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A reaction–diffusion model for a single species with age structure. I Travelling wavefronts on unbounded domains

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In this paper, we derive the equation for a single species population with two age classes and a fixed maturation period living in a spatially unbounded environment. We show that if the mature death and diffusion rates are age independent, then the total mature population is governed by a reaction–diffusion equation with time delay and non-local effect. We also consider the existence, uniqueness and positivity of solution to the initial-value problem for this type of equation. Moreover, we establish the existence of a travelling-wave front for the special case when the birth function is the one which appears in the well-known Nicholson's blowflies equation and we consider the dependence of the minimal wave speed on the mobility of the immature population.

Keywords: delay; diffusion; structured population; non-local effect; travelling waves

1. Introduction

When incorporating diffusion into a time delay model, many investigators generally simply add a diffusion term to the corresponding delay ordinary differential equation (ODE) model (Yoshida 1982; Memory 1989; Yang & So 1998; Feng & Lu 1999). But in recent years it has become recognized that there are modelling difficulties with this approach. The problem is that individuals have not been at the same point in space at previous times. It appears that the first comprehensive attempt to address this difficulty was made by Britton (1990), who addressed the problem for a delayed Fisher equation on an infinite spatial domain. His idea was that, to account for the drift of individuals to their present position from all possible positions at previous times, the delay term has to involve a weighted spatial averaging over the whole of the infinite domain, the weighting to be properly derived using probabilistic arguments and the assumptions being made about the motion of the individuals. Gourley & Britton (1996) developed the ideas further by studying a predator–prey system with time delays and associated spatial averaging, again on an infinite domain, and they developed a general approach to the study of linear stability of the uniform steady states in the resulting non-local delay system. Another approach, which is motivated by Smith (1994), is to divide the population into two age classes—immature and mature—with the time delay being the maturation period. The appropriate delay system for the case of a patchy environment was derived in So *et al*. (2001), where various bifurcations of stable synchronized periodic oscillations and unstable phase-locked oscillations were studied. In this paper, we continue this study for the case of a continuous infinite spatial domain. The resulting equation is a reaction–diffusion equation, where the reaction term contains a time delay as well as non-local spatial averaging.

In § 2, we derive the model equation. The existence, uniqueness and positivity of solution to the initial-value problem is considered in § 3. In § 4, we prove the existence of travelling wavefronts for a particular choice of birth function, the one used in Nicholson's blowflies equation. Some observations about the minimal wave speed are also made in this section.

2. Derivation of the model

Let $u(t,a,x)$ denote the density of the population of the species under consideration at time $t \geqslant 0$, age $a \geqslant 0$ and location $x \in \Omega$. In this paper, we will consider the unbounded case when $\Omega = \mathbb{R}^n$ and leave the case of a bounded Ω to be studied in a separate paper. In fact, for simplicity of presentation, we assume $n = 1$, that is, $\Omega = \mathbb{R}$. In that case, it is natural to assume that

$$|u(t,a,\pm\infty)| < \infty, \quad \text{for } t \geqslant 0, \quad a \geqslant 0. \tag{2.1}$$

A standard argument on population with age structure and diffusion (Metz & Diekmann 1986) gives

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = D(a)\frac{\partial^2 u}{\partial x^2} - d(a)u, \tag{2.2}$$

where $D(a)$ and $d(a)$ are the diffusion rate and death rate, respectively, at age a. Let $r \geqslant 0$ be the maturation time for the species. Then the total matured population at time t and location x is given by

$$w(t,x) = \int_r^\infty u(t,a,x)\,\mathrm{d}a.$$

Therefore,

$$\begin{aligned}\frac{\partial w}{\partial t} &= \int_r^\infty \frac{\partial}{\partial t}u(t,a,x)\,\mathrm{d}a = \int_r^\infty \left[-\frac{\partial u}{\partial a} + D(a)\frac{\partial^2 u}{\partial x^2} - d(a)u\right]\mathrm{d}a \\ &= u(t,r,x) + \int_r^\infty \left[D(a)\frac{\partial^2 u}{\partial x^2} - d(a)u\right]\mathrm{d}a,\end{aligned}$$

where we have made the biologically realistic assumption

$$u(t,\infty,x) = 0. \tag{2.3}$$

Also, since only the mature can reproduce, we have

$$u(t,0,x) = b(w(t,x)), \tag{2.4}$$

where $b(\cdot)$ is the birth function. In order to proceed further, next we assume that the diffusion and death rates for the mature population are age independent, that is, $D(a) = D_{\mathrm{m}}$ and $d(a) = d_{\mathrm{m}}$ for $a \in [r, \infty)$, where D_{m} and d_{m} are constants. Then

$$\frac{\partial w}{\partial t} = u(t, r, x) + D_{\mathrm{m}} \frac{\partial^2 w}{\partial x^2} - d_{\mathrm{m}} w. \tag{2.5}$$

To obtain an equation for w, we need to evaluate $u(t, r, x)$. For this purpose, fix $s \geqslant 0$ and let $V^s(t, x) = u(t, t - s, x)$ for $s \leqslant t \leqslant s + r$. Then

$$\begin{aligned} \frac{\partial}{\partial t} V^s(t, x) &= \frac{\partial u}{\partial t}(t, a, x)\bigg|_{a=t-s} + \frac{\partial u}{\partial a}(t, a, x)\bigg|_{a=t-s} \\ &= D(t - s) \frac{\partial^2}{\partial x^2} V^s(t, x) - d(t - s) V^s(t, x), \end{aligned} \tag{2.6}$$

with

$$|V^s(t, \pm\infty)| < \infty. \tag{2.7}$$

Note that (2.6) is a linear reaction–diffusion equation. Applying the method of separation of variables to (2.6)–(2.7), we obtain

$$\begin{aligned} V^s(t, x) &= \int_{-\infty}^{\infty} k(s, \omega) \exp\left[-\int_s^t (\omega^2 D(\theta - s) + d(\theta - s))\,\mathrm{d}\theta\right] \mathrm{e}^{-\mathrm{i}\omega x}\,\mathrm{d}\omega \\ &= \int_{-\infty}^{\infty} k(s, \omega) \exp\left[-\int_0^{t-s} (\omega^2 D(a) + d(a))\,\mathrm{d}a\right] \mathrm{e}^{-\mathrm{i}\omega x}\,\mathrm{d}\omega, \end{aligned} \tag{2.8}$$

where $k(s, w)$ is determined as follows:

$$b(w(s, x)) = u(s, 0, x) = V^s(s, x) = \int_{-\infty}^{\infty} k(s, \omega) \mathrm{e}^{-\mathrm{i}\omega x}\,\mathrm{d}\omega.$$

In other words, $b(w(s, x))$ is the Fourier transform of $k(s, \omega)$. Therefore, $k(s, \omega)$ is the inverse Fourier transform of $b(w(s, x))$ and hence

$$k(s, \omega) = \frac{1}{2\pi} \int_{-\infty}^{\infty} b(w(s, y)) \mathrm{e}^{\mathrm{i}\omega y}\,\mathrm{d}y.$$

We denote by D_{I} and d_{I} the diffusion and death rates of the immature, respectively, i.e. $D(a) = D_{\mathrm{I}}(a)$ and $d(a) = d_{\mathrm{I}}(a)$ for $a \in [0, r]$. Then, provided

$$\alpha := \int_0^r D_{\mathrm{I}}(a)\,\mathrm{d}a > 0 \tag{2.9}$$

(in other words, there is some mobility among the immature), we have

$$\begin{aligned} &u(t, r, x) \\ &\quad = V^{t-r}(t, x) \\ &\quad = \int_{-\infty}^{\infty} k(t - r, \omega) \exp\left[-\int_0^r (\omega^2 D_{\mathrm{I}}(a) + d_{\mathrm{I}}(a))\,\mathrm{d}a\right] \mathrm{e}^{-\mathrm{i}\omega x}\,\mathrm{d}\omega \\ &\quad = \int_{-\infty}^{\infty} \left[\frac{1}{2\pi} \int_{-\infty}^{\infty} b(w(t - r, y)) \mathrm{e}^{\mathrm{i}\omega y}\,\mathrm{d}y\right] \exp\left[-\int_0^r (\omega^2 D_{\mathrm{I}}(a) + d_{\mathrm{I}}(a))\,\mathrm{d}a\right] \mathrm{e}^{-\mathrm{i}\omega x}\,\mathrm{d}\omega \end{aligned}$$

$$
\begin{aligned}
&= \frac{1}{2\pi}\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} b(w(t-r,y))\mathrm{e}^{\mathrm{i}\omega(y-x)}\exp\left[-\int_0^r(\omega^2 D_{\mathrm{I}}(a)+d_{\mathrm{I}}(a))\,\mathrm{d}a\right]\mathrm{d}y\,\mathrm{d}\omega\\
&= \frac{1}{2\pi}\int_{-\infty}^{\infty} b(w(t-r,y))\exp\left[-\int_0^r d_{\mathrm{I}}(a)\,\mathrm{d}a\right]\left[\int_{-\infty}^{\infty}\mathrm{e}^{-\alpha\omega^2}\mathrm{e}^{\mathrm{i}\omega(y-x)}\,\mathrm{d}\omega\right]\mathrm{d}y\\
&= \frac{1}{2\pi}\int_{-\infty}^{\infty} b(w(t-r,y))\exp\left[-\int_0^r d_{\mathrm{I}}(a)\,\mathrm{d}a\right]\sqrt{\frac{\pi}{\alpha}}\mathrm{e}^{-(x-y)^2/4\alpha}\,\mathrm{d}y\\
&= \frac{\exp[-\int_0^r d_{\mathrm{I}}(a)\,\mathrm{d}a]}{\sqrt{4\pi\alpha}}\int_{-\infty}^{\infty} b(w(t-r,y))\mathrm{e}^{-(x-y)^2/4\alpha}\,\mathrm{d}y. \qquad (2.10)
\end{aligned}
$$

Hence $w(t,x)$ satisfies

$$
\begin{aligned}
\frac{\partial w}{\partial t} &= D_{\mathrm{m}}\frac{\partial^2 w}{\partial x^2} - d_{\mathrm{m}}w\\
&\quad + \frac{\exp[-\int_0^r d_{\mathrm{I}}(\theta)\,\mathrm{d}\theta]}{\sqrt{4\pi\alpha}}\int_{-\infty}^{\infty} b(w(t-r,y))\mathrm{e}^{-(x-y)^2/4\alpha}\,\mathrm{d}y, \quad \text{for } t>r. \qquad (2.11)
\end{aligned}
$$

Let

$$
\varepsilon = \exp\left[-\int_0^r d_{\mathrm{I}}(a)\,\mathrm{d}a\right] \quad \text{and} \quad f_\alpha(x) = \frac{1}{\sqrt{4\pi\alpha}}\mathrm{e}^{-x^2/4\alpha}.
$$

Then $0<\varepsilon\leqslant 1$ and (2.11) becomes

$$
\frac{\partial w}{\partial t} = D_{\mathrm{m}}\frac{\partial^2 w}{\partial x^2} - d_{\mathrm{m}}w + \varepsilon\int_{-\infty}^{\infty} b(w(t-r,y))f_\alpha(x-y)\,\mathrm{d}y. \qquad (2.12)
$$

Equation (2.12) is a reaction–diffusion equation with time delays and non-local effects. Here ε reflects the impact of the death rate for the immature population and α represents the effect of the dispersal rate of the immature on the matured population. Notice that the death rate and diffusion rate of the immature enter (2.12) in a totally different way from that of the matured. When $\alpha\to 0$, that is as the immature become immobile, (2.12) reduces to

$$
\frac{\partial w}{\partial t} = D_{\mathrm{m}}\frac{\partial^2 w}{\partial x^2} - d_{\mathrm{m}}w + \varepsilon b(w(t-r,x)), \qquad (2.13)
$$

and the non-local effect disappears. If we further let $\varepsilon\to 1$, that is, all immatures live to maturity, then equation (2.13) becomes

$$
\frac{\partial w}{\partial t} = D_{\mathrm{m}}\frac{\partial^2 w}{\partial x^2} - d_{\mathrm{m}}w + b(w(t-r,x)), \qquad (2.14)
$$

which has been widely studied for different choices of the birth function $b(\cdot)$. See, for example, Yoshida (1982), Memory (1989), So & Yang (1998), Yang & So (1998) and So *et al*. (2000) for the finite-domain case, and So & Zou (2001) for a particular case of infinite domain.

For the rest of this paper we will concentrate on equation (2.12). Our goal is to describe the long-term behaviour of the mature population w. It is therefore useful to consider solutions to this equation for all $t\geqslant 0$, although technically (2.12) describes the evolution of the mature population only when $t\geqslant r$.

3. Existence, uniqueness and positivity of solutions of the Cauchy problem

Equation (2.12) is a delay equation with non-local interaction on the whole spatial domain $\mathbb{R}$. Naturally, as far as existence and uniqueness of solutions are concerned, an initial condition of delayed type should be considered. In other words, we consider the following initial-value problem (IVP),

$$\left.\begin{aligned}\frac{\partial w}{\partial t} &= D_{\mathrm{m}}\Delta w - d_{\mathrm{m}}w + \varepsilon\int_{-\infty}^{\infty} b(w(t-r,y))f_\alpha(x-y)\,\mathrm{d}y, \quad x\in\mathbb{R}, \quad t>0,\\ w(s,x) &= \phi(s,x), \quad x\in\mathbb{R}, \quad s\in[-r,0],\end{aligned}\right\} \tag{3.1}$$

where Δ is the Laplacian operator on $\mathbb{R}$, and ϕ is an initial function which will be specified below. The initial-value problem (3.1) can be solved using the method of steps, that is, we first solve (3.1) on $(0,r]\times\mathbb{R}$ and then on $(r,2r]\times\mathbb{R}$, etc. However, this leaves us with the question of smoothness of $w(t,x)$ on $(0,\infty)\times\mathbb{R}$; so instead we will use the following abstract approach.

Let $X = \mathrm{BUC}\,(\mathbb{R},\mathbb{R})$ be the Banach space of all bounded and uniformly continuous functions from $\mathbb{R}$ to $\mathbb{R}$ with the usual supremum norm $|\cdot|_X$, and let $X^+ = \{\phi\in X : \phi(x)\geqslant 0, \text{ for all } x\in\mathbb{R}\}$. It is easily seen that X^+ is a closed cone of X and X is a Banach lattice under the partial ordering induced by X^+. From Daners & Koch Medina (1992, theorem 1.5), it follows that the X-realization $D_{\mathrm{m}}\Delta_X$ of $D_{\mathrm{m}}\Delta$ generates an analytic semigroup $T(t)$ on X. Moreover, since solutions of the heat equation

$$\left.\begin{aligned}\frac{\partial w}{\partial t} &= D_{\mathrm{m}}\Delta w, \quad x\in\mathbb{R}, \quad t>0,\\ w(x,0) &= \phi(x), \quad x\in\mathbb{R},\end{aligned}\right\} \tag{3.2}$$

can be expressed in terms of the heat kernel, we have

$$(T(t)\phi)(x) = \frac{1}{\sqrt{4\pi D_{\mathrm{m}}t}}\int_{-\infty}^{\infty}\exp\biggl(-\frac{(x-y)^2}{4D_{\mathrm{m}}t}\biggr)\phi(y)\,\mathrm{d}y, \quad x\in R, \quad t>0, \quad \phi\in X. \tag{3.3}$$

It follows immediately from (3.3) that $T(t)X^+\subset X^+$.

Let $C = C([-r,0],X)$ be the Banach space of continuous functions from $[-r,0]$ into X with the supremum norm $\|\cdot\|$ and let $C^+ = \{\phi\in C : \phi(s)\in X^+, \text{for all } s\in[-r,0]\}$. Then C^+ is a closed cone of C. For convenience, we will also identify an element $\phi\in C$ as a function from $[-r,0]\times\mathbb{R}$ into $\mathbb{R}$ defined by $\phi(s,x)=\phi(s)(x)$. For any continuous function $y(\cdot):[-r,b)\to X$, where $b>0$, we define $y_t\in C, t\in[0,b)$, by $y_t(s) = y(t+s)$, $s\in[-r,0]$. It is easily seen that $t\mapsto y_t$ is a continuous function from $[0,b)$ to C. The right-hand side of (3.1) induces a nonlinear functional $F: C^+\to X$ by

$$F(\phi)(x) = -d_{\mathrm{m}}\phi(0,x) + \varepsilon\int_{\infty}^{\infty} b(\phi(-r,y))f_\alpha(x-y)\,\mathrm{d}y, \quad x\in\mathbb{R}, \quad \phi\in C^+,$$

if the birth function $b:\mathbb{R}\to\mathbb{R}$ is continuous. Moreover, if the restriction of b to $[0,\infty)$ is positive and locally Lipschitz continuous, then

$$\lim_{h\to 0} d(\phi(0)+hF(\phi),X^+) := \lim_{h\to 0}\inf\{|\phi(0)+hF(\phi)-\xi|_X : \xi\in X^+\} = 0, \quad \text{for } \phi\in C^+,$$

and for any $R > 0$, there exists $L_R > 0$ such that

$$|F(\phi) - F(\psi)|_X \leqslant L_R\|\phi - \psi\| \quad \text{if } \phi, \psi \in C^+ \quad \text{and} \quad \|\phi\|, \|\psi\| \leqslant R.$$

Consequently, from Martin & Smith (1990) (see also corollary 1.3 on p. 270 of Wu 1996), we know that for each $\phi \in C^+$ there exists a unique non-continuable solution u on $[0, t_\phi)$, for some $t_\phi > 0$, of the following initial-value problem for the abstract integral equation

$$\left.\begin{aligned} u(t) &= T(t)u(0) + \int_0^t T(t-s)F(u_s)\,\mathrm{d}s, \\ u_0 &= \phi \in C^+, \end{aligned}\right\} \tag{3.4}$$

which satisfies $u(t) \in X^+$ for all $t \in [0, t_\phi)$. Such a solution is called a *mild solution* of (3.1). Since the semigroup $T(t)$ is analytic, such a mild solution of (3.1) must also be a classical solution of (3.1) for $t > r$ (see corollary 2.5 on p. 50 of Wu 1996).

4. Travelling wavefronts

In this section we consider a particular birth function for equation (2.12), namely, we let $b(w) = pw\mathrm{e}^{-aw}$. This function has been used in the well-studied Nicholson's blowflies equation (see Gurney *et al*. 1980). In the discrete case, it is commonly known as Ricker's model (Ricker 1954). With this birth function, equation (2.12) becomes

$$\frac{\partial w}{\partial t} = D_\mathrm{m}\frac{\partial^2 w}{\partial x^2} - d_\mathrm{m}w + \varepsilon p\int_{-\infty}^{\infty} w(t-r,y)\mathrm{e}^{-aw(t-r,y)}f_\alpha(x-y)\,\mathrm{d}y. \tag{4.1}$$

It should be emphasized that we choose the above birth function mainly for the sake of simplicity of presentation, and that our method below should be independent of this specific choice. Our focus in this section is about travelling wavefronts of (4.1). More precisely, a *travelling-wave solution* of (4.1) is a solution of the form $w(t, x) = \phi(x + ct)$, where $c > 0$ is the *wave speed*. In the event that (2.12) has two equilibria w_1 and w_2 with $w_1 < w_2$ and the *profile* ϕ of the wave is monotonic and satisfies $\lim_{s\to-\infty}\phi(s) = w_1$ and $\lim_{s\to\infty}\phi(s) = w_2$, the travelling-wave solution is called a *travelling-wave front*.

The case when $D_\mathrm{I}(\theta) \equiv 0$ and $d_\mathrm{I}(\theta) \equiv 0$, i.e. $\alpha = 0$, $\varepsilon = 1$ and (4.1) reduces to

$$\frac{\partial w}{\partial t} = D_\mathrm{m}\frac{\partial^2 w}{\partial x^2} - d_\mathrm{m}w + pw(t-r,y)\mathrm{e}^{-aw(t-r,x)}, \tag{4.2}$$

which was studied in So & Zou (2001), where the monotone iteration scheme and the method of upper–lower solutions in Wu & Zou (2001) were used to show that a travelling-wave front exists. Notice that the reaction term in (4.2) is local, whereas that of (4.1) is non-local. Since the method in Wu & Zou (2001) was only for the local case, there arises a natural question: can the method be extended to reaction–diffusion systems with non-local reaction terms like (4.1)? We will see in this section that the answer to this question is affirmative, at least for (4.1).

It is easily seen that when $(\varepsilon p)/d_\mathrm{m} > 1$, (4.1) has two spatially homogeneous equilibria

$$w_1 = 0 \quad \text{and} \quad w_2 = \frac{1}{a}\ln\frac{\varepsilon p}{d_\mathrm{m}} > 0.$$

To look for a travelling-wave front $w(t,x) = \phi(x+ct)$, with ϕ saturating at w_1 and w_2, we need to find a monotonic function $\phi(\xi)$, where $\xi = x + ct$, for the following equation

$$c\phi'(t) = D_{\mathrm{m}}\phi''(t) - d_{\mathrm{m}}\phi(t) + \varepsilon p \int_{-\infty}^{\infty} \phi(t - cr - y)\mathrm{e}^{-a\phi(t-cr-y)} f_{\alpha}(y)\,\mathrm{d}y, \tag{4.3}$$

subject to the boundary conditions

$$\phi(-\infty) = w_1, \qquad \phi(\infty) = w_2. \tag{4.4}$$

Notice that, without causing unnecessary confusion, we are using t in place of ξ in (4.3) as well as in the following presentation. Equation (4.3) is a second-order functional equation of *mixed type* (namely, with both advanced and delayed arguments), whereas a similar substitution for (4.2) gives rise to a second-order *delayed* differential equation only.

Let $K = w_2$. Based on (4.3), (4.4), we define the *profile set* for travelling wavefronts of (4.1) as

$$\boldsymbol{\Gamma} = \left\{ \phi \in C(\mathbb{R};\mathbb{R}) : \begin{array}{ll} \text{(i)} & \phi(t) \text{ is non-decreasing in } t \in \mathbb{R}, \\ \text{(ii)} & \lim_{t\to-\infty} \phi(t) = 0, \quad \lim_{t\to\infty} \phi(t) = K. \end{array} \right\}.$$

We also define $H : C(\mathbb{R};\mathbb{R}) \to C(\mathbb{R};\mathbb{R})$ by

$$H(\phi)(t) = \varepsilon p \int_{-\infty}^{\infty} \phi(t - cr - y)\mathrm{e}^{-a\phi(t-cr-y)} f_{\alpha}(y)\,\mathrm{d}y, \quad \phi \in C(\mathbb{R},\mathbb{R}), \quad t \in \mathbb{R}.$$

The operator H has some nice properties as stated below.

Lemma 4.1. *Assume*$1 < (\varepsilon p)/d_{\mathrm{m}} \leqslant \mathrm{e}$. *Then, for any* $\phi \in \boldsymbol{\Gamma}$, *we have*

(i) $H(\phi)(t) \geqslant 0$, *for all* $t \in \mathbb{R}$;

(ii) $H(\phi)(t)$ *is non-decreasing in* $t \in \mathbb{R}$; *and*

(iii) $H(\psi)(t) \leqslant H(\phi)(t)$, *for all* $t \in \mathbb{R}$, *provided* $\psi \in C(\mathbb{R};\mathbb{R})$ *is such that* $0 \leqslant \psi(t) \leqslant \phi(t) \leqslant K$ *for* $t \in \mathbb{R}$.

Proof. Note that when $1 < (\varepsilon p)/d_{\mathrm{m}} \leqslant \mathrm{e}$, the birth function $b(w) = pw\mathrm{e}^{-aw}$ is increasing on the interval

$$[w_1, w_2] = [0, K] = \left[0, \frac{1}{a} \ln \frac{\varepsilon p}{d_{\mathrm{m}}}\right].$$

Based on this observation, (i)–(iii) can be easily verified. ■

Note that in the case when $(\epsilon p)/d_{\mathrm{m}} > \mathrm{e}$, we are unable to verify the monotonicity of H, and therefore our method developed below cannot be used to find travelling wavefronts from the profile set Γ consisting of non-decreasing functions. We suspect that the method developed in Wu & Zou (2001) for travelling waves of reaction–diffusion equations without non-local effects and based on a non-standard ordering could be used in this case. However, for the sake of simplicity, from now on we will always assume that $1 < (\varepsilon p)/d_{\mathrm{m}} \leqslant \mathrm{e}$.

Next we will define upper and lower solutions for (4.3) as follows.

Definition 4.2. A function $\phi \in C(\mathbb{R};\mathbb{R})$ is called an *upper* (respectively *lower*) *solution* of (4.3) if it is differentiable almost everywhere (a.e.) and satisfies the inequality

$$c\phi' \geqslant D_{\mathrm{m}}\phi''(t) - d_{\mathrm{m}}\phi(t) + H(\phi)(t), \quad \text{a.e. in } \mathbb{R}$$
$$(\text{respectively } c\phi' \leqslant D_{\mathrm{m}}\phi''(t) - d_{\mathrm{m}}\phi(t) + H(\phi)(t), \quad \text{a.e. in } \mathbb{R}).$$

First, we assume that an upper solution $\bar{\phi} \in \boldsymbol{\Gamma}$ and a lower solution of $\underline{\phi}$ (which is not necessarily in $\boldsymbol{\Gamma}$) of (4.3) are given (we will see how to obtain such a pair in a moment) so that

(A1) $0 \leqslant \underline{\phi}(t) \leqslant \bar{\phi}(t) \leqslant K$, for all $t \in \mathbb{R}$; and

(A2) $\underline{\phi}(t) \not\equiv 0$.

Consider the following iteration scheme:

$$cw_n'(t) = D_{\mathrm{m}}w_n''(t) - d_{\mathrm{m}}w_n(t) + H(w_{n-1})(t), \quad t \in \mathbb{R}, \quad n = 1, 2, \dots, \tag{4.5}$$

with the boundary conditions

$$\lim_{t\to-\infty} w_n(t) = 0, \qquad \lim_{t\to\infty} w_n(t) = K, \tag{4.6}$$

where $w_0 = \bar{\phi}$. Solving (4.5), (4.6) for $n = 1, 2, \dots,$ leads to a sequence of functions $\{w_n\}_{n=1}^{\infty}$, given by

$$\left.\begin{aligned} w_0(t) &= \bar{\phi}(t), \quad t \in \mathbb{R}, \\ w_n(t) &= \frac{1}{D_{\mathrm{m}}(\beta_2 - \beta_1)}\left[\int_{-\infty}^{t} \mathrm{e}^{\beta_1(t-s)} H(w_{n-1})(s)\,\mathrm{d}s + \int_{t}^{\infty} \mathrm{e}^{\beta_2(t-s)} H(w_{n-1})(s)\,\mathrm{d}s\right], \end{aligned}\right\} \tag{4.7}$$

where $t \in \mathbb{R}$, $n = 1, 2, \dots,$ and

$$\beta_1 = \frac{c - \sqrt{c^2 + 4D_{\mathrm{m}}d_{\mathrm{m}}}}{2D_{\mathrm{m}}}, \qquad \beta_2 = \frac{c + \sqrt{c^2 + 4D_{\mathrm{m}}d_{\mathrm{m}}}}{2D_{\mathrm{m}}}. \tag{4.8}$$

Using lemma 4.1, one can establish the following result (see Wu & Zou 2001, lemmas 3.3 and 3.4 and proposition 3.5).

Theorem 4.3. *The sequence of functions* $\{w_n\}_{n=0}^{\infty}$ *satisfies*

(i) $w_n \in \boldsymbol{\Gamma}$, *for all* $n = 1, 2, \dots,$

(ii) $\underline{\phi}(t) \leqslant w_n(t) \leqslant w_{n-1}(t) \leqslant \bar{\phi}(t)$, *for all* $n = 1, 2, \dots,$ *and* $t \in \mathbb{R}$,

(iii) *each* w_n *is an upper solution of (4.3), and*

(iv) $\phi(t) := \lim_{n\to\infty} w_n(t)$ *is a solution of (4.3) and (4.4).*

Based on theorem 4.3, we see that the existence of travelling fronts for equation (4.1) follows from the existence of a pair of upper and lower solutions of (4.3) satisfying (A1) and (A2). Theorem 4.3 also provides a way of approximating the travelling-wave front. In the remainder of this section, we will construct such a pair of upper and lower solutions.

For $\lambda \in \mathbb{R}$, define the function

$$\Delta_c(\lambda) = \varepsilon p \mathrm{e}^{\alpha\lambda^2 - \lambda cr} - [c\lambda + d_{\mathrm{m}} - D_{\mathrm{m}}\lambda^2].$$

It is easy to show the following.

Lemma 4.4. *There exist $c^* > 0$ and $\lambda^* > 0$ such that*

(i) $\Delta_{c^*}(\lambda^*) = 0$ *and*

$$\frac{\partial}{\partial\lambda}\Delta_{c^*}(\lambda)\bigg|_{\lambda=\lambda^*} = 0;$$

(ii) *for $0 < c < c^*$ and $\lambda > 0$, we have $\Delta_c(\lambda) > 0$; and*

(iii) *for $c > c^*$ the equation $\Delta_c(\lambda) = 0$ has two positive real roots λ_1, λ_2, such that $0 < \lambda_1 < \lambda_2$ and*

$$\Delta_c(\lambda) = \begin{cases} > 0 & \text{for } \lambda < \lambda_1, \\ < 0 & \text{for } \lambda \in (\lambda_1, \lambda_2), \\ > 0 & \text{for } \lambda > \lambda_2. \end{cases}$$

Now fix $c > c^*$ and let $0 < \lambda_1 < \lambda_2$ as in lemma 4.4. Choose $\epsilon > 0$ sufficiently small so that $\epsilon < \lambda_1 < \lambda_1 + \epsilon < \lambda_2$. Define the functions $\bar{\phi}$ and $\underline{\phi}$ by

$$\begin{aligned} \bar{\phi}(t) &= \min\{K, K\mathrm{e}^{\lambda_1 t}\}, \\ \underline{\phi}(t) &= \max\{0, K(1 - M\mathrm{e}^{\epsilon t})\mathrm{e}^{\lambda_1 t}\}, \end{aligned}$$

where $M > 1$ is a constant to be determined. Clearly, $\bar{\phi}$ and $\underline{\phi}$ satisfy (A1) and (A2).

Lemma 4.5. *$\bar{\phi}(t)$ is an upper solution of (4.3) and $\bar{\phi}(t) \in \Gamma$.*

Proof. $\bar{\phi} \in \Gamma$ is obvious. We only need to verify that $\bar{\phi}$ is an upper solution of (4.3).

Case (i): $t \in (0, \infty)$. Then $\bar{\phi}(t) = K$ and $\bar{\phi}'(t) = 0 = \bar{\phi}''(t)$. Using the facts that $0 \leqslant \bar{\phi}(t) \leqslant K$ and that the function $a \mapsto w\mathrm{e}^{-aw}$ is increasing on the interval $[0, K]$, we have

$$\begin{aligned} c\bar{\phi}'(t) - D_{\mathrm{m}}\bar{\phi}''(t) + d_{\mathrm{m}}\bar{\phi}(t) - \varepsilon p \int_{-\infty}^{\infty} \bar{\phi}(t - cr - y)\mathrm{e}^{-a\bar{\phi}(t-cr-y)} f_\alpha(y)\,\mathrm{d}y \\ = d_{\mathrm{m}}K - \varepsilon p \int_{-\infty}^{\infty} \bar{\phi}(t - cr - y)\mathrm{e}^{-a\bar{\phi}(t-cr-y)} f_\alpha(y)\,\mathrm{d}y \\ \geqslant d_{\mathrm{m}}K - \varepsilon p \int_{-\infty}^{\infty} K\mathrm{e}^{-aK} f_\alpha(y)\,\mathrm{d}y \\ = K(d_{\mathrm{m}} - p\varepsilon\mathrm{e}^{-aK}) = 0, \quad \text{since } K = w_2. \end{aligned}$$

Case (ii): $t \in (-\infty, 0)$. Then $\bar{\phi}(t) = K\mathrm{e}^{\lambda_1 t}$, $\bar{\phi}'(t) = K\lambda_1 \mathrm{e}^{\lambda_1 t}$ and $\bar{\phi}''(t) = K\lambda_1^2 \mathrm{e}^{\lambda_1 t}$. Noting that $\bar{\phi}(s) \leqslant K\mathrm{e}^{\lambda_1 s}$ for all $s \in \mathbb{R}$, we have

$$\begin{aligned}
c\bar{\phi}'(t) - D_{\mathrm{m}}\bar{\phi}''(t) + d_{\mathrm{m}}\bar{\phi}(t) - \varepsilon p \int_{-\infty}^{\infty} \bar{\phi}(t - cr - y)\mathrm{e}^{-a\bar{\phi}(t-cr-y)} f_\alpha(y)\,\mathrm{d}y \\
&\geqslant [c\lambda_1 - D_{\mathrm{m}}\lambda_1^2 + d_{\mathrm{m}}]K\mathrm{e}^{\lambda_1 t} - \varepsilon p \int_{-\infty}^{\infty} \bar{\phi}(t - cr - y) f_\alpha(y)\,\mathrm{d}y \\
&\geqslant [c\lambda_1 - D_{\mathrm{m}}\lambda_1^2 + d_{\mathrm{m}}]K\mathrm{e}^{\lambda_1 t} - \varepsilon p \int_{-\infty}^{\infty} \mathrm{e}^{\lambda(t-y-cr)} f_\alpha(y)\,\mathrm{d}y \\
&= K\mathrm{e}^{\lambda_1 t}[c\lambda_1 - D_{\mathrm{m}}\lambda_1^2 + d_{\mathrm{m}} - \epsilon p \mathrm{e}^{\alpha^2\lambda_1^2 - \lambda_1 cr}] \\
&= \Delta_c(\lambda_1) = 0.
\end{aligned}$$

This completes the proof. ∎

Lemma 4.6. *For sufficiently large M, $\underline{\phi}(t)$ is a lower solution of (4.3).*

Proof. Let

$$t_1 = \frac{1}{\epsilon} \ln \frac{1}{M}.$$

Then $t_1 < 0$ for $M > 1$ and

$$\underline{\phi}(t) = \begin{cases} 0 & \text{for } t > t_1, \\ K(1 - M\mathrm{e}^{\epsilon t})\mathrm{e}^{\lambda_1 t} & \text{for } t < t_1. \end{cases}$$

Case (i): $t \in (t_1, \infty)$. Then $\underline{\phi}(t) = 0$ and $\underline{\phi}(t - cr - y) \geqslant 0$ for all $y \in \mathbb{R}$. Thus,

$$\begin{aligned}
c\underline{\phi}'(t) - D_{\mathrm{m}}\underline{\phi}''(t) + d_{\mathrm{m}}\underline{\phi}(t) - \varepsilon p \int_{-\infty}^{\infty} \underline{\phi}(t - cr - y)\mathrm{e}^{-a\underline{\phi}(t-cr-y)} f_\alpha(y)\,\mathrm{d}y \\
&= -\varepsilon p \int_{-\infty}^{\infty} \underline{\phi}(t - cr - y)\mathrm{e}^{-a\underline{\phi}(t-cr-y)} f_\alpha(y)\,\mathrm{d}y \leqslant 0.
\end{aligned}$$

Case (ii): $t \in (-\infty, t_1)$. Then $\underline{\phi}(t) = K[1 - M\mathrm{e}^{\epsilon t}]\mathrm{e}^{\lambda_1 t}$, $\underline{\phi}'(t) = K[\lambda_1 - M(\epsilon + \lambda_1)\mathrm{e}^{\epsilon t}]\mathrm{e}^{\lambda_1 t}$ and $\underline{\phi}''(t) = K[\lambda_1^2 - M(\lambda_1 + \epsilon)^2 \mathrm{e}^{\epsilon t}]\mathrm{e}^{\lambda_1 t}$. Note that the function $w \mapsto w\mathrm{e}^{-aw}$ is increasing on the interval $(-\infty, (1/a))$, and $\underline{\phi}(t) \geqslant K(1 - M\mathrm{e}^{\epsilon t})\mathrm{e}^{\lambda_1 t} =: h(t)$ for all $t \in \mathbb{R}$. Using the inequalities $h(s) \leqslant \underline{\phi}(s) \leqslant \bar{\phi}(s) \leqslant K \leqslant (1/a)$, for all $s \in \mathbb{R}$ and $\mathrm{e}^y \geqslant 1 + y$, for $y \in \mathbb{R}$, we have

$$\begin{aligned}
\varepsilon p &\int_{-\infty}^{\infty} \underline{\phi}(t - cr - y)\mathrm{e}^{-a\underline{\phi}(t-cr-y)} f_\alpha(y)\,\mathrm{d}y \\
&\geqslant \varepsilon p \int_{-\infty}^{\infty} h(t - cr - y)\mathrm{e}^{-ah(t-cr-y)} f_\alpha(y)\,\mathrm{d}y \\
&\geqslant \varepsilon p \int_{-\infty}^{\infty} h(t - cr - y)[1 - ah(t - cr - y)] f_\alpha(y)\,\mathrm{d}y
\end{aligned}$$

$$
\begin{aligned}
&= \varepsilon pK\mathrm{e}^{\lambda_1 t}\int_{-\infty}^{\infty}\mathrm{e}^{-\lambda_1(y+cr)}f_\alpha(y)\,\mathrm{d}y - \varepsilon pKM\mathrm{e}^{(\lambda_1+\epsilon)t}\int_{-\infty}^{\infty}\mathrm{e}^{-(\lambda_1+\epsilon)(y+cr)}f_\alpha(y)\,\mathrm{d}y \\
&\quad - \varepsilon pK^2 a\mathrm{e}^{2\lambda_1 t}\int_{-\infty}^{\infty}\mathrm{e}^{-2\lambda_1(y+cr)}[1-M\mathrm{e}^{\epsilon(t-y-cr)}]^2 f_\alpha(y)\,\mathrm{d}y \\
&= \varepsilon pK\mathrm{e}^{\lambda_1 t}\mathrm{e}^{\lambda_1[\alpha\lambda_1-cr]} - \varepsilon pKM\mathrm{e}^{(\lambda_1+\epsilon)t}\mathrm{e}^{(\lambda_1+\epsilon)[\alpha(\lambda_1+\epsilon)-cr]} \\
&\quad - \varepsilon pK^2 a\mathrm{e}^{2\lambda_1 t}\int_{-\infty}^{\infty}\mathrm{e}^{-2\lambda_1(y+cr)}[1-M\mathrm{e}^{\epsilon(t-y-cr)}]^2 f_\alpha(y)\,\mathrm{d}y. \qquad (4.9)
\end{aligned}
$$

Since $t \leqslant t_1 < 0$ and $0 < \epsilon < \lambda_1$, the third term above can be bounded as follows:

$$
\begin{aligned}
&\mathrm{e}^{2\lambda_1 t}\int_{-\infty}^{\infty}\mathrm{e}^{-2\lambda_1(y+cr)}[1-M\mathrm{e}^{\epsilon(t-y-cr)}]^2 f_\alpha(y)\,\mathrm{d}y \\
&\qquad \leqslant \mathrm{e}^{(\lambda_1+\epsilon)t}\int_{-\infty}^{\infty}\mathrm{e}^{-2\lambda_1(y+cr)}[1+M\mathrm{e}^{\epsilon(t-y-cr)}]^2 f_\alpha(y)\,\mathrm{d}y \\
&\qquad \leqslant \mathrm{e}^{(\lambda_1+\epsilon)t}\int_{-\infty}^{\infty}\mathrm{e}^{-2\lambda_1(y+cr)}[1+M\mathrm{e}^{\epsilon t_1}\mathrm{e}^{-\epsilon(y+cr)}]^2 f_\alpha(y)\,\mathrm{d}y \\
&\qquad = \mathrm{e}^{(\lambda_1+\epsilon)t}\int_{-\infty}^{\infty}\mathrm{e}^{-2\lambda_1(y+cr)}[1+\mathrm{e}^{-\epsilon(y+cr)}]^2 f_\alpha(y)\,\mathrm{d}y. \qquad (4.10)
\end{aligned}
$$

It is obvious that the last integral in (4.10) is convergent, that is

$$
G = G(\lambda_1,\epsilon,r,c,\alpha) := \int_{-\infty}^{\infty}\mathrm{e}^{-2\lambda_1(y+cr)}[1+\mathrm{e}^{-\epsilon(y+cr)}]^2 f_\alpha(y)\,\mathrm{d}y < \infty.
$$

By (4.9) and (4.10), we have

$$
\begin{aligned}
&c\underline{\phi}'(t) - D_{\mathrm{m}}\underline{\phi}''(t) + d_{\mathrm{m}}\underline{\phi}(t) - \varepsilon p\int_{-\infty}^{\infty}\underline{\phi}(t-cr-y)\mathrm{e}^{-a\underline{\phi}(t-cr-y)}f_\alpha(y)\,\mathrm{d}y \\
&\qquad \leqslant -K\mathrm{e}^{\lambda_1 t}\Delta_\alpha(\lambda_1) + KM\mathrm{e}^{(\lambda_1+\epsilon)t}\Delta_\alpha(\lambda_1+\epsilon) \\
&\qquad\qquad + \varepsilon pK^2 a\mathrm{e}^{2\lambda_1 t}\int_{-\infty}^{\infty}\mathrm{e}^{-2\lambda_1(y+cr)}[1-M\mathrm{e}^{\epsilon(t-y-cr)}]^2 f_\alpha(y)\,\mathrm{d}y \\
&\qquad \leqslant KM\mathrm{e}^{(\lambda_1+\epsilon)t}\Delta_\alpha(\lambda_1+\epsilon) + \varepsilon paK^2\mathrm{e}^{(\lambda_1+\epsilon)t}G \\
&\qquad = K\mathrm{e}^{(\lambda_1+\epsilon)t}\Delta_\alpha(\lambda_1+\epsilon)\left[M + \frac{\varepsilon paKG}{\Delta_\alpha(\lambda_1+\epsilon)}\right]. \qquad (4.11)
\end{aligned}
$$

Since $\Delta_\alpha(\lambda_1+\epsilon) < 0$, the right-hand side in (4.11) is negative for sufficiently large M. This completes the proof. ■

Combining theorem 4.3 and lemmas 4.4–4.6, we obtain the existence of a travelling-wave front for (4.3).

Theorem 4.7. *If $1 < (\varepsilon p)/d_{\mathrm{m}} \leqslant \mathrm{e}$, then there exists a $c^* > 0$ such that for every $c > c^*$, (4.3) has a travelling-wave front solution, which connects the trivial equilibrium $w_1 = 0$ and the positive equilibrium*

$$
w_2 = \frac{1}{a}\ln\frac{\varepsilon p}{d_{\mathrm{m}}}.
$$

We now give a heuristic explanation that c^* is the 'minimal wave speed' in the sense that equation (4.1) has no travelling-wave front with wave speed c which is less than c^*. This can be seen from the observation that the formal linearization of (4.3) at the zero solution is given by

$$c\phi'(t) = D_{\mathrm{m}}\phi''(t) - d_{\mathrm{m}}\phi(t) + \varepsilon p \int_{-\infty}^{\infty} \phi(t - cr - y) f_\alpha(y)\,\mathrm{d}y,$$

and the function $\Delta_c(\lambda)$ is obtained by substituting $\mathrm{e}^{\lambda t}$ for $\phi(t)$ in the above linearization. Therefore, by lemma 4.4 (ii), (4.3) should not have a solution (ϕ, c) with $c < c^*$ and $\phi(-\infty) = 0$.

Also, since the graph of $\lambda \mapsto \Delta_c(\lambda)$ moves upwards as α increases, by lemma 4.4 it is easily seen that the minimal wave speed c^* is an increasing function of α. Hence, waves with speeds near the minimal wave speed go faster as the mobility of the immature population increases.

As a final remark, we note that as $(\epsilon p)/d_{\mathrm{m}}$ increases beyond e, the map H is no longer order preserving. As a consequence, we are unable to employ our approach to prove the existence of a travelling-wave front. Preliminary numerical simulations seem to indicate that travelling wavefronts persist, except that the front becomes non-monotonic when $(\epsilon p)/d_{\mathrm{m}}$ increases past a critical value. More precisely, we have numerically observed non-monotonic travelling wavefronts, very much similar to those reported in Gourley (2000) for a Fisher equation with non-local effect. It is important and challenging, both theoretically and numerically, to find this critical value and to understand the mechanism behind this loss of monotonicity of wavefronts.

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