

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

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Abstract

This paper is concerned with a diffusive predator-prey model with prey-taxis and prey-structure under the homogeneous Neumann boundary condition. The stability of the unique positive constant equilibrium of the predator-prey model is derived. Hopf bifurcation and steady state bifurcation are also concluded.

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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1 In the spatial-temporal predator-prey interaction, with the exception of the
2 random diffusion of predators and the prey, the variations of the predator's ve-
3 locity are often directed by prey gradient i.e. prey-taxis. Kareiva and Odell
4 [23] first derived a prey-taxis model to describe the predator aggregation in
5 high prey density areas. Since then, more and more scholars have studied the
6 predator-prey model with prey-taxis. For example, Lee et al showed that the
7 prey-taxis tends to reduce the likelihood of pattern formation and effective bio-
8 control in [24]. Wang et al. [25] investigated the global existence, boundedness
9 and global stabilities of the equilibria for a two predators and one prey model
10 with prey-taxis. We refer to [26, 27, 28, 29, 30] for other interesting works on
11 models with prey-taxis. It has been recognized that the systems with prey-taxis
12 may undergo more rich dynamics and generate different spatial patterns than
13 without prey-taxis.

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

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

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

19 $g(0) = 0, g'(u) > 0 (u \geq 0)$, and $0 < g(u) < L$, L is a positive constant.

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

23 It is known that the distributions of populations, in general, being heteroge-
24 neous, depend not only on time, but also on the spatial positions in habitat. So it
25 is natural and more precise to study the corresponding PDE problem. In paper
26 [12], the authors also considered the following corresponding reaction-diffusion
27 system:

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

1 where $\Omega \subseteq R^N (N \geq 1)$ is a bounded domain with smooth boundary $\partial\Omega$, n
 2 is the outward unit normal vector of the boundary $\partial\Omega$. d_1 , d_2 and d_3 are
 3 positive constants which stand for the random diffusion rates of the three species,
 4 respectively. The homogeneous Neumann boundary condition indicates that
 5 the predator-prey system is self-contained with zero population flux across the
 6 boundary. $u_0(x)$, $v_0(x)$ and $w_0(x)$ are nonnegative smooth functions on $\bar{\Omega}$. In
 7 [12], the existence and uniform boundedness of global solutions and stability
 8 of equilibrium points for the corresponding reaction-diffusion problem (2) were
 9 discussed. In addition, by using the topological degree theory, the existence
 10 of nontrivial steady states of system (2) under certain situations was showed,
 11 and some nonexistence of nontrivial steady state results were also obtained. We
 12 refer to [31, 32, 33, 34, 35] for the studies on the reaction-diffusion in other
 13 three-species predator-prey models.

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

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

17 where the terms $\chi \nabla(u \nabla v)$ and $\rho \nabla(w \nabla u)$ are actually taxis mechanisms and
 18 $\chi, \rho > 0$ are their taxis rates, respectively. The term $\chi \nabla(u \nabla v)$ models the
 19 movement of the immature prey which is directed toward the increasing mature
 20 prey densities. The term $\rho \nabla(w \nabla u)$ accounts for prey-taxis which describes the
 21 phenomenon that the predator has the tendency to move increasingly toward
 22 the immature prey gradient direction. In the following paper, we will study the
 23 Hopf bifurcation and steady-state bifurcation of problem (3) by choosing the
 24 prey-taxis rate.

25 The outline of this paper is as follows. In Section 2, after analyzing the
 26 characteristic equation, we conclude the stability of constant equilibria of prob-
 27 lem (3). In Section 3, we research the existence of periodic solutions bifurcating
 28 from the unique positive constant equilibrium of problem (3). In Section 4,
 29 we consider steady state bifurcations to show the existence of nontrivial steady
 30 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

$$a - b - \gamma u^* > 0, \quad \text{and} \quad \delta L > r \quad (4)$$

a unique positive constant equilibrium (u^*, v^*, w^*) also exists, where

$$u^* = v^* = g^{-1}\left(\frac{r}{\delta}\right), \quad w^* = \frac{\delta}{r}(a - b - \gamma u^*)u^*.$$

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*

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

where

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

then (u^*, v^*, w^*) 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

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

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

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

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

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

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

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

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

- 4 then $(\bar{u}, \bar{v}, 0)$ is locally asymptotically stable.
- 5 (3) Due to the standard linearized stability principle, the linearized stability
- 6 of (u^*, v^*, w^*) is determined by eigenvalues of the following matrixes

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

- 7 Hence, the characteristic equation for N_k is as follows:

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

1 where

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

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

$$\chi < \chi_3, \quad a < \eta + \delta w^*g(u^*)g'(u^*), \quad (8)$$

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

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

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

Next, direct computations show that

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

5 where

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

6 According to the above formula, we can easily get $B_1 > 0$ for any $k \geq 0$; if
7 $\chi \leq \chi_1$, then $B_2 > 0$ holds; if $\chi \leq \chi_1$, and $a \leq \eta$, then $B_3 > 0$; if $a \leq \eta$, then
8 $B_4 > 0$. Therefore, $A_1A_2 - A_3 > 0$ holds if $\chi \leq \chi_1$, and $a \leq \eta$, where χ_1, η have
9 been mentioned above.

10 In summary, if (8), (9) and $\chi \leq \chi_1, a \leq \eta$ hold, that is $\chi \leq \min\{\chi_1, \chi_2, \chi_3\} =$
11 $\min\{\chi_1, \chi_2\}$ and $a \leq \eta$ hold, then we have $A_1, A_2, A_3 > 0$ and $A_1A_2 - A_3 > 0$.
12 According to Routh-Hurwitz criterion, if (4) and (5) hold, then (u^*, v^*, w^*) is
13 locally asymptotically stable.

14 Remark

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

1 $\rho \neq 0$, we have $\chi_1 < \chi_3$, but the relationship between χ_2 and χ_1, χ_3 cannot be
2 determined. It can be seen that ρ has a direct influence on the size relationship
3 of χ_1, χ_2 and χ_3 , also indirectly affects the stability conditions.
4 Compared with the case of $\chi = \rho = 0$, the stability of constant equilibria of
5 the model after introducing the prey-taxis is controlled by the prey-taxis rates.
6 The fluctuation of the value of χ has a direct impact on the stability.

7 3 Hopf bifurcation of problem (3)

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

Denote

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

12 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

$$\min\{\chi_1, \chi_2\} < \chi_j^H \leq \min\{\chi_2, \chi_3\}$$

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 $(\chi, u, v, w) = (\chi_j^H, u^*, v^*, w^*)$. 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

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

and

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

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 $\tilde{U}(x, t)$
of period T for some $\chi \in \mathbb{R}$ with

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

13 then $\chi = \chi_j(s)$ and $\tilde{U}(x, t) = U_j(s, x, t + \theta)$ 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 $\chi_j^H \leq \chi_2$ and $a \leq \eta$, it is easy to see that $A_3(\chi_j^H) > 0$. And due to $\chi_j^H < \chi_3$ and $a \leq \eta$, 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 $\chi_j^H \neq \chi_k^H$ for $j \neq k$, 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 $\sigma'(\chi_j^H) \neq 0$.

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 $\sigma'(\chi_j^H) \neq 0$.

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

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

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

$$\alpha' + 2\sigma' = 0, \quad 2\sigma\sigma' + 2\nu\nu' + 2\alpha'\sigma + 2\alpha\sigma' = -u^*\mu_j, \quad (11)$$

$$\alpha'\nu^2 + \alpha'\sigma^2 + 2\alpha\nu\nu' + 2\alpha\sigma\sigma' = d_3u^*\mu_j^2. \quad (12)$$

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

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

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

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

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

which implies

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

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 $\gamma = \gamma^*$ by choosing γ as bifurcation parameter, where $\gamma^* = \frac{\zeta_0 - b - \frac{\delta}{r}u^*g'(u^*)(a-b)}{(2 - \frac{\delta}{r}u^*g'(u^*))u^*}$. 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

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

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 $(u, v, w, \chi) = (u^, v^*, w^*, \chi_j^S)$. 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*

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

and

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

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

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

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

2 We apply Theorem 4.3 of [37] to the equation $F(u, v, w, \chi) = 0$ at $(u^*, v^*, w^*, \chi_j^S)$.
 3 Clearly, $F(u^*, v^*, w^*, \chi_j^S) = 0$, and F is continuously differentiable. We verify
 4 the conditions in Theorem 4.3 of [37] in the following steps.
 5 **Step 1** $F_U(u^*, v^*, w^*, \chi_j^S)$ is a Fredholm operator with index zero, and the kernel
 6 space $N(F_U(u^*, v^*, w^*, \chi_j^S))$ is a one-dimensional, where $U = (u, v, w)$.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Define

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

and its adjoint operator

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

1 Thus, we have

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

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

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

2 then

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

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

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

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

Now it's worth noting that

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

4 then according to (15), we get

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

5 Hence, $F_{\chi_U}(u^*, v^*, w^*, \chi_j^S)[(\bar{a}_j, \bar{b}_j, \bar{c}_j)y_j] \notin R(F_U(u^*, v^*, w^*, \chi_j^S))$. This conclu-

6 sion 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^*, v^*, w^*) , the following two cases are analyzed:

(i) We choose that $\gamma = 0.45$, $\chi = 2$ which satisfy $a - b - \gamma u^* > 0$ and $\chi \leq \chi_2 = 2.8680$. Theorem 2.1 tell us that if (4), and (5) hold, (u^*, v^*, w^*) is locally asymptotically stable. The local stability of (u^*, v^*, w^*) 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^*, v^*, w^*) with the bifurcation value $\chi = \chi_2 = 2.5880$. The period solutions bifurcating from (u^*, v^*, w^*) are illustrated in Fig 2.

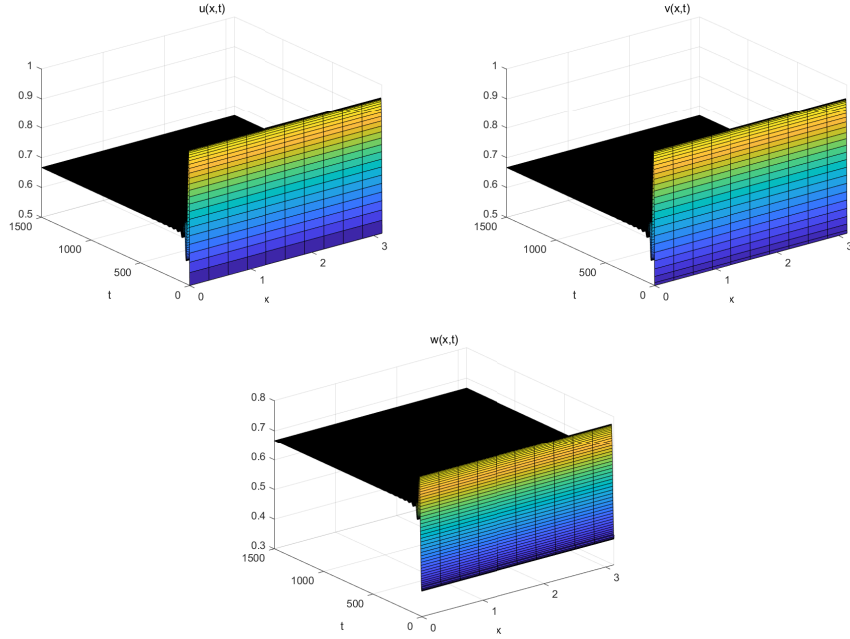


Figure 1: When $\gamma = 0.45$, $\chi = 2$, the unique positive constant solution $(u^*, v^*, w^*) = (0.6667, 0.6667, 0.6667)$ with $(u_0, v_0, w_0) = (0.5, 0.5, 0.4)$ is locally stable. Line 1-Left: component u . Line 1-Right: component v . Line 2: component w .

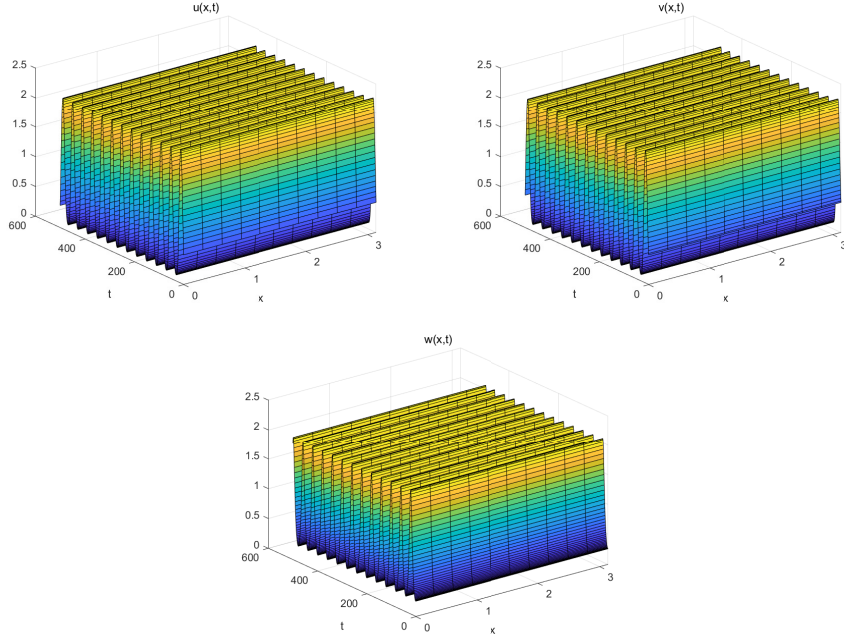


Figure 2: When $\gamma = 0.2$, $\chi = \chi_2 = 2.5880$, the homogeneous periodic solutions bifurcate from $(u^*, v^*, w^*) = (0.6667, 0.6667, 0.9444)$ with $(u_0, v_0, w_0) = (0.5, 0.5, 0.26)$. Line 1-Left: component u . Line 1-Right: component v . Line 2: component w .

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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