

Stability of steady states and existence of travelling waves in a vector-disease model

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In this paper, a host-vector model is considered for a disease without immunity in which the current density of infectious vectors is related to the number of infectious hosts at earlier times. Spatial spread in a region is modelled in the partial integro-differential equation by a diffusion term. For the general model, we first study the stability of the steady states using the contracting-convex-sets technique. When the spatial variable is one dimensional and the delay kernel assumes some special form, we establish the existence of travelling wave solutions by using the linear chain trick and the geometric singular perturbation method.

1. Introduction

Throughout recorded history, non-indigenous vectors that arrive, establish and spread in new areas have fomented epidemics of human diseases such as malaria, yellow fever, typhus, plague and West Nile (see [19]). Such vector-borne diseases are now major public health problems throughout the world. The spatial spread of newly introduced diseases is a subject of continuing interest to both theoreticians and empiricists.

In his pioneering work, Fisher [12] used a logistic-based reaction–diffusion model to investigate the spread of an advantageous gene in a spatially extended population. Kermack and McKendrick [18] proposed a simple deterministic model for a directly transmitted viral or bacterial agent in a closed population consisting of susceptibles, infectives and recovered. Their model leads to a nonlinear integral equation, which has been studied extensively. The typical feature of the Kermack–McKendrick model is the existence of a critical threshold density of the susceptibles for the occurrence of an epidemic, that is, if the initial population density of the susceptibles exceeds this threshold value, then the population density of infectives at first grows and then diminishes. The Kermack–McKendrick model and the threshold theorem derived from it have played a pivotal role in subsequent developments in the study of the transmission dynamics of infective diseases.

The deterministic model of Barlett [6] predicts a wave of infection moving out from the initial source of infection. Kendall [17] generalized the Kermack–McKendrick model to a space-dependent integro-differential equation. For such an epidemic model described by an integro-differential system with a general weight function, Atkinson and Reuter [4] studied the existence and non-existence of travelling waves (see also [5] and [7]). Aronson [1] argued that the three-component Kendall model can be reduced to a scalar one and extended the concept of asymptotic speed of propagation developed in [2] to the scalar epidemic model (see also a recent paper by Medlock and Kot [21] (and the references cited therein) on travelling waves in scalar integrodifferential equation epidemic models).

The Kendall model (or the scalar Aronson model) assumes that the infected individuals become immediately infectious and does not take into account the fact that most infectious diseases have an incubation period. Taking the incubation period into consideration, Diekmann [10, 11] and Thieme [31, 32] simultaneously proposed a nonlinear (double) integral equation model. Aronson and Weinberger's concept of asymptotic speed of propagation has been successfully extended to such models (see [10, 11, 29–33]). All these models are integral equations in which the spatial migration of the population or host was not explicitly modelled.

Griffiths [15] considered the initial growth of a host-vector epidemic such as malaria using the approximation that the numbers of susceptibles remain constant and formulated the problem as a bivariate birth–death process. Radcliffe [25] generalized the results of Barlett [6] concerning the initial spatial spread of an epidemic to host-vector and carrier-borne epidemics. Radcliffe *et al.* [26] investigated the travelling wave problem for the host-vector epidemic (see also [27]).

In this paper, following Cooke [9], Busenberg and Cooke [8], Marcati and Pozio [20] and Volz [34], we consider a host-vector model for a disease without immunity in which the current density of infectious vectors is related to the number of infectious hosts at earlier times. Spatial spread in a region is modelled in the partial integro-differential equation by a diffusion term. For the general model, we first study the stability of the steady states using the contracting-convex-sets technique (see [22, 23]). When the spatial variable is one dimensional and the delay kernel assumes some special forms, we establish the existence of travelling wave solutions by using the linear chain trick and the geometric singular perturbation method (see [12, 16]).

2. The model

Consider a host in a bounded region $\Omega \in R^N$ ($N \leq 3$), where a disease is carried by a vector, such as in a human population malaria is carried by a mosquito. The host is divided into two classes, susceptible and infectious, whereas the vector population is divided into three classes, infectious, exposed and susceptible.

Suppose that the infection in the host confers negligible immunity and does not result in death or isolation. All newborns are susceptible. The host population is assumed to be stable, that is, the birth rate is constant and equal to the death rate. Moreover, the total host population is homogeneously distributed in Ω and both susceptible and infectious populations are allowed to diffuse inside Ω ; however, there is no migration through $\partial\Omega$, the boundary of Ω .

For the transmission of the disease, it is assumed that a susceptible host can receive the infection only by contacting infected vectors, and a susceptible vector

can receive the infection only from the infectious host. Also, a susceptible vector becomes exposed when it receives the infection from an infected host. It remains exposed for some time and then becomes infectious. The total vector population is also constant and homogeneous in Ω . All three vector classes diffuse inside Ω and cannot cross the boundary of Ω .

Denote

$u(t, x) :=$ normalized spatial density of infectious host at time t in x ,

$v(t, x) :=$ normalized spatial density of susceptible host at time t in x ,

where the normalization is done with respect to the spatial density of the total population. Hence we have

$$u(t, x) + v(t, x) = 1, \quad (t, x) \in R_+ \times \Omega,$$

where $R_+ = [0, \infty)$. Similarly, define

$I(t, x) :=$ normalized spatial density of infectious vector at time t in x ,

$S(t, x) :=$ normalized spatial density of susceptible vector at time t in x .

If α denotes the host-vector contact rate, then the density of new infections in host is given by

$$\alpha v(t, x)I(t, x) = \alpha[1 - u(t, x)]I(t, x).$$

The density of infections vanishes at a rate

$$au(t, x),$$

where a is the cure/recovery rate of the infected host. The difference of host densities of arriving and leaving infections per unit time is given by

$$d\Delta u(t, x),$$

where d is the diffusion constant, Δ is the Laplacian operator. We then obtain the following equation:

$$\frac{\partial u}{\partial t}(t, x) = d\Delta u(t, x) - au(t, x) + \alpha[1 - u(t, x)]I(t, x). \tag{2.1}$$

If the vector population is large enough, we can assume that the density of vectors that become exposed at time t in $x \in \Omega$ is proportional to the density of the infectious hosts at time t in x . That is,

$$S(t, x) = hu(t, x),$$

where h is a positive constant. Let $\xi(t, s, x, y)$ denote the proportion of vectors that arrive in x at time t , starting from y at time $t - s$. Then

$$\int_{\Omega} \xi(t, s, x, y)S(t - s, y) \, dy$$

is the density of vectors that became exposed at time $t - s$ and are in x at time t . Let $\eta(s)$ be the proportion of vectors that are still infectious s units of time after

they became exposed. Then

$$\begin{aligned} I(t, x) &= \int_0^\infty \int_\Omega \xi(t, s, x, y) S(t - s, y) \eta(s) \, dy ds \\ &= \int_0^\infty \int_\Omega \xi(t, s, x, y) h \eta(s) u(t - s, y) \, dy ds. \end{aligned}$$

Substituting $I(t, x)$ into equation (2.1), changing the limits and writing

$$b = \alpha h, \quad F(t, s, x, y) = \xi(t, s, x, y) \eta(s),$$

we obtain the following diffusive integro-differential equation modelling the vector disease:

$$\frac{\partial u}{\partial t}(t, x) = d\Delta u(t, x) - au(t, x) + b[1 - u(t, x)] \int_{-\infty}^t \int_\Omega F(t, s, x, y) u(s, y) \, dy ds, \quad (t, x) \in R_+ \times \Omega. \quad (2.2)$$

The initial value condition is given by

$$u(\theta, x) = \phi(\theta, x), \quad (\theta, x) \in (-\infty, 0] \times \Omega, \quad (2.3)$$

where ϕ is a continuous function for $(\theta, x) \in (-\infty, 0] \times \Omega$, and the boundary value condition is given by

$$\frac{\partial u}{\partial n}(t, x) = 0, \quad (t, x) \in R_+ \times \partial\Omega, \quad (2.4)$$

where $\partial/\partial n$ represents the outward normal derivative on $\partial\Omega$.

The convolution kernel $F(t, s, x, y)$ is a positive continuous function in its variables $t \in R, s \in R_+, x, y \in \Omega$. We normalize the kernel so that

$$\int_0^\infty \int_\Omega F(t, s, x, y) \, dy ds = 1.$$

Various types of equations can be derived from equation (2.2) by taking different kernels. Some examples are given as follows.

- (i) If $F(t, s, x, y) = \delta(x - y)G(t, s)$, then equation (2.2) becomes the following integro-differential equation with a local delay:

$$\frac{\partial u}{\partial t} = d\Delta u(t, x) - au(t, x) + b[1 - u(t, x)] \int_{-\infty}^t G(t - s) u(s, x) \, ds, \quad (t, x) \in R_+ \times \Omega. \quad (2.5)$$

If $u = u(t)$ depends on time only, then the equation becomes

$$\frac{du}{dt} = -au(t) + b[1 - u(t)] \int_{-\infty}^t G(t - s) u(s) \, ds, \quad t > 0. \quad (2.6)$$

- (ii) If $F(t, s, x, y) = \delta(x - y)\delta(t - s)$, then equation (2.2) becomes the following reaction-diffusion equation without delay:

$$\frac{\partial u}{\partial t} = d\Delta u(t, x) - au(t, x) + b[1 - u(t, x)]u(t, x), \quad (t, x) \in R_+ \times \Omega. \quad (2.7)$$

(iii) If $F(t, s, x, y) = \delta(x - y)\delta(t - s - \tau)$, where $\tau > 0$ is a constant, and u does not depend on the spatial variable, then equation (2.2) becomes the following ordinary differential equation with a constant delay:

$$\frac{du}{dt} = -au(t) + b[1 - u(t)]u(t - \tau). \tag{2.8}$$

Cooke [9] studied the stability of equation (2.8) and showed that, when $0 < b \leq a$, the trivial equilibrium $u_0 = 0$ is globally stable; when $0 \leq a < b$, the trivial equilibrium is unstable and the positive equilibrium $u_1 = (b - a)/b$ is globally stable. Busenberg and Cooke [8] assumed that the coefficients are periodic and investigated the existence and stability of periodic solutions of (2.8). Marcati and Pozio [20] proved the global stability of the constant solution to (2.2) when the delay is finite. Volz [34] assumed that all coefficients are periodic and discussed the existence and stability of periodic solutions of equation (2.2).

In this paper, we first discuss the stability of the steady-state solutions for the general equation (2.2). Then, for $x \in (-\infty, \infty)$, we establish the existence of travelling front solutions to the diffusive integro-differential equation with specific convolution kernels.

3. Stability of the steady states

Denote $E = C(\bar{\Omega}, R)$. Then E is a Banach space with respect to the norm

$$|u|_E = \max_{x \in \bar{\Omega}} |u(x)|, \quad u \in E.$$

Denote $\mathcal{C} = BC((-\infty, 0], E)$. For $\phi \in \mathcal{C}$, define

$$\|\phi\| = \sup_{\theta \in (-\infty, 0]} |\phi(\theta)|_E.$$

For any $\beta \in (0, \infty)$, if $u : (-\infty, \beta) \rightarrow E$ is a continuous function, then u_t is defined by $u_t(\theta) = u(t + \theta), \theta \in (-\infty, 0]$.

Define

$$\mathcal{D}(A) = \left\{ u \in E : \Delta u \in E, \frac{\partial u}{\partial n} = 0 \text{ on } \partial\Omega \right\},$$

$$Au = d\Delta u \quad \text{for all } u \in \mathcal{D}(A),$$

$$f(\phi)(x) = -a\phi(0, x) + b[1 - \phi(0, x)] \int_{-\infty}^0 \int_{\Omega} F(0, s, x, y)\phi(s, y) dy ds,$$

where $\phi \in \mathcal{C}, x \in \bar{\Omega}$. Then we can rewrite equation (2.2) in the following abstract form:

$$\left. \begin{aligned} \frac{du}{dt} &= Au + f(u_t), \quad t \geq 0, \\ u_0 &= \phi \in \mathcal{C}, \end{aligned} \right\} \tag{3.1}$$

where

- (a) $A : \mathcal{D}(A) \rightarrow E$ is the infinitesimal generator of a strongly continuous semi-group e^{tA} for $t \geq 0$ on E endowed with the maximum norm; and

(b) $f : \mathcal{C} \rightarrow E$ is Lipschitz continuous on bounded sets of \mathcal{C} .

Associated to equation (3.1), we also consider the following integral equation:

$$\left. \begin{aligned} u(t) &= e^{tA}\phi(0) + \int_0^t e^{(t-s)A}f(u_s) \, ds, \quad t \geq 0, \\ u_0 &= \phi. \end{aligned} \right\} \tag{3.2}$$

A continuous solution of the integral equation (3.2) is called a *mild solution* to the abstract equation (3.1). The existence and uniqueness of the maximal mild solution to equation (3.1) follow from a standard argument (see [28, 35]). When the initial value is taken inside an invariant bounded set in \mathcal{C} , the boundedness of the maximal mild solution implies the global existence.

Define

$$M = \{u \in E : 0 \leq u(x) \leq 1, x \in \bar{\Omega}\}.$$

We shall use the results on invariance and attractivity of sets for general partial functional differential equations established by Pozio [22, 23] and follow the arguments in Marcati and Pozio [20] to study the invariance of the set M and the stability of the steady-state solutions.

DEFINITION 3.1. Let K_1, K_2 be two given subsets in E . We say that $f \in \mathcal{E}(K_1, K_2)$ if and only if, for any $r > 0$, there is $\gamma = \gamma(r) > 0$ such that $\phi(0) + \gamma f(\theta) \in K_2$ if $\phi \in \mathcal{C}$ with $\|\phi\| \leq r$ and $\phi(\theta) \in K_1$ for all $\theta \in (-\infty, 0]$.

The following invariance result was established in Pozio [22, 23].

LEMMA 3.2 (invariance). Let $K \subset E$ be a closed convex subset such that

- (i) $f \in \mathcal{E}(K, K)$;
- (ii) $e^{tA}K \subseteq K$ for $t > 0$.

Then $u(\phi)(t, \cdot) \in K$ if $\phi \in BC((-\infty, 0], K)$.

We first prove that M is invariant by using lemma 3.2 with $K = M$.

THEOREM 3.3. The set M is invariant, that is, if $\phi \in BC((-\infty, 0]; M)$, then $u(\phi)$ exists globally and $u(\phi)(t) \in M$ for all $t \geq 0$.

Proof. Let $\gamma = 1/(a + b)$. For any $y, z \in [0, 1]$, we have

$$\begin{aligned} y + \gamma bz(1 - y) - \gamma ay &\geq y(1 - \gamma a) \\ &\geq 0 \end{aligned}$$

and

$$\begin{aligned} y + \gamma bz(1 - y) - \gamma ay &= y[1 - \gamma(bz + a)] + \gamma bz \\ &\leq [1 - \gamma(bz + a)] + \gamma bz \\ &= 1 - \gamma a \\ &\leq 1. \end{aligned}$$

Thus $0 \leq y + \gamma bz(1 - y) - \gamma ay \leq 1$ for any $y, z \in [0, 1]$, which implies that if $\phi \in BC((-\infty, 0], M)$, then we have

$$0 \leq \phi(0, x) + \gamma f(\phi)(x) \leq 1 \quad \text{for all } x \in \bar{\Omega}.$$

Therefore, condition (i) of lemma 3.2 is satisfied. Condition (ii) follows by the strong maximum principle (see [23, 24]). This completes the proof. □

To study the stability of the steady-state solutions, we need the following attractivity result of Pozio [22, 23].

LEMMA 3.4 (attractivity). *Let $\{K_n\}_{n \in \mathbb{N}}$, $\{K'_n\}_{n \in \mathbb{N}}$ be sequences of subsets in E such that, for all $n \in \mathbb{N}$, we have*

- (i) $f \in \mathcal{E}(K_n, K'_n)$;
- (ii) $e^{tA}K_n \subseteq K_n$ and $e^{tA}K'_n \subseteq K'_n$ for $t > 0$;
- (iii) K'_n is convex and there exists $\varepsilon_n > 0$ such that $(K'_n)_{\varepsilon_n} \cap K_n \subseteq K_{n+1}$, where

$$(K'_n)_{\varepsilon_n} = \{v \in E : \text{dist}(v, K'_n) < \varepsilon_n\};$$

- (iv) there exists $K \subset E$ such that

$$\lim_{n \rightarrow \infty} \delta\left(\bigcap_{j=0}^n K_j, K\right) = 0,$$

where $\delta(S_1, S_2)$ is the Hausdorff distance between the two sets $S_1, S_2 \subset E$, that is,

$$\delta(S_1, S_2) = \max\{\text{dist}(u, S_1), \text{dist}(v, S_2) : (u, v) \in S_1 \times S_2\};$$

- (v) $K_0 \subset E$ is a bounded invariant subset.

Then

$$\lim_{t \rightarrow \infty} \text{dist}(u(\phi)(t), K) = 0$$

for any $\phi \in BC((-\infty, 0], K_0)$.

THEOREM 3.5. *The following statements hold.*

- (i) *If $0 < b \leq a$, then $u_0 = 0$ is the unique steady-state solution of (2.2) in M and it is globally asymptotically stable in $BC((-\infty, 0]; M)$.*
- (ii) *If $0 \leq a < b$, then there are two steady-state solutions in M , $u_0 = 0$ and $u_1 = (b - a)/b$, where u_0 is unstable and u_1 is globally asymptotically stable in $BC((-\infty, 0]; M)$.*

Proof. To use lemma 3.4, define a map by

$$T_\gamma(y) = y[1 + \gamma b(1 - y) - \gamma a],$$

where $y \in [0, 1]$ and $\gamma > 0$. Set $\gamma = 1/(b + a)$. Then

$$T_{\gamma/2}([0, 1]) \subseteq [0, 1], \quad T_{\gamma}([0, 1]) \subseteq [0, 1].$$

Let $\omega = \max\{(b - a)/b, 0\}$ and fix any $\xi, \eta \in [0, 1]$ such that $0 \leq \xi \leq w \leq \eta \leq 1$ with $\xi > 0$ if $w > 0$ and $\eta > \xi$. Thus, for any $n \in N$, we have

$$0 \leq T_{\gamma/2}^n \xi \leq w \leq T_{\gamma/2}^n \eta \leq 1.$$

Let

$$K_n = C(\bar{\Omega}, [T_{\gamma/2}^n \xi, T_{\gamma/2}^n \eta]), \quad K'_n = C(\bar{\Omega}, [T_{\gamma}^n \xi, T_{\gamma}^n \eta]), \quad n \in N.$$

We verify that all conditions in lemma 3.4 are satisfied.

(i) If $y, z \in [T_{\gamma/2}^n \xi, T_{\gamma/2}^n \eta]$, then

$$\begin{aligned} y + \gamma bz(1 - y) - \gamma ay &= y[(1 - \gamma a) - \gamma bz] + \gamma bz \\ &\geq T_{\gamma/2}^n \xi(1 - \gamma a) - T_{\gamma/2}^n \xi \cdot \gamma bz + \gamma bz \\ &= T_{\gamma/2}^n \xi(1 - \gamma a) + \gamma bz(1 - T_{\gamma/2}^n \xi) \\ &\geq T_{\gamma/2}^n \xi[1 + \gamma b(1 - T_{\gamma/2}^n \xi) - \gamma a] \\ &\geq T_{\gamma} T_{\gamma/2}^n \xi \end{aligned}$$

and

$$\begin{aligned} y + \gamma bz(1 - y) - \gamma ay &= y[(1 - \gamma a) - \gamma bz] + \gamma bz \\ &\leq T_{\gamma/2}^n \eta(1 - \gamma a) - T_{\gamma/2}^n \eta \cdot \gamma bz + \gamma bz \\ &= T_{\gamma/2}^n \eta(1 - \gamma a) + \gamma bz(1 - T_{\gamma/2}^n \eta) \\ &\leq T_{\gamma/2}^n \eta[1 + \gamma bz(1 - T_{\gamma/2}^n \eta) - \gamma a] \\ &= T_{\gamma} T_{\gamma/2}^n \eta. \end{aligned}$$

Thus we have

$$T_{\gamma} T_{\gamma/2}^n \xi \leq y + \gamma bz(1 - y) - \gamma ay \leq T_{\gamma} T_{\gamma/2}^n \eta,$$

which implies that $f \in \mathcal{E}(K_n, K'_n)$.

(ii) It follows by the maximum principle arguments.

(iii) Define

$$\delta_n = \frac{1}{2} b T_{\gamma/2}^n \xi \cdot \left(\frac{b - a}{b} - T_{\gamma/2}^n \xi \right), \quad \sigma_n = \frac{1}{2} b T_{\gamma/2}^n \eta \cdot \left(T_{\gamma/2}^n \eta - \frac{b - a}{b} \right), \quad n \in N,$$

and choose

$$\varepsilon_n = \begin{cases} \min\{\delta_n, \sigma_n\} & \text{if } \delta_n \sigma_n > 0, \\ \max\{\delta_n, \sigma_n\} & \text{if } \delta_n \sigma_n = 0. \end{cases}$$

Then we have

$$\min\{T_{\gamma} T_{\gamma/2}^n \eta + \varepsilon_n, T_{\gamma/2}^n \eta\} \leq T_{\gamma/2}^{n+1} \eta, \quad \max\{T_{\gamma} T_{\gamma/2}^n \xi - \varepsilon_n, T_{\gamma/2}^n \xi\} \geq T_{\gamma/2}^{n+1} \xi.$$

This implies that $(K'_n)_{\varepsilon_n} \cap K_n \subseteq K_{n+1}$.

(iv) For ω defined above, let $K = \{v \in E : v(x) = \omega\}$. Then, for all n , we have

$$\delta\left(\bigcap_{j=0}^n K_j, K\right) = \delta(K_n, K) < T_{\gamma/2}^n \eta - T_{\gamma/2}^n \xi. \tag{3.3}$$

We can see that $\{T_{\gamma/2}^n \eta\}$ is a monotone non-increasing sequence bounded from below by ω . Thus it converges to some $y_0 \geq \omega$, which is a fixed point of $T_{\gamma/2}$, that is,

$$y_0[1 + \frac{1}{2}b(1 - y_0) - \frac{1}{2}a] = y_0 \geq \omega.$$

Thus:

- (a) if $b \leq a$, we have $\omega = 0$, and then $y_0 = \omega = 0$;
- (b) if $b > a$, we have $\omega > 0$, and then $y_0 = (b - a)/b = \omega > 0$.

Similarly, $\{T_{\gamma/2}^n \xi\}$ is a monotone non-decreasing sequence bounded from above by ω . Thus, if $b > a$ and $h > 0$, it converges to some fixed point z_0 of $T_{\gamma/2}$. We have

$$z_0[1 + \frac{1}{2}b(1 - z_0) - \frac{1}{2}a] = z_0 \geq \omega.$$

Therefore:

- (a) if $b \leq a$, that is, $\omega = 0$, we have $h = 0$ and $T_{\gamma/2} 0 = 0$ for each $n \in N$;
- (b) if $b > a$, we have $\omega > 0$, and then $z_0 = (b - a)/b = \omega > 0$.

Combining the above two cases and using (3.3), we have the following.

- (a) If $0 < b \leq a$, since $T_{\gamma/2} \eta \rightarrow \omega = 0$, we have

$$\lim_{n \rightarrow \infty} \delta\left(\bigcap_{j=0}^n K_j, \{0\}\right) = 0. \tag{3.4}$$

- (b) If $0 \leq a < b$ and $h > 0$, since $T_{\gamma/2} \eta \rightarrow \omega = (b - a)/b$ and $T_{\gamma/2} \xi \rightarrow \omega = (b - a)/b$, we have

$$\lim_{n \rightarrow \infty} \delta\left(\bigcap_{j=0}^n K_j, \left\{\frac{b - a}{b}\right\}\right) = 0. \tag{3.5}$$

(v) Let $K_0 = C(\bar{\Omega}, [\xi, \eta])$. By lemma 3.2, we have $f \in \mathcal{E}(K_0, K_0)$. Thus K_0 is invariant.

Conclusion (i) of theorem 3.5 follows by (3.4). To prove conclusion (ii) by applying (3.5), we have to verify that the initial value satisfies the following condition:

$$\phi(\theta, x) \geq \xi > 0, \quad (\theta, x) \in (-\infty, 0] \times \bar{\Omega}. \tag{3.6}$$

(I) Assume that $\phi(0, \cdot) \in \mathcal{D}(A)$ with $\phi(0, \cdot) \not\equiv 0$. Then there exist a time $t_0 = t_0(\phi) > r$ and a number $h_0 = h_0(\phi)$ such that, for $x \in \bar{\Omega}$, $t \in [t_0 - r, t_0]$ and $\gamma > 0$, we have

$$e^{-t/\gamma}[e^{tA}\phi(0)](x) \geq h_0 > 0. \tag{3.7}$$

Notice that the mild solution of (3.1) satisfies

$$u(\phi)(t, x) = e^{-t/\gamma}[e^{tA}\phi(0)](x) + \frac{1}{\gamma} \int_0^t e^{(t-s)(-1/\gamma+A)}[u(\phi)(s, x) + \gamma f(u_s(\phi))(x)] ds, \tag{3.8}$$

provided $\gamma > 0$. By the proof of lemma 3.2, we know that there exists $\gamma > 0$ such that $u(\phi)(s, x) + \gamma f(u_s(\phi))(x) \geq 0$. Thus (3.7) and (3.8) imply that there exist a time $t_0 = t_0(\phi)$ and a number $h_0 = h_0(\phi)$ such that u_{t_0} satisfies (3.6) when $h = h_0$.

(II) If $\phi(0) \in M \setminus \{0\}$, consider $\psi \in \mathcal{D}(A) \setminus \{0\}$ such that $0 \leq \psi(x)\phi(0, x), x \in \Omega$. Then

$$e^{-t/\gamma}[e^{tA}\phi(0)](x) \geq e^{-t/\gamma}[e^{tA}\psi](x).$$

We can show that the same conclusion holds.

(III) Finally, if $\phi \in BC((-\infty, 0], M)$ with $\phi \neq 0$, then there exists $(\theta_0, x_0) \in (-\infty, 0] \times \Omega$ such that

$$\phi(\theta_0, x_0) > 0. \tag{3.9}$$

Assume that $u_t(0, \cdot) \equiv 0$ for all $t \geq 0$. Then (3.2) implies that

$$\int_0^t e^{(t-s)A} f(u_s) ds = 0, \quad t \geq 0, \quad x \in \bar{\Omega}. \tag{3.10}$$

By the properties of the kernel and inequality (3.9), we can find $t_0 > 0$ such that

$$\int_0^{t_0} e^{(t_0-s)A} f(u_s) ds > 0,$$

which contradicts (3.10). Thus there exists a $\bar{t} > 0$ such that $u_{\bar{t}}(0, \cdot) \neq 0$. Following the previous arguments, we can show that condition (3.6) is satisfied.

Now conclusion (ii) follows by (3.5). This completes the proof. □

Recall that b represents the contact rate and a represents the recovery rate. The stability results indicate that there is a *threshold* at $b = a$. If $b \leq a$, then the proportion u of infectious individuals tends to zero as t becomes large and the disease dies out. If $b > a$, the proportion of infectious individuals tends to an endemic level $u_1 = (b - a)/b$ as t becomes large. There is no non-constant periodic solutions in the region $0 \leq u \leq 1$.

The above results also apply to the special cases (2.5), (2.7) and (2.8), and thus include the following results on global stability of the steady states of the discrete delay model (2.8) obtained by Cooke [9] (using the Liapunov functional method).

COROLLARY 3.6. *For the discrete delay model (2.8), we have the following statements.*

- (i) *If $0 < b \leq a$, then the steady-state solution $u_0 = 0$ is asymptotically stable and the set*

$$\{\phi \in C([-\tau, 0], R) : 0 \leq \phi(\theta) \leq 1 \text{ for } -\tau \leq \theta \leq 0\}$$

is a region of attraction.

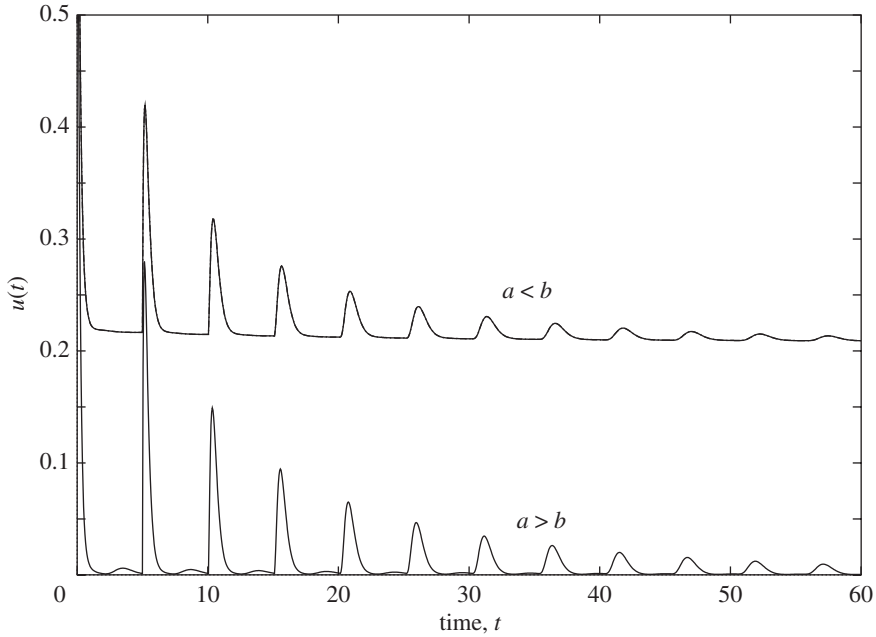


Figure 1. Numerical simulations for the discrete delay equation (2.8). When $a = 5.8$, $b = 4.8$ ($a > b$), the zero steady state $u = 0$ is asymptotically stable; when $a = 3.8$, $b = 4.8$ ($a < b$), the positive steady state u^* is asymptotically stable for all delay values. Here, for both cases, $\tau = 5$.

- (ii) If $0 \leq a < b$, then the steady-state solution $u_1 = (b - a)/b$ is asymptotically stable and the set

$$\{\phi \in C([-\tau, 0], R) : 0 < \phi(\theta) \leq 1 \text{ for } -\tau \leq \theta \leq 0\}$$

is a region of attraction.

Numerical simulations are given in figure 1.

Similarly, we can obtain stability conditions for the integrodifferential equation (2.6) when $u = u(t)$ does not depend on the spatial variable x . Numerical simulations are presented in figure 2.

4. Existence of travelling waves

We know that, when $b > a$, equation (2.2) has two steady-state solutions, $u_0 = 0$ and $u_1 = (b - a)/b$. In this section, we consider $x \in (-\infty, \infty)$ and establish the existence of travelling wave solutions of the form $u(x, t) = U(z)$ such that

$$\lim_{z \rightarrow -\infty} U(z) = \frac{b - a}{b}, \quad \lim_{z \rightarrow \infty} U(z) = 0,$$

where $z = x - ct$ is the wave variable and $c \geq 0$ is the wave speed. We consider two cases:

- (a) without delay, i.e. equation (2.7);

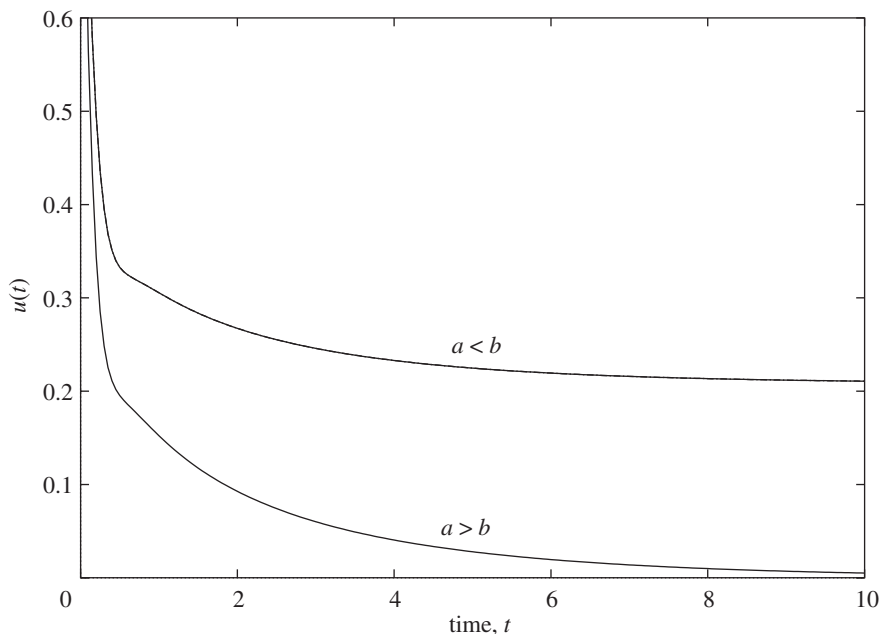


Figure 2. Numerical simulations for the integrodifferential equation (2.6) with a strong kernel $G(t) = (t/\tau^2)e^{-t/\tau}$. When $a = 5.8$, $b = 4.8$ ($a > b$), the zero steady state $u = 0$ is asymptotically stable; when $a = 3.8$, $b = 4.8$ ($a < b$), the positive steady state u^* is asymptotically stable for all delay values. Here, for both cases, $\tau = 0.2$.

(b) with local delay, i.e. equation (2.5).

Throughout this section, we scale the model so that $d = 1$.

4.1. The model without delay

Substituting $u(x, t) = U(z)$ into the reaction-diffusion equation (2.7) without delay, i.e.

$$\frac{\partial u}{\partial t} = \Delta u(t, x) - au(t, x) + b[1 - u(t, x)]u(t, x),$$

we obtain the travelling wave equation

$$U'' + cU' + (b - a - bU)U = 0,$$

which is equivalent to the following system of first-order equations

$$\left. \begin{aligned} U' &= V, \\ V' &= -cV - (b - a - bU)U. \end{aligned} \right\} \quad (4.1)$$

System (4.1) has two equilibria, $E_0 = (0, 0)$ and $E_1 = ((b - a)/b, 0)$. The following result shows that there is a travelling front solution of equation (4.1) connecting E_0 and E_1 .

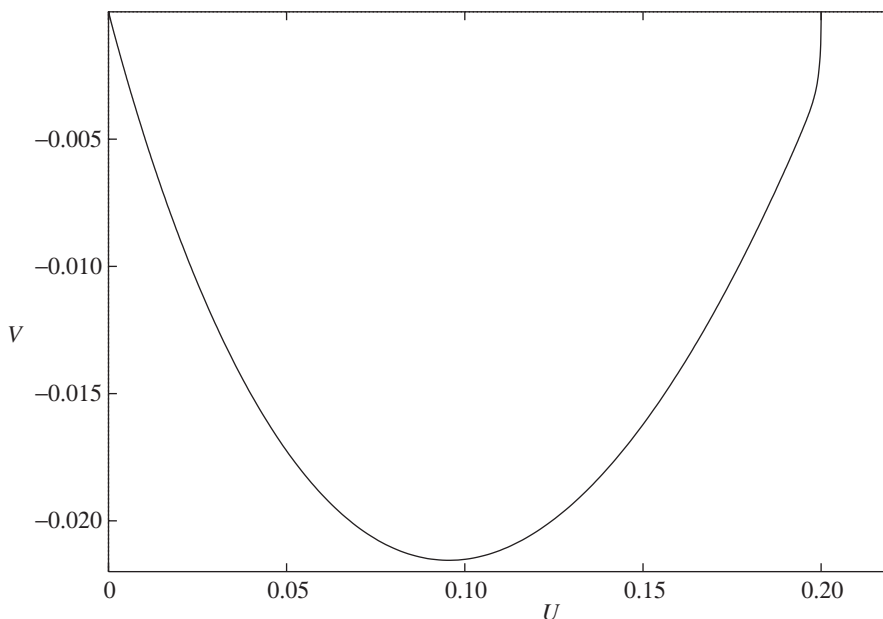


Figure 3. The heteroclinic orbit connecting the critical points $E_0 = (0, 0)$ and $E_1 = (0.2, 0)$. Here, $a = 3.8$, $b = 4.8$ and $c = 2.4$.

THEOREM 4.1. *If $c \geq 2\sqrt{b-a}$, then, in the (U, V) phase plane for system (4.1), there is a heteroclinic orbit connecting the critical points E_0 and E_1 . The heteroclinic connection is confined to $V < 0$ and the travelling wave $U(z)$ is strictly monotonically decreasing.*

Proof. Linear analysis of system (4.1) shows that E_0 is a node (under the condition on c) and E_1 is a saddle. To establish the existence of a heteroclinic orbit connecting the two equilibria for $V < 0$, we shall show that, for a suitable value of $\mu > 0$, the triangular set

$$B = \left\{ (U, V) : 0 \leq U \leq \frac{b-a}{b}, -\mu U \leq V \leq 0 \right\}$$

is positively invariant. Let \mathbf{f} be the vector defined by the right-hand sides of system (4.1) and \mathbf{n} be the inward normal vector on the boundary of B . We only need to consider the side $V = -\mu U$, $0 < U \leq (b-a)/b$ of the triangle and have

$$\mathbf{f} \cdot \mathbf{n} = U[-\mu^2 + c\mu - (b-a)] + bU^2 > 0,$$

with

$$\mu = \frac{1}{2}[-c + \sqrt{c^2 + 4(b-a)}].$$

This implies that one branch of the unstable manifold of E_1 enters the region B and joins E_0 to form a heteroclinic orbit. This completes the proof. \square

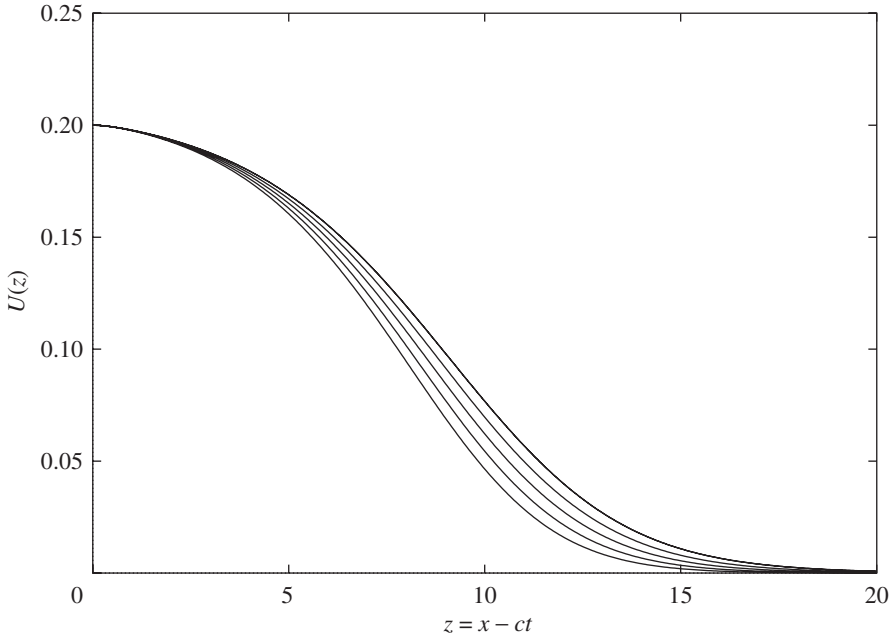


Figure 4. The travelling front profiles for the wave form equations (4.1). Here, $a = 3.8$, $b = 4.8$ and $c = 2.0 - 2.4$.

4.2. The model with local delay

Consider the diffusive integro-differential equation (2.5) with a local delay kernel

$$G(t) = \frac{t}{\tau^2} e^{-t/\tau},$$

which is called the *strong* kernel. The parameter $\tau > 0$ measures the delay, which implies that a particular time in the past, namely, τ time units ago, is more important than any other, since the kernel achieves its unique maximum when $t = \tau$. Equation (2.5) becomes

$$\frac{\partial u}{\partial t} = \Delta u(t, x) - au(t, x) + b[1 - u(t, x)] \int_{-\infty}^t \frac{t-s}{\tau^2} e^{-(t-s)/\tau} u(s, x) ds, \quad (t, x) \in \mathbb{R}_+ \times \Omega. \quad (4.2)$$

Define $U(z) = u(x, t)$ and

$$W(z) = \int_0^\infty \frac{t}{\tau^2} e^{-t/\tau} U(z + ct) dt, \quad Y(z) = \int_0^\infty \frac{1}{\tau} e^{-t/\tau} U(z + ct) dt.$$

Differentiating with respect to z , we have

$$\begin{aligned} -c \frac{dU}{dz} &= \frac{d^2U}{dz^2} - aU + b(1 - U)W, \\ \frac{dW}{dz} &= \frac{1}{c\tau}(W - Y), \end{aligned}$$

$$\frac{dY}{dz} = \frac{1}{c\tau}(Y - U).$$

Denote $U' = V$. Then we obtain the following travelling wave equations:

$$\left. \begin{aligned} U' &= V, \\ V' &= aU - cV - bW + bUW, \\ c\tau W' &= W - Y, \\ c\tau Y' &= -U + Y. \end{aligned} \right\} \tag{4.3}$$

For $\tau > 0$, system (4.3) has two equilibria,

$$(0, 0, 0, 0) \quad \text{and} \quad \left(\frac{b-a}{b}, 0, \frac{b-a}{b}, \frac{b-a}{b} \right).$$

A travelling front solution of the original equation exists if there exists a heteroclinic orbit connecting these two critical points (see [3, 13, 14]).

Note that, when τ is very small, system (4.3) is a singularly perturbed system. Let $z = \tau\eta$. Then system (4.3) becomes

$$\left. \begin{aligned} \dot{U} &= \tau V, \\ \dot{V} &= \tau(aU - cV - bW + bUW), \\ c\dot{W} &= W - Y, \\ c\dot{Y} &= -U + Y, \end{aligned} \right\} \tag{4.4}$$

where dots denote differentiation with respect to η . While these two systems are equivalent for $\tau > 0$, the different time-scales give rise to two different limiting systems. Letting $\tau \rightarrow 0$ in (4.3), we obtain

$$\left. \begin{aligned} \dot{U} &= \tau V, \\ \dot{V} &= \tau(aU - cV - bW + bUW), \\ 0 &= W - Y, \\ 0 &= -U + Y. \end{aligned} \right\} \tag{4.5}$$

Thus the flow of system (4.5) is confined to the set

$$\mathcal{M}_0 = \{(U, V, W, Y) \in \mathbf{R}^4 : W = U, Y = U\}, \tag{4.6}$$

and its dynamics are determined by the first two equations only. On the other hand, setting $\tau \rightarrow 0$ in (4.4) results in the system

$$\left. \begin{aligned} U' &= 0, \\ V' &= 0, \\ cW' &= W - Y, \\ cY' &= -U + Y. \end{aligned} \right\} \tag{4.7}$$

Any points in \mathcal{M}_0 are the equilibria of system (4.7). Generally, system (4.3) is referred to as the *slow system*, since the time-scale z is slow, and (4.4) is referred

to as the *fast system*, since the time-scale η is fast. Hence U and V are called *slow variables* and W and Y are called the *fast variables*. \mathcal{M}_0 is the *slow manifold*.

If \mathcal{M}_0 is *normally hyperbolic*, then we can use the geometric singular perturbation theory of Fenichel [12] to obtain a two-dimensional invariant manifold \mathcal{M}_τ for the flow when $0 < \tau \ll 1$, which implies the persistence of the slow manifold as well as the stable and unstable foliations. As a consequence, the dynamics in the vicinity of the slow manifold are completely determined by the one on the slow manifold. Therefore, we only need to study the flow of the slow system (4.3) restricted to \mathcal{M}_τ and show that the two-dimensional reduced system has a heteroclinic orbit.

Recall that \mathcal{M}_0 is a normally hyperbolic manifold if the linearization of the fast system (4.4), restricted to \mathcal{M}_0 , has exactly $\dim \mathcal{M}_0$ eigenvalues with zero real part. The eigenvalues of the linearization of the fast system restricted to \mathcal{M}_0 are $0, 0, 1/c, 1/c$. Thus \mathcal{M}_0 is normally hyperbolic.

We need the following results on invariant manifolds, which is due to Fenichel [12]. We use a form of this theorem due to Jones [16].

LEMMA 4.2 (geometric singular perturbation theorem). *Given a C^∞ vector field of the form*

$$\begin{aligned} x' &= f(x, y, \varepsilon), \\ y' &= \varepsilon g(x, y, \varepsilon) \end{aligned}$$

such that, when $\varepsilon = 0$, the system has a compact normally hyperbolic manifold of critical points M_0 , which is given as the graph of a C^∞ function $h^0(y)$, then, for every $r > 0$, there exists an $\varepsilon_0 > 0$ such that, if $|\varepsilon| < \varepsilon_0$, there exists a manifold M_ε such that the following hold.

- (1) M_ε is locally invariant under the flow of the system.
- (2) M_ε is C^r in x, y and ε .
- (3) $M_\varepsilon = \{(x, y) \mid x = h^\varepsilon(y)\}$ for some C^r function h^ε and y in some compact set K .
- (4) There are local stable and unstable manifolds, $W^s(M_\varepsilon)$ and $W^u(M_\varepsilon)$, that lie within $\mathcal{O}(\varepsilon)$ of and are diffeomorphic to $W^s(M_0)$ and $W^u(M_0)$.

The geometric singular perturbation theorem now implies that there exists a two-dimensional manifold \mathcal{M}_τ for $\tau > 0$. To determine \mathcal{M}_τ explicitly, we have

$$\mathcal{M}_\tau = \{(U, V, W, Y) \in \mathbb{R}^4 : W = U + g(U, V; \tau), Y = U + h(U, V; \tau)\}, \tag{4.8}$$

where the functions g and h are to be determined and satisfy

$$g(U, V; 0) = h(U, V; 0) = 0. \tag{4.9}$$

By substituting into the slow system (4.3), we know that g and h satisfy

$$\begin{aligned} c\tau \left[\left(1 + \frac{\partial h}{\partial U} + \frac{\partial g}{\partial U} \right) V \right. \\ \left. + \left(\frac{\partial h}{\partial V} + \frac{\partial g}{\partial V} \right) (aU - cV - b(U + h + g) + bU(U + h + g)) \right] = g, \end{aligned}$$

$$c\tau \left[\left(1 + \frac{\partial h}{\partial U} \right) V + \frac{\partial h}{\partial V} (aU - cV - b(U + h + g) + bU(U + h + g)) \right] = h.$$

Since h and g are zero when $\tau = 0$, we set

$$\left. \begin{aligned} g(U, V; \tau) &= \tau g_1(U, V) + \tau^2 g_2(U, V) + \dots, \\ h(U, V; \tau) &= \tau h_1(U, V) + \tau^2 h_2(U, V) + \dots. \end{aligned} \right\} \quad (4.10)$$

Substituting $g(U, V; \tau)$ and $h(U, V; \tau)$ into the above equations and comparing powers of τ , we obtain

$$\left. \begin{aligned} g_1(U, V) &= cV, \\ h_1(U, V) &= cV, \\ g_2(U, V) &= 2c^2(aU - cV - b(1 - U)U), \\ h_2(U, V) &= c^2(aU - cV - b(1 - U)U). \end{aligned} \right\} \quad (4.11)$$

The slow system (4.3) restricted to \mathcal{M}_τ is therefore given by

$$\left. \begin{aligned} U' &= V, \\ V' &= aU - cV - b(1 - U)[U + g(U, V; \tau) + h(U, V; \tau)], \end{aligned} \right\} \quad (4.12)$$

where g and h are given by (4.10) and (4.11). Note that, when $\tau = 0$, system (4.12) reduces to the corresponding system (4.1) for the non-delay equation. We can see that, for $0 < \tau \ll 1$, system (4.12) still has critical points E_0 and E_1 . The following theorem shows that there is a heteroclinic orbit connecting E_0 and E_1 and thus equation (4.2) has a travelling wave solution connecting $u_0 = 0$ and $u_1 = (b - a)/b$.

THEOREM 4.3. *For any $\tau > 0$ sufficiently small, there exist a speed c such that the system (4.12) has a heteroclinic orbit connecting the two equilibrium points E_0 and E_1 .*

Proof. We write system (4.12) as

$$\left. \begin{aligned} U' &= V, \\ V' &= \Phi(U, V, c, \tau). \end{aligned} \right\} \quad (4.13)$$

Note that

$$\Phi(U, V, c, 0) = aU - cV - b(1 - U)U.$$

We know that when $\tau = 0$ the travelling front $U(z)$ is strictly monotone if its speed $c \geq 2\sqrt{b - a}$. Therefore, in the (U, V) plane, it can be characterized as the graph of some function, i.e.

$$V = w(U, c).$$

By the stable manifold theorem, for sufficiently small τ , we can also characterize the unstable manifold at $((b - a)/b, 0)$ as the graph of some function,

$$V = w_1(U, c, \tau),$$

where $w_1((b - a)/b, c, \tau) = 0$. Furthermore, by continuous dependence of the solutions on parameters, this manifold must cross the line $U = (b - a)/(2b)$ somewhere if τ is sufficiently small.

Similarly, let $V = w_2(U, c, \tau)$ be the equation for the stable manifold at the origin. Clearly, $w_2(0, c, \tau) = 0$, and it also crosses the line $U = (b - a)/(2b)$ somewhere for suitably small τ . Thus

$$w_1(U, c, 0) = w_2(U, c, 0) = w(U, c).$$

For $\tau = 0$, fix $c = c_0 \geq 2\sqrt{b - a}$, so that the equation of the corresponding wave in the phase plane is $V = w(U, c_0)$. To show that there is a heteroclinic connection when $\tau > 0$, we want to show that there exists a unique value of $c = c(\tau)$, near c_0 , such that the manifolds w_1 and w_2 cross the line $U = (b - a)/(2b)$ at the same point. Define

$$G(c, \tau) = w_1\left(\frac{b - a}{2b}, c, \tau\right) - w_2\left(\frac{b - a}{2b}, c, \tau\right).$$

Note that both $V = w_1(U, c, \tau)$ and $V = w_2(U, c, \tau)$ satisfy the equation

$$\frac{dV}{dU} = \frac{\Phi(U, V, c, \tau)}{U}.$$

We have

$$\begin{aligned} \frac{d}{dU} \left(\frac{\partial w_1}{\partial c}(U, c_0, 0) \right) &= \frac{\partial}{\partial c} \left(\frac{dw_1}{dU}(U, c, 0) \right) \Big|_{c=c_0} \\ &= \frac{\partial}{\partial c} \left(\frac{\Phi(U, w_1(U, c, 0), c, 0)}{w_1(U, c, 0)} \right) \Big|_{c=c_0} \\ &= \frac{\partial}{\partial c} \left(\frac{aU - cw_1(U, c, 0) - b(1 - U)U}{w_1(U, c, 0)} \right) \Big|_{c=c_0} \\ &= \frac{\partial}{\partial c} \left(-c + \frac{aU - b(1 - U)U}{w_1(U, c, 0)} \right) \Big|_{c=c_0} \\ &= -1 - \frac{(b - a)U - bU^2}{w(U, c_0)^2} \frac{\partial w_1}{\partial c}(U, c_0, 0). \end{aligned}$$

Integrating from $(b - a)/(2b)$ to $(b - a)/b$, we have

$$\frac{\partial w_1}{\partial c} \left(\frac{b - a}{2b}, c_0, 0 \right) = \int_{(b-a)/2b}^{(b-a)/b} \exp \left[\int_{(b-a)/2b}^s \frac{(b - a)\xi - b\xi^2}{w(\xi, c_0)^2} d\xi \right] ds. \tag{4.14}$$

Similarly, we have

$$\frac{d}{dU} \left(\frac{\partial w_2}{\partial c}(U, c_0, 0) \right) = 1 - \frac{(b - a)U - bU^2}{w(U, c_0)^2} \frac{\partial w_2}{\partial c}(U, c_0, 0).$$

Integrating from 0 to $(b - a)/(2b)$ yields

$$\frac{\partial w_2}{\partial c} \left(\frac{b - a}{2b}, c_0, 0 \right) = - \int_0^{(b-a)/2b} \exp \left[\int_{(b-a)/2b}^s \frac{(b - a)\xi - b\xi^2}{w(\xi, c_0)^2} d\xi \right] ds. \tag{4.15}$$

Combining (4.14) and (4.15), we have

$$\begin{aligned} \frac{\partial G}{\partial c}(c_0, 0) &= \frac{\partial w_1}{\partial c}\left(\frac{b-a}{2b}, c_0, 0\right) - \frac{\partial w_2}{\partial c}\left(\frac{b-a}{2b}, c_0, 0\right) \\ &= \int_0^{(b-a)/b} \exp\left[\int_{(b-a)/2b}^s \frac{(b-a)\xi - b\xi^2}{w(\xi, c_0)^2} d\xi\right] ds > 0. \end{aligned}$$

Thus, by the implicit function theorem, for sufficiently small τ , $G(c, \tau) = 0$ has a root $c = c(\tau)$ near c_0 . This implies that the manifolds w_1 and w_2 cross the line $U = (b-a)/(2b)$ at the same point. This establishes the existence of a heteroclinic connection. \square

REMARK 4.4. The existence of travelling wave solutions can be similarly established if the local delay kernel is a weak kernel, i.e. $G(t) = (1/\tau)e^{-t/\tau}$.

5. Discussion

Recently, great attention has been paid to the existence of travelling wave solutions in epidemic models. The basic idea is that epidemic models described by reaction–diffusion systems can give rise to a moving zone of transition from an infective state to a disease-free state.

In this paper, following Cooke [9], Busenberg and Cooke [8], Marcati and Pozio [20] and Volz [34], we have considered a host-vector model for a disease without immunity in which the current density of infectious vectors is related to the number of infectious hosts at earlier times. Spatial spread in a region was modelled in the partial integro-differential equation by a diffusion term. For the general model, we studied the stability of the steady states using the contracting-convex-sets technique (see [22,23]). The stability results indicate that there is a *threshold* at $b = a$. If $b \leq a$, then the proportion u of infectious individuals tends to zero as t becomes large and the disease dies out. If $b > a$, the proportion of infectious individuals tends to an endemic level $u_1 = (b-a)/b$ as t becomes large.

When the spatial variable is one dimensional and the delay kernel assumes some special form, we first transformed the travelling wave equations into a finite-dimensional system of ordinary differential equations by using the linear chain trick, then we applied the geometric singular perturbation method (see [12,16]) to prove the existence of heteroclinic orbits, which are travelling wave solutions for the original partial integro-differential equation. Our results (theorems 4.1 and 4.3) also show that, for the small delay, the travelling waves are qualitatively similar to those of the non-delay equation. The existence of travelling front solutions show that there is a moving zone of transition from the disease-free state to the infective state.

We only established the existence of travelling front waves in the vector-disease model when the kernel takes some specific forms, namely, a delta kernel and a local strong kernel. The case with a general non-local kernel deserves further investigation. Also, the minimal wave speed, the asymptotic wave speed, the uniqueness and stability of the travelling waves in such vector-disease models are interesting and challenging problems. We leave these for future consideration.

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References

- 1 D. G. Aronson. The asymptotic speed of propagation of a simple epidemic. In *Nonlinear diffusion* (ed. W. E. Fitzgibbon and H. F. Walker). Research Notes in Mathematics, vol. 14, pp. 1–23 (Boston, MA: Pitman, 1977).
- 2 D. G. Aronson and H. F. Weinberger. Nonlinear diffusion in population genetics, combustion, and nerve pulse propagation. In *Partial differential equations and related topics* (ed. J. A. Goldstein). Lecture Notes in Mathematics, vol. 446, pp. 5–49 (Springer, 1975).
- 3 P. Ashwin, M. V. Bartuccelli, T. J. Bridges and S. A. Gourley. Travelling fronts for the KPP equation with spatio-temporal delay. *Z. Angew. Math. Phys.* **53** (2002), 103–122.
- 4 C. Atkinson and G. E. H. Reuter. Deterministic epidemic waves. *Math. Proc. Camb. Phil. Soc.* **80** (1976), 315–330.
- 5 A. D. Barbour. The uniqueness of Atkinson and Reuter’s epidemic waves. *Math. Proc. Camb. Phil. Soc.* **82** (1977), 127–130.
- 6 M. S. Bartlett. Deterministic and stochastic models for recurrent epidemics. *Proc. 3rd Berkeley Symp. Math. Stat. Prob.* **4** (1956), 81–109.
- 7 K. J. Brown and J. Carr. Deterministic epidemic waves of critical velocity. *Math. Proc. Camb. Phil. Soc.* **81** (1977), 431–433.
- 8 S. Busenberg and K. L. Cooke. Periodic solutions for a vector disease model. *SIAM J. Appl. Math.* **35** (1978), 704–721.
- 9 K. L. Cooke. Stability analysis for a vector disease model. *Rocky Mt. J. Math.* **9** (1979), 31–42.
- 10 O. Diekmann. Thresholds and travelling waves for the geographical spread of infection. *J. Math. Biol.* **6** (1978), 109–130.
- 11 O. Diekmann. Run for life: a note on the asymptotic spread of propagation of an epidemic. *J. Diff. Eqns* **33** (1979), 58–73.
- 12 N. Fenichel. Geometric singular perturbation theory for ordinary differential equations. *J. Diff. Eqns* **31** (1979), 53–98.
- 13 S. A. Gourley. Travelling fronts in the diffusive Nicholson’s blowflies equation with distributed delays. *Math. Comput. Modelling* **32** (2000), 843–853.
- 14 S. A. Gourley and M. A. J. Chaplain. Travelling fronts in a food-limited population model with time delay. *Proc. R. Soc. Edinb. A* **132** (2002), 75–89.
- 15 D. A. Griffiths. A bivariate birth–death process which approximates to the spread of a disease involving a vector. *J. Appl. Prob.* **9** (1972), 65–75.
- 16 C. K. R. T. Jones. Geometric singular perturbation theory. In *Dynamical systems* (ed. R. Johnson). Lecture Notes in Mathematics, vol. 1609 (Springer, 1995).
- 17 D. G. Kendall. Discussion of ‘Measles periodicity and community size’ by M. S. Bartlett. *J. R. Stat. Soc. A* **120** (1957), 64–76.
- 18 W. O. Kermack and A. G. McKendrick. A contribution to the mathematical theory of epidemics. *Proc. R. Soc. Lond. A* **115** (1927), 700–721.
- 19 L. P. Lounibos. Invasions by insect vectors of human disease. *A. Rev. Entomol.* **47** (2002), 233–266.
- 20 P. Marcati and M. A. Pozio. Global asymptotic stability for a vector disease model with spatial spread. *J. Math. Biol.* **9** (1980), 179–187.
- 21 J. Medlock and M. Kot. Spreading disease: integro-differential equations old and new. *Math. Biosci.* **184** (2003), 201–222.
- 22 M. A. Pozio. Behavior of solutions of some abstract functional differential equations and application to predator–prey dynamics. *Nonlin. Analysis* **4** (1980), 917–938.
- 23 M. A. Pozio. Some conditions for global asymptotic stability of equilibria of integrodifferential equations. *J. Math. Analysis Applic.* **95** (1983), 501–527.

- 24 M. H. Protter and H. F. Weinberger. *Maximum principle in differential equations* (Englewood Cliffs, NJ: Prentice-Hall, 1967).
- 25 J. Radcliffe. The initial geographical spread of host-vector and carrier-borne epidemics. *J. Appl. Prob.* **10** (1973), 703–717.
- 26 J. Radcliffe, L. Rass and W. D. Stirling. Wave solution for the deterministic host-vector epidemic. *Math. Proc. Camb. Phil. Soc.* **91** (1982), 131–152.
- 27 L. Rass and J. Radcliffe. *Spatial deterministic epidemics*. Mathematical Surveys Monographs, vol. 102 (Providence, RI: American Mathematical Society, 2003).
- 28 S. Ruan and J. Wu. Reaction–diffusion equations with infinite delay. *Can. Appl. Math. Q.* **2** (1994), 485–550.
- 29 K. Schumacher. Travelling-front solution for integro-differential equation. I. *J. Reine Angew. Math.* **316** (1980), 54–70.
- 30 K. Schumacher. Travelling-front solution for integro-differential equation. II. In *Biological growth and spread*. Lecture Notes in Biomathematics, vol. 38, pp. 296–309 (ed. W. Jäger *et al.*) (Springer, 1980).
- 31 H. R. Thieme. A model for the spatial spread of an epidemic. [*J. Math. Biol.* **4** \(1977\), 337–351.](#)
- 32 H. R. Thieme. Asymptotic estimates of the solutions of nonlinear integral equation and asymptotic speeds for the spread of populations. *J. Reine Angew. Math.* **306** (1979), 94–121.
- 33 H. R. Thieme and X.-Q. Zhao. Asymptotic speeds of spread and traveling waves for integral equations and delayed reaction–diffusion models. *J. Diff. Eqns* **195** (2003), 430–470.
- 34 R. Volz. Global asymptotic stability of a periodic solution to an epidemic model. [*J. Math. Biol.* **15** \(1982\), 319–338.](#)
- 35 J. Wu. *Theory and applications of partial functional differential equations* (Springer, 1996).

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