

Dynamics of a diffusive predator–prey model with herd behavior*

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Abstract. This paper is devoted to considering a diffusive predator–prey model with Leslie–Gower term and herd behavior subject to the homogeneous Neumann boundary conditions. Concretely, by choosing the proper bifurcation parameter, the local stability of constant equilibria of this model without diffusion and the existence of Hopf bifurcation are investigated by analyzing the distribution of the eigenvalues. Furthermore, the explicit formula for determining the direction of Hopf bifurcation and the stability of the bifurcating periodic solutions are also derived by applying the normal form theory. Next, we show the stability of positive constant equilibrium, the existence and stability of periodic solutions near positive constant equilibrium for the diffusive model. Finally, some numerical simulations are carried out to support the analytical results.

Keywords: diffusive predator–prey model, herd behavior, stability, Leslie-Gower term, Hopf bifurcation.

1 Introduction

A fundamental goal of theoretical ecology is to understand the interactions between different species, and between species and natural environment. Predator–prey model is one of the important models in ecosystems and has become a subject of intense research activities. In population dynamics, the functional response refers to the number of prey eaten per predator per unit time as a function of prey density. Generally, the functional response can be classified into many different types, such as Holling I–IV types [10, 11, 16, 19], Hassell–Varley type [9], Beddington–DeAngelis type [3, 6], Crowley–Martin type [5], Leslie–Gower type [13] and so on, and have been proposed and investigated widely [2, 7, 15, 18, 20, 21, 25, 31, 32].

Recently, predator–prey interactions have been studied for a more elaborated social model in which the individuals of one population gather together in herds, while the

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other one shows a more individualistic behavior. Based on the fact that predator–prey interactions occur mainly through the perimeter of the herd, a new predator–prey model described by the following ordinary differential equations (ODEs) was proposed in [1]:

$$\begin{aligned}\frac{du}{dt} &= u(1 - u) - \sqrt{uv}, \quad t > 0, \\ \frac{dv}{dt} &= \gamma v(-\beta + \sqrt{u}), \quad t > 0,\end{aligned}$$

where $u(t)$ and $v(t)$ stand for the prey and predator densities at time t , respectively. $\beta\gamma$ is the death rate of the predator in the absence of prey; γ is the conversion or consumption rate of prey to predator. This model is also known as the predator–prey model with herd behavior, and it has been shown that the sustained limit cycles are possible and the solution behavior near the origin is more subtle and interesting than the classical predator–prey models [1, 4].

In paper [23], taking into account the inhomogeneous distribution of the prey and predators in different spatial locations within a fixed bounded domain $\Omega \subset R$ at any given time, and the natural tendency of each species to diffuse to areas of smaller population concentration, the authors considered the following model:

$$\begin{aligned}\frac{\partial u}{\partial t} - d_1 \Delta u &= u(1 - u) - \sqrt{uv}, \quad (x, t) \in (0, \pi) \times (0, \infty), \\ \frac{\partial v}{\partial t} - d_2 \Delta v &= \gamma v(-\beta + \sqrt{u(t - \tau)}), \quad (x, t) \in (0, \pi) \times (0, \infty), \\ u_x(0, t) = u_x(\pi, t) &= v_x(0, t) = v_x(\pi, t) = 0, \quad t > 0, \\ u(x, t) = \phi(x, t) \geq 0, \quad v(x, t) &= \psi(x, t) \geq 0, \quad (x, t) \in [0, \pi] \times [-\tau, 0],\end{aligned}$$

subject to the homogeneous Neumann boundary conditions, $\tau \geq 0$ represents the time delay, $x \in (0, \pi)$ is the spatial habitat of the two species, $\Delta = \partial^2 / \partial x^2$ is the usual Laplacian operator, which is used to describe the Brownian motion, $d_1, d_2 > 0$ are the diffusion coefficients of species, β, γ are positive. The authors studied the stability of the positive equilibria and the existence of Hopf bifurcation induced by diffusion and delay, respectively. In paper [27], the authors considered the following spatial predator–prey model with herd behavior:

$$\begin{aligned}\frac{\partial u}{\partial t} &= u(1 - u) - \sqrt{uv} + \Delta u, \quad (x, t) \in (0, \pi) \times (0, \infty), \\ \frac{\partial v}{\partial t} &= v(-sv + c\sqrt{u}) + \delta \Delta v, \quad (x, t) \in (0, \pi) \times (0, \infty).\end{aligned}$$

The authors chose s as bifurcation parameter and obtained complex pattern replication: spotted pattern, stripe pattern, and coexistence of both were found by numerical simulations, where s is the coefficient of quadratic mortality.

Based on the assumptions in papers [13, 28] that the carrying capacity of the predator’s environment is assumed to be proportional to the prey abundance, we proposed the

following model:

$$\begin{aligned}u_t &= u(p - \alpha u) - \beta\sqrt{uv}, \quad t > 0, \\v_t &= sv\left(1 - \frac{v}{u}\right), \quad t > 0, \\u(0) &= u_0 \geq 0, \quad v(0) = v_0 \geq 0.\end{aligned}\tag{1}$$

Here the parameters p , s , α , β are positive, p is the birth rate of prey, α is the death rate of prey, β is the predation coefficient, s is the birth rate of the predator. The term v/u is called Leslie–Gower term, which was firstly proposed by Leslie and Gower in papers [12, 13]. Spatial diffusion is ubiquitous and can generate the rich spatiotemporal dynamics. So, we introduce the spatial diffusion into (1) and have the corresponding partial differential equations (PDEs) of (1) with homogeneous Neumann boundary conditions as follows:

$$\begin{aligned}\frac{\partial u}{\partial t} - d_1\Delta u &= u(p - \alpha u) - \beta\sqrt{uv}, \quad x \in \Omega, t > 0, \\ \frac{\partial v}{\partial t} - d_2\Delta v &= sv\left(1 - \frac{v}{u}\right), \quad x \in \Omega, t > 0, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} &= 0, \quad x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) &= v_0(x) \geq 0, \quad x \in \Omega,\end{aligned}\tag{2}$$

where $\Omega \subset R^n$ is a smooth and bounded domain, and ν is the outward unit normal vector of the smooth boundary $\partial\Omega$, $\Delta = \partial^2/\partial x_1^2 + \partial^2/\partial x_2^2 + \cdots + \partial^2/\partial x_n^2$ is the usual Laplacian operator in n -dimensional space $x = (x_1, x_2, \dots, x_n)$, which is used to describe the Brownian motion,

In fact, there are many papers with herb behavior, such as [17, 22, 27, 29]. In [27], the authors focused on the quadratic mortality and chose the quadratic mortality coefficient as bifurcation parameter. In [22], the authors discussed the steady-state bifurcation, that is to say, bifurcation of the elliptic equations. In [29], the authors investigated the predator–prey model with herd behavior, prey taxis and linear mortality for predator, while the authors investigated the predator–prey model with herd behavior, prey taxis and nonlinear mortality for predator in [17]. The two papers are concerned in the steady-state bifurcation of the model and point out that prey taxis play an important role in the determination of dynamics.

In this paper, we concentrate our attention on the dynamics of problems (1) and (2), such as the stability and analysis of Hopf bifurcation. The paper is organized as follows. In Section 2, the stability of constant solutions of problem (1) is obtained and the direction of Hopf bifurcation is also derived by choosing s as bifurcation parameter. The stability of the positive constant equilibrium of problem (2) and the existence of Hopf bifurcation are investigated by treating s as bifurcation parameter respectively in Section 3. Numerical simulations are shown in Section 4. Finally, the conclusions are given in Section 5.

2 Hopf bifurcation of ODE

In this section, we analyze problem (1) and derive the stability of constant solutions.

It is easy to see that problem (1) has two constant solutions $(p/\alpha, 0)$ and (u^*, v^*) , where $u^* = v^* = (\beta^2 + 2p\alpha - \beta\sqrt{\beta^2 + 4p\alpha})/2\alpha^2$.

- (I) The eigenvalues of (1) at $(p/\alpha, 0)$ are $\lambda_1 = -p < 0$, $\lambda_2 = s > 0$. Then $(p/\alpha, 0)$ is unstable.
- (II) At (u^*, v^*) , the Jacobian matrix takes the form

$$J(u^*, v^*) = \begin{pmatrix} \frac{1}{2}\beta\sqrt{u^*} - \alpha u^* & -\beta\sqrt{u^*} \\ s & -s \end{pmatrix}.$$

The characteristic equation is

$$\xi^2 + \xi \left(s - \frac{\beta}{2}\sqrt{u^*} + \alpha u^* \right) + \frac{\beta}{2}s\sqrt{u^*} + \alpha s u^* = 0. \quad (3)$$

Set

$$s_0 = \frac{\beta}{2}\sqrt{u^*} - \alpha u^*. \quad (4)$$

The two eigenvalues ξ_1, ξ_2 of (3) satisfy

$$\xi_1 + \xi_2 = s_0 - s, \quad (5)$$

$$\xi_1 \xi_2 = \frac{\beta}{2}s\sqrt{u^*} + \alpha s u^* > 0. \quad (6)$$

Obviously, if $s_0 \leq 0$, i.e., $3\beta^2 \leq 4\alpha p$, then $\xi_1 + \xi_2 < 0$, which implies that (u^*, v^*) is locally asymptotically stable.

Assume that $s_0 > 0$, i.e., $3\beta^2 > 4\alpha p$, we shall analyze the Hopf bifurcation occurring at (u^*, v^*) by treating s as the bifurcating parameter. When $s > s_0$, $\xi_1 + \xi_2 < 0$, then (u^*, v^*) is locally asymptotically stable; when $s < s_0$, $\xi_1 + \xi_2 > 0$, then (u^*, v^*) is unstable; when $s = s_0$, the Jacobi matrix $J((u^*, v^*))$ has a pair of imaginary eigenvalues $\xi = \pm i\omega(s_0)$. Let $\xi(s) = q(s) \pm i\omega(s)$ be the roots of (3), then

$$\begin{aligned} q(s) &= \frac{1}{2}(s_0 - s), & \omega(s) &= \frac{1}{2}\sqrt{4\xi_1\xi_2 - (\xi_1 + \xi_2)^2}, \\ q'(s)|_{s=s_0} &= -\frac{1}{2} < 0, \end{aligned} \quad (7)$$

where $s_0, \xi_1 + \xi_2$ and $\xi_1\xi_2$ are defined in (4), (5) and (6), respectively.

By the Poincaré–Andronov–Hopf bifurcation theorem, we know that problem (1) undergoes a Hopf bifurcation at (u^*, v^*) when $s = s_0$. However, the detailed nature of the Hopf bifurcation needs further analysis of the normal form of (1). Now we investigate the direction of Hopf bifurcation and stability of the bifurcating periodic solutions. After

a change of scale, we change (u^*, v^*) to the origin, and problem (1) is translated into

$$\begin{aligned} u_t &= (u + u^*)(p - \alpha(u + u^*)) - \beta\sqrt{(u + u^*)(v + u^*)}, \quad t > 0, \\ v_t &= s(v + u^*)\left(1 - \frac{(v + u^*)}{(u + u^*)}\right), \quad t > 0. \end{aligned} \tag{8}$$

Rewrite (8) as

$$\begin{pmatrix} u_t \\ v_t \end{pmatrix} = L_0(s) \begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} f(u, v, s) \\ g(u, v, s) \end{pmatrix} \tag{9}$$

with

$$\begin{aligned} L_0(s) &= \begin{pmatrix} \frac{\beta}{2}\sqrt{u^*} - \alpha u^* & -\beta\sqrt{u^*} \\ s & -s \end{pmatrix}, \\ f(u, v, s) &= \left(\frac{\beta}{8\sqrt{u^*}} - \alpha\right)u^2 - \frac{\beta}{2\sqrt{u^*}}uv - \frac{\beta}{16u^{*\frac{3}{2}}}u^3 + \frac{\beta}{8u^{*\frac{3}{2}}}u^2v + \dots, \\ g(u, v, s) &= -\frac{s}{u^*}u^2 + \frac{2s}{u^*}uv - \frac{s}{u^*}v^2 + \frac{s}{u^{*2}}u^3 - \frac{2s}{u^{*2}}u^2v + \frac{s}{u^{*2}}uv^2 + \dots. \end{aligned}$$

Set

$$B = \begin{pmatrix} 1 & 0 \\ M & N \end{pmatrix}$$

with $M = (\beta\sqrt{u^*} - \alpha u^* - 2q(s))/(2\beta\sqrt{u^*})$, $N = \omega(s)/(\beta\sqrt{u^*})$, where $q(s)$ and $\omega(s)$ are defined in (7). By the transformation

$$\begin{pmatrix} u \\ v \end{pmatrix} = B \begin{pmatrix} x \\ y \end{pmatrix},$$

problem (8) becomes

$$\begin{pmatrix} \dot{x}(t) \\ \dot{y}(t) \end{pmatrix} = L_1(s) \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} F^1(x, y, s) \\ F^2(x, y, s) \end{pmatrix}, \tag{10}$$

where

$$L_1(s) = \begin{pmatrix} q(s) & -\omega(s) \\ \omega(s) & q(s) \end{pmatrix},$$

$$\begin{aligned} F^1(x, y, s) &= \left[\frac{\beta(1-4M)}{8\sqrt{u^*}} - \alpha\right]x^2 - \frac{N\beta}{2\sqrt{u^*}}xy + \frac{\beta(2M-1)}{16u^{*3/2}}x^3 + \frac{N\beta}{8u^{*3/2}}x^2y + \dots, \\ F^2(x, y, s) &= \frac{1}{Nu^*} \left[M\alpha u^* - \frac{\beta}{8}M(1-4M)\sqrt{u^*} - s(M-1)^2 \right] x^2 \\ &+ \frac{1}{2u^*} (M\beta\sqrt{u^*} + 4s(1-M))xy \\ &- \frac{s}{u^*}Ny^2 + \frac{1}{Nu^{*3/2}} \left[s(1-M)^2\sqrt{u^*} - \frac{\beta M}{16} \right] x^3 \\ &+ \frac{1}{u^{*2}} \left[2s(M+1) - \frac{\beta}{8}M\sqrt{u^*} \right] x^2y + \frac{s}{u^*}Nxy^2 + \dots. \end{aligned}$$

In order to verify the stability of the periodic solutions, we need to calculate the sign of $\alpha(s_0)$ given by

$$\begin{aligned} \alpha(s_0) &= \frac{1}{16} [F^1_{xxx} + F^1_{xyy} + F^2_{xxy} + F^2_{xxx}] + \frac{1}{16\omega(s_0)} [F^1_{xy}(F^1_{xx} + F^1_{yy}) \\ &\quad - F^2_{xy}(F^2_{xx} + F^2_{yy}) - F^1_{xx}F^2_{xx} + F^1_{yy}F^2_{yy}] \\ &= \frac{1}{16} \left[\frac{3\beta(2M-1)}{8(u^*)^{3/2}} + \frac{1}{u^{*2}} (4s(1+M) - \frac{\beta}{4}M\sqrt{u^*}) \right] \\ &\quad + \frac{1}{16\omega(s_0)} \left[\frac{\beta}{8u^*} N(8\alpha\sqrt{u^*} - \beta(1-4M)) - \frac{1}{u^*} (4s(1-M) + \beta M\sqrt{u^*}) \right] \\ &\quad \times \left(\frac{\alpha M}{N} - \frac{\beta M(1-4M)}{8N\sqrt{u^*}} - \frac{s(M-1)^2}{Nu^*} - \frac{sN}{u^*} \right) \\ &\quad - \frac{4}{Nu^*} \left(-\frac{\beta}{8\sqrt{u^*}}(1-4M) - \alpha \right) \\ &\quad \times \left(\alpha Mu^* - \frac{\beta}{8}M(1-4M)\sqrt{u^*} - s(M-1)^2 \right). \end{aligned}$$

Then we denote that

$$\Lambda(s_0) = -\frac{\alpha(s_0)}{q(s_0)}.$$

Now, from the Poincaré–Andronov–Hopf theorem, $q'(s)|_{s=s_0} = -1/2 < 0$ and the above calculations of $\alpha(s_0)$, we obtain the following conclusions:

Theorem 1. For problem (1),

- (i) $(p/\alpha, 0)$ is unstable;
- (ii) When $3\beta^2 \leq 4\alpha p$, then the unique positive constant solution (u^*, v^*) is locally asymptotically stable;
- (iii) When $3\beta^2 > 4\alpha p$, if $s > s_0$, then (u^*, v^*) is locally asymptotically stable; if $s < s_0$, then (u^*, v^*) is unstable; if $s = s_0$, problem (1) undergoes a Hopf bifurcation. Moreover, if $\alpha(s_0) < 0$, the bifurcating periodic solutions are unstable, and the direction of Hopf bifurcation is subcritical; if $\alpha(s_0) > 0$, the bifurcating periodic solutions are stable, and the direction of Hopf bifurcation is supercritical.

3 Hopf bifurcation of PDE

In this section, we do analysis of problem (2). Firstly, we analyze the stability of trivial and nontrivial equilibria.

We know that problems (2) and (1) have the same equilibria. It is well known that stability can be yielded by eigenvalue analysis, and the matrix of linearization of system (2) at point (u, v) is

$$J_k(u, v) = \begin{pmatrix} -d_1\mu_k + p - 2\alpha u - \frac{1}{2}\beta\frac{v}{\sqrt{u}} & -\beta\sqrt{u} \\ s\frac{v^2}{u^2} & -d_2\mu_k + s - 2s\frac{v}{u} \end{pmatrix}, \quad (11)$$

where $k = 0, 1, 2, \dots$, μ_k is the eigenvalue of the following eigenvalue problem:

$$-\Delta\phi = \lambda\phi, \quad x \in \Omega,$$

$$\frac{\partial\phi}{\partial n} = 0, \quad x \in \partial\Omega,$$

and satisfies $0 = \mu_0 < \mu_1 \leq \mu_2 \leq \dots \leq \mu_k \rightarrow \infty$.

For $(p/\alpha, 0)$, we get

$$\text{Tr } J_k\left(\frac{p}{\alpha}, 0\right) = s - p - (d_1 + d_2)\mu_k,$$

$$\det J_k\left(\frac{p}{\alpha}, 0\right) = (d_1\mu_k + p)(d_2\mu_k - s).$$

It is easy to see that $\det J_0(p/\alpha, 0) = -ps < 0$, this means $(p/\alpha, 0)$ is unstable.

Substituting (u^*, v^*) into (11), we have

$$\text{Tr } J_k(u^*, v^*) = s_0 - s - (d_1 + d_2)\mu_k, \tag{12}$$

$$\det J_k(u^*, v^*) = (d_1\mu_k - s_0)(d_2\mu_k + s) + s\beta\sqrt{u^*}. \tag{13}$$

When $s_0 \leq 0$, for all $k = 0, 1, 2, \dots$, $\text{Tr } J_k(u^*, v^*) < 0$ and $\det J_k(u^*, v^*) > 0$ hold, which indicates that (u^*, v^*) is locally asymptotically stable. Similarly, when $s_0 > 0$, if $s > s_0$ and $s \geq d_2s_0/d_1$, then (u^*, v^*) is locally asymptotically stable. This indicates that the possible Hopf bifurcation value exists in the interval $s \in (0, s_0]$.

In what follows, we shall treat s as a bifurcation parameter and conclude the existence of Hopf bifurcation. From (12) and (13) we define

$$T(s, \mu) = -(d_1 + d_2)\mu + s_0 - s, \tag{14}$$

$$D(s, \mu) = d_1d_2\mu^2 + \mu(d_1s - d_2s_0) + s\left(\alpha u^* + \frac{1}{2}\beta\sqrt{u^*}\right), \tag{15}$$

$$H = \{(s, \mu) \in (0, s_0] \times (0, \infty) : T(s, \mu) = 0\}. \tag{16}$$

Then H is the Hopf bifurcation curve.

Let s_H be the possible Hopf bifurcation value. By [8, 26], to identify s_H be the Hopf bifurcation point, we recall the following sufficient conditions:

- (A) There exists $i \in N$ such that $T_i(s_H) = 0$ and $D_i(s_H) > 0$ hold, and as $i \neq j$, $T_j(s_H), D_j(s_H) \neq 0$, and the unique pair of complex eigenvalues $\lambda(s) = \sigma(s) \pm i\omega(s)$ near the imaginary axis satisfy $\sigma'(s_H) \neq 0, \omega(s_H) > 0$, where $T_i(s_H) = T(s_H, \mu_i), D_i(s_H) = D(s_H, \mu_i)$.

Let $T(s, \mu) = 0$, we can derive $s = s_0 - (d_1 + d_2)\mu$, so s is decreasing with respect to μ , thus there exists $n_0 \in N$ such that $\mu^* = s_0/(d_1 + d_2) \in (\mu_{n_0}, \mu_{n_0+1})$, and for problem (2), there are $n_0 + 1$ possible Hopf bifurcation points satisfying

$$s_0 = s_H^0 > s_H^1 > s_H^2 > \dots > s_H^{n_0} > s_H(\mu^*) = 0.$$

Next, we will show that under some additional conditions, $D_j(s_H^i) > 0$ holds for $0 \leq i \leq n_0$ and $j \in N$, then we must have $D_i(s_H^i) > 0$ and $D_j(s_H^i) \neq 0$ for $0 \leq i \leq n_0$ and $j \in N$ as required in condition (A).

We apply the technique adopted in [14, 30] and find

$$\begin{aligned} D_j(s_H^i) &= d_1 d_2 \mu_j^2 + \mu_j (d_1 s_H^i - d_2 s_0) - s_H^i (s_0 - \beta \sqrt{u^*}) \\ &\geq d_1 d_2 \mu_j^2 + \mu_j (d_1 s_H^{n_0} - d_2 s_0) - s_H^{n_0} (s_0 - \beta \sqrt{u^*}). \end{aligned}$$

If $d_1 s_H^{n_0} - d_2 s_0 \geq 0$, then $D_j(s_H^i) > 0$. Otherwise, when $d_1 s_H^{n_0} - d_2 s_0 < 0$, we have

$$\begin{aligned} D_j(s_H^i) &\geq d_1 d_2 \mu_j^2 + \mu_j (d_1 s_H^{n_0} - d_2 s_0) - s_H^{n_0} (s_0 - \beta \sqrt{u^*}) \\ &= \left(\sqrt{d_1 d_2} \mu_j + \frac{d_1 s_H^{n_0} - d_2 s_0}{2\sqrt{d_1 d_2}} \right)^2 - \frac{(d_1 s_H^{n_0} - d_2 s_0)^2}{4d_1 d_2} - s_H^{n_0} (s_0 - \beta \sqrt{u^*}) \\ &> -\frac{(d_1 s_H^{n_0} - d_2 s_0)^2}{4d_1 d_2} - s_H^{n_0} (s_0 - \beta \sqrt{u^*}). \end{aligned}$$

If $(d_1 s_H^{n_0} + d_2 s_0)^2 < 4d_1 d_2 \beta \sqrt{u^*} s_H^{n_0}$, then we also verify $D_j(s_H^i) > 0$.

Collecting the above analysis and using the monotonicity of $T(s, \mu)$ with respect to s , we have that if $i \neq j$, $T_j(s_H^i) \neq 0$ holds, then

$$\sigma'(s_H^i) = \frac{1}{2} T'_i(s_H^i) = -\frac{1}{2} < 0, \quad \omega(s_H^i) = \sqrt{D_i(s_H^i)} > 0.$$

By the Hopf bifurcation theorem in [8, 26], we can conclude the following result.

Theorem 2. For problem (2),

- (i) $(p/\alpha, 0)$ is unstable;
- (ii) When $3\beta^2 \leq 4\alpha p$, the unique positive constant equilibrium solution (u^*, v^*) is locally asymptotically stable;
- (iii) When $3\beta^2 > 4\alpha p$, if $s > s_0$ and $s \geq d_2 s_0 / d_1$, then (u^*, v^*) is locally asymptotically stable;
- (iv) When $3\beta^2 > 4\alpha p$, if $d_1 s_H^{n_0} - d_2 s_0 \geq 0$ or $(d_1 s_H^{n_0} + d_2 s_0)^2 < 4d_1 d_2 \beta \sqrt{u^*} s_H^{n_0}$ holds, let Ω be a bounded smooth domain so that the spectral set $W = \{\mu_i\}$ satisfies

(W) All the eigenvalues μ_i are simple for $i \geq 0$.

Then there exists $n_0 \in \mathbb{N}$ such that $s_H^{n_0} > s_H(\mu^*) \geq s_H^{n_0+1}$, and for problem (2), there are $n_0 + 1$ Hopf bifurcation points satisfying

$$s_0 = s_H^0 > s_H^1 > s_H^2 > \dots > s_H^{n_0} > s_H(\mu^*) = 0.$$

where $s_H^j = s_H(\mu_j)$, $j = 0, 1, 2, \dots, n_0$.

For every Hopf bifurcation point $s = s_H^j$, problem (2) undergoes a Hopf bifurcation, and the bifurcation periodic orbits near $(s, (u, v)) = (s_H^j, (u^*, v^*))$ can be parameterized as $(s(r), (u(r), v(r)))$, so that $s(r) \in C^\infty$ in the form $s(r) = s_H^j + o(r)$, $r \in (0, \delta)$ for small δ , and

$$\begin{aligned} u(r)(x, t) &= u^* + ra_j \cos(\omega(s_H^j)t)\phi_j(x) + o(r), \\ v(r)(x, t) &= v^* + ra_j \cos(\omega(s_H^j)t)\phi_j(x) + o(r), \end{aligned} \tag{17}$$

where $\omega(s_H^j) = (D_j(s_H^j))^{1/2}$ is the corresponding time frequency, $\phi_j(x)$ is the corresponding spatial eigenfunction, and (a_j, b_j) is the corresponding eigenvector, that is to say,

$$[L(s_H^j) - i\omega(s_H^j)I] [(a_j, b_j)^T \phi_j(x)] = (0, 0)^T.$$

Here $D_j(s) = D(s, \mu_j)$ is defined in (15).

Moreover,

- (i) The bifurcating periodic orbits from $s = s_0 = s_H^0$ are spatially homogeneous, which coincide with the periodic orbits of the corresponding ODE system;
- (ii) The bifurcating periodic orbits from $s = s_H^j$ are spatially nonhomogeneous, $0 < j \leq n_0$.

Remark 1. Comparing Theorem 2 with Theorem 1, we can find that the occurrence of self-diffusions can cause the change of the number of Hopf bifurcation points, which is the reason of the introduce of diffusion.

Denote

$$\gamma = -\frac{\operatorname{Re}(c_1(s_H^j))}{\operatorname{Re}(\lambda'(s_H^j))}, \quad \beta_2^* = 2 \operatorname{Re}(c_1(s_H^j)),$$

where

$$c_1(s_H^j) = \frac{i}{2_0} \left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3} \right) + \frac{g_{21}}{2}.$$

$\omega_0 = \omega(s_H^j)$ is the purely imaginary root, and $g_{20}, g_{11}, g_{21}, g_{02}$ will be given in the following proof.

Since $\sigma'(s_H^j) < 0$, from Theorem 2.1 in [26], we have

Theorem 3. For system (2),

- (i) the direction of Hopf bifurcation at $s = s_H^j$ is forward (resp. backward) if $\gamma > 0$ (resp. < 0), that is, the bifurcating periodic solutions exist for $s > s_H^j$ ($s < s_H^j$), $j = 0, 1, \dots, n_0$;
- (ii) the bifurcating periodic solutions are orbitally asymptotically stable (resp. unstable) if $\beta_2^* < 0$ (resp. > 0).

Remark 2. The calculation of $\operatorname{Re}(c_1(s_H^j))$ is lengthy, and we will show it in Appendix.

In the following, we get the positivity and long behavior of the solution of model (2). We first state the following lemma, which will be used later.

Lemma 1. (See [24].) Let $f(s)$ be a positive C^1 function for $s \geq 0$, and let $d > 0$, $\beta \geq 0$ be constants. Further, let $T \in [0, \infty)$ and $w \in C^{2,1}(\Omega \times (T, \infty)) \cap C^{1,0}(\bar{\Omega} \times [T, \infty))$ be a positive function.

(i) If w satisfies

$$w_t - d\Delta w \leq (\geq) w^{1+\beta} f(w)(\alpha - w), \quad (x, t) \in \Omega \times (T, \infty),$$

$$\frac{\partial w}{\partial n} = 0, \quad (x, t) \in \Omega \times (T, \infty),$$

and the constant $\alpha > 0$, then

$$\limsup_{t \rightarrow \infty} \max_{\bar{\Omega}} w(\cdot, t) \leq \alpha \left(\liminf_{t \rightarrow \infty} \min_{\bar{\Omega}} w(\cdot, t) \geq \alpha \right).$$

(ii) If w satisfies

$$w_t - d\Delta w \leq w^{1+\beta} f(w)(\alpha - w), \quad (x, t) \in \Omega \times (T, \infty),$$

$$\frac{\partial w}{\partial n} = 0, \quad (x, t) \in \Omega \times (T, \infty),$$

and the constant $\alpha \leq 0$, then $\limsup_{t \rightarrow \infty} \max_{\bar{\Omega}} w(\cdot, t) \leq 0$.

Proposition 1. By the maximum principle of parabolic equations, for any initial values $(u_0(x), v_0(x)) > (0, 0)$, solutions $(u(x, t), v(x, t))$ of problem (2) are positive.

Following Lemma 1, we can easily derive

Proposition 2. The following statements hold:

$$\limsup_{t \rightarrow \infty} \max_{\bar{\Omega}} u(\cdot, t) \leq \frac{p}{\alpha}, \quad \limsup_{t \rightarrow \infty} \max_{\bar{\Omega}} v(\cdot, t) \leq \frac{p}{\alpha}.$$

Proof. The proof is so easy, so we omit it here. □

4 Numerical simulations and discussion

In this subsection, by using mathematical software Matlab, we show some numerical simulations to depict our theoretical analysis of the existence of periodic solutions.

For Theorem 1, we obtain a rather complete picture for problem (1). We choose $\alpha = 0.2$, $p = 0.8$. Then a series of calculations show that $\beta = \sqrt{4\alpha p/3} = 0.4619$. By Theorem 1, (u^*, v^*) is locally asymptotically stable when $\beta < 0.4619$. When $\beta > 0.4619$, if $s > s_0$, then (u^*, v^*) is locally asymptotically stable; if $s < s_0$, then (u^*, v^*) is unstable; if $s = s_0$, problem (1) undergoes a Hopf bifurcation. We can illustrate our results in a bifurcation diagram as in Fig. 1.

For problem (1), choose $\alpha = 0.225$, $\beta = 0.8$, $p = 0.75$, and $(u_0, v_0) = (0.65, 0.525)$. Then a series of calculations show that $s_0 = 0.1746$ and $(u^*, v^*) = (0.5937, 0.5937)$,

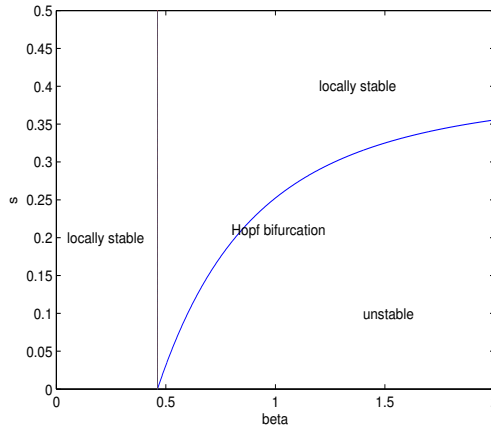


Figure 1. Bifurcation diagram in (β, s) parameter space. Here $\alpha = 0.2, p = 0.8$. The vertical line is: $\beta = 0.4619$. The parabolic curve line is the line s_0 .

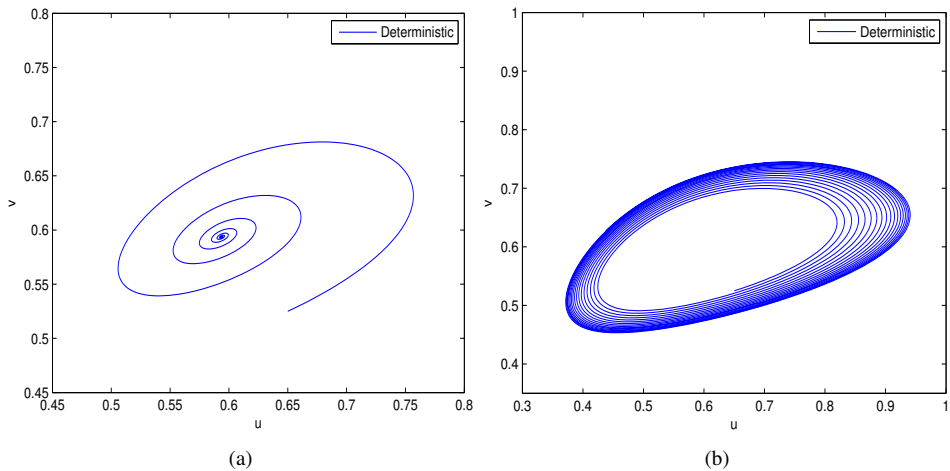


Figure 2. (a) The positive constant solution (u^*, v^*) of (1) is asymptotically stable, where $s = 0.2746 > s_0$. (b) The periodic solutions bifurcating from (u^*, v^*) of (1), where $s = 0.1746 = s_0$.

which implies the conditions in Theorem 1 are satisfied. Hence, by Theorem 1, (u^*, v^*) is locally stable when $s > s_0$. When $s = s_0$, (u^*, v^*) loses its stability, and Hopf bifurcation occurs, i.e., a family of periodic solutions are bifurcated from (u^*, v^*) , the periodic solutions are depicted in Fig. 2.

For problem (2), choose $\Omega = (0, \pi), d_1 = 1, d_2 = 0.8, \alpha = 0.5, \beta = 0.8, p = 0.5$, and $(u_0, v_0) = (0.17 + 0.1 \cos x, 0.17 + 0.1 \cos x)$. Then a series of calculations show that $s_0 = 0.0767$ and $(u^*, v^*) = (0.2310, 0.2310), \text{Re } c_1(s_H^0) = \text{Re } c_1(s_0) = -29.9663 < 0$, which implies the conditions in Theorem 2 are satisfied. Hence, by Theorem 2, (u^*, v^*) is locally stable when $s > s_0$. When $s = s_0$, (u^*, v^*) loses its stability and Hopf

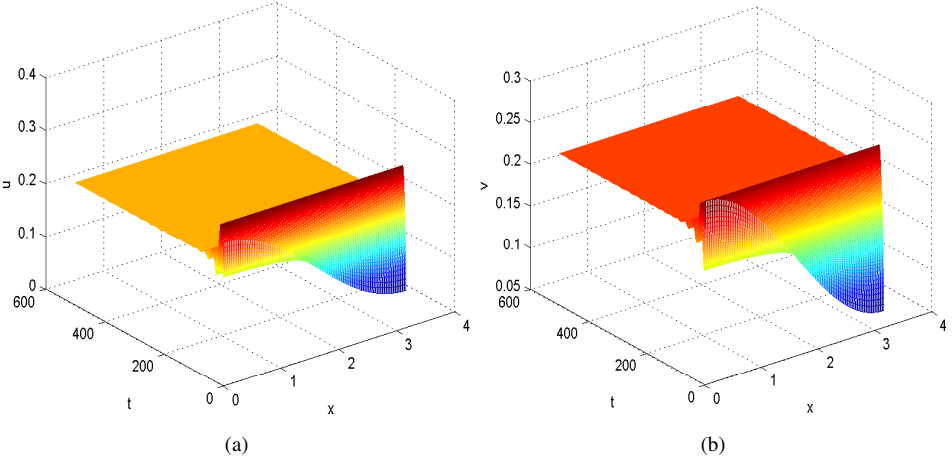


Figure 3. The homogeneous positive constant solution (u^*, v^*) of (2) is asymptotically stable, where $s_H^0 = 0.1767 > s_0$: (a) component u , (b) component v .

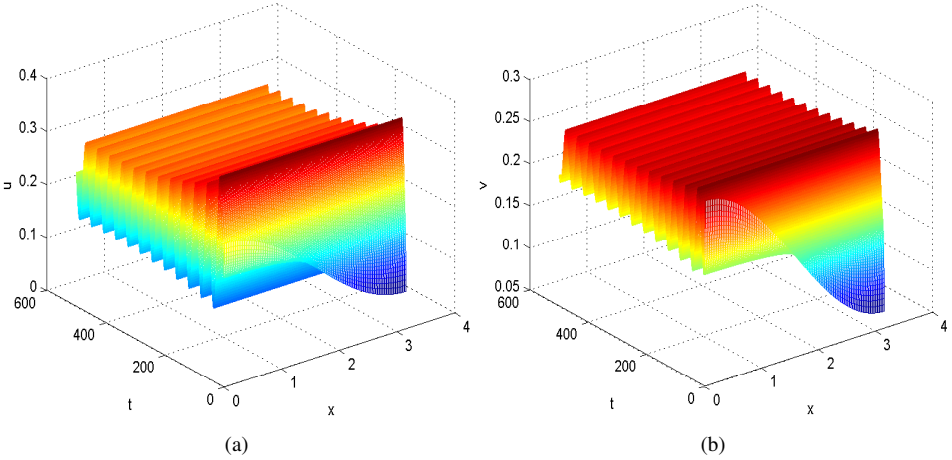


Figure 4. The homogeneous periodic solutions bifurcate from (u^*, v^*) of (2), where $s_H^0 = 0.0767 = s_0$, and the periodic solutions are stable, and the direction of Hopf bifurcation is backward: (a) component u , (b) component v .

bifurcation occurs, i.e., a family of periodic solutions are bifurcated from (u^*, v^*) , the periodic solutions are depicted in Figs. 3 and 4.

For both Figs. 3 and 4, the simulations were done with the same initial condition $(u_0, v_0) = (0.17 + 0.1 \cos x, 0.17 + 0.1 \cos x)$, and finite difference method was used to discretize the spatial and time domains with spacial step size $dx = 0.314$ and the time step size $t = 0.5$, and the iteration number is $H = 1000$. To show the stabilization and periodic property by time series, the numerical simulations are also given by increasing simulation time to 2500 in Figs. 5 and 6 corresponding to Figs. 3 and 4, respectively.

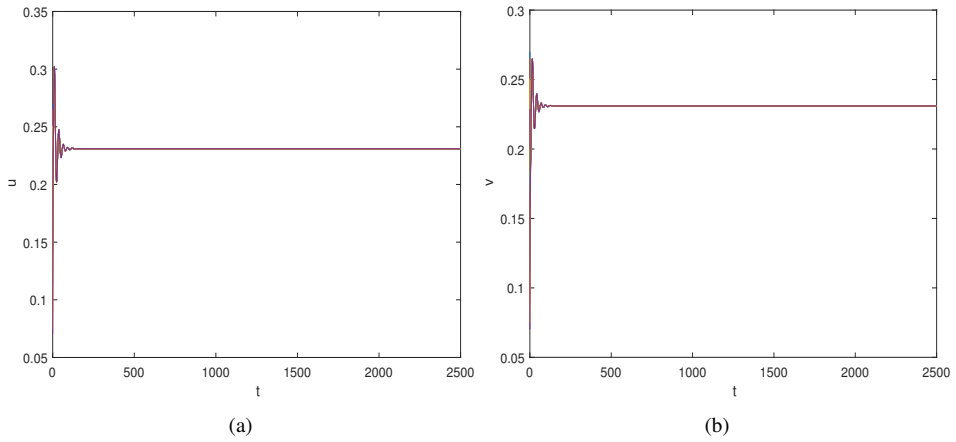


Figure 5. The homogeneous positive constant solution (u^*, v^*) of (2) is asymptotically stable by time series, where $s_H^0 = 0.1767 > s_0$: (a) component u , (b) component v .

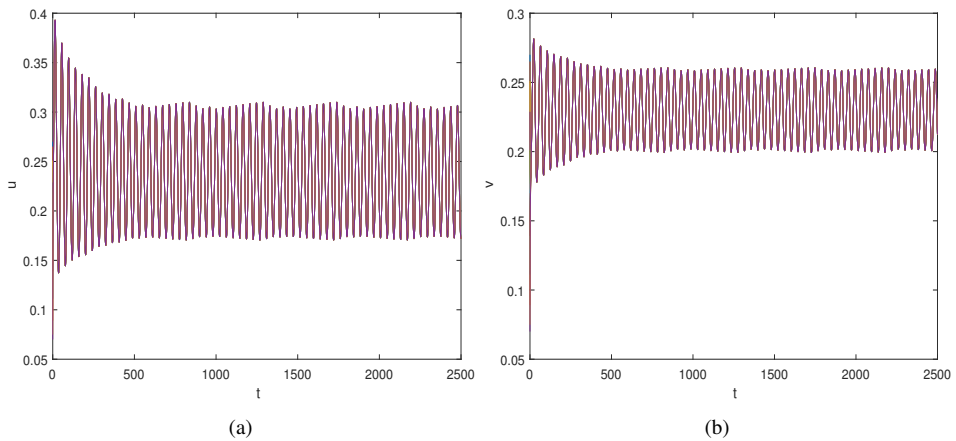


Figure 6. The homogeneous periodic solutions bifurcate from (u^*, v^*) of (2) by time series, where $s_H^0 = 0.0767 = s_0$: (a) component u , (b) component v .

5 Conclusions

In this paper, the dynamics of a diffusive predator–prey model with Leslie–Gower term and herd behavior are studied under the homogeneous Neumann boundary conditions. Firstly, by choosing the appropriate bifurcation parameter, the stability of the constant solutions of ODEs and the existence of Hopf bifurcation are discussed by analyzing the corresponding characteristic equation. Especially, the results determining the stability of bifurcating periodic solutions and the direction of Hopf bifurcation are derived by the normal form theory. Then, in order to investigate the influence of diffusion coefficients, the stability of positive constant equilibrium of PDEs and the existence of Hopf

bifurcation are also presented, and conclude that both the spatially homogeneous and nonhomogeneous bifurcating periodic solutions can arise under suitable conditions. Finally, numerical simulations illustrate the above theory results. In addition, we find from Theorems 1 and 2 that the diffusion coefficients can cause the change of the number of Hopf bifurcation points, which is one of the most exciting features in the ecosystem. Obviously, the emergence of spatially nonhomogeneous periodic solutions is also due to the effect of diffusion.

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Appendix: Direction of Hopf Bifurcation

For simplicity of calculation, in this appendix, we calculate $\text{Re}(c_1(s_H^0))$, where $s_H^0 = s_0$. We choose

$$q = \left(1, \frac{s_H^0 - i\omega_0}{\beta\sqrt{u^*}}\right)^T, \quad q^* = \left(\frac{is_H^0 + \omega_0}{2\omega_0 l\pi}, \frac{-i\beta\sqrt{u^*}}{2\omega_0 l\pi}\right)^T,$$

where

$$\omega_0 = \omega(s_H^0) = \sqrt{s_H^0(\beta\sqrt{u^*} - s_H^0)}.$$

It is straightforward to compute that

$$\begin{aligned} f_{uu} &= \frac{\beta\sqrt{u^*}}{4} - 2\alpha, & f_{uv} &= -\frac{\beta}{2\sqrt{u^*}}, & f_{vv} &= 0, \\ f_{uuu} &= -\frac{3\beta}{8u^*\sqrt{u^*}}, & f_{uuv} &= \frac{\beta}{4u^*\sqrt{u^*}}, & f_{uvv} &= 0, & f_{vvv} &= 0, \\ g_{uu} &= -\frac{2s_H^0}{u^*}, & g_{uv} &= \frac{2s_H^0}{u^*}, & g_{vv} &= -\frac{2s_H^0}{u^*}, \\ g_{uuu} &= \frac{6s_H^0}{u^{*2}}, & g_{uuv} &= -\frac{4s_H^0}{u^{*2}}, & g_{uvv} &= \frac{2s_H^0}{u^{*2}}, & g_{vvv} &= 0 \end{aligned}$$

and

$$\begin{aligned} c_0 &= \frac{\beta\sqrt{u^*}}{4} - \alpha - \frac{\beta}{2\sqrt{u^*}} + i\frac{\omega_0}{u^*}, \\ d_0 &= 3\alpha + \frac{4\alpha^2\sqrt{u^*}}{\beta} - \frac{4\alpha}{u^*} + \frac{4\alpha^3 u^*}{\beta^2} - \frac{4\alpha}{\beta\sqrt{u^*}} - i\frac{2\omega_0}{\beta u^*} \left(\frac{\beta}{2} - \frac{2\alpha^2 u^*}{\beta}\right), \\ e_0 &= \frac{\beta\sqrt{u^*}}{4} - \alpha - \frac{\beta}{2\sqrt{u^*}}, & f_0 &= \frac{2\alpha^2\sqrt{u^*}}{\beta} - \frac{\beta}{2\sqrt{u^*}}, \\ g_0 &= f_{uuu} + f_{uuv}(2b_0 + \bar{b}_0) = -\frac{3\alpha}{4u^*}, \end{aligned}$$

$$\begin{aligned}
 h_0 &= g_{uuu} + g_{uvv}(2b_0 + \bar{b}_0) + g_{uvv}(2|b_0|^2 + b_0^2) \\
 &= \frac{\alpha}{u^*} - \frac{4\alpha^2}{\beta\sqrt{u^*}} + \frac{1}{\beta u^* \sqrt{u^*}} - \frac{4\alpha^3}{\beta^2} - i\omega_0 \left(\frac{1}{u^{*2}} + \frac{4\alpha^2}{\beta^2 u^*} - \frac{4\alpha}{\beta u^* \sqrt{u^*}} \right),
 \end{aligned}$$

and

$$\begin{aligned}
 \langle q^*, Q_{qq} \rangle &= l\pi(\bar{a}_0^* c_0 + \bar{b}_0^* d_0), & H_{11} &= Q_{q\bar{q}} - \langle q^*, Q_{q\bar{q}} \rangle q - \langle \bar{q}^*, Q_{q\bar{q}} \rangle \bar{q} = 0, \\
 \langle q^*, Q_{q\bar{q}} \rangle &= l\pi(\bar{a}_0^* e_0 + \bar{b}_0^* f_0), & H_{20} &= Q_{qq} - \langle q^*, Q_{qq} \rangle q - \langle \bar{q}^*, Q_{qq} \rangle \bar{q} = 0, \\
 \langle q^*, C_{qq\bar{q}} \rangle &= l\pi(\bar{a}_0^* g_0 + \bar{b}_0^* h_0),
 \end{aligned}$$

which implies that $W_{11} = W_{20} = 0$. Hence,

$$\begin{aligned}
 \operatorname{Re}(c_1(s_H^0)) &= \operatorname{Re}\langle q^*, Q_{w_{11}q} \rangle + \frac{1}{2} \operatorname{Re}\langle q^*, C_{qq\bar{q}} \rangle + \frac{1}{2} \operatorname{Re}\langle q^*, Q_{w_{20}\bar{q}} \rangle \\
 &\quad + \operatorname{Re}\left(\frac{i}{2w_0} \langle q^*, Q_{qq} \rangle \cdot \langle q^*, Q_{q\bar{q}} \rangle\right) \\
 &= \operatorname{Re}\left(\frac{1}{2} \langle q^*, C_{qq\bar{q}} \rangle + \frac{i}{2w_0} \langle q^*, Q_{qq} \rangle \cdot \langle q^*, Q_{q\bar{q}} \rangle\right) \\
 &= \operatorname{Re}\left\{ \frac{l\pi}{2} (\bar{a}_0^* g_0 + \bar{b}_0^* h_0) + \frac{l^2 \pi^2 i}{2w_0} (\bar{a}_0^* c_0 + \bar{b}_0^* d_0) (\bar{a}_0^* e_0 + \bar{b}_0^* f_0) \right\} \\
 &= -\frac{19\alpha}{16u^*} + \frac{\beta}{4u^* \sqrt{u^*}} + \frac{\alpha^2}{\beta \sqrt{u^*}} + \left(\frac{(s_H^0)^2}{4\omega_0^2} - \frac{1}{4} \right) \frac{e_0 \operatorname{Im} c_0}{2\omega_0} + \frac{s_H^0 \operatorname{Re} c_0}{2\omega_0 l\pi} \\
 &\quad - \frac{\beta \sqrt{u^*}}{8\omega_0^3} (\omega_0 (f_0 \operatorname{Re} c_0 + e_0 \operatorname{Re} d_0) + s_H^0 (f_0 \operatorname{Im} c_0 + e_0 \operatorname{Im} d_0)) \\
 &\quad + \frac{\beta^2 u^* f_0 \operatorname{Im} d_0}{8\omega_0^3}.
 \end{aligned}$$

References

1. V. Ajraldi, M. Pittavino, E. Venturino, Modeling herd behavior in population systems, *Nonlinear Anal., Real World Appl.*, **12**(4):2319–2338, 2011.
2. N. Ali, M. Jazar, Global dynamics of a modified Leslie–Gower predator–prey model with Crowley–Martin functional responses, *J. Appl. Math. Comput.*, **43**(1-2):271–293, 2013.
3. J.R. Beddington, Mutual interference between parasites or predators and its effect on searching efficiency, *J. Anim. Ecol.*, **44**(1):331–340, 1975.
4. P.A. Braza, Predator-prey dynamics with square root functional responses, *Nonlinear Anal., Real World Appl.*, **13**(4):1837–1843, 2012.
5. P.H. Crowley, E.K. Martin, Functional responses and interference within and between year classes of a dragonfly population, *J. N. Am. Benthol. Soc.*, **8**(3):211–221, 1989.

6. D.L. Deangelis, R.A. Goldstein, R.V. O'Neill, A model for trophic interaction, *Ecology*, **56**(4):881–892, 1975.
7. M. Haque, Existence of complex patterns in the Beddington–DeAngelis predator–prey model, *Math. Biosci.*, **239**(2):179–190, 2012.
8. B. Hassard, N. Kazarinoff, Y.H. Wan, *Theory and Applications of Hopf Bifurcation*, Cambridge Univ. Press, Cambridge, 1981.
9. M.P. Hassell, G.C. Varley, New inductive population model for insect parasites and its bearing on biological control, *Nature*, **223**:1133–1137, 1969.
10. C.S. Holling, The components of predation as revealed by a study of small-mammal predation of the European pine sawfly, *Can. Entomol.*, **91**:293–320, 1959.
11. C.S. Holling, The functional response of predators to prey density and its role in mimicry and population dynamics, *Mem. Entomol. Soc. Can.*, **97**(45):1–60, 1965.
12. P.H. Leslie, A stochastic model for studying the properties of certain biological systems by numerical methods, *Biometrika*, **45**(1–2):16–31, 1958.
13. P.H. Leslie, J.C. Gower, The properties of a stochastic model for the predator–prey type of interaction between two species, *Biometrika*, **47**(3–4):219–234, 1960.
14. Y. Li, M.X. Wang, Dynamics of a diffusive predator–prey model with modified Leslie–Gower term and Michaelis–Menten type prey harvesting, *Acta Appl. Math.*, **140**(1):147–172, 2015.
15. Y.Q. Li, S.D. Huang, T.W. Zhang, Dynamics of a non-selective harvesting predator–prey model with Hassell–Varley type functional response and impulsive effects, *Math. Methods Appl. Sci.*, **39**(2):189–201, 2016.
16. B. Liu, Y. Tian, B.L. Kang, Dynamics on a Holling II predator–prey model with state-dependent impulsive control, *Int. J. Biomath.*, **05**(3):93–110, 2012.
17. X. Liu, T.H. Zhang, X.Z. Meng, T.Q. Zhang, Turing–Hopf bifurcations in a predator–prey model with herd behavior, quadratic mortality and prey-taxis, *Physica A*, **496**:446–460, 2018.
18. H. Mohammadi, M. Mahzoon, Effect of weak prey in Leslie–Gower predator–prey model, *Appl. Math. Comput.*, **224**:196–204, 2013.
19. P.J. Pal, P.K. Mandal, K.K. Lahiri, A delayed ratio-dependent predator–prey model of interacting populations with Holling type III functional response, *Nonlinear Dyn.*, **76**(1):201–220, 2014.
20. P.J. Pal, S. Sarwardi, T. Saha, P.K. Mandal, Mean square stability in a modified Leslie–Gower and Holling-type II predator–prey model, *J. Appl. Math. Inform.*, **29**(3):781–802, 2011.
21. F.A. Rihan, S. Lakshmanan, A.H. Hashish, R. Rakkiyappan, E. Ahmed, Fractional-order delayed predator–prey systems with Holling type-II functional response, *Nonlinear Dyn.*, **80**(1–2):777–789, 2015.
22. Y.L. Song, X. S. Tang, Stability, steady-state bifurcations, and Turing patterns in a predator–prey model with herd behavior and prey-taxis, *Stud. Appl. Math.*, **139**(3):371–404, 2017.
23. X.S. Tang, Y.L. Song, Stability, Hopf bifurcations and spatial patterns in a delayed diffusive predator–prey model with herd behavior, *Appl. Math. Comput.*, **254**(C):375–391, 2015.
24. M.X. Wang, P.Y.H. Pang, Global asymptotic stability of positive steady states of a diffusive ratio-dependent prey–predator model, *Appl. Math. Lett.*, **21**(11):1215–1220, 2008.

25. R.Z. Yang, J.J. Wei, The effect of delay on a diffusive predator–prey system with modified Leslie–Gower functional response, *Bull. Malays. Math. Sci. Soc. (2)*, **40**(1):51–73, 2017.
26. F.Q. Yi, J.J. Wei, J.P. Shi, Bifurcation and spatiotemporal patterns in a homogeneous diffusive predator–prey system, *J. Differ. Equations*, **246**(5):1944–1977, 2009.
27. S.L. Yuan, C.Q. Xu, T.H. Zhang, Spatial dynamics in a predator–prey model with herd behavior, *Chaos*, **23**(3):033102, 2013.
28. J.F. Zhang, H. Fang, Nonlinear dynamics of a delayed Leslie predator–prey model, *Nonlinear Dyn.*, **77**(4):1577–1588, 2014.
29. T.H. Zhang, X. Liu, X.Z. Meng, Spatio-temporal dynamics near the steady state of a planktonic system, *Comput. Math. Appl.*, **75**:4490–4504, 2018.
30. J. Zhou, J.P. Shi, Pattern formation in a general glycolysis reaction–diffusion system, *IMA J. Appl. Math.*, **80**(6):1703–1738, 2015.
31. X.Y. Zhou, Y.L. Li, The coexistence of a modified Holling-IV type predator–prey model with Michaelis–Menten type prey harvesting, *Basic Sciences Journal of Textile Universities*, **29**:141–147, 2016.
32. W.J. Zuo, Global stability and hopf bifurcations of a Beddington–DeAngelis type predator–prey system with diffusion and delays, *Appl. Math. Comput.*, **223**(4):423–435, 2013.