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ASYMPTOTICAL BEHAVIORS OF A DIFFUSIVE PREDATOR-PREY SYSTEM WITH RATIO-DEPENDENT FUNCTIONAL RESPONSE AND MATURATION DELAY

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Abstract. In this paper, we consider a delayed ratio-dependent predator-prey reaction-diffusion system with homogenous Neumann boundary conditions. We study the existence of nonnegative solutions and the stability of the nonnegative equilibria to the system. In particular, we provide a sufficient condition for the positive equilibrium to be globally asymptotically stable.

1. Introduction

In this paper, we deal with the following predator-prey reaction-diffusion system with a ratio-dependent functional response and time delay effect:

$$(1.1)\quad \begin{cases} \dfrac{\partial u(x,t)}{\partial t} = \Delta u(x,t) + u(x,t)(1-u(x,t)) \\ \qquad\qquad -\dfrac{\alpha u(x,t)v(x,t)}{u(x,t)+v(x,t)} \quad \text{in } \Omega\times(0,\infty), \\ \dfrac{\partial v(x,t)}{\partial t} = \rho\Delta v(x,t) + \dfrac{\beta u(x,t-\tau)v(x,t-\tau)}{u(x,t-\tau)+v(x,t-\tau)} \\ \qquad\qquad -dv(x,t) \quad \text{in } \Omega\times(0,\infty), \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0 \quad \text{on } \partial\Omega\times(0,\infty), \\ u(x,\theta) = u_0(x) \geq 0, \quad v(x,\theta) = v_0(x) \geq 0 \quad \text{in } \Omega\times[-\tau,0], \end{cases}$$

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where $\Omega \subseteq \mathbb{R}^N$ is a bounded domain with a smooth boundary $\partial\Omega$, the given coefficients α, β, ρ and d are positive constants, τ is a nonnegative constant, ν is the outward directional derivative normal to $\partial\Omega$, and the initial data u_0, v_0 are continuous functions that are not identically zero. Moreover, $u(x,t)$ and $v(x,t)$ are the population densities of the prey and predators in spatial location x and at time t, respectively, and ρ denotes the diffusion rate of the predator species. In addition, α is the consumption (or predation) rate of the prey by the predators, β represents the conversion rate of the prey into a predator, d denotes the predator's death rate, and τ represents the time-delay effect for predators.

Based on the biological background given in [2, 4, 5, 6], we are able to propose the following diffusive stage-structured predator-prey model with a ratio-dependent function response (e.g., see [6]):

(1.2)

$$
\begin{cases}
\dfrac{\partial u(x,t)}{\partial t} = d_1\Delta u(x,t) + ru(x,t)\left(1 - \dfrac{u(x,t)}{K}\right) \\
\qquad\qquad - \dfrac{\alpha u(x,t)v(x,t)}{u(x,t)+mv(x,t)} & \text{in } \Omega \times (0,\infty), \\
\dfrac{\partial v(x,t)}{\partial t} = d_2\Delta v(x,t) + \beta e^{-\gamma\tau}\dfrac{\alpha u(x,t-\tau)v(x,t-\tau)}{u(x,t-\tau)+mv(x,t-\tau)} \\
\qquad\qquad - dv(x,t) & \text{in } \Omega \times (0,\infty), \\
\dfrac{\partial w(x,t)}{\partial t} = \beta\dfrac{\alpha u(x,t)v(x,t)}{u(x,t)+mv(x,t)} - \beta e^{-\gamma\tau}\dfrac{\alpha u(x,t-\tau)v(x,t-\tau)}{u(x,t-\tau)+mv(x,t-\tau)} \\
\qquad\qquad - \gamma w(x,t) & \text{in } \Omega \times (0,\infty), \\
\dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = \dfrac{\partial w}{\partial \nu} = 0, & \text{on } \partial\Omega \times (0,\infty), \\
u(x,\theta) = u_0(x) \geq 0, \quad v(x,\theta) = v_0(x) \geq 0 & \text{in } \Omega \times [-\tau, 0], \\
w(x,0) = \displaystyle\int_{-\tau}^{0} \beta e^{\gamma s}\dfrac{\alpha u(x,s)v(x,s)}{u(x,s)+mv(x,s)}\,\mathrm{d}s & \text{in } \Omega,
\end{cases}
$$

where $u(x,t)$, $v(x,t)$ and $w(x,t)$ represent the density of the prey, mature predators and immature predators, respectively. The given coefficients d_1, d_2, r, K, α, β, m, d, γ are positive constants and τ is the nonnegative constant. These coefficients given in (1.2) have appropriate biological meanings as in [2, 4, 5, 6] since (1.2) is designed to account for a robust predator-prey interaction system with stage structure with constant maturation time delay (through-stage time delay). One important feature of this model is that immature (juvenile) predators suffer a mortality rate of γ and take a constant τ time to mature, and another is that the per capita predator growth rate depends on the ratio of prey to predator abundance (so-called the ratio-dependent functional response [1, 4]).

For convenience, when studying the above system, after introducing a new typical length scale and the following dimensionless quantities and then dropping the upper bars:

$$\bar{t} = rt,\ \bar{x} = \sqrt{\frac{d_1}{r}}x,\ \bar{u} = \frac{u}{K},\ \bar{v} = \frac{m}{K}v,\ \bar{w} = \frac{m}{K}w,\ \bar{\alpha} = \frac{\alpha}{rm},$$

$$\bar{\beta} = \frac{\alpha}{r}e^{-\gamma\tau}\beta,\ \bar{\gamma} = \frac{\gamma}{r},\ \bar{\tau} = r\tau,\ \bar{s} = rs,\ \bar{d} = \frac{d}{r},\ \rho = \frac{d_2}{d_1},$$

then we can eventually obtain the dimensionless form:

(1.3)
$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} = \Delta u(x,t) + u(x,t)\,(1 - u(x,t)) & \\ \qquad\qquad -\dfrac{\alpha u(x,t)v(x,t)}{u(x,t)+v(x,t)} & \text{in } \Omega \times (0,\infty), \\ \dfrac{\partial v(x,t)}{\partial t} = \rho\Delta v(x,t) + \dfrac{\beta u(x,t-\tau)v(x,t-\tau)}{u(x,t-\tau)+v(x,t-\tau)} & \\ \qquad\qquad -dv(x,t) & \text{in } \Omega \times (0,\infty), \\ \dfrac{\partial w(x,t)}{\partial t} = e^{\gamma\tau}\dfrac{\beta u(x,t)v(x,t)}{u(x,t)+v(x,t)} - \dfrac{\beta u(x,t-\tau)v(x,t-\tau)}{u(x,t-\tau)+mv(x,t-\tau)} & \\ \qquad\qquad -\gamma w(x,t) & \text{in } \Omega \times (0,\infty), \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = \dfrac{\partial w}{\partial \nu} = 0, & \text{on } \partial\Omega \times (0,\infty), \\ u(x,\theta) = u_0(x) \geq 0, \quad v(x,\theta) = v_0(x) \geq 0 & \text{in } \Omega \times [-\tau, 0], \\ w(x,0) = \displaystyle\int_{-\tau}^{0} e^{\gamma(s+\tau)}\frac{\beta u(x,s)v(x,s)}{u(x,s)+v(x,s)}\,\mathrm{d}s & \text{in } \Omega. \end{cases}$$

We see that the first two differential equations in system (1.3) are decoupled from the immature predators. Moreover, from the third differential equation in system (1.3), we have

$$\begin{aligned} w(x,t) &= \int_{t-\tau}^{t} e^{\gamma\tau}e^{-\gamma(t-s)}\frac{\beta u(x,s)v(x,s)}{u(x,s)+v(x,s)}\,\mathrm{d}s \\ &= \int_{0}^{\tau} e^{\gamma(\tau-s)}\frac{\beta u(x,t-s)v(x,t-s)}{u(x,t-s)+v(x,t-s)}\,\mathrm{d}s \ \text{ in } \Omega. \end{aligned}$$

Thus, the dynamics of system (1.3) is entirely determined by its first two equations. Therefore, we study system (1.1) which is a subsystem of (1.3).

In this present paper, we study the global existence of nonnegative solutions to system (1.1) using the upper-lower solution method [7]. We also investigate whether the nonnegative solutions of the system satisfy the uniform boundedness and persistence properties. We finally provide sufficient conditions for local and global stability of the semitrivial and positive equilibria to the system. To the end, we analyze the characteristic equations, and we use the comparison argument and monotone iteration scheme.

The remainder of this paper is organized as follows. In Section 2, we summarize the main results on the existence of nonnegative solutions to system (1.1), the uniform boundedness and persistence of the solutions, and the local/global stability of nonnegative equilibria of the system. In Section 3, we provide proofs for these results.

2. Main theorems

In this section, without giving proofs, we just state our main results: the existence of nonnegative solutions to system (1.1), and the stability of the prey-only and coexistence equilibria of (1.1).

THEOREM 2.1. *System (1.1) has a unique global nonnegative solution* $(u(x,t), v(x,t))$ *in* $[C(\overline{\Omega} \times [0,\infty))]^2$.

We study the boundedness and persistence of the solution to (1.1).

THEOREM 2.2. *Let* $(u(x,t), v(x,t))$ *be the nonnegative solution to (1.1). Then*

(i)

$$\limsup_{t\to\infty} u(x,t) \le 1 \ \ \text{and} \ \ \limsup_{t\to\infty} v(x,t) \le \frac{\beta}{d} \ \ \text{on } \overline{\Omega}.$$

(ii) If $\alpha < 1$,

$$\liminf_{t\to\infty} u(x,t) \ge 1-\alpha \ \ \text{and} \ \ \liminf_{t\to\infty} v(x,t) \ge \frac{\beta}{d}(1-\alpha) \ \ \text{on } \overline{\Omega}.$$

The following is a simple result of the global stability at $(1,0)$.

THEOREM 2.3. *Let* $(u(x,t), v(x,t))$ *be the nonnegative solution to (1.1). If* $\alpha < 1$ *and* $\beta \le d$,

$$\lim_{t\to\infty} (u(x,t), v(x,t)) = (1,0) \ \ \text{on } \overline{\Omega}.$$

In the following, we study the ranges of α in which system (1.1) has a unique positive equilibrium which is globally asymptotically stable.

THEOREM 2.4. *If $\beta > d$ and $\alpha < \frac{\beta}{\beta-d}$, then (1.1) has a unique positive constant solution*

$$(u_*, v_*) = \left(1 - \alpha\frac{\beta - d}{\beta}, \frac{\beta - d}{d}u_*\right).$$

In addition, if $\alpha < \frac{\beta^2}{\beta^2+d(\beta-d)}$, then (u_*, v_*) is globally asymptotically stable.

Finally, we study the local stability at $(1, 0)$ and (u_*, v_*).

THEOREM 2.5. *(i) If $\beta < d$, then $(1, 0)$ is locally asymptotically stable.*
(ii) If $\beta > d$ and $\alpha \leq \frac{\beta(\beta+d)}{(\beta-d)(\beta+3d)}$, then (u_*, v_*) is locally asymptotically stable.

3. Proofs of main theorems

In this section, we prove the main results given in the previous section.

Proof of Theorem 2.1. The right-hand sides of the differential equations in (1.1) satisfy the mixed quasi-monotone property and Lipschitz condition (see [7]) in $(\mathbb{R}^+)^2 = [0, \infty)^2$. Let

$$(\underline{u}, \underline{v}) = (0, 0) \quad \text{and}$$

$$(\overline{u}, \overline{v}) = \left(\max\{||u_0||_\infty, 1\}, \max\left\{\frac{\beta}{d}\overline{u}, ||v_0||_\infty\right\}\right).$$

Then we see that $(\underline{u}, \underline{v})$ and $(\overline{u}, \overline{v})$ are the lower and upper solution (see [7]) to (1.1), respectively. Thus from the upper-lower solution method [7, Chap. 8] (see also [8, Theorem 2.1]), (1.1) has a unique globally defined solution (u, v) in $[C(\overline{\Omega} \times [0, \infty))]^2$. □

Proof of Theorem 2.2 (i). From the first equation in (1.1), we know that

$$\frac{\partial u(x, t)}{\partial t} \leq \Delta u(x, t) + u(x, t)(1 - u(x, t)) \quad \text{in } \Omega \times (0, \infty).$$

Thus, from the standard comparison argument, we obtain the boundedness of u.

According to the first result, there exists $T > 0$ such that

$$u(x, t) \leq 1 + \epsilon \quad \text{in } \overline{\Omega} \times [T, \infty),$$

where $\epsilon > 0$ is an arbitrary constant. Using it in the second equation of (1.1), we can derive that

$$\frac{\partial v(x,t)}{\partial t} \leq \rho \Delta v(x,t) + \beta(1+\epsilon) - dv(x,t) \quad \text{in } \overline{\Omega} \times [T+\tau, \infty).$$

Hence, the comparison argument and arbitrariness of ϵ give the second result. □

We now introduce the following result from [6, Lemma 4.3], which plays an important role in studying the stability of the constant steady-states to (1.1).

LEMMA 3.1. *Let $v(x,t)$ be the nonnegative solution to the delayed differential equation*

(3.1)
$$\begin{cases} \dfrac{\partial v(x,t)}{\partial t} = \rho \Delta v(x,t) + \dfrac{\beta M v(x,t-\tau)}{M + v(x,t-\tau)} - dv(x,t) & \text{in } \Omega \times (0,\infty), \\ \dfrac{\partial v}{\partial \nu} = 0 & \text{on } \partial\Omega \times (0,\infty), \\ v(x,\theta) = \phi(x,\theta) & \text{in } \Omega \times [-\tau, 0], \end{cases}$$

where M is a positive constant and $\phi \geq 0 (\not\equiv 0)$ is a continuous function in $\Omega \times [-\tau, 0]$.

(i) If $\beta > d$,

$$\lim_{t\to\infty} v(x,t) = \left(\frac{\beta}{d} - 1\right) M \quad \text{on } \overline{\Omega}.$$

(ii) If $\beta \leq d$, then

$$\lim_{t\to\infty} v(x,t) = 0 \quad \text{on } \overline{\Omega}.$$

Proof of Theorem 2.2 (ii). From the first equation in (1.1), we can derive that

$$\frac{\partial u(x,t)}{\partial t} \geq \Delta u(x,t) + u(x,t)(1 - \alpha - u(x,t)) \quad \text{in } \Omega \times (0,\infty).$$

Thus, from the standard comparison argument, we obtain the desired first result.

Using the result obtained above in the second equation of (1.1), we see that there exists $T > 0$ such that

$$\frac{\partial v(x,t)}{\partial t} \geq \rho \Delta v(x,t) + \frac{\beta(1-\alpha-\epsilon) v(x,t-\tau)}{1-\alpha-\epsilon+v(x,t-\tau)} - dv(x,t)$$

in $\Omega \times (T+\tau, \infty)$, where ϵ is an arbitrary positive constant. Thus, from the standard comparison argument,

$$v(x,t) \geq \widehat{v}(x,t) \quad \text{in } \Omega \times (T+\tau, \infty), \tag{3.2}$$

where $\widehat{v}(x,t)$ is the nonnegative solution to problem (3.1) with $M = 1-\alpha-\epsilon$ and $\phi(x,\theta) = v(x,\theta)$ in $\Omega \times [T, T+\tau]$. Moreover, by Lemma 3.1,

$$\lim_{t\to\infty} \widehat{v}(x,t) = \left(\frac{\beta}{d} - 1\right)(1-\alpha-\epsilon) \ \text{ on } \overline{\Omega}.$$

Hence, this and the arbitrariness of ϵ, together with (3.2), implies the second desired result. $\square$

Proof of Theorem 2.3. Let ϵ be an arbitrary positive constant. According to the first result in Theorem 2.2(i), there exists $T_1 > 0$ such that $u(x,t) \leq 1+\epsilon$ in $\Omega \times (T_1, \infty)$. Thus, using it, we derive that

$$\frac{\partial v(x,t)}{\partial t} \leq \rho \Delta v(x,t) + \frac{\beta(1+\epsilon)v(x,t-\tau)}{1+\epsilon+v(x,t-\tau)} - dv(x,t)$$

in $\Omega \times (T_1+\tau, \infty)$. Thus, from the standard comparison argument,

$$v(x,t) \leq \widetilde{v}(x,t) \quad \text{in } \Omega \times (T_1+\tau, \infty),$$

where $\widetilde{v}(x,t)$ is the nonnegative solution to problem (3.1) with $M = 1+\epsilon$ and $\phi(x,\theta) = v(x,\theta)$ in $\Omega \times [T_1, T_1+\tau]$, and furthermore it follows from Lemma 3.1 that $\lim_{t\to\infty} \widehat{v}(x,t) = 0$ holds on $\overline{\Omega}$. Hence, similar to the proof of the previous theorem, we can obtain that $\lim_{t\to\infty} v(x,t) = 0$ on $\overline{\Omega}$.

From the result obtained above and Theorem 2.2(ii), we see that exists $T_2 \geq T_1 + \tau$ such that $v(x,t) \leq \epsilon$ and $u(x,t) \geq 1-\alpha-\epsilon$ in $\Omega \times (T_2, \infty)$. Using it in the first equation in (1.1), we can have

$$\frac{\partial u(x,t)}{\partial t} \geq \Delta u(x,t) + u(x,t)\left(1 - \frac{\epsilon}{1-\alpha-\epsilon} - u(x,t)\right) \ \text{ in } \Omega \times (T_2, \infty).$$

Hence, by the comparison argument and arbitrariness of ϵ, we have $\liminf_{t\to\infty} u(x,t) \geq 1$ on $\overline{\Omega}$, which, together with the first result in Theorem 2.2(i), imply $\lim_{t\to\infty} u(x,t) = 1$ on $\overline{\Omega}$. $\square$

Proof of Theorem 2.4. When the given assumptions hold ture, we can easily see that (1.1) has the positive equilibrium (u_*, v_*).

Let $\epsilon > 0$ be a sufficiently small constant. First, since $\alpha < 1$ and $\beta > d$, as in the proofs of the previous theorems, we can have from the comparison argument and Lemma 3.1 that there exists $T_1 > 0$ such that

$$1-\alpha-\epsilon := \underline{u}_1 \le u(x,t) \le \overline{u}_1 := 1+\epsilon,$$
$$\left(\frac{\beta}{d}-1\right)\underline{u}_1-\epsilon := \underline{v}_1 \le v(x,t) \le \overline{v}_1 := \left(\frac{\beta}{d}-1\right)\overline{u}_1+\epsilon$$

in $\Omega \times (T_1+\tau,\infty)$. Using these results in the first equation of (1.1),

$$\frac{\partial u(x,t)}{\partial t} \le \Delta u(x,t) + u(x,t)\left(1-\frac{\alpha \underline{v}_1}{\overline{u}_1+\underline{v}_1}-u(x,t)\right),$$
$$\frac{\partial u(x,t)}{\partial t} \ge \Delta u(x,t) + u(x,t)\left(1-\frac{\alpha \overline{v}_1}{\underline{u}_1+\overline{v}_1}-u(x,t)\right)$$

in $\Omega \times (T_1+\tau,\infty)$. Thus, from the comparison argument and Lemma 3.1, we see that there exists $T_2 \ge T_1+\tau$ such that

$$1-\frac{\alpha\overline{v}_1}{\underline{u}_1+\overline{v}_1}-\epsilon := \underline{u}_2 \le u(x,t) \le \overline{u}_2 := 1-\frac{\alpha\underline{v}_1}{\overline{u}_1+\underline{v}_1}+\epsilon$$

in $\Omega \times (T_2,\infty)$. Using this derived result in the second equation of (1.1), we sequentially obtain that

$$\frac{\partial v(x,t)}{\partial t} \le \rho\Delta v(x,t) + \frac{\beta\overline{u}_2 v(x,t-\tau)}{\overline{u}_2+v(x,t-\tau)} - dv(x,t),$$
$$\frac{\partial v(x,t)}{\partial t} \ge \rho\Delta v(x,t) + \frac{\beta\underline{u}_2 v(x,t-\tau)}{\underline{u}_2+v(x,t-\tau)} - dv(x,t),$$

in $\Omega \times (T_2,\infty)$. Thus, using the comparison argument and Lemma 3.1 again, we can derive that there exists $T_3 \ge T_2$ such that

$$\left(\frac{\beta}{d}-1\right)\underline{u}_2-\epsilon := \underline{v}_2 \le v(x,t) \le \overline{v}_2 := \left(\frac{\beta}{d}-1\right)\overline{u}_2+\epsilon$$

in $\Omega \times (T_2,\infty)$. Furthermore, it is obvious from the definitions of u_*, v_*, $\underline{u}_i$, $\underline{v}_i$, $\overline{u}_i$ and $\overline{v}_i$ $(i=1,2)$ that

$$\underline{u}_1 \le \underline{u}_2 \le u_* \le \overline{u}_2 \le \overline{u}_1, \quad \underline{v}_1 \le \underline{v}_2 \le v_* \le \overline{v}_2 \le \overline{v}_1.$$

Now, repeating the above arguments with $\underline{u}_2 \le u(x,t) \le \overline{u}_2$ and $\underline{v}_2 \le v(x,t) \le \overline{v}_2$ in $\Omega \times (T_2,\infty)$, we can eventually obtain that

$$\begin{aligned} &\underline{u}_1 \le \underline{u}_2 \le \cdots \le \underline{u}_n \le \cdots \le u_* \le \cdots \le \overline{u}_n \le \cdots \le \overline{u}_2 \le \overline{u}_1, \\ &\underline{v}_1 \le \underline{v}_2 \le \cdots \le \underline{v}_n \le \cdots \le v_* \le \cdots \le \overline{v}_n \le \cdots \le \overline{v}_2 \le \overline{v}_1, \end{aligned} \tag{3.3}$$

where

$$\underline{u}_n = 1-\frac{\alpha\overline{v}_{n-1}}{\underline{u}_{n-1}+\overline{v}_{n-1}}-\epsilon, \quad \overline{u}_n = 1-\frac{\alpha\underline{v}_{n-1}}{\overline{u}_{n-1}+\underline{v}_{n-1}}+\epsilon,$$

$$\overline{v}_n = \left(\frac{\beta}{d} - 1\right)\overline{u}_n + \epsilon, \quad \underline{v}_n = \left(\frac{\beta}{d} - 1\right)\underline{u}_n - \epsilon.$$

Since the constant sequences $\{\overline{u}_n\}$, $\{\overline{v}_n\}$, $\{\underline{u}_n\}$ and $\{\underline{v}_n\}$ satisfy (3.3), the limits of these sequences exist. Denote

$$\lim_{n\to\infty} \overline{u}_n = \overline{u}, \quad \lim_{n\to\infty} \underline{u}_n = \underline{u}, \quad \lim_{n\to\infty} \overline{v}_n = \overline{v}, \quad \lim_{n\to\infty} \underline{v}_n = \underline{v}.$$

To complete the proof, we are going to prove that $\overline{u} = \underline{u}$ and $\overline{v} = \underline{v}$. Suppose for a contradiction that $\overline{u} > \underline{u}$. By using the definitions of $\overline{u}_n$, $\underline{u}_n$, $\overline{v}_n$ and $\underline{v}_n$, and by letting $n \to \infty$, we can see that

$$\begin{aligned} &\underline{u} = 1 - \frac{\alpha\overline{v}}{\underline{u}+\overline{v}} - \epsilon, \quad \overline{u} = 1 - \frac{\alpha\underline{v}}{\overline{u}+\underline{v}} + \epsilon, \\ &\overline{v} = \left(\frac{\beta}{d} - 1\right)\overline{u} + \epsilon, \quad \underline{v} = \left(\frac{\beta}{d} - 1\right)\underline{u} - \epsilon, \end{aligned} \tag{3.4}$$

which lead to

(3.5)
$$(1-\underline{u})(\underline{u} + (\frac{\beta}{d}-1)\overline{u}) - \alpha(\frac{\beta}{d}-1)\overline{u} = \epsilon(\alpha - 1 + 2\underline{u} + (\frac{\beta}{d}-1)\overline{u} + \epsilon),$$

(3.6)
$$(1-\overline{u})(\overline{u} + (\frac{\beta}{d}-1)\underline{u}) - \alpha(\frac{\beta}{d}-1)\underline{u} = \epsilon(-\alpha + 1 - 2\overline{u} - (\frac{\beta}{d}-1)\underline{u} + \epsilon).$$

By subtracting (3.6) from (3.5), we have

$$\begin{aligned} &(\overline{u} - \underline{u})\left(-1 + (1-\alpha)(\frac{\beta}{d}-1) + \overline{u} + \underline{u}\right) \\ &\quad = \epsilon\left(-2(1-\alpha) + (\frac{\beta}{d}+1)(\overline{u}+\underline{u})\right). \end{aligned} \tag{3.7}$$

It is obvious that

$$-2(1-\alpha) + (\frac{\beta}{d}+1)(\overline{u}+\underline{u}) \geq -2(1-\alpha) + 4(1-\alpha-\epsilon) > 0 \tag{3.8}$$

for a sufficiently small $\epsilon > 0$, since $\overline{u}$, $\underline{u} \geq 1-\alpha-\epsilon$, and $\beta > d$. Moreover, using the given assumption and the fact that $\overline{u} \geq u_*$ and $\underline{u} \geq 1-\alpha-\epsilon$, we know that

$$\begin{aligned} &-1 + (1-\alpha)(\frac{\beta}{d}-1) + \overline{u} + \underline{u} \\ &\geq -1 + (1-\alpha)(\frac{\beta}{d}-1) + u_* + 1 - \alpha - \epsilon \\ &= \frac{\beta^2 + d(\beta-d)}{\beta d}\left(\frac{\beta^2}{\beta^2+d(\beta-d)} - \alpha\right) - \epsilon > 0 \end{aligned} \tag{3.9}$$

holds for a sufficiently small $\epsilon > 0$. Using (3.8) and (3.9) in (3.7), and noting that $\epsilon > 0$ can be arbitrarily small, we have $\overline{u} = \underline{u}$. Sequentially, $\overline{v} = \underline{v}$ follows from (3.4). The proof is completed. □

We now prove the local stability of the constant equilibria $(1, 0)$ and (u_*, v_*) (if it exists).

We let

$$0 = \mu_0 < \mu_1 \leq \mu_2 \leq \cdots \leq \mu_k \leq \mu_{k+1} \cdots$$

be the eigenvalues of $-\Delta$ in Ω under the homogeneous Neumann boundary condition on $\partial\Omega$.

When $\mathbf{u_0} = (u_0, v_0)$ is a nonnegative constant solution of (1.1), the linearization of (1.1) at $\mathbf{u_0}$ can be written as follows:

$$\begin{pmatrix} \dfrac{\partial \phi(t)}{\partial t} \\ \dfrac{\partial \psi(t)}{\partial t} \end{pmatrix} = \mathcal{D}\begin{pmatrix} \phi(t) \\ \psi(t) \end{pmatrix} + \mathcal{L}_1 \begin{pmatrix} \phi(t) \\ \psi(t) \end{pmatrix} + \mathcal{L}_2 \begin{pmatrix} \phi(t-\tau) \\ \psi(t-\tau) \end{pmatrix} \tag{3.10}$$

for $(\phi, \psi) \in [C([-\tau, 0], L^2(\Omega))]^2$, where

$$\mathcal{D} = \begin{pmatrix} \Delta & 0 \\ 0 & \rho\Delta \end{pmatrix} : \mathrm{Dom}(\mathcal{D}) \to [L^2(\overline{\Omega})]^2,$$

$$\mathrm{Dom}(\mathcal{D}) = \left\{ (u, v)^T : u, v \in W^{2,2}(\Omega),\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0 \text{ on } \partial\Omega \right\},$$

$$\mathcal{L}_1 = \begin{pmatrix} -u_0 + \dfrac{\alpha u_0 v_0}{(u_0 + v_0)^2} & -\dfrac{\alpha u_0^2}{(u_0 + v_0)^2} \\ 0 & -d \end{pmatrix},$$

$$\mathcal{L}_2 = \begin{pmatrix} 0 & 0 \\ \dfrac{\beta v_0^2}{(u_0 + v_0)^2} & \dfrac{\beta u_0^2}{(u_0 + v_0)^2} \end{pmatrix}.$$

Then the characteristic equation for the linear system (3.10) at $\mathbf{u_0}$ takes the form

$$\lambda\varphi - \mathcal{D}(\varphi) - \mathcal{L}_1(\varphi) - \mathcal{L}_2(e^{\lambda}\varphi) = 0, \quad \varphi \in \mathrm{Dom}(\mathcal{D}), \quad \varphi \neq 0.$$

Using the eigenfunction expansions of φ in the characteristic equation, we see that the eigenvalue λ satisfies

$$\det \begin{pmatrix} \lambda + \mu_k + u_0 - \dfrac{\alpha u_0 v_0}{(u_0 + v_0)^2} & \dfrac{\alpha u_0^2}{(u_0 + v_0)^2} \\ -\dfrac{\beta v_0^2}{(u_0 + v_0)^2} e^{-\lambda\tau} & \lambda + \rho\mu_k + d - \dfrac{\beta u_0^2}{(u_0 + v_0)^2} e^{-\lambda\tau} \end{pmatrix} = 0$$

for $k = 0, 1, 2, \cdots$. Thus according to [3, Chap. 5], if all roots of

$$
\begin{aligned}
\mathrm{D}_k(\lambda, \tau) =&\lambda^2 + \lambda\left((1+\rho)\mu_k + d + u_0 - \frac{\alpha u_0 v_0}{(u_0+v_0)^2}\right)\\
&+\left(\mu_k + u_0 - \frac{\alpha u_0 v_0}{(u_0+v_0)^2}\right)(\rho\mu_k + d) \qquad (3.11)\\
&-\frac{\beta u_0^2}{(u_0+v_0)^2}e^{-\lambda\tau}\left(\lambda + \mu_k + u_0 - \frac{\alpha u_0 v_0}{(u_0+v_0)^2} - \frac{\alpha v_0^2}{(u_0+v_0)^2}\right)\\
=&0
\end{aligned}
$$

have negative real parts, then $\mathbf{u}_0$ is locally asymptotically stable, whereas if at least one eigenvalue has a positive real part, it is unstable.

Proof of Theorem 2.5. (i) When $\mathbf{u}_0 = (1, 0)$ in (3.11),

$$\mathrm{D}_k(\lambda, \tau) = (\lambda + \mu_k + 1)\left(\lambda + \rho\mu_k + d - \beta e^{-\lambda\tau}\right).$$

It is obvious that $\lambda = -(\mu_k + 1) < 0$ is a root of $\mathrm{D}_k(\lambda, \tau) = 0$, so that it suffices to show that the roots of

$$\lambda + \rho\mu_k + d - \beta e^{-\lambda\tau} = 0 \qquad (3.12)$$

have negative real parts. Assume that $\lambda = A + iB$ with $A \geq 0$. Then (3.12) can be rewritten as

$$(A + \rho\mu_k + d) + iB = \beta e^{-A\tau}(\cos\tau B - i\sin\tau B), \quad k \geq 0.$$

Furthermore, using it, we can derive that

$$A + \rho\mu_k + d \leq |(A + \rho\mu_k + d) + Bi| \leq \beta,$$

which is a contradiction to $\beta < d$. The proof is complete.

(ii) Using the definitions of u_* and v_*, when $\mathbf{u}_0 = (u_*, v_*)$ in (3.11),

$$\mathrm{D}_k(\lambda, \tau) = (\lambda + A_k)(\lambda + P_k) - \frac{d^2}{\beta}e^{-\lambda\tau}(\lambda + Q_k),$$

where

$$A_k = \rho\mu_k + d, \quad P_k = \mu_k + 1 - \alpha(1 - \frac{d^2}{\beta^2}), \quad Q_k = \mu_k + 1 - 2\alpha(1 - \frac{d}{\beta}).$$

If $\lambda = 0$, then

$$
\begin{aligned}
\mathrm{D}_k(0, \tau) &= A_k P_k - \frac{d^2}{\beta}Q_k\\
&= \rho\mu_k^2 + \left(\rho P_0 + d - \frac{d^2}{\beta}\right)\mu_k + d\left(P_0 - \frac{d}{\beta}Q_0\right).
\end{aligned}
$$

Since $\beta > d$ and $\alpha < \frac{\beta}{\beta-d}$,

$$P_0 - \frac{d}{\beta}Q_0 = \left(1 - \frac{d}{\beta}\right)\left(1 - \alpha(1 - \frac{d}{\beta})\right) > 0$$

holds. Moreover, when $\beta > d$,

$$\begin{aligned} \rho P_0 + d - \frac{d^2}{\beta} &= \rho + d(1 - \frac{d}{\beta}) - \rho\alpha(1 - \frac{d^2}{\beta^2}) \\ &\geq 0 \ \text{ iff } \ \alpha \leq \frac{\rho\beta^2 + \beta d(\beta - d)}{\rho(\beta^2 - d^2)}. \end{aligned}$$

Thus $\mathrm{D}_k(0,\tau) > 0$ for all $k \geq 0$ if

$$\begin{aligned} &\text{either} \quad \beta > d, \ \ \rho > \beta - d \ \text{ and } \ \alpha \leq \frac{\rho\beta^2 + \beta d(\beta - d)}{\rho(\beta^2 - d^2)}, \\ &\text{or} \quad \beta > d, \ \ \rho \leq \beta - d \ \text{ and } \ \alpha < \frac{\beta}{\beta - d}. \end{aligned}$$

To consider the case that $\rho P_0 + d - \frac{d^2}{\beta} < 0$, find the discriminant of $\mathrm{D}_k(0,\tau)$ in μ_k,

$$H(\alpha) := \left(\rho P_0 + d - \frac{d^2}{\beta}\right)^2 - 4\rho d\left(P_0 - \frac{d}{\beta}Q_0\right).$$

The equation $H(\alpha) = 0$ has two positive roots, say α_1 and α_2 with $\alpha_1 < \alpha_2$, if $\rho > \beta - d$. Moreover, through straightforward calculations, we can see that if $\beta > d$ and $\rho > \beta - d$, then

$$\begin{aligned} H\left(\frac{\beta}{\beta - d}\right) &= \left(\rho\frac{d}{\beta} - d(1 - \frac{d}{\beta})\right)^2 \geq 0, \\ H\left(\frac{\rho + d(1 - \frac{d}{\beta})}{\rho(1 - \frac{d^2}{\beta^2})}\right) &= -4d\left(\rho\frac{d}{\beta} - d(1 - \frac{d}{\beta})\right)\frac{\beta - d}{\beta + d} < 0. \end{aligned}$$

Thus if

$$\beta > d, \ \ \rho > \beta - d \ \text{ and } \ \frac{\rho\beta^2 + \beta d(\beta - d)}{\rho(\beta^2 - d^2)} < \alpha < \alpha_2,$$

then $H(\alpha) < 0$ holds, and so $\mathrm{D}_k(0,\tau) > 0$ for all $k \geq 0$. Hence, $\lambda = 0$ can not be a root of $\mathrm{D}_k(\lambda,\tau) = 0$ for all $k \geq 0$ if

$$\begin{aligned} &\text{either} \quad \beta > d, \ \ \rho > \beta - d \ \text{ and } \ \alpha < \alpha_2, \\ &\text{or} \quad \beta > d, \ \ \rho \leq \beta - d \ \text{ and } \ \alpha < \frac{\beta}{\beta - d}. \end{aligned} \tag{3.13}$$

We now investigate whether $\mathrm{Re}(\lambda) < 0$ holds, when $\tau = 0$. Note that

$$\mathrm{D}_k(\lambda, 0) = \lambda^2 + \left(A_k + P_k - \frac{d^2}{\beta}\right)\lambda + A_k P_k - \frac{d^2}{\beta} Q_k,$$

and if (3.13) and

$$\alpha < \frac{\beta^2 + \beta d(\beta - d)}{\beta^2 - d^2} \tag{3.14}$$

hold, then

$$A_k P_k - \frac{d^2}{\beta} Q_k = \mathrm{D}_k(0, \tau) > 0$$

$$A_k + P_k - \frac{d^2}{\beta} = (\rho + 1)\mu_k + 1 + d(1 - \frac{d}{\beta}) - \alpha(1 - \frac{d^2}{\beta^2}) > 0$$

for all $k \geq 0$, and thus $\mathrm{Re}(\lambda) < 0$. Hence if (3.13) and (3.14) are given, all the roots of $\mathrm{D}_k(\lambda, 0) = 0$ have negative real parts, so that (u_*, v_*) is locally asymptotically stable when $\tau = 0$.

We finally investigate whether stability switches occurs for increasing $\tau \geq 0$. We know that stability switches may occur only when a root of (3.11) crosses the imaginary axis, that is, (3.11) has a pair of roots $\lambda = \pm i\sigma(\tau)$ with $\sigma(\tau) > 0$. We now assume that $\lambda = \pm i\sigma(\tau)$ $(\sigma(\tau) > 0)$ in (3.11). Then from

$$\begin{aligned}\mathrm{D}_k(i\sigma, \tau) = & - \sigma^2 + A_k P_k - \frac{d^2}{\beta} Q_k \cos\tau\sigma - \frac{d^2}{\beta}\sigma \sin\tau\sigma \\ & + i\left(\sigma(A_k + P_k) - \frac{d^2}{\beta}\sigma\cos\tau\sigma + \frac{d^2}{\beta} Q_k \sin\tau\sigma\right) = 0,\end{aligned}$$

we have

$$\cos\tau\sigma = \frac{\beta}{d^2}\left(\frac{\sigma^2(A_k + P_k - Q_k) + A_k P_k Q_k}{\sigma^2 + Q_k^2}\right)$$

and

$$\sin\tau\sigma = \frac{\beta}{d^2}\sigma\left(\frac{-\sigma^2 + A_k P_k - P_k Q_k - A_k Q_k}{\sigma^2 + Q_k^2}\right).$$

Furthermore, using these equalities, we can deduce

$$1 = \cos^2\tau\sigma + \sin^2\tau\sigma = \frac{\beta^2}{d^4}\frac{(\sigma^2 + P_k^2)(\sigma^2 + A_k^2)}{\sigma^2 + Q_k^2},$$

which is equivalent to

$$\sigma^4 + \left(A_k^2 + P_k^2 - \frac{d^4}{\beta^2}\right)\sigma^2 + A_k^2 P_k^2 - \frac{d^4}{\beta^2} Q_k^2 = 0. \tag{3.15}$$

Through simple calculations, we see that

$$A_k^2 + P_k^2 - \frac{d^4}{\beta^2} = P_k^2 + \left(\rho\mu_k + d(1+\frac{d}{\beta})\right)\left(\rho\mu_k + d(1-\frac{d}{\beta})\right) > 0$$

for all $k \geq 0$ if $\beta > d$. Note that

$$\begin{aligned} &A_k^2 P_k^2 - \frac{d^4}{\beta^2} Q_k^2 \\ &= \mathrm{D}_k(0,\tau)\left[\rho\mu_k^2 + \left(\rho P_0 + d + \frac{d^2}{\beta}\right)\mu_k + d\left(P_0 + \frac{d}{\beta}Q_0\right)\right]. \end{aligned}$$

We already know that if (3.13) is given, then $\mathrm{D}_k(0,\tau) > 0$ for all $k \geq 0$, and

$$\rho P_0 + d + \frac{d^2}{\beta} > \rho P_0 + d - \frac{d^2}{\beta} > 0.$$

We determine the sign of

$$P_0 + \frac{d}{\beta}Q_0 = d\left(1 + \frac{d}{\beta} - \alpha(1-\frac{d}{\beta})(1+3\frac{d}{\beta})\right).$$

Obviously, $P_0 + \frac{d}{\beta}Q_0 \geq 0$ if

$$\alpha \leq \frac{\beta(\beta+d)}{(\beta-d)(\beta+3d)}. \tag{3.16}$$

Thus a contradiction is deduced since the left-hand side of (3.15) is positive if (3.13) and (3.16) hold. Hence (3.15) has no positive roots $\sigma(\tau)$ for all $\tau \geq 0$ when (3.13) and (3.16) are given.

We can easily check that $\beta > d$ implies

$$\frac{\beta(\beta+d)}{(\beta-d)(\beta+3d)} < \frac{\beta}{\beta-d}, \ \frac{\beta^2+\beta d(\beta-d)}{\beta^2-d^2}, \ \frac{\rho\beta^2+\beta d(\beta-d)}{\rho(\beta^2-d^2)}.$$

Thus the given assumption $\beta > d$ and $\alpha \leq \frac{\beta(\beta+d)}{(\beta-d)(\beta+3d)}$ is the only case that simultaneously satisfies (3.13), (3.14) and (3.16). Consequently under the given assumption, (3.11) can not have $\lambda = 0$, and (u_*, v_*) is stable at $\tau = 0$ and it has no stability switches as τ increases. The proof is completed. □

References

[1] R. Arditi and L. R. Ginzburg, *Coupling in predator-prey dynamics: ratio dependence,* J. Theoret. Biol., **139** (1989), 311-326.

[2] S. A. Gourley and Y. Kuang, *A delay reaction-diffusion model of the spread of bacteriophage infection,* SIAM J. Appl. Math., **65** (2005), 550-566.

[3] D. Henry, *Geometric Theory of Semilinear Parabolic Equations: Lecture Notes in Mathematics,* Springer-Verlag, Berlin-New York, 1981.

[4] S. B. Hsu, T. W. Hwang and Y. Kuang, *A ratio-dependent food chain model and its applications to biological control,* Math. Biosci., **181** (2003), 55-83.

[5] S. Liu and E. Beretta, *Stage-structured Predator-prey Model with the Beddington-DeAngelis functional response,* SIAM J. Appl. Math., **66** (2006), 1101-1129.

[6] W. Ko, I. Ahn and S. Liu, *Asymptotical behaviors of a general diffusive consumer-resource model with maturation delay,* Discrete Contin. Dyn. Syst., **23** (2015), 1715-1733.

[7] C. V. Pao, *Nonlinear Parabolic and Elliptic Equations,* Plenum Press, New York, 1992.

[8] C. V. Pao, *Coupled nonlinear parabolic systems with time delays,* J. Math. Anal. Appl., **196** (1995), 237-265.

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