar{d}(t_0) f * \phi(t_0, x_0) > 0.$$

Due to time continuity of ϕ , there exists $\varepsilon > 0$ such that

$$\phi(\tau, x_0) < 0 \quad \text{for } \tau \in (t_0 - \varepsilon, t_0).$$

This is impossible.

Suppose that $\phi_0 \geq 0$. Now, we take an arbitrary element $h \in X$ such that $h > 0$ and consider the equation in (2.1) for initial condition $\phi_0 + \varepsilon h$. We obtain, by the previous reasoning, solutions ϕ^ε which are positive everywhere. By Proposition 2.3, we have

$$\lim_{\varepsilon \rightarrow 0} \phi^\varepsilon = \phi^0 \geq 0 \quad \text{in } Y_T.$$

Finally, we check (2.17). For this we simply integrate (2.1) over \mathbb{R} with respect to x . We obtain

$$\begin{aligned} \frac{d}{dt} \int_{\mathbb{R}} \phi(t, x) dx &= (1 - U) \bar{d}(t) \int_{\mathbb{R}} \phi(t, x) dx - \bar{d}(t) + U \bar{d}(t) \int_{\mathbb{R}} f * \phi(t, x) dx \\ &= \bar{d}(t) \left(\int_{\mathbb{R}} \phi(t, x) dx - 1 \right). \end{aligned}$$

That is, $y(t) = \int_{\mathbb{R}} \phi(t, x) dx$ satisfies an ODE

$$y' = \bar{d}(t)(y - 1),$$

and thus, by uniqueness of solutions, if $y(0) = 1$, then $y(t) = 1$ for all $t \geq 0$. Our theorem follows. ■

3. Existence of solution to the linearized problem. Let $\phi = \phi_0 + \varepsilon\phi_1 + \varepsilon^2\phi_2 + \dots$, where ϕ_0 is the solution of the travelling wave equation (1.3), and define $\bar{d}_0 = \int_{-\infty}^{\infty} d(x - ct)\phi_0(x, t) dx$. We substitute this into the equation and we take the coefficient of the ε term. We have, with $\bar{d}_1 = \int_{-\infty}^{\infty} d(x - ct)\phi_1(x, t) dx$,

$$(3.1) \quad -\frac{\partial\phi_1}{\partial t} = [d(x - ct) - \bar{d}_0(1 - U)]\phi_1 - (1 - U)\bar{d}_1(t)\phi_0 \\ - U\bar{d}_0 f \star \phi_1 - U\bar{d}_1(t)f \star \phi_0,$$

$$(3.2) \quad \phi_1(0, x) = \phi_{10}(x).$$

The function f is the Gaussian distribution as in the standard biological theory. If we consider $\phi_i \in Y_T$, $i = 0, 1$, then it is clear that the quantities \bar{d}_i are well defined. If we take into account that $\phi_0 = \phi_0(x - ct)$, we see that \bar{d}_0 is independent of time.

Considering (3.1) pointwise for each x , we have a linear ODE in t . Using an integrating factor, we obtain

$$(3.3) \quad \phi_1(t, x) = \exp\left(-\int_0^t [d(x - cs) - (1 - U)\bar{d}_0] ds\right)\phi_{10}(x) \\ + \int_0^t \exp\left(-\int_s^t [d(x - c\tau) - (1 - U)\bar{d}_0] d\tau\right) \left((1 - U)\bar{d}_1(s)\phi_0(s, x) ds \right. \\ \left. + U \int_0^t \exp\left(-\int_s^t [d(x - c\tau) - (1 - U)\bar{d}_0] d\tau\right) f \star (\bar{d}_0\phi_1 + \bar{d}_1(s)\phi_0(s, x)) ds\right) ds.$$

We are now ready to state the main result of this section.

THEOREM 3.1. *Suppose that $\phi_{10} \in X$ and $\int_{\mathbb{R}} \phi_{10}(x) dx = 0$. Then there exists a unique global in time solution to (3.1) such that $\phi_1 \in C^1((0, \infty), X)$. Moreover, for all $t > 0$, we have $\int_{\mathbb{R}} \phi_1(t) dx = 0$.*

Before we start the proof of this theorem we recall inequalities (2.7), (2.10), (2.11) that we used in the previous section:

$$p_k(f \star \phi) \leq \sum_{i=0}^k C(k, i) M_{k-i}(f) p_i(\phi), \quad k = 0, 2, 4,$$

where

$$(3.4) \quad M_i(f) = \int_{\mathbb{R}} x^i f(x) dx, \quad i = 0, 2, 4.$$

We also note that if $\phi \in X_T$, then

$$(3.5) \quad \left| \int_{\mathbb{R}} d(x - ct)\phi(t, x) dx \right| \leq \sum_{i=0}^2 c(i, t)p_i(\phi(t)),$$

where

$$c(4, t) = 2, \quad c(2, t) = 2(1 + 2c^2t^2), \quad c(0, t) = 2(3 + 2c^2t^2).$$

Sketch of proof of Theorem 3.1. We essentially follow the reasoning of Theorem 2.1. We use the space Y_T , and $B = \{\phi \in C([0, T], X) : \phi(0) = \phi_{10}, \|\phi - \phi_{10}\|_{Y_T} \leq R\}$, where $T, R > 0$. We define $\Psi : Y_T \rightarrow Y_T$ by the formula

$$\begin{aligned} \Psi(\phi)(t, x) &= e^{-tG(t,0)}\phi_{10}(x) \\ &\quad + \int_0^t e^{-(t-s)G(t,s,x)}((1-U)\bar{d}_1s\phi_0 + Uf \star (\bar{d}_0\phi_1 + \bar{d}_1s\phi_0)) ds. \end{aligned}$$

It is now possible to establish the first two steps below by modifying slightly Proposition 2.2.

STEP (i). Ψ is well defined and maps B into itself, i.e. $\|\Psi(\phi) - \phi_{10}\|_{Y_T} \leq R$ for $\phi \in B$.

STEP (ii). Ψ is a contraction for sufficiently small $T > 0$, i.e. $\|\Psi(\phi_1) - \Psi(\phi_2)\|_{Y_T} \leq \frac{1}{2}\|\phi_1 - \phi_2\|_{Y_T}$ for sufficiently small $T > 0$. Thus, we immediately conclude that Ψ has a unique fixed point ϕ_1 .

STEP (iii). It is also easy to see that the fixed point ϕ_1 of Ψ is in $C^1([0, T], X)$.

STEP (iv). We calculate the X norm of both sides of (3.2). Using (3.3) and (3.4) it is fairly easy to see that $\|\phi_1\|_X$ satisfies

$$\|\phi_1\|_X(t) \leq a(t) + \int_0^t b(s)\|\phi_1\|_X(s) ds$$

for some functions a and b . Thus, by the Gronwall inequality our solution is global in time.

STEP (v). Finally, we check that $\frac{d}{dt} \int_{\mathbb{R}} \phi_1(t, x) dx = 0$. For this purpose we integrate (3.1) over \mathbb{R} with respect to x . Reasoning as in the proof of Theorem 2.4, we see that $y(t) := \int_{\mathbb{R}} \phi_1(t, x) dx$ satisfies an ODE

$$\frac{d}{dt}y = \bar{d}_0y.$$

Due to $y(0) = 0$ and uniqueness of solutions to ODE's we deduce that $y(t) \equiv 0$, i.e.

$$\int_{\mathbb{R}} \phi_1(t, x) dx = 0. \quad \blacksquare$$

REFERENCES

- [1] J. F. Crow and M. Kimura, *The theory of genetic loads*, in: Proc. XI Internat. Congress of Genetics, S. J. Geerts (ed.), Pergamon, Oxford, 1964, 495–505.
- [2] A. Hastings, *Population Biology*, Springer, New York, 1997.
- [3] M. Kimura, *A stochastic model concerning the maintenance of genetic variability in quantitative characters*, Proc. Natl. Acad. Sci. U.S.A. 54 (1965), 731–736.
- [4] M. Ridley, *Evolution*, Blackwell, Boston, 1996.
- [5] Q. Tang and D. Waxman, *An integral equation describing an asexual population in a changing environment*, Nonlinear Anal. 53 (2003), 683–699.
- [6] M. Turelli, *Heritable genetic variation via mutation-selection balance: Lerch's zeta meets the abdominal bristle*, Theor. Pop. Biol. 25 (1984), 138–193.
- [7] D. Waxman and J. R. Peck, *Sex and adaptation in a changing environment*, Genetics 154 (1999), 1041–1053.

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