Research Article

Bifurcation Analysis in a Delayed Diffusive Leslie-Gower Model

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We investigate a modified delayed Leslie-Gower model under homogeneous Neumann boundary conditions. We give the stability analysis of the equilibria of the model and show the existence of Hopf bifurcation at the positive equilibrium under some conditions. Furthermore, we investigate the stability and direction of bifurcating periodic orbits by using normal form theorem and the center manifold theorem.

1. Introduction

The dynamic relationship between predators and their preys has long been and will continue to be one of dominant themes in both ecology and mathematical ecology due to its universal existence and importance. A major trend in theoretical work on prey-predator dynamics has been to derive more realistic models, trying to keep to maximum the unavoidable increase in complexity of their mathematics [1]. In this optic, recent years, the important Leslie-Gower predator-prey model [2,3] has been extensively studied in [4–7]. A modified version of Leslie-Gower predator-prey model with Holling-type II functional response takes the form

\[
\begin{align*}
\frac{dH}{dt} &= H\left(a_1 - bH\right) - \frac{c_1 HP}{k_1 + H}, \\
\frac{dP}{dt} &= P\left(a_2 - \frac{c_2 P}{k_2 + H}\right),
\end{align*}
\]

where \(H\) and \(P\) represent prey and predator population densities at time \(t\), respectively. \(a_1, a_2, b, c_1, c_2, k_1,\) and \(k_2\) are positive constants. \(a_1\) is the growth rate of prey \(H\). \(a_2\) describes the growth rate of predator \(P\). \(b\) measures the strength of competition among individuals of species \(H\). \(c_1\) is the maximum value of the per capita reduction of \(H\) due to \(P\), and \(c_2\) is the maximum value of the per capita reduction of \(P\) due to \(H\), which is not available in abundance. \(k_1\) measures the extent to which environment provides protection to prey \(H\). \(k_2\) measures the extent to which environment provides protection to the predator \(P\).

On the other hand, time delay plays an important role in many biological dynamical systems, being particularly relevant in ecology [1]. For some predator-prey systems, the rate of the prey population depends on the predation of predator in the earlier times [8–14]. The results indicated that delay differential equations exhibit much more complicated dynamics than ordinary differential equations since a time delay could cause a stable equilibrium to become unstable and induce bifurcations.

In this paper, we will focus on the complex dynamics of the delay effect in the extended reaction-diffusion model. The reproduction of the individuals is modeled by diffusion with diffusion coefficients \(D_1 > 0\) and \(D_2 > 0\) for the prey and predator, respectively. This basic model is described by a system of two partial differential equations:

\[
\begin{align*}
\frac{\partial H}{\partial t} &= H\left(a_1 - bH\right) - \frac{c_1 HP(t - \tau)}{k_1 + H} + D_1 \Delta H, \quad x \in \Omega, \quad t > 0, \\
\frac{\partial P}{\partial t} &= P\left(a_2 - \frac{c_2 P}{k_2 + H}\right) + D_2 \Delta P, \quad x \in \Omega, \quad t > 0, \\
\frac{\partial H}{\partial n} &= \frac{\partial P}{\partial n} = 0, \quad x \in \partial \Omega, \quad t > 0,
\end{align*}
\]

where \(H = H(t, x), P = P(t, x), \Delta = \partial^2/\partial x^2, \Omega\) is a bounded open domain in \(\mathbb{R}\) with boundary \(\partial \Omega\), \(n\) is the outward unit normal vector of \(\partial \Omega\).
normal vector on $\partial \Omega$, and homogeneous Neumann boundary conditions reflect the situation where the population cannot move across the boundary of the domain. And we incorporate a single discrete delay $\tau > 0$ in the negative feedback of the predator's density.

The rest of the paper is organized as follows. In Section 2, we give the stability property of the equilibria of model (1). In Section 3, we mainly analyze the distribution of the roots of the characteristic equation and show the occurrence of Hopf bifurcation at the positive equilibrium of model (2) under some conditions. In Section 4, we investigate the stability and direction of bifurcating periodic orbits by using normal form theorems and the center manifold theorem, corresponding to theorems we also give some numerical simulations.

## 2. Equilibria Stability

In this section, we consider the existence and stability of the equilibria of model (1).

It is easy to verify that model (1) always has three boundary equilibria:

(i) $E_1 = (0, 0)$ (extinction of prey and predator), which is a nodal source point;

(ii) $E_2 = (a_1/b, 0)$ (extinction of the predator), which is a saddle point;

(iii) $E_3 = (0, a_2 k_2/c_2)$ (extinction of the prey), which is a stable node when $a_2 k_2/c_2 > a_1 k_1/c_1$.

For the positive equilibria, we have

$$a_1 - b H - \frac{c_2 P}{k_1 + H} = 0, \quad a_2 - \frac{c_2 P}{k_2 + H} = 0, \quad (3)$$

which yields

$$b c_2 H^2 - (a_1 c_2 - a_2 c_1 - b c_2 k_1) H + a_2 c_1 k_2 - a_1 c_1 k_1 = 0. \quad (4)$$

For simplicity, we define

$$A = b c_2, \quad B = a_1 c_2 - a_2 c_1 - b c_2 k_1, \quad C = a_2 c_1 k_2 - a_1 c_2 k_1, \quad (5)$$

then (4) can be written as

$$AH^2 - BH + C = 0, \quad (6)$$

which has two roots given by

$$h_+ = \frac{B + \sqrt{B^2 - 4AC}}{2A}, \quad h_- = \frac{B - \sqrt{B^2 - 4AC}}{2A}. \quad (7)$$

Case 1 ($C < 0$, i.e., $k_2 < a_1 c_2 k_1/a_2 c_1$). Model (1) has a unique positive equilibrium $E^* = (h^*, p^*) = (h_+, (a_2/c_2)(h_+ + k_2))$.

Case 2 ($C = 0$, i.e., $k_2 = a_1 c_2 k_1/a_2 c_1$).

(i) If $B > 0$, that is, $k_1 < (a_1 c_2 - a_2 c_1)/b c_2$, model (1) has a unique positive equilibrium $E = (h, p) = (h_+, (a_2/c_2)(h_+ + k_2))$;

(ii) If $B \leq 0$, that is, $k_1 \geq (a_1 c_2 - a_2 c_1)/b c_2$, (4) has no positive root; hence model (1) has no positive equilibrium.

Case 3 ($C > 0$, i.e., $k_2 > a_1 c_2 k_1/a_2 c_1$).

(i) Suppose that $B > 0$, that is, $k_1 < (a_1 c_2 - a_2 c_1)/b c_2$, then

(ii) If $B^2 - 4AC > 0$, that is, $k_2 < (a_1 c_2 - a_2 c_1 - b c_2 k_1)^2/4a_1 b c_2 c_1 + k_1$, model (1) has two positive equilibria $E_1 = (h_1, p_1) = (h_+, (a_2/c_2)(h_+ + k_2))$ and $E_2 = (h_+, p_2) = (h_+, (a_2/c_2)(h_+ + k_2))$;

(iii) If $B^2 - 4AC = 0$, that is, $k_2 = (a_1 c_2 - a_2 c_1 - b c_2 k_1)^2/4a_1 b c_2 c_1 + k_1$, (4) has a unique positive root of multiplicity 2 given by $h_+ = B/2A = h_+ = h_+$, then model (1) has a unique positive equilibrium $E = (h_+, p_2) = (h_+, (a_2/c_2)(h_+ + k_2))$;

(iv) If $B^2 - 4AC < 0$, that is, $k_2 > (a_1 c_2 - a_2 c_1 - b c_2 k_1)^2/4a_1 b c_2 c_1 + k_1$, (4) has no positive root; hence model (1) has no positive equilibrium.

We show the bifurcation diagram to display the distribution of the positive roots; in Figure 1, the whole region has been divided into six parts; the number indicates the number of positive equilibria.

Next, we analyze the stability of these positive equilibria. Let $E = (h, p)$ be arbitrary positive equilibrium, and the Jacobian matrix for $E = (h, p)$ is given by

$$J(E) = \begin{pmatrix} -bh + \frac{c_1 hp}{(h + k_1)^2} & -c_1 h \\ \frac{a_2 k_1}{c_2} & -a_2 \end{pmatrix}. \quad (8)$$
Hence, \( \det(J(E^*)) > 0, \det(J(\overline{E})) > 0, \det(J(E_3)) > 0, \det(J(E_-)) < 0, \) and \( \det(J(E_2)) = 0. \) Obviously, the positive equilibrium \( E_+ \) is a saddle point.

In the following, we study the stability of other positive equilibria. The sign of \( \text{tr}(J(E)) \) is determined by

\[
G_1(h) = h(a_1 - a_2 - 2bh) - (a_2 + bh)k_1, \tag{13}
\]

Then we can get

\[
G_1(h^*) = \frac{h^*a_2(c_1 - c_2)}{c_2} - \frac{h^*\sqrt{B^2 - 4AC}}{c_2} - a_2k_1,
\]

\[
G_1(h) = \frac{\overline{h}a_2(c_1 - c_2)}{c_2} - \frac{\overline{h}B}{c_2} - a_2k_1,
\]

\[
G_1(h_-) = \frac{h_-a_2(c_1 - c_2)}{c_2} - a_2k_1.
\]

Hence, if \( c_1 \leq c_2, \) then \( \text{tr}(J(E^*)) < 0, \text{tr}(J(\overline{E})) < 0, \) and \( \text{tr}(J(E_2)) < 0 \) are true. Summarizing the above, we can obtain the following theorem.

**Theorem 1.** For model (1),

(i) if \( k_2 < a_1c_1k_1/a_2c_1 \) holds, the unique positive equilibrium \( E^+ \) is locally asymptotically stable for \( c_1 \leq c_2; \)

(ii) if \( k_2 = a_1c_1k_1/a_2c_1 \) and \( k_1 < (a_1c_2 - a_2c_2)/bc_2 \) hold, the unique positive equilibrium \( \overline{E} \) is locally asymptotically stable for \( c_1 \leq c_2; \)

(iii) if \( a_1c_2k_1/a_2c_1 < k_2 < (a_1c_1 - a_1c_2 - bc_2k_1)^2/4a_2bc_2c_1 + k_1 \) and \( k_1 < (a_1c_2 - a_2c_1)/bc_2 \) hold, model (1) has two positive equilibria, the positive equilibrium \( E_+ \) is locally asymptotically stable for \( c_1 \leq c_2, \) and \( E_- \) is a saddle point.

Figure 2 shows the dynamics of model (1). In this case, \( E_1 \) is a nodal source point; \( E_2 \) is a saddle point; \( E_3 \) is a nodal sink point, which is locally asymptotically stable; \( E_+ \) is locally asymptotically stable; \( E_- \) is a saddle point. There exists a separatrix curve determined by the stable manifold of \( E_+, \) which divides the behavior of trajectories; that is, the stable manifold of saddle \( E_- \) splits the feasible region into two parts such that orbits initiating inside tend to the positive equilibrium \( E_+, \) while orbits initiating outside tend to \( E_3 \) except for the stable manifolds of \( E_- \). This means that, in this situation, the trajectories of the model can have different behavior strongly depending on the initial conditions.

**Theorem 2.** For model (1), if the unique positive equilibrium \( E_+ = \left(h_+, (a_2/c_2)(h_+ + k_2)\right) \) exists, and \( k_1 = (a_1c_2 - a_2c_1)(c_1 - c_2)/bc_2(c_1 + c_2), \) then it is a cusp of codimension 2.
Proof. The Jacobian matrix at $E_c = (h_c, p_c)$ is

$$J_{E_c} = \begin{pmatrix} \frac{a_2 c_1 (a_2 c_1 - a_1 c_2 + b c_1 k_1)}{c_1 (a_2 c_1 - a_1 c_2 + b c_1 k_1)} & \frac{c_1 (a_2 c_1 - a_1 c_2 + b c_1 k_1)}{b c_1 k_1 - a_2 c_1 + a_1 c_2} \\ \frac{a_2^2}{c_2} & -a_2 \end{pmatrix},$$

we have know that $\det(J_{E_c}) = 0$. Moreover, $\text{tr}(J_{E_c}) = 0$, if and only if

$$k_1 = \frac{(a_1 c_2 - a_2 c_2) (c_1 - c_2)}{b c_1 (c_1 + c_2)}.$$

Then

$$J_{E_c} = \begin{pmatrix} a_2 & -c_2 \\ a_2^2 & -a_2 \end{pmatrix} = a_2 \begin{pmatrix} 1 & -\frac{c_2}{a_2} \\ \frac{a_2}{c_2} & -1 \end{pmatrix},$$

and the associate Jordan matrix is

$$\tilde{J} = \begin{pmatrix} 0 & \frac{c_1 (a_1 c_2 - a_2 c_2 + b c_1 k_1)}{b c_1 k_1 - a_2 c_1 + a_1 c_2} \\ 0 & 0 \end{pmatrix}.$$

Hence, following [15, 16], we know that the unique positive equilibrium $E_c$ is a cusp of codimension 2. $\square$

3. Stability and Hopf Bifurcation Analysis in Delayed Reaction-Diffusion Model (2)

According to the previous section, for model (1), we know that $E_1, E_2$, and $E_3$ are unstable and $E_c$ is a saddle point, and note that a solution of the model (1) is also a solution of the model (2), so they are also unstable for model (2). In the following, we will focus on the dynamics of the positive equilibria of model (2). As an example, we only give the proof of the unique positive equilibrium $E^*_{\gamma}$ of model (2).

Introducing small perturbations $\tilde{H} = H - h^*$, and $\tilde{P} = P - p^*$ and dropping the hats for simplicity of notation, then we have

$$\frac{\partial H}{\partial t} = (H + h^*) (a_1 - b (H + h^*))$$

$$+ \frac{c_1 (H + h^*) (P (t - \tau) + p^*)}{k_1 + H + h^*}$$

$$+ D_1 \Delta H, \quad x \in \Omega, \quad t > 0,$n

$$\frac{\partial P}{\partial t} = (P + p^*) (a_2 - \frac{c_2 (P + p^*)}{k_2 + H + h^*})$$

$$+ D_2 \Delta P, \quad x \in \Omega, \quad t > 0,$$n

$$\frac{\partial H}{\partial \nu} = \frac{\partial P}{\partial \nu} = 0, \quad x \in \partial \Omega, \quad t > 0.$$

Denote

$$X = \left\{ H, P \in W^{2,2} (\Omega) : \frac{\partial H}{\partial \nu} = \frac{\partial P}{\partial \nu} = 0, \quad x \in \partial \Omega \right\}. \quad (20)$$

In the abstract space $C([-\tau, 0], X)$, model (19) can be regarded as the following abstract functional differential equation.

$$\frac{dU}{dt} = D \Delta U + L (U_t) + F (\phi), \quad (21)$$

where $U = (H, P)^T, U_t = U (t + \theta, \theta \in [-\tau, 0], D = \left( \frac{D_1}{D_2} \right)$, dom$(\Delta) \subset X$, and $L : C([-\tau, 0], X) \mapsto X, F : C([-\tau, 0], X) \mapsto X$ are given by

$$L (\phi) = \begin{pmatrix} -bh^* + \frac{c_1 h^* p^*}{(h^* + k_1)^2} \phi_1 (0) + \frac{c_1 h^*}{h^* + k_1} \phi_2 (0) \\ \frac{a_2}{c_2} \phi_1 (0) - a_2 \phi_2 (0) \end{pmatrix},$$

$$F (\phi) = \begin{pmatrix} -\frac{c_1 k_1 p^*}{(k_1 + h^*)^2} \phi_1 (0) + \frac{c_1 k_1}{(k_1 + h^*)} \phi_2 (0) - \frac{c_1 k_1 p^*}{(k_1 + h^*)^2} \phi_1 (0) \phi_2 (0) - \frac{c_1 k_1}{(k_1 + h^*)^2} \phi_2 (0) \phi_2 (0) \end{pmatrix} \quad (22)$$

here $\phi = (\phi_1, \phi_2)^T = U_t \in C([-\tau, 0], X).$ Then the linearization of model (19) near $(h^*, p^*)$ is

$$\frac{dU}{dt} = D \Delta U + L (U_t). \quad (23)$$

Following [17], we obtain that the characteristic equation for liner model (23) is

$$\lambda y - D \Delta y - L (e^{\lambda \tau} y) = 0, \quad y \in \text{dom}(\Delta) \subset X, \quad y \neq 0. \quad (24)$$

It is well known that the eigenvalue problem

$$-\Delta \psi = \mu \psi, \quad x \in \Omega, \quad \frac{\partial \psi}{\partial \nu} = 0, \quad x \in \partial \Omega, \quad (25)$$

has eigenvalues $\mu_n = \{ \mu_n = -D_n \nu^2, i = 1, 2, \ldots, n = 0, 1, 2, \ldots \}$, with the corresponding eigenfunctions $\psi_n (x) = \cos nx$ ($n \in \mathbb{N} = \{0, 1, 2, \ldots \}$).

Substituting $y = \sum_{n=0}^{\infty} \cos nx (y_{1n}, y_{2n})^T$ into characteristic equation (24), we obtain

$$\begin{pmatrix} -bh^* + \frac{c_1 h^* p^*}{(h^* + k_1)^2} - \frac{c_1 h^*}{h^* + k_1} e^{-\lambda \tau} \end{pmatrix} y_{1n} = \begin{pmatrix} \frac{a_2}{c_2} \\ -a_2 - D_n n^2 \end{pmatrix} \begin{pmatrix} y_{2n} \\ y_{2n} \end{pmatrix} \quad (26)$$
Therefore the characteristic equation (24) is equivalent to
\[ \lambda^2 + A_n \lambda + B_n e^{-\lambda \tau} + C_n = 0, \quad n \in \mathbb{N}, \] (27)
where
\[ A_n = (D_1 + D_2) n^2 + a_2 + bh^* - \frac{c_1 h^* p^*}{(h^* + k_1)^2}, \]
\[ B_n = \frac{a_2 c_1 h^*}{c_2 (h^* + k_1)^2}, \]
\[ C_n = D_1 D_2 n^4 + \left( D_1 + D_2 + a_2 + bh^* - \frac{c_1 h^* p^*}{(h^* + k_1)^2} \right) n^2 + a_2 bh^* - \frac{a_2 c_1 h^* p^*}{(h^* + k_1)^2}. \] (28)

The stability of the positive equilibrium \( E^* \) can be determined by the distribution of the roots of (27); that is, the equilibrium \( E^* \) is locally asymptotically stable if all the roots of (27) have negative real parts. From the result of [18], the sum of the multiplicities of the roots of (27) in the open right half plane changes only if a root appears on or crosses the imaginary axis. It can be verified that \( \lambda = 0 \) is not a root of (27) for \( n \in \mathbb{N} \).

**Theorem 3.** If \( k_2 < \min(a_1c_1k_1/a_1c_1, bc_2(h^* + k_1)^2/a_2c_2 - 2h^* - k_1) \) holds, then the unique positive equilibrium \( E^* \) of model (2) is locally asymptotically stable.

**Proof.** Let \( \pm i \omega \) (\( \omega > 0 \)) be a pair of roots of (27); substituting \( i \omega \) into (27), then we have
\[ -\omega^2 + A_n \omega + B_n e^{-\omega \tau} + C_n = 0. \] (29)
Separating the real part from image part, we have
\[ -\omega^2 + B_n \cos \omega \tau + C_n = 0, \]
\[ A_n \omega - B_n \sin \omega \tau = 0, \] (30)
then
\[ \omega^4 + \left( A_n^2 - 2C_n \right) \omega^2 + C_n^2 - B_n^2 = 0, \] (31)
where
\[ A_n^2 - 2C_n = \left( bh^* - \frac{c_1 h^* p^*}{(h^* + k_1)^2} + D_1 n^2 \right)^2 + \left( a_2 + D_2 n^2 \right)^2 > 0, \]
\[ C_n^2 - B_n^2 = D_1 D_2 n^4 + \left( D_1 + D_2 + a_2 + bh^* - \frac{c_1 h^* p^*}{(h^* + k_1)^2} \right) n^2 \]
\[ - \frac{a_2 c_1 h^* p^*}{(h^* + k_1)^2} - \frac{a_2 c_1^2 (h^*)^2}{c_2^2 (h^* + k_1)^2} + a_2 bh^*. \] (32)

Obviously, if \( k_2 < bc_2(h^* + k_1)^2/a_2c_2 - 2h^* - k_1, C_n^2 - B_n^2 > 0 \) is true. Thus (31) has no positive roots for all \( n \in \mathbb{N} \). Hence, all the roots of (27) have negative real part. This completes the proof.

If there exists an integer \( n_0 \in \mathbb{N} \) such that for \( 0 \leq n \leq n_0 \), \( C_n^2 - B_n^2 < 0 \), then (31) has a unique positive real root
\[ \omega_n^0 = \sqrt{\frac{-\left( A_n^2 - 2C_n \right) + \sqrt{(A_n^2 - 2C_n)^2 - 4C_n^2 B_n^2}}{2}}, \] (33)
and (27) has a pair of pure imaginary roots \( \pm i \omega_n^0 \), and
\[ \tau_n^j = \tau_n^0 + \frac{2\pi j}{\omega_n^0}, \quad j = 0, 1, 2, \ldots, 0 \leq n \leq n_0, \quad n_0 \in \mathbb{N}, \] (34)
where \( \tau_n^0 = \arccos((\omega_n^0, -C_n)/B_n)/\omega_n^0 \).

Let \( \lambda(\tau) = y(\tau) + i \omega(\tau) \) be the root of (24), where \( y(\tau_n^j) = 0 \) and \( \omega(\tau_n^j) = \omega_n^0 \) when \( \tau \) is close to \( \tau_n^j \). Then we have the following transversality condition.

**Lemma 4.** For \( 0 \leq n \leq n_0 (n_0 \in \mathbb{N}) \), if

(H1) \( D_1 D_2 n^4 + (D_1 + D_2 + a_2 + bh^* - c_1 h^* p^*/(h^* + k_1)^2) n^2 < \frac{a_2 c_1^2 (h^*)^2}{c_2^2 (h^* + k_1)^2} - a_2 bh^* \) holds, then \( (dy/d\tau)_{\tau=\tau_n^j} > 0 \) for \( j = 0, 1, 2, \ldots \).

From this transversality condition, we know that when \( \tau \) passes through these critical values \( \tau_n^j \), the sum of the multiplicities of the roots of (27) in the open right half plane will increases at least two.

Summarizing the above results, we can obtain the following theorem.

**Theorem 5.** For \( 0 \leq n \leq n_0 (n_0 \in \mathbb{N}) \) if (H1) holds, the following statements are true:

(i) if \( \tau < \tau_n^0 \), then the equilibrium point \( E^* \) is locally asymptotically stable;

(ii) if \( \tau > \tau_n^0 \), then the equilibrium \( E^* \) is unstable;

(iii) \( \tau = \tau_n^j (j = 0, 1, 2, \ldots) \) are Hopf bifurcation values of model (2).

### 4. Direction and Stability of Spatial Hopf Bifurcation

In the previous section, we have obtained the conditions under which model (2) undergoes a Hopf bifurcation at the equilibrium point \( E^* \) when \( \tau \) crosses though the critical value \( \tau_n^j (0 \leq n \leq n_0, n_0 \in \mathbb{N}, j = 0, 1, 2, \ldots) \). In this section, we will study the direction of the Hopf bifurcation and the stability of the bifurcating periodic solutions by employing the center manifold theorem and normal form method [17, 19] for partial differential equations with delay.
Then we compute the direction and stability of the Hopf bifurcation when \( \tau = \tau_0^* \) for fixed \( j \in \{0, 1, 2, \ldots \} \).

Define

\[
\begin{align*}
\mu &= - \frac{\text{Re}(c_1(0))}{\text{Re}(\lambda'(\tau))}, \\
\beta_2 &= 2 \text{Re}(c_1(0)), \\
T_2 &= - \frac{\text{Im}(c_1(0)) + \mu \text{Im}(\lambda'(\tau))}{\omega_0^2 \tau},
\end{align*}
\]

where \( c_1(0) \) is defined in the appendix. Then we can get the following theorem.

**Theorem 6.** For model (19), if (H1) holds, we have the following:

(i) \( \mu \) determines the direction of the Hopf bifurcation: if \( \mu > 0 (\mu < 0) \), then the bifurcating periodic solutions exist for \( \tau > \tau (\tau < \tau) \);

(ii) \( \beta_2 \) determines the stability of bifurcating periodic solutions: the bifurcating periodic solutions are orbitally asymptotically stable (unstable) if \( \beta_2 < 0 (\beta_2 > 0) \);

(iii) \( T_2 \) determines the period of the bifurcating periodic solutions: the period increases (decreases) if \( T_2 > 0 (T_2 < 0) \).

The proof is deferred to the appendix.

**5. Conclusions and Remarks**

In this paper, we have considered a modified version of Leslie-Gower model with Holling-type II functional and delayed diffusive predator-prey model under homogeneous Neumann boundary conditions. The value of this study lies in two folds. First, it presents local asymptotic stability of the equilibria of model with and without delay and the existence of Hopf bifurcation, which indicates that the dynamics induced by time delay are rich and complex. Second, it gives the analysis of direction and stability of spatial Hopf bifurcation, from which one can find that small sufficiently delays cannot change the stability of the positive equilibrium and large delays cannot only destabilize the positive equilibrium but also induce oscillatory behaviors near the positive equilibrium.

In the following, we give some numerical examples to illustrate the dynamical behaviors of model (2). In Figure 3, \( \tau = 2 < \tau_0^* = 3.435144529 \), the unique positive equilibrium \( E^* = (2, 1.5) \) remains the stability; the population of the predator and the prey will tend to a steady state. However, in Figure 4, \( \tau = 4 > \tau_0^* = 3.435144529 \), the positive equilibrium \( E^* \) loses its stability and Hopf bifurcation occurs, which means that a family of stable periodic solutions bifurcate from \( E^* \) and the system goes into oscillations; it means that the predator coexists with the prey with oscillatory behaviors.

Our results show that time-delay can make a stable equilibrium to become unstable and induce Hopf bifurcation and the system goes into oscillations; that's to say, the dynamical behaviors of the delay reaction-diffusion equations are much more complex and rich than reaction-diffusion equations.

**Appendix**

**A. The Proof of Theorem 6**

Setting \( \tau = \tau + \alpha \), then \( \alpha = 0 \) is the Hopf bifurcation of model (19). Let \( \bar{H}(t,x) = H(\tau t,x), \bar{P}(t,x) = P(\tau t,x) \), and drop the tilde for the sake of simplicity, then (19) can be transformed into

\[
\begin{align*}
\frac{\partial H}{\partial t} &= \tau (H + h^*)(a_1 - b (H + h*)) \\
&\quad - \frac{c_1 (H + h^*)(P (t - 1) + p^*)}{k_1 + H + h^*} \\
&\quad + D_1 \Delta H, \quad x \in \Omega, \ t > 0, \\
\frac{\partial P}{\partial t} &= \tau (P + p^*)(a_2 - \frac{c_2 (P + p^*)}{k_2 + H + h^*}) \\
&\quad + D_2 \Delta P, \quad x \in \Omega, \ t > 0, \\
\frac{\partial H}{\partial n} &= \frac{\partial P}{\partial n} = 0, \quad x \in \partial \Omega, \ t > 0.
\end{align*}
\]

And the abstract functional differential equation can also be written in the form

\[
\frac{dU}{dt} = \tau D \Delta U + \tau L(U_t) + G(U, \alpha),
\]

where

\[
L(\phi) = \left( \begin{array}{c}
- b h^* + \frac{c_1 h^* p^*}{(h^* + k_1)^2} \\
\frac{c_1 h^* (k_1 + h^*)}{(h^* + k_1)} \phi_1(0) - \frac{c_1 h^*}{k_1} \phi_2(-1) \\
\frac{a_2}{c_2} \phi_1(0) - a \phi_2(0)
\end{array} \right),
\]

\[
G(\phi, \alpha) = \alpha D \Delta \phi + \alpha L(\phi) + (\tau + \alpha) F(\phi),
\]

\[
F(\phi) = \left( \begin{array}{c}
\frac{c_1 k_1 p^*}{(k_1 + h^*)^3} \phi_1^2(0) - \frac{c_1 k_1}{(k_1 + h^*)^2} \phi_1(0) \phi_2(-1) \\
\frac{c_2 p^*}{(k_2 + h^*)^3} \phi_1^2(0) + \frac{2 c_2 p^*}{(k_2 + h^*)^2} \phi_1(0) \phi_2(0) - \frac{c_2}{k_2 + h^*} \phi_2^2(0)
\end{array} \right),
\]

for \( \phi = (\phi_1, \phi_2) = U_t \in C([-1,0], X) \).

From Section 2, we know that \( \tau i \omega_0^2 \tau \) are a pair of simple purely imaginary eigenvalues of the liner system

\[
\frac{dU}{dt} = \tau L(U_t) + \tau D \Delta U,
\]

where \( U(t) = (H(t), P(t))^T \in R^2 \), and \( U_t(\theta) \) is defined by \( U_t(\theta) = U(t + \theta) \).
By using the Riesz representation theorem [20], we have a function $\eta(\theta, \alpha)$ of bounded variation for $\theta \in [-1, 0]$ such that

$$L(\phi) + D\Delta \phi(0) = \int_{-1}^{0} d\eta(\theta, \alpha) \phi(\theta),$$

(A.5)

for $\phi(\theta) \in C([-1, 0], R^2)$. Because in this paper, we discuss the existence of the Hopf bifurcation when $\tau = \tau^0$, that is $n = 0$; here we choose

$$\eta(\theta, \alpha) = \begin{pmatrix}
\frac{-bh^* + c_1 h^* p^*}{(h^* + k_1)^2} & 0 \\
\frac{\alpha_2}{c_2} & -\alpha_2 \\
0 & -\frac{-c_1 h^*}{h^* + k_1}
\end{pmatrix}\delta(\theta) \quad \begin{pmatrix}
0 \\
0 \\
\delta(\theta + 1)
\end{pmatrix},$$

(A.6)

where $\delta$ is the Dirac delta function. For $\phi(\theta) \in C^1([-1, 0], R^2)$, define $A(\alpha)$ as

$$A(\alpha) \phi = \begin{cases}
\frac{d\phi(\theta)}{d\theta}, & \theta \in [-1, 0), \\
\int_{-1}^{0} d\eta(\theta, \alpha) \phi(\theta), & \theta = 0.
\end{cases}$$

(A.7)

and for $\psi = (\psi_1, \psi_2) \in C^1([0, 1], (R^2)^*)$, define

$$A^*(\psi(s)) = \begin{cases}
\frac{d\psi(s)}{ds}, & s \in [-1, 0), \\
\int_{-1}^{0} \psi(-\xi) \, d\eta(\theta, 0), & s = 0.
\end{cases}$$

(A.8)
Then $A(0)$ and $A^*$ are adjoint operators under the bilinear form
\[
(\psi(s), \phi(\theta)) = \overline{\psi}(0)\phi(0) - \int_{-1}^{0} \int_{0}^{\theta} \overline{\psi}(\xi - \theta) \, d\eta(\theta, \alpha) \phi(\xi) \, d\xi.
\] (A.9)

We know that $\pm ia_0^\gamma$ are eigenvalues of $A(0)$. Since $A(0)$ and $A^*(0)$ are two adjoint operators, then $\pm ia_0^\gamma$ are also eigenvalue of $A^*$; we shall first try to obtain eigenvector of $A(0)$ and $A^*$ corresponding to the eigenvalues $ia_0^\gamma$ and $-ia_0^\gamma$, respectively. Let $q(\theta) = (1, \rho)^T e^{i\omega_0^\gamma t}$ be the eigenvector of $A(0)$ corresponding to the eigenvalue $ia_0^\gamma$. Then by definition of eigenvector we have $A(0)q(\theta) = q(\theta)i\omega_0^\gamma$. Therefore, from (A.5), (A.6), and definition of $A(0)$ we get
\[
\begin{pmatrix}
-bh^* + \frac{c_1 h^* p^*}{(h^* + k_1)^2} + ia_0^\gamma & -\frac{a_2}{c_2} \\
-\frac{c_1 h^* e^{-i\omega_0^\gamma \xi}}{h^* + k_1} & -a_2 - ia_0^\gamma
\end{pmatrix}
\begin{pmatrix}
1 \\
0
\end{pmatrix}
= (0, 0)^T.
\] (A.10)

we choose $\rho = a_2^2/c_2 (a_2 + ia_0^\gamma)$, and then we get $q(\theta)$. On the other hand, $q^*(s) = M(1, \gamma)e^{i\omega_0^\gamma s}$ is the eigenvector of $A^*$ corresponding to the eigenvalue $-ia_0^\gamma$. From the definition of $A^*$, we have
\[
\begin{pmatrix}
-bh^* + \frac{c_1 h^* p^*}{(h^* + k_1)^2} + ia_0^\gamma & \frac{a_2}{c_2} \\
-\frac{c_1 h^* e^{-i\omega_0^\gamma \xi}}{h^* + k_1} & -a_2 - ia_0^\gamma
\end{pmatrix}
\begin{pmatrix}
M \\
My
\end{pmatrix}
= (0, 0)^T.
\] (A.11)

where
\[
\gamma = \left( \frac{bh^* - \frac{c_1 h^* p^*}{(h^* + k_1)^2} - ia_0^\gamma}{a_2^2} \right) \frac{c_2}{a_2^2}.
\] (A.12)

We also assume that $(q^*(s), q(\theta)) = 1$. To obtain the value of $M$, from (A.9) we have
\[
(q^*(s), q(\theta)) = M \left\{ (1, \gamma)^T \right. \\
- \int_{-1}^{0} \int_{0}^{\theta} (1, \gamma) e^{-i(\xi - \theta) \omega_0^\gamma} \, d\eta(\theta, \alpha) (1, \rho)^T e^{i\omega_0^\gamma \xi} \, d\xi \right\},
\] (A.13)

then we choose
\[
M = \left( 1 + \rho \gamma + \frac{\rho c_1 h^*}{h^* + k_1} \right)^{-1} e^{i\omega_0^\gamma}
\] (A.14)
such that $(q^*(s), q(\theta)) = 0$ and $(q^*(s), q(\theta)) = 1$. In other words, let $\Phi = (q(\theta), \overline{q}(\theta))$, $\Psi = (q^*(s), \overline{q}^*(s))^T$, then $(\Psi, \Phi) = I$, and $I$ is unit matrix.

Then the center subspace of model (A.4) is $P = \text{span}[q(\theta), \overline{q}(\theta)]$, and the adjoint subspace is $P^* = \text{span}[q^*(s), \overline{q}^*(s)]$. Let $v = (v^1, v^2)^T$, where
\[
v^1 = (1, 0)^T, \quad v^2 = (0, 1)^T.
\] (A.15)

Let $m \cdot v$ be defined by
\[
m \cdot v = m_1 v^1 + m_2 v^2,
\] (A.16)

for $m = (m_1, m_2)^T \in \{ (-1, 0), X \}$. Hence the center subspace of linear system (A.4) is given by $P_{CN} \mathcal{C}$, where
\[
P_{CN} = \{ (q(\theta) z + \overline{q}(\theta) \overline{z}) \cdot v, z \in \mathbb{C} \},
\] (A.17)

and $\mathcal{C} = P_{CN} \mathcal{C} \oplus P_2 \mathcal{C}$, where $P_2 \mathcal{C}$ is the stable subspace.

From [17], we know that the infinitesimal generator $A_U$ of linear model (A.4) satisfies $A_U \psi = \psi(\theta)$; moreover $\psi \in \text{dom}(A_U)$ if and only if
\[
\psi(\theta) \in \mathcal{C}, \quad \psi(0) \in \text{dom}(\Delta),
\] (A.18)

First we define the coordinate to describe the center manifold at $\alpha = 0$; from center manifold we have
\[
w(t, \theta) = \omega(z(t), \overline{z}(t), \theta) = \omega_{20}(\theta) \frac{z^2}{2} + \omega_{11}(\theta) z \overline{z} + \omega_{02}(\theta) \frac{\overline{z}^2}{2} + \cdots.
\] (A.19)

The flow of model (A.2) in the center manifold can be written as follows:
\[
U_1 = \Phi(z, \overline{z})^T \cdot v + w(z, \overline{z}),
\] (A.20)

where
\[
\dot{z} = i\omega_0^\gamma z + q^*(0) \left( F(\Phi(z, \overline{z})^T \cdot v + w(z, \overline{z}), 0), v \right) = i\omega_0^\gamma z + g(z, \overline{z})
\] (A.21)

with
\[
g(z, \overline{z}) = q^*(0) \left( \frac{F(\Phi(z, \overline{z})^T \cdot v + w(z, \overline{z}), 0) \right), v \\
= g_{20} \frac{z^2}{2} + g_{11} z \overline{z} + g_{02} \frac{\overline{z}^2}{2} + g_{21} \frac{z^2}{2} \overline{z} \cdot \cdots.
\] (A.22)

Let
\[
f^1 = (H + h^*) (a_1 - b (H + h^*)^T) \\
- \frac{c_1 (H + h^*) (P (t - 1) + p^*)}{k_1 + H + h^*},
\] (A.23)
From above equations, we have
\[
\begin{align*}
\theta_{20} &= \frac{g_{20}}{2} \\
&= M \left( \rho \left( f_{110} + \bar{f}_{110} \right) + \rho e^{i\omega_0} \left( f_{101} + \bar{f}_{101} \right) + \rho^2 e^{-i\omega_0} \left( f_{011} + \bar{f}_{011} \right) + \frac{f_{100} + \bar{f}_{100}^2}{2} + \frac{\rho^2 (f_{010} + \bar{f}_{010})}{2} \right), \\
\theta_{11}(\theta) &= M \left( \rho \left( f_{110} + \bar{f}_{110} \right) + \rho e^{i\omega_0} \left( f_{101} + \bar{f}_{101} \right) \right) \\
&= M \left( \rho \left( f_{110} + \bar{f}_{110} \right) + \rho e^{i\omega_0} \left( f_{101} + \bar{f}_{101} \right) + \rho e^{-i\omega_0} \left( f_{101} + \bar{f}_{101} \right) + (f_{100} + \bar{f}_{100}^2) + \rho^2 (f_{010} + \bar{f}_{010}) + \rho \rho e^{i\omega_0} \left( f_{011} + f_{011} \right) \right) \\
\theta_{21} &= \frac{g_{21}}{2} \left( \rho \left( w_{110} + \bar{w}_{110} \right) + \rho e^{i\omega_0} \left( w_{101} + \bar{w}_{101} \right) \right)
\end{align*}
\]
From [17], we can know that \( \omega(z, \bar{z}) \) satisfies
\[
\dot{\omega} = A_{\omega} \omega + H(z, \bar{z}),
\]
where
\[
H(z, \bar{z}) = H_{20}(\theta) \frac{z^2}{2} + H_{11}(\theta) z \bar{z} + H_{02}(\theta) \frac{\bar{z}^2}{2} + \cdots
= X_0 F(U_1, 0) - \Phi(\Psi, (X_0 F(U_1, 0), v)) \cdot v.
\]
Again we write near the origin on \( C_0 \)
\[
\dot{\omega} = z \dot{w}_z + \bar{z} \dot{w}_{\bar{z}}
\]
By comparing (A.21) and (A.25) we get
\[
(A_{\omega} - 2 i \omega_0) \omega_{20}(\theta) = -H_{20}(\theta),
\]
\[
A_{\omega} \omega_{11}(\theta) = -H_{11}(\theta).
\]
When \(-1 \leq \theta < 0, H(z, \bar{z}) = -\Phi(\Psi(0) F(U_1, 0), v) \cdot v. \)
Therefore, for \(-1 \leq \theta < 0, H_{20}(\theta) = -[g_{20}q(\theta) + \bar{g}_{20}\bar{q}(\theta)] \cdot v,
\]
and for \(\theta = 0, H(z, \bar{z})(0) = F(U_1, 0) - \Phi(\Psi, (F(U_1, 0), v)) \cdot v, \)
then we obtain
\[
H_{20}(0) = -\left[ g_{20}q(0) + \bar{g}_{20}\bar{q}(0) \right] \cdot v
\]
\[
+ \bar{\tau} \left( \rho \left( f_{110} + \bar{f}_{110} \right) + \rho e^{i\omega_0} \left( f_{101} + \bar{f}_{101} \right) + \rho^2 e^{-i\omega_0} \left( f_{011} + \bar{f}_{011} \right) \right)
+ \frac{f_{200}^2}{2} + \frac{\rho^2 f_{200}^2}{2} + \frac{1}{2} \rho^2 e^{-i\omega_0} \frac{f_{020}^2}{2}
\]
\[
\left( \rho \rho e^{i\omega_0} \left( f_{110} + \bar{f}_{110} \right) \right)
+ \frac{f_{100}^2}{2} + \frac{\rho^2 f_{100}^2}{2} + \frac{1}{2} \rho^2 e^{-i\omega_0} \frac{f_{010}^2}{2}
\right)
\]
\[
H_{11}(0) = -\left[ g_{11}q(0) + \bar{g}_{11}\bar{q}(0) \right] \cdot v
+ \bar{\tau} \left( f_{110}^2 (\bar{p} + \rho) + f_{101}^2 (\bar{p} e^{i\omega_0} + \rho e^{-i\omega_0}) \right)
+ \bar{\tau} \left[ f_{011} (\rho \bar{p} e^{i\omega_0} + \rho \rho e^{-i\omega_0}) + f_{100}^2 \right]
\]
\[
+ f_{020}^2 (\bar{p} + \rho) + f_{200}^2 (\bar{p} e^{i\omega_0} + \rho e^{-i\omega_0})
+ f_{010} (\rho \bar{p} e^{i\omega_0} + \rho \rho e^{-i\omega_0}) + f_{200}^2
\right).
\]
By the definition of $A_U$, we have from (A.28)

$$w_{20} (\theta) = \frac{i g_{20}}{\omega_0^2} q - (0) e^{i \omega_0^0 \nu} \cdot v - \frac{i g_{20}}{3 \omega_0^0} \bar{q} (0) e^{-i \omega_0^0 \nu} \cdot v + E e^{i \omega_0^0 \nu},$$

(A.31)

where $E = (E^1, E^2) \in \mathbb{R}^2$ is a constant vector.

Similarly, we get

$$w_{11} (\theta) = -\frac{i g_{11}}{\omega_0^2} q (0) e^{i \omega_0^0 \nu} \cdot v + \frac{i g_{11}}{\omega_0^2} \bar{q} (0) e^{-i \omega_0^0 \nu} \cdot v + \bar{E},$$

(A.32)

where $\bar{E} = (\bar{E}^1, \bar{E}^2) \in \mathbb{R}^2$ is a constant vector.

Combining (A.5) and (A.28), we obtain

$$H_{20} (0) = 2i \omega_0^0 \bar{E} w_{20} (0) - \tau D \Delta w_{20} (0) - \tau L (w_{20} (\theta)),$$

(A.33)

therefore

$$
\left( \begin{array}{c}
\left( \rho \left( f_{110}^1 \right) + \rho e^{-i \omega_0^0} \left( f_{110}^0 \right) \right) \\
+ f_{200}^1 + \frac{\rho^2 f_{201}^0}{2} + \frac{1}{2} \rho^2 e^{-2i \omega_0^0} f_{002}^1 \\
\end{array} \right) \\
\left( \begin{array}{c}
\left( \rho \bar{f}_{110}^1 + \rho e^{-i \omega_0^0} \left( \bar{f}_{110}^0 \right) \right) \\
+ \bar{f}_{200}^1 + \frac{\rho^2 \bar{f}_{201}^0}{2} + \frac{1}{2} \rho^2 e^{-2i \omega_0^0} \bar{f}_{002}^1 \\
\end{array} \right)
= g_{20} q (\theta) + \overline{g}_{20} \bar{q} (\theta) + 2i \omega_0^0 n w_{20} (\theta)
$$

$$- \int_{-1}^{0} d \eta (\theta) w_{20} (\theta)

= -g_{20} q (0) + \frac{\overline{g}_{20} \bar{q} (0)}{3} + E 2i \omega_0^0 n
$$

$$- \int_{-1}^{0} d \eta (\theta) \left[ \frac{i g_{20}}{\omega_0^2} q (0) - \frac{i g_{20}}{3 \omega_0^0} \bar{q} (0) - E e^{2i \omega_0^0 \nu} \right]
$$

$$E \left( 2i \omega_0^0 n - \int_{-1}^{0} d \eta (\theta) e^{2i \omega_0^0 \nu} \right)
$$

$$= 2i E \omega_0^0 \left( \begin{array}{c}
1 \\
0 \\
0 \\
1
\end{array} \right)
$$

$$- \left( \begin{array}{c}
-b h + \frac{c_i h_p}{(h_i + k_i)^2} \\
\frac{a_2^2}{c_2} \\
\end{array} \right)
$$

$$E
$$

$$= \left( \begin{array}{c}
2i \omega_0^0 + b h + \frac{c_i h_p}{(h_i + k_i)^2} \\
\frac{a_2^2}{c_2} \\
\end{array} \right)
$$

from the above equation we can find the values of $E^1$ and $E^2$. From (A.28) we have

$$\int_{-1}^{0} d \eta (\theta) w_{11} (\theta) = -H_{11} (\theta).$$

Therefore

$$
\left( \begin{array}{c}
f_{110} (\overline{p} + \rho) + f_{110} (\rho \overline{p} e^{-i \omega_0^0} + \rho e^{-i \omega_0^0}) \\
+ f_{110} (\rho \overline{p} e^{-i \omega_0^0} + \rho e^{-i \omega_0^0}) + f_{200}^1 + f_{002}^1 \rho \overline{p} + f_{002}^1 \overline{p} \rho
\end{array} \right)
$$

$$\left( f_{110} (\overline{p} + \rho) + f_{110} (\rho \overline{p} e^{-i \omega_0^0} + \rho e^{-i \omega_0^0}) \\
+ f_{110} (\rho \overline{p} e^{-i \omega_0^0} + \rho e^{-i \omega_0^0}) + f_{200}^1 + f_{002}^1 \rho \overline{p} + f_{002}^1 \overline{p} \rho
\right)
$$

$$= g_{11} q (0) + \overline{g}_{11} \bar{q} (0) - \int_{-1}^{0} d \eta (\theta) w_{11} (\theta)
$$

$$= g_{11} q (0) + \overline{g}_{11} \bar{q} (0)
$$

$$- \int_{-1}^{0} d \eta (\theta) \left[ \frac{i g_{11}}{\omega_0^2} q (0) e^{i \omega_0^0 \nu} + \frac{i g_{11}}{\omega_0^2} e^{-i \omega_0^0 \nu} + \bar{E} \right]
$$

$$= -\int_{-1}^{0} d \eta (\theta) \bar{E}
$$

$$= \left( \begin{array}{c}
b h + \frac{c_i h_p}{(h_i + k_i)^2} \\
\frac{a_2^2}{c_2} \\
\end{array} \right)
$$

$$\left( \begin{array}{c}
\frac{c_i h_p}{(h_i + k_i)^2} \\
\frac{a_2^2}{c_2} \\
\end{array} \right)
$$

$$\bar{E}.$$ (A.35)

In a similar manner we can compute the corresponding results in $E^1$ and $E^2$. Then $g_{21}$ can be determined. Based on the above analysis, we can see that each $g_{ij}$ can be determined by the parameters. Thus we can compute the following values which determine the direction and stability of bifurcating periodic orbits:

$$c_1 (0) = \frac{i}{2 \omega_0^0} \left( g_{11} g_{20} - 2 |g_{20}|^2 - \frac{|g_{002}|^2}{3} \right) + \frac{g_{21}}{2},$$

$$\mu = \frac{\Re (c_1 (0))}{\Re (\lambda' (\overline{\tau}))},$$

$$T_2 = -\frac{\Im (c_1 (0)) + \mu_1 \Im (\lambda' (\overline{\tau}))}{\omega_0^0 \overline{\tau}}.$$ (A.36)

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