THE STABILITY AND BIFURCATION OF HOMOGENEOUS DIFFUSIVE PREDATOR–PREY SYSTEMS WITH SPATIO–TEMPORAL DELAYS

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Abstract. In this paper, we consider a generalized predator-prey system described by a reaction-diffusion system with spatio-temporal delays. We study the local stability for the constant equilibria of predator-prey system with the generalized delay kernels. Moreover, using the specific delay kernels, we perform a qualitative analysis of the solutions, including existence, uniqueness, and boundedness of the solutions; global stability, and Hopf bifurcation of the nontrivial equilibria.

1. Introduction. In recent years, there is a increasing evidence that environmental heterogeneity and individual motility have significant impact on the ecological balance [1, 5, 20, 23, 11]. A typical interaction of predator and prey is well known as the Rosenzweig-MacArthur model, which aims to investigate the roles of movement and environmental heterogeneity on the habitat [19, 12, 24, 4, 26, 25, 18, 10], and it has also been used to describe the spatiotemporal dynamics of an aquatic community of phytoplankton and zooplankton system [13].

Among these works, in [24], Wang, Wei, and Shi gave a complete and rigorous analysis of the global dynamics of the following general predator-prey system

\[
\begin{align*}
  u_t(x,t) &= d_1 u_{xx} + g(u)(f(u) - v), & x \in \Omega, t > 0, \\
  v_t(x,t) &= d_2 v_{xx} + (g(u) - d)v, & x \in \Omega, t > 0, \\
  \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} &= 0, & x \in \partial \Omega, t > 0, \\
  u(x,0) &= u_0(x) \geq 0, & x \in \Omega, t = 0, \\
  v(x,0) &= v_0(x) \geq 0, & x \in \Omega, t = 0,
\end{align*}
\]

where \( f, g \) satisfy the following conditions:

(i) \( f \in C^1(\mathbb{R}^+), f(0) > 0, \) there exists \( K > 0, \) such that for any \( u > 0, u \neq K, \) 
\( f(u)(u - K) < 0 \) and \( f(K) = 0, \) there exists \( \bar{\lambda} \in (0, K) \) such that \( f'(u) > 0 \) on \( [0, \bar{\lambda}), f'(u) < 0 \) on \( (\bar{\lambda}, K]. \)

(ii) \( g \in C^1(\mathbb{R}^+), g(0) = 0, g(u) > 0 \) for \( u > 0 \) and \( g'(u) > 0 \) for \( u \geq 0, \) there exists a unique \( \lambda > 0 \) such that \( g(\lambda) = d. \)

Here, \( u(x,t) \) and \( v(x,t) \) denote the density of predator and prey at location \( x \) and time \( t, \) where \( x \) is in the bounded domain \( \Omega \) in \( \mathbb{R}^m \) \((m \geq 1)\) with smooth

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boundary $\partial \Omega$. For simplicity, in the following, we only consider the case $m = 1$, where $\Omega = [0, \pi]$. $d_1$ and $d_2$ represent the diffusion coefficients for individuals. The function $g(u)$ denotes the predator functional response, $g(u)f(u)$ represents the net growth rate of the prey in the absence of predators, $d$ is the mortality rate of the predator. Some examples of $f(u)$ and $g(u)$ are shown in Figure 1.

However, realizing that the interaction of predator and prey should be mediated by some time-lag required for the maturing of the species and regeneration resources instead of being instantaneous, we propose a general predator-prey system with spatio-temporal delays. The system takes the form

\[
\begin{align*}
    u_t(x,t) &= d_1 u_{xx} + g(u)f(u) - \tau_1 * g(u)v, & x \in (0, l\pi), t > 0, \\
    v_t(x,t) &= d_2 v_{xx} + \tau_2 * g(u)v - dv, & x \in (0, l\pi), t > 0, \\
    \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, & x = 0, l\pi, t > 0, \\
    u(x,0) &= u_0(x) \geq 0, & x \in [0, \pi], t \in [-\infty, 0].
\end{align*}
\]

(1.2)

Generally, for $u(x,t)$ the delayed operator can be described as

\[
(\tau_i * u)(x,t) = \int_{-\infty}^{t} \int_{0}^{\pi} G_i(x, y, t - s) \tau_i(t - s)u(y, s)\,dy\,ds, \quad i = 1, 2.
\]

(1.3)

The function $\tau_i$ in (1.3) is called the delay kernel and it satisfies $\tau(t) \geq 0$ for all $t \geq 0$ together with the normalisation condition

\[
\int_{0}^{\infty} \tau_i(t)\,dt = 1, \quad i = 1, 2.
\]

(1.4)

The function $G_i$ in (1.3) is chosen from the appropriately normalised solution of the heat equation with the homogeneous Neumann boundary conditions,
\[ \begin{align*}
G_{tt} &= d_i G_{iyy}, & y \in (0, l\pi), \\
G_{ty} &= 0, & y = 0, l\pi, \\
G_i(x, y, 0) &= \delta(x - y), & y \in (0, l\pi).
\end{align*} \] (1.5)

Solve (1.5) and integrate the solution with respect to \( x \) yields that
\[ \int_0^\pi G_i(x, y, t) dx = 1. \] (1.6)

The term (1.3) involves a temporal convolution and therefore introduces delay effects into the system. The convolution in space then arises because the animals are moving (by diffusion), and have therefore not been at the same point in space at previous times. Thus intraspecific interaction depends not simply on species density at one point in space and time, but on a weighted average involving values at all previous time \( s \) and at all points in space. This non-local term was first proposed by Gourley and Bartuccelli in [6], and was widely used in ecological or biological system [7, 6, 3, 21, 8]. For example, Gourley and Britton incorporated a spatio-temporal delay to a predator-prey model [7], Chen and Yu introduced a population model with non-local delay in [3].

This paper is organized as follows. We show how the system (1.2) may be linearized about its spatially uniform steady states and therefore can obtain various results on the local stability of the equilibria of (1.2) with generalized delay kernels in section 2. In section 3, we present a priori bound and global stability of equilibria for subsystem of (1.2) by using specific delay kernels. Besides, to illustrate the effects of the two delays separately, we study the Hopf bifurcation of subsystems of (1.2). In section 4 we summarize and conclude our findings and discuss their implications.

2. Stability of the uniform equilibria. The equations (1.4) and (1.6) imply that the non-local delay terms have no effect on the spatially uniform steady state solutions. Hence, the system (1.2) has three nonnegative constant equilibrium solutions \((0, 0), (K, 0), (\lambda, v_\lambda)\), where \( \lambda \) is the unique one satisfied \( g(\lambda) = d \) and \( v_\lambda = f(\lambda) \). The coexistence equilibrium \((\lambda, v_\lambda)\) is in the first quadrant if and only if \( 0 < \lambda < K \). These solutions are clearly stated in [24].

We first recall some well known results for the delay term (1.3), see for example [22, 21]. Since the boundary conditions are homogeneous Neumann on the domain \((0, \pi)\), the appropriate trial solution is
\[(u, v) = (c_1, c_2)e^{\phi t} \cos nx, \ n = 0, 1, 2, ...\]

Here \( n \) is the wave number, \( \phi \) is the eigenvalue. The term (1.3) can be written as
\[(\tau_i * u)(t, x) = \int_{-\infty}^t \int_0^\pi G_i(x, y, t - s) \tau_i(t - s) e^{\phi s} \cos n y dy ds.\]

After some algebra,
\[(\tau_i * u)(t, x) = \tilde{\tau}_i(\phi + d_i n^2) e^{\phi t} \cos nx. \] (2.1)

Here, \( \tilde{\tau}_i \) denotes the Laplace transform of \( \tau_i \). And for all unspecified kernels we have
\[\tilde{\tau}_i(iR + d_i n^2) = \int_0^\infty \tau_i(t) e^{-(iR + d_i n^2)t} dt = C_i(R, n) - iS_i(R, n),\]
where
\[ C_i(R, n) = \int_0^\infty \tau_i(t)e^{-dn^2t} \cos Rtdt, \quad S_i(R, n) = \int_0^\infty \tau_i(t)e^{-dn^2t} \sin Rtdt. \] (2.2)

It is obvious that,
\[ |C_i(R, n)| \leq 1 \text{ and } |S_i(R, n)| \leq 1. \]

This is provided by \(|\sin x| \leq x\) for \(x \geq 0\).

The linearization of (1.2) at a constant solution \(e^* = (u^*, v^*)\) can be expressed by
\[
\begin{pmatrix}
\psi_1 \\
\varphi_t
\end{pmatrix} = L \begin{pmatrix}
\psi \\
\varphi
\end{pmatrix} := J_{(u^*, v^*)} \begin{pmatrix}
\psi \\
\varphi
\end{pmatrix} + D \begin{pmatrix}
\psi_{xx} \\
\varphi_{xx}
\end{pmatrix},
\]
with domain \(X = \{ (\psi, \varphi) \in H^2(\Omega) \times H^2(\Omega) : \frac{\partial \psi}{\partial \nu} = \frac{\partial \varphi}{\partial \nu} = 0 \}\), where
\[
D = \begin{pmatrix}
d_1 & 0 \\
0 & d_2
\end{pmatrix}, \quad J_{(u^*, v^*)} = \begin{pmatrix}
A(u, v, \tau_1) - d_1n^2 & B(u, v, \tau_1) \\
C(u, v, \tau_2) & D(u, v, \tau_2) - d_2n^2
\end{pmatrix},
\]
and
\[
A(u, v, \tau_1) = g'(u)f(u) - vg'(u)\tau_1(\phi + d_1n^2) + g(u)f'(u),
\]
\[
B(u, v, \tau_1) = -g(u)\tau_1(\phi + d_1n^2),
\]
\[
C(u, v, \tau_2) = vg'(u)\tau_2(\phi + d_2n^2),
\]
\[
D(u, v, \tau_2) = g(u)\tau_2(\phi + d_2n^2) - d.
\]

The eigenvalue equation at \(e^* = (u^*, v^*)\) is
\[
\Phi(\phi, n^2, q) = \text{Det} \begin{pmatrix}
A(u^*, v^*, \tau_1) - \phi - d_1n^2 & B(u^*, v^*, \tau_1) \\
C(u^*, v^*, \tau_2) & D(u^*, v^*, \tau_2) - \phi - d_2n^2
\end{pmatrix} = 0, \] (2.3)
where \(q\) is simply a list of all the parameters, and \(\phi\) is the eigenvalue.

Due to the existence of the Laplace transform in (2.1), the Laplace transform is analytic in the half plane of convergence and the function \(\Phi(\phi, n^2, q) = 0\) is analytic for \(\Re \phi > 0\). By a well known result in complex variable theory [17], for any given solution of the system (1.2), it will be asymptotically local stable if for every wave number \(n = 0, 1, 2, \ldots\), the roots of the equation \(\Phi(\phi, n^2, q) = 0\) are all in the left half complex plane. In the following, we call the solution is local stable if the roots of the equation \(\Phi(\phi, n^2, q) = 0\) are all in the left half complex plane when wave number \(n = 1, 2, 3, \ldots\).

From Gourley and Bartuccelli [6] we have the following lemma.

**Lemma 1.** The number of roots of the characteristic equation (2.3) in the right half complex plane equals
\[
\lim_{R \to \infty} 1 - \frac{1}{\pi} \arg \Phi(iR, n^2, q).
\]

**Lemma 2.** All the roots of (2.3) have negative real parts if
\[
\Phi(0, n^2, q) > 0, \quad \lim_{R \to \infty} \text{Im}(\Phi(iR, n^2, q)) \to \infty, \quad \text{Im}(\Phi'(0, n^2, q)) > 0,
\]
where the dot is the derivative with respect to \(R\).

To illustrate the effect of the spatio-temporal delays on the local stability results of three equilibria, we recall the stability results of (1.1) in [24]. Here, the functional responses for the prey and predator are instantaneous. Notice that \(\lambda \in (0, K)\) is the unique root of \(f'(\lambda) = 0\).
Lemma 3. Suppose that $d, d_1, d_2 > 0$,
1. $(0, 0)$ is unstable for all $\lambda > 0$.
2. When $\lambda > K$, $(K, 0)$ is locally asymptotically stable, when $\lambda < K$, $(K, 0)$ is unstable.
3. When $\bar{\lambda} < \lambda < K$, $(\lambda, v_\lambda)$ is locally asymptotically stable, when $0 < \lambda < \bar{\lambda}$, $(\lambda, v_\lambda)$ is unstable.

The local stability of equilibrium solutions of (1.2) can be analyzed as follows. The cases for $n \neq 0$ and for $n = 0$ are considered separately.

Theorem 1. Suppose that $d, d_1, d_2 > 0$, for wave number $n = 1, 2, \ldots$
1. $(0, 0)$ is locally stable if $f(0)g'(0) < d_1$.
2. When $\lambda > K$, $(K, 0)$ is locally stable; when $\lambda < K$, $(K, 0)$ is locally stable if $g(K) < d_2 + d$.
3. When $0 < \lambda < \bar{\lambda}$, $(\lambda, v_\lambda)$ is locally stable for $0 < v_\lambda g'(\lambda) + df'(\lambda) < d_1$, when $\bar{\lambda} < \lambda < K$, $(\lambda, v_\lambda)$ is locally stable for $0 < v_\lambda g'(\lambda) < d_1$.

Proof. 1. If $e^* = (0, 0)$, the Jacobian matrix is
$$J_{(0,0)} = \begin{pmatrix} f(0)g'(0) - d_1n^2 & 0 \\ 0 & -d - d_2n^2 \end{pmatrix}.$$ 

The eigenvalue equation is then:
$$\Phi_1(\phi, n^2, q) := (f(0)g'(0) - d_1n^2 - \phi)(-d - d_2n^2 - \phi) = 0. \quad (2.4)$$

It is clear that the roots of (2.4) are
$$f(0)g'(0) - d_1n^2, -d - d_2n^2.$$ 

Then, if $f(0)g'(0) < d_1$, all roots are negative when $n \geq 1$. Thus, $(0, 0)$ is locally stable.

2. If $e^* = (K, 0)$, the Jacobian matrix is
$$J_{(K,0)} = \begin{pmatrix} f'(K)g(K) - d_1n^2 & -g(K)\tau_1(\phi + d_1n^2) \\ 0 & -d + g(K)\tau_2(\phi + d_2n^2) - d_2n^2 \end{pmatrix}.$$ 

The eigenvalue equation is then:
$$\Phi_2(\phi, n^2, q) := (d_1n^2 + \phi - f'(K)g(K))(d_2n^2 + \phi + d - g(K)\tau_2(\phi + d_2n^2)) = 0.$$ 

When $\phi = iR$, for $R \to \infty$,
$$\text{Re}\Phi_2(iR, n^2, q) \sim -R^2,$$
$$\text{Im}\Phi_2(iR, n^2, q) \sim (d - C_1(R, n)g(K) - f'(K)g(K) + (d_1 + d_2)n^2)R.$$ 

Also, when $R = 0$,
$$\Phi_2(0, n^2, q) = (d_1n^2 - f'(K)g(K))(d - C_1(0, n)g(K) + d_2n^2).$$

(2a). When $\lambda > K$, then $f'(K) < 0$ and $d - C_1g(K) > d - g(K) > 0$, which is supported by (2). Thus,
$$\Phi_2(0, n^2, q) > (d_1n^2 - f'(K)g(K))(d - g(K) + d_2n^2) > 0,$$
$$\text{Im}\Phi_2(0, n^2, q) = (d - C_1(0, n)g(K) - f'(K)g(K) + (d_1 + d_2)n^2) > 0,$$
and
$$\lim_{R \to \infty} \text{Im}\Phi_2(iR, n^2, q) \to \infty.$$ 

Then, according to Lemma 2, $\Phi_2(\phi, n^2, q) = 0$ has no roots in the right half complex plane for every wave number. Therefore, $(K, 0)$ is locally stable.
(2b). When \( \lambda < K \), we have \( d - g(K) < 0, f'(K) < 0 \), and then \( d_1 n^2 - f'(K)g(K) > 0 \). When wave number \( n \geq 1 \) and \( g(K) < d_2 + d \), we have \( d + d_2 n^2 - g(K) > 0 \). Based on the above analysis, we have \( \Phi_2(0, n^2, q) > 0, \lim_{K \to \infty} \text{Im} \Phi_2(iR, n^2, q) = \infty \), and \( \text{Im} \Phi'_2(0, n^2, q) > 0 \). Then, the result follows from Lemma 2.

3. If \( e^* = (\lambda, v_\lambda) \), then

\[
J_{(\lambda, v_\lambda)} = \begin{pmatrix}
A_1(\lambda) - B_1(\lambda) \bar{\tau}_1(\phi + d_1 n^2) - d_1 n^2 & -d_1 \bar{\tau}_1(\phi + d_1 n^2) \\
B_1(\lambda) \bar{\tau}_2(\phi + d_2 n^2) & -d_2 \bar{\tau}_2(\phi + d_2 n^2) - d_2 n^2
\end{pmatrix},
\]

with

\[
A_1(\lambda) = v_\lambda g'(\lambda) + df'(\lambda), \quad B_1(\lambda) = v_\lambda g'(\lambda) > 0.
\]

The eigenvalue equation is then:

\[
\Phi_3(\phi, n^2, q) := (d + \phi + d_2 n^2 - d\bar{\tau}_2(\phi + d_2 n^2))(\phi + d_1 n^2 + B_1 \bar{\tau}_1(\phi + d_1 n^2) - A_1) + B_1 d \bar{\tau}_1(\phi + d_1 n^2)\bar{\tau}_2(\phi + d_2 n^2) = 0.
\]

When \( \phi = iR \), for \( R \to \infty \),

\[
\text{Re} \Phi_3(iR, n^2, q) \sim -R^2,
\]

\[
\text{Im} \Phi_3(iR, n^2, q) \sim (B_1 C_1(R, n) - A_1 + (1 - C_2(R, n))d + (d_1 + d_2)n^2)R.
\]

Also, when \( R = 0 \),

\[
\Phi_3(0, n^2, q) = dB_1 C_1(0, n)C_2(0, n) - (A_1 - B_1 C_1(0, n) - d_1 n^2)((1 - C_2(0, n))d + d_2 n^2),
\]

\[
\text{Im} \Phi'_3(0, n^2, q) = B_1 C_1(0, n) - A_1 + (1 - C_2(0, n))d + (d_1 + d_2)n^2.
\]

Since \( (1 - C_2)d + d_2 n^2 > 0 \), according to Lemma 2, we need \( A_1 - d_1 n^2 < 0 \) to guarantee the local stability.

(3a). When \( 0 < \lambda < \lambda \), then \( f'(\lambda) > 0 \). For wave number \( n \geq 1 \), under the assumption \( v_\lambda g'(\lambda) + df'(\lambda) < d_1 \), then \( A_1 - d_1 n^2 < 0 \). Then, the result follows from Lemma 2.

(3b). When \( \lambda < K < K \), then \( f'(\lambda) < 0 \). For wave number \( n \geq 1 \), under the assumption \( v_\lambda g'(\lambda) < d_1 \), then \( A_1 - d_1 n^2 < 0 \). Then, the result follows from Lemma 2.

Next, we discuss the case for \( n = 0 \). In view of (2.2), we obtain that \( C_i(0, 0) = 1 \), \( S_i(0, 0) = 0 \).

(I). If \( e^* = (0, 0) \), the Jacobian matrix is

\[
J_{(0, 0)} = \begin{pmatrix}
f(0)g'(0) & 0 \\
0 & -d
\end{pmatrix}.
\]

The eigenvalue equation is then:

\[
\Phi_1(\phi, n^2, q) := (f(0)g'(0) - \phi)(-d - \phi) = 0.
\]

It is clear that when \( n = 0 \), the roots of (2.5) are \( f(0)g'(0), -d \), where there exists a positive eigenvalue. Thus, \( (0, 0) \) is unstable.

(II). If \( e^* = (K, 0) \), the Jacobian matrix is

\[
J_{(K, 0)} = \begin{pmatrix}
f'(K)g(K) & -g(K)\bar{\tau}_1(\phi) \\
0 & -d + g(K)\bar{\tau}_2(\phi)
\end{pmatrix}.
\]

The eigenvalue equation is then:

\[
\Phi_2(\phi, 0, q) := (\phi - f'(K)g(K))(\phi + d - g(K)\bar{\tau}_2(\phi)) = 0.
\]
When \( \phi = iR \), for \( R \to \infty \),
\[
\begin{align*}
\text{Re} \Phi_2(iR, 0, q) & \sim -R^2, \\
\text{Im} \Phi_2(iR, 0, q) & \sim (d - C_1(R, 0)g(K) - f'(K)g(K))R.
\end{align*}
\]

Also, when \( R = 0 \),
\[
\Phi_2(0, 0, q) = -f'(K)g(K)(d - g(K)).
\]

(i). When \( \lambda > K \), \( d - C_1(R, 0)g(K) > d - g(K) > 0 \) and \( f'(K) < 0 \). Then,
\[
\begin{align*}
\Phi_2(0, 0, q) & > -f'(K)g(K)(d - g(K)) > 0, \\
\text{Im} \Phi_2(0, 0, q) & = d - g(K) - f'(K)g(K) > 0,
\end{align*}
\]

and
\[
\lim_{R \to \infty} \text{Im} \Phi_2(iR, 0, q) \to \infty.
\]

According to Lemma 2 and Theorem 1, \((K, 0)\) is locally asymptotically stable.
(ii). When \( \lambda < K \), we have \( d - g(K) < 0, f'(K) < 0 \). One can easily find that \( \Phi_2(0, 0, q) < 0 \), therefore when \( n = 0 \), \((K, 0)\) is unstable.

(III). If \( e^* = (\lambda, v_\lambda) \), the Jacobian matrix is
\[
J_{(\lambda, v_\lambda)} = \begin{pmatrix}
A_1(\lambda) - B_1(\lambda) \bar{\tau}_1(\phi) & -d \bar{\tau}_1(\phi) \\
B_1(\lambda) \bar{\tau}_2(\phi) & -d + d \bar{\tau}_2(\phi)
\end{pmatrix},
\]
with
\[
A_1(\lambda) = v_\lambda g'(\lambda) + df'(\lambda), \quad B_1(\lambda) = v_\lambda g'(\lambda) > 0.
\]

The eigenvalue equation is then:
\[
\Phi_3(\phi, 0, q) := (d + df(\phi) + B_1 \bar{\tau}_1(\phi) - A_1) + B_1 d \bar{\tau}_1(\phi) \bar{\tau}_2(\phi) = 0.
\]

When \( \phi = iR \), for \( R \to \infty \),
\[
\begin{align*}
\text{Re} \Phi_3(iR, 0, q) & \sim -R^2, \\
\text{Im} \Phi_3(iR, 0, q) & \sim (B_1 C_1(R, 0) + (1 - C_2(R, 0))d - A_1)R.
\end{align*}
\]

Also, when \( R = 0 \),
\[
\begin{align*}
\Phi_3(0, 0, q) &= dB_1 > 0, \\
\text{Im} \Phi_3'(0, 0, q) &= B_1 - A_1 = -df'(\lambda).
\end{align*}
\]

(i). When \( 0 < \lambda < \bar{\lambda} \), then \( f'(\lambda) > 0 \), then \( \text{Im} \Phi_3'(0, 0, q) < 0 \). Thus, when \( n = 0 \), \((\lambda, v_\lambda)\) is unstable.

(ii). When \( \bar{\lambda} < \lambda < K \), then \( f'(\lambda) < 0 \). Under the assumption \( A_1 < 0 \), we have
\[
\lim_{R \to \infty} \text{Im} \Phi_3(iR, 0, q) \to \infty \quad \text{and} \quad \text{Im} \Phi_3'(0, 0, q) > 0.
\]

Then, follows from Lemma 2 and Theorem 1, \((\lambda, v_\lambda)\) is locally asymptotically stable.

Based on the above analysis, we have the following results.

**Theorem 2.** Suppose that \( d, d_1, d_2 > 0 \), for every wave number \( n = 0, 1, 2, \ldots, \),
1. When \( \lambda > K \), \((K, 0)\) is locally asymptotically stable.
2. When \( \lambda < \lambda < K \), \((\lambda, v_\lambda)\) is locally asymptotically stable for \( v_\lambda g'(\lambda) + df'(\lambda) < 0 \).
3. Global behavior of the uniform equilibria. In this section, we shall consider the global behaviour of the case when the predator functional response for the predator is instantaneous. Such a system can be considered as an approximation to the case when this particular time-scale is negligible to that on which the predator functional response for the prey. This subsystem can be extracted as a particular case of (1.2) by setting
\[
\tau_1(t) = \delta(t), \quad \tau_2(t) = \frac{1}{\tau_2} e^{-\frac{t}{\tau_2}}. \tag{3.1}
\]
One is the Dirac delta function, the other is the weak delay kernel. It is useful to define the following component, which can be thought of the detritus in the system,
\[
q(x,t) = \int_{-\infty}^{t} \int_{0}^{\pi} G_2(x,y,t-s) e^{-\frac{t-s}{\tau_2}} g(u(y,s)) v(y,s) dy ds. \tag{3.2}
\]
Note that although \(G_2(x,y,t)\) is defined by being the solution of (1.5). In view of this fact, if we differentiate (3.2) with respect to \(t\) we shall find that
\[
q_t(x,t) = d_2 q_{xx} + g(u) v - \frac{1}{\tau_2} q.
\]
Thus, for the particular kernels (3.1), (1.2) can formally be recast as
\[
\begin{align*}
& u_t(x,t) = d_1 u_{xx} + g(u)(f(u) - v), & x \in (0,l\pi), t > 0, \\
& v_t(x,t) = d_2 v_{xx} + \frac{1}{\tau_2} q - dv, & x \in (0,l\pi), t > 0, \\
& q_t(x,t) = d_2 q_{xx} + g(u) v - \frac{1}{\tau_2} q, & x \in (0,l\pi), t > 0, \\
& \frac{\partial u}{\partial x} = \frac{\partial v}{\partial x} = \frac{\partial q}{\partial x} = 0, & x = 0,l\pi, t > 0, \\
& u(x,0) = u_0(x) \geq 0, v(x,0) = v_0(x) \geq 0, & x \in [0,l\pi], \\
& q(x,0) = \int_{-\infty}^{0} \int_{0}^{\pi} G_2(x,y,t-s) e^{\frac{s}{\tau_2}} g(u(x,s)) v(x,s) dy ds \geq 0, & t \in [-\infty,0].
\end{align*}
\]  
(3.3)

Since the nonlocal delay terms have no effect on the spatially uniform steady state solutions, we can see that (3.3) has three nonnegative constant equilibrium solutions \((0,0,0), (K,0,0), \) and \((\lambda,v_\lambda,\tau_2 v_\lambda g(\lambda))\).

To show the existence of a classical solution to (3.3), we use the method of upper and lower solutions for mixed quasimonotone functions. Recall that a vector function
\[
m(\cdot,u) = (m_1(\cdot,u),...,m_N(\cdot,u)),
\]
is said to have a mixed quasimonotone property in a subset \(A\) of \(\mathbb{R}^N\) if for each \(i = 1,...,N\) there exist nonnegative integers \(a_i, b_i\) with \(a_i + b_i = N - 1\) such that \(m_i(\cdot,u,[u|\alpha_i],[u|\beta_i])\) is nondecreasing in \([u|\alpha_i]\) and is nonincreasing in \([u|\beta_i]\) for all \(u \in A\). Let \(X_T = (0,T] \times \Omega\). The definition of upper and lower solutions (Definition 2.1, [16]) depends on the mixed quasimonotone properties and is given by the following:
Theorem 3. Suppose that

\[ \begin{align*}
\partial \hat{u}_i / \partial t - \nabla \cdot (\alpha_1^* \partial_i u_i \nabla \hat{u}_i) + \beta_1^* (D_i \partial_i u_i) & \geq m_i(t, x, \hat{u}_i, [\hat{u}]_{\alpha_i}, [\hat{u}]_{\beta_i}), &(t,x) \in (0,T] \times \Omega, \\
\partial \hat{u}_i / \partial t - \nabla \cdot (\alpha_2^* \partial_i u_i \nabla \hat{u}_i) + \beta_2^* (D_i \partial_i u_i) & \leq m_i(t, x, \hat{u}_i, [\hat{u}]_{\alpha_i}, [\hat{u}]_{\beta_i}), &(t,x) \in (0,T] \times \Omega, \\
D_i(\hat{u}_i) \frac{\partial \hat{u}_i}{\partial n} & \geq 0 \geq D_i(\hat{u}_i) \frac{\partial \hat{u}_i}{\partial n}, &(t,x) \in (0,T] \times \partial \Omega, \\
\hat{u}_i(0, x) & \geq \varphi(x) \geq \hat{u}_i(0, x), & t = 0, x \in \Omega.
\end{align*} \]

System (3.3) has a unique solution \( \hat{u} = (\hat{u}_1, ..., \hat{u}_N) \), \( u = (\hat{u}_1, ..., \hat{u}_N) \) in \( C^{1,0}(\bar{X}_T) \cap C^{2,1}(X_T) \) are called coupled upper and lower solutions if \( \hat{u} \geq u > 0 \) in \( X_T \) and if

\[ \begin{align*}
\frac{\partial \hat{u}_i}{\partial t} - \nabla \cdot (\alpha_1^* \partial_i u_i \nabla \hat{u}_i) + \beta_1^* (D_i \partial_i u_i) & \geq m_i(t, x, \hat{u}_i, [\hat{u}]_{\alpha_i}, [\hat{u}]_{\beta_i}), &(t,x) \in (0,T] \times \Omega, \\
\frac{\partial \hat{u}_i}{\partial t} - \nabla \cdot (\alpha_2^* \partial_i u_i \nabla \hat{u}_i) + \beta_2^* (D_i \partial_i u_i) & \leq m_i(t, x, \hat{u}_i, [\hat{u}]_{\alpha_i}, [\hat{u}]_{\beta_i}), &(t,x) \in (0,T] \times \Omega, \\
D_i(\hat{u}_i) \frac{\partial \hat{u}_i}{\partial n} & \geq 0 \geq D_i(\hat{u}_i) \frac{\partial \hat{u}_i}{\partial n}, &(t,x) \in (0,T] \times \partial \Omega, \\
\hat{u}_i(0, x) & \geq \varphi(x) \geq \hat{u}_i(0, x), & t = 0, x \in \Omega.
\end{align*} \]

Theorem 3. Suppose that \( d, d_1, d_2 > 0 \),

1. System (3.3) has a unique solution \( (u(x,t), v(x,t), q(x,t)) \) such that \( u(x,t) > 0 \), \( v(x,t) > 0 \), \( q(x,t) > 0 \) for \( t \in (0, \infty) \) and \( x \in [0, \pi] \).

2. For any solution of (3.3), \( \lim_{t \to \infty} \sup v(x,t) \leq K \), and if \( d_1 = d_2 \),

\[ \int_0^\pi v(x,t)dt \leq (K + \frac{g(K)f(\bar{\lambda})}{d})\pi. \]

Proof. 1. Define

\[ m_1(x,t) = g(u)(f(u) - v), \quad m_2(x,t) = \frac{1}{\tau_2} q - dv, \quad m_3(x,t) = g(u)v - \frac{1}{\tau_2} q. \]

For

\[ \frac{\partial m_1}{\partial v} = - g(u) < 0, \quad \frac{\partial m_1}{\partial q} = 0, \]

\[ \frac{\partial m_2}{\partial u} = \frac{\partial m_2}{\partial q} = \frac{1}{\tau_2} > 0, \quad \frac{\partial m_3}{\partial u} = g'(u)v > 0, \quad \frac{\partial m_3}{\partial v} = g(u) > 0, \]

in \( \bar{R}^3_+ = \{u \geq 0, v \geq 0, q \geq 0 \} \), and then (3.3) is a mixed quasi-monotone system.

Let \( (\hat{u}(x,t), \hat{v}(x,t), \hat{q}(x,t)) = (0,0,0) \) and \( (\hat{u}(x,t), \hat{v}(x,t), \hat{q}(x,t)) = (\hat{u}^*(t), \hat{v}^*(t), \hat{q}^*(t)) \), where \( (\hat{u}^*(t), \hat{v}^*(t), \hat{q}^*(t)) \) is the unique solution of

\[ \begin{align*}
\frac{du}{dt} & = f(u)g(u), \\
\frac{dv}{dt} & = \frac{1}{\tau_2} q, \\
\frac{dq}{dt} & = g(u)v, \\
u(0) & = \sup_{[0,\pi]} u_0(x), \quad v(0) = \sup_{[0,\pi]} v_0(x), \quad q(0) = \sup_{[0,\pi]} q_0(x).
\end{align*} \]

Then, \( (\hat{u}(x,t), \hat{v}(x,t), \hat{q}(x,t)) \) and \( (\hat{u}(x,t), \hat{v}(x,t), \hat{q}(x,t)) \) are the lower and upper solution to (3.3), since

\[ \begin{align*}
\frac{\partial \hat{u}(x,t)}{\partial t} - \Delta \hat{u}(x,t) - m_1(\hat{u}(x,t), \hat{v}(x,t), \hat{q}(x,t)) & = 0, \\
\frac{\partial \hat{v}(x,t)}{\partial t} - \Delta \hat{v}(x,t) - m_2(\hat{v}(x,t), \hat{u}(x,t), \hat{q}(x,t)) & = 0, \\
\frac{\partial \hat{q}(x,t)}{\partial t} - \Delta \hat{q}(x,t) - m_3(\hat{q}(x,t), \hat{u}(x,t), \hat{v}(x,t)) & = 0,
\end{align*} \]
and
\[
\begin{align*}
\frac{\partial \bar{u}(x,t)}{\partial t} - \triangle \bar{u}(x,t) - m_1(\bar{u}(x,t), \bar{v}(x,t), \bar{q}(x,t)) &= 0, \\
\frac{\partial \bar{v}(x,t)}{\partial t} - \triangle \bar{v}(x,t) - m_2(\bar{v}(x,t), \bar{u}(x,t), \bar{q}(x,t)) &= \bar{d}\bar{v}^*(t) \geq 0, \\
\frac{\partial \bar{q}(x,t)}{\partial t} - \triangle \bar{q}(x,t) - m_3(\bar{q}(x,t), \bar{u}(x,t), \bar{v}(x,t)) &= \frac{1}{\tau_2} \bar{q}^*(t) \geq 0.
\end{align*}
\]

Also, the boundary conditions and the initial conditions are satisfied. Therefore, Lemma 2.1 in [16] shows that (3.3) has a unique globally defined solution \((u(x,t), v(x,t), q(x,t))\), which satisfies
\[
0 \leq u(x,t) \leq \bar{u}^*(t), \quad 0 \leq v(x,t) \leq \bar{v}^*(t), \quad 0 \leq q(x,t) \leq \bar{q}^*(t), \quad t \geq 0.
\]
The strong maximum principle implies that \(u(x,t), v(x,t), q(x,t) > 0\) for \(t > 0\) and \(x \in [0,\pi]\).

2. From the proof above, we obtain that \(u(x,t) \leq \bar{u}^*(t)\) for all \(t > 0\). From the ODE satisfied by \(u^*(t)\) and \(f, g\) satisfying (i),(ii), one can see that \(u^*(t) \to K\) as \(t \to \infty\). Thus for any \(\varepsilon > 0\), there exists \(T > 0\) such that \(u(x,t) \leq K + \varepsilon\) in \(X_T\).

For the estimate of \(v(x,t)\), let \(d_1 = d_2\), then
\[
r_t = u_t + q_t = d_1(u_{xx} + q_{xx}) + f(u)g(u) - \frac{1}{\tau_2}q,
\]
by the comparison principle of parabolic equations, we have
\[
r(x,t) \leq u^*(t) \leq K + \varepsilon.
\]

Define
\[
\int_0^\pi u(x,t)dx = U(t), \quad \int_0^\pi v(x,t)dx = V(t), \\
\int_0^\pi q(x,t)dx = Q(t), \quad \int_0^\pi r(x,t)dx = R(t).
\]

By the virtue of the Neumann boundary condition, we obtain
\[
\frac{d(U + V + Q)}{dt} = \int_0^\pi d_1(u_{xx} + v_{xx} + q_{xx})dx + \int_0^\pi g(u)(f(u) - v)dx \\
+ \int_0^\pi g(u)vdx - d \int_0^\pi vdx,
\]
\[
= \int_0^\pi g(u)f(u)dx - dV.
\]

Then we have
\[
(U + V + Q)_t = -d(U + V + Q) + dR + \int_0^\pi g(u)f(u)dx,
\]
\[
\leq -d(U + V + Q) + \pi(d(K + \varepsilon) + g(K + \varepsilon)f(\bar{\lambda})).
\]

Integration of the inequality leads to
\[
\int_0^\pi v(x,t)dx = V(t) < U(t) + V(t) + Q(t) \leq \frac{\pi}{d}(d(K + \varepsilon) + g(K + \varepsilon)f(\bar{\lambda})).
\]

Thus, any solution \(v(x,t)\) satisfies an \(L^1\) a priori estimate
\[
K_1 = \frac{\pi(d(K + \varepsilon) + g(K + \varepsilon)f(\bar{\lambda}))}{d}.
\]

This completes the proof. \(\square\)
Then ally stable. For PDEs [26]. Here we choose \( d > g(K) \), then \( (K,0,0) \) is globally asymptotically stable.

\[ V(x,t) = \int_0^\pi \int_\lambda^u \frac{g(\zeta) - d}{g(\zeta)} \, d\zeta \, dx + \int_0^\pi \int_{v_\lambda+q}^{u+q} \frac{\eta - q - v_\lambda}{\eta - q} \, dy \, dx. \]

Then
\[
\frac{dV}{dt} = \int_0^\pi g(u) - \frac{d}{g(u)} u_t \, dx + \int_0^\pi \frac{v - v_\lambda}{v} (v_t + q_t) \, dx,
\]
\[
\leq \int_0^\pi (g(u) - g(\lambda))(f(u) - f(\lambda)) \, dx - d_1 \int_0^\pi g'(u) \, dx - d_2 \int_0^\pi \frac{g''(u)}{g'(u)} |\nabla u|^2 \, dx.
\]

Therefore, the definition of \( \lambda_0 \) and (ii) imply that \( V_t \leq 0 \) along an orbit \( (u(x,t),v(x,t),q(x,t)) \) of system (3.3) with non-negative initial value. Therefore \( (u(x,t),v(x,t),q(x,t)) \) is globally stable.

2. When \( \lambda > K \), we construct a similar Lyapunov functional as follows:
\[
V(x,t) = \int_0^\pi \int_K^u \frac{g(\zeta) - g(K)}{g(\zeta)} \, d\zeta \, dx + \int_0^\pi (v + q) \, dx.
\]

Then
\[
\frac{dV}{dt} = \int_0^\pi g(u) - \frac{g(K)}{g(u)} u_t \, dx + \int_0^\pi (v_t + q_t) \, dx,
\]
\[
\leq - d_1 g(K) \int_0^\pi \frac{g'(u)}{g^2(u)} |\nabla u|^2 \, dx + \int_0^\pi (g(u) - g(K)) f(u) + (g(K) - d) v \, dx
\]
\[
- d_2 v_\lambda \int_0^\pi \frac{|\nabla v||\nabla q|}{v^2} \, dx.
\]

Therefore, \( g(K) < d \) and (i), (ii) imply that \( V_t \leq 0 \) along an orbit \( (u(x,t),v(x,t),q(x,t)) \) of system (3.3) with non-negative initial value. Therefore, \( (K,0,0) \) is globally stable.

Next, we study the Hopf bifurcation of (3.3), using the Hopf bifurcation theorem for PDEs [26]. Here we choose \( d_1 \) as the bifurcation parameter.

For the nontrivial solution \((\lambda,v_\lambda,v_\lambda \tau_2 g(\lambda))\), the Jacobi matrix is
\[
J_{(\lambda,v_\lambda,v_\lambda \tau_2 g(\lambda))} = \begin{pmatrix}
A_1(\lambda) - d_1 n^2 & -d & 0 \\
0 & -d - d_2 n^2 & \frac{1}{\tau_2} \\
B_1(\lambda) & d & -\frac{1}{\tau_2} - d_2 n^2
\end{pmatrix}.
\]
Then the roots of (3.8) are

\[ \Phi_4(\phi, n^2, q) = \phi^3 + b_2\phi^2 + b_1\phi + b_0 = 0, \]  

where

\[ b_0 = d_2n^2(\gamma_2 - d_2n^2)(d_1n^2 - A_1) + \frac{dB_1}{\tau_2}, \]
\[ b_1 = n^2(d_2(\gamma_1 + d_1n^2) + (d_1 + d_2)(d + \frac{1}{\tau_2})) - A_1\gamma_2, \]
\[ b_2 = d + (d_1 + 2d_2)n^2 + \frac{1}{\tau_2} - A_1, \]

with \( \gamma_1 = (d_1 + d_2)n^2 > 0, \gamma_2 = d + 2d_2n^2 + \frac{1}{\tau_2} > 0. \)

**Theorem 5.** Suppose that \( d, d_1, d_2 > 0, \) and

\[ v_\lambda g'(\lambda) + df'(\lambda) < 0, \]  

for wave number \( n = 1, 2, \ldots, \) (3.9) undergoes a Hopf bifurcation at \( (\lambda, v_\lambda, v_\lambda\tau_2d), \) and the bifurcation parameter \( d_1 \) satisfies

\[ \tau_2\gamma_2(A_1(A_1 - \gamma_2 - 2d_1n^2) + \gamma_1(d + \gamma_1 + \frac{1}{\tau_2})) = dv_\lambda g'(\lambda). \]

**Proof.** The assumption (3.6) can guarantee that \( b_2, b_1, b_0 \) are positive, which implies that any potential Hopf bifurcation point exists in the interval \([0, \bar{\lambda})\). Further, it can be shown that \( b_2b_1 = b_0 \), when \( d_1 \) satisfies (3.7). Then, equation (3.5) becomes

\[ \Phi_4(\phi, n^2, q) = (\phi^3 + b_1)(\phi + b_2). \]

Then the roots of (3.8) are

\[ \phi_{1,2} = \pm \sqrt{b_1}, \phi_3 = -b_2 < 0, \]

which are supported by \( A_1 < 0. \) We now derive the transversality condition.

\[ \frac{d\phi}{dd_1} = -\frac{d\Phi_4}{dd_1} \cdot \frac{d\Phi_4}{d\phi} = -\frac{\zeta_2\phi^2 + \zeta_1\phi + \zeta_0}{3\phi^2 + 2b_2\phi + b_1}, \]

where

\[ \zeta_2 = n^2 > 0, \zeta_1 = n^2(d + 2d_2n^2 + \frac{1}{\tau_2}) > 0, \zeta_0 = d_2n^4(d + d_2n^2 + \frac{1}{\tau_2}) > 0. \]

And then when \( b_2b_1 = b_0 > 0 \) and \( n \geq 1, \)

\[ \text{Re}\left(\frac{d\phi}{dd_1}\right) = \frac{-b_1\zeta_2 + \zeta_0 - \zeta_1b_2}{2(b_1 + b_2^2)}, \]
\[ = \frac{-n^2(d_2^2n^4 + b_1 + (d + \gamma_1 + \frac{1}{\tau_2} - A_1)\gamma_2)}{2(b_1 + b_2^2)} < 0. \]

Therefore, (3.9) undergoes a Hopf bifurcation at \( (\lambda, v_\lambda, v_\lambda\tau_2d). \)

In the following, to gain more Hopf bifurcation informations, we shall consider the case when the predator functional response for the prey is instantaneous. Such a system can be considered as an approximation to the case when this particular time-scale is negligible to that on which the predator functional response for the predator. This subsystem can be extracted as a particular case of (1.2) by setting

\[ \tau_1(t) = \frac{1}{\tau_1}e^{-\frac{t}{\tau_1}}, \tau_2(t) = \delta(t). \]
Similarly, (1.2) can be reformulated as

\[
\begin{aligned}
u_t(t, x) &= d_1 u_{xx} + g(u) f(u) - \frac{1}{\tau_1} p, \quad x \in (0, \pi), t > 0, \\
v_t(t, x) &= d_2 v_{xx} + g(u) v - dv, \quad x \in (0, \pi), t > 0, \\
p_t(t, x) &= d_1 p_{xx} + g(u) v - \frac{1}{\tau_1} p, \quad x \in (0, \pi), t > 0, \\
\frac{\partial u}{\partial x} = \frac{\partial v}{\partial x} = \frac{\partial p}{\partial x} = 0, \quad x = 0, \pi, t > 0, \\
u(0, x) = u_0(x) \geq 0, v(0, x) = v_0(x) \geq 0, \quad x \in [0, \pi], \\
p(0, x) = \int_0^\infty \int_0^\pi G_1(x, y, -s) e^{\pi} g(u(y, s)) v(y, s) dy ds \geq 0, \quad t \in [-\infty, 0].
\end{aligned}
\]

System (3.9) has three nonnegative constant equilibrium solutions \((0, 0, 0), (K, 0, 0)\), and \((\lambda, v_\lambda, \lambda v_\lambda \tau_1)\). In the following, we discuss the Hopf bifurcation near \((\lambda, v_\lambda, \lambda v_\lambda \tau_1)\), choosing \(d_1\) as the bifurcation parameter.

For the nontrivial solution \((\lambda, v_\lambda, \lambda v_\lambda \tau_1)\), the Jacobi matrix is

\[
J(\lambda, v_\lambda, \lambda v_\lambda \tau_1) = \begin{pmatrix}
A_1(\lambda) - d_1 n^2 & 0 & -\frac{1}{\tau_1} \\
0 & B_1(\lambda) & -d_2 n^2 \\
0 & -d & B_1(\lambda) - d - \frac{1}{\tau_1} - d_1 n^2
\end{pmatrix}.
\]

The characteristic equation is,

\[
\Phi_5(\phi, n^2, q) = \phi^3 + \phi^2 a_2 + \phi a_1 + a_0 = 0,
\]

where

\[
a_0 = d_2 n^2(d_1 n^2 + \frac{1}{\tau_1})(d_1 n^2 - A_1) + \frac{B_1}{\tau_1}(d_2 n^2 - d), \\
a_1 = d_1(d_1 + 2d_2)n^2 + (B_1 + (d_1 + d_2)n^2) \frac{1}{\tau_1} - A_1((d_1 + d_2)n^2 + \frac{1}{\tau_1}), \\
a_2 = (2d_1 + d_2)n^2 + \frac{1}{\tau_1} - A_1.
\]

Assume that

\[
A_1 = v_\lambda g'(\lambda) + df'(\lambda) < 0, d < d_2.
\]

Then the inequalities (3.11) guarantee that \(a_2, a_1, a_0 > 0\) for \(n \geq 1\). Further, it can be shown that when \(a_2 a_1 = a_0\), equation (3.10) becomes

\[
\Phi_5(\phi, n^2, q) = (\phi^2 + a_1)(\phi + a_2).
\]

Then the roots of (3.12) are

\[
\phi_{1,2} = \pm \sqrt{a_1}, \quad \phi_3 = -a_2 < 0.
\]

For convenience, we denote \(A_2 = A_1 - 2d_1 n^2 - \frac{1}{\tau_1} < 0\). By calculation, under the inequalities (3.11), we obtain

\[
a_2 a_1 - a_0 = A_1 \tau_1 (A_2 - (d_1 + d_2)n^2)((d_1 + d_2)n^2 + \frac{1}{\tau_1}) - B_1(A_2 - d) > 0,
\]

which leads a contradiction. Hence, when \(d, d_1, d_2 > 0, d < d_2\), and \(v_\lambda g'(\lambda) + df'(\lambda) < 0\), for wave number \(n = 1, 2, ...\), (3.9) does not undergoes a Hopf bifurcation at \((\lambda, v_\lambda, \tau_1 f(\lambda) g(\lambda))\).
4. Discussion. We study a diffusion-reaction model with spatio-temporal delays to offer insights into the predator-prey systems by studying how the dynamics depend on the delays and diffusion rates.

For the full general system (1.2) (with both delays present), we show the local stability for the three types of equilibrium. The local stability of the equilibrium solutions depends on the diffusion rates of predator and prey. By comparing the conditions of the system (1.1) and those of the system (1.2), we find that the delays affect the local stability of all three equilibrium solutions. Besides, with specific delay kernels, we present the existence, uniqueness, and boundedness of the solutions.

To study the effects of the two delays separately, we have considered two special cases: when the delay is present only in the prey term, and when the delay is present only in the predator term. We have shown that under the same conditions, the first of these subsystems can occur Hopf bifurcation near the positive constant equilibrium, while the second one does not occur Hopf bifurcation.

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