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TRAVELING WAVE SOLUTIONS OF A DIFFUSIVE RATIO-DEPENDENT HOLLING-TANNER SYSTEM WITH DISTRIBUTED DELAY

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Abstract. The existence of traveling wave solutions and wave train solutions of a diffusive ratio-dependent predator-prey system with distributed delay is proved. For the case without distributed delay, we first establish the existence of traveling wave solution by using the upper and lower solutions method. Second, we prove the existence of periodic traveling wave train by using the Hopf bifurcation theorem. For the case with distributed delay, we obtain the existence of traveling wave and traveling wave train solutions when the mean delay is sufficiently small via the geometric singular perturbation theory. Our results provide theoretical basis for biological invasion of predator species.

1. Introduction.

The biological invasion of some non-native species can potentially cause devastating consequences in an existing ecosystem [21, 43], and spatiotemporal mathematical models have been used to study, analyze, predict and prevent the occurrence of harmful biological invasions [11, 19, 31, 39]. One of the common scenarios is the invasion of a predator species into a territory occupied by a prey species [11, 31], and reaction-diffusion predator-prey models have been established to describe the invasion of a predator species [9, 39, 41].

On the other hand, the growth of biological organisms may depend on the population density of previous times. Moreover the time delay can be a distributed one over all past time and spatially nonlocal one[6, 19, 25, 46, 48].

In this article, we consider a reaction-diffusion predator-prey model with a distributed delay on the growth rate of the prey species, and we are interested in the spatial spreading of the predator and the corresponding retreating of the prey which emulate the biological invasion of a non-native predator species into an established ecosystem. To be more precise, we consider a reaction-diffusion Holling-Tanner

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type predator-prey system with ratio-dependent functional response and a distributed delay as follows:

$$\begin{cases} u_t(x,t) = du_{xx}(x,t) + u(x,t)(1 - G * u(x,t)) - \dfrac{Au(x,t)v(x,t)}{u(x,t)+av(x,t)}, & x \in \mathbb{R},\ t > 0, \\ v_t(x,t) = v_{xx}(x,t) + Bv(x,t)\left(1 - \dfrac{v(x,t)}{u(x,t)}\right), & x \in \mathbb{R},\ t > 0. \end{cases} \tag{1.1}$$

Here $u(x,t)$ and $v(x,t)$ are the population densities of the prey and predator species at the location x and time t respectively; the two species move randomly along a one-dimensional region $\mathbb{R}$, and the parameter $d > 0$ is a rescaled diffusion coefficient of the prey species while the diffusion coefficient for the predator is rescaled to be 1. The prey population has a logistic growth pattern with the growth rate per-capita depending on population density in previous time. That is, the term $G * u$ shows the effect of a distributed delay term with a distribution kernel function G:

$$(G * u)(x,t) = \int_{-\infty}^{t} G(t-s)u(x,s)ds.$$

In this article, we will consider the following kernel functions $G : \mathbb{R}_+ \to \mathbb{R}_+$:

$$(i) \text{ the Dirac kernel } G(t) = \delta(t),$$

$$(ii) \text{ the strong kernel } G(t) = \frac{t}{\tau^2}e^{-t/\tau},$$

$$(iii) \text{ the weak kernel } G(t) = \frac{1}{\tau}e^{-t/\tau}.$$

In the cases of (ii) and (iii), $\tau > 0$ is the mean value of $G(t)$ over $\mathbb{R}_+$. The predator-prey structure in (1.1) follows the one used in [22, 44], which is typically called Holling-Tanner predator-prey model. Here the predator functional response is Holling type II, but also a ratio-dependent one following the proposal in [1, 2, 17] as the predators may share or complete for food. The parameter A is the capturing rate, a is the half-capturing saturation constant, and B denotes the predator intrinsic growth rate. All the parameters are assumed to be positive. Some previous work for dynamics of diffusive Holling-Tanner predator-prey systems on a bounded region can be found in [5, 40].

When the distribution kernel is the Dirac delta function, (1.1) becomes a reaction-diffusion system without delay effect:

$$\begin{cases} u_t(x,t) = du_{xx}(x,t) + u(x,t)(1 - u(x,t)) - \dfrac{Au(x,t)v(x,t)}{u(x,t)+av(x,t)}, & x \in \mathbb{R},\ t > 0, \\ v_t(x,t) = v_{xx}(x,t) + Bv(x,t)\left(1 - \dfrac{v(x,t)}{u(x,t)}\right), & x \in \mathbb{R},\ t > 0. \end{cases} \tag{1.2}$$

Indeed our strategy of studying the spreading is to first consider the delay-free system (1.2), then consider the distributed delay system (1.1) when the mean delay τ is small.

It is easy to check that the system (1.2) has two nonnegative equilibria $E_1(1,0)$ and $E_2(u^*,u^*)$, where $u^* = 1 - A/(a+1) > 0$, if and only if the following condition holds:

(H1) $0 < A < a + 1$.

Throughout this article, we assume the condition **(H1)** always holds unless otherwise noted.

Our first result is on the existence, nonexistence and the minimal wave speed of traveling wave solutions of the delay-free system (1.2) connecting the equilibria $E_1(1,0)$ to $E_2(u^*,u^*)$:

Theorem 1.1. *Suppose d, A, a, B are all positive constants which satisfy*

(H2) $0 < A < \dfrac{(1+a)a}{a+2}$.

Then the following statements are true:

1. *For each $c \geq c^* = 2\sqrt{B}$, the system (1.2) has a positive traveling wave solution $(u(x,t), v(x,t)) = (U(x+ct), V(x+ct))$ connecting $E_1(1,0)$ and $E_2(u^*,u^*)$.*
2. *For $0 < c < c^* = 2\sqrt{B}$, the system (1.2) has no nonnegative traveling wave solution connecting $E_1(1,0)$ and $E_2(u^*,u^*)$. That is, $c^* = 2\sqrt{B}$ is the minimal wave speed.*

Note that **(H1)** is satisfied if **(H2)** holds. Hence **(H2)** requires more restricted condition on a and A for the existence of traveling wave solutions. The result on the minimal wave speed shows a linear determinacy on the predator growth rate B similar to the Fisher type equation. The proof of Theorem 1.1 relies on a fixed point theorem argument.

Our second result is on the existence of small amplitude periodic traveling wave train solutions for the system (1.2). Wave trains or periodic traveling waves are spatio-temporal patterns which have periodic profile, maintain their shape and move at a constant speed. For that purpose, we make another sets of assumptions on the parameters:

(H3) $\sqrt{\dfrac{A}{B}}\left(\dfrac{A(a+2)}{(a+1)^2} - B - 1\right) > a + 1 - A$, or

(H3') $0 < \sqrt{\dfrac{A}{B}}\left(\dfrac{A(a+2)}{(a+1)^2} - B - 1\right) < a + 1 - A$.

Then we have the following results:

Theorem 1.2. 1. *Assume that* **(H1)** *and* **(H3)** *hold. Then for any $c > 0$, the system (1.2) has a family of small amplitude positive periodic traveling wave train solutions $(u(x,t), v(x,t)) = (U(x+ct), V(x+ct))$ with periodic (U,V), when the diffusion coefficient d is near $d = d(c)$ which is defined by*

$$d(c) = \frac{(a+1)^2}{2B(A - B(a+1)^2)}\left(-\rho(c^2+2B) + \sqrt{\Delta}\right) - 1, \qquad (1.3)$$

where

$$\rho = B + 1 - \frac{A(a+2)}{(a+1)^2}, \quad \Delta = \rho^2(c^2+2B)^2 + 4\rho^2 B\left(\frac{A}{(a+1)^2} - B\right); \qquad (1.4)$$

2. *Assume* **(H1)** *and* **(H3')** *hold. Then there exists a unique $c^* > 0$ such that for $c > c^*$, the system (1.2) has a family of periodic traveling wave train solutions near $d = d(c)$, where $d(c)$ is defined by (1.3) and c^* is the unique zero of $d(c) = 0$.*

Here the conditions **(H3)** and **(H3')** actually complement each other, so it only makes a difference on the range of wave speed c. The results are proved using the Hopf bifurcation theorem [20] for the corresponding ODE system around the positive equilibrium $E_2(u^*,u^*)$.

Finally the traveling wave solutions and traveling wave train solutions found in Theorems 1.1 and 1.2 also exist for the distributed delay system(1.1) with a small mean delay τ. More precisely we have

Theorem 1.3. *For the system (1.1) with the strong kernel or the weak kernel, there exists a $\tau_0 > 0$ such that for any $\tau \in (0, \tau_0)$, the following statements are true:*

1. *if the condition* **(H2)** *holds, then for each $c \geq c^* = 2\sqrt{B}$, there exists a nonnegative traveling wave solution connecting $E_1(1, 0)$ and $E_2(u^*, u^*)$.*
2. *if the conditions* **(H1)** *and* **(H3)** *(or* **(H3')***) hold, then there exists a family of small amplitude periodic traveling wave train solutions when d is near $d = d(c)$ for all $c > 0$ (or for $c > c^*$), where $d(c)$ is defined in Theorem 1.2.*

The last results are proved by applying the geometric singular perturbation theory [14, 30, 4, 18] when the mean delay is sufficiently small. We note that there have been very few results on the existence of traveling wave solutions for the diffusive predator-prey systems with distributed delays.

The existence of traveling wave solutions and traveling wave train solutions for reaction-diffusion systems has been a hot subject of study for the last a few decades, and important applications in biology can be found in [15, 47]. If the underlying dynamical system has a monotone structure (for example cooperative systems or two-species competition systems), then the theory of monotone dynamical systems provides a powerful tool to prove the existence of spreading speed and traveling wave solutions [12, 32, 45]. However the predator-prey systems do not generate monotone semi-flows so these theories cannot be applied.

In [8, 9, 10] the existence of traveling wave solutions connecting two equilibria of diffusive predator-prey systems was proved by using the ODE shooting arguments and Lyapunov theory, and this method has been improved and refined in [23, 24, 26, 27, 35]. Another approach of proving the existing of traveling wave solutions is to use topological index method, see [16, 38]. Finally upper-lower solution and fixed point theory have also be used to prove the existence of traveling wave solutions in a quasimonotone system, see [13, 29, 33, 34, 36]. For the proof of the existence of traveling wave solutions in Theorem 1.1, we use the fixed point theory similar to the ones in [13, 33, 34]. Note that the existence of weak traveling wave solution for a spatio-temporal Holling-Tanner system was also considered in [7]. In [37, 42], the wave train solutions modeling predator invasion have been considered with some less rigorous way.

The rest of the paper is organized as follows. Section 2 is devoted to the existence of the traveling wave solution of the system (1.2) and obtain the minimum wave speed. In Section 3, we study the existence of small amplitude periodic traveling waves train of the system (1.2). In Section 4, we discuss the existence of traveling wave solutions and periodic traveling waves of the system (1.1) when the mean delay is treated as a small parameter. Finally, numerical simulations are given to illustrate our theoretical results.

2. Traveling wave solutions.

2.1. Preliminaries.

We first present a general existence result of the traveling wave solutions of a two-species reaction-diffusion system with mixed quasimonotone nonlinearity. Consider a general two-species reaction-diffusion system:

$$\begin{cases} u_t(x,t) = du_{xx}(x,t) + H_1(u(x,t),v(x,t)), & x \in \mathbb{R},\ t > 0, \\ v_t(x,t) = v_{xx}(x,t) + H_2(u(x,t),v(x,t)), & x \in \mathbb{R},\ t > 0, \end{cases} \tag{2.1}$$

where $d > 0$, and $H_i(u,v)$ $(i = 1,2)$ are continuously differential functions.

Set $(u(x,t), v(x,t)) = (U(\xi), V(\xi))$ with $\xi = x + ct$ where $c > 0$ is a wave speed. Then $(U(x+ct), V(x+ct))$ is a traveling wave solution of (2.1) if and only if $(U(\xi), V(\xi))$ is a solution of the following system:

$$\begin{cases} d\ddot{U}(\xi) - c\dot{U}(\xi) + H_1(U(\xi),V(\xi)) = 0, & \xi \in \mathbb{R}, \\ \ddot{V}(\xi) - c\dot{V}(\xi) + H_2(U(\xi),V(\xi)) = 0, & \xi \in \mathbb{R}. \end{cases} \tag{2.2}$$

For convenience, we introduce some notations. Define

$$X = \{\mathbf{U} : \mathbf{U} \text{ is a bounded and absolutely continuous function from } \mathbb{R} \text{ to } \mathbb{R}^2\},$$

which is a Banach space with the maximum norm $|\cdot|$. If $\mathbf{a}, \mathbf{b} \in \mathbb{R}^2$ with $\mathbf{a} \le \mathbf{b}$, then the order interval $X_{[\mathbf{a},\mathbf{b}]}$ is defined by

$$X_{[\mathbf{a},\mathbf{b}]} = \{\mathbf{U} \in X : \mathbf{a} \le \mathbf{U}(\xi) \le \mathbf{b},\ \xi \in \mathbb{R}\}.$$

We assume the following conditions hold:

(A1) (Mixed quasi-monotonicity) For $\mathbf{a} \le (u,v) \le \mathbf{b}$, the function $H_1(u,v)$ is monotone nonincreasing in v and $H_2(u,v)$ is monotone nondecreasing in u. Also, there exists a constant $\beta_0 \ge 0$ such that $\beta_0 u + H_1(u,v)$ is nondecreasing in u and $\beta_0 v + H_2(u,v)$ is nondecreasing in v.

(A2) (Lipschitz condition) H_i $(i = 1,2)$ satisfies the Lipschitz condition for $\mathbf{a} \le (u,v) \le \mathbf{b}$. That is, there is a constant $L > 0$ such that for any $\mathbf{a} \le (\phi_j, \psi_j) \le \mathbf{b}$,

$$|H_i(\phi_1,\psi_1) - H_i(\phi_2,\psi_2)| \le L(|\phi_1 - \phi_2| + |\psi_1 - \psi_2|), \quad i = 1,2.$$

For convenience, we first recall the definition of a pair of coupled upper and lower solutions of (2.2) (see for example [33]):

Definition 2.1. $\overline{\Phi} = (\overline{\phi}_1, \overline{\phi}_2)$ and $\underline{\Phi} = (\underline{\phi}_1, \underline{\phi}_2) \in X_{[\mathbf{a},\mathbf{b}]}$ are called a pair of upper and lower solutions of Eq.(2.2), if $\overline{\Phi} \ge \underline{\Phi}$ and there exists a finite set $T = \{T_i \in \mathbb{R} : i = 1,2,\cdots,n\}$ such that $\ddot{\overline{\Phi}}(\xi)$, $\ddot{\underline{\Phi}}(\xi)$ exist for $\xi \in \mathbb{R}\backslash T$, and $\overline{\Phi}, \underline{\Phi}$ satisfy

$$\begin{cases} d\ddot{\overline{\phi}}_1 - c\dot{\overline{\phi}}_1 + H_1(\overline{\phi}_1, \underline{\phi}_2) \le 0 \le d\ddot{\underline{\phi}}_1 - c\dot{\underline{\phi}}_1 + H_1(\underline{\phi}_1, \overline{\phi}_2), & \xi \in \mathbb{R}\backslash T, \\ \ddot{\overline{\phi}}_2 - c\dot{\overline{\phi}}_2 + H_2(\overline{\phi}_1, \overline{\phi}_2) \le 0 \le \ddot{\underline{\phi}}_2 - c\dot{\underline{\phi}}_2 + H_2(\underline{\phi}_1, \underline{\phi}_2), & \xi \in \mathbb{R}\backslash T. \end{cases} \tag{2.3}$$

We have the following general existence result of solution of (2.2) using the upper-lower solutions:

Theorem 2.2. *Assume that* **(A1)**-**(A2)** *hold, and (2.2) has a pair of upper and lower solutions* $(\overline{\phi}_1, \overline{\phi}_2)$ *and* $(\underline{\phi}_1, \underline{\phi}_2)$ *as defined in Definition 2.1 which also satisfy*

$$\dot{\overline{\phi}}_i(\xi+) \le \dot{\overline{\phi}}_i(\xi-),\ \dot{\underline{\phi}}_i(\xi-) \le \dot{\underline{\phi}}_i(\xi+),\ \xi \in \mathbb{R},\ i = 1,2,\ \textit{where}\ \dot{\phi}(\xi\pm) = \lim_{t \to \xi\pm} \dot{\phi}(t),$$

if $\phi(t)$ *is differentiable in a deleted neighborhood of* ξ. *Then the system (2.2) has a solution* (ϕ_1, ϕ_2) *satisfying* $(\underline{\phi}_1, \underline{\phi}_2) \le (\phi_1, \phi_2) \le (\overline{\phi}_1, \overline{\phi}_2)$.

Proof. Define the operators $F_i : X \to X$, $i = 1, 2$, by

$$F_1(U,V) = \beta_0 U + H_1(U,V),\ F_2(U,V) = \beta_0 V + H_2(U,V).$$

Obviously, $F_1(U,V)$ is nondecreasing in U and nonincreasing in V and $F_2(U,V)$ is monotone nondecreasing in U and V. Then Eq.(2.2) is equivalent to the following equation:

$$\begin{cases} d\ddot{U}(\xi) - c\dot{U}(\xi) - \beta_0 U(\xi) + F_1(U(\xi), V(\xi)) = 0, \\ \ddot{V}(\xi) - c\dot{V}(\xi) - \beta_0 V(\xi) + F_2(U(\xi), V(\xi)) = 0. \end{cases}$$

Define

$$\lambda_1 = \frac{1}{2d}(c - \sqrt{c^2 + 4d\beta_0}),\ \lambda_2 = \frac{1}{2d}(c + \sqrt{c^2 + 4d\beta_0}),$$
$$\lambda_3 = \frac{1}{2}(c - \sqrt{c^2 + 4\beta_0}),\ \lambda_4 = \frac{1}{2}(c + \sqrt{c^2 + 4\beta_0}),$$

and an operator $P = (P_1, P_2) : X_{[\mathbf{a},\mathbf{b}]} \to X$ as follows:

$$\begin{aligned} P_1(U,V)(\xi) &= \frac{1}{d(\lambda_2 - \lambda_1)} \left(\int_{-\infty}^{\xi} e^{\lambda_1(\xi - s)} + \int_{\xi}^{+\infty} e^{\lambda_2(\xi - s)} \right) F_1(U,V)(s) ds, \\ P_2(U,V)(\xi) &= \frac{1}{\lambda_4 - \lambda_3} \left(\int_{-\infty}^{\xi} e^{\lambda_3(\xi - s)} + \int_{\xi}^{+\infty} e^{\lambda_4(\xi - s)} \right) F_2(U,V)(s) ds. \end{aligned} \tag{2.4}$$

Clearly, a fixed point of $P = (P_1, P_2)$ is a solution of (2.2). We prove the existence of the fixed point by using the Schauder's fixed point theorem. The remaining part of the proof is standard and similar to Lemma 3.2 of [33] and Lemma 3.2 of [29], thus we omit it here. □

Remark 2.3. A very general existence result of a traveling wave solution for a mixed quasimonotone system was recently proved in [13]. However the upper and lower solutions there are required to be smooth ones, while the upper and lower solutions in Definition 2.1 may be not differentiable at finitely many points. On the other hand, we do not specify the asymptotic behavior of the solution obtained in Theorem 2.2, as such behavior is often implied by the choices of upper and lower solutions.

2.2. **Traveling wave solutions of (1.2).** In this subsection, we seek for a traveling wave solution of (1.2), which satisfies

$$\begin{cases} d\ddot{U}(\xi) - c\dot{U}(\xi) + U(\xi)(1 - U(\xi)) - \dfrac{AU(\xi)V(\xi)}{U(\xi) + aV(\xi)} = 0, & \xi \in \mathbb{R}, \\ \ddot{V}(\xi) - c\dot{V}(\xi) + BV(\xi)\left(1 - \dfrac{V(\xi)}{U(\xi)}\right) = 0, & \xi \in \mathbb{R}, \end{cases} \tag{2.5}$$

with the boundary conditions:

$$\lim_{\xi \to -\infty} (U(\xi), V(\xi)) = (1, 0),\ \lim_{\xi \to +\infty} (U(\xi), V(\xi)) = (u^*, u^*).$$

Denote $H_i(u,v),\ i = 1, 2$ by

$$H_1(u,v) = u(1-u) - \frac{Auv}{u + av},\ H_2(u,v) = Bv\left(1 - \frac{v}{u}\right).$$

We recall some well-known results for the Fisher equation on unbounded domain [3].

Consider

$$\begin{cases} z_t(x,t) = Dz_{xx}(x,t) + Rz(x,t)\left(1 - \dfrac{z(x,t)}{K}\right), & x \in \mathbb{R},\ t > 0, \\ z(x,0) = z_0(x) \geq 0, & x \in \mathbb{R}, \end{cases} \tag{2.6}$$

where $D, R, K > 0$ and $z_0(x) \geq 0$ is a bounded uniformly continuous function with nonempty support set. Then the following results were proved in ([3], Corollary 1 and Proposition 2.1).

Lemma 2.4. *Assume that $z(x,t)$ is a solution of (2.6) in $\mathbb{R} \times \mathbb{R}^1$. Then for any given $\epsilon \in (0, 2\sqrt{DR})$,*

$$\lim_{t\to+\infty} \min_{|x|<(2\sqrt{DR}-\epsilon)t} z(x,t) = K.$$

Lemma 2.5. *Assume that $z(x,t)$ is the solution of (2.6), $\bar{z}(x,t)$ is bounded for $x \in \mathbb{R}, t \geq 0$, twice differentiable in $x \in \mathbb{R}$, differentiable in $t > 0$ and satisfies:*

$$\begin{cases} \bar{z}_t(x,t) \geq D\bar{z}_{xx}(x,t) + R\bar{z}(x,t)\left(1 - \dfrac{\bar{z}(x,t)}{K}\right), & x \in \mathbb{R},\ t > 0, \\ \bar{z}(x,0) \geq z_0(x), & x \in \mathbb{R}. \end{cases}$$

Then $\bar{z}(x,t) \geq z(x,t)$ for $x \in \mathbb{R}, t \geq 0$.

We first prove the existence of the semi-traveling wave solution by using Theorem 2.2. Define a set

$$X_{[\mathbf{M_1},\mathbf{M_2}]} \triangleq \{(u,v) \in X: \ (\theta_0, 0) \leq (u,v)(\xi) \leq (1,1)\}, \tag{2.7}$$

where $\mathbf{M_1} = (\theta_0, 0)$, and $\mathbf{M_2} = (1,1)$, where $\theta_0 < 1 - A/a$ is a fixed small positive constant. It is easy to check that the conditions **(A1)-(A2)** hold in the invariant set $X_{[\mathbf{M_1},\mathbf{M_2}]}$. Now we construct a pair of upper and lower solutions.

Define

$$\begin{aligned} &\overline{\phi}_1(\xi) = 1,\ \underline{\phi}_1(\xi) = \max\left\{1 - \frac{A}{a}, 1 - \frac{a}{A}e^{r_1\xi}\right\}, \\ &\overline{\phi}_2(\xi) = \min\left\{1, \frac{a}{A^2}e^{r_2\xi}\right\},\ \underline{\phi}_2(\xi) = \max\left\{0, \frac{a}{A^2}e^{r_2\xi} - qe^{\eta r_1\xi}\right\}, \end{aligned} \tag{2.8}$$

where

$$r_2 = \frac{c - \sqrt{c^2 - 4B}}{2},\ r_1 = \min\left\{r_2, \frac{c}{d}\right\},\ \eta \in \left(\frac{r_2}{r_1},\ \min\left\{\frac{c}{2r_1}, \frac{2r_2}{r_1}\right\}\right), \tag{2.9}$$

and

$$q = \frac{Ba^3}{-A^4(a-A)(\eta^2 r_1^2 - c\eta r_1 + B)} + \frac{a}{A^2} + 1. \tag{2.10}$$

Lemma 2.6. *Suppose that $c > 2\sqrt{B}$ and $r_1,\ r_2,\ \eta,\ q$ are defined as in (2.9)-(2.10). Let $(\overline{\phi}_1, \overline{\phi}_2)$ and $(\underline{\phi}_1, \underline{\phi}_2)$ be defined as in (2.8). Then $(\overline{\phi}_1, \overline{\phi}_2)$, $(\underline{\phi}_1, \underline{\phi}_2) \in X_{[\mathbf{M_1},\mathbf{M_2}]}$, $(\underline{\phi}_1, \underline{\phi}_2) \leq (\overline{\phi}_1, \overline{\phi}_2)$, and $(\overline{\phi}_1, \overline{\phi}_2)$ and $(\underline{\phi}_1, \underline{\phi}_2)$ are a pair of upper and lower solutions of the system (2.5).*

Proof. Note that $r_1,\ r_2,\ \eta > 0$ are well-defined since $c > 2\sqrt{B}$, and it is easy to see that $(\overline{\phi}_1, \overline{\phi}_2)$, $(\underline{\phi}_1, \underline{\phi}_2) \in X_{[\mathbf{M_1},\mathbf{M_2}]}$, and $(\underline{\phi}_1, \underline{\phi}_2) \leq (\overline{\phi}_1, \overline{\phi}_2)$.

Next we verify the conditions of upper and lower solutions separately.

(i) Since $\overline{\phi}_1(\xi)=1$, then it is easy to verify that

$$d\ddot{\overline{\phi}}_1 - c\dot{\overline{\phi}}_1 + \overline{\phi}_1(1-\overline{\phi}_1) - \frac{A\overline{\phi}_1\underline{\phi}_2}{\overline{\phi}_1 + a\underline{\phi}_2} = -\frac{A\underline{\phi}_2}{1+a\underline{\phi}_2} \le 0.$$

(ii) One can see that

$$\underline{\phi}_1(\xi) = \begin{cases} 1-\dfrac{A}{a}, & \xi \ge \dfrac{2}{r_1}\ln\dfrac{A}{a}, \\ 1-\dfrac{a}{A}e^{r_1\xi}, & \xi < \dfrac{2}{r_1}\ln\dfrac{A}{a}. \end{cases}$$

For $\xi \ge \frac{2}{r_1}\ln\frac{A}{a}$, from $\underline{\phi}_1(\xi) = 1-\frac{A}{a}$, we get

$$\begin{aligned} & d\ddot{\underline{\phi}}_1 - c\dot{\underline{\phi}}_1 + \underline{\phi}_1(1-\underline{\phi}_1) - \frac{A\underline{\phi}_1\overline{\phi}_2}{\underline{\phi}_1 + a\overline{\phi}_2} \\ =& \left(1-\frac{A}{a}\right)\left(\frac{A}{a} - \frac{A\overline{\phi}_2}{1-\frac{A}{a}+a\overline{\phi}_2}\right) \ge \left(1-\frac{A}{a}\right)\left(\frac{A}{a}-\frac{A}{a}\right) = 0. \end{aligned}$$

And for $\xi < \frac{2}{r_1}\ln\frac{A}{a}$, we have $\underline{\phi}_1(\xi) = 1-\frac{a}{A}e^{r_1\xi}$, and

$$\begin{aligned} & 1-\underline{\phi}_1 - \frac{A\overline{\phi}_2}{\underline{\phi}_1 + a\overline{\phi}_2} = \frac{a}{A}e^{r_1\xi} - \frac{A\overline{\phi}_2}{\underline{\phi}_1 + a\overline{\phi}_2} \\ \ge & \frac{a}{A}e^{r_1\xi} - \frac{\frac{a}{A}e^{r_1\xi}}{1-\frac{a}{A}e^{r_1\xi} + \frac{a^2}{A^2}e^{r_1\xi}} \ge \frac{a}{A}e^{r_1\xi} - \frac{\frac{a}{A}e^{r_1\xi}}{1-\frac{a}{A}e^{r_1\xi}+\frac{a}{A}e^{r_1\xi}} = 0, \end{aligned}$$

according to that $\overline{\phi}_2(\xi) \le \frac{a}{A^2}e^{r_2\xi} \le \frac{a}{A^2}e^{r_1\xi}$ since $r_1 = \min\{r_2, c/d\}$. Hence from (2.9),

$$\begin{aligned} & d\ddot{\underline{\phi}}_1 - c\dot{\underline{\phi}}_1 + \underline{\phi}_1(1-\underline{\phi}_1) - \frac{A\underline{\phi}_1\overline{\phi}_2}{\underline{\phi}_1 + a\overline{\phi}_2} \\ =& -\frac{a}{A}r_1e^{r_1\xi}(dr_1 - c) + \underline{\phi}_1(1-\underline{\phi}_1) - \frac{A\underline{\phi}_1\overline{\phi}_2}{\underline{\phi}_1 + a\overline{\phi}_2} \ge \underline{\phi}_1(1-\underline{\phi}_1) - \frac{A\underline{\phi}_1\overline{\phi}_2}{\underline{\phi}_1 + a\overline{\phi}_2} \ge 0. \end{aligned}$$

(iii) We have

$$\overline{\phi}_2(\xi) = \begin{cases} 1, & \xi \ge \dfrac{1}{r_2}\ln\dfrac{A^2}{a}, \\ \dfrac{a}{A^2}e^{r_2\xi}, & \xi < \dfrac{1}{r_2}\ln\dfrac{A^2}{a}. \end{cases}$$

For $\xi \ge \frac{1}{r_2}\ln\frac{A^2}{a}$, $\overline{\phi}_2(\xi) = 1$. Then,

$$\ddot{\overline{\phi}}_2 - c\dot{\overline{\phi}}_2 + B\overline{\phi}_2\left(1-\frac{\overline{\phi}_2}{\overline{\phi}_1}\right) = B(1-1) = 0.$$

Otherwise for $\xi < \frac{1}{r_2}\ln\frac{A^2}{a}$, $\overline{\phi}_2(\xi) = \frac{a}{A^2}e^{r_2\xi} \le 1$, then from (2.9),

$$\ddot{\overline{\phi}}_2 - c\dot{\overline{\phi}}_2 + B\overline{\phi}_2\left(1-\frac{\overline{\phi}_2}{\overline{\phi}_1}\right) = \frac{a}{A^2}e^{r_2\xi}(r_2^2 - cr_2 + B) - \frac{Ba^2}{A^4}e^{2r_2\xi} = -\frac{Ba^2}{A^4}e^{2r_2\xi} \le 0.$$

(iv) Note that

$$\underline{\phi}_2(\xi) = \begin{cases} 0, & \xi \geq \dfrac{1}{\eta r_1 - r_2} \ln \dfrac{a}{A^2 q}, \\ \dfrac{a}{A^2} e^{r_2 \xi} - q e^{\eta r_1 \xi}, & \xi < \dfrac{1}{\eta r_1 - r_2} \ln \dfrac{a}{A^2 q}. \end{cases}$$

For $\xi \geq \dfrac{1}{\eta r_1 - r_2} \ln \dfrac{a}{A^2 q}$, $\underline{\phi}_2(\xi) = 0$. Then

$$\ddot{\underline{\phi}}_2 - c\dot{\underline{\phi}}_2 + B\underline{\phi}_2 \left(1 - \frac{\underline{\phi}_2}{\underline{\phi}_1}\right) = 0.$$

On the other hand, for $\xi < \dfrac{1}{\eta r_1 - r_2} \ln \dfrac{a}{A^2 q}$, we have $\underline{\phi}_2(\xi) = \dfrac{a}{A^2} e^{r_2 \xi} - q e^{\eta r_1 \xi}$. Then,

$$\begin{aligned} &\ddot{\underline{\phi}}_2 - c\dot{\underline{\phi}}_2 + B\underline{\phi}_2 \left(1 - \frac{\underline{\phi}_2}{\underline{\phi}_1}\right) = \ddot{\underline{\phi}}_2 - c\dot{\underline{\phi}}_2 + B\underline{\phi}_2 - \frac{B\underline{\phi}_2^2}{\underline{\phi}_1} \\ \geq &\frac{a}{A^2} e^{r_2 \xi}(r_2^2 - c r_2 + B) - q e^{\eta r_1 \xi}(\eta^2 r_1^2 - c\eta r_1 + B) - \frac{B(\frac{a}{A^2} e^{r_2 \xi} - q e^{\eta r_1 \xi}) \frac{a}{A^2} e^{r_2 \xi}}{1 - \frac{A}{a}} \\ \geq & - q e^{\eta r_1 \xi}(\eta^2 r_1^2 - c\eta r_1 + B) - \frac{B a^3}{A^4 (a - A)} e^{2 r_2 \xi} \\ \geq & e^{\eta r_1 \xi} \left(-q(\eta^2 r_1^2 - c\eta r_1 + B) - \frac{B a^3}{A^4 (a - A)} \right) \geq 0, \end{aligned}$$

by using the facts that $\underline{\phi}_1(\xi) \geq 1 - A/a$ and $\underline{\phi}_2^2(\xi) \leq \dfrac{a}{A^2} \underline{\phi}_2(\xi) e^{r_2 \xi}$, (2.9) and (2.10).

Now from (i)-(iv), $(\overline{\phi}_1, \overline{\phi}_2)$ and $(\underline{\phi}_1, \underline{\phi}_2)$ are a pair of upper and lower solutions of the system (2.5). □

Now we are ready to prove Theorem 1.1.

Proof of Theorem 1.1. 1. It is sufficient to show that there exists a traveling wave solution for all $c > 2\sqrt{B}$. The case of $c = 2\sqrt{B}$ can be proved by letting $c \downarrow 2\sqrt{B}$ (for the validity of such a limiting argument we refer readers to the proof of [28, Theorem 4.1] or [45, Theorem 4.2]). In the following, we prove the existence of traveling wave solution when $c > 2\sqrt{B}$ in two steps.

Step 1. We claim that there exists a semi-traveling wave solution $(\phi_1(\xi), \phi_2(\xi))$ satisfying $\lim_{\xi \to -\infty} (\phi_1(\xi), \phi_2(\xi)) = (1, 0)$.

From Lemma 2.6, there exists a pair of upper and lower solutions $(\overline{\phi}_1, \overline{\phi}_2)$ and $(\underline{\phi}_1, \underline{\phi}_2)$ for the system (2.5). Then from Theorem 2.2, there exists a solution $(\phi_1(\xi), \phi_2(\xi))$ of Eq.(2.5) satisfying $(\underline{\phi}_1, \underline{\phi}_2) \leq (\phi_1, \phi_2) \leq (\overline{\phi}_1, \overline{\phi}_2)$. It is clear that

$$\begin{aligned} 1 = \lim_{\xi \to -\infty} \underline{\phi}_1(\xi) \leq \lim_{\xi \to -\infty} \phi_1(\xi) \leq \lim_{\xi \to -\infty} \overline{\phi}_1(\xi) = 1, \\ 0 = \lim_{\xi \to -\infty} \underline{\phi}_2(\xi) \leq \lim_{\xi \to -\infty} \phi_2(\xi) \leq \lim_{\xi \to -\infty} \overline{\phi}_2(\xi) = 0, \end{aligned}$$

hence $\lim_{\xi \to -\infty} (\phi_1(\xi), \phi_2(\xi)) = (1, 0)$.

Step 2. Next we show that $\lim_{\xi \to +\infty} (\phi_1(\xi), \phi_2(\xi)) = (u^*, u^*)$.

Denote

$$\overline{u}_1 = \limsup_{\xi \to +\infty} \phi_1(\xi),\ \ \underline{u}_1 = \liminf_{\xi \to +\infty} \phi_1(\xi),$$
$$\overline{u}_2 = \limsup_{\xi \to +\infty} \phi_2(\xi),\ \ \underline{u}_2 = \liminf_{\xi \to +\infty} \phi_2(\xi).$$

Let $(u(x,t), v(x,t)) = (\phi_1(x+ct), \phi_2(x+ct))$. Then $(u(x,t), v(x,t))$ is a solution of Eq.(1.2).

Clearly, we have that

$$\phi_1(\xi) \geq \underline{\phi}_1(\xi) \geq 1 - \frac{A}{a} > 0,\ \text{for } \xi \in \mathbb{R}. \tag{2.11}$$

That is,

$$\underline{u}_1 = \liminf_{\xi \to +\infty} \phi_1(\xi) \geq 1 - \frac{A}{a} > 0. \tag{2.12}$$

Consequently by the second equation of (1.2), we have that

$$\begin{cases} v_t(x,t) \geq v_{xx}(x,t) + Bv(x,t)\left(1 - \dfrac{v(x,t)}{1-\frac{A}{a}}\right), & x \in \mathbb{R},\ t > 0, \\ v(x,0) = \phi_2(x), & x \in \mathbb{R}. \end{cases}$$

Hence, by Lemmas 2.4 and 2.5, $\underline{u}_2 = \liminf_{\xi \to +\infty} \phi_2(\xi) \geq 1 - A/a > 0$.

From the definition of limit superior and limit inferior, for $\epsilon > 0$ sufficiently small, we choose $N = \dfrac{1}{\lambda_1} \ln \dfrac{-\epsilon d(\lambda_2 - \lambda_1)\lambda_1}{\beta_0} > 0$, then there exist a pair of constants $M_1 > 0$ and $\xi_1 > M_1 + N$ satisfying

$$\phi_1(\xi) < \overline{u}_1 + \epsilon,\ \phi_2(\xi) > \underline{u}_2 - \epsilon,\ \text{for } \xi \geq M_1, \quad \phi_1(\xi_1) > \overline{u}_1 - \epsilon.$$

Since $(\phi_1(\xi), \phi_2(\xi))$ is a fixed point of P defined by (2.4) and based on the mixed monotonicity of F_1 and F_2, we have the following inequality:

$$\begin{aligned}
\overline{u}_1 - \epsilon < & \phi_1(\xi_1) = \frac{1}{d(\lambda_2 - \lambda_1)}\left(\int_{-\infty}^{\xi_1 - N} e^{\lambda_1(\xi_1 - s)} F_1(\phi_1, \phi_2)(s) ds \right. \\
& \left. + \int_{\xi_1 - N}^{\xi_1} e^{\lambda_1(\xi_1 - s)} F_1(\phi_1, \phi_2)(s) ds + \int_{\xi_1}^{+\infty} e^{\lambda_2(\xi_1 - s)} F_1(\phi_1, \phi_2)(s) ds \right) \\
\leq & \frac{F_1(\overline{u}_1 + \epsilon, \underline{u}_2 - \epsilon)}{d(\lambda_2 - \lambda_1)} \left(\int_{\xi_1 - N}^{\xi_1} e^{\lambda_1(\xi_1 - s)} ds + \int_{\xi_1}^{+\infty} e^{\lambda_2(\xi_1 - s)} ds \right) \\
& + \frac{F_1(1,0)}{d(\lambda_2 - \lambda_1)} \int_{-\infty}^{\xi_1 - N} e^{\lambda_1(\xi_1 - s)} ds \\
\leq & \frac{F_1(\overline{u}_1 + \epsilon, \underline{u}_2 - \epsilon)}{d(\lambda_2 - \lambda_1)} \left(\int_{-\infty}^{\xi_1} e^{\lambda_1(\xi_1 - s)} ds + \int_{\xi_1}^{+\infty} e^{\lambda_2(\xi_1 - s)} ds \right) - \frac{\beta_0 e^{\lambda_1 N}}{d(\lambda_2 - \lambda_1)\lambda_1} \\
= & - \frac{F_1(\overline{u}_1 + \epsilon, \underline{u}_2 - \epsilon)}{d\lambda_1 \lambda_2} + \epsilon \\
= & \frac{1}{\beta_0} \left(\beta_0(\overline{u}_1 + \epsilon) + (\overline{u}_1 + \epsilon)(1 - \overline{u}_1 - \epsilon) - \frac{A(\overline{u}_1 + \epsilon)(\underline{u}_2 - \epsilon)}{\overline{u}_1 + \epsilon + a(\underline{u}_2 - \epsilon)} \right) + \epsilon.
\end{aligned}$$

By the arbitrariness of ϵ, we have that

$$\overline{u}_1(1 - \overline{u}_1) - \frac{A\overline{u}_1 \underline{u}_2}{\overline{u}_1 + a\underline{u}_2} \geq 0. \tag{2.13}$$

Similarly we can prove that

$$\underline{u}_1(1-\underline{u}_1) - \frac{A\underline{u}_1\overline{u}_2}{\underline{u}_1 + a\overline{u}_2} \le 0, \tag{2.14}$$

$$\overline{u}_2\left(1-\frac{\overline{u}_2}{\overline{u}_1}\right) \ge 0, \tag{2.15}$$

$$\underline{u}_2\left(1-\frac{\underline{u}_2}{\underline{u}_1}\right) \le 0. \tag{2.16}$$

From (2.13) and (2.16) and $\overline{u}_1,\ \underline{u}_2 > 0$, we have,

$$1-\overline{u}_1 \ge \frac{A\underline{u}_2}{\overline{u}_1 + a\underline{u}_2} \ge \frac{A\underline{u}_1}{\overline{u}_1 + a\underline{u}_1}.$$

That is,

$$\overline{u}_1 - \overline{u}_1{}^2 + a\underline{u}_1 - a\overline{u}_1\underline{u}_1 - A\underline{u}_1 \ge 0. \tag{2.17}$$

In the same way, we have from (2.14) and (2.15),

$$-\underline{u}_1 + \underline{u}_1{}^2 - a\overline{u}_1 + a\overline{u}_1\underline{u}_1 + A\overline{u}_1 \ge 0. \tag{2.18}$$

Adding (2.17) and (2.18), we have,

$$(\overline{u}_1 - \underline{u}_1)(1-a+A-\overline{u}_1-\underline{u}_1) \ge 0. \tag{2.19}$$

Since the condition **(H2)** holds, we have

$$\overline{u}_1 + \underline{u}_1 \ge 2\underline{u}_1 \ge 2\left(1-\frac{A}{a}\right) > 1-a+A.$$

That is,

$$1-a+A-\overline{u}_1-\underline{u}_1 < 0,$$

which, combining (2.19) and $\overline{u}_1 \ge \underline{u}_1$, implies $\overline{u}_1 = \underline{u}_1$.

By (2.15) and (2.16) again, we have that,

$$\overline{u}_1 = \underline{u}_1 = \overline{u}_2 = \underline{u}_2 \triangleq x^*. \tag{2.20}$$

Substituting (2.20) into (2.13) and (2.14) induces that

$$x^* \le 1-\frac{A}{1+a},\ x^* \ge 1-\frac{A}{a+1}.$$

That is,

$$\overline{u}_1 = \underline{u}_1 = 1-\frac{A}{1+a} = u^*,\ \overline{u}_2 = \underline{u}_2 = u^*.$$

This completes the proof of existence of a traveling wave solution connecting $(1,0)$ and (u^*,u^*).

2. If the statement is false, then there exists c_0 satisfying $0 < c_0 < c^* = 2\sqrt{B}$ such that the system (1.2) has a positive solution $(u(x,t), v(x,t)) = (\phi_1(x+c_0t), \phi_2(x+c_0t))$ satisfying

$$\lim_{\xi\to-\infty}(\phi_1(\xi),\phi_2(\xi)) = (1,0),\ \lim_{\xi\to+\infty}(\phi_1(\xi),\phi_2(\xi)) = (u^*,u^*). \tag{2.21}$$

By the continuity of $\phi_1(\xi)$ and (2.21), there exists a $\delta > 0$ such that $\phi_1(\xi) > \delta$ for $\xi \in \mathbb{R}$. Hence, from the second equation of (1.2) again, we have that

$$\begin{cases} v_t(x,t) \ge v_{xx}(x,t) + Bv(x,t)\left(1-\dfrac{v(x,t)}{\delta}\right), & x\in\mathbb{R},\ t>0, \\ v(x,0) = \phi_2(x) > 0, & x\in\mathbb{R}. \end{cases} \tag{2.22}$$

By Lemmas 2.4 and 2.5, we have, for any $\epsilon \in (0, 2\sqrt{B})$,

$$\lim_{t\to\infty} \min_{|x|<(2\sqrt{B}-\epsilon)t} v(x,t) \geq \delta > 0. \tag{2.23}$$

We choose $\theta_0 \in (0,1)$ such that $c_0 < 2\sqrt{\theta_0 B}$ since $c_0 < 2\sqrt{B}$. We let $x(t) = -2\sqrt{\theta_0 B}t$ and $\epsilon = \sqrt{B} - \sqrt{\theta_0 B}$. Then $|x| = 2\sqrt{\theta_0 B}t < (2\sqrt{B}-\epsilon)t$. Then by (2.23), we have

$$\lim_{t\to\infty} \inf_{|x|=2\sqrt{\theta_0 B}t} v(x,t) \geq \delta > 0.$$

On the other hand, $x(t) + c_0 t = (c_0 - 2\sqrt{\theta_0 B})t \to -\infty$, (2.21) implies that $\liminf_{\xi\to-\infty} \phi_2(\xi) = 0$, which is a contraction. Thus (1.2) has no positive traveling wave solution connecting $(1,0)$ and (u^*, u^*). □

3. **Existence of wave train solutions.** In this section, we prove Theorem 1.2. To achieve that, we first give the following two lemmas.

Lemma 3.1. *Assume* **(H1)** *and* **(H3)** *or* **(H3')** *hold. Then* $B < \dfrac{A}{(a+1)^2}$.

Proof. From **(H3)** or **(H3')** and $A < 1 + a$, we observe that

$$\frac{(a+1)^2}{a+2}(B+1) < 1 + a,$$

which is equivalent to the inequality $B < 1/(a+1)$. That is,

$$\frac{B+1}{a+2} - B = \frac{-B(1+a)+1}{a+2} > 0.$$

Thereby, $A > \dfrac{(a+1)^2(B+1)}{a+2} > B(a+1)^2$. □

Consider a quartic polynomial equation:

$$\lambda^4 + P_1(d)\lambda^3 + P_2(d)\lambda^2 + P_3(d)\lambda + P_4(d) = 0, \tag{3.1}$$

where $P_i(d)$ $(1 \leq i \leq 4)$ are continuously differentiable functions of a parameter d.

Lemma 3.2. *Assume (3.1) has a pair of simple imaginary roots $\lambda = \pm i\omega$ with $\omega > 0$ at $d = d_0$. Then*

$$\operatorname{Re}\left(\frac{d\lambda}{dd}\right)^{-1}\Bigg|_{d=d_0} = \frac{2P_3(d_0)g'(d_0)}{MP_1^2(d_0)},$$

where

$$M = (P_4'(d_0) - \omega^2 P_2'(d_0))^2 + (P_3'(d_0) - \omega^2 P_1'(d_0))^2\omega^2,$$
$$g(d) = P_3^2(d) - P_1(d)P_2(d)P_3(d) + P_1^2(d)P_4(d).$$

Proof. Let $\lambda = \pm i\omega$ with $\omega > 0$ be a pair of roots of Eq.(3.1) at $d = d_0$. Then

$$\omega^4 - P_1(d_0)\omega^3 i - P_2(d_0)\omega^2 + P_3(d_0)\omega i + P_4(d_0) = 0.$$

Separating the real and imaginative parts leads to

$$\omega^2 = \frac{P_3(d_0)}{P_1(d_0)}, \ \ \omega^4 - P_2(d_0)\omega^2 + P_4(d_0) = 0. \tag{3.2}$$

Then $g(d_0) = 0$ and

$$\begin{aligned} g'(d_0) =& 2P_3(d_0)P_3'(d_0) - P_1'(d_0)P_2(d_0)P_3(d_0) - P_1(d_0)P_2'(d_0)P_3(d_0) \\ & - P_1(d_0)P_2(d_0)P_3'(d_0) + 2P_1(d_0)P_1'(d_0)P_4(d_0) + P_1^2(d_0)P_4'(d_0). \end{aligned} \tag{3.3}$$

Differentiating (3.1) results in the following equality:

$$\left(\frac{d\lambda}{dd}\right)^{-1}\Bigg|_{d=d_0} = -\frac{\lambda(4\lambda^2 + 3P_1(d)\lambda + 2P_2(d)) + P_3(d)}{P_1'(d)\lambda^3 + P_2'(d)\lambda^2 + P_3'(d)\lambda + P_4'(d)}\Bigg|_{d=d_0}.$$

Thus, by using (3.2) and (3.3), we have that

$$\begin{aligned} &\operatorname{Re}\left(\frac{d\lambda}{dd}\right)^{-1}\Bigg|_{d=d_0} \\ =& -\operatorname{Re}\left\{\frac{i\omega(-4\omega^2 + 3P_1(d_0)i\omega + 2P_2(d_0)) + P_3(d_0)}{P_4'(d_0) - P_2'(d_0)\omega^2 + i\omega(P_3'(d_0) - \omega^2 P_1'(d_0))}\right\} \\ =& \frac{1}{M}\left(3P_1(d_0)\omega^2 - P_3(d_0)\right)(P_4'(d_0) - \omega^2 P_2'(d_0)) \\ & - \frac{\omega^2}{M}(2P_2(d_0) - 4\omega^2)(P_3'(d_0) - \omega^2 P_1'(d_0)) \\ =& \frac{2P_3(d_0)}{MP_1^2(d_0)}\Bigg(P_4'(d_0)P_1^2(d_0) - P_1(d_0)P_2'(d_0)P_3(d_0) + P_1'(d_0)P_2(d_0)P_3(d_0) \\ & - P_1(d_0)P_2(d_0)P_3'(d_0) - \frac{2P_3^2(d_0)P_1'(d_0)}{P_1(d_0)} + 2P_3(d_0)P_3'(d_0)\Bigg) \\ =& \frac{2P_3(d_0)}{MP_1^2(d_0)}\left(g'(d_0) + 2P_1'(d_0)P_2(d_0)P_3(d_0)\right) \\ & - \frac{4P_3(d_0)P_1'(d_0)}{KP_1^3(d_0)}(P_1^2(d_0)P_4(d_0) + P_3^2(d_0)) \\ =& \frac{2P_3(d_0)}{MP_1^2(d_0)}\left(g'(d_0) - \frac{2P_1'(d_0)}{P_1(d_0)}g(d_0)\right) = \frac{2P_3(d_0)g'(d_0)}{MP_1^2(d_0)}. \end{aligned}$$

□

Now we are ready to prove Theorem 1.2.

Proof of Theorem 1.2. We use the Hopf bifurcation theorem to prove the existence of small amplitude periodic solutions of (2.5), which is equivalent to wave train solutions of (1.2). For that purpose, we convert (2.5) to a system of first order ODEs. We set $\dot{U}(\xi) = W(\xi)$, $\dot{V}(\xi) = X(\xi)$ and rewrite the system (2.5) as follows:

$$\begin{cases} \dot{U}(\xi) = W(\xi), \\ \dot{W}(\xi) = \dfrac{c}{d}W(\xi) - \dfrac{U(\xi)(1-U(\xi))}{d} + \dfrac{AU(\xi)V(\xi)}{d(U(\xi)+aV(\xi))}, \\ \dot{V}(\xi) = X(\xi), \\ \dot{X}(\xi) = cX(\xi) - BV(\xi)\left(1 - \dfrac{V(\xi)}{U(\xi)}\right). \end{cases} \tag{3.4}$$

The system (3.4) has two equilibria $E_1(1,0,0,0)$ and $E_2(u^*,0,u^*,0)$.

The Jaccobian matrix of the linearization of Eq.(3.4) at $E(U,0,V,0)$ is given by

$$\begin{pmatrix} 0 & 1 & 0 & 0 \\ \alpha & c/d & \beta & 0 \\ 0 & 0 & 0 & 1 \\ r & 0 & \mu & c \end{pmatrix}$$

where

$$\alpha = \frac{1}{d}\left(2U - 1 + \frac{AaV^2}{(U+aV)^2}\right),\ r = -\frac{BV^2}{U^2},$$
$$\beta = \frac{AU^2}{d(U+aV)^2},\ \mu = -B\left(1 - \frac{2V}{U}\right),$$

and the corresponding characteristic equation is given as follows:

$$Q(\lambda, d) = \lambda^4 - c\left(1 + \frac{1}{d}\right)\lambda^3 + \left(\frac{c^2}{d} - \alpha - \mu\right)\lambda^2 + c\left(\frac{\mu}{d} + \alpha\right)\lambda + \alpha\mu - \beta r = 0.$$

Hence at the equilibrium $E_2(u^*, 0, u^*, 0)$, the corresponding characteristic polynomial is

$$\begin{aligned} Q_2(\lambda, d) =& \lambda^4 - c\left(1 + \frac{1}{d}\right)\lambda^3 + \left(\frac{c^2}{d} - B - \frac{1}{d}\left(1 - \frac{A(a+2)}{(a+1)^2}\right)\right)\lambda^2 \\ &+ \frac{c}{d}\left(B + 1 - \frac{A(a+2)}{(a+1)^2}\right)\lambda + \frac{Bu^*}{d} = 0. \end{aligned} \tag{3.5}$$

We define

$$\rho = B + 1 - \frac{A(a+2)}{(a+1)^2},\ \theta = c^2 - B(d-1).$$

Then (3.5) is simplified to

$$Q_2(\lambda, d) = \lambda^4 - c\left(1 + \frac{1}{d}\right)\lambda^3 + \frac{\theta - \rho}{d}\lambda^2 + \frac{c\rho}{d}\lambda + \frac{Bu^*}{d} = 0. \tag{3.6}$$

To obtain the existence of periodic solutions induced by Hopf bifurcation, we seek for a pair of pure imaginary roots of (3.6). Let $\lambda = i\omega$ ($\omega > 0$) be a root of Eq. (3.6). Then

$$\omega^4 + c\left(1 + \frac{1}{d}\right)\omega^3 i - \frac{\theta - \rho}{d}\omega^2 + \frac{c\rho}{d}\omega i + \frac{Bu^*}{d} = 0. \tag{3.7}$$

Separating the real and imaginary parts in (3.7), we obtain

$$\begin{cases} \omega^4 - \dfrac{\theta - \rho}{d}\omega^2 + \dfrac{Bu^*}{d} = 0, \\ c\left(1 + \dfrac{1}{d}\right)\omega^2 = -\dfrac{c\rho}{d}. \end{cases} \tag{3.8}$$

From (3.8), we have

$$\omega = \sqrt{-\frac{\rho}{d+1}} > 0, \tag{3.9}$$

as **(H3)** or **(H3')** implies that $\rho < 0$. Substituting (3.9) into (3.8), we find that

$$B\left(\frac{A}{(a+1)^2} - B\right)(d+1)^2 + \rho(c^2 + 2B)(d+1) - \rho^2 = 0. \tag{3.10}$$

By Lemma 3.1, (3.10) has a unique root $d = d(c) > -1$ given by (1.3) with Δ defined as in (1.4).

To show that $d(c)$ is indeed positive, we analyze the dependence of $d(c)$ on the wave speed c. One can observe that $d(c)$ is strictly increasing on c, and

$$\begin{aligned} d(0) =& \frac{(a+1)^2}{2B(A-B(a+1)^2)}\left(-2\rho B - \frac{2\rho\sqrt{AB}}{a+1}\right) - 1 \\ =& \frac{a+1}{A-B(a+1)^2}\left(A-(a+1)+\left(\frac{A(a+2)}{(a+1)^2} - B - 1\right)\sqrt{\frac{A}{B}}\right). \end{aligned}$$

Therefore, if **(H3)** holds, then $d(0) \geq 0$ and consequently $d(c) > 0$ for $c > 0$. On the other hand, if **(H3')** holds, $d(0) < 0$, then there exists a unique $c^* > 0$ such that $d(c^*) = 0$, and $d(c) > 0$ for $c > c^*$. In either case, we have shown that, when $d = d(c)$, (3.6) has a pair of pure imaginary roots $\pm i\omega$ where ω is given by (3.9).

From the characteristic equation (3.6), $P_3(d) = c\rho/d < 0$ and $g'(d(c)) > 0$, then by Lemma 3.2, the transversity condition holds. That is,

$$\mathrm{Re}\left(\frac{d\lambda}{dd}\right)\Bigg|_{d=d(c)} = \frac{2c\rho g'(d(c))}{d(c)P_1^2(d(c))M} < 0. \tag{3.11}$$

Now from the standard Hopf bifurcation theorem [20], we obtain the result of Theorem 1.2. □

Figure 1 shows the graphs of the Hopf bifurcation curve $d = d(c)$ for two examples satisfying **(H3)** and **(H3')**. Note that the transversality condition (3.11) suggests that when d decreases across $d(c)$, the real part of one pair of eigenvalues changes from negative to positive, hence for smaller diffusion coefficient d, there exists time-periodic oscillations.

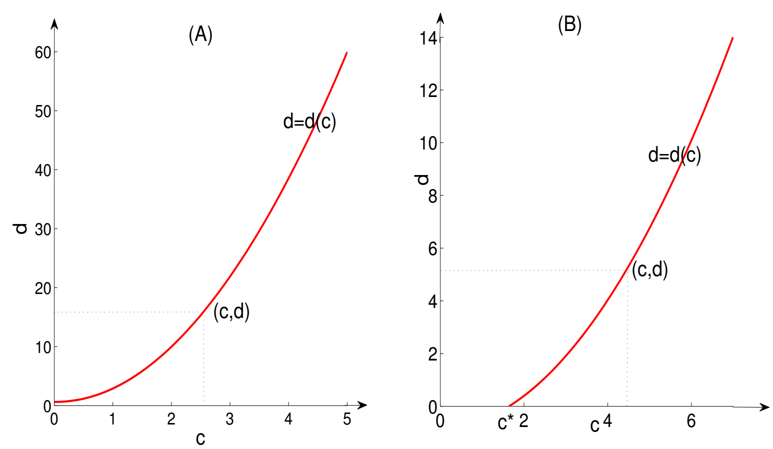

FIGURE 1. Hopf bifurcation curves of (3.4). Left: $A = 1.9$, $B = 0.3$, $a = 1$ (satisfying **(H3)**); Right: $A = 1.75$, $B = 0.3$, $a = 1$ (satisfying **(H3')**).

4. **Distributed delay systems.** In this section, we investigate the existence of traveling wave solution and periodic traveling waves of the system (1.1) with distributed delay when τ is small by using the geometric singular theory [14].

Similar to Section 2, we know that $(U(x+ct), V(x+ct))$ is a traveling wave solution of (1.1) if and only if $(U(\xi), V(\xi))$ is a solution of the following integro-differential system:

$$\begin{cases} d\ddot{U}(\xi) - c\dot{U}(\xi) + U(\xi)(1-(G*U)(\xi)) - \dfrac{AU(\xi)V(\xi)}{U(\xi)+aV(\xi)} = 0, \\ \ddot{V}(\xi) - c\dot{V}(\xi) + BV(\xi)\left(1 - \dfrac{V(\xi)}{U(\xi)}\right) = 0. \end{cases} \tag{4.1}$$

We only consider in detail the case that the distribution kernel is a strong one, that is, $G(t) = \dfrac{t}{\tau^2}e^{-\frac{t}{\tau}}$.

Define

$$\begin{aligned} Y(\xi) &= (G*U)(\xi) = \int_0^{+\infty} \frac{t}{\tau^2}e^{-\frac{t}{\tau}}U(\xi-ct)dt, \\ Z(\xi) &= \int_0^{+\infty} \frac{1}{\tau}e^{-\frac{t}{\tau}}U(\xi-ct)dt. \end{aligned} \tag{4.2}$$

Differentiating Y, Z with respect to ξ and further denoting

$$\dot{U} = W, \ \ \dot{V} = X, \tag{4.3}$$

we obtain from (4.1) and (4.2):

$$\begin{cases} \dot{U}(\xi) = W(\xi), \\ \dot{W}(\xi) = \dfrac{c}{d}W(\xi) - \dfrac{U(\xi)(1-Y(\xi))}{d} + \dfrac{AU(\xi)V(\xi)}{d(U(\xi)+aV(\xi))}, \\ \dot{V}(\xi) = X(\xi), \\ \dot{X}(\xi) = cX(\xi) - BV(\xi)\left(1 - \dfrac{V(\xi)}{U(\xi)}\right), \\ c\tau\dot{Y}(\xi) = Z(\xi) - Y(\xi), \\ c\tau\dot{Z}(\xi) = U(\xi) - Z(\xi). \end{cases} \tag{4.4}$$

Or equivalently, we make a coordinate change $\delta = \xi/\tau$, and obtain that

$$\begin{cases} U' = \tau W, \\ W' = \tau\left(\dfrac{c}{d}W - \dfrac{U(1-Y)}{d} + \dfrac{AUV}{d(U+aV)}\right), \\ V' = \tau X, \\ X' = \tau\left(cX - BV\left(1 - \dfrac{V}{U}\right)\right), \\ cY' = Z - Y, \\ cZ' = U - Z, \end{cases} \tag{4.5}$$

where $'$ denotes the derivative in δ. When $\tau > 0$, the slow ODE system (4.4) and the fast ODE system (4.5) are equivalent and have the same equilibria $E_1(1,0,0,0,1,1)$ and $E_2(u^*, 0, u^*, 0, u^*, u^*)$.

Next we prove the existence of a heteroclinic orbit connecting E_1 and E_2 for sufficiently small $\tau > 0$. Notice that when $\tau \to 0$, the slow system (4.4) is reduced into a limit system (3.4). On the other hand, when $\tau \to 0$, the fast system (4.5) has the limit form:

$$\begin{cases} U' = 0, \\ W' = 0, \\ V' = 0, \\ X' = 0, \\ Y' = \dfrac{Z}{c} - \dfrac{Y}{c}, \\ Z' = \dfrac{U}{c} - \dfrac{Z}{c}. \end{cases} \tag{4.6}$$

The set $M(0) = \{(U, W, V, X, Y, Z) \in \mathbb{R}^6 : Y = Z \text{ and } Z = U\}$ is a four-dimensional invariant manifold of (4.6). The linearization of (4.6) at any point in M_0 has a zero eigenvalue with multiplicity 4 and two negative eigenvalues $\lambda = -1/c$. From Fenichel's First Theorem [14], $M(0)$ is a normally hyperbolic invariant manifold. By the geometric singular perturbation theory [14, 30], we know that there exists an invariant set $M(\tau)$ for (4.4) with $\tau > 0$ small enough, defined by

$$\begin{aligned} M(\tau) = \{(U, W, V, X, Y, Z) \in \mathbb{R}^6 : Y = Z + g(U, W, V, X, \tau) \\ \text{and } Z = U + h(U, W, V, X, \tau)\}, \end{aligned} \tag{4.7}$$

where $g,\ h$ will be determined later and satisfy

$$g(U, W, V, X, 0) = h(U, W, V, X, 0) = 0.$$

Substituting (4.7) into the (4.4) induces

$$\begin{aligned} &c\tau \left(\dot{U} \left(1 + \frac{\partial g}{\partial U} + \frac{\partial h}{\partial U} \right) + \dot{W} \left(\frac{\partial g}{\partial W} + \frac{\partial h}{\partial W} \right) \right. \\ &\left. + \dot{V} \left(\frac{\partial g}{\partial V} + \frac{\partial h}{\partial V} \right) + \dot{X} \left(\frac{\partial g}{\partial X} + \frac{\partial h}{\partial X} \right) \right) = -g, \\ &c\tau \left(\dot{U} \left(1 + \frac{\partial h}{\partial U} \right) + \dot{W} \frac{\partial h}{\partial W} + \dot{V} \frac{\partial h}{\partial V} + \dot{X} \frac{\partial h}{\partial X} \right) = -h. \end{aligned}$$

We write the Taylor expansion of g, h on τ as follows:

$$\begin{aligned} g(U, W, V, X, \tau) &= \tau g_1(U, W, V, X) + \tau^2 g_2(U, W, V, X) + O(\tau^3), \\ h(U, W, V, X, \tau) &= \tau h_1(U, W, V, X) + \tau^2 h_2(U, W, V, X) + O(\tau^3). \end{aligned}$$

Comparing the coefficients of τ leads to the results:

$$\begin{aligned} &g_1(U, W, V, X) = h_1(U, W, V, X) = -cW, \\ &g_2(U, W, V, X) = 2c^2 \left(\frac{c}{d} W - \frac{U(1-U)}{d} + \frac{AUV}{d(U + aV)} \right) = 2h_2(U, W, V, X). \end{aligned} \tag{4.8}$$

Hence the slow system (4.4) is reduced into an equivalent system:

$$\begin{cases} \dot{U} = W, \\ \dot{W} = \dfrac{c}{d} W - \dfrac{U(1-U)}{d} + \dfrac{AUV}{d(U + aV)} + \dfrac{U}{d}(\tau(h_1 + g_1) + \tau^2(h_2 + g_2)), \\ \dot{V} = X, \\ \dot{X} = cX - BV \left(1 - \dfrac{V}{U} \right), \end{cases} \tag{4.9}$$

where g_1, g_2, h_1, h_2 are defined by (4.8). It is easy to check when $\tau > 0$, the system (4.9) still has critical points $E_1(1, 0, 0, 0)$ and $E_2 = (u^*, 0, u^*, 0)$. In Sections 2 and 3, we have shown that, the system (1.2) $(\tau = 0)$ has a heteroclinic orbit connecting between E_1 and E_2 for $c \geq c^* = 2\sqrt{B}$ if **(H2)** holds, and has a small amplitude periodic traveling wave train at $d = d(c)$ if **(H1)**, and **(H3)** or **(H3')** hold. Then by the geometric singular perturbation theory, there is a sufficiently small $\tau_0 > 0$ such that for each $0 < \tau < \tau_0$, these orbits persist as solutions of the full system (4.9).

For the weak kernel $G(t) = \frac{1}{\tau}e^{-t/\tau}$, define

$$Y(\xi) = (G * U)(\xi) = \int_0^{+\infty} \frac{1}{\tau}e^{-t/\tau}U(\xi - ct)dt.$$

Then combining (4.1) and (4.3), we obtain the four-dimensional slow system

$$\begin{cases} \dot{U}(\xi) = W(\xi), \\ \dot{W}(\xi) = \dfrac{c}{d}W(\xi) - \dfrac{U(\xi)(1 - Y(\xi))}{d} + \dfrac{AU(\xi)V(\xi)}{d(U(\xi) + aV(\xi))}, \\ \dot{V}(\xi) = X(\xi), \\ \dot{X}(\xi) = cX(\xi) - BV(\xi)\left(1 - \dfrac{V(\xi)}{U(\xi)}\right), \\ c\tau\dot{Y}(\xi) = U(\xi) - Y(\xi). \end{cases}$$

The proof is similar to the one for the strong kernel thus we omit it here. This completes the proof of Theorem 1.3.

5. **Numerical simulations.**

We present some numerical simulations to illustrate our main results in Sections 2 and 4. We choose parameters $d = 0.1,\ a = 1,\ A = 0.4,\ B = 0.01$ such that the condition **(H2)** holds. Then the system (1.2) admits a boundary equilibrium $E_1(1, 0)$ and a positive equilibrium $E_2(0.8, 0.8)$. In order to perform numerical simulation of (1.2), we truncate the infinite domain $\mathbb{R}$ to finite domain $[-L, L]$, where L is sufficiently large, and we use a homogeneous Neumann boundary condition at both ends and we choose an initial condition close to a wave profile. The corresponding solution profiles of the initial value problem (1.2) for $t = 40$, $t = 80$ and $t = 120$ are given in Figure 2. Note that the solution exhibits a traveling wave profile which moves at a constant speed close to $2\sqrt{B}$.

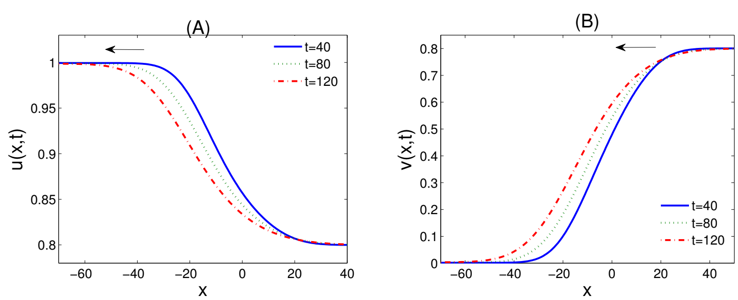

FIGURE 2. Wave profiles for prey (A) and predator (B) of the traveling wave solutions of (1.2) with $d = 0.1,\ a = 1,\ A = 0.4,\ B = 0.01$.

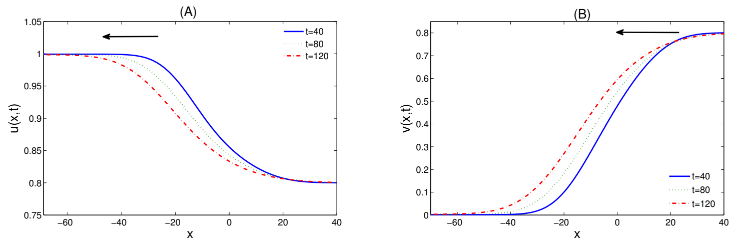

FIGURE 3. Wave profiles for prey (A) and predator (B) of the traveling wave solutions of (1.1) with $d = 0.1,\ a = 1,\ A = 0.4,\ B = 0.01$ and $\tau = 1$.

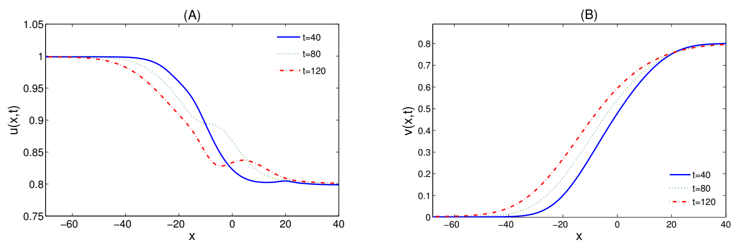

FIGURE 4. Wave profiles for prey (A) and predator (B) of the traveling wave solutions of (1.1) with $d = 0.1,\ a = 1,\ A = 0.4,\ B = 0.01$ and $\tau = 1.5$.

To carry out numerical simulation for the system with distributed delay Eq.(1.1) with the strong kernel $G(t) = \dfrac{t}{\tau^2} e^{-\frac{t}{\tau}}$, we define

$$X(x,t) = (G * u)(x,t) = \int_{-\infty}^{t} \frac{t-s}{\tau^2} e^{-\frac{t-s}{\tau}} u(x,s)ds,$$
$$Y(x,t) = \int_{-\infty}^{t} \frac{1}{\tau} e^{-\frac{t-s}{\tau}} u(x,s)ds.$$

Then Eq.(1.1) can be recast as a system of four reaction-diffusion equations without delay:

$$\begin{cases} u_t(x,t) = du_{xx} + u(x,t)(1 - X(x,t)) - \dfrac{Au(x,t)v(x,t)}{u(x,t) + av(x,t)}, \\ X_t(x,t) = \dfrac{1}{\tau}(Y(x,t) - X(x,t)), \\ Y_t(x,t) = \dfrac{1}{\tau}(u(x,t) - Y(x,t)), \\ v_t(x,t) = v_{xx}(x,t) + Bv(x,t)\left(1 - \dfrac{v(x,t)}{u(x,t)}\right). \end{cases} \tag{5.1}$$

We simulate the solution of (5.1) (which is equivalent to that of (1.1)) by carefully choosing the initial conditions. Figure 3 shows the wave profile of the traveling wave solutions for the distributed delay model (1.1) with the strong kernel and $\tau = 1$. Both Figures 2 and 3 show that the spreading speed $c \approx 0.2 = 2\sqrt{B}$, and in both cases the traveling wave solutions appear to be monotone in ξ. Note that our existence results do not guarantee the monotonicity of the wave solutions. However when τ increases to 1.5, Figure 4 shows that the wave profile does not persist, so the system (1.1) may not have a stable traveling wave solution with larger τ.

6. Conclusion.

In this paper, we study the spatiotemporal patterns of a reaction-diffusion predator-prey system with ratio-dependent Holling-Tanner type interaction and a distributed delay in the prey species growth. We rigorously prove the existence of traveling wave and traveling wave train solutions for both the non-delay system (1.2) and also the delayed case (1.1) with a small mean delay. We apply mathematical tools of upper-lower solution method, Hopf bifurcation theorem and geometric singular perturbation methods to achieve our results. Note that the first two methods can be applied to many other similar models of spatiotemporal resource-consumer type models arising from biological, chemical and physical models, while the geometric singular perturbation methods can only be applied to the models with weak or strong type distribution kernels. The existence of these types of solutions for (1.1) with other distribution kernels and/or larger mean delays remain as interesting open questions. Another challenging mathematical question is the stability of traveling wave and traveling wave train solutions obtained here.

The rigorous mathematical results proved here have profound biological meaning. The existence of traveling wave solutions with specific wave speeds for a realistic predator-prey model provides theoretical basis for the biological invasion of predator species. Numerical simulations show that the spreading speed is exactly the minimal speed of the traveling wave solutions. Note that for monotone systems such as diffusive cooperative or two-species competition systems, there have been algorithms for determining the spreading speeds, but these methods cannot be applied to predator-prey systems.

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