Dynamics of a diffusive predator-prey model with prey-stage structure and prey-taxis

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Keywords: Predator-prey model; Hopf bifurcation; Steady state bifurcation; Prey-taxis.

1 Introduction

Predator-prey models have always been considered to be classical, and the source of all the research work in population models during the past century is the Lotka-Volterra model [1, 2]. In the predator-prey models, the functional response is one of the crucial factors, which affect population dynamics. Typically, the Lotka-Volterra interaction term can be classified into many different types, for instance, Holling type I-IV [3, 4], Holling-Tanner type [5, 6], Beddington-DeAngelis type [7, 8, 9], ratio-dependent type [10], and Ivlev type [11]. Dynamic structure of the system is not only related to the response function but also may depend on many other factors such as location, age and mature delay and so on. The life histories of plants, insects, and animal life histories exhibit enormous diversity. Metamorphosis may carry the same individual through several totally different niches during a lifetime. Specialized stages may exist for dispersal or dormancy. The vital rates (rates of survival, development, and reproduction) almost always depend on age, size, or development stage. Population growth models that include age, stage or body size structure often predict complex population dynamics. Due to the above realistic evidences, the stage-structured models have received much attention in recent years, see [13, 14, 15, 16, 17, 18, 19, 20, 21, 22]. Generally speaking, population growth models that include stage structure predict more complex population dynamics than those without stage structure.

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In the spatial-temporal predator-prey interaction, with the exception of the random diffusion of predators and the prey, the variations of the predator's velocity are often directed by prey gradient i.e. prey-taxis. Kareiva and Odell [23] first derived a prey-taxis model to describe the predator aggregation in high prey density areas. Since then, more and more scholars have studied the predator-prey model with prey-taxis. For example, Lee et all showed that the prey-taxis tends to reduce the likelihood of pattern formation and effective biocontrol in [24]. Wang et al. [25] investigated the global existence, boundedness and global stabilities of the equilibria for a two predators and one prey model with prey-taxis. We refer to [26, 27, 28, 29, 30] for other interesting works on models with prey-taxis. It has been recognized that the systems with prey-taxis may undergo more rich dynamics and generate different spatial patterns than without prey-taxis.

In [12], the authors established the following predator-prey model with general functional response and stage-structure for the prey:

$$\begin{cases} \dfrac{du}{dt} = av - bu - \gamma u^2 - g(u)w, & t > 0, \\ \dfrac{dv}{dt} = u - v, & t > 0, \\ \dfrac{dw}{dt} = w(-r + \delta g(u)), & t > 0 \end{cases} \tag{1}$$

where u, v are the population densities of immature and mature prey species, respectively. w denotes the density of predator population. $a, b, r, \delta > 0$, and the functional response $g(u)$ also satisfies

$$g(0) = 0,\ g'(u) > 0 (u \geq 0), \text{ and } 0 < g(u) < L,\ L \text{ is a positive constant.}$$

For the background of (1), the readers can refer to [12]. The authors studied the stability of equilibrium points for this ODE system via linearization and the Lyapunov method, and showed that Hopf bifurcation occurs in paper [12].

It is known that the distributions of populations, in general, being heterogeneous, depend not only on time, but also on the spatial positions in habitat. So it is natural and more precise to study the corresponding PDE problem. In paper [12], the authors also considered the following corresponding reaction-diffusion system:

$$\begin{cases} \dfrac{\partial u}{\partial t} - d_1 \Delta u = av - bu - \gamma u^2 - g(u)w, & x \in \Omega, t > 0, \\ \dfrac{\partial v}{\partial t} - d_2 \Delta v = u - v, & x \in \Omega, t > 0, \\ \dfrac{\partial w}{\partial t} - d_3 \Delta w = w(-r + \delta g(u)), & x \in \Omega, t > 0, \\ \dfrac{\partial u}{\partial n} = \dfrac{\partial v}{\partial n} = \dfrac{\partial w}{\partial n} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x), v(x,0) = v_0(x), w(x,0) = w_0(x) \geq 0 & x \in \Omega \end{cases} \tag{2}$$

where $\Omega \subseteq R^N (N \geq 1)$ is a bounded domain with smooth boundary $\partial\Omega$, n is the outward unit normal vector of the boundary $\partial\Omega$. d_1, d_2 and d_3 are positive constants which stand for the random diffusion rates of the three species, respectively. The homogeneous Neumann boundary condition indicates that the predator-prey system is self-contained with zero population flux across the boundary. $u_0(x)$, $v_0(x)$ and $w_0(x)$ are nonnegative smooth functions on $\bar{\Omega}$. In [12], the existence and uniform boundedness of global solutions and stability of equilibrium points for the corresponding reaction-diffusion problem (2) were discussed. In addition, by using the topological degree theory, the existence of nontrivial steady states of system (2) under certain situations was showed, and some nonexistence of nontrivial steady state results were also obtained. We refer to [31, 32, 33, 34, 35] for the studies on the reaction-diffusion in other three-species predator-prey models.

In this paper, we introduce prey-taxis term into problem (2) and investigate the effect of the prey-taxis on the dynamics of predator-prey model. Thus, we shall consider the following model:

$$\begin{cases} \dfrac{\partial u}{\partial t} - d_1 \Delta u + \chi \nabla (u \nabla v) = av - bu - \gamma u^2 - g(u)w, & x \in \Omega, t > 0, \\ \dfrac{\partial v}{\partial t} - d_2 \Delta v = u - v, & x \in \Omega, t > 0, \\ \dfrac{\partial w}{\partial t} - d_3 \Delta w + \rho \nabla (w \nabla u) = w(-r + \delta g(u)), & x \in \Omega, t > 0, \\ \dfrac{\partial u}{\partial n} = \dfrac{\partial v}{\partial n} = \dfrac{\partial w}{\partial n} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x), v(x,0) = v_0(x), w(x,0) = w_0(x) \geq 0 & x \in \Omega \end{cases} \tag{3}$$

where the terms $\chi \nabla (u \nabla v)$ and $\rho \nabla (w \nabla u)$ are actually taxis mechanisms and $\chi, \rho > 0$ are their taxis rates, respectively. The term $\chi \nabla (u \nabla v)$ models the movement of the immature prey which is directed toward the increasing mature prey densities. The term $\rho \nabla (w \nabla u)$ accounts for prey-taxis which describes the phenomenon that the predator has the tendency to move increasingly toward the immature prey gradient direction. In the following paper, we will study the Hopf bifurcation and steady-state bifurcation of problem (3) by choosing the prey-taxis rate.

The outline of this paper is as follows. In Section 2, after analyzing the characteristic equation, we conclude the stability of constant equilibria of problem (3). In Section 3, we research the existence of periodic solutions bifurcating from the unique positive constant equilibrium of problem (3). In Section 4, we consider steady state bifurcations to show the existence of nontrivial steady state solutions of (3).

Throughout the paper, μ_k denotes the eigenvalues of $-\Delta$ in Ω under the homogeneous Neumann boundary condition satisfying

$$0 = \mu_0 < \mu_1 \leq \mu_2 < \cdots \mu_k < \cdots < \infty.$$

2 Stability of constant equilibria of problem (3)

In this section we will study the stability of constant equilibria of problem (3).

It is easy to see that the trivial equilibrium point $(0, 0, 0)$ always exists. If $a > b$, semi-trivial equilibrium point $(\bar{u}, \bar{v}, 0) = (\frac{a-b}{\gamma}, \frac{a-b}{\gamma}, 0)$ exists. Especially if

$$a - b - \gamma u^\star > 0, \quad \text{and} \quad \delta \mathrm{L} > \mathrm{r} \tag{4}$$

a unique positive constant equilibrium $(u^\star, v^\star, w^\star)$ also exists, where

$$u^\star = v^\star = g^{-1}(\frac{r}{\delta}), \qquad w^\star = \frac{\delta}{r}(a - b - \gamma u^\star)u^\star.$$

When $\chi = \rho = 0$, in [12], the stability of constant equilibria of (1) and (2) has been studied. We shall perform linearized stability analysis to see the effects of prey-taxis coefficients χ and ρ.

Theorem 2.1. *For problem (3),*

(1) If $a < b$, then $(0, 0, 0)$ is locally asymptotically stable; if $a > b$, then $(0, 0, 0)$ is unstable;

(2) Let $a > b$, $r > \delta L$ hold. If

$$\chi \leq \frac{\gamma}{a - b}[d_1 + d_2(2a - b)],$$

$(\bar{u}, \bar{v}, 0)$ is locally asymptotically stable;

(3) Assume that (4) holds. If

$$\chi \leq \min\{\chi_1, \chi_2\}, \quad \text{and} \quad \mathrm{a} \leq \eta \tag{5}$$

where

$$\begin{aligned} \chi_1 &= \tfrac{d_1 + d_2\eta + d_3(\eta+1)}{u^\star}, \\ \chi_2 &= \tfrac{d_1 + d_2\eta + \frac{d_2}{d_3}\rho w^\star g(u^\star)}{u^\star}, \\ \eta &= b + 2\gamma u^\star + g'(u^\star)w^\star, \end{aligned}$$

then $(u^\star, v^\star, w^\star)$ is locally asymptotically stable.

Proof We will prove the above points in turn.

(1) Linearizing problem (3) at the trivial equilibrium $(0, 0, 0)$, the Jacobi matrix at $(0, 0, 0)$ is as follows

$$J_{(0,0,0)} = \begin{pmatrix} -d_1\mu_k - b & a & 0 \\ 1 & -d_2\mu_k - 1 & 0 \\ 0 & 0 & -d_3\mu_k - r \end{pmatrix}, \ k = 0, 1, 2, ...,$$

so the characteristic equation is

$$[\lambda^2+(d_1\mu_k+b+d_2\mu_k+1)\lambda+d_1d_2\mu_k^2+(d_1+d_2b)\mu_k+b-a](\lambda+d_3\mu_k+r)=0.$$

Hence, according to Routh-Hurwitz criterion, we obtain that if $a<b$, then $(0,0,0)$ is locally asymptotically stable; if $a>b$, then $(0,0,0)$ is unstable; if $a=b$, when $k=0$, we have $\mu_k=0$, so the characteristic equation is

$$\lambda(\lambda+b+1)(\lambda+r)=0,$$

then the roots of the equation are $\lambda_1=0, \lambda_2=-(b+1)<0, \lambda_3=-r<0$. There is a zero eigenvalue, so we need to use the manifold theorem to judge the stability, which will not be discussed here.

(2) Similar to the above, the Jacobi matrix at $(\bar{u},\bar{v},0)$ is

$$J_{(\bar{u},\bar{v},0)}=\begin{pmatrix} -d_1\mu_k-b-2\gamma\bar{u} & \mu_k\chi\bar{u}+a & -g(\bar{u}) \\ 1 & -d_2\mu_k-1 & 0 \\ 0 & 0 & -d_3\mu_k-r+\delta g(\bar{u}) \end{pmatrix}, \ k=0,1,2,...,$$

the characteristic equation at $(\bar{u},\bar{v},0)$ is

$$[\lambda^2+(d_1\mu_k+2a-b+d_2\mu_k+1)\lambda+(d_1\mu_k+2a-b)(d_2\mu_k+1)-(\chi\frac{a-b}{\gamma}\mu_k+a)](\lambda+d_3\mu_k+r-\delta g(\frac{a-b}{\gamma}))=0.$$

It is observed that $r-\delta g(\frac{a-b}{\gamma})>0$ since $r>\delta L$ holds. Moreover according to Routh-Hurwitz criterion, it is easy to get that if

$$\chi\le\frac{\gamma}{a-b}[d_1+d_2(2a-b)],$$

then $(\bar{u},\bar{v},0)$ is locally asymptotically stable.

(3) Due to the standard linearized stability principle, the linearized stability of $(u^\star,v^\star,w^\star)$ is determined by eigenvalues of the following matrixes

$$N_k=\begin{pmatrix} -d_1\mu_k-\eta & \mu_k\chi u^\star+a & -g(u^\star) \\ 1 & -d_2\mu_k-1 & 0 \\ \mu_k\rho w^\star+\delta w^\star g'(u^\star) & 0 & -d_3\mu_k \end{pmatrix}, \quad k=0,1,2,.... \qquad (6)$$

Hence, the characteristic equation for N_k is as follows:

$$\lambda^3+A_1\lambda^2+A_2\lambda+A_3=0, \qquad (7)$$

where

$$\begin{aligned}
A_1 &= (d_1+d_2+d_3)\mu_k+\eta+1,\\
A_2 &= (d_1d_2+d_1d_3+d_2d_3)\mu_k^2+[d_1+d_2\eta+d_3(\eta+1)+\rho w^\star g(u^\star)-\chi u^\star]\mu_k\\
&\quad +[\eta+\delta w^\star g(u^\star)g'(u^\star)-a],\\
A_3 &= d_1d_2d_3\mu_k^3+[(d_1+d_2\eta)d_3+d_2\rho w^\star g(u^\star)-d_3\chi u^\star]\mu_k^2\\
&\quad +[d_3\eta+d_2\delta w^\star g(u^\star)g'(u^\star)+\rho w^\star g(u^\star)-ad_3]\mu_k+\delta w^\star g(u^\star)g'(u^\star).
\end{aligned}$$

Firstly it is noted that $A_1>0$ for any $k\geq 0$. In addition, if

$$\chi<\chi_3,\quad a<\eta+\delta w^\star g(u^\star)g'(u^\star), \tag{8}$$

then $A_2>0$ for any $k\geq 0$, where $\chi_3=\frac{d_1+d_2\eta+d_3(\eta+1)+\rho w^\star g(u^\star)}{u^\star}$. And if

$$\chi\leq\chi_2,\quad a\leq\eta+\frac{d_2}{d_3}\delta w^\star g(u^\star)g'(u^\star)+\frac{1}{d_3}\rho w^\star g(u^\star), \tag{9}$$

then $A_3>0$ for any $k\geq 0$, where χ_2 has been mentioned above.

Next, direct computations show that

$$A_1A_2-A_3=B_1\mu_k^3+B_2\mu_k^2+B_3\mu_k+B_4$$

where

$$\begin{aligned}
B_1 &= (d_1+d_2+d_3)(d_1d_2+d_1d_3+d_2d_3)-d_1d_2d_3,\\
B_2 &= (d_1d_2+d_1d_3+d_2d_3)(\eta+1)+d_1[d_1+d_2\eta+d_3(\eta+1)+\rho w^\star g(u^\star)-\chi u^\star]\\
&\quad +d_2[d_1+d_2\eta+d_3(\eta+1)-\chi u^\star]+d_3[d_3(\eta+1)+\rho w^\star g(u^\star)],\\
B_3 &= \eta[d_1+d_2\eta+d_3(\eta+1)+\rho w^\star g(u^\star)-\chi u^\star]+d_1[\eta+\delta w^\star g(u^\star)g'(u^\star)-a]\\
&\quad +d_2(\eta-a)+d_3\delta w^\star g(u^\star)g'(u^\star)+[d_1+d_2\eta+d_3(\eta+1)-\chi u^\star],\\
B_4 &= \eta[\eta+\delta w^\star g(u^\star)g'(u^\star)-a]+\eta-a.
\end{aligned}$$

According to the above formula, we can easily get $B_1>0$ for any $k\geq 0$; if $\chi\leq\chi_1$, then $B_2>0$ holds; if $\chi\leq\chi_1$, and $a\leq\eta$, then $B_3>0$; if $a\leq\eta$, then $B_4>0$. Therefore, $A_1A_2-A_3>0$ holds if $\chi\leq\chi_1$, and $a\leq\eta$, where χ_1,η have been mentioned above.

In summary, if (8), (9) and $\chi\leq\chi_1, a\leq\eta$ hold, that is $\chi\leq\min\{\chi_1,\chi_2,\chi_3\}=\min\{\chi_1,\chi_2\}$ and $a\leq\eta$ hold, then we have $A_1,A_2,A_3>0$ and $A_1A_2-A_3>0$. According to Routh-Hurwitz criterion, if (4) and (5) hold, then $(u^\star,v^\star,w^\star)$ is locally asymptotically stable.

Remark

When $\rho=0$, we get $\chi_2<\chi_1=\chi_3$. Therefore, condition (5) can be changed to $\chi\leq\chi_2$ and $a\leq\eta$, which makes the stability conditions more concise. When

$\rho \neq 0$, we have $\chi_1 < \chi_3$, but the relationship between χ_2 and χ_1, χ_3 cannot be determined. It can be seen that ρ has a direct influence on the size relationship of χ_1, χ_2 and χ_3, also indirectly affects the stability conditions.

Compared with the case of $\chi = \rho = 0$, the stability of constant equilibria of the model after introducing the prey-taxis is controlled by the prey-taxis rates. The fluctuation of the value of χ has a direct impact on the stability.

3 Hopf bifurcation of problem (3)

In this section we are going to analyze the conditions about the parameters under which Hopf bifurcation occurs near the unique positive constant solution $(u^\star, v^\star, w^\star)$ of problem (3). We shall apply Theorem 6.1 of paper [31] to derive the emergence of Hopf bifurcation.

Denote

$$H = \{\chi_j^H : A_1 A_2(\chi_j^H) - A_3(\chi_j^H) = 0\},$$

where H is the Hopf bifurcation curve.

Theorem 3.1. *Assume that (4) and $a \leq \eta$ hold. There exists $j \geq 1$ such that*

$$\min\{\chi_1, \chi_2\} < \chi_{\mathrm{j}}^{\mathrm{H}} \leq \min\{\chi_2, \chi_3\}$$

holds, where χ_1, χ_2 and χ_3 have been mentioned in Theorem 2.1. Suppose that
(H1) *for some $j \in N$, μ_j is a simple eigenvalue of $-\Delta$ in Ω with Neumann boundary condition and the corresponding eigenfunction is $y_j(x)$;*
(H2) *for any $k \neq j$, $\chi_j^H \neq \chi_k^H$.*
Then
1. *(3) has a unique one-parameter family $\{\beta(s) : 0 < s < \varepsilon\}$ of nontrivial periodic orbits near $(\chi, u, v, w) = (\chi_j^H, u^\star, v^\star, w^\star)$. More precisely, let $X = \{u \in H^2(\Omega) \mid \frac{\partial u}{\partial n}|_{\partial\Omega} = 0\}$, there exist $\varepsilon > 0$ and C^∞ function $s \mapsto (U_j(s), T_j(s), \chi_j(s))$ from $s \in (-\varepsilon, \varepsilon)$ to $C^1(\mathbb{R}, X^3) \times (0, \infty) \times \mathbb{R}$ satisfying*

$$(U_j(0), T_j(0), \chi_j(0)) = \left((u^\star, v^\star, w^\star), \frac{2\pi}{\nu_0}, \chi_j^H\right),$$

and

$$U_j(s, x, t) = (u^\star, v^\star, w^\star) + s y_j(x)[V_j^+ \mathrm{exp}(\mathrm{i}\nu_0 \mathrm{t}) + \mathrm{V_j^- exp(i\nu_0 t)}] + \mathrm{o(s)},$$

where $\nu_0 = \sqrt{A_2}$, A_2 has been mentioned in (7), and $V_j^\pm$ is an eigenvector satisfying $N_j V_j^\pm = i\nu_0 V_j^\pm$;
2. *for $0 < |s| < \varepsilon, \beta(s) = \beta(U_j(s)) = \{U_j(s, \cdot, t) : t \in \mathbb{R}\}$ is a nontrivial periodic orbit of (3) of period $T_j(s)$;*
3. *if $0 < s_1 < s_2 < \varepsilon$, then $\beta(s_1) \neq \beta(s_2)$;*
4. *there exists $\tau > 0$ such that if (3) has a nontrivial periodic solution $\widetilde{U}(x, t)$ of period T for some $\chi \in \mathbb{R}$ with*

$$|\chi - \chi_j^H| < \tau, \quad |T - \frac{2\pi}{\nu_0}| < \tau, \quad \max|\mathrm{\widetilde{U}(x, t) - (u^\star, v^\star, w^\star)}| < \tau,$$

then $\chi = \chi_j(s)$ and $\widetilde{U}(x, t) = U_j(s, x, t + \theta)$ for some $s \in (0, \varepsilon)$ and some $\theta \in \mathbb{R}$.

Proof We illustrate all the conditions listed in Theorem 6.1 of paper [31] one by one.

Step 1: we first show that, at $\chi = \chi_j^H$, there is $\omega_0 > 0$ such that $\pm i\omega_0$ are simple eigenvalues of (7). By $\chi_j^H \le \chi_2$ and $a \le \eta$, it is easy to see that $A_3(\chi_j^H) > 0$. And due to $\chi_j^H < \chi_3$ and $a \le \eta$, we have $A_2(\chi_j^H) > 0$. The roots of the characteristic equation (7) with $\chi = \chi_j^H$ are

$$\lambda_j = -A_1 < 0, \quad \lambda_j^{\pm} = \pm\sqrt{A_2(\chi_j^H)}.$$

Therefore, the matrix $N_j(\chi_j^H)$ defined in (6) admits a pair of purely imaginary eigenvalues $\pm i\sqrt{A_2(\chi_j^H)}$.

Step 2: we next show that, at $\chi = \chi_j^H$, (7) has not eigenvalues of the form $\pm iq\sqrt{A_2(\chi_j^H)}$ for $q \in N \setminus \{\pm 1\}$. Due to μ_j is a simple eigenvalue of $-\Delta$ and $\chi_j^H \ne \chi_k^H$ for $j \ne k$, the characteristic equation (7) has no root of the form $iq\sqrt{A_2(\chi_j^H)}$ with $q \in N^+ \setminus \{\pm 1\}$.

Step 3: finally, we prove that, for χ near χ_j^H, N_j has a unique eigenvalue $\sigma(\chi) + i\nu(\chi)$ such that $\sigma(\chi_j^H) = 0$, $\nu(\chi_j^H) > 0$ and $\sigma'(\chi_j^H) \ne 0$.

Let $\alpha(\chi)$ and $\sigma(\chi) \pm i\nu(\chi)$ be the three roots of (7) in a neighbourhood of χ_j^H. Clearly, $\alpha(\chi)$, $\sigma(\chi)$ and $\nu(\chi)$ are real analytic function of χ, and $\alpha(\chi_j^H) = -A_1 < 0$, $\sigma(\chi_j^H) = 0$, $\nu(\chi_j^H) = \sqrt{A_2(\chi_j^H)} > 0$.

Next, we show the transversality condition $\sigma'(\chi_j^H) \ne 0$.

Plugging $\alpha(\chi)$, $\sigma(\chi) \pm i\nu(\chi)$ into (7), we obtain

$$A_1 = -\alpha - 2\sigma, \quad A_2(\chi) = \sigma^2 + \nu^2 + 2\alpha\sigma, \quad A_3(\chi) = -\alpha(\sigma^2 + \nu^2). \tag{10}$$

By differentiating the three equations in (10) with respect to χ and using the definitions of A_1, A_2 and A_3, we have

$$\alpha' + 2\sigma' = 0, \quad 2\sigma\sigma' + 2\nu\nu' + 2\alpha'\sigma + 2\alpha\sigma' = -u^\star\mu_j, \tag{11}$$

$$\alpha'\nu^2 + \alpha'\sigma^2 + 2\alpha\nu\nu' + 2\alpha\sigma\sigma' = d_3u^\star\mu_j^2. \tag{12}$$

Note that $\sigma(\chi_j^H) = 0$. It follows from (11) and (12) that, at $\chi = \chi_j^H$,

$$2\nu\nu' + 2\alpha\sigma' = -u^\star\mu_j, \quad 2\alpha\nu\nu' + \alpha'\nu^2 = d_3u^\star\mu_j^2.$$

Observe that $\alpha(\chi_j^H) = -A_1$ and $\alpha'(\chi_j^H) = -2\sigma'(\chi_j^H)$. Thus, at $\chi = \chi_j^H$,

$$2\alpha\nu\nu' + 2\alpha^2\sigma' = 2\alpha\nu\nu' - \alpha'\alpha^2 = -\alpha u^\star\mu_j,$$

$$2\alpha\nu\nu' + \alpha'\nu^2 = d_3u^\star\mu_j^2,$$

which implies

$$\begin{aligned} \alpha'(\chi_j^H) &= \tfrac{(d_3\mu_j+\alpha)u^\star\mu_j}{\alpha^2+\nu^2}\big|_{\chi=\chi_j^H} \\ &= \tfrac{(d_3\mu_j-A_1)u^\star\mu_j}{A_1^2+A_2}\big|_{\chi=\chi_j^H}. \end{aligned}$$

Due to the definition of A_1 such that $d_3\mu_j - A_1 < 0$, so we obtain that $\alpha'(\chi_j^H) < 0$, and hence $\sigma'(\chi_j^H) = -\frac{1}{2}\alpha'(\chi_j^H) > 0$. This gives the transversality condition mentioned above.

Noticing that (3) is normally parabolic and steps $1-3$ ensure the conditions $(H_1)-(H_3)$ given in Theorem 6.1 of [31], respectively. Our desired conclusions are deduced by Theorem 6.1 of [31].

Remark

In paper [12], the authors derived the emergence of Hopf bifurcation at $\gamma = \gamma^\star$ by choosing γ as bifurcation parameter, where $\gamma^\star = \frac{\zeta_0 - b - \frac{\delta}{r}u^\star g'(u^\star)(a-b)}{(2-\frac{\delta}{r}u^\star g'(u^\star))u^\star}$. Compared with [12], we introduced the prey-taxis rates χ and ρ. By choosing χ as a bifurcation parameter, Hopf bifurcation can also be generated at χ_j^H. When $\rho = 0$, it can be accurately shown that periodic solutions will arise near χ_2.

4 Steady state bifurcation of problem (3)

Note that the steady state solutions of (3) satisfy

$$\begin{cases} -d_1\Delta u + \chi\nabla(u\nabla v) = av - bu - \gamma u^2 - g(u)w, & x \in \Omega, \\ -d_2\Delta v = u - v, & x \in \Omega, \\ -d_3\Delta w + \rho\nabla(w\nabla u) = w(-r + \delta g(u)), & x \in \Omega, \\ \dfrac{\partial u}{\partial n} = \dfrac{\partial v}{\partial n} = \dfrac{\partial w}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{13}$$

In this section, we prove the existence of nonconstant solutions of (13). In order to achieve this goal, we shall use χ as bifurcation parameter and apply the bifurcation theory in Theorem 4.3 of [37].

Denote

$$S = \{\chi_j^S : A_3(\chi_j^S) = 0\},$$

where S is the steady state bifurcation curve.

Theorem 4.1. *Assume that the parameters that condition **(H1)** in Theorem* 3.1 *is satisfied, and also*
(S1) *for any $k \neq j$, $\chi_j^S \neq \chi_k^S$.*
Then (13) has a unique one-parameter family $\Gamma_j = \{(\hat{U}_j(s), \hat{\chi}_j(s)) : -\varepsilon < s < \varepsilon\}$ of nontrivial solutions near $(u, v, w, \chi) = (u^\star, v^\star, w^\star, \chi_j^S)$. More precisely, there exist $\varepsilon > 0$ and C^∞ function $s \mapsto (\hat{U}_j(s), \hat{\chi}_j(s))$ from $s \in (-\varepsilon, \varepsilon)$ to $X^3 \times \mathbb{R}$ satisfying

$$(\hat{U}_j(0), \hat{\chi}_j(0)) = ((u^\star, v^\star, w^\star), \chi_j^S),$$

and

$$\begin{aligned} \hat{U}_j(s,x) &= (u^\star, v^\star, w^\star) + sy_j(x)\left(d_2\mu_j + 1, 1, \tfrac{(\rho w^\star\mu_j + \delta w^\star g'(u^\star))(d_2\mu_j+1)}{d_3\mu_j}\right) \\ &\quad + s(h_{1,j}(s), h_{2,j}(s), h_{3,j}(s)), \end{aligned}$$

such that $h_{1,j}(0) = h_{2,j}(0) = h_{3,j}(0) = 0$.

Proof Let $X = H^2(\Omega) = \{u \in H^2(\Omega) \mid \frac{\partial u}{\partial n}\big|_{\partial\Omega} = 0\}$, $Y = L^2(\Omega)$, $Y_0 = \{u \in L^2(\Omega) \mid \int_\Omega u(x)dx = 0\}$. Define a mapping $F : X^3 \times \mathbb{R} \to Y_0 \times Y^2 \times \mathbb{R}$ by

$$F(u, v, w, \chi) = \begin{pmatrix} d_1\Delta u - \chi\nabla(u\nabla v) + av - bu - \gamma u^2 - g(u)w \\ d_2\Delta v + u - v \\ d_3\Delta w - \rho\nabla(w\nabla u) + w(-r + \delta g(u)) \end{pmatrix}.$$

We apply Theorem 4.3 of [37] to the equation $F(u, v, w, \chi) = 0$ at $(u^\star, v^\star, w^\star, \chi_j^S)$. Clearly, $F(u^\star, v^\star, w^\star, \chi_j^S) = 0$, and F is continuously differentiable. We verify the conditions in Theorem 4.3 of [37] in the following steps.

Step 1 $F_U(u^\star, v^\star, w^\star, \chi_j^S)$ is a Fredholm operator with index zero, and the kernel space $N(F_U(u^\star, v^\star, w^\star, \chi_j^S))$ is a one-dimensional, where $U = (u, v, w)$.

According to the Lemma 2.3 in [36], one can show that the linear operator $F_U(u^\star, v^\star, w^\star, \chi_j^S) : X^3 \to Y_0 \times Y^2 \times \mathbb{R}$ is a Fredholm operator with index zero. To prove that $N(F_U(u^\star, v^\star, w^\star, \chi_j^S)) \neq \{0\}$, we calculate that

$$F_U(u^\star, v^\star, w^\star, \chi_j^S)[\phi, \psi, \varphi] = \begin{pmatrix} d_1\Delta\phi - \chi_j^S\nabla(u^\star\nabla\psi) + a\psi - b\phi - 2\gamma u^\star\phi - g(u^\star)\varphi \\ d_2\Delta\psi + \phi - \psi \\ d_3\Delta\varphi - \rho\nabla(w^\star\nabla\phi) + \varphi(-r + \delta g(u^\star)) \end{pmatrix}.$$

Let $(\phi, \psi, \varphi)(\neq 0) \in NF_U(u^\star, v^\star, w^\star, \chi_j^S)$, so

$$F_U(u^\star, v^\star, w^\star, \chi_j^S)[\phi, \psi, \varphi] = 0.$$

The above equation has a non-zero solution, which is equivalent to that 0 is the eigenvalue of N_j. It is easy to verify that when $\chi = \chi_j^S$, 0 is the eigenvalue of N_j and the corresponding eigenfunction is

$$(\bar{a}_j, \bar{b}_j, \bar{c}_j)y_j = \left(d_2\mu_j + 1, 1, \frac{(\rho w^\star\mu_j + \delta w^\star g'(u^\star))(d_2\mu_j + 1)}{d_3\mu_j}\right) y_j. \tag{14}$$

From the condition (**H1**), the eigenvector is unique up to a constant multiple. Thus one has $N(F_U(u^\star, v^\star, w^\star, \chi_j^S)) = \text{span}\{(\bar{a}_j, \bar{b}_j, \bar{c}_j)y_j\}$, which is one-dimensional.

Step 2 $F_{\chi U}(u^\star, v^\star, w^\star, \chi_j^S)[(\bar{a}_j, \bar{b}_j, \bar{c}_j)y_j] \notin R(F_U(u^\star, v^\star, w^\star, \chi_j^S))$.

We claim that the range space $R(F_U(u^\star, v^\star, w^\star, \chi_j^S))$ can be characterized as follows:

$$\begin{aligned} &R(F_U(u^\star, v^\star, w^\star, \chi_j^S)) \\ &= \left\{(h_1, h_2, h_3, \tau) \in Y_0 \times Y^2 \times \mathbb{R} : \int_\Omega (a_j^\star h_1 + b_j^\star h_2 + c_j^\star h_3)y_j \, dx = 0\right\}, \end{aligned} \tag{15}$$

where $(a_j^\star, b_j^\star, c_j^\star)$ is a non-zero eigenvector for the eigenvalue $\lambda = 0$ of N_j^T(the transpose of N_j defined in (6)):

$$(a_j^\star, b_j^\star, c_j^\star)y_j = \left(d_2\mu_j + 1, \chi_j^S\mu_j u^\star + a, -\frac{g(u^\star)(d_2\mu_j + 1)}{d_3\mu_j}\right) y_j.$$

Indeed if $(h_1, h_2, h_3, \tau) \in R(F_U(u^\star, v^\star, w^\star, \chi_j^S))$, then there exists $(\phi_1, \psi_1, \varphi_1) \in X^3$ such that

$$F_U(u^\star, v^\star, w^\star, \chi_j^S)[(\phi_1, \psi_1, \varphi_1)] = (h_1, h_2, h_3, \tau).$$

Define

$$L[\phi, \psi, \varphi] = \begin{pmatrix} d_1\Delta\phi - \chi_j^S u^\star \Delta\psi + a\psi - b\phi - 2\gamma u^\star \phi - g(u^\star)\varphi \\ d_2\Delta\psi + \phi - \psi \\ d_3\Delta\varphi - \rho w^\star \Delta\phi + \varphi(-r + \delta g(u^\star)) \end{pmatrix},$$

and its adjoint operator

$$L^\star[\phi, \psi, \varphi] = \begin{pmatrix} d_1\Delta\phi - b\phi - 2\gamma u^\star \phi + \psi - \rho w^\star \Delta\varphi \\ d_2\Delta\psi - \chi_j^S u^\star \Delta\phi + a\phi - \psi \\ d_3\Delta\varphi - g(u^\star)\phi + \varphi(-r + \delta g(u^\star)) \end{pmatrix}.$$

Thus, we have

$$\begin{aligned} < (h_1, h_2, h_3), (a_j^\star, b_j^\star, c_j^\star)y_j > &= < L[(\phi_1, \psi_1, \varphi_1)], (a_j^\star, b_j^\star, c_j^\star)y_j > \\ &= < (\phi_1, \psi_1, \varphi_1), L^\star[(a_j^\star, b_j^\star, c_j^\star)y_j] > \\ &= < (\phi_1, \psi_1, \varphi_1), N_j^\star(a_j^\star, b_j^\star, c_j^\star)y_j > \\ &= 0, \end{aligned}$$

where $< \cdot, \cdot >$ is the inner product in $[L^2(\Omega)]^3$. This illustrates that if

$$(h_1, h_2, h_3, \tau) \in R(F_U(u^\star, v^\star, w^\star, \chi_j^S)),$$

then

$$\int_\Omega (a_j^\star h_1 + b_j^\star h_2 + c_j^\star h_3) y_j \ dx = 0. \tag{16}$$

Due to (16) defines a codimension-1 set in $Y_0 \times Y^2 \times \mathbb{R}$, and we obtain that

$$\text{codim } R(F_U(u^\star, v^\star, w^\star, \chi_j^S)) = \dim N(F_U(u^\star, v^\star, w^\star, \chi_j^S)) = 1,$$

therefore, $R(F_U(u^\star, v^\star, w^\star, \chi_j^S))$ must be in form of (15).

Now it's worth noting that

$$F_{\chi U}(u^\star, v^\star, w^\star, \chi_j^S)[(\bar{a}_j, \bar{b}_j, \bar{c}_j)y_j] = (-u^\star \bar{b}_j \Delta y_j, 0, 0) = (u^\star \mu_j y_j, 0, 0),$$

then according to (15), we get

$$\begin{aligned} \textstyle\int_\Omega (a_j^\star h_1 + b_j^\star h_2 + c_j^\star h_3) y_j \ dx &= \textstyle\int_\Omega u^\star \mu_j y_j a_j^\star y_j \ dx \\ &= \textstyle\int_\Omega u^\star \mu_j (d_2\mu_j + 1) y_j^2 \ dx > 0. \end{aligned}$$

Hence, $F_{\chi U}(u^\star, v^\star, w^\star, \chi_j^S)[(\bar{a}_j, \bar{b}_j, \bar{c}_j)y_j] \notin R(F_U(u^\star, v^\star, w^\star, \chi_j^S))$. This conclusion has been proved.

5 Numerical Simulation

In this section, by using mathematical software Matlab, for the case of $\rho = 0$, we show some numerical simulations to depict our theoretical analysis of the existence of homogeneous periodic solutions. We choose $g(u) = \frac{u}{u+1}$, $0 < g(u) < 1$.

For problem (3), we choose that $d_1 = 1,\ d_2 = 0.8,\ d_3 = 1,\ \delta = 0.5,\ r = 0.2,\ a = 1,\ b = 0.3$, which satisfy $\delta > r, a \leq \eta$. Since the value of χ will affect the local stability of the problem (3) at point $(u^\star, v^\star, w^\star)$, the following two cases are analyzed:

(i) We choose that $\gamma = 0.45,\ \chi = 2$ which satisfy $a - b - \gamma u^\star > 0$ and $\chi \leq \chi_2 = 2.8680$. Theorem 2.1 tell us that if (4), and (5) hold, $(u^\star, v^\star, w^\star)$ is locally asymptotically stable. The local stability of $(u^\star, v^\star, w^\star)$ is depicted in Fig 1;

(ii) We choose that $\gamma = 0.2,\ \chi = \chi_2 = 2.5880$. Theorem 3.1 tell us that problem (3) has a homogeneous Hopf bifurcation near $(u^\star, v^\star, w^\star)$ with the bifurcation value $\chi = \chi_2 = 2.5880$. The period solutions bifurcating from $(u^\star, v^\star, w^\star)$ are illustrated in Fig 2.

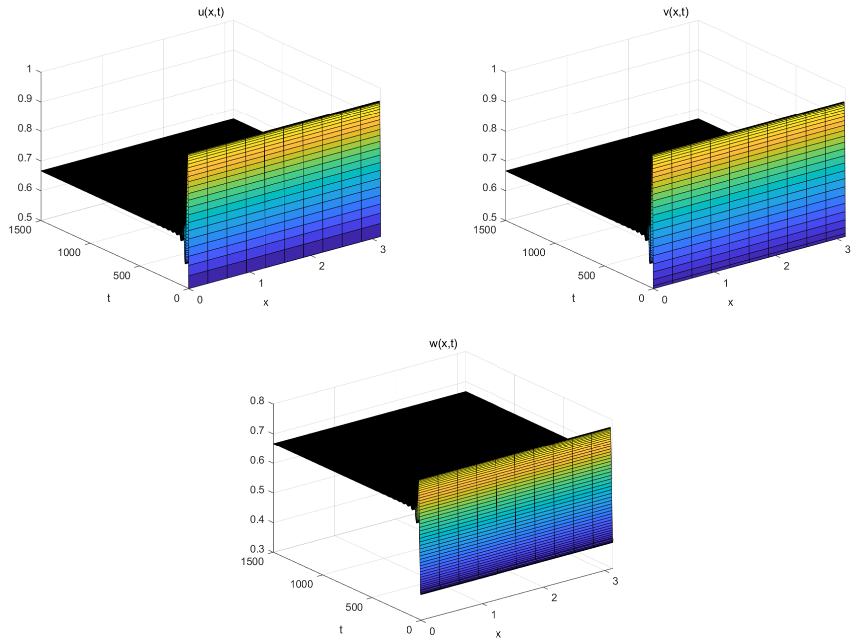

Figure 1: When $\gamma = 0.45,\ \chi = 2$, the unique positive constant solution $(u^\star, v^\star, w^\star) = (0.6667, 0.6667, 0.6667)$ with $(u_0, v_0, w_0) = (0.5, 0.5, 0.4)$ is locally stable. Line 1-Left: component u. Line 1-Right: component v. Line 2: component w.

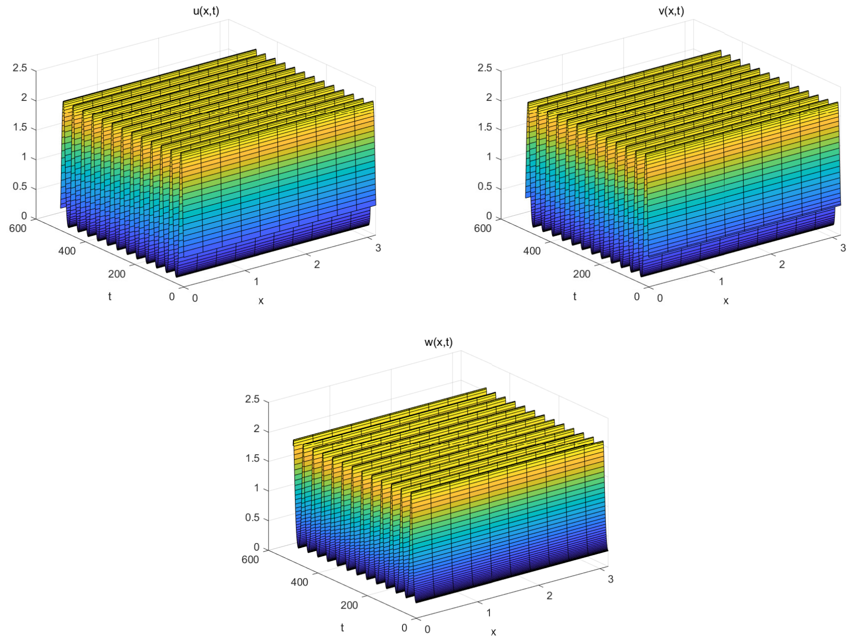

Figure 2: When $\gamma = 0.2$, $\chi = \chi_2 = 2.5880$, the homogeneous periodic solutions bifurcate from $(u^\star, v^\star, w^\star) = (0.6667, 0.6667, 0.9444)$ with $(u_0, v_0, w_0) = (0.5, 0.5, 0.26)$. Line 1-Left: component u. Line 1-Right: component v. Line 2: component w.

6 Conclusions

In this paper, we study the dynamics of a three-component predator-prey model with prey-taxis and stage structure for the prey under the homogeneous Neumann boundary condition. The main contributions of the present paper consist of three parts: stability analysis of constant equilibria, Hopf bifurcation analysis and steady state bifurcation analysis. For the first problem, we mainly use the eigenvalue method to analyze and obtain the stability of the constant equilibria. We conclude that the sufficiently strong taxis effect χ destabilizes the stability of the positive equilibrium regardless of the influence of another taxis mechanism ρ; for the second problem, choosing the prey-taxis sensitivity coefficient as a bifurcation parameter, we get the existence of Hopf bifurcation; for the third problem, the emergence of non-constant steady state is concluded at a chemotactic parameter by the bifurcation theorem. Our conclusions show that taxis rate χ plays an important role in determining the stability of the interior equilibrium and influencing the existence of time-periodic patterns and non-constant steady state. However, we shall not perform related numerical simulations in the present framework and we leave it for the interested readers.

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References

[1] A.J. Lotka. Elements of physical biology[M]. Williams and Wilkins. (1925).

[2] H. Malchow, S.V. Petrovskii, E. Venturino. Spatiotemporal patterns in ecology and epidemiology: theory, models, and simulation[M]. (2007).

[3] C.S. Holling. The functional response of predators to prey density and its role in mimicry and population regulation[J]. Memoirs of the Entomological Society of Canada. 97(45): 5-60(1965).

[4] J.F. Andrews. A mathematical model for the continuous culture of microorganisms utilizing inhibitory substrates[J]. Biotechnology and Bioengineering. 10(6): 707-723(1968).

[5] J.T. Tanner. The stability and the intrinsic growth rates of prey and predator populations[J]. Ecology. 56(4): 855-867(1975).

[6] P.A. Braza. The bifurcation structure of the Holling-Tanner model for predator-prey interactions using two-timing[J]. SIAM Journal on Applied Mathematics. 63(3): 889-904(2002).

[7] J. Beddington. Mutual interference between parasites or predators and its effect on searching efficiency[J]. Journal of Animal Ecology. 44(1): 331-340(1975).

[8] D.L. DeAngelis, R.A. Goldstein, R.V. O'Neill. A model for trophic interaction[J]. Ecology. 56(2): 881-892(1975).

[9] X.C. Zhang, G.Q. Sun, Z. Jin. Spatial dynamics in a predator-prey model with Beddington-DeAngelis functional response[J]. Physical Review E. 85(2): 021924(2012).

[10] R. Arditi, L.R. Ginzburg. Coupling in predator-prey dynamics: ratio-dependence[J]. Journal of Theoretical Biology. 139(3): 311-326(1989).

[11] R.E. Kooij, A. Zegeling. A predator-prey model with Ivlev's functional response[J]. Journal of Mathematical Analysis and Applications. 198: 473-489(1996).

[12] S.H. Xu. Dynamics of a general prey-predator model with prey-stage structure and diffusive effects[J]. Computers and Mathematics with Applications. 68(3): 405-423(2014).

[13] S.M. Baer, B.W. Kooi, Y.A. Kuznetsov, H.R. Thieme. Multiparametric bifurcation analysis of a basic two-stage population model[J]. SIAM Journal on Applied Mathematics. 66(4): 1339-1365(2006).

[14] K.L. Cooke, R.H. Elderkin, W. Huang. Predator-prey interactions with delays due to juvenile maturation[J]. SIAM Journal on Applied Mathematics. 66(3): 1050-1079(2006).

[15] S.A. Gourley, Y. Kuang. A stage structured predator-prey model and its dependence on maturation delay and death rate[J]. Journal of Mathematical Biology. 49(2): 188-200(2004).

[16] A. Hastings, Age-dependent predation is not a simple process. I. Continuous time models[J]. Theoretical Population Biology. 23(3): 347-362(1983).

[17] S.Q. Liu, E. Berett. A stage-structured predator-prey model of Beddington-Deangelis type[J]. SIAM Journal on Applied Mathematics. 66(4): 1101-1129(2006).

[18] S.Q. Liu, L.S. Chen, R. Agarwal. Recent progress on stage-structured population dynamics[J]. Mathematical and Computer Modelling. 36(11-13): 1319-1360(2002).

[19] C.H. Ou, J.H. Wu. Spatial spread of rabies revisited: Influence of age-dependent diffusion on nonlinear dynamics[J]. SIAM Journal on Applied Mathematics. 67(1): 138-163(2006).

[20] W.D. Wang, G. Mulone, F. Salemi, V. Salone. Permanence and stability of a stage-structured predator-prey model[J]. Journal of Mathematical Analysis and Applications. 262(2): 499-528(2001).

[21] N.X. Yan, L.S. Chen. Global stability of a predator-prey system with stage structure for the predator[J]. Acta Mathematica Sinica. 20(001): 63-70(2004).

[22] X. Rui, M. Chaplain, F.A. Davidson. Persistence and global stability of a ratio-dependent predator-prey model with stage structure[J]. Applied Mathematics and Computation. 158(3): 729-744(2004).

[23] P. Kareiva, G. Odell. Swarms of predators exhibit preytaxis if individual predators use area-restricted search[J]. The American Naturalist. 130(2): 233-270(1987).

[24] J.M. Lee, T. Hillen, M.A. Lewis. Pattern formation in prey-taxis systems[J]. Journal of Biological Dynamics. 3(6): 551-573(2009).

[25] J.P. Wang, M.X. Wang. Boundedness and global stability of the two-predator and one-prey models with nonlinear prey-taxis[J]. Zeitschrift für Angewandte Mathematik und Physik. 69(3): 63(2018).

[26] B.E. Ainseba, M. Bendahmane, A. Noussair. A reaction-diffusion system modeling predator-prey with prey-taxis[J]. Nonlinear Analysis: Real World Applications. 9(5): 2086-2105(2008).

[27] C. Hauzy, F.D. Hulot, A. Gins, M. Loreau. Intra- and interspecific density-dependent dispersal in an aquatic prey-predator system[J]. The Journal of Animal Ecology. 76: 552-558(2007).

[28] J.I. Tello,D. Wrzosek. Predator-prey model with diffusion and indirect prey-taxis[J]. Mathematical Models and Methods in Applied Sciences. 26(11): 2129-2162(2016).

[29] J.P. Wang, M.X. Wang. Global solution of a diffusive predator-prey model with prey-taxis[J]. Computers and Mathematics with Applications. 77(10): 2676-2694(2019).

[30] M. Winkler. Asymptotic homogenization in a three-dimensional nutrient taxis system involving food-supported proliferation[J]. Journal of Differential Equations. 263(8): 4826-4869(2017).

[31] P. Liu, J.P. Shi, Z. Wang. Pattern formation of the attraction-repulsion Keller-Segel system[J]. Discrete and Continuous Dynamical Systems Series B. 18(10): 2597-2625(2013).

[32] J.P. Wang, M.X. Wang. A predator-prey model with taxis mechanisms and stage structure for the predator[J]. Nonlinearity. 33(7): 1-39(2020).

[33] P. Panja. Stability and dynamics of a fractional-order three-species predator-prey model[J]. Theory in Biosciences. 138: 251-259(2019).

[34] L. Jia. Analysis for a delayed three-species predator-prey model with feedback controls and prey diffusion[J]. Journal of Mathematics. 2020: 1-26(2020).

[35] M. Sambath, C. Gokila. Stability and bifurcation analysis of three species predator-prey model with Holling Type II[J]. Discontinuity, Nonlinearity, and Complexity. 8(2): 127-144(2019).

[36] X. Wang, Q. Xu. Spiky and transition layer steady states of chemotaxis systems via global bifurcation and Helly's compactness theorem[J]. Journal of Mathematical Biology. 66(6): 1241-1266(2013).

[37] J.P. Shi, X.F. Wang. On global bifurcation for quasilinear elliptic systems on bounded domains[J]. Journal of Differential Equations. 246(7): 2788-2812(2009).