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Minimal wave speed and spread speed in a system modelling the geographic spread of black-legged tick *Ixodes scapularis*

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Abstract

In a recent work [1], a mathematical model is derived to explore the role that the white-tail deer plays in the geographic spread of the black-legged tick *Ixodes scapularis* in the northeast of the United States of America. The threshold dynamics is rigorously investigated in terms of the basic reproduction number, for the cases of the 1-D whole space $\Omega = \mathbb{R}$ and general bounded spatial domain Ω with homogeneous Neumann and Direchlet boundary conditions. However, the minimal wave speed and spread speed of the model, which are the motivation of this model and thus most important, are only explored numerically. In the present paper, we offer a rigorous theoretical confirmation of what are numerically observed in [1], concluding that if the basic reproduction number is larger than one, the model allows a spread speed which is also the minimal speed of traveling wave fronts, and this speed is linearly deterministic.

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Keywords: Tick Ixodes scapularis; Spatial invasion; Spread speed; Traveling wave front; Minimal wave speed; Upper-lower solutions

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Table 1
Explanation of parameters.

Parameters	*Meaning*
b	Birth rate of tick
$1/r_1$	Average time that a questing larvae needs to feed and moult
$1/r_2$	Average time that a questing nymph needs to feed and moult
$1/r_3$	Average time that a questing adult needs to successfully attach to a deer
r_4	Proportion of fed adults that can lay eggs
d_1	Per-capita death rate of larvae
d_2	Per-capita death rate of nymphs
d_3	Per-capita death rate of questing adults
d_4	Per-capita death rate of fed adults
τ_1	Average time between last blood feeding and hatch of laid eggs
τ_2	Average time tick is attached to a deer

1. Introduction

Lyme disease is transmitted via blacklegged tick *Ixodes scapularis*, and thus, the spatial spread of this tick is responsible for the spread of the Lyme disease. It has been conjectured that the geographical expansion of the blacklegged tick's habitat in some eastern states of the USA is mainly through the transport on white-tailed deer when successful questing adult ticks are having blood meals on the deer. In order to model the role of the deer's random diffusion on the spatial spread of the blacklegged ticks, Gourley et al. [1] recently have derived a mathematical model to describe the tick's spatial dynamics. The model is given by the following system differential equations with time delays and spatial non-locality:

$$\begin{cases} \dfrac{\partial L(x,t)}{\partial t} = br_4 \mathrm{e}^{-d_4\tau_1} A_f(x,t-\tau_1) - d_1 L(x,t) - r_1 L(x,t), \\ \dfrac{\partial N(x,t)}{\partial t} = r_1 g(L(x,t)) - d_2 N(x,t) - r_2 N(x,t), \\ \dfrac{\partial A_q(x,t)}{\partial t} = r_2 N(x,t) - d_3 A_q(x,t) - r_3 A_q(x,t), \\ \dfrac{\partial A_f(x,t)}{\partial t} = \dfrac{r_3}{2} \displaystyle\int_\Omega k(x,y)\mathrm{e}^{-d_3\tau_2} A_q(y,t-\tau_2)dy - r_4 A_f(x,t) - d_4 A_f(x,t). \end{cases} \tag{1.1}$$

Here $L(x,t)$ and $N(x,t)$ be the population densities of larvae and nymphs at time t, location $x \in \Omega$. Denote by $A_q(x,t)$ and $A_f(x,t)$ the populations of questing adults and female fed adults respectively. The model parameters are described in Table 1.

The nonlinear function $g(L)$ is increasing and saturating function. A prototype is

$$g(L) = \frac{N_{cap}k_2L}{k_1 + k_2L} = \frac{N_{cap}L}{k_1/k_2 + L} =: \frac{N_{cap}L}{h+L}. \tag{1.2}$$

The kernel function $k(x, y)$ depends on the diffusion rate of the deer and the average time τ_2 that an adult tick needs to be fully fed on dear, and it accounts for the probability that an adult tick attached a dear at location y will drop to the ground in location x. It tracks the movement of the dear when a tick is on the dear feeling itself and can be determined by solving a heat equation with the respective boundary conditions, depending on the situation of the spatial domain Ω. In particular, when $\Omega = \mathbb{R}$, $k(x, y)$ is given by the following formula

$$k(x, y) = \frac{1}{\sqrt{4D\pi\tau_2}} e^{\frac{-(x-y)^2}{4D\tau_2}} \tag{1.3}$$

In addition to the well-posedness of the model, Gourley et al. [1] also analyzed the threshold dynamics in terms of the basic reproduction number $\mathcal{R}_0$, which predicts whether the tick population will go to extinction or become persistent. In the persistence scenario ($\mathcal{R}_0 > 1$) and for the case of $\Omega = \mathbb{R}$, they also performed some numerical simulations, which seem to suggest that the tick population spread at a speed c^* to both direction in $\mathbb{R}$, and this spread speed is also precisely the minimum speed of traveling wave fronts connecting the extinction equilibrium and the unique positive equilibrium (persistence equilibrium). In this paper, we theoretically prove the above results that have been numerically observed in Gourley et al. [1].

The rest of the following the paper is organized as below. In Section 2, by following the framework and applying the results in [2,3], we rigorously prove that the existence of spread speed. The proof also gives the way this speed is determined. In Section 3, by employing the approach developed in Wu and Zou [4], that is, by constructing a pair of suitable upper-lower solution and establishing a monotone iteration scheme, we show that the spread speed confirmed in Section 2 is actually the minimal wave speed from traveling wavefronts. We point out that since the model is a system of four equations containing a time delay and spatial non-locality, the construction of upper-lower solution is quite challenging, involving some subtle inequalities and estimates. Our results also imply that both spread speed and minimal wave speed are linearly deterministic.

2. Asymptotic speed of spread

In this section, we follow the framework of [2,3,5,6] to prove the existence of spread speed. To this end, we first note that in the model system (1.1), there is an heterogeneity in delays for different unknown variables. This requires some slight modifications in notations. For readers' convenience, we will introduce the and notions and notations from [2,3] with minor modifications to accommodate the heterogeneity in delays.

For convenience of tracking the indices of delays, we let $\hat{\tau}_1 = 0$, $\hat{\tau}_2 = 0$, $\hat{\tau}_3 = \tau_2$ and $\hat{\tau}_4 = \tau_1$. Denote by $\mathcal{C}$ the set of all bounded and continuous functions from $\prod_{i=1}^4([-\hat{\tau}_i, 0] \times \mathbb{R})$. Let $\bar{\mathcal{C}} = \prod_{i=1}^4 C_i$ where $C_i = C([-\hat{\tau}_i, 0], \mathbb{R})$ for $i = 1, 2, 3, 4$ and X be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}^4$. Clearly, any vector in $\mathbb{R}^4$ or any element in the space $\bar{\mathcal{C}}$ or X can be regarded as a function in $\mathcal{C}$. We equip $\mathcal{C}$ with the compact open topology, meaning that the convergence $\phi^n \to \phi \in \mathcal{C}$ with respect this topology is equivalent to $\phi^n(\theta, x) \to \phi(\theta, x)$ uniformly for (θ, x) in every compact set. Moreover, we can define the metric function $d(\cdot, \cdot)$ in $\mathcal{C}$ with respect to this topology by

$$d(\phi, \psi) = \sum_{k=1}^{\infty} \frac{\max_{i\in\{1,2,3,4\}} \max_{\theta\in[-\hat{\tau}_i,0],|x|\le k} |\phi_i(\theta, x) - \psi_i(\theta, x)|}{2^k}, \quad \forall \phi, \psi \in \mathcal{C},$$

so that $(\mathcal{C}, d)$ is a metric space.

Define the reflection operator $\mathcal{R}$ on $\mathcal{C}$ by $\mathcal{R}[u](\theta, x) = u(\theta, -x)$. Given $y \in \mathbb{R}$, define the translation operator T_y by $T_y[u](\theta, x) = u(\theta, x - y)$. For any given $\beta > 0$, define $\mathcal{C}_\beta := \{\phi \in \mathcal{C} : 0 \le \phi \le \beta\}$ and $\bar{\mathcal{C}}_\beta := \{\phi \in \bar{\mathcal{C}} : 0 \le \phi \le \beta\}$. In order to use the theory developed in [2], for a given operator $Q : \mathcal{C}_\beta \to \mathcal{C}_\beta$, we make the following assumptions:

(A1) $Q[\mathcal{R}[\phi]] = \mathcal{R}[Q[\phi]]$, $T_y[Q[\phi]] = Q[T_y[\phi]]$, $\forall y \in \mathbb{R}$.
(A2) $Q : \mathcal{C}_\beta \to \mathcal{C}_\beta$ is continuous with respect to the compact open topology.
(A3) One of the following two properties holds:
(a) $\{Q[u](\cdot, x) : u \in \mathcal{C}_\beta, x \in \mathbb{R}\}$ is precompact in $\bar{\mathcal{C}}_\beta$.
(b) The set $Q[\mathcal{C}_\beta](0, \cdot)$ is precompact in X, and there is a positive number $\zeta \le \tau$ such that $Q[\phi](\theta, x) = \phi(\theta + \zeta, x)$ for $-\tau \le \theta \le -\zeta$, and the operator

$$S[\phi](\theta, x) := \begin{cases} \phi(0, x), & -\tau\theta < -\zeta, \\ Q[\phi](\theta, x), -\zeta \le \theta \le 0, & \end{cases}$$

has the property that $S[D](\cdot, 0)$ is precompact in $\bar{\mathcal{C}}_\beta$ for any T-invariant set $D \subset \mathcal{C}_\beta$, with $D(0, \cdot)$ precompact in X.
(A4) $Q : \mathcal{C}_\beta \to \mathcal{C}_\beta$ is monotone (order preserving) in the sense that $Q[\phi] \ge Q[\psi]$ whenever $\phi \ge \psi$ in $\mathcal{C}_\beta$.
(A5) $Q : \bar{\mathcal{C}}_\beta \to \bar{\mathcal{C}}_\beta$ admits exactly two fixed points 0 and β, and for any positive number ϵ, there is $\alpha \in \bar{\mathcal{C}}_\beta$ with $\|\alpha\| < \epsilon$ such that $Q[\alpha] \gg \alpha$.

Define

$$[T_i(t)\phi_i](x) = \mathrm{e}^{-(d_i + r_i)t}\phi_i(x), \forall \phi \in X,\ t > 0,\ x \in \mathbb{R},\ i = 1, 2, 3, 4.$$

Then

$$L(t, x) = T_1(t)L(0, x) + br_4 e^{-d_4\tau_1} \int_0^t T_1(t - s)A_f(s - \tau_1, x)ds,$$

$$N(t, x) = T_2(t)N(0, x) + r_1 N_{cap} \int_0^t T_2(t - s)\frac{L(s, x)}{h + L(s, x)}ds,$$

$$A_q(t, x) = T_3(t)A_q(0, x) + r_2 \int_0^t T_3(t - s)N(s, x)ds,$$

$$A_f(t, x) = T_4(t)A_f(0, x) + \frac{r_3}{2}d^{-d_3\tau_2} \int_0^t \int_\Omega k(x, y)T_4(t - s)A_q(s - \tau_2, y)dyds,$$

for $t > 0$.

Let Q_t be the solution map of (1.1), that is,

$$\begin{aligned}Q_t[\phi](\theta,x) &:= u(t+\theta,x;\phi)\\ &= (L(t,x;L_0), N(t,x;N_0), A_q(t+\theta_q,x;\phi_q), A_f(t+\theta_f,x;\phi_f)),\\ &\quad \forall\theta_q\in[-\tau_2,0],\ \theta_f\in[-\tau_1,0],\ x\in\mathbb{R},\ \phi=(L_0,N_0,\phi_q,\phi_f)\in\mathcal{C}_\beta.\end{aligned}$$

Lemma 2.1. *For each $t>0$, the map Q_t satisfies (A1)-(A5) with $\beta=(L^+,N^+,A_q^+,A_f^+)$.*

Proof. (A1) is confirmed by the property that both $u(t,-x)$ and $u(t,x+y)$, $y\in\mathbb{R}$, are also solutions whenever $u(t,x)$ is a solution, which holds for Q_t, since the kernel function $k(x)$ is symmetric at $x=0$. (A2) follows from the continuity of solutions for initial values with respect to the compact open topology. Since the model system (1.1) is cooperative and irreducible, Q_t satisfies (A4). Furthermore, using the similar argument as proof of Lemma 2.4 in [3], we get that Q_t satisfies (A5), where the spatially homogeneous equilibria of (1.1) are $u_0=(0,0,0,0)$ and $\beta=(L^+,N^+,A_q^+,A_f^+)$. In the following, we prove that Q_t satisfies (A3).

Since $\{L(t,x;\phi):\phi\in\mathcal{C}_\beta,\ x\in\mathbb{R}\}$ and $\{N(t,x;\phi):\phi\in\mathcal{C}_\beta,\ x\in\mathbb{R}\}$ are bounded subsets of $\mathbb{R}$, for any $t>0$. Therefore, $L(t,x;L_0)$ and $N(t,x;N_0)$ satisfy (A3)(a). (A3) is equivalent to that $\{Q_t[u](\cdot,x):u\in\mathcal{C}_\beta,x\in\mathbb{R}\}$ is a family of equicontinuous functions of $\theta\in[-\tau,0]$. We only need to prove A_q and A_f are equicontinuous functions of $\theta\in[-\tau_2,0]$ and $\theta\in[-\tau_1,0]$ respectively. For A_q, we need to prove, for every $\epsilon>0$, there exists a $\delta>0$ such that

$$|A_q(t+\theta_1,x;\phi)-A_q(t+\theta_2,x;\phi)|<\epsilon,$$

for all $\theta_1,\theta_2\in[-\tau_2,0]$ with $|\theta_1-\theta_2|<\delta$.

For $t>\tau_2$,

$$\begin{aligned}&|A_q(t+\theta_1,x;\phi_q)-A_q(t+\theta_2,x;\phi_q)|\\ &\le |T_3(t+\theta_1)-T_3(t+\theta_2)|\phi_q(0,x)\\ &\quad +r_2\left|\int_0^{t+\theta_1}T_3(t+\theta_1-s)N(s,x)ds-\int_0^{t+\theta_2}T_3(t+\theta_2-s)N(s,x)ds\right|\\ &\le |T_3(t+\theta_1)-T_3(t+\theta_2)|\phi_q(0,x)\\ &\quad +r_2\left|\int_0^{t+\theta_1}|T_3(t+\theta_1-s)-T_3(t+\theta_2-s)|N(s,x)ds\right|\\ &\quad +r_2\left|\int_{t+\theta_1}^{t+\theta_2}T_3(t+\theta_2-s)N(s,x)ds\right|\\ &= |T_3(t+\theta_1)-T_3(t+\theta_2)|\phi_q(0,x)\end{aligned}$$

$$+r_2\left|\int\limits_0^{t+\theta_1}|T_3(t+\theta_1)-T_3(t+\theta_2)|e^{-(d_3+r_3)s}N(s,x)ds\right|$$

$$+r_2\left|\int\limits_{t+\theta_1}^{t+\theta_2}T_3(t+\theta_2)e^{-(d_3+r_3)s}N(s,x)ds\right|,$$

$$\begin{aligned}|T_3(t+\theta_1)-T_3(t+\theta_2)| &= |e^{-(d_3+r_3)(t+\theta_1)}-e^{-(d_3+r_3)(t+\theta_2)}|\\ &= e^{-(d_3+r_3)t}|e^{-(d_3+r_3)\theta_1}-e^{-(d_3+r_3)\theta_2}|\\ &= e^{-(d_3+r_3)(t+\theta_m)}|1-e^{-(d_3+r_3)(\theta_M-\theta_m)}|\\ &\leq \left|1-e^{-(d_3+r_3)(\theta_M-\theta_m)}\right|\\ &= \left|1-e^{-(d_3+r_3)|\theta_1-\theta_2|}\right|,\end{aligned}$$

where $\theta_M=\max\{\theta_1,\theta_2\}$, $\theta_m=\min\{\theta_1,\theta_2\}$.

$$\begin{aligned}&\left|\int\limits_0^{t+\theta_1}|T_3(t+\theta_1)-T_3(t+\theta_2)|e^{-(d_3+r_3)s}N(s,x)ds\right|\\ &=|T_3(t+\theta_1)-T_3(t+\theta_2)|\left|\int\limits_0^{t+\theta_1}e^{-(d_3+r_3)s}N(s,x)ds\right|\\ &\leq |T_3(t+\theta_1)-T_3(t+\theta_2)|\left|1-e^{-(d_3+r_3)(t+\theta_1)}\right|\frac{N^+}{d_3+r_3}\\ &\leq |T_3(t+\theta_1)-T_3(t+\theta_2)|\frac{N^+}{d_3+r_3},\end{aligned}$$

$$\begin{aligned}&\left|\int\limits_{t+\theta_1}^{t+\theta_2}T_3(t+\theta_2)e^{-(d_3+r_3)s}N(s,x)ds\right|\\ &\leq |T_3(t+\theta_2)|\left|e^{-(d_3+r_3)(t+\theta_1)}-e^{-(d_3+r_3)(t+\theta_2)}\right|\frac{N^+}{d_3+r_3}\\ &\leq |T_3(t+\theta_1)-T_3(t+\theta_2)|\,\frac{N^+}{d_3+r_3}.\end{aligned}$$

$$\begin{aligned}&|A_q(t+\theta_1,x;\phi_q)-A_q(t+\theta_2,x;\phi_q)|\\ &\leq\left(\frac{2r_2N^+}{d_3+r_3}+A_q^+\right)|T_3(t+\theta_1)-T_3(t+\theta_2)|\\ &\leq\frac{N^+}{d_3+r_3}\left|1-e^{-(d_3+r_3)|\theta_2-\theta_1|}\right|<\epsilon,\end{aligned}$$

when

$$\delta = -\frac{1}{d_3 + r_3} \log\left(1 - \frac{(d_3 + r_3)\epsilon}{N}\right).$$

In the similar way, we can prove that $A_f(t+\theta, x; \phi_f)$ are equicontinuous functions of $\theta \in [-\tau_1, 0]$. $\square$

According to Theorem 2.11 and Theorem 2.15 in [2], the map $Q_1 : \mathcal{C}_\beta \to \mathcal{C}_\beta$ admits a spreading speed c^*.

Theorem 2.1. *Assume that $R_0 > 1$. Let $u(t, x; \phi)$ be the solution of system (1.1) with $u(o, \cdot; \phi) = \phi \in \mathcal{C}_\beta$. Then the following statements are valid:*
(i) For any $c > c^*$, if $\phi \in \mathcal{C}_\beta$ with $0 \le \phi \ll \beta$, and $\phi(\cdot, x) = 0$ for x outside a bounded interval, then $\lim_{t\to\infty, |x|\ge ct} u(t, x; \phi) = (0, 0, 0, 0)$.
(ii) For any $c \in (0, c^*)$, if $\phi \in \mathcal{C}_\beta$ and $\phi \not\equiv 0$, then $\lim_{t\to\infty, |x|\le ct} u(t, x; \phi) = \beta$.

Proof. Since Q_t satisfies (A1)-(A5), the statement (i) holds according to Theorem 2.17(i) in [2]. Because $u \equiv 0$ and $u \equiv \beta$ are solutions of (1.1), it follows from comparison principle that $Q_t(C_\beta) \subset C_\beta$, $t > 0$. For any $\phi \in C_\beta$ and $\rho \in [0, 1]$, $\rho u(t, x; \phi)$ is a lower solution to (1.1), which implies $\rho Q_t(\phi) \le Q_t(\rho\phi)$. Hence, Q_t is subhomogeneous on C_β. By Theorem 2.17(ii) in [2], we can choose $\beta = \beta_\sigma$ to be independent of $\sigma > 0$. Let $\phi \in C_\beta \backslash \{0\}$, and $t_0 = t_0(\phi) \ge 0$ such that $u(t, x; \phi) > 0$, $\forall t \ge t_0$, $x \in \mathbb{R}$, by Lemma 3.1 in [1]. Define $\sigma := \min_{(t,x)\in[t_0,t_0+\tau]\times[-\beta,\beta]} \frac{u(t,x;\phi)}{2}$, then $0 < \sigma < Q_{t_0+\tau}[\phi](\cdot, x)$ for $x \in [-\beta, \beta]$. For any $\phi \in C_\beta \backslash \{0\}$ and any $0 < c < c^*$, we use Theorem 2.17(ii) of [2] with $\nu = Q_{t_0+\tau}[\phi]$ to obtain

$$\lim_{t\to\infty, |x|\le ct} Q_t[Q_{t_0+\tau}[\phi]](\theta, x) = \beta, \text{ uniformly for } \theta \in [-\tau, 0].$$

This implies that $\lim_{t\to\infty, |x|\le ct} u(t, x; \phi) = \beta$. $\square$

In order to compute c^*, we consider the linearized system of (1.1) at the zero solution

$$\begin{aligned}
\frac{\partial u_1(t,x)}{\partial t} &= br_4 e^{-d_4\tau_1} u_4(t-\tau_1, x) - (d_1 + r_1)u_1(t, x), \\
\frac{\partial u_2(t,x)}{\partial t} &= \frac{r_1 N_{cap}}{h} u_1(t, x) - (d_2 + r_2)u_2(t, x), \\
\frac{\partial u_3(t,x)}{\partial t} &= r_2 u_2(t, x) - (d_3 + r_3)u_3(t, x), \\
\frac{\partial u_4(t,x)}{\partial t} &= \frac{r_3}{2} \int_{\mathbb{R}} k(x, y) e^{-d_3\tau_2} u_3(t-\tau_2, y)dy - (d_4 + r_4)u_4(t, x).
\end{aligned} \tag{2.1}$$

Let $M_t : \mathcal{C} \to \mathcal{C}$ be the solution map of this linear system, that is, $M_t[\phi] := u_t(\theta, x; \phi)$, $\phi \in \mathcal{C}$.

For any $\mu \in \mathbb{R}_+$, let $u_i(t,x) = \mathrm{e}^{-\mu x} v_i(t)$. Then $v(t) = (v_1(t), ..., v_4(t))$ satisfies

$$\begin{aligned}
\frac{dv_1(t)}{dt} &= br_4 \mathrm{e}^{-d_4\tau_1} v_4(t-\tau_1) - (d_1+r_1)v_1(t), \\
\frac{dv_2(t)}{dt} &= \frac{r_1 N_{cap}}{h} v_1(t) - (d_2+r_2)v_2(t), \\
\frac{dv_3(t)}{dt} &= r_2 v_2(t) - (d_3+r_3)v_3(t), \\
\frac{dv_4(t)}{dt} &= \frac{r_3}{2} K_\mu \mathrm{e}^{-d_3\tau_2} v_3(t-\tau_2) - (d_4+r_4)v_4(t),
\end{aligned} \tag{2.2}$$

where

$$K_\mu = \int_{\mathbb{R}} \Gamma(s)\mathrm{e}^{-\mu s} ds = \mathrm{e}^{D\tau_2\mu^2}.$$

Notice that

$$\begin{aligned}
\int_{\mathbb{R}} k(x,y)e^{-\mu y} dy = \int_{\mathbb{R}} \Gamma(y-x)e^{-\mu y} dy = \int_{\mathbb{R}} \Gamma(s)e^{-\mu(s+x)} ds \\
= e^{-\mu x} \int_{\mathbb{R}} \Gamma(s)e^{-\mu s} ds = e^{-\mu x} e^{D\tau_2\mu^2},
\end{aligned}$$

$$k(x,y) = \frac{1}{\sqrt{4D\tau_2\pi}} \int_{\mathbb{R}} e^{\frac{(x-y)^2}{4D\tau_2}} dy, \quad \Gamma(y) = \frac{1}{\sqrt{4D\tau_2\pi}} \int_{\mathbb{R}} e^{\frac{y^2}{4D\tau_2}} dy.$$

Define the linear map $B_\mu^t : \bar{\mathcal{C}} \to \bar{\mathcal{C}}$ by

$$B_\mu^t[v_0](\theta) = M_t[v_0 \mathrm{e}^{-\mu x}](\theta, 0), \quad \forall \theta \in [-\tau, 0],\ \forall v_0 \in \bar{\mathcal{C}}.$$

Then B_μ^t is the solution map of (2.2). Since (2.2) is cooperative and irreducible, it follows that its characteristic equations

$$\begin{pmatrix}
\lambda + (d_1+r_1) & 0 & 0 & -br_4\mathrm{e}^{-d_4\tau_1}\mathrm{e}^{-\tau_1\lambda}, \\
-\frac{r_1 N_{cap}}{h} & \lambda + (d_2+r_2) & 0 & 0 \\
0 & -r_2 & \lambda + (d_3+r_3), & 0 \\
0 & 0 & -\frac{r_3}{2} K_\mu \mathrm{e}^{-d_3\tau_2}\mathrm{e}^{-\tau_2\lambda} & \lambda + (d_4+r_4)
\end{pmatrix}
\begin{pmatrix} \eta_1 \\ \eta_2 \\ \eta_3 \\ \eta_4 \end{pmatrix} = 0$$

admit a real root $\lambda(\mu)$ which is greater than the real parts of other ones, that is, $\lambda(\mu)$ is the principal eigenvalue. Then $e^{\lambda(\mu)t}$ is the principal eigenvalue of B_μ^t with a positive eigenfunction. Now we define the function

$$\Phi(\mu) := \frac{1}{\mu} \ln \mathrm{e}^{\lambda(\mu)} = \frac{\lambda(\mu)}{\mu}, \quad \forall \mu > 0.$$

Lemma 2.2. *Let c^* be the spreading speed of the map Q_1 on $\mathcal{C}_\beta$. Then*

$$c^* = \inf_{\mu>0} \Phi(\mu), \tag{2.3}$$

where $\inf_{\mu>0}\Phi(\mu)$ *is attained at some finite* $\mu^* > 0$ *and hence* $c^* > 0$.

Proof. Note that $\lambda(0) = s(P)$. Since $R_0 > 1$, we then have $\lambda(0) = s(P) > 0$. We see that $\lim_{\mu\to+\infty}\Phi(\mu) = +\infty$ and $\lim_{\mu\to 0}\Phi(\mu) = +\infty$. Therefore, $\Phi(\mu)$ has a finite infimum which is attained at some $\mu^* > 0$, i.e., $\Phi(\mu^*) = \inf_{\mu>0}\Phi(\mu)$ for some finite $\mu^* > 0$. The map M_t satisfies the assumptions (C1)-(C7) in [2] for each $t > 0$. Since each mild solution of (1.1) is a lower solution of (2.1), it follows that $Q_t[\phi] \le M_t[\phi]$, $\forall t > 0$, $\phi \in \mathcal{C}_\beta$. It follows from Theorem 3.10 of [2] that

$$c^* < \inf_{\mu>0} \Phi(\mu).$$

By the continuous dependence on initial values of solutions to the spatially homogeneous system, we have that $\forall \epsilon > 0$, $t_0 > 0$, $\exists \eta > 0$ such that the solution $u(t;\bar\eta)$ of the spatially homogeneous system with $u(0,\bar\eta) = \bar\eta$ satisfies $u(t;\bar\eta) \le \bar\epsilon$, $\forall t \in [0,t_0]$, where $\bar\epsilon = (\epsilon,\epsilon,\epsilon,\epsilon)$ and $\bar\eta = (\eta,\eta,\eta,\eta)$. Thus, for the solution $u(t,x;\phi)$ of (1.1), the comparison principle implies that

$$u(t,x;\phi) \le u(t;\bar\eta) \le \bar\epsilon, \quad \forall x \in \mathbb{R},\ \phi \in \mathcal{C}_{\bar\eta},\ t \in [0,t_0].$$

It then follows that for all $t \in [0,t_0]$ and $x \in \mathbb{R}$, $u(t,x;\phi) = (L,N,A_q,A_f)(t,x;\phi)$ with $\phi \in \mathcal{C}_{\bar\eta}$ satisfies

$$\begin{aligned}
\frac{\partial L(t,x)}{\partial t} &\ge br_4 e^{-d_4\tau_1} A_f(t-\tau_1,x) - (d_1+r_1)L(t,x),\\
\frac{\partial N(t,x)}{\partial t} &\ge \frac{r_1 N_{cap}}{h+\epsilon} L(t,x) - (d_2+r_2)N(t,x),\\
\frac{\partial A_q(t,x)}{\partial t} &\ge r_2 N(t,x) - (d_3+r_3)A_q(t,x),\\
\frac{\partial A_f(t,x)}{\partial t} &\ge \frac{r_3}{2}\int_\Omega k(x,y) e^{-d_3\tau_2} A_q(t-\tau_2,y)\,dy - (d_4+r_4)A_f(t,x).
\end{aligned}$$

Let $\{M_t^\epsilon\}_{t\ge 0}$ be the solution semiflow associated with the linear system

$$\begin{aligned}
\frac{\partial u_1(t,x)}{\partial t} &= br_4 e^{-d_4\tau_1} u_4(t-\tau_1,x) - (d_1+r_1)u_1(t,x),\\
\frac{\partial u_2 N(t,x)}{\partial t} &= \frac{r_1 N_{cap}}{h+\epsilon} u_1(t,x) - (d_2+r_2)u_2(t,x),\\
\frac{\partial u_3(t,x)}{\partial t} &= r_2 u_2(t,x) - (d_3+r_3)u_3(t,x),\\
\frac{\partial u_4(t,x)}{\partial t} &= \frac{r_3}{2}\int_\Omega k(x,y) e^{-d_3\tau_2} u_3(t-\tau_2,y)\,dy - (r_4+d_4)u_4(t,x).
\end{aligned} \tag{2.4}$$

Since $Q_t[\phi]$ is an upper solution of system (2.4) for $t \in [0, t_0]$ and $\phi \in \mathcal{C}_{\bar{\eta}}$, it follows that

$$M_t^{\epsilon}[\phi] \le Q_t[\phi], \quad \forall \phi \in \mathcal{C}_{\bar{\eta}},\ t \in [0, t_0].$$

In particular, $M_1^{\epsilon}[\phi] \le Q_1[\phi]$, $\forall \phi \in \mathcal{C}_{\bar{\eta}}$. As we did for $\{M_t\}_{t\ge 0}$, a similar analysis can be made for $\{M_t^{\epsilon}\}_{t\ge 0}$. By Theorem 3.10 in [2], we have

$$\inf_{\mu>0} \Phi_{\epsilon}(\mu) \le c^* < \inf_{\mu>0} \Phi(\mu), \quad \forall \epsilon > 0.$$

Letting $\epsilon \to 0$, we then obtain $c^* = \inf_{\mu>0} \Phi(\mu)$, proving (2.3). Moreover, $c^* = \Phi(\mu^*) = \frac{\lambda(\mu^*)}{\mu^*} > 0$, and the proof is completed. □

3. Traveling wave solution

A traveling wave front solution of (1.1) is a solution with the form

$$L(x,t) = \varphi_1(x+ct),\ N(x,t) = \varphi_2(x+ct),\ A_q(x,t) = \varphi_3(x+ct),\ A_f(x,t) = \varphi_4(x+ct), \tag{3.1}$$

where $c > 0$ is the wave speed, and $\varphi = (\psi_1, \varphi_2.\varphi_3, \varphi_4)$ is the wave profile. Let the traveling wave variable be $s = x + ct$. Substituting (3.1) into (1.1) yields

$$\begin{aligned}
c\varphi_1'(s) &= br_4 e^{-d_4\tau_1}\varphi_4(s - c\tau_1) - (d_1 + r_1)\varphi_1(s),\\
c\varphi_2'(s) &= r_1 g(\varphi_1(s)) - (d_2 + r_2)\varphi_2(s),\\
c\varphi_3'(s) &= r_2\varphi_2(s) - (d_3 + r_3)\varphi_3(s),\\
c\varphi_4'(s) &= \frac{r_3}{2}\int_{-\infty}^{+\infty} k(y) e^{-d_3\tau_2}\varphi_3(s - y - c\tau_2)dy - (d_4 + r_4)\varphi_4(s),
\end{aligned} \tag{3.2}$$

where

$$k(y) = \frac{1}{\sqrt{4D\tau_2\pi}} e^{-\frac{y^2}{4D\tau_2}}.$$

According to Lemma 2.2, there is a $\mu^* \in (0, \infty)$, such that $\Phi(\mu^*) = \inf_{\mu>0} \Phi(\mu)$, that is, $c^* = \Phi(\mu^*) = \frac{\lambda(\mu^*)}{\mu^*} > 0$. Furthermore, by Lemma 3.8 in [2], (c^*, μ^*) actually also solves the following system

$$P(c, \mu) = 0, \quad \frac{\partial P}{\partial \mu}(c, \mu) = 0, \tag{3.3}$$

where

$$P(c,\mu) = \begin{vmatrix}
c\mu + (d_1 + r_1) & 0 & 0 & -br_4 \mathrm{e}^{-d_4\tau_1}\mathrm{e}^{-\tau_1 c\mu}, \\
-\frac{r_1 N_{cap}}{h} & c\mu + (d_2 + r_2) & 0 & 0 \\
0 & -r_2 & c\mu + (d_3 + r_3), & 0 \\
0 & 0 & -\frac{r_3}{2} K_{\mu} \mathrm{e}^{-d_3\tau_2}\mathrm{e}^{-\tau_2 c\mu} & c\mu + (d_4 + r_4)
\end{vmatrix},$$

that is,

$$P(c,\mu)=\prod_{i=1}^{4}[c\mu+(d_i+r_i)]-R_0\left[\prod_{i=1}^{4}(d_i+r_i)\right]e^{D\tau_2\mu^2-(\tau_1+\tau_2)c\mu}.$$

Let $c=\Phi(\mu)$, and $c^*=\Phi(\mu^*)$. Then $\frac{dc}{d\mu}|_{\mu=\mu^*}=0$. Let $c>c^*$ be given. There exist at least one $\mu_1\in(0,\infty)$ such that $\Phi(\mu_1)=c$. If there are two values μ_1 and μ_2 such that $\Phi(\mu_i)=c$, $i=1,2$, we always choose the smaller one, say μ_1, such that $\Phi(\mu_1)=c$. Let $\lambda_1=\lambda(\mu_1)$, and $\eta:=\eta(\mu_1)\gg 0$ be the eigenvector associated with $\lambda(\mu_1)$. For any $\mu>0$, if $v(t;v_0)$ is a solution of (2.2), then $u(t,x)=\mathrm{e}^{-\mu x}v(t;v_0)$ is a solution of (2.1). Note that $u(t,-x)=\mathrm{e}^{\mu x}v(t;v_0)$ is also a solution of (2.1). Taking $\mu=\mu_1$, $v_0=\eta(\mu_1)$, we have

$$u(t,-x)=\mathrm{e}^{\mu_1 x}\mathrm{e}^{\lambda(\mu_1)t}\eta(\mu_1)=\mathrm{e}^{\mu_1\left(x+\frac{\lambda(\mu_1)}{\mu_1}t\right)}\eta(\mu_1).$$

Let $s=x+\frac{\lambda(\mu_1)}{\mu_1}t$, then $\varphi(s):=u(t,-x)=\mathrm{e}^{\mu_1 s}\eta(\mu_1)$ is a solution of the linearized wave equations of (3.2) at zero solution

$$\begin{aligned}
c\varphi_1'(s)&=br_4e^{-d_4\tau_1}\varphi_4(s-c\tau_1)-(d_1+r_1)\varphi_1(s),\\
c\varphi_2'(s)&=\frac{r_1N_{cap}}{h}\varphi_1(s)-(d_2+r_2)\varphi_2(s),\\
c\varphi_3'(s)&=r_2\varphi_2(s)-(d_3+r_3)\varphi_3(s),\\
c\varphi_4'(s)&=\frac{r_3}{2}\int_{-\infty}^{+\infty}k(y)e^{-d_3\tau_2}\varphi_3(s-y-c\tau_2)dy-(d_4+r_4)\varphi_4(s).
\end{aligned}\tag{3.4}$$

Thus, μ_1 is the positive root of $P(\mu,c)=0$.

In the following, we construct upper and lower solutions of the system (3.1) as in [4]. For $\epsilon>0$, let $\mu_\epsilon:=\mu_1+\epsilon$, $\lambda_\epsilon:=\lambda(\mu_\epsilon)$, $c_\epsilon:=\frac{\lambda_\epsilon}{\mu_\epsilon}=\Phi(\mu_\epsilon)$. For sufficiently small $\epsilon>0$, we have $c^*<c_\epsilon<c$. Assume that the strongly positive eigenvector associated with λ_ϵ is

$$\eta^\epsilon:=(\eta_1^\epsilon,...,\eta_4^\epsilon)\gg 0.$$

Notice that

$$u(t,-x)=\mathrm{e}^{\mu_\epsilon x}\mathrm{e}^{\lambda_\epsilon t}=\mathrm{e}^{\mu_\epsilon(x+c_\epsilon t)}\eta_\epsilon$$

is also a solution of (2.1). Thus $\varphi(s):=\mathrm{e}^{\mu_\epsilon s}w_\epsilon$ is a solution of the linearized wave equations system (3.4), where $s=x+c_\epsilon t$. Therefore, c_ϵ and μ_ϵ also satisfy $P(c_\epsilon,\mu_\epsilon)=0$. Thus,

$$\begin{bmatrix}
c_\epsilon\mu_\epsilon+(d_1+r_1) & 0 & 0 & -br_4\mathrm{e}^{-d_4\tau_1}\mathrm{e}^{-\tau_1c_\epsilon\mu_\epsilon}, \\
-\frac{r_1N_{cap}}{h} & c_\epsilon\mu_\epsilon+(d_2+r_2) & 0 & 0\\
0 & -r_2 & c_\epsilon\mu_\epsilon+(d_3+r_3), & 0\\
0 & 0 & -\frac{r_3}{2}K_{\mu_\epsilon}\mathrm{e}^{-d_3\tau_2}\mathrm{e}^{-\tau_2c_\epsilon\mu_\epsilon} & c_\epsilon\mu_\epsilon+(d_4+r_4)
\end{bmatrix}\begin{pmatrix}\eta_1^\epsilon\\ \eta_2^\epsilon\\ \eta_3^\epsilon\\ \eta_4^\epsilon\end{pmatrix}$$

$$=0.$$

Let $\delta_\epsilon := c - c_\epsilon$. Then we have

$$\begin{bmatrix} c\mu_\epsilon + (d_1+r_1) & 0 & 0 & -br_4 \mathrm{e}^{-d_4\tau_1}\mathrm{e}^{-\tau_1 c\mu_\epsilon}, \\ -\frac{r_1 N_{cap}}{h} & c\mu_\epsilon + (d_2+r_2) & 0 & 0 \\ 0 & -r_2 & c\mu_\epsilon + (d_3+r_3), & 0 \\ 0 & 0 & -\frac{r_3}{2}K_{\mu_\epsilon}\mathrm{e}^{-d_3\tau_2}\mathrm{e}^{-\tau_2 c\mu_\epsilon} & c\mu_\epsilon + (d_4+r_4) \end{bmatrix} \begin{pmatrix} \eta_1^\epsilon \\ \eta_2^\epsilon \\ \eta_3^\epsilon \\ \eta_4^\epsilon \end{pmatrix}$$
$$\geq \begin{bmatrix} c\mu_\epsilon + (d_1+r_1) & 0 & 0 & -br_4 \mathrm{e}^{-d_4\tau_1}\mathrm{e}^{-\tau_1 c_\epsilon\mu_\epsilon}, \\ -\frac{r_1 N_{cap}}{h} & c\mu_\epsilon + (d_2+r_2) & 0 & 0 \\ 0 & -r_2 & c\mu_\epsilon + (d_3+r_3), & 0 \\ 0 & 0 & -\frac{r_3}{2}K_{\mu_\epsilon}\mathrm{e}^{-d_3\tau_2}\mathrm{e}^{-\tau_2 c_\epsilon\mu_\epsilon} & c\mu_\epsilon + (d_4+r_4) \end{bmatrix} \begin{pmatrix} \eta_1^\epsilon \\ \eta_2^\epsilon \\ \eta_3^\epsilon \\ \eta_4^\epsilon \end{pmatrix}$$
$$= \delta_\epsilon \mu_\epsilon \eta^\epsilon \gg 0.$$

Let $\eta = (\eta_1, ..., \eta_4)$ and $\eta^\epsilon := (\eta_1^\epsilon, ..., \eta_4^\epsilon)$ be the strongly positive eigenvectors associated with $\lambda(\mu_1)$ and $\lambda(\mu_\epsilon)$, respectively, such that $\eta^\epsilon \gg \eta$ and

$$\delta_\epsilon \mu_\epsilon \eta_2^\epsilon > \frac{N_{cap}}{h^2}\eta_1^2.$$

Define the function $\overline{\varphi}(s) = (\overline{\varphi}_1(s), ..., \overline{\varphi}_4(s))$, where

$$\overline{\varphi}_j(s) = \min\left\{\eta_j e^{\mu_1 s}, \varphi_j^*\right\}, \quad \overline{s}_j := \frac{1}{\mu_1}\ln\frac{\varphi_j^*}{\eta_j}, \ \forall s \in \mathbb{R}, \ j = 1, ..., 4.$$

We see that $= \varphi_j^*$ and

$$\eta_j e^{\mu_1 s}\begin{cases} < \varphi_j^*, & s < \overline{s}_j, \\ = \varphi_j^* & s = \overline{s}_j, \\ > \varphi_j^*, & s > \overline{s}_j, \end{cases} \quad \text{and} \quad \overline{\varphi}_j(s) = \begin{cases} \eta_j e^{\mu_1 s}, & s < \overline{s}_j, \\ \varphi_j^*, & s \geq \overline{s}_j. \end{cases}$$

Lemma 3.1. *For any $c > c^*$, the above defined $\overline{\varphi}(s)$ is an upper solution of (3.2), whenever $\epsilon > 0$ is sufficiently small.*

Proof. We consider the equations of (3.2) separately in each different location cases of s.

(i) $j = 1$:

Case 1. $s > \max\{\overline{s}_1, \overline{s}_4 + c\tau_1\}$:

$$\begin{aligned} & c\overline{\varphi}_1'(s) - br_4 e^{-d_4\tau_1}\overline{\varphi}_4(s - c\tau_1) + (d_1+r_1)\overline{\varphi}_1(s) \\ =& -br_4 e^{-d_4\tau_1}\varphi_4^* + (d_1+r_1)\varphi_1^* = 0. \end{aligned}$$

Case 2. $s < \min\{\overline{s}_1, \overline{s}_4 + c\tau_1\}$:

$$\begin{aligned} & c\overline{\varphi}_1'(s) - br_4 e^{-d_4\tau_1}\overline{\varphi}_4(s - c\tau_1) + (d_1+r_1)\overline{\varphi}_1(s) \\ =& c\eta_1\mu_1 e^{\mu_1 s} - br_4 e^{-d_4\tau_1}\eta_4 e^{\mu_1(s - c\tau_1)} + (d_1+r_1)\eta_1 e^{\mu_1 s} \\ =& e^{\mu_1 s}\left[(c\mu_1 + d_1 + r_1)\eta_1 - br_4 e^{-d_4\tau_1}e^{-\mu_1 c\tau_1}\eta_4\right] = 0. \end{aligned}$$

Case 3. $\overline{s}_1 < s < \overline{s}_4 + c\tau_1$:

$$\begin{aligned}
&c\overline{\varphi}_1'(s) - br_4e^{-d_4\tau_1}\overline{\varphi}_4(s-c\tau_1) + (d_1+r_1)\overline{\varphi}_1(s) \\
&= -br_4e^{-d_4\tau_1}\eta_4e^{\mu_1(s-c\tau_1)} + (d_1+r_1)\varphi_1^*, \\
&\geq -br_4e^{-d_4\tau_1}\varphi_4^* + (d_1+r_1)\varphi_1^* = 0.
\end{aligned}$$

Case 4. $\overline{s}_4 + c\tau_1 < s < \overline{s}_1$:

$$\begin{aligned}
&c\overline{\varphi}_1'(s) - br_4e^{-d_4\tau_1}\overline{\varphi}_4(s-c\tau_1) + (d_1+r_1)\overline{\varphi}_1(s) \\
&= \eta_1c\mu_1e^{\mu_1s} - br_4e^{-d_4\tau_1}\varphi_4^* + (d_1+r_1)\eta_1e^{\mu_1s} \\
&\geq \eta_1c\mu_1e^{\mu_1s} - br_4e^{-d_4\tau_1}\eta_4e^{\mu_1(s-c\tau_1)} + (d_1+r_1)\eta_1e^{\mu_1s} \\
&= e^{\mu_1s}[(c\mu_1+d_1+r_1)\eta_1 - br_4e^{-d_4\tau_1}e^{-\mu_1c\tau_1}\eta_4] = 0.
\end{aligned}$$

(ii) $j = 2$:
Case 1. $s > \max\{\overline{s}_1, \overline{s}_2\}$:

$$\begin{aligned}
&c\overline{\varphi}_2'(s) - r_1g(\overline{\varphi}_1(s)) + (d_2+r_2)\overline{\varphi}_2(s) \\
&= -r_1g(\varphi_1^*) + (d_2+r_2)\varphi_2^* = 0.
\end{aligned}$$

Case 2. $s < \min\{\overline{s}_1, \overline{s}_2\}$:

$$\begin{aligned}
&c\overline{\varphi}_2'(s) - r_1g(\overline{\varphi}_1(s)) + (d_2+r_2)\overline{\varphi}_2(s) \\
&\geq c\overline{\varphi}_2'(s) - \frac{r_1N_{cap}}{h}\overline{\varphi}_1(s) + (d_2+r_2)\overline{\varphi}_2(s) \\
&= \left[(c\mu_1+d_2+r_2)\eta_2 - \frac{r_1N_{cap}}{h}\eta_1\right]e^{\mu_1s} = 0.
\end{aligned}$$

Case 3. $\overline{s}_1 < s < \overline{s}_2$:

$$\begin{aligned}
&c\overline{\varphi}_2'(s) - r_1g(\overline{\varphi}_1(s)) + (d_2+r_2)\overline{\varphi}_2(s) \\
&\geq c\overline{\varphi}_2'(s) - \frac{r_1N_{cap}}{h}\overline{\varphi}_1(s) + (d_2+r_2)\overline{\varphi}_2(s) \\
&= (c\mu_1+d_2+r_2)\eta_2e^{\mu_1s} - \frac{r_1N_{cap}}{h}\varphi_1^* \\
&\geq (c\mu_1+d_2+r_2)\eta_2e^{\mu_1s} - \frac{r_1N_{cap}}{h}\eta_1e^{\mu_1s} \\
&= \left[(c\mu_1+d_2+r_2)\eta_2 - \frac{r_1N_{cap}}{h}\eta_1\right]e^{\mu_1s} = 0.
\end{aligned}$$

Case 4. $\overline{s}_2 < s < \overline{s}_1$:

$$\begin{aligned}
&c\overline{\varphi}_2'(s) - r_1 g(\overline{\varphi}_1(s)) + (d_2 + r_2)\overline{\varphi}_2(s) \\
&= -r_1 g(\eta_1 e^{\mu_1 s}) + (d_2 + r_2)\varphi_2^* \\
&\geq -r_1 g(\varphi_1^*) + (d_2 + r_2)\varphi_2^* = 0.
\end{aligned}$$

(iii) $j = 3$:
Case 1. $s > \max\{\overline{s}_2, \overline{s}_3\}$:

$$\begin{aligned}
&c\overline{\varphi}_3'(s) - r_2\overline{\varphi}_2(s) + (d_3 + r_3)\overline{\varphi}_3(s) \\
&= -r_2\varphi_2^* + (d_3 + r_3)\varphi_3^* = 0.
\end{aligned}$$

Case 2. $s < \min\{\overline{s}_2, \overline{s}_3\}$:

$$\begin{aligned}
&c\overline{\varphi}_3'(s) - r_2\overline{\varphi}_2(s) + (d_3 + r_3)\overline{\varphi}_3(s) \\
&= e^{\mu_1 s}\left[(c\mu_1 + d_3 + r_3)\eta_3 - r_2\eta_2\right] = 0.
\end{aligned}$$

Case 3. $\overline{s}_2 < s < \overline{s}_3$:

$$\begin{aligned}
&c\overline{\varphi}_3'(s) - r_2\overline{\varphi}_2(s) + (d_3 + r_3)\overline{\varphi}_3(s) \\
&= (c\mu_1 + d_3 + r_3)\eta_3 e^{\mu_1 s} - r_2\varphi_2^* \\
&\geq (c\mu_1 + d_3 + r_3)\eta_3 e^{\mu_1 s} - r_2\eta_2 e^{\mu_1 s} \\
&= e^{\mu_1 s}[(c\mu_1 + d_3 + r_3)\eta_3 - r_2\eta_2] = 0.
\end{aligned}$$

Case 4. $\overline{s}_3 < s < \overline{s}_2$:

$$\begin{aligned}
&c\overline{\varphi}_3'(s) - r_2\overline{\varphi}_2(s) + (d_3 + r_3)\overline{\varphi}_3(s) \\
&= -r_2\eta_2 e^{\mu_1 s} + (d_3 + r_3)\varphi_3^* \\
&\geq -r_2\varphi_2^* + (d_3 + r_3)\varphi_3^* = 0.
\end{aligned}$$

(iv) $j = 4$:

$$\begin{aligned}
&\frac{r_3}{2}\int_{-\infty}^{+\infty} k(y)e^{-d_3\tau_2}\overline{\varphi}_3(s - y - c\tau_2)dy \\
&= \frac{r_3}{2}e^{-d_3\tau_2}\left[\int_{-\infty}^{s-c\tau_2-s_3} k(y)\varphi_3^* dy + \int_{s-c\tau_2-s_3}^{+\infty} k(y)\eta_3 e^{\mu_1(s-y-c\tau_2)}dy\right] \\
&\leq \frac{r_3}{2}e^{-d_3\tau_2}\left[\int_{-\infty}^{s-c\tau_2-s_3} k(y)\eta_3 e^{\mu_1(s-y-c\tau_2)}dy + \int_{s-c\tau_2-s_3}^{+\infty} k(y)\eta_3 e^{\mu_1(s-y-c\tau_2)}dy\right]
\end{aligned}$$

$$
\begin{aligned}
&= \frac{r_3}{2} e^{-d_3\tau_2} \int_{-\infty}^{+\infty} k(y)\eta_3 e^{\mu_1(s-y-c\tau_2)} dy \\
&= \frac{r_3}{2} e^{-d_3\tau_2} e^{-\mu_1 c\tau_2} \bar{k}(\mu_1) e^{\mu_1 s} \eta_3.
\end{aligned}
$$

Similarly,

$$
\begin{aligned}
&\frac{r_3}{2} \int_{-\infty}^{+\infty} k(y) e^{-d_3\tau_2} \overline{\varphi}_3(s-y-c\tau_2) dy \\
&= \frac{r_3}{2} e^{-d_3\tau_2} \left[\int_{-\infty}^{s-c\tau_2-s_3} k(y)\varphi_3^* dy + \int_{s-c\tau_2-s_3}^{+\infty} k(y)\eta_3 e^{\mu_1(s-y-c\tau_2)} dy \right] \\
&\le \frac{r_3}{2} e^{-d_3\tau_2} \left[\int_{-\infty}^{s-c\tau_2-s_3} k(y)\varphi_3^* dy + \int_{s-c\tau_2-s_3}^{+\infty} k(y)\varphi_3^* dy \right] \\
&= \frac{r_3}{2} e^{-d_3\tau_2} \int_{-\infty}^{+\infty} k(y)\varphi_3^* dy \\
&= \frac{r_3}{2} e^{-d_3\tau_2} \varphi_3^*.
\end{aligned}
$$

Case 1. $s > \overline{s}_4$:

$$
\begin{aligned}
&c\overline{\varphi}_4'(s) - \frac{r_3}{2} \int_{-\infty}^{+\infty} k(y) e^{-d_3\tau_2} \overline{\varphi}_3(s-y-c\tau_2) dy + (d_4+r_4)\overline{\varphi}_4(s) \\
&= -\frac{r_3}{2} e^{-d_3\tau_2} \varphi_3^* + (d_4+r_4)\varphi_4^* = 0.
\end{aligned}
$$

Case 2. $s < \overline{s}_4$:

$$
\begin{aligned}
&c\overline{\varphi}_4'(s) - \frac{r_3}{2} \int_{-\infty}^{+\infty} k(y) e^{-d_3\tau_2} \overline{\varphi}_3(s-y-c\tau_2) dy + (d_4+r_4)\overline{\varphi}_4(s) \\
&= (c\mu_1 + d_4 + r_4)\eta_4 e^{\mu_1 s} - \frac{r_3}{2} \int_{-\infty}^{+\infty} k(y) e^{-d_3\tau_2} \overline{\varphi}_3(s-y-c\tau_2) dy \\
&\ge (c\mu_1 + d_4 + r_4)\eta_4 e^{\mu_1 s} - \frac{r_3}{2} e^{-d_3\tau_2} e^{-\mu_1 c\tau_2} \bar{k}(\mu_1) e^{\mu_1 s} \eta_3 \\
&= e^{\mu_1 s} \left[(c\mu_1 + d_4 + r_4)\eta_4 - \frac{r_3}{2} e^{-d_3\tau_2} e^{-\mu_1 c\tau_2} \bar{k}(\mu_1)\eta_3 \right] = 0.
\end{aligned}
$$

This proves that $\overline{\varphi}(s)$ is an upper solution of (3.2). □

Let

$$\underline{\varphi}_j(s) = \max\{0, \eta_j e^{\mu_1 s} - \eta_j^\epsilon e^{\mu_\epsilon s}\}, \quad \underline{s}_j := \frac{1}{\epsilon} \ln \frac{\eta_j}{\eta_j^\epsilon} < 0, \quad j = 1, 2, 3, 4. \tag{3.5}$$

We see that

$$\eta_j e^{\mu_1 s} - \eta_j^\epsilon e^{\mu_\epsilon s} \begin{cases} > 0, & s < \underline{s}_j, \\ = 0, & s = \underline{s}_j, \\ < 0, & s > \underline{s}_j, \end{cases} \quad \text{and} \quad \underline{\varphi}_j(s) = \begin{cases} \eta_j e^{\mu_1 s} - \eta_j^\epsilon e^{\mu_\epsilon s}, & s < \underline{s}_j, \\ 0, & s \geq \underline{s}_j. \end{cases}$$

Lemma 3.2. *For any $c > c^*$, the above defined $\underline{\varphi}(s) = (\underline{\varphi}_1(s), ..., \underline{\varphi}_4(s))$ is a lower solution of (3.2), whenever $\epsilon > 0$ is sufficiently small.*

Proof. We consider the equations of (3.2) separately in each different location cases of s.

(i) $j = 1$:

Case 1. $s > \max\{\underline{s}_1, \underline{s}_4 + c\tau_1\}$:

$$c\underline{\varphi}_1'(s) - br_4 e^{-d_4\tau_1} \underline{\varphi}_4(s - c\tau_1) + (d_1 + r_1)\underline{\varphi}_1(s) = 0.$$

Case 2. $s < \min\{\underline{s}_1, \underline{s}_4 + c\tau_1\}$:

$$\begin{aligned}
&c\underline{\varphi}_1'(s) - br_4 e^{-d_4\tau_1} \underline{\varphi}_4(s - c\tau_1) + (d_1 + r_1)\underline{\varphi}_1(s) \\
&= c(\eta_1\mu_1 e^{\mu_1 s} - \eta_1^\epsilon \mu_\epsilon e^{\mu_\epsilon s}) - br_4 e^{-d_4\tau_1}[\eta_4 e^{\mu_1(s - c\tau_1)} - \eta_4^\epsilon e^{\mu_\epsilon(s - c\tau_1)}] \\
&\quad + (d_1 + r_1)(\eta_1 e^{\mu_1 s} - \eta_1^\epsilon e^{\mu_\epsilon s}) \\
&= [c\eta_1\mu_1 - br_4 e^{-d_4\tau_1} e^{-c\tau_1\mu_1}\eta_4 + (d_1 + r_1)\eta_1] e^{\mu_1 s} \\
&\quad - [c\mu_\epsilon\eta_1^\epsilon - br_4 e^{-d_4\tau_1} e^{-c\tau_1\mu_\epsilon}\eta_4^\epsilon + (d_1 + r_1)\eta_1^\epsilon] e^{\mu_\epsilon s} \\
&= -[c\mu_\epsilon\eta_1^\epsilon - br_4 e^{-d_4\tau_1} e^{-c\tau_1\mu_\epsilon}\eta_4^\epsilon + (d_1 + r_1)\eta_1^\epsilon] e^{\mu_\epsilon s} \\
&= [(c_\epsilon - c)\mu_\epsilon\eta_1^\epsilon - br_4 e^{-d_4\tau_1}(e^{-c_\epsilon\tau_1\mu_\epsilon} - e^{-c\tau_1\mu_\epsilon})\eta_4^\epsilon] e^{\mu_\epsilon s} \\
&\leq 0.
\end{aligned}$$

Case 3. $\underline{s}_1 < s < \underline{s}_4 + c\tau_1$:

$$\begin{aligned}
&c\underline{\varphi}_1'(s) - br_4 e^{-d_4\tau_1} \underline{\varphi}_4(s - c\tau_1) + (d_1 + r_1)\underline{\varphi}_1(s) \\
&= -br_4 e^{-d_4\tau_1}[\eta_4 e^{\mu_1(s - c\tau_1)} - \eta_4^\epsilon e^{\mu_\epsilon(s - c\tau_1)}] \leq 0.
\end{aligned}$$

Case 4. $\underline{s}_4 + c\tau_1 < s < \underline{s}_1$:

$$
\begin{aligned}
& c\underline{\varphi}_1'(s) - br_4 e^{-d_4\tau_1}\underline{\varphi}_4(s-c\tau_1) + (d_1+r_1)\underline{\varphi}_1(s) \\
&= c(\eta_1\mu_1 e^{\mu_1 s} - \eta_1^\epsilon \mu_\epsilon e^{\mu_\epsilon s}) + (d_1+r_1)(\eta_1 e^{\mu_1 s} - \eta_1^\epsilon e^{\mu_\epsilon s}) \\
&= (c\mu_1 + d_1 + r_1)\eta_1 e^{\mu_1 s} - (c\mu_\epsilon + d_1 + r_1)\eta_1^\epsilon e^{\mu_\epsilon s} \\
&\le (c\mu_1 + d_1 + r_1)\eta_1 e^{\mu_1 s} - (c_\epsilon\mu_\epsilon + d_1 + r_1)\eta_1^\epsilon e^{\mu_\epsilon s} \\
&= br_4 e^{-d_4\tau_1}\eta_4 e^{\mu_1(s-c\tau_1)} - br_4 e^{-d_4\tau_1}\eta_4^\epsilon e^{\mu_\epsilon(s-c_\epsilon\tau_1)} \\
&\le br_4 e^{-d_4\tau_1}[\eta_4 e^{\mu_1(s-c\tau_1)} - \eta_4^\epsilon e^{\mu_\epsilon(s-c\tau_1)}] \\
&\le 0.
\end{aligned}
$$

(ii) $j = 2$:
Case 1. $s > \max\{\underline{s}_1, \underline{s}_2\}$:

$$c\underline{\varphi}_2'(s) - r_1 g(\underline{\varphi}_1(s)) + (d_2+r_2)\underline{\varphi}_2(s) = 0.$$

Case 2. $s < \min\{\underline{s}_1, \underline{s}_2\}$:
Notice that

$$g(\underline{\varphi}_1) = \frac{N_{cap}\underline{\varphi}_1}{1+\underline{\varphi}_1} = \frac{N_{cap}}{h}\underline{\varphi}_1 - \frac{N_{cap}}{h}\underline{\varphi}_1\frac{\underline{\varphi}_1}{h+\underline{\varphi}_1}.$$

Since

$$
\begin{aligned}
\frac{N_{cap}}{h}\frac{\underline{\varphi}_1^2}{h+\underline{\varphi}_1} &\le \frac{N_{cap}}{h^2}\underline{\varphi}_1^2 \\
&= \frac{N_{cap}}{h^2}\left[\eta_1 e^{\mu_1 s} - \eta_1^\epsilon e^{\mu_\epsilon s}\right]^2 \\
&\le \frac{N_{cap}}{h^2}\eta_1^2 e^{2\mu_1 s} \quad (\text{Note, } \eta_1 e^{\mu_1 s} > \eta_1^\epsilon e^{\mu_\epsilon s}) \\
&\le \frac{N_{cap}}{h^2}\eta_1^2 e^{\mu_\epsilon s}, \quad (\epsilon < \mu_1)
\end{aligned}
$$

we have

$$g(\underline{\varphi}_1) \ge \frac{N_{cap}}{h}\left[\eta_1 e^{\mu_1 s} - \eta_1^\epsilon e^{\mu_\epsilon s}\right] - \frac{N_{cap}}{h^2}\eta_1^2 e^{\mu_\epsilon s}.$$

$$
\begin{aligned}
& c\underline{\varphi}_2'(s) - r_1 g(\underline{\varphi}_1(s)) + (d_2+r_2)\underline{\varphi}_2(s) \\
&= c(\eta_2\mu_1 e^{\mu_1 s} - \eta_2^\epsilon\mu_\epsilon e^{\mu_\epsilon s}) + (d_2+r_2)(\eta_2 e^{\mu_1 s} - \eta_2^\epsilon e^{\mu_\epsilon s}) - r_1 g(\eta_1 e^{\mu_1 s} - \eta_1^\epsilon e^{\mu_\epsilon s}) \\
&= (c\mu_1 + d_2 + r_2)\eta_2 e^{\mu_1 s} - (c\mu_\epsilon + d_2 + r_2)\eta_2^\epsilon e^{\mu_\epsilon s} - r_1 g(\eta_1 e^{\mu_1 s} - \eta_1^\epsilon e^{\mu_\epsilon s}) \\
&\le (c\mu_1 + d_2 + r_2)\eta_2 e^{\mu_1 s} - (c\mu_\epsilon + d_2 + r_2)\eta_2^\epsilon e^{\mu_\epsilon s} - \frac{r_1 N_{cap}}{h}[\eta_1 e^{\mu_1 s} - \eta_1^\epsilon e^{\mu_\epsilon s}] \\
&\quad + \frac{N_{cap}}{h^2}\eta_1^2 e^{\mu_\epsilon s}
\end{aligned}
$$

$$= \left[(c_\epsilon - c)\mu_\epsilon \eta_2^\epsilon + \frac{N_{cap}}{h^2}\eta_1^2 \right] e^{\mu_\epsilon s}$$
$$\leq 0.$$

Case 3. $\underline{s}_1 < s < \underline{s}_2$:

$$\begin{aligned}
& c\underline{\varphi}_2'(s) - r_1 g(\underline{\varphi}_1(s)) + (d_2 + r_2)\underline{\varphi}_2(s) \\
&= c(\eta_2\mu_1 e^{\mu_1 s} - \eta_2^\epsilon \mu_\epsilon e^{\mu_\epsilon s}) + (d_2 + r_2)(\eta_2 e^{\mu_1 s} - \eta_2^\epsilon e^{\mu_\epsilon s}) \\
&= (c\mu_1 + d_2 + r_2)\eta_2 e^{\mu_1 s} - (c\mu_\epsilon + d_2 + r_2)\eta_2^\epsilon e^{\mu_\epsilon s} \\
&\leq (c\mu_1 + d_2 + r_2)\eta_2 e^{\mu_1 s} - (c_\epsilon \mu_\epsilon + d_2 + r_2)\eta_2^\epsilon e^{\mu_\epsilon s} \\
&= \frac{r_1 N_{cap}}{h}(\eta_1 e^{\mu_1 s} - \eta_1^\epsilon e^{\mu_\epsilon s}) \\
&\leq 0.
\end{aligned}$$

Case 4. $\underline{s}_2 < s < \underline{s}_1$:

$$\begin{aligned}
& c\underline{\varphi}_2'(s) - r_1 g(\underline{\varphi}_1(s)) + (d_2 + r_2)\underline{\varphi}_2(s) \\
&= -r_1 g(\underline{\varphi}_1(s)) \leq 0.
\end{aligned}$$

(iii) $j = 3$: Case 1. $s > \max\{\underline{s}_2, \underline{s}_3\}$:

$$c\underline{\varphi}_3'(s) - r_2\underline{\varphi}_2(s) + (d_3 + r_3)\underline{\varphi}_3(s) = 0.$$

Case 2. $s < \min\{\underline{s}_2, \underline{s}_3\}$:

$$\begin{aligned}
& c\underline{\varphi}_3'(s) - r_2\underline{\varphi}_2(s) + (d_3 + r_3)\underline{\varphi}_3(s) \\
&= c(\eta_3\mu_1 e^{\mu_1 s} - \eta_3^\epsilon \mu_\epsilon e^{\mu_\epsilon s}) - r_2(\eta_2 e^{\mu_1 s} - \eta_2^\epsilon e^{\mu_\epsilon s}) + (d_3 + r_3)(\eta_3 e^{\mu_1 s} - \eta_3^\epsilon e^{\mu_\epsilon s}) \\
&= [(c\mu_1 + d_3 + r_3)\eta_3 - r_2\eta_2]e^{\mu_1 s} - [(c\mu_\epsilon + d_3 + r_3)\eta_3^\epsilon - r_2\eta_2^\epsilon]e^{\mu_\epsilon s} \\
&= (c_\epsilon - c)\mu_\epsilon e^{\mu_\epsilon s} \\
&\leq 0.
\end{aligned}$$

Case 3. $\underline{s}_2 < s < \underline{s}_3$:

$$\begin{aligned}
& c\underline{\varphi}_3'(s) - r_2\underline{\varphi}_2(s) + (d_3 + r_3)\underline{\varphi}_3(s) \\
&= c(\eta_3\mu_1 e^{\mu_1 s} - \eta_3^\epsilon \mu_\epsilon e^{\mu_\epsilon s}) + (d_3 + r_3)(\eta_3 e^{\mu_1 s} - \eta_3^\epsilon e^{\mu_\epsilon s}) \\
&= (c\mu_1 + d_3 + r_3)\eta_3 e^{\mu_1 s} - (c\mu_\epsilon + d_3 + r_3)\eta_3^\epsilon e^{\mu_\epsilon s} \\
&\leq (c\mu_1 + d_3 + r_3)\eta_3 e^{\mu_1 s} - (c_\epsilon \mu_\epsilon + d_3 + r_3)\eta_3^\epsilon e^{\mu_\epsilon s} \\
&= r_2(\eta_2 e^{\mu_1 s} - \eta_2^\epsilon e^{\mu_\epsilon s}) \\
&\leq 0.
\end{aligned}$$

Case 4. $\underline{s}_3 < s < \underline{s}_2$:

$$\begin{aligned}&c\underline{\varphi}_3'(s) - r_2\underline{\varphi}_2(s) + (d_3+r_3)\underline{\varphi}_3(s)\\ =& -r_2\underline{\varphi}_2(s) \le 0.\end{aligned}$$

(iv) $j = 4$:

$$\begin{aligned}&\frac{r_3}{2}\int_{-\infty}^{+\infty} k(y)e^{-d_3\tau_2}\underline{\varphi}_3(s-y-c\tau_2)dy\\
=&\frac{r_3}{2}e^{-d_3\tau_2}\left[\int_{-\infty}^{s-c\tau_2-s_3} k(y)\underline{\varphi}_3(s-y-c\tau_2)dy + \int_{s-c\tau_2-s_3}^{+\infty} k(y)\underline{\varphi}_3(s-y-c\tau_2)dy\right]\\
=&\frac{r_3}{2}e^{-d_3\tau_2}\int_{s-c\tau_2-s_3}^{+\infty} k(y)\left[\eta_3 e^{\mu_1(s-y-c\tau_2)} - \eta_3^\epsilon e^{\mu_\epsilon(s-y-c\tau_2)}\right]dy\\
\ge&\frac{r_3}{2}e^{-d_3\tau_2}\int_{-\infty}^{+\infty} k(y)\left[\eta_3 e^{\mu_1(s-y-c\tau_2)} - \eta_3^\epsilon e^{\mu_\epsilon(s-y-c\tau_2)}\right]dy\end{aligned}$$

Case 1. $s > \underline{s}_4$:

$$\begin{aligned}&c\underline{\varphi}_4'(s) - \frac{r_3}{2}\int_{-\infty}^{+\infty} k(y)e^{-d_3\tau_2}\underline{\varphi}_3(s-y-c\tau_2)dy + (d_4+r_4)\underline{\varphi}_4(s)\\
=& -\frac{r_3}{2}\int_{-\infty}^{+\infty} k(y)e^{-d_3\tau_2}\underline{\varphi}_3(s-y-c\tau_2)dy \le 0.\end{aligned}$$

Case 2. $s < \underline{s}_4$:

$$\begin{aligned}&c\underline{\varphi}_4'(s) - \frac{r_3}{2}\int_{-\infty}^{+\infty} k(y)e^{-d_3\tau_2}\underline{\varphi}_3(s-y-c\tau_2)dy + (d_4+r_4)\underline{\varphi}_4(s)\\
=& c(\eta_4\mu_1 e^{\mu_1 s} - \eta_4^\epsilon\mu_\epsilon e^{\mu_\epsilon s}) + (d_4+r_4)(\eta_4 e^{\mu_1 s} - \eta_4^\epsilon e^{\mu_\epsilon s})\\
&-\frac{r_3}{2}e^{-d_3\tau_2}\int_{s-c\tau_2-s_3}^{+\infty} k(y)\left[\eta_3 e^{\mu_1(s-y-c\tau_2)} - \eta_3^\epsilon e^{\mu_\epsilon(s-y-c\tau_2)}\right]dy\\
\le& (c\mu_1+d_4+r_4)\eta_4 e^{\mu_1 s} - (c\mu_\epsilon+d_4+r_4)\eta_4^\epsilon e^{\mu_\epsilon s})\\
&-\frac{r_3}{2}e^{-d_3\tau_2}\int_{-\infty}^{+\infty} k(y)\left[\eta_3 e^{\mu_1(s-y-c\tau_2)} - \eta_3^\epsilon e^{\mu_\epsilon(s-y-c\tau_2)}\right]dy\end{aligned}$$

$$
\begin{aligned}
&= -(c\mu_\epsilon + d_4 + r_4)\eta_4^\epsilon e^{\mu_\epsilon s} + \frac{r_3}{2} e^{-d_3\tau_2} \int_{-\infty}^{+\infty} k(y)\eta_3^\epsilon e^{\mu_\epsilon(s-y-c\tau_2)}dy \\
&\le -(c_\epsilon\mu_\epsilon + d_4 + r_4)\eta_4^\epsilon e^{\mu_\epsilon s} + \frac{r_3}{2} e^{-d_3\tau_2} \int_{-\infty}^{+\infty} k(y)\eta_3^\epsilon e^{\mu_\epsilon(s-y-c\tau_2)}dy \\
&= 0.
\end{aligned}
$$

Thus, $\underline{\varphi}(s)$ is a lower solution of (3.2). □

Notice that (3.2) is equivalent to the following system

$$
\frac{d\varphi_j(s)}{ds} + \delta\varphi_j(s) = \left(\delta - \frac{d_j + r_j}{c}\right)\varphi_j(s) + \frac{1}{c} f_j(\varphi(s)), \quad j = 1, ..., 4, \tag{3.6}
$$

where $\varphi(s) = (\varphi_1(s), ..., \varphi_4(s))$ and

$$
\begin{aligned}
&f_1(\varphi(s)) = br_4 e^{-d_4\tau_1}\varphi_4(s - c\tau_1), \quad f_2(\varphi(s)) = r_1 g(\varphi_1(s)), \\
&f_3(\varphi(s)) = r_2\varphi_2(s), \quad f_4(\varphi(s)) = \frac{r_3}{2}\int_{-\infty}^{+\infty} k(y)e^{-d_3\tau_2}\varphi_3(s - y - c\tau_2)dy.
\end{aligned}
$$

Let $\delta_j(c) := \delta - \frac{d_j + r_j}{c}$, where $\delta > 0$ is large enough constant. Thus, (3.6) reduces to

$$
\varphi_j(s) = e^{-\delta s}\int_{-\infty}^{s} e^{\delta t}[F\varphi]_j(t)dt, \quad j = 1, ..., 4, \tag{3.7}
$$

where $F\varphi = ([F\varphi]_1, ..., [F\varphi]_4)$ and

$$
[F\varphi]_j(s) = \delta_j(c)\varphi_j(s) + f_j(\varphi(s)), \quad j = 1, ..., 4.
$$

It follows that $[F\varphi](t) \ge [F\psi](t)$, $\forall t \in \mathbb{R}$, provided that $\varphi, \psi \in C(\mathbb{R}, [0, \varphi^*])$ with $\varphi(t) > \psi(t)$, $t \in \mathbb{R}$. Moreover, we have $F(0) = 0$ and $F(\varphi^*) = \mathrm{diag}(\delta, ..., \delta)\varphi^*$.

Define an operator $T = (T_1, ..., T_4)$ on $C(\mathbb{R}, [0, \varphi^*])$ by

$$
T_j[\varphi](s) = e^{-\delta s}\int_{-\infty}^{s} e^{\delta t}[F\varphi]_j(t)dt, \quad \forall s \in \mathbb{R}, \ j = 1, ..., 4.
$$

The following observation is straightforward.

Lemma 3.3. *The operator T has the following properties:*
(i) If $\varphi \in C(\mathbb{R}, [0, \beta])$ is nondecreasing, then so is $T\varphi$.
(ii) If $\varphi \geq \psi$, then $T\varphi \geq T\psi$.
(iii) If φ is an upper (lower) solution of (3.2), then $\varphi(s) \geq [T\varphi](s)$ ($\varphi(s) \leq [T\psi](s)$) for all $s \in \mathbb{R}$.
(iv) If φ is an upper (lower) solution of (3.2), then $T\varphi$ is also an upper (lower) solution of (3.2).

Theorem 3.1. *Assume $R_0 > 1$ and c^* is the asymptotic speed of spread of Q_1. Then for any $c \geq c^*$, system (1.1) has a traveling wave solution $\varphi(x+ct)$ connecting 0 to φ^* (that is, β) such that $\varphi(s)$ is continuous and nondecreasing in $s \in \mathbb{R}$.*

Proof. In the case where $c > c^*$, we construct a sequence of functions by the iteration scheme

$$\varphi^{(0)} = \overline{\varphi}, \quad \varphi^{(m)} = T\varphi^{(m-1)}, \quad \forall m \geq 1.$$

By Lemmas 3.1, 3.2 and 3.3, we have

$$0 \leq \underline{\varphi}(s) \leq ... \leq \varphi^{(m)}(s) \leq \varphi^{(m-1)}(s) \leq ... \leq \overline{\varphi}(s) \leq \varphi^*, \quad \forall s \in \mathbb{R}.$$

By the Lebesgue's dominated convergence theorem, it follows that $\lim_{m\to\infty} \varphi^{(m)}(s) =: \varphi(s)$ exists, and $\varphi(\cdot)$ is a fixed point of T. Since $\varphi(\cdot)$ is nondecreasing and

$$\underline{\varphi}(s) \leq \overline{\varphi}(s), \forall s \in \mathbb{R},$$

it follows that $\varphi(-\infty) = 0$ and $\varphi(+\infty) > 0$. It is easy to see that $\varphi(+\infty)$ is an equilibrium of (3.2). By the uniqueness of the positive equilibrium, we have $\varphi(+\infty) = \varphi^*$. Consequently, $\varphi(x+ct)$ is a monotone traveling wave of (1.1) connecting 0 to φ^* (that is, β).

In the case where $c = c^*$, we use a limiting argument. Let $\{c_n\} \subset (c^*, c^*+1]$ with $\lim_{n\to\infty} c_n = c^*$. Since $c_n > c^*$, (3.2) with $c = c_n$ admits a nondecreasing solution $\varphi^{(n)}(s) = (\varphi_1^{(n)}, ..., \varphi_4^{(n)})$ such that $\varphi^{(n)}(-\infty) = 0$ and $\varphi^{(n)}(+\infty) = \varphi^*$. Without loss of generality (due to translation invariance), we may assume that $\varphi_1^{(n)}(0) = \frac{1}{2}\beta_1$. Note that $\varphi_j^{(n)}(s)$ satisfies

$$\varphi_j^{(n)}(s) = e^{-\delta s} \int_{-\infty}^{s} e^{\delta t}[\delta_j(c_n)\varphi_j^{(n)}(s) + f_j(\varphi^{(n)}(s))]dt, \quad j = 1, ..., 4, \tag{3.8}$$

and

$$c_n \frac{d\varphi_j^{(n)}(s)}{ds} = f_j(\varphi^{(n)}(s)) - (d_j + r_j)\varphi_j^{(n)}(s), \quad j = 1, ..., 4. \tag{3.9}$$

Since $\{\varphi^{(n)}(s)\}$ and $\frac{d\varphi_j^{(n)}(s)}{ds}$ are uniformly bounded on $\mathbb{R}$, $\{\varphi^{(n)}(s)\}$ is equicontinuous on $\mathbb{R}$. Using the Arzelia Ascoli theorem and the standard diagonal method, we can obtain a subsequence of functions $\varphi^{(n_k)}(s)$, which converges to $\varphi^*(s)$, as $k \to \infty$, uniformly for s in any bounded subset of $\mathbb{R}$. Clearly, $\varphi^*(s)$ is nondecreasing, $\varphi^*(-\infty) = 0$ and $\varphi^*(\infty)$ is an equilibrium of

(3.2). Moreover $\varphi_1^*(0) = \frac{1}{2}\beta_1 > 0$, implying that $\varphi_1^*(\infty) > 0$. This together with the structure of equilibria of (3.2) further implies that $\varphi^*(+\infty) = \beta$. By the dominated convergence theorem and (3.8), it follows that

$$\varphi_j^*(s) = e^{-\delta s} \int_{-\infty}^{s} e^{\delta t}[\delta_j(c^*)\varphi_j^*(s) + f_j(\varphi^*(s))]dt, \quad j = 1, ..., 4. \tag{3.10}$$

Thus, $\varphi^*(x + c^*t)$ is a monotone traveling wave of (1.1) connecting 0 and β. □

For the nonexistence of traveling wave solutions, we have the following result, according to Theorem 4.3 in [2].

Theorem 3.2. *Assume $R_0 > 1$, and c^* is the spreading speed of spread of Q_1. Then for any $c \in (0, c^*)$, system (1.1) does not have traveling wave solution $\varphi(x + ct)$ connecting 0 to β.*

It follows from Theorem 3.1 and 3.2 that the asymptotic speed of spread is exactly the minimum wave speed for monotone traveling waves.

We conclude the paper by pointing out that the method provided in a more recent work [7] (than [2]) may also provide an alternative way to prove the existence of traveling waves for the model system (1.1).

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