J Nonlinear Sci (2007) 17: 505–525
DOI 10.1007/s00332-007-9003-9

Journal of
Nonlinear
Science

On the Diffusive Nicholson's Blowflies Equation with Nonlocal Delay

W.-T. Li · S. Ruan · Z.-C. Wang

Received: 17 December 2006 / Accepted: 16 May 2007 / Published online: 20 September 2007

Abstract This paper is concerned with the diffusive Nicholson's blowflies model with nonlocal (or spatiotemporal) delay. When the spatial variable is one-dimensional, we establish the existence of travelling wave-front solutions by using the approach developed by Wang, Li, and Ruan (J. Differ. Equ. 222, 185–232, 2006) on the existence of travelling front solutions of reaction–diffusion systems with nonlocal delay. Moreover, we consider the dependence of the minimal wave speed on the delay and the mobility of the population. Our main finding here is that delay can induce slow travelling wave-fronts and the mobility of the population can increase fast travelling wave-fronts. In particular, if we choose some special kernel forms, then our results include and improve some known results.

Keywords Nicholson's blowflies model · Reaction-diffusion · Nonlocal delay · Travelling wave-front

Mathematics Subject Classification (2000) 35K57 · 92D25 · 35R20

Communicated by J. Belair.

W.-T. Li (✉) · Z.-C. Wang
School of Mathematics and Statistics, Lanzhou University, Lanzhou, Gansu 730000, People's Republic of China
e-mail: wtli@lzu.edu.cn

S. Ruan
Department of Mathematics, University of Miami, P.O. Box 249085, Coral Gables, FL 33124-4250, USA

1 Introduction

In 1954, Nicholson (1954a, 1954b) published his famous findings concerning competition for food (sheep's liver) in laboratory populations of blowflies, *Lucilia cuprina*. In a typical experiment, the caged blowflies were fed a limited amount (500 mg) of ground liver daily as a source of protein, which they required for egg production. Sugar and water were supplied ad lib. Each day's production of eggs was transferred to a separate and unlimited supply of fresh liver and reared through to adults, which emerged in the cage a generation later. Under the conditions of his experiments Nicholson (1954a, 1954b) gave the duration of egg to adult development as "more than two weeks" (i.e. 15 days). The essential feature of the experiments was that the populations were left free to develop under predetermined environmental conditions for long periods. The total numbers of blowflies were recorded every two or three days. It was observed that there occurred characteristic periodic oscillations or cycles during the course of the experiments.

Nicholson concluded that the basic cause of the oscillations was the time-lag between stimulus and reaction of the density-related responses. May (1976) used the delayed logistic model (i.e. Hutchinson model, 1948) to simulate one of Nicholson's experiments and inferred an egg to adult duration of nine days. This is far from the actual observed time of about 15 days stated by Nicholson (1954b).

To overcome the discrepancy in estimating the delay value, Gurney et al. (1990) proposed the following delay equation:

$$\frac{\mathrm{d}u}{\mathrm{d}t} = -\delta u(t) + pu(t-\tau)\exp\bigl[-au(t-\tau)\bigr], \tag{1.1}$$

to model the population of the Australian sheep-blowfly *Lucilia cuprina*, where p is the maximum per capita daily egg production rate, $1/a$ is the size at which the blowfly population reproduces at its maximum rate, δ is the per capita daily adult death rate, and τ is the generation time.

Notice that, after recalling $u^* = au, t^* = \tau t$, $\tau^* = \delta\tau$, $\beta = p/\delta$ and dropping the asterisks, the equation becomes

$$\frac{\mathrm{d}u}{\mathrm{d}t} = -\tau u(t) + \beta\tau u(t-1)\exp\bigl[-u(t-1)\bigr]. \tag{1.2}$$

There is a positive equilibrium,

$$u^* = \ln\beta = \ln(p/\delta),$$

if the maximum possible per capita reproduction rate is greater than the per capita death rate, that is, if $p > \delta$. As in Hutchinson's equation, there is a critical value of the time delay. The positive equilibrium is stable when the delay is less than the critical value, becomes unstable when it is greater than the value, and there are oscillations (Ruan 2006; Wei and Li 2005). Testing Nicholson's data, (1.2) not only provides self-sustaining limit cycles as Hutchinson's equation did, but also gives an accurate measurement of the delay value as 15 days. Gurney et al. (1990) showed that the fluctuations observed by Nicholson are of limit-cycle type. The period of the cycles is set mainly by the delay and adult death rate. High values of $p\tau$ and $\delta\tau$ will give large amplitude cycles. Moving deeper into instability produces a number of successive doublings of the repeated time until a region is reached where the solution becomes aperiodic (chaotic). Since this equation explains Nicholson's data (1957) of blowflies more accurately, it is now referred to as the Nicholson's blowflies equation and has been studied by many researchers; see Gourley (2000), Gourley and Ruan (2000), Li and Fan (2007), Ruan (2006), So et al. (2000), So and Yang (1998), So and Zou (2001), Wei and Li (2005), Yang and So (1998), and the references therein.

Spatial structure may make it impossible for organisms to encounter each other in proportion to their average density (Law et al. 2003). The random collision of individuals assumed in the above models may not represent interactions among organisms. Taking the spatial structure into account, Yang and So (1998) extended (1.2) to the following diffusive form:

$$\frac{\partial u}{\partial t} = d\Delta u - \tau u(x,t) + \beta\tau u(x,t-1)\exp\big[-u(x,t-1)\big] \tag{1.3}$$

on a finite domain with homogeneous Neumann boundary conditions, and obtained results on the global attractivity of positive steady state and on the oscillation of solutions. The case of Dirichlet boundary conditions was studied by So and Yang (1998), where the global attractivity of the equilibrium was proved by developing a new approach to deal with the fact that the delay term is nonmonotone. Some numerical and Hopf bifurcation analysis of this model was carried out by So et al. (2000). For the problem on the whole real line, $x \in (-\infty, \infty)$, So and Zou (2001) obtained results on the existence of travelling wave-fronts. The existence of nonmonotone travelling waves was studied by Faria and Trofimchuk (2006).

It has been observed that distributed delays are more reasonable than discrete delays in modeling maturation periods (Blythe et al. 1984, 1985; Bernard et al. 2001). Taking the distributed maturation periods into account, Gourley and Ruan (2000) proposed and investigated the following generalized Nicholson's blowflies model with distributed delay:

$$\begin{aligned}\frac{\partial u}{\partial t} &= d\Delta u - \tau u(x,t)\\ &\quad + \beta\tau\left(\int_{-\infty}^{t} k(t-s)u(x,s)\,\mathrm{d}s\right)\exp\left[-\int_{-\infty}^{t} k(t-s)u(x,s)\,\mathrm{d}s\right],\end{aligned} \tag{1.4}$$

for $(x,t) \in \Omega \times [0,\infty)$, where Ω is either all of $\mathbb{R}^n$ or some finite domain, and the kernel $k(t)$ satisfies $k(t) \geq 0$ and the conditions

$$\int_0^\infty k(t)\,\mathrm{d}t = 1 \quad \text{and} \quad \int_0^\infty t k(t)\,\mathrm{d}t = 1.$$

They studied the uniform states $u \equiv 0$ and $u \equiv \ln\beta$ of (1.4) in terms of both their local (linearized) stability and their global stability and showed that the zero state is globally asymptotically stable if $\beta < 1$ and the nonzero steady state $u \equiv \ln\beta$ is globally stable if $1 < \beta \leq \mathrm{e}$, where a theory of sub- and supersolutions for delay differential equations is employed. For the problem on the whole real line, $x \in (-\infty, \infty)$, the existence of travelling wave-fronts was considered by Gourley (2000) under a special kernel form, where the travelling wave equations were recasted into a four-dimensional system of nondelay ordinary differential equations and then geometric singular perturbation theory was applied to this system for the case when the delay is *small*.

In ecology, since populations take time to move in space and usually were not at the same position in space at previous times, sometimes it is not sufficient to include only a discrete delay or a finite delay in a population model. Motivated by this, Britton (1989, 1990) considered the two factors comprehensively and introduced the so-called *spatiotemporal delay* or *nonlocal delay*, that is, the delay term involves a weighted spatiotemporal average over the whole infinite spatial domain and the whole times internal up to now. Since then, great progress has been made on the existence of travelling wave-fronts in reaction–diffusion equations with spatiotemporal delays; see Ai (2007), Ashwin et al. (2002), Billingham (2004), Gourley (2000), Gourley and Britton (1993), Gourley et al. (2001), Gourley and Kuang (2003), Gourley and Ruan (2003), Liang and Wu (2003), Ruan and Xiao (2004), So et al. (2003), Wang et al. (2006), and the recent survey of Gourley and Wu (2006).

Since the delay term in the Nicholson's blowflies equation models the larval and pupa stage in development (when they are not moving very much or not at all) the use of a time-delay term that remains purely local in space is probably not unreasonable. However, the basic assumptions behind the Nicholson's blowflies equation are such that it is probably applicable to many other species that have a maturation phase when the individuals may indeed move about. For such cases, nonlocal delays are indeed essential. Motivated by the above consideration, in this paper we shall study the following generalization of (1.4):

$$\frac{\partial u}{\partial t} = d\Delta u - \tau u(x,t) + \beta\tau\big((g*u)(x,t)\big)\exp\big[-(g*u)(x,t)\big], \tag{1.5}$$

for $(x,t) \in \Omega \times [0,\infty)$, where

$$(g*u)(x,t) = \int_{\Omega}\int_{-\infty}^{t} g(x-y, t-s)u(y,s)\,\mathrm{d}y\,\mathrm{d}s,$$

and the convolution kernel $g(y,s)$ is an integrable and nonnegative function in its variables $s \in \mathbb{R}_+$, $y \in \Omega$. We normalize the kernel so that

$$\int_{\Omega}\int_{0}^{\infty} g(y,s)\,\mathrm{d}y\,\mathrm{d}s = 1. \tag{1.6}$$

We remark that (1.5) contains many special equations by taking different kernels. Some examples are given as follows.

(i) If $g(x,y,t,s) = \delta(x-y)k(t-s)$, then (1.5) becomes (1.4).
(ii) If $g(x,y,t,s) = \delta(x-y)\delta(t-s-1)$, then (1.5) becomes (1.3). If $u = u(t)$ depends on time only, then (1.3) reduces to (1.2).

In this paper, we are interested in the existence of travelling wave-fronts in (1.5) when $\Omega = \mathbb{R}$. The paper is organized as follows. In Sect. 2, we list some results we developed in Wang et al. (2006) for reaction–diffusion systems with spatiotemporal delays that are needed in Sect. 3. In Sect. 3, we establish the existence of travelling front solutions to (1.5) with general convolution kernels. Moreover, we consider the dependence of the minimal wave speed on the delay and the mobility of the population. Our main finding here is that delay can induce slow travelling wave-fronts and the mobility of the population can increase fast travelling wave-fronts. In the final section, we summarize our conclusions.

2 Preliminaries

The theory developed in Wang et al. (2006) is quite general and extends to coupled systems as well as scalar equations. Our theorem on the existence of travelling wave-front solutions involves different hypotheses depending on whether γ-monotonicity properties hold or not. In this section, we set up the notation and summarize the relevant results.

Consider the following reaction–diffusion systems with nonlocal delay:

$$\frac{\partial u(x,t)}{\partial t} = D\frac{\partial^2 u(x,t)}{\partial x^2} + f\big(u(x,t),(g_1 * u)(x,t),\dots,(g_m * u)(x,t)\big), \tag{2.1}$$

where $t \geq 0$, $x \in \mathbb{R}$, $D = \operatorname{diag}(d_1,\dots,d_n)$, $d_i > 0$, $i = 1,\dots,n$, $n \in \mathbb{N}$; $u(x,t) = (u_1(x,t),\dots,u_n(x,t))^T$, $f \in C(\mathbb{R}^{(m+1)n},\mathbb{R}^n)$, and

$$(g_j * u)(x,t) = \int_{-\infty}^{t}\int_{-\infty}^{+\infty} g_j(x-y,t-s)u(y,s)\,\mathrm{d}y\,\mathrm{d}s,$$

the kernel $g_j(x,t)$ is an integrable nonnegative function satisfying

$$\begin{aligned} &g_j(-x,t) = g_j(x,t) \quad \text{and} \\ &\int_0^{+\infty}\int_{-\infty}^{+\infty} g_j(y,s)\,\mathrm{d}y\,\mathrm{d}s = 1, \qquad j = 1,\dots,m, \qquad m \in \mathbb{N}. \end{aligned} \tag{2.2}$$

Assume $u(x,t) = \varphi(x+ct)$ and replace $x+ct$ with t; then we can rewrite (2.1) in the form

$$-D\varphi''(t) + c\varphi'(t) = f\big(\varphi(t),(g_1 * \varphi)(t),\dots,(g_m * \varphi)(t)\big), \quad t \in \mathbb{R}, \tag{2.3}$$

where

$$(g_j * \varphi)(t) = \int_0^{+\infty}\int_{-\infty}^{+\infty} g_j(y,s)\varphi(t-y-cs)\,\mathrm{d}y\,\mathrm{d}s, \qquad j = 1,\dots,m.$$

A travelling wave-front with a wave speed $c > 0$ to (2.1) is a function $\varphi \in BC^2(\mathbb{R},\mathbb{R}^n)$, $\varphi(x+ct)$, which satisfies (2.3) and the following boundary condition:

$$\begin{aligned} &\varphi(-\infty) = \mathbf{0} \quad \text{and} \\ &\varphi(+\infty) = \mathbf{K} = (K_1,\dots,K_n)^{\mathrm{T}} \quad \text{with } K_i > 0,\ i = 1,2,\dots,n. \end{aligned} \tag{2.4}$$

We make an assumption on the kernels $g_j(x,t)$, $j = 1,\dots,m$:

(H$_0$) $\int_{-\infty}^{+\infty} g_j(x,t)\,\mathrm{d}x$ is uniformly convergent for $t \in [0,a]$, $a>0$, $j=1,\dots,m$. In other words, given $\varepsilon > 0$, there exists an $M>0$ such that $\int_M^{+\infty} g_j(x,t)\,\mathrm{d}x < \varepsilon$ for any $t \in [0,a]$.

In order to study the existence of travelling wave-fronts, we need the following monotonicity condition and assumptions:

(H$_1$) There exists a matrix $\gamma =$diag$(\gamma_1,\dots,\gamma_n)$ with $\gamma_i > 0$, $i=1,\dots,n$ such that

$$\begin{aligned} &f\big(\varphi_2(t),(g_1*\varphi_2)(t),\dots,(g_m*\varphi_2)(t)\big)+\gamma\varphi_2(t)\\ &\quad\ge f\big(\varphi_1(t),(g_1*\varphi_1)(t),\dots,(g_m*\varphi_1)(t)\big)+\gamma\varphi_1(t),\end{aligned}$$

where $\varphi_1,\varphi_2 \in C(\mathbb{R},\mathbb{R}^n)$ satisfy $\mathbf{0}\le\varphi_1(t)\le\varphi_2(t)\le\mathbf{K}$ in $t\in\mathbb{R}$.

(H$_2$) $f(\mu,\dots,\mu)\ne\mathbf{0}$ for $\mathbf{0}<\mu<\mathbf{K}$;

(H$_3$) $f(\mu,\dots,\mu)=\mathbf{0}$ when $\mu=\mathbf{0}$ or $\mathbf{K}$.

Next we give definitions of the sub- and supersolutions of (2.3).

Definition 2.1 A continuous function $\phi:\mathbb{R}\to\mathbb{R}^n$ is called a supersolution of (2.3) if ϕ' and ϕ'' exist almost everywhere and are essentially bounded on $\mathbb{R}$, and φ satisfies

$$-D\phi''(t)+c\phi'(t)\ge f\big(\phi(t),(g_1*\phi)(t),\dots,(g_m*\phi)(t)\big),\quad \text{a.e. on } \mathbb{R}. \tag{2.5}$$

A subsolution of (2.3) is defined in a similar way by reversing the inequality in (2.5).

Let

$$\Gamma=\left\{\varphi\in Y\colon \begin{array}{ll}\text{(i)} & \varphi \text{ is increasing in } \mathbb{R};\\ \text{(ii)} & \mathbf{0}\le\lim_{t\to-\infty}\varphi(t)<\mathbf{K} \text{ and } \lim_{t\to+\infty}\varphi(t)=\mathbf{K}\end{array}\right\},$$

and

$$BC[\mathbf{0},\mathbf{K}]=\big\{\varphi\in BC\big(\mathbb{R},\mathbb{R}^n\big);\mathbf{0}\le\varphi\le\mathbf{K}\big\},$$

where $Y=\{\varphi\in BC(\mathbb{R},\mathbb{R}^n):\varphi',\varphi''\in L^\infty(\mathbb{R},\mathbb{R}^n)\}$.

Theorem 2.2 *Assume that* (H$_1$), (H$_2$), (H$_3$), *and* (H$_0$) *hold. Assume further that* ϕ *and* ψ, *where* $\psi\in BC[\mathbf{0},\mathbf{K}]\cap Y$ *with* $\psi\not\equiv\mathbf{0}$ *and* $\lim_{t\to-\infty}\psi(t)=\mathbf{0}$, $\phi\in\Gamma$ *with* $\psi\le\phi$, *are sub- and supersolutions of* (2.3), *respectively. Then* (2.1) *has a travelling wave-front* ϕ^* *which is increasing and satisfies* (2.4) *with* $\psi\le\phi^*\le\phi$ *and for* $a,b\in\mathbb{R}$ *with* $a<b$,

$$\big\|\phi^m-\phi^*\big\|_{C([a,b],\mathbb{R}^n)}\to 0, \tag{2.6}$$

where

$$-D\big(\phi^m\big)''+c\big(\phi^m\big)'+\gamma\phi^m=F\psi^{m-1}+\gamma\phi^{m-1}\quad(m\in\mathbb{N}), \tag{2.7}$$

and

$$\psi\le\phi^*\le\cdots\le\phi^m\le\cdots\le\phi^1\le\phi^0=\phi. \tag{2.8}$$

In particular, if $\lim_{t\to-\infty}\phi(t)=\mathbf{0}$, *then* $\|\phi^m-\phi^*\|\to 0$.

In the subsequent section of this paper, we shall use the above results to prove the existence of monotone travelling waves of (1.5).

3 Existence of Travelling Wave Fronts

Conversion of (1.5) into travelling wave form, with $u(x,t)=\varphi(z), z=x+ct$ and replacing z with t, yields

$$d\varphi''(t)-c\varphi'(t)+f\big(\varphi(t),(g*\varphi)(t)\big)=0,\quad t\in\mathbb{R},\tag{3.1}$$

where

$$(g*\varphi)(t)=\int_0^{+\infty}\int_{-\infty}^{+\infty}g(y,s)\varphi(t-y-cs)\,\mathrm{d}y\,\mathrm{d}s,$$
$$f\big(\varphi(t),(g*\varphi)(t)\big)=-\tau\varphi(t)+\beta\tau(g*\varphi)(t)\mathrm{e}^{-(g*\varphi)(t)},$$

and solutions of this equation are sought satisfying

$$\varphi(-\infty)=0\quad\text{and}\quad\varphi(\infty)=\ln\beta:=k.\tag{3.2}$$

We first establish an upper bound on any travelling wave-front, which is an extension of a result in Gourley (2000).

Lemma 3.1 *Any travelling wave-front $\varphi(t)$ of (3.1) satisfies $\varphi(t)\le\beta/\mathrm{e}$ everywhere.*

Proof If φ exceeds β/e anywhere, then φ must attain a global maximum, i.e., a point t_0 such that $\varphi(t_0)>\beta/\mathrm{e}$, $\varphi'(t_0)=0$, and $\varphi''(t_0)\le 0$. Equation (3.1) yields

$$\varphi(t_0)\le\beta(g*\varphi)(t_0)\exp\big(-(g*\varphi)(t_0)\big)\le\frac{\beta}{\mathrm{e}},$$

since $x\mathrm{e}^{-x}\le 1/\mathrm{e}$ for all x. □

The following result extends Proposition 3 of Gourley (2000) for the wave equation (3.1).

Lemma 3.2 *If $\beta\le\mathrm{e}$, then any travelling wave-front $\varphi(t)$ of (3.1) satisfies $\varphi(t)\le\ln\beta$ everywhere.*

Proof If φ exceeds $\ln\beta$, then there must exist a global maximum t_0. At t_0, $\varphi'=0$ and $\varphi''\le 0$. Also,

$$\begin{aligned}(g*\varphi)(t_0)&=\int_0^{+\infty}\int_{-\infty}^{+\infty}g(y,s)\varphi(t_0-y-cs)\,\mathrm{d}y\,\mathrm{d}s\\&\le\int_0^{+\infty}\int_{-\infty}^{+\infty}g(y,s)\varphi(t_0)\,\mathrm{d}y\,\mathrm{d}s=\varphi(t_0),\end{aligned}$$

and furthermore, by Lemma 3.1, both sides of the above inequality are less than or equal to 1. In view of this fact, together with the fact that xe^{-x} is an increasing function for $x \le 1$, we can write

$$\begin{aligned} 0 &= d\varphi''(t_0) - c\varphi'(t_0) + f\big(\varphi(t), (g*\varphi)(t_0)\big) \\ &\le -\tau\varphi(t_0) + \beta\tau\varphi(t_0)\mathrm{e}^{-\varphi(t_0)}. \end{aligned}$$

This gives $\varphi(t_0) \le \ln\beta$, which is a contradiction. □

Lemma 3.3 *$f(\varphi(t), (g*\varphi)(t))$ satisfies* (H$_1$).

Proof Let $\varphi_1, \varphi_2 \in C(\mathbb{R}, \mathbb{R})$ with $0 \le \varphi_1(t) \le \varphi_2(t) \le k$. Then,

$$\begin{aligned} &f\big(\varphi_2(t), (g*\varphi_2)(t)\big) - f\big(\varphi_1(t), (g*\varphi_1)(t)\big) \\ &\quad = -\tau\varphi_2(t) + \beta\tau(g*\varphi_2)(t)\mathrm{e}^{-(g*\varphi_2)(t)} + \tau\varphi_1(t) - \beta\tau(g*\varphi_1)(t)\mathrm{e}^{-(g*\varphi_1)(t)} \\ &\quad = -\tau\big[\varphi_2(t) - \varphi_1(t)\big] + \beta\tau\big[(g*\varphi_2)(t)\mathrm{e}^{-(g*\varphi_2)(t)} - (g*\varphi_1)(t)\mathrm{e}^{-(g*\varphi_1)(t)}\big]. \end{aligned}$$

Consider the function $h(y) = y\mathrm{e}^{-y}$. Then,

$$h'(y) = \mathrm{e}^{-y}(1-y)\begin{cases} > 0 & \text{for } y < 1, \\ < 0 & \text{for } y > 1. \end{cases} \tag{3.3}$$

So, $h(y)$ is increasing on [0, 1]. Now, since $\beta \le \mathrm{e}$,

$$0 \le \varphi_1(t) \le \varphi_2(t) \le k \le 1.$$

Thus,

$$(g*\varphi_2)(t)\mathrm{e}^{-(g*\varphi_2)(t)} - (g*\varphi_1)(t)\mathrm{e}^{-(g*\varphi_1)(t)} > 0.$$

Therefore,

$$f\big(\varphi_2(t), (g*\varphi_2)(t)\big) - f\big(\varphi_1(t), (g*\varphi_1)(t)\big) \ge -\tau\big[\varphi_2(t) - \varphi_1(t)\big]. \qquad \square$$

Based on Theorem 2.2, we see that the existence of travelling wave-fronts for (1.6) follows from the existence of a pair of upper and lower solutions of (3.1). In the remainder of this section, we will construct such a pair of upper and lower solutions by choosing a different kernel function g. Here we consider five cases:

(i) $g(x,t) = \frac{1}{\tau_0}\mathrm{e}^{-\frac{t}{\tau_0}}\delta(x)$, $\tau_0 > 0$.

(ii) $g(x,t) = \delta(t)\frac{1}{\sqrt{4\pi\rho_0}}\mathrm{e}^{-\frac{x^2}{4\rho_0}}$, $\rho_0 > 0$.

(iii) $g(x,t) = \frac{t}{\tau_0^2}\mathrm{e}^{-\frac{t}{\tau_0}}\delta(x)$, $\tau_0 > 0$.

(iv) $g(x,t) = \frac{1}{\tau_0}\mathrm{e}^{-\frac{t}{\tau_0}}\frac{1}{\sqrt{4\pi\rho_0}}\mathrm{e}^{-\frac{x^2}{4\rho_0}}$, $\tau_0 > 0$, $\rho_0 > 0$.

(v) $g(x,t) = \frac{1}{\tau_0}\mathrm{e}^{-\frac{t}{\tau_0}}\frac{1}{\sqrt{4\pi t}}\mathrm{e}^{-\frac{x^2}{4t}}$, $\tau_0 > 0$.

From the results of Wang et al. (2006), we know that these functions satisfy the condition (H_0).

Our main result in this section is the following theorem.

Theorem 3.4 *If* $1 < \beta \leq \mathrm{e}$, *then there exists* $c^* > 0$ *such that for every* $c > c^*$, (1.5) *has a travelling wave-front solution that connects the trivial equilibrium* $u = 0$ *and the positive equilibrium* $u = \ln \beta$.

We remark that the wave speed c^* depends on the choice of different kernel functions.

3.1 The case $g(x,t) = \frac{1}{\tau_0}\mathrm{e}^{-\frac{t}{\tau_0}}\delta(x)$, $\tau_0 > 0$

In this case, we define the function

$$\Delta_{1c}(\lambda) = \left(\frac{1}{1+\lambda\tau_0 c} - 1\right)\beta\tau - \left[\tau(1-\beta) + c\lambda - d\lambda^2\right], \quad \lambda \in \mathbb{R}.$$

Then, $\Delta_{10}(\lambda) = d\lambda^2 + (\beta - 1)\tau > 0$. Hence, it is easy to show the following.

Lemma 3.5 *There exist* $c^* > 0$ *and* $\lambda^* > 0$ *such that*

(i) $\Delta_{1c^*}(\lambda^*) = 0$ *and*

$$\frac{\partial}{\partial\lambda}\Delta_{1c^*}(\lambda)\bigg|_{\lambda=\lambda^*} = 0;$$

(ii) *for* $0 < c < c^*$, *and* $\lambda > 0$, *we have* $\Delta_{1c}(\lambda) > 0$; *and*

(iii) *for* $c > c^*$ *the equation* $\Delta_{1c}(\lambda) = 0$ *has two positive real roots* $\lambda_{11}, \lambda_{12}$, *such that* $0 < \lambda_{11} < \lambda_{12}$ *and*

$$\Delta_{1c}(\lambda) = \begin{cases} > 0 & \text{for } \lambda < \lambda_{11}, \\ < 0 & \text{for } \lambda \in (\lambda_{11}, \lambda_{12}), \\ > 0 & \text{for } \lambda > \lambda_{12}. \end{cases}$$

Now fix $c > c^*$ and let $0 < \lambda_{11} < \lambda_{12}$ as in Lemma 3.5. Choose $\varepsilon > 0$ sufficiently small so that $\varepsilon < \lambda_{11} < \lambda_{11} + \varepsilon < \lambda_{12}$. Define the functions ϕ and ψ by

$$\phi(t) = \min\left\{k, k\mathrm{e}^{\lambda_{11}t}\right\} \quad \text{and} \quad \psi(t) = \max\left\{0, k\left(1 - M_0\mathrm{e}^{\varepsilon t}\right)\mathrm{e}^{\lambda_{11}t}\right\}, \tag{3.4}$$

where $M_0 > 1$ is a constant to be determined. Clearly, $0 \leq \psi(t) \leq \phi(t) \leq k$ for $t \in \mathbb{R}$ and $\psi(t) \not\equiv 0$.

Lemma 3.6 $\phi(t)$ *defined by* (3.4) *is an upper solution of* (3.1) *and* $\phi(t) \in \Gamma$.

Proof $\phi(t) \in \Gamma$ is obvious. We only need to verify that $\phi(t)$ is an upper solution of (3.1).

For $t \geq 0$, $\phi(t) = k$, $\phi'(t) = 0$, $\phi''(t) = 0$. In view of $0 \leq \phi(t) \leq k$ and the fact that the function $h(y)$ defined by (3.3) is increasing on $[0, k]$, we have

$$\begin{aligned}
&d\phi''(t) - c\phi'(t) + f\big(\phi(t), (g * \phi)(t)\big) \\
&\quad = -\tau k + \beta\tau(g * \phi)(t)\mathrm{e}^{-(g*\phi)(t)} \\
&\quad \leq -\tau k + \beta\tau k \mathrm{e}^{-k} = -\tau \ln\beta + \tau\ln\beta = 0.
\end{aligned}$$

For $t < 0$, $\phi(t) = k\mathrm{e}^{\lambda_{11}t}$, $\phi'(t) = k\lambda_{11}\mathrm{e}^{\lambda_{11}t}$, $\phi''(t) = k\lambda_{11}^2\mathrm{e}^{\lambda_{11}t}$. Hence, we have

$$\begin{aligned}
&d\phi''(t) - c\phi'(t) + f\big(\phi(t), (g * \phi)(t)\big) \\
&\quad = k\left[\big(d\lambda_{11}^2 - c\lambda_{11} - \tau\big)\mathrm{e}^{\lambda_{11}t} + \frac{\beta\tau}{k}(g * \phi)(t)\mathrm{e}^{-(g*\phi)(t)}\right] \\
&\quad \leq k\left[\big(d\lambda_{11}^2 - c\lambda_{11} - \tau\big)\mathrm{e}^{\lambda_{11}t} + \frac{\beta\tau}{k}(g * \phi)(t)\right] \\
&\quad = k\left[\big(d\lambda_{11}^2 - c\lambda_{11} - \tau\big)\mathrm{e}^{\lambda_{11}t} + \frac{\beta\tau}{k}\int_0^{+\infty}\int_{-\infty}^{+\infty}\frac{1}{\tau_0}\mathrm{e}^{-\frac{s}{\tau_0}}\delta(y)\phi(t - y - cs)\,\mathrm{d}y\,\mathrm{d}s\right] \\
&\quad = k\left[\big(d\lambda_{11}^2 - c\lambda_{11} - \tau\big)\mathrm{e}^{\lambda_{11}t} + \beta\tau\int_0^{+\infty}\frac{1}{\tau_0}\mathrm{e}^{-\frac{s}{\tau_0}}\mathrm{e}^{\lambda_{11}(t-cs)}\,\mathrm{d}s\right] \\
&\quad = k\left[\big(d\lambda_{11}^2 - c\lambda_{11} - \tau\big)\mathrm{e}^{\lambda_{11}t} + \beta\tau\mathrm{e}^{\lambda_{11}t}\int_0^{+\infty}\frac{1}{\tau_0}\mathrm{e}^{-\frac{(1+\lambda_{11}\tau_0 c)s}{\tau_0}}\,\mathrm{d}s\right] \\
&\quad = k\mathrm{e}^{\lambda_{11}t}\left[\big(d\lambda_{11}^2 - c\lambda_{11} - \tau\big) + \frac{\beta\tau}{1 + \lambda_{11}\tau_0 c}\right] \\
&\quad = k\mathrm{e}^{\lambda_{11}t}\left[d\lambda_{11}^2 - c\lambda_{11} + \tau(\beta - 1) + \left(\frac{1}{1 + \lambda_{11}\tau_0 c} - 1\right)\beta\tau\right] = 0.
\end{aligned}$$

□

Lemma 3.7 *For sufficiently large $M_0 > 1$, $\psi(t)$ is a lower solution of* (3.1).

Proof Let

$$t_1 = \frac{1}{\varepsilon}\ln\frac{1}{M_0}.$$

Then $t_1 < 0$ and

$$\psi(t) = \begin{cases} 0 & \text{for } t \geq t_1, \\ k(1 - M_0\mathrm{e}^{\varepsilon t})\mathrm{e}^{\lambda_{11}t} & \text{for } t < t_1. \end{cases}$$

For $t \geq t_1$, $\psi(t) = 0$ and $\psi(t - y - cs) \geq 0$ for all $y \in \mathbb{R}$. Thus,

$$\begin{aligned}
&d\psi''(t) - c\psi'(t) + f\big(\psi(t), (g * \psi)(t)\big) \\
&\quad = d\psi''(t) - c\psi'(t) - \tau\psi(t) + \beta\tau(g * \psi)(t)\mathrm{e}^{-(g*\psi)(t)} \\
&\quad \geq 0.
\end{aligned}$$

For $t < t_1$, $\psi(t) = k(1 - M_0 e^{\varepsilon t})e^{\lambda_{11} t}$, $\psi'(t) = k[\lambda_{11} - M_0(\lambda_{11}+\varepsilon)e^{\varepsilon t}]e^{\lambda_{11} t}$ and $\psi''(t) = k[\lambda_{11}^2 - M_0(\lambda_{11}+\varepsilon)^2 e^{\varepsilon t}]e^{\lambda_{11} t}$. Hence, we have

$$\begin{aligned}
(g*\psi)(t) &= k\int_0^{+\infty}\int_{-\infty}^{+\infty}\frac{1}{\tau_0}e^{-\frac{s}{\tau_0}}\delta(y)\psi(t-y-cs)\,\mathrm{d}y\,\mathrm{d}s\\
&= k\int_0^{+\infty}\frac{1}{\tau_0}e^{-\frac{s}{\tau_0}}\psi(t-cs)\,\mathrm{d}s\\
&\geq k\int_0^{+\infty}\frac{1}{\tau_0}e^{-\frac{s}{\tau_0}}e^{\lambda_{11}(t-cs)}\,\mathrm{d}s - kM_0\int_0^{+\infty}\frac{1}{\tau_0}e^{-\frac{s}{\tau_0}}e^{\varepsilon(t-cs)}e^{\lambda_{11}(t-cs)}\,\mathrm{d}s\\
&= \frac{ke^{\lambda_{11}t}}{1+\lambda_{11}\tau_0 c} - \frac{kM_0 e^{(\lambda_{11}+\varepsilon)t}}{1+(\lambda_{11}+\varepsilon)\tau_0 c},
\end{aligned}$$

and

$$(g*\psi)(t) \leq k\int_0^{+\infty}\frac{1}{\tau_0}e^{-\frac{s}{\tau_0}}e^{\lambda_{11}(t-cs)}\,\mathrm{d}s = \frac{ke^{\lambda_{11}t}}{1+\lambda_{11}\tau_0 c}.$$

Thus, using the inequality $e^x \geq 1 + x$ for $x \in \mathbb{R}$, we have

$$\begin{aligned}
&d\psi''(t) - c\psi'(t) + f\big(\psi(t), (g*\psi)(t)\big)\\
&= d\psi''(t) - c\psi'(t) - \tau\psi(t) + \beta\tau(g*\psi)(t)e^{-(g*\psi)(t)}\\
&\geq ke^{\lambda_{11}t}\left[d\lambda_{11}^2 - c\lambda_{11} + \tau(\beta-1) + \left(\frac{1}{1+\lambda_{11}\tau_0 c} - 1\right)\beta\tau\right]\\
&\quad - kM_0 e^{(\lambda_{11}+\varepsilon)t}\bigg[d(\lambda_{11}+\varepsilon)^2 - c(\lambda_{11}+\varepsilon) + \tau(\beta-1)\\
&\quad + \left(\frac{1}{1+(\lambda_{11}+\varepsilon)\tau_0 c} - 1\right)\beta\tau\bigg]\\
&\quad + \beta\tau(g*\psi)(t)\big[e^{-(g*\psi)(t)} - 1\big]\\
&\geq -kM_0 e^{(\lambda_{11}+\varepsilon)t}\Delta_{1c}(\lambda_{11}+\varepsilon) - \beta\tau\big[(g*\psi)(t)\big]^2\\
&\geq -kM_0 e^{(\lambda_{11}+\varepsilon)t}\Delta_{1c}(\lambda_{11}+\varepsilon) - \frac{\beta\tau k^2 e^{(\lambda_{11}+\varepsilon)t}}{(1+\lambda_{11}\tau_0 c)^2}\\
&= -ke^{(\lambda_{11}+\varepsilon)t}\Delta_{1c}(\lambda_{11}+\varepsilon)\left[M_0 + \frac{\beta\tau k}{\Delta_{1c}(\lambda_{11}+\varepsilon)(1+\lambda_{11}\tau_0 c)^2}\right].
\end{aligned}\tag{3.5}$$

Since $\Delta_{1c}(\lambda_{11}+\varepsilon) < 0$, the right-hand side in (3.5) is positive for sufficiently large M_0. □

From Lemmas 3.3, 3.6, and 3.7 and Theorem 2.2, we see that Theorem 3.4 is true. In order to estimate the value of c^*, we define

$$h_{11}(\lambda) = \tau(1-\beta) + c\lambda - d\lambda^2 \quad\text{and}\quad h_{12}(\lambda) = \left(\frac{1}{1+\tau_0 c\lambda} - 1\right)\beta\tau.$$

Then,

$$\Delta_{1c}(\lambda) = h_{12}(\lambda) - h_{11}(\lambda).$$

Obviously, the function $h_{11}(\lambda)$ is concave down with the maximum $\frac{c^2}{4d} - \tau(\beta - 1)$ attained at $\frac{c}{2d}$ and the function $h_{12}(\lambda)$ is decreasing in $[0, \infty)$ and

$$h_{12}\left(\frac{c}{2d}\right) = \frac{-\tau_0 c^2 \beta\tau}{2d + \tau_0 c^2}.$$

Thus, if $\frac{c^2}{4d} \geq \tau(\beta - 1)$, that is, $c \geq 2\sqrt{d\tau(\beta - 1)}$, then $\Delta_{1c}(\lambda) = 0$ has two positive real roots, regardless of the value of τ_0, and if $c = 0$, then $\Delta_{1c}(\lambda) = 0$ has no real roots. Hence, we have $c^* \in (0, 2\sqrt{d\tau(\beta - 1)})$. Furthermore, if $c \in (0, 2\sqrt{d\tau(\beta - 1)})$, then $\Delta_{1c}(\lambda) = 0$ has two positive real roots provided that

$$\tau_0 \geq \frac{4d\tau(\beta - 1) - c^2}{2\tau c^2 + \frac{c^4}{2d}}.$$

Thus, we have the following result.

Corollary 3.8 *Assume that* $1 < \beta \leq \mathrm{e}$. *Then the following statements are true*:

(i) *For every* $c \geq 2\sqrt{d\tau(\beta - 1)}$, *regardless of the value of* $\tau_0 \geq 0$, (1.5) *has a travelling wave-front solution, which connects the trivial equilibrium* $u = 0$ *and the positive equilibrium* $u = \ln\beta$.

(ii) *For every* $c \in (0, 2\sqrt{d\tau(\beta - 1)})$, (1.5) *also admits a travelling wave-front solution, which connects the trivial equilibrium* $u = 0$ *and the positive equilibrium* $u = \ln\beta$, *provided that*

$$\tau_0 \geq \frac{2d\tau(\beta - 1) - \frac{c^2}{2}}{\tau c^2 + \frac{c^4}{4d}}.$$

We know from Sect. 1 that if $g(x, y, t, s) = \delta(x - y)\delta(t - s)$, then (1.5) becomes equation

$$\frac{\partial u}{\partial t} = d\Delta u - \tau u(x, t) + \beta\tau u(x, t)\exp[-u(x, t)]. \tag{3.6}$$

For (3.6), Gourley (2000) obtained the following result.

Theorem 3.9 *Equation* (3.6) *has a travelling wave-front with speed c if and only if* $c \geq 2\sqrt{d\tau(\beta - 1)}$.

If $g(x, y, t, s) = \delta(x - y)\delta(t - s - 1)$, then (1.5) becomes (1.3). For the discrete delay model (1.3), So and Zou (2001) obtained the following result by applying Wu and Zou's results for reaction–diffusion equations with discrete delays (Wu and Zou 2001).

Theorem 3.10 *If* $1 < \beta \leq e$, *then there exists* $c^* > 0$ *such that for every* $c > c^*$ *there exists a travelling wave-front for* (1.3) *with speed* c.

Remark 3.11 The constant c^* is the "minimal wave speed" in the sense that (1.4) has no travelling wave-front when the wave speed c is less than c^*. This can be seen from the observation that the formal linearization of (3.1) at the zero solution is given by

$$d\varphi''(t) - c\varphi'(t) - \tau\varphi(t) + \beta\tau(g * \varphi)(t) = 0,$$

and the function $\Delta_{1c}(\lambda)$ is obtained by substituting $e^{\lambda t}$ for $\varphi(t)$ in the above linearization. Therefore, by Lemma 3.5(ii), (3.1) should not have a solution (φ, c) with $c < c^*$ and $\varphi(-\infty) = 0$.

Remark 3.12 From the expression of the function

$$\begin{aligned}\Delta_{1c}(\lambda) &= \left(\frac{1}{1+\lambda\tau_0 c} - 1\right)\beta\tau - \left[\tau(1-\beta) + c\lambda - d\lambda^2\right] \\ &= \frac{\beta\tau}{1+\lambda\tau_0 c} - \tau - c\lambda + d\lambda^2,\end{aligned}$$

we see that the graph of $\lambda \mapsto \Delta_{1c}(\lambda)$ moves downwards as τ_0 increases. By Lemma 3.5 it is easily seen that the minimal wave speed c^* is a decreasing function of τ_0.

Remark 3.13 Corollary 3.8 and Theorems 3.9 and 3.10 indicate that the time delay can induce slow wave-fronts, which was also reported by Zou (2002) for the equation of KPP-Fisher type.

3.2 The case $g(x,t) = \delta(t)\frac{1}{\sqrt{4\pi\rho_0}}e^{-\frac{x^2}{4\rho_0}}$, $\rho_0 > 0$

In this case, we define the function

$$\Delta_{2c}(\lambda) = \left(e^{\rho_0\lambda^2} - 1\right)\beta\tau - \left[\tau(1-\beta) + c\lambda - d\lambda^2\right], \quad \lambda \in \mathbb{R}.$$

It is easy to show the following.

Lemma 3.14 *There exist $c^* > 0$ and $\lambda^* > 0$ such that*

(i) $\Delta_{2c^*}(\lambda^*) = 0$ *and*

$$\left.\frac{\partial}{\partial\lambda}\Delta_{2c^*}(\lambda)\right|_{\lambda=\lambda^*} = 0.$$

(ii) *For $0 < c < c^*$ and $\lambda > 0$, we have $\Delta_{2c}(\lambda) > 0$.*

(iii) *For $c > c^*$, the equation $\Delta_{2c}(\lambda) = 0$ has two positive real roots $\lambda_{21}, \lambda_{22}$, such that $0 < \lambda_{21} < \lambda_{22}$ and*

$$\Delta_{2c}(\lambda)\begin{cases} > 0 & \text{for } \lambda < \lambda_{21}, \\ < 0 & \text{for } \lambda \in (\lambda_{21}, \lambda_{22}), \\ > 0 & \text{for } \lambda > \lambda_{22}. \end{cases}$$

Now fix $c > c^*$ and let $0 < \lambda_{21} < \lambda_{22}$ as in Lemma 3.14. Choose $\varepsilon > 0$ sufficiently small so that $\varepsilon < \lambda_{21} < \lambda_{21} + \varepsilon < \lambda_{22}$. Define the functions ϕ and ψ as (3.4).

Lemma 3.15 *$\phi(t)$ defined by (3.4) is an upper solution of (3.1) and $\phi(t) \in \Gamma$.*

Proof $\phi(t) \in \Gamma$ is obvious. We only need to verify that $\phi(t)$ is an upper solution of (3.1).

For $t \geq 0$, the proof is similar to that of Lemma 3.6.

For $t < 0$, $\phi(t) = k\mathrm{e}^{\lambda_{21}t}$, $\phi'(t) = k\lambda_{21}\mathrm{e}^{\lambda_{21}t}$, $\phi''(t) = k\lambda_{21}^2\mathrm{e}^{\lambda_{21}t}$. Hence, using the fact that $\phi(t) \leq k\mathrm{e}^{\lambda_{21}t}$ for $t \in \mathbb{R}$, we have

$$\begin{aligned}
&d\phi''(t) - c\phi'(t) + f\big(\phi(t), (g*\phi)(t)\big) \\
&\quad = k\left[\big(d\lambda_{21}^2 - c\lambda_{21} - \tau\big)\mathrm{e}^{\lambda_{21}t} + \frac{\beta\tau}{k}(g*\phi)(t)\mathrm{e}^{-(g*\phi)(t)}\right] \\
&\quad \leq k\left[\big(d\lambda_{21}^2 - c\lambda_{21} - \tau\big)\mathrm{e}^{\lambda_{21}t} + \frac{\beta\tau}{k}(g*\phi)(t)\right] \\
&\quad = k\left[\big(d\lambda_{21}^2 - c\lambda_{21} - \tau\big)\mathrm{e}^{\lambda_{21}t} + \frac{\beta\tau}{k}\int_0^{+\infty}\int_{-\infty}^{+\infty} g(s,y)\phi(t-y-cs)\,\mathrm{d}y\,\mathrm{d}s\right] \\
&\quad = k\left[\big(d\lambda_{21}^2 - c\lambda_{21} - \tau\big)\mathrm{e}^{\lambda_{21}t} + \frac{\beta\tau}{k}\int_{-\infty}^{+\infty} \frac{1}{\sqrt{4\pi\rho_0}}\mathrm{e}^{-\frac{y^2}{4\rho_0}}\phi(t-y)\,\mathrm{d}s\right] \\
&\quad \leq k\left[\big(d\lambda_{21}^2 - c\lambda_{21} - \tau\big)\mathrm{e}^{\lambda_{21}t} + \beta\tau\int_{-\infty}^{+\infty} \frac{1}{\sqrt{4\pi\rho_0}}\mathrm{e}^{-\frac{y^2}{4\rho_0}}\mathrm{e}^{\lambda_{21}(t-y)}\,\mathrm{d}s\right] \\
&\quad = k\mathrm{e}^{\lambda_{21}t}\big[\big(d\lambda_{21}^2 - c\lambda_{21} - \tau\big) + \beta\tau\mathrm{e}^{\lambda_{21}^2\rho_0}\big] \\
&\quad = k\mathrm{e}^{\lambda_{21}t}\big[d\lambda_{21}^2 - c\lambda_{21} + \tau(\beta-1) + \big(\mathrm{e}^{\lambda_{21}^2\rho_0} - 1\big)\beta\tau\big] = 0.
\end{aligned}$$

□

Lemma 3.16 *For sufficiently large $M_0 > 1$, $\psi(t)$ is a lower solution of (3.1).*

Proof Let $t_1 = \frac{1}{\varepsilon}\ln\frac{1}{M_0}$. For $t \geq t_1$, the proof is similar to that of Lemma 3.7.

For $t < t_1$, $\psi(t) = k(1 - M_0\mathrm{e}^{\varepsilon t})\mathrm{e}^{\lambda_{21}t}$, $\psi'(t) = k[\lambda_{21} - M_0(\lambda_{21}+\varepsilon)\mathrm{e}^{\varepsilon t}]\mathrm{e}^{\lambda_{21}t}$ and $\psi''(t) = k[\lambda_{21}^2 - M_0(\lambda_{21}+\varepsilon)^2\mathrm{e}^{\varepsilon t}]\mathrm{e}^{\lambda_{21}t}$. Noting that $k(1 - M_0\mathrm{e}^{\varepsilon t})\mathrm{e}^{\lambda_{21}t} \leq \psi(t) \leq k\mathrm{e}^{\lambda_{21}t}$ for all $t \in \mathbb{R}$, we have

$$\begin{aligned}
(g*\psi)(t) &= \int_0^{+\infty}\int_{-\infty}^{+\infty} \delta(s)\frac{1}{\sqrt{4\pi\rho_0}}\mathrm{e}^{-\frac{y^2}{4\rho_0}}\psi(t-y-cs)\,\mathrm{d}y\,\mathrm{d}s \\
&\geq k\int_{-\infty}^{+\infty}\frac{1}{\sqrt{4\pi\rho_0}}\mathrm{e}^{-\frac{y^2}{4\rho_0}}\big(1 - M_0\mathrm{e}^{\varepsilon(t-y)}\big)\mathrm{e}^{\lambda_{21}(t-y)}\,\mathrm{d}y \\
&= k\mathrm{e}^{\lambda_{21}t}\int_{-\infty}^{+\infty}\frac{1}{\sqrt{4\pi\rho_0}}\mathrm{e}^{-\frac{y^2}{4\rho_0}}\mathrm{e}^{-\lambda_{21}y}\,\mathrm{d}y \\
&\quad - kM_0\mathrm{e}^{(\lambda_{21}+\varepsilon)t}\int_{-\infty}^{+\infty}\frac{1}{\sqrt{4\pi\rho_0}}\mathrm{e}^{-\frac{y^2}{4\rho_0}}\mathrm{e}^{-(\lambda_{21}+\varepsilon)y}\,\mathrm{d}y \\
&= k\mathrm{e}^{\lambda_{21}t}\mathrm{e}^{\rho_0\lambda_{21}^2} - kM_0\mathrm{e}^{(\lambda_{21}+\varepsilon)t}\mathrm{e}^{\rho_0(\lambda_{21}+\varepsilon)^2},
\end{aligned}$$

and

$$(g*\psi)(t)\le k\mathrm{e}^{\lambda_{21}t}\int_{-\infty}^{+\infty}\frac{1}{\sqrt{4\pi\rho_0}}\mathrm{e}^{-\frac{y^2}{4\rho_0}}\mathrm{e}^{-\lambda_{21}y}\,\mathrm{d}y=k\mathrm{e}^{\lambda_{21}t}\mathrm{e}^{\rho_0\lambda_{21}^2}.$$

Thus, using the inequality $\mathrm{e}^x\ge 1+x$ for $x\in\mathbb{R}$, we have

$$\begin{aligned}
&d\psi''(t)-c\psi'(t)+f\big(\psi(t),(g*\psi)(t)\big)\\
&\quad=d\psi''(t)-c\psi'(t)-\tau\psi(t)+\beta\tau(g*\psi)(t)\mathrm{e}^{-(g*\psi)(t)}\\
&\quad\ge k\mathrm{e}^{\lambda_{21}t}\big[d\lambda_{21}^2-c\lambda_{21}+\tau(\beta-1)+\big(\mathrm{e}^{\rho_0\lambda_{21}^2}-1\big)\beta\tau\big]\\
&\qquad-kM_0\mathrm{e}^{(\lambda_{21}+\varepsilon)t}\big[d(\lambda_{21}+\varepsilon)^2-c(\lambda_{21}+\varepsilon)+\tau(\beta-1)+\big(\mathrm{e}^{\rho_0(\lambda_{21}+\varepsilon)^2}-1\big)\beta\tau\big]\\
&\qquad+\beta\tau(g*\psi)(t)\big[\mathrm{e}^{-(g*\psi)(t)}-1\big]\\
&\quad=-kM_0\mathrm{e}^{(\lambda_{21}+\varepsilon)t}\Delta_{2c}(\lambda_{21}+\varepsilon)+\beta\tau(g*\psi)(t)\big[\mathrm{e}^{-(g*\psi)(t)}-1\big]\\
&\quad\ge -kM_0\mathrm{e}^{(\lambda_{21}+\varepsilon)t}\Delta_{2c}(\lambda_{21}+\varepsilon)-\beta\tau\big[(g*\psi)(t)\big]^2\\
&\quad\ge -kM_0\mathrm{e}^{(\lambda_{21}+\varepsilon)t}\Delta_{2c}(\lambda_{21}+\varepsilon)-\beta\tau k^2\mathrm{e}^{2\rho_0\lambda_{21}^2}\mathrm{e}^{(\lambda_{21}+\varepsilon)t}\\
&\quad=-k\mathrm{e}^{(\lambda_{21}+\varepsilon)t}\Delta_{2c}(\lambda_{21}+\varepsilon)\left[M_0+\frac{\beta\tau k^2\mathrm{e}^{2\rho_0\lambda_{21}^2}}{\Delta_{2c}(\lambda_{21}+\varepsilon)}\right].
\end{aligned}\tag{3.7}$$

Since $\Delta_{2c}(\lambda_{21}+\varepsilon)<0$, the right-hand side in (3.7) is positive for sufficiently large M_0. □

From Lemmas 3.3, 3.15, and 3.16 and Theorem 2.2, we see that Theorem 3.4 is true.

In order to estimate the value of c^*, we define

$$h_{21}(\lambda)=\tau(1-\beta)+c\lambda-d\lambda^2\quad\text{and}\quad h_{22}(\lambda)=\big(\mathrm{e}^{\rho_0\lambda^2}-1\big)\beta\tau.$$

Then,

$$\Delta_{2c}(\lambda)=h_{22}(\lambda)-h_{21}(\lambda).$$

Obviously, the function $h_{21}(\lambda)$ is concave down with the maximum $\frac{c^2}{4d}-\tau(\beta-1)$ attained at $\frac{c}{2d}$ and the function $h_{22}(\lambda)$ is increasing in $[0,\infty)$ and

$$h_{22}\left(\frac{c}{2d}\right)=\left(\exp\left(\frac{c^2\rho_0}{4d^2}\right)-1\right)\beta\tau.$$

Thus, if $c=0$, then $\Delta_{2c}(\lambda)=0$ has no real roots and if $0<c\le 2\sqrt{d\tau(\beta-1)}$, then $h_{22}(\lambda)>0$ and $h_{21}(\lambda)\le 0$ for $\lambda>0$ and so $\Delta_{2c}(\lambda)>0$. Hence, $c^*\in(2\sqrt{d\tau(\beta-1)},\infty)$.

Remark 3.17 Similar to Remark 3.11, we can see that the constant c^* is the "minimal wave speed" in the sense that (1.4) has no travelling wave-front when the wave speed c is less than c^*.

Remark 3.18 From the expression of the function

$$\Delta_{2c}(\lambda) = \left(e^{\rho_0\lambda^2} - 1\right)\beta\tau - \left[\tau(1-\beta) + c\lambda - d\lambda^2\right] = \beta\tau e^{\rho_0\lambda^2} - \tau - c\lambda + d\lambda^2,$$

we can see that the graph of $\lambda \mapsto \Delta_{2c}(\lambda)$ moves upwards as ρ_0 increases. By Lemma 3.14 it is easily seen that the minimal wave speed c^* is an increasing function of ρ_0.

Remark 3.19 Theorem 3.4 shows that the mobility of the population can increase the fast wave-fronts.

3.3 The case $g(x,t) = \frac{t}{\tau_0^2} e^{-\frac{t}{\tau_0}} \delta(x)$, $\tau_0 > 0$

In this case, we define the function

$$\Delta_{3c}(\lambda) = \left(\frac{1}{(1+\lambda\tau_0 c)^2} - 1\right)\beta\tau - \left[\tau(1-\beta) + c\lambda - d\lambda^2\right], \quad \lambda \in \mathbb{R}.$$

We have the following lemma.

Lemma 3.20 *There exist $c^* > 0$ and $\lambda^* > 0$ such that*

(i) $\Delta_{3c^*}(\lambda^*) = 0$ *and*

$$\frac{\partial}{\partial\lambda}\Delta_{3c^*}(\lambda)\bigg|_{\lambda=\lambda^*} = 0;$$

(ii) *for $0 < c < c^*$ and $\lambda > 0$, we have $\Delta_{3c}(\lambda) > 0$; and*

(iii) *for $c > c^*$ the equation $\Delta_{3c}(\lambda) = 0$ has two positive real roots $\lambda_{31}, \lambda_{32}$, such that $0 < \lambda_{31} < \lambda_{32}$ and*

$$\Delta_{3c}(\lambda) \begin{cases} > 0 & \text{for } \lambda < \lambda_{31}, \\ < 0 & \text{for } \lambda \in (\lambda_{31}, \lambda_{32}), \\ > 0 & \text{for } \lambda > \lambda_{32}. \end{cases}$$

Now fix $c > c^*$ and let $0 < \lambda_{31} < \lambda_{32}$ as in Lemma 3.20. Choose $\varepsilon > 0$ sufficiently small so that $\varepsilon < \lambda_{31} < \lambda_{31} + \varepsilon < \lambda_{32}$. Define the functions ϕ and ψ as (3.4).

Similarly, we can prove the following lemmas.

Lemma 3.21 *$\phi(t)$ defined by (3.4) is an upper solution of (3.1) and $\phi(t) \in \Gamma$.*

Lemma 3.22 *For sufficiently large $M_0 > 1$, $\psi(t)$ is a lower solution of (3.1).*

From Lemmas 3.3, 3.21, and 3.22 and Theorem 2.2, we see that Theorem 3.4 is true.

In order to estimate the value of c^*, we define

$$h_{31}(\lambda) = \tau(1-\beta) + c\lambda - d\lambda^2 \quad \text{and} \quad h_{32}(\lambda) = \left(\frac{1}{(1+\lambda\tau_0 c)^2} - 1\right)\beta\tau.$$

Then,

$$\Delta_{3c}(\lambda) = h_{32}(\lambda) - h_{31}(\lambda).$$

Obviously, the function $h_{31}(\lambda)$ is concave down with the maximum $\frac{c^2}{4d} - \tau(\beta - 1)$ attained at $\frac{c}{2d}$ and the function $h_{32}(\lambda)$ is decreasing in $[0, \infty)$ and

$$h_{32}\left(\frac{c}{2d}\right) = -\beta\tau \frac{4d\tau_0 c^2 + \tau_0^2 c^4}{(2d + \tau_0 c^2)^2}.$$

Thus, if $\frac{c^2}{4d} \geq \tau(\beta - 1)$, that is, $c \geq 2\sqrt{d\tau(\beta - 1)}$, then $\Delta_{3c}(\lambda) = 0$ has two positive real roots, regardless of the value of τ_0, and if $c = 0$, then $\Delta_{3c}(\lambda) = 0$ has no real roots. Hence, we have $c^* \in (0, 2\sqrt{d\tau(\beta - 1)})$. Furthermore, if $c \in (0, 2\sqrt{d\tau(\beta - 1)})$, then $\Delta_{3c}(\lambda) = 0$ has two positive real roots provided that

$$\tau_0 \geq \frac{-(c^4 + 4d\tau c^2) + \sqrt{(c^4 + 4d\tau c^2)^2 + 4d(\tau c^4 + \frac{c^6}{4d})(4d\tau(\beta - 1) - c^2)}}{2(\tau c^4 + \frac{c^6}{4d})}. \quad (3.8)$$

Thus, we have the following result.

Corollary 3.23 *Assume that* $1 < \beta \leq e$. *Then the following statements are true*:

(i) *For every* $c \geq 2\sqrt{d\tau(\beta - 1)}$, *regardless of the value of* $\tau_0 \geq 0$, (1.5) *has a travelling wave-front solution that connects the trivial equilibrium* $u = 0$ *and the positive equilibrium* $u = \ln \beta$.
(ii) *For every* $c \in (0, 2\sqrt{d\tau(\beta - 1)})$, (1.5) *also admits a travelling wave-front solution that connects the trivial equilibrium* $u = 0$ *and the positive equilibrium* $u = \ln \beta$, *provided that* (3.8) *holds*.

If $g(x, y, t, s) = \delta(x - y)k(t - s)$, then (1.5) becomes (1.4), where the kernel function $k(t)$ is a strong generic delay, that is, $k(t) = \frac{t}{\tau_0^2}e^{-t/\tau_0}$, $\tau_0 > 0$. Gourley (2000) considered (1.4) and established the existence of travelling wave-front solutions by using geometric singular perturbation theory.

Theorem 3.24 *For any* $\tau_0 > 0$ *sufficiently small, there exists speed* $c \geq 2\sqrt{d\tau(\beta - 1)}$ *such that* (1.4) *has a travelling wave-front*.

Remark 3.25 Clearly, Corollary 3.23 improves Theorem 3.24 by dropping the assumption that τ_0 is sufficiently small and relaxing the condition $c \geq 2\sqrt{d\tau(\beta - 1)}$.

3.4 The case $g(t, x) = \frac{1}{\tau_0}e^{-\frac{t}{\tau_0}} \frac{1}{\sqrt{4\pi\rho_0}}e^{-\frac{x^2}{4\rho_0}}$, $\tau_0 > 0$, $\rho_0 > 0$

In this case, we define the function

$$\Delta_{4c}(\lambda) = \left(\frac{e^{\rho_0\lambda^2}}{(1 + \lambda\tau_0 c)} - 1\right)\beta\tau - \left[\tau(1 - \beta) + c\lambda - d\lambda^2\right], \quad \lambda \in \mathbb{R}.$$

Similarly, we have

Lemma 3.26 *There exist* $c^* > 0$ *and* $\lambda^* > 0$ *such that*

(i) $\Delta_{4c^*}(\lambda^*) = 0$ *and*

$$\frac{\partial}{\partial\lambda}\Delta_{4c^*}(\lambda)\bigg|_{\lambda=\lambda^*} = 0.$$

(ii) *For* $0 < c < c^*$ *and* $\lambda > 0$, *we have* $\Delta_{4c}(\lambda) > 0$.

(iii) *For* $c > c^*$, *the equation* $\Delta_{4c}(\lambda) = 0$ *has two positive real roots* $\lambda_{41}, \lambda_{42}$, *such that* $0 < \lambda_{41} < \lambda_{42}$ *and*

$$\Delta_{4c}(\lambda) = \begin{cases} > 0 & \text{for } \lambda < \lambda_{41}, \\ < 0 & \text{for } \lambda \in (\lambda_{41}, \lambda_{42}), \\ > 0 & \text{for } \lambda > \lambda_{42}. \end{cases}$$

Similarly, we can prove that $\phi(t)$ defined by (3.4) is an upper solution of (3.1) and $\phi(t) \in \Gamma$, and for sufficiently large $M_0 > 1$, $\psi(t)$ defined by (3.4) is a lower solution of (3.1). Thus, Theorem 3.4 holds.

3.5 The case $g(t,x) = \frac{1}{\tau_0}e^{-\frac{t}{\tau_0}}\frac{1}{\sqrt{4\pi t}}e^{-\frac{x^2}{4t}}$, $\tau_0 > 0$

For $c > 0$, let $\lambda_5(c) = \frac{c\tau_0+\sqrt{c^2\tau_0^2+4\tau_0}}{2\tau_0}$, and for $\lambda \in (0, \lambda_5(c))$, define the function

$$\Delta_{5c}(\lambda) = \left(\frac{1}{1+\lambda c\tau_0 - \tau_0\lambda^2} - 1\right)\beta\tau - \left[\tau(1-\beta) + c\lambda - d\lambda^2\right].$$

Obviously,

$$\begin{aligned} &\Delta_{5c}(0) \equiv (\beta - 1)\tau, \qquad \lim_{\lambda\to\lambda_5(c)-0}\Delta_{5c}(\lambda) = +\infty, \\ &1 + \lambda c\tau_0 - \lambda^2\tau_0 > 0, \quad \text{for } \lambda \in \big(0, \lambda_5(c)\big). \end{aligned} \tag{3.9}$$

Lemma 3.27 *There exist* $c^* > 0$ *and* $\lambda^* > 0$ *such that*

(i) $\Delta_{5c^*}(\lambda^*) = 0$ *and*

$$\frac{\partial}{\partial\lambda}\Delta_{5c^*}(\lambda)\bigg|_{\lambda=\lambda^*} = 0.$$

(ii) *For* $0 < c < c^*$, *and* $\lambda_5(c) > \lambda > 0$, *we have* $\Delta_{5c}(\lambda) > 0$.

(iii) *For* $c > c^*$ *the equation* $\Delta_{5c}(\lambda) = 0$ *has two positive real roots* $\lambda_{51}, \lambda_{52}$, *such that* $0 < \lambda_{51} < \lambda_{52} < \lambda_5(c)$ *and*

$$\Delta_{5c}(\lambda) \begin{cases} > 0 & \text{for } 0 < \lambda < \lambda_{51}, \\ < 0 & \text{for } \lambda \in (\lambda_{51}, \lambda_{52}), \\ > 0 & \text{for } \lambda_5(c) > \lambda > \lambda_{52}. \end{cases}$$

Proof If $c = 0$, then $\lambda_5(0) = \frac{1}{\sqrt{\tau_0}} > 0$ for $\lambda \in (0, \lambda_5(0))$, and

$$\Delta_{50}(\lambda) = \left(\frac{1}{1-\lambda^2\tau_0} - 1\right)\beta\tau - \left[\tau(1-\beta) - d\lambda^2\right] > 0.$$

If $c_0 = d + \beta\tau + 1$, then $\lambda_5(c_0) > 1$, and

$$\Delta_{5c_0}(1) = \left(\frac{1}{1+c_0\tau_0-\tau_0} - 1\right)\beta\tau - \left[\tau(1-\beta) + \beta\tau + 1\right] < -1.$$

Furthermore, for any $c \geq 0$ and $\lambda \in (0, \lambda(c))$, we have

$$\frac{\partial^2}{\partial\lambda^2}\Delta_{5c}(\lambda) = 2d + \frac{4\tau_0(1+\lambda c\tau_0 - \lambda^2\tau_0) + 2(c\tau_0 - 2\lambda\tau_0)^2}{(1+\lambda c\tau_0 - \lambda^2\tau_0)^3} > 0,$$

and

$$\frac{\partial}{\partial c}\Delta(\lambda, c) = -\lambda - \frac{\lambda\tau_0}{(1+\lambda c\tau_0 - \lambda^2\tau_0)^2} < 0.$$

This implies that for $c \geq 0$, the image of $y = \Delta_{5c}(\lambda)$ in the plane (λ, y) $(0 < \lambda < \lambda(c))$ is strictly convex down and satisfies (3.9). Also, when $c \geq 0$ is increasing, the image strictly drops and there are no common points for $\lambda > 0$. Combining the arguments for $c = 0$ and $c = c_0$, the conclusion follows. □

Using this lemma, we can prove that Theorem 3.4 is true for this case.

4 Discussion

We have established the existence of travelling wave-fronts for a version of Nicholson's blowflies model that is more general than that studied by Gourley (2000), Gourley and Ruan (2003), So et al. (2000), So and Yang (1998), and Yang and So (1998) by considering a nonlocal delay, which involves a weighted spatiotemporal average over the whole space domain and the whole time interval. Our method is the approach developed in Wang et al. (2006) on the existence of travelling-front solutions to reaction–diffusion systems with nonlocal delays. Moreover, we have considered the dependence of the minimal wave speed on the delay and the mobility of the population. Our main finding here is that the time delay can induce slow travelling wave-fronts and the mobility of the population can increase fast travelling wave-fronts if $\beta \leq \mathrm{e}$. In particular, if we choose some special kernel forms, then our results include and improve some known results obtained by Gourley (2000), Gourley and Ruan (2003), and So and Zou (2001).

Note that in terms of the original parameters, the condition $\beta \leq \mathrm{e}$ is equivalent to $p/\delta \leq \mathrm{e}$, where p is the maximum per capita daily egg production rate and δ is the per capita daily adult death rate. The main results demonstrate that when the ratio of the maximum per capita daily egg production rate and the per capita daily adult death rate is relatively small (less than the exponential number e), then the generalized Nicholson's blowflies model has travelling wave-fronts connecting the two uniform steady states $u = 0$ and $u = \ln\beta = \ln(p/\delta)$. Thus, there is a moving zone of transition for the species from the zero steady-state to the positive steady-state. In other words, the species successfully invade the environment by "waves of invasion."

We established only the existence of travelling-front solutions in the Nicholson's blowflies model with nonlocal delay when the ratio β of the maximum per capita daily egg production rate and the per capita daily adult death rate is less than e. In the case when $\beta > \mathrm{e}$, the delay model undergoes a Hopf bifurcation at the positive steady-state $u = \ln\beta$, and there are bifurcating periodic solutions surrounding the positive steady state (Gurney et al. 1990; Wei and Li 2005; Ruan 2006). We expect that in this case there are travelling wave-train solutions connecting the zero steady state and the periodic solution (see Dunbar 1986 and Huang et al. 2003) that can be established by using a topological argument (see, for example, Ruan 1998). This deserves further investigation.

Acknowledgements Research by Li was partially supported by the NNSF of China (10571078), NSF of Gansu Province of China (3ZS061-A25-001), and the Teaching and Research Award Program for Outstanding Young Teachers in Higher Education Institutions of the Ministry of Education of China. Research by Ruan was partially supported by the NSF grant DMS-0412047 and DMS-0715772.

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