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Steady-state bifurcation and pattern formation in a predator–prey model with prey-taxis

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Abstract. In this paper, the bifurcation structure and stability of the nonconstant positive steady states in a ratio-dependent predator–prey model with prey-taxis are described. First, the stability results for the positive constant equilibrium will extend to the derivative of prey's functional response with prey is positive. It is found that attractive prey-taxis can stabilize equilibrium even self-diffusion-driven instability has occurred, and repulsive prey-taxis can destabilize equilibrium. Then, several numerical simulations are performed to visualize the complex dynamic behavior: The model exhibits taxis-controlled spatial patterns such as spots pattern, spots-stripe pattern and stripe pattern. Finally, the stationary problem in one-dimensional domain is investigated. Choosing prey-taxis coefficient as bifurcation parameter, we derive the existence and stability of nonconstant positive steady states by applying Crandall–Rabinowitz bifurcation theory, and obtain the stable bifurcating solutions near the bifurcation point under suitable conditions.

Keywords: prey-taxis, steady-state bifurcation, stability, pattern.

2020 Mathematics Subject Classification: 35B32, 35B35, 35B36, 35Q92.

1 Introduction

In the field of mathematical ecology, one of the hottest topics is to study the dynamical relationship between predator and prey and exhibited the rich biodiversity of ecosystem. It has been recognized that, in the spatial predator–prey interaction, in addition to the random movement of the population, which is modeled by diffusion equations, the spatiotemporal variations of the predator's velocity are affected by the prey gradient, i.e. prey-taxis [4, 6, 19, 21, 22, 27]. It plays important roles in biological control and ecological balance, such as regulating prey (pest) population to avoid incipient outbreaks, forming large-scale aggregation for survival and so on. The prey-taxis describes active movement of predators towards the area of higher prey density, which was first observed in the experiment and treated as biased random

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walks by Karevia and Odell [21]. Over the past few decades, various reaction-diffusion models have been proposed to interpret the prey-taxis phenomenon ([17,26,28,29] and references therein).

In the present paper, we introduce prey-taxis into the following ratio-dependent predator–prey model

$$\begin{cases} \dfrac{\partial u}{\partial t} - d_1 \triangle u = u(1-u) - \dfrac{\alpha u v}{u+v}, & x \in \Omega,\ t>0, \\ \dfrac{\partial v}{\partial t} - d_2 \triangle v + \nabla \cdot (\chi \phi(u,v) \nabla u) = v\left(-\gamma + \dfrac{\beta u}{u+v}\right), & x \in \Omega,\ t>0, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega,\ t>0, \\ u(x,0) = u_0(x),\ v(x,0) = v_0(x), & x \in \Omega, \end{cases} \tag{1.1}$$

where Ω is a bounded domain in $\mathbb{R}^N$ with smooth boundary $\partial\Omega$, ν is the outward unit normal vector on $\partial\Omega$, u and v are the densities of prey and predator, respectively. α, β, γ stand for the capturing rate, the conversion rate and predator death rate. d_1 and d_2 are the diffusion coefficients. In order to preserve the biological meaning of this model, all parameters are assumed to be strictly positive. The initial data $u_0(x), v_0(x)$ are nonnegative smooth functions which are all not identically zero.

The function $\frac{\alpha u}{u+v}$ is called the ratio-dependent type functional response, which is put forward by Arditi and Ginzburg [1] based on the Holling type II. It is a more suitable realistic predation term of predator–prey model depends upon the amount of prey that each predator can search, share and compete. This conclusion is supported by numerous fields including observations and laboratory experiments [1,2,12].

The term $\nabla \cdot (\chi \phi(u,v) \nabla u)$ stands for prey-taxis, χ is a constant that measures the intensity of interference sensitivity between the species, and the smooth function $\phi(u,v)$ reflects the strength of prey-taxis with respect to variation in the population densities of both interacting species. Various specific forms of ϕ can be chosen, depending on the biological situation that one tries to model. In particular, $\chi\phi(u,v) > 0$ represents that predator forage prey, that is prey-taxis is attractive, and $\chi\phi(u,v) < 0$ means that predator retreat the habitat of prey which can defend themselves as a group when the population density is high, i.e. prey-taxis is repulsive. Please see [11, 31] and the references therein for more examples and further discussions about anti-predation of prey through group defense.

The ratio-dependent ODE model (1.1) of dynamics have been well studied (see [13,14,16, 30] etc.). For the corresponding pure diffusion system of model (1.1) ($\chi = 0$), Pang et al. [20] established the stability results of both constant and nonconstant steady states showed that the diffusion is a factor inducing pattern formation. In [9], the authors obtained the global stability of homogeneous steady states by the method of upper-lower solutions combined with the monotone iteration and construction of suitable Lyapunoval functions. Moreover, pattern formation, Hopf bifurcation and Hopf–Turing bifurcation were investigated in [3,10,18,25].

Prey-taxis models with different population dynamics have been extensively studied in recent years. For example, Lee et al. [17] investigated pattern formation in prey-taxis model under a variety of nonlinear functional responses. Wang et al. [28] considered a prey-taxis model with Holling II presented that a branch of nonconstant solutions can bifurcate from the positive equilibrium only when the chemotactic is repulsive. Wu et al. [29] studied the global existence and boundedness of solutions to a general reaction-diffusion model with prey-taxis. Song and Tang [24] proved the steady-state bifurcation and Turing patterns in predator–prey model with herd behavior and prey-taxis. Recently, the authors [5] investigated asymptotic dynamics and spatial patterns of the classic ratio-dependent model when $\phi(u,v) = v$, numerical simulations found that the pattern formation can arise and prey-taxis is a factor driving the evolution of spatial inhomogeneity into homogeneity.

The first purpose of the present paper is to prove the stability of positive constant equilibrium of model (1.1). It is shown that attractive prey-taxis can stabilize equilibrium even self-diffusion-driven instability has occurred, and repulsive prey-taxis can destabilize equilibrium. Moreover, the formation and evolution of taxis-controlled spatial patterns such as spots pattern, spots-stripe pattern and stripe pattern are simulated. Our second purpose is to investigate the bifurcation structure and stability of nonconstant positive steady states by an Crandall–Rabinowitz bifurcation theory. And we provide detailed and complete calculations to determine properties such as pitchfork and turning direction of the local branches. It is found that model (1.1) can undergo the stable bifurcating solutions near the bifurcation point under suitable conditions.

The organization of the rest of this paper is as following. In Section 2, the stability of the positive equilibrium for (1.1) in a multi-dimensional domains is discussed (Theorem 2.1). In Section 3, by using the abstract bifurcation theory in 1D, the existence of nonconstant positive steady state solutions bifurcating from the unique positive equilibrium is obtained (Theorem 3.1). In Section 4, the stability of these nontrivial bifurcating solutions is analyzed in detail under some conditions (Theorem 4.2). We make some comments on our studies and propose some interesting problems for future studies in Section 5.

2 Local stability of the positive equilibrium

In this section, we summarize the linear stability criterion for model (1.1). Obviously, model (1.1) has a unique positive constant equilibrium (u^*, v^*) if and only if

$$(\mathbf{H_1}) \qquad \max\left\{0, \beta - \frac{\beta}{\alpha}\right\} < \gamma < \beta,$$

where

$$u^* = \frac{\gamma(\beta - \alpha\beta + \alpha\gamma)}{\beta\gamma}, \qquad v^* = \left(\frac{\beta - \gamma}{\gamma}\right)u^*.$$

For convenience, denote

$$f(u,v) = u(1-u) - \frac{\alpha uv}{u+v}, \qquad g(u,v) = v\left(-\gamma + \frac{\beta u}{u+v}\right),$$

$$f_1 = f_u(u^*,v^*) = -u^* + \frac{\alpha u^* v^*}{(u^*+v^*)^2}, \qquad f_2 = f_v(u^*,v^*) = -\frac{\alpha u^{*2}}{(u^*+v^*)^2} < 0,$$

$$g_1 = g_u(u^*,v^*) = \frac{(\gamma-\beta)^2}{\beta} > 0, \qquad g_2 = g_v(u^*,v^*) = \frac{(\gamma-\beta)\gamma}{\beta} < 0.$$

Similarly, we can denote f_{11}, g_{11}, ϕ_1 and so on. Clearly, we have $f_1 g_2 - f_2 g_1 > 0$ if $(\mathbf{H_1})$ holds. Throughout this paper, we assume the condition

$$(\mathbf{H_2}) \qquad f_1 + g_2 < 0$$

is satisfied to ensure that (u^*, v^*) is stable for the corresponding ODE system of (1.1).

Let $0 = \mu_0 < \mu_1 < \cdots < \mu_i < \cdots$ be the sequence of eigenvalues for the elliptic operator $-\triangle$ subject to the Neumann boundary condition on Ω, and $E(\mu_i)$ be the eigenspace corresponding to μ_i in $H^1(\Omega)$. Set $\{\zeta_{ij} : j = 1, 2, \ldots, \dim E(\mu_i)\}$ be the orthonormal basis of $E(\mu_i)$, $\mathbf{X}$ is the closure of $[u \in C^1(\overline{\Omega}) | \frac{\partial u}{\partial \nu}, x \in \partial\Omega]^2$ in $[H^1(\Omega)]^2$, $\mathbf{X_{ij}} = \{\mathbf{c}\zeta_{ij} : \mathbf{c} \in \mathbb{R}^2\}$. Then

$$\mathbf{X} = \bigoplus_{i=1}^{+\infty} \mathbf{X_i} \quad \text{and} \quad \mathbf{X_i} = \bigoplus_{j=1}^{\dim E(\mu_i)} \mathbf{X_{ij}}.$$

The linearization operator of model (1.1) at (u^*, v^*) is

$$L = \begin{pmatrix} d_1\Delta + f_1 & f_2 \\ -\chi\phi^*\Delta + g_1 & d_2\Delta + g_2 \end{pmatrix},$$

where $\phi^* = \phi(u^*, v^*)$.

Suppose $(\varphi(x), \psi(x))$ is an eigenfunction of L corresponding to an eigenvalue λ and

$$\varphi(x) = \sum_{0 \le i < \infty, 1 \le j \le \dim E(\mu_i)} a_{ij}\zeta_{ij}, \qquad \psi(x) = \sum_{0 \le i < \infty, 1 \le j \le \dim E(\mu_i)} b_{ij}\zeta_{ij},$$

we find that

$$\sum_{0 \le i < \infty, 1 \le j \le \dim E(\mu_i)} L(\mu_i, \chi) \begin{pmatrix} a_{ij} \\ b_{ij} \end{pmatrix} \zeta_{ij} = 0, \qquad L(\mu_i, \chi) = \begin{pmatrix} -\mu_i d_1 + f_1 & f_2 \\ \mu_i\chi\phi^* + g_1 & -\mu_i d_2 + g_2 \end{pmatrix}.$$

In fact, λ is an eigenvalue of L if and only if $\det L(\mu_i, \chi) = 0$ for some $i \ge 1$, i.e.,

$$\lambda^2 - T_i(\mu_i)\lambda + D_i(\mu_i, \chi) = 0, \tag{2.1}$$

where

$$T_i(\mu_i) = -(d_1 + d_2)\mu_i + f_1 + g_2 < 0$$

(by $(\mathbf{H_2})$) and

$$D_i(\mu_i, \chi) = d_1 d_2 \mu_i^2 - (\chi\phi^* f_2 + d_1 g_2 + d_2 f_1)\mu_i + f_1 g_2 - f_2 g_1.$$

Obviously,

$$D_i(\mu_i, \chi) = D_i(\mu_i, 0) - \chi\phi^* f_2 \mu_i. \tag{2.2}$$

If there exist some $i \ge 1$ such that $D_i(\mu_i, 0) < 0$, we denote

$$\Lambda = \{i \mid i \ge 1, D_i(\mu_i, 0) < 0\}.$$

Clearly, $D_i(\mu_i, 0) > 0$ for i large, hence there are only finitely many i such that $D_i(\mu_i, 0) < 0$. Let

$$\chi_i = \frac{d_1 d_2 \mu_i^2 - (d_1 g_2 + d_2 f_1)\mu_i + f_1 g_2 - f_2 g_1}{\phi^* f_2 \mu_i}, \qquad i \ge 1. \tag{2.3}$$

$$\overline{\chi} := \max_{1 \le i \le +\infty} \chi_i, \quad \text{and} \quad \underline{\chi} := \min_{1 \le i \le +\infty} \chi_i. \tag{2.4}$$

The stability of the positive equilibrium (u^*, v^*) with respect to (1.1) can be summarized as follows.

Theorem 2.1. *Assume* $(\mathbf{H_1})$, $(\mathbf{H_2})$ *and* $d_1 \ne d_2$ *hold. For model* (1.1), *the following statements are true.*

(a) Suppose that $\phi(u^*, v^*) > 0$.

(a1) If $D_i(\mu_i, 0) > 0$ *for all* $i \geq 1$*, then* (u^*, v^*) *is locally asymptotically stable for all* $\chi > 0$ *or* $\overline{\chi} < \chi < 0$ *and it is unstable if* $\chi < \overline{\chi} < 0$.

(a2) If there exist some $i \geq 1$ *such that* $D_i(\mu_i, 0) < 0$*, then* (u^*, v^*) *is locally asymptotically stable for* $0 < \overline{\chi} < \chi$ *and it is unstable if* $0 < \chi < \overline{\chi}$.

(b) Suppose that $\phi(u^*, v^*) < 0$.

(b1) If $D_i(\mu_i, 0) > 0$ *for all* $i \geq 1$*, then* (u^*, v^*) *is locally asymptotically stable for all* $\chi < 0$ *or* $0 < \chi < \underline{\chi}$ *and it is unstable if* $\chi > \underline{\chi} > 0$.

(b2) If there exist some $i \geq 1$ *such that* $D_i(\mu_i, 0) < 0$*, then* (u^*, v^*) *is locally asymptotically stable for* $\chi < \underline{\chi} < 0$ *and it is unstable if* $\underline{\chi} < \chi < 0$.

Proof. We shall only prove case (a), case (b) can be treated by the same arguments. Since $T_i(\mu_i) < 0$ for all $i \geq 1$, we need consider the sign of $D_i(\mu_i, \chi)$.

(a1) If $D_i(\mu_i, 0) > 0$ for all $i \geq 1$, then by $f_2 < 0$, we have $D_i(\mu_i, \chi) > 0$ for all $i \geq 1$ when $\chi > 0$ by (2.2). In addition, $\chi_i < 0$ by (2.3) and $D_i(\mu_i, \chi) > 0$ if $\overline{\chi} < \chi < 0$ for all i. This implies that the positive equilibrium (u^*, v^*) is locally asymptotically stable. If $\chi < \overline{\chi} < 0$, then $D_i(\mu_i, \chi) < 0$. The result leads to the instability of (u^*, v^*).

(a2) If there exist some $i \geq 1$ such that $D_i(\mu_i, 0) < 0$ and $0 < \overline{\chi} < \chi$, then $\chi > \chi_i$ for $i \in \Lambda$, it follows that $D_i(\mu_i, \chi) > 0$ for all $i \in \Lambda$. Furthermore, if $i \notin \Lambda$, then $D_i(\mu_i, 0) > 0$ and $D_i(\mu_i, \chi) > 0$ by (2.2). The argument leads to the asymptotical stability of (u^*, v^*) again.

If there exist some $i \geq 1$ such that $D_i(\mu_i, 0) < 0$ and $0 < \chi < \overline{\chi}$, then we may assume that the maximum in (2.4) is attained by $k \in \Lambda$, thus $0 < \chi < \overline{\chi}$ implies $D_k(\mu_k, \chi) < 0$ and so (2.1) has a positive eigenvalue when $i = k$. Hence, the instability of (u^*, v^*) follows. This finishes the proof of the theorem. □

Remark 2.2. Lee et al. in [17] obtained the stability of positive equilibrium for the $f_1 < 0$ in $\Omega = (0, l)$ with constant $l > 0$. In the view of above theorem, we extend their results, i.e. the conditions for the stability are established for general dimensional $N \geq 1$. And there are also some results when $f_1 > 0$, which includes the effects of the prey-taxis.

Remark 2.3. Case (a1) and (b1) in Theorem 2.1 show that (u^*, v^*) is stable for model (1.1) without prey-taxis, then it still keeps stable when the prey-taxis is attractive. However, repulsive prey-taxis can destabilize (u^*, v^*), which instability is caused by prey-taxis. Case (a2) and (b2) imply that attractive prey-taxis can stabilize (u^*, v^*) and inhibit the formation of spatial patterns even diffusion-driven instability has occurred.

Remark 2.4. Under the assumptions of $(\mathbf{H_1})$ and $(\mathbf{H_2})$, it is straightforward to derive that $T_i(\mu_i) < 0$, $D_i(\mu_i, 0) > 0$ and $D_i(\mu_i, \chi) > 0$ when $d_1 = d_2$ and $\chi\phi^* = 1$, in which case no any diffusion driven instability can happen.

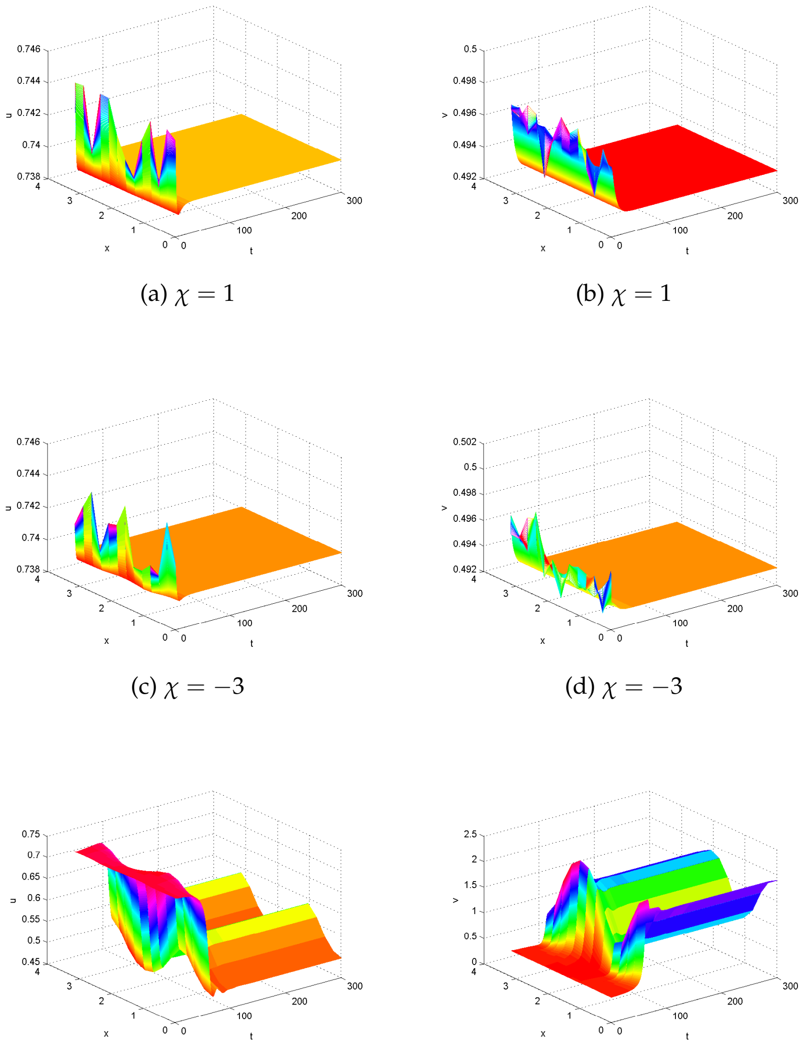
To illustrate Theorem 2.1, we give some numerical examples.

Example 2.5. We fix the parameter values $\alpha, \beta, \gamma, d_1, d_2$ and let χ as the variable parameter in model (1.1). In particular, we shall choose sensitivity function $\phi(u, v) = u(M - u)v$ to describe the situation that prey species can defend themselves in a group when the population density surpasses the threshold value M.

Firstly, let us choose

$$\alpha = 0.65, \quad \beta = 0.5, \quad \gamma = 0.3, \quad d_1 = 0.02, \quad d_2 = 0.2, \quad M = 1. \tag{2.5}$$

We can see that $\phi(u^*, v^*) \approx 0.09 > 0$ and $D_i(\mu_i, 0) > 0$ for all $i \geq 1$, and $\overline{\chi} \approx -7.1$. Then, the positive equilibrium (u^*, v^*) is stable for the diffusive model without prey-taxis. For model (1.1), by Theorem 2.1 (a1), (u^*, v^*) is locally asymptotically stable for $\chi = 1$ (Fig. 2.1(a)–2.1(b)) and $\chi = -3 \in (\overline{\chi}, 0)$ (Fig. 2.1(c)–2.1(d)), and it is unstable for $\chi = -7.5 < \overline{\chi}$ (Fig. 2.1(e)–2.1(f)), which instability is induced by prey-taxis.



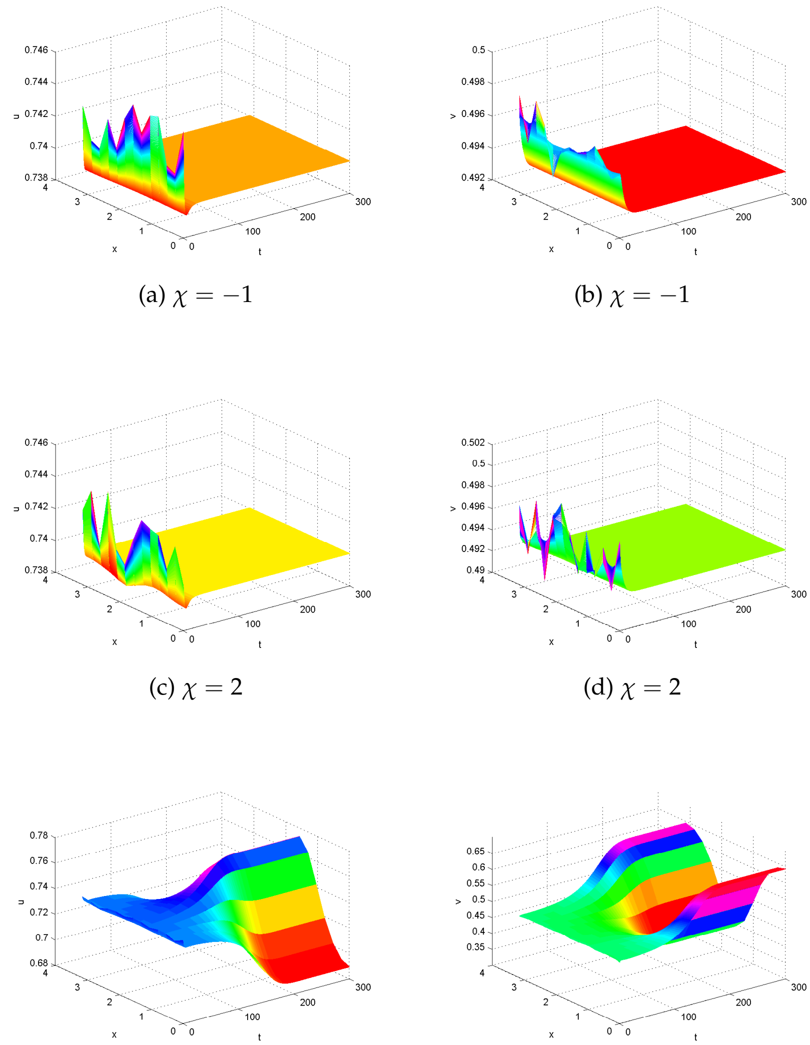
(a) $\chi = 1$ (b) $\chi = 1$

(c) $\chi = -3$ (d) $\chi = -3$

(e) $\chi = -7.5$ (f) $\chi = -7.5$

Figure 2.1: Numerical simulations of the solution $(u(x,t), v(x,t))$ for model (1.1) with $M = 1$ and $\phi(u^*, v^*) > 0$. When $\chi = 1$ or $\chi = -3 > \overline{\chi}$, (u^*, v^*) is stable (see (a)–(d)). When $\chi = -7.5 < \overline{\chi}$, (u^*, v^*) is unstable (see (e)–(f)).

Secondly, choose $M = 0.1$ in (2.5), then $\phi(u^*, v^*) \approx -0.2 < 0$, $D_i(\mu_i, 0) > 0$ for all $i \geq 1$ and $\underline{\chi} \approx 2.9$. For model (1.1), by Theorem 2.1 (b1), (u^*, v^*) is locally asymptotically stable for $\chi = -1$ (Fig. 2.2(a)–2.2(b)) and $\chi = 2 < \underline{\chi}$ (Fig. 2.2(c)–2.2(d)), it is unstable for $\chi = 3.1 > \underline{\chi}$ (Fig. 2.2(e)–2.2(f)).



(a) $\chi = -1$ (b) $\chi = -1$

(c) $\chi = 2$ (d) $\chi = 2$

(e) $\chi = 3.1$ (f) $\chi = 3.1$

Figure 2.2: Numerical simulations of the solution $(u(x,t), v(x,t))$ for model (1.1) with $M = 0.1$ and $\phi(u^*, v^*) < 0$. When $\chi = -1$ and $\chi = 2 < \underline{\chi}$, (u^*, v^*) is stable (see (a)–(d)). When $\chi = 3.1 > \underline{\chi}$, (u^*, v^*) is unstable (see (e)–(f)).

Now, we show spatial patterns for model (1.1) through varying χ. The numerical integration is performed by using a finite difference approximation for the spatial derivatives and an explicit Euler method for the time integration with a time step size of $1/100$ in a spatial domain of size 100×100 (the lattice size). The initial condition is always a small amplitude random perturbation around (u^*, v^*). We only show the results of pattern formation about the distribution of prey due to predator and prey are always of the similar type.

Example 2.6. We continue to choose the parameters values in (2.5). The critical value of $\overline{\chi} \approx -7.1$ and taxis-controlled spatial patterns generate in this case that χ is less than this value by Theorem 2.1(a1). Thus, choosing three values of χ: -7.5, -7.8, -8 and -8.5, we find that as the value of χ decrease, pattern formation change from spots pattern, spots-stripe pattern into stripe pattern in turn, see Fig. 2.3–2.4. Our numerical results reveal that random diffusion cannot drive instability, but prey-taxis can create Turing instability, and it does not belong to the classical Turing instability.

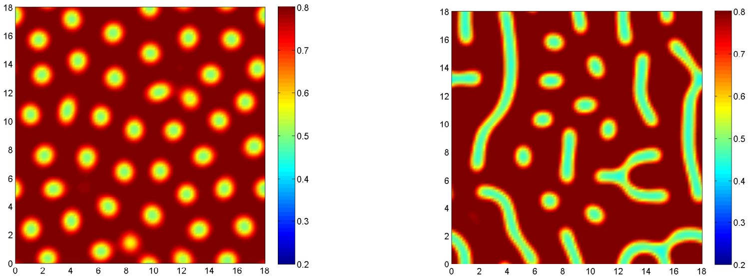


Figure 2.3: Spots and spots-stripe patterns of u in model (1.1) for $\chi = -7.5$ and $\chi = -7.8$.

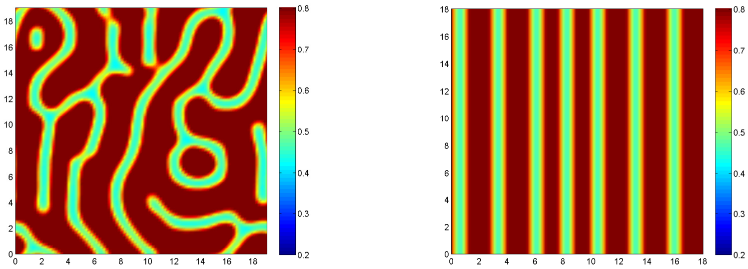


Figure 2.4: Stripe patterns of u in model (1.1) for $\chi = -8$ and $\chi = -8.5$.

3 Existence of nonconstant positive steady states

In this section, we shall proceed a rigorous bifurcation analysis in a one-dimensional interval $\Omega = (0, l)$ $(l > 0)$ to study a branch of nonconstant positive steady state solutions, which bifurcating from the constant steady state (u^*, v^*) by applying Crandall–Rabinowitz bifurcation theory [7] and its user-friendly version developed in [23].

The steady-state problem associated with model (1.1) as the following form

$$\begin{cases} -d_1 u'' = u(1-u) - \dfrac{\alpha u v}{u+v} & \text{on } (0,l), \\ -d_2 v'' + (\chi \phi(u,v) u')' = v\left(-\gamma + \dfrac{\beta u}{u+v}\right) & \text{on } (0,l), \\ u' = v' = 0 & \text{at } x = 0, l. \end{cases} \tag{3.1}$$

Let

$$\begin{aligned} X &= \{(u,v) : u, v \in H^2(0,l),\ u' = v' = 0, x = 0, l\}, \\ W &= \{(\chi; u, v) \in \mathbb{R} \times X \times X \mid u > 0, v > 0\}, \\ Y &= L^2(0,l) \times L^2(0,l). \end{aligned}$$

To apply the bifurcation theory, we treat χ as the bifurcation parameter. Define a nonlinear mapping $F : \mathbb{R} \times X \times X \to Y \times Y$ by

$$F(\chi; u, v) = \begin{pmatrix} d_1 u'' + u(1-u) - \dfrac{\alpha uv}{u+v} \\ d_2 v'' - (\chi\phi(u,v)u')' + v\left(-\gamma + \dfrac{\beta u}{u+v}\right) \end{pmatrix}. \tag{3.2}$$

Then $F(\chi; u^*, v^*) = 0$ for any $\chi \in \mathbb{R}$. For any fixed $(u_1, v_1) \in X \times X$, the Fréchet derivative of F is given by

$$\begin{aligned} &F_{(u,v)}(\chi; u_1, v_1)(u, v) \\ &= \begin{pmatrix} d_1 u'' + f_u(u_1, v_1)u + f_v(u_1, v_1)v \\ d_2 v'' - \chi(\phi(u_1, v_1)u' + u_1'(\phi_u(u_1, v_1)u + \phi_v(u_1, v_1)v))' + g_u(u_1, v_1)u + g_v(u_1, v_1)v \end{pmatrix} \end{aligned} \tag{3.3}$$

We now show that all the conditions for Theorem 4.3 in [23] are satisfied. In fact, $F(\chi; u_1, v_1)$ is continuous and differentiable with respect to χ, u, v in W. Furthermore, by (3.3), we have

$$F_{\chi(u,v)}(\chi; u_1, v_1)(u, v) = \begin{pmatrix} 0 \\ -(\phi(u_1, v_1)u' + u_1'(\phi_u(u_1, v_1)u + \phi_v(u_1, v_1)v))' \end{pmatrix}, \tag{3.4}$$

which is continuous.

To seek for the possible bifurcation points, we first check $\mathrm{Ker}(F_{(u,v)}(\chi; u^*, v^*)) \neq \{0\}$ and this implies that the system

$$\begin{cases} d_1 u'' + f_1 u + f_2 v = 0 & \text{on } (0, l), \\ d_2 v'' - \chi\phi^* u'' + g_1 u + g_2 v = 0 & \text{on } (0, l), \\ u' = v' = 0 & \text{at } x = 0, l \end{cases} \tag{3.5}$$

has a nontrivial solution (u, v), expanding which as their eigenexpansions

$$u(x) = \sum_{i=0}^{\infty} a_i \cos\frac{i\pi x}{l}, \qquad v(x) = \sum_{i=0}^{\infty} b_i \cos\frac{i\pi x}{l},$$

where $\cos\frac{i\pi x}{l}$ is all eigenfunctions corresponding to the eigenvalue $(\frac{i\pi}{l})^2$ of $-\frac{d^2}{dx^2}$ under the Neumann boundary condition in $(0, l)$. Then, at least one of these coefficients in the expansions is nonzero if (u, v) is nonzero. Substituting these series into (3.5) gives

$$\begin{pmatrix} -d_1\left(\dfrac{i\pi}{l}\right)^2 + f_1 & f_2 \\ \chi\phi^*\left(\dfrac{i\pi}{l}\right)^2 + g_1 & -d_2\left(\dfrac{i\pi}{l}\right)^2 + g_2 \end{pmatrix} \begin{pmatrix} a_i \\ b_i \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \qquad i \in \mathbb{N}. \tag{3.6}$$

Clearly, $i = 0$ can be easily ruled out. Then, for $i \in \mathbb{N}^+$, system (3.5) has nontrivial solutions if and only if

$$\begin{vmatrix} -d_1\left(\dfrac{i\pi}{l}\right)^2 + f_1 & f_2 \\ \chi\phi^*\left(\dfrac{i\pi}{l}\right)^2 + g_1 & -d_2\left(\dfrac{i\pi}{l}\right)^2 + g_2 \end{vmatrix} = 0, \tag{3.7}$$

which implies that

$$\chi = \chi_i = \frac{d_1 d_2 \left(\frac{i\pi}{l}\right)^4 - (d_1 g_2 + d_2 f_1)\left(\frac{i\pi}{l}\right)^2 + f_1 g_2 - f_2 g_1}{\phi^* f_2 \left(\frac{i\pi}{l}\right)^2}. \tag{3.8}$$

In the following, we prove $F_{(u,v)}(\chi; u_1, v_1)$ is the Fredholm operator with zero index and $\operatorname{codim} \operatorname{Range} F(\chi_i; u^*, v^*) = 1$. Define $\mathbf{u} = (u,v)^T$ and rewrite (3.3) as

$$F_{\mathbf{u}}(\chi; \mathbf{u_1})\mathbf{u} = F_0(\chi; \mathbf{u_1})\mathbf{u}'' + F_1(\chi; \mathbf{u}, \mathbf{u}'), \tag{3.9}$$

where

$$F_0(\chi; \mathbf{u_1}) = \begin{pmatrix} d_1 & 0 \\ -\chi\phi(\mathbf{u_1}) & d_2 \end{pmatrix},$$

$$F_1(\chi; \mathbf{u}, \mathbf{u}') = \begin{pmatrix} f_u(\mathbf{u_1})u + f_v(\mathbf{u_1})v \\ -\chi(\phi'(\mathbf{u_1})u' + ({u_1}'(\phi_u(\mathbf{u_1})u + \phi_v(\mathbf{u_1})v))') + g_u(\mathbf{u_1})u + g_v(\mathbf{u_1})v \end{pmatrix}.$$

Operator $F_{\mathbf{u}}(\chi; \mathbf{u_1})$ is strictly elliptic due to $d_1 > 0, d_2 > 0$ and it satisfies the Agmon's condition for angles $\theta \in [-\pi/2, \pi/2]$ according to [23], then $F_{\mathbf{u}}(\chi; \mathbf{u_1})$ is the Fredholm operator with zero index.

In fact, the null space $\operatorname{Ker}(F_{(u,v)}(\chi_i; u^*, v^*))$ is one-dimensional and

$$\operatorname{Ker}(F_{(u,v)}(\chi_i; u^*, v^*)) = \operatorname{span}\{\tilde{u}_i, \tilde{v}_i\},$$

where

$$(\tilde{u}_i, \tilde{v}_i) = \{1, Q_i\} \cos\frac{i\pi x}{l} \tag{3.10}$$

with

$$Q_i = \frac{d_1(\frac{i\pi}{l})^2 - f_1}{f_2}, \qquad i \in \mathbb{N}^+. \tag{3.11}$$

Because we have proved that $F_{(u,v)}(\chi; u^*, v^*)$ is the Fredholm operator with zero index, then $\operatorname{codim} \operatorname{Range} F(\chi_i; u^*, v^*) = 1$.

To prove the following transversality condition

$$F_{\chi(u,v)}(\chi_i; u^*, v^*)(\tilde{u}_i, \tilde{v}_i) \notin \operatorname{Range}(F_{(u,v)}(\chi_i; u^*, v^*)),$$

we shall argue by contradiction. Obviously,

$$F_{\chi(u,v)}(\chi_i; u^*, v^*)(\tilde{u}_i, \tilde{v}_i) = \begin{pmatrix} 0 \\ -\phi^* {\tilde{u}_i}'' \end{pmatrix}. \tag{3.12}$$

If there exists a nontrivial pair $(\hat{u}, \hat{v})$ such that the condition fails, then $(\hat{u}, \hat{v})$ satisfies

$$\begin{pmatrix} d_1\hat{u}'' + f_1\hat{u} + f_2\hat{v} \\ d_2\hat{v}'' - \chi_i\phi^*\hat{u}'' + g_1\hat{u} + g_2\hat{v} \end{pmatrix} = \begin{pmatrix} 0 \\ -\phi^* {\tilde{u}_i}'' \end{pmatrix} \tag{3.13}$$

Substituting the following eigenexpansions of $\hat{u}$ and $\hat{v}$

$$\hat{u}(x) = \sum_{i=0}^{\infty} \tilde{a}_i \cos\frac{i\pi x}{l}, \qquad \hat{v}(x) = \sum_{i=0}^{\infty} \tilde{b}_i \cos\frac{i\pi x}{l}$$

into (3.13) gives

$$\begin{pmatrix} -d_1\left(\frac{i\pi}{l}\right)^2+f_1 & f_2 \\ \chi_i\phi^*\left(\frac{i\pi}{l}\right)^2+g_1 & -d_2\left(\frac{i\pi}{l}\right)^2+g_2 \end{pmatrix}\begin{pmatrix}\tilde{a}_i\\ \tilde{b}_i\end{pmatrix}=\begin{pmatrix}0\\ \phi^*\left(\frac{i\pi}{l}\right)^2\end{pmatrix}. \tag{3.14}$$

However, the determinant of the coefficient matrix on the left-hand is zero by (3.7), so (3.14) is impossible. Thus, we obtain the contradiction. In addition, we must have that $\chi_i \neq \chi_j$ for $i \neq j$ in order to apply the bifurcation theory, and obtain the following result.

Theorem 3.1. *Assume that* $(\mathbf{H_1}), (\mathbf{H_2})$ *and*

$$d_1d_2i^2j^2\left(\frac{\pi}{l}\right)^4 \neq f_1g_2-f_2g_1, \qquad \forall i\neq j,\ i,j\in\mathbb{N}^+ \tag{3.15}$$

hold. There exists a small positive constant δ *such that* (3.1) *admits nonconstant positive solutions* $(\chi_i(\epsilon); u_i(\epsilon,x), v_i(\epsilon,x))$ *for* $\epsilon\in(-\delta,\delta)$ *that bifurcate from* $(\chi_i; u^*, v^*)$*. Moreover, the solutions are smooth functions of* ϵ *such that*

$$\begin{aligned} \chi_i(\epsilon) &= \chi_i+\epsilon K_1+\epsilon^2K_2+O(\epsilon^3),\\ u_i(\epsilon,x) &= u^*+\epsilon\cos\frac{i\pi x}{l}+O(\epsilon),\\ v_i(\epsilon,x) &= v^*+\epsilon Q_i\cos\frac{i\pi x}{l}+O(\epsilon), \end{aligned} \tag{3.16}$$

and $\left((u_i(\epsilon,x),v_i(\epsilon,x))-(u^*,v^*)-\epsilon(1,Q_i)\cos\frac{i\pi x}{l}\right)\in Z$*, where*

$$Z=\left\{(u,v)\in X\times X \;\middle|\; \int_0^l(u\tilde{u}_i+v\tilde{v}_i)dx=0\right\}, \tag{3.17}$$

and $(\tilde{u}_i,\tilde{v}_i)$ *is given by* (3.10)*.*

4 Stability analysis of the bifurcation branches near $(\chi_i; u^*, v^*)$

In this section, we will provide criterion and explicit formulas to determine the direction of steady-state bifurcation and stability of the bifurcating solutions $(\chi_i(\epsilon); u_i(\epsilon,x), v_i(\epsilon,x))$ established in Theorem 3.1 for model (3.1). To this end, we can expand them as follows

$$\begin{aligned} \chi_i(\epsilon) &= \chi_i+\epsilon K_1+\epsilon^2K_2+\cdots,\\ u_i(\epsilon,x) &= u^*+\epsilon\cos\frac{i\pi x}{l}+\epsilon^2p_1(x)+\epsilon^3p_2(x)+\cdots,\\ v_i(\epsilon,x) &= v^*+\epsilon Q_i\cos\frac{i\pi x}{l}+\epsilon^2q_1(x)+\epsilon^3q_2(x)+\cdots, \end{aligned} \tag{4.1}$$

where Q_i is given by (3.11), $(p_k,q_k)\in Z$ for $k=1,2$, and

$$\begin{aligned} d_1u_i''(\epsilon,x) &= \epsilon d_1\cos''\frac{i\pi x}{l}+\epsilon^2d_1p_1''(x)+\epsilon^3d_1p_2''(x)+\cdots,\\ d_2v_i''(\epsilon,x) &= \epsilon d_2Q_i\cos''\frac{i\pi x}{l}+\epsilon^2d_2q_1''(x)+\epsilon^3d_2q_2''(x)+\cdots. \end{aligned} \tag{4.2}$$

Moreover, we have from the Taylor's expansion that

$$\begin{aligned}
&f(u_i(\epsilon,x),v_i(\epsilon,x))\\
&\quad= f(u^*,v^*)+\epsilon\Big((f_1+f_2Q_i)\cos\frac{i\pi x}{l}\Big)\\
&\qquad+\epsilon^2\Big(f_1p_1+f_2q_1+\frac{1}{2}(f_{11}+2f_{12}Q_i+f_{22}Q_i^2)\cos^2\frac{i\pi x}{l}\Big)\\
&\qquad+\epsilon^3\Big(f_1p_2+f_2q_2+(f_{11}+f_{12}Q_i)p_1\cos\frac{i\pi x}{l}+(f_{12}+f_{22}Q_i)q_1\cos\frac{i\pi x}{l}\\
&\qquad\quad+\frac{1}{6}(f_{111}+3f_{112}Q_i+3f_{122}Q_i^2+f_{222}Q_i^3)\cos^3\frac{i\pi x}{l}\Big)+\cdots,
\end{aligned}\tag{4.3}$$

$$\begin{aligned}
&g(u_i(\epsilon,x),v_i(\epsilon,x))\\
&\quad= g(u^*,v^*)+\epsilon\Big((g_1+g_2Q_i)\cos\frac{i\pi x}{l}\Big)\\
&\qquad+\epsilon^2\Big(g_1p_1+g_2q_1+\frac{1}{2}(g_{11}+2g_{12}Q_i+g_{22}Q_i^2)\cos^2\frac{i\pi x}{l}\Big)\\
&\qquad+\epsilon^3\Big(g_1p_2+g_2q_2+(g_{11}+g_{12}Q_i)p_1\cos\frac{i\pi x}{l}+(g_{12}+g_{22}Q_i)q_1\cos\frac{i\pi x}{l}\\
&\qquad\quad+\frac{1}{6}(g_{111}+3g_{112}Q_i+3g_{122}Q_i^2+g_{222}Q_i^3)\cos^3\frac{i\pi x}{l}\Big)+\cdots,
\end{aligned}\tag{4.4}$$

and

$$\begin{aligned}
&(\phi(u_i(\epsilon,x),v_i(\epsilon,x))u_i'(\epsilon,x))'\\
&= \epsilon\phi^*\cos''\frac{i\pi x}{l}+\epsilon^2\Big(\phi^*p_1''+(\phi_1+\phi_2Q_i)\Big(\cos\frac{i\pi x}{l}\cos'\frac{i\pi x}{l}\Big)'\Big)\\
&\quad+\epsilon^3\Big(\phi^*p_2''+(\phi_1+\phi_2Q_i)\Big(p_1'\cos\frac{i\pi x}{l}\Big)'+\phi_1\Big(p_1\cos'\frac{i\pi x}{l}\Big)'+\phi_2\Big(q_1\cos'\frac{i\pi x}{l}\Big)'\\
&\qquad+\frac{1}{2}(\phi_{11}+2\phi_{12}Q_i+\phi_{22}Q_i^2)\Big(\cos^2\frac{i\pi x}{l}\cos'\frac{i\pi x}{l}\Big)'\Big)+\cdots.
\end{aligned}\tag{4.5}$$

To evaluate K_1, substituting (4.1)–(4.5) into the second equation in (3.1) and collecting their s^2-terms, we have

$$\begin{aligned}
&d_2q_1''+g_1p_1+g_2q_1+\frac{1}{2}(g_{11}+2g_{12}Q_i+g_{22}Q_i^2)\cos^2\frac{i\pi x}{l}\\
&\quad=\chi_i\Big(\phi^*p_1''+(\phi_1+\phi_2Q_i)\Big(\cos\frac{i\pi x}{l}\cos'\frac{i\pi x}{l}\Big)'\Big)+K_1\phi^*\cos''\frac{i\pi x}{l}.
\end{aligned}\tag{4.6}$$

Multiplying (4.6) by $\cos\frac{i\pi x}{l}$ and integrating it over $(0,l)$ lead to

$$\begin{aligned}
K_1=&-\frac{2l}{\phi^*(i\pi)^2}\Big(\Big(g_1+\chi_i\phi^*\Big(\frac{i\pi}{l}\Big)^2\Big)\int_0^l p_1\cos\frac{i\pi x}{l}dx\\
&+\Big(g_2-d_2\Big(\frac{i\pi}{l}\Big)^2\Big)\int_0^l q_1\cos\frac{i\pi x}{l}dx\Big).
\end{aligned}\tag{4.7}$$

Likewise, substituting (4.1)–(4.5) into the first equation in (3.1) and collecting their s^2-terms, we obtain

$$d_1 p_1'' + f_1 p_1 + f_2 q_1 + \frac{1}{2}(f_{11} + 2f_{12}Q_i + f_{22}Q_i^2)\cos^2\frac{i\pi x}{l} = 0. \tag{4.8}$$

Multiplying (4.8) by $\cos\frac{i\pi x}{l}$ and integrating it over $(0, l)$, we derive

$$\left(-d_1\left(\frac{i\pi}{l}\right)^2 + f_1\right)\int_0^l p_1\cos\frac{i\pi x}{l}dx + f_2\int_0^l q_1\cos\frac{i\pi x}{l}dx = 0. \tag{4.9}$$

On the other hand, since $(p_1, q_1) \in Z$ as defined in (3.17), then

$$\left(d_1\left(\frac{i\pi}{l}\right)^2 - f_1\right)\int_0^l q_1\cos\frac{i\pi x}{l}dx + f_2\int_0^l p_1\cos\frac{i\pi x}{l}dx = 0. \tag{4.10}$$

From (4.9) and (4.10), we have the following system

$$\begin{pmatrix} -d_1\left(\frac{i\pi}{l}\right)^2 + f_1 & f_2 \\ f_2 & d_1\left(\frac{i\pi}{l}\right)^2 - f_1 \end{pmatrix}\begin{pmatrix} \int_0^l p_1\cos\frac{i\pi x}{l}dx \\ \int_0^l q_1\cos\frac{i\pi x}{l}dx \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}. \tag{4.11}$$

Obviously, the coefficient matrix in (4.11) is not singular. Then

$$\int_0^l p_1\cos\frac{i\pi x}{l}dx = \int_0^l q_1\cos\frac{i\pi x}{l}dx = 0. \tag{4.12}$$

So $K_1 = 0$ by (4.7). Hence, the bifurcation curve $\Gamma_i(\epsilon)$ is of pitchfork type, we present the following lemma.

Lemma 4.1. *Suppose that all conditions in Theorem 3.1 hold. Then for each $i \in \mathbb{N}^+$, $K_1 = 0$ and the bifurcation curve $\Gamma_i(\epsilon)$ around $(\chi_i; u^*, v^*)$ is pitchfork, that is, is of one-sided.*

We now proceed to discuss the sign of K_2 to determine the bifurcation direction and the stability of $\Gamma_i(\epsilon)$ around $(\chi_i; u^*, v^*)$. Equating ϵ^3-terms in the second equation of (3.1) by (4.1)–(4.5)

$$\begin{aligned} d_2 q_2'' &+ g_1 p_2 + g_2 q_2 + (g_{11} + g_{12}Q_i)p_1\cos\frac{i\pi x}{l} + (g_{12} + g_{22}Q_i)q_1\cos\frac{i\pi x}{l} \\ &+ \frac{1}{6}\left(g_{111} + 3g_{112}Q_i + 3g_{122}Q_i^2 + g_{222}Q_i^3\right)\cos^3\frac{i\pi x}{l} \\ &= \chi_i\left(\phi^* p_2'' + (\phi_1 + \phi_2 Q_i)\left(p_1'\cos\frac{i\pi x}{l}\right)' + \phi_1\left(p_1\cos'\frac{i\pi x}{l}\right)' + \phi_2\left(q_1\cos'\frac{i\pi x}{l}\right)'\right. \\ &\left.+ \frac{1}{2}(\phi_{11} + 2\phi_{12}Q_i + \phi_{22}Q_i^2)\left(\cos^2\frac{i\pi x}{l}\cos'\frac{i\pi x}{l}\right)'\right) + K_2\phi^*\cos''\frac{i\pi x}{l}, \end{aligned} \tag{4.13}$$

and multiplying (4.13) by $\cos\frac{i\pi x}{l}$ and integrating it over $(0, l)$ give rise to

$$\begin{aligned} K_2 = -\frac{2l}{\phi^*(i\pi)^2}&\left(A_1\int_0^l p_2\cos\frac{i\pi x}{l}dx + A_2\int_0^l q_2\cos\frac{i\pi x}{l}dx\right. \\ &+ A_3\int_0^l p_1\cos\frac{2i\pi x}{l}dx + A_4\int_0^l q_1\cos\frac{2i\pi x}{l}dx \\ &\left.+ A_5\int_0^l p_1 dx + A_6\int_0^l q_1 dx + A_7\right), \end{aligned} \tag{4.14}$$

where

$$A_1 = \chi_i \phi^* \Big(\frac{i\pi}{l}\Big)^2 + g_1, \quad A_2 = -d_2 \Big(\frac{i\pi}{l}\Big)^2 + g_2,$$

$$A_3 = \frac{1}{2}(g_{11} + g_{12}Q_i) + \chi_i \Big(\frac{1}{2}\phi_1 + \phi_2 Q_i\Big)\Big(\frac{i\pi}{l}\Big)^2,$$

$$A_4 = \frac{1}{2}(g_{12} + g_{22}Q_i) - \frac{1}{2}\chi_i \phi_2 \Big(\frac{i\pi}{l}\Big)^2,$$

$$A_5 = \frac{1}{2}(g_{11} + g_{12}Q_i) + \frac{1}{2}\chi_i \phi_1 \Big(\frac{i\pi}{l}\Big)^2,$$

$$A_6 = \frac{1}{2}(g_{12} + g_{22}Q_i) + \frac{1}{2}\chi_i \phi_2 \Big(\frac{i\pi}{l}\Big)^2,$$

and

$$A_7 = \frac{l}{16}\left((g_{111} + 3g_{112}Q_i + 3g_{122}Q_i^2 + g_{222}Q_i^3) + \chi_i \left(\frac{i\pi}{l}\right)^2 (\phi_{11} + 2\phi_{12}Q_i + \phi_{22}Q_i^2)\right).$$

Similarly, equating ϵ^3-terms in the first equation of (3.1) to obtain

$$\begin{aligned} d_1 p_2'' + f_1 p_2 + f_2 q_2 + (f_{11} + f_{12}Q_i)p_1 \cos\frac{i\pi x}{l} + (f_{12} + f_{22}Q_i)q_1 \cos\frac{i\pi x}{l} \\ + \frac{1}{6}(f_{111} + 3f_{112}Q_i + 3f_{122}Q_i^2 + f_{222}Q_i^3)\cos^3\frac{i\pi x}{l} = 0. \end{aligned} \tag{4.15}$$

Multiplying (4.15) by $\cos\frac{i\pi x}{l}$ and integrating it over $(0, l)$, we have

$$\left(-d_1\left(\frac{i\pi}{l}\right)^2 + f_1\right)\int_0^l p_2 \cos\frac{i\pi x}{l}dx + f_2\int_0^l q_2 \cos\frac{i\pi x}{l}dx = B_0, \tag{4.16}$$

where

$$\begin{aligned} B_0 = &-\frac{1}{2}(f_{11} + f_{12}Q_i)\int_0^l p_1 \cos\frac{2i\pi x}{l}dx - \frac{1}{2}(f_{12} + f_{22}Q_i)\int_0^l q_1 \cos\frac{2i\pi x}{l}dx \\ &-\frac{1}{2}(f_{11} + f_{12}Q_i)\int_0^l p_1 - \frac{1}{2}(f_{12} + f_{22}Q_i)\int_0^l q_1 dx - \frac{l}{16}(f_{111} + 3f_{112}Q_i + 3f_{122}Q_i^2 + f_{222}Q_i^3). \end{aligned}$$

Since $(p_2, q_2) \in Z$, we obtain

$$\left(d_1\left(\frac{i\pi}{l}\right)^2 - f_1\right)\int_0^l q_2 \cos\frac{i\pi x}{l}dx + f_2\int_0^l p_2 \cos\frac{i\pi x}{l}dx = 0. \tag{4.17}$$

From (4.16) and (4.17), we have the following system

$$\begin{pmatrix} -d_1\left(\frac{i\pi}{l}\right)^2 + f_1 & f_2 \\ f_2 & d_1\left(\frac{i\pi}{l}\right)^2 - f_1 \end{pmatrix}\begin{pmatrix} \int_0^l p_2 \cos\frac{i\pi x}{l}dx \\ \int_0^l q_2 \cos\frac{i\pi x}{l}dx \end{pmatrix} = \begin{pmatrix} B_0 \\ 0 \end{pmatrix} \tag{4.18}$$

and solving (4.18) gives

$$\int_0^l p_2 \cos\frac{i\pi x}{l}dx = \frac{B_2}{B_1}, \qquad \int_0^l q_2 \cos\frac{i\pi x}{l} = \frac{B_3}{B_1}, \tag{4.19}$$

where

$$B_1 = -\left(d_1\left(\frac{i\pi}{l}\right)^2 - f_1\right)^2 - f_2^2, \qquad B_2 = B_0\left(d_1\left(\frac{i\pi}{l}\right)^2 - f_1\right), \qquad B_3 = -f_2 B_0.$$

To calculate K_2, it is necessary to evaluate the following integrals

$$\int_0^l p_1 dx, \ \int_0^l q_1 dx, \ \int_0^l p_1 \cos\frac{2i\pi x}{l}dx, \text{ and } \int_0^l q_1 \cos\frac{2i\pi x}{l}dx.$$

Integrating (4.6) and (4.8) over $(0, l)$, we derive

$$\begin{pmatrix} f_1 & f_2 \\ g_1 & g_2 \end{pmatrix}\begin{pmatrix} \int_0^l p_1 dx \\ \int_0^l q_1 dx \end{pmatrix} = \begin{pmatrix} -\frac{l}{4}(f_{11} + 2f_{12}Q_i + f_{22}Q_i^2) \\ -\frac{l}{4}(g_{11} + 2g_{12}Q_i + g_{22}Q_i^2) \end{pmatrix}. \tag{4.20}$$

Solving (4.20) gives

$$\int_0^l p_1 dx = \frac{C_1}{C_0}, \qquad \int_0^l q_1 dx = \frac{C_2}{C_0}, \tag{4.21}$$

where

$$\begin{aligned} C_0 &= f_1 g_2 - f_2 g_1, \\ C_1 &= -\frac{l}{4}\Big((f_{11} + 2f_{12}Q_i + f_{22}Q_i^2)g_2 - (g_{11} + 2g_{12}Q_i + g_{22}Q_i^2)f_2\Big), \\ C_2 &= \frac{l}{4}\Big((f_{11} + 2f_{12}Q_i + f_{22}Q_i^2)g_1 - (g_{11} + 2g_{12}Q_i + g_{22}Q_i^2)f_1\Big). \end{aligned}$$

Multiplying (4.6) and (4.8) by $\cos\frac{2i\pi x}{l}$ and integrating them over $(0, l)$, we have

$$\begin{pmatrix} -d_1\left(\frac{2i\pi}{l}\right)^2 + f_1 & f_2 \\ \chi_i \phi^* \left(\frac{2i\pi}{l}\right)^2 + g_1 & -d_2\left(\frac{2i\pi}{l}\right)^2 + g_2 \end{pmatrix}\begin{pmatrix} \int_0^l p_1 \cos\frac{2i\pi x}{l}dx \\ \int_0^l q_1 \cos\frac{2i\pi x}{l}dx \end{pmatrix} = \begin{pmatrix} C_3 \\ C_4 \end{pmatrix}, \tag{4.22}$$

where

$$\begin{aligned} C_3 &= -\frac{l}{8}(f_{11} + 2f_{12}Q_i + f_{22}Q_i^2), \\ C_4 &= -\frac{l}{8}(g_{11} + 2g_{12}Q_i + g_{22}Q_i^2) - \frac{i^2\pi^2}{2l}\chi_i(\phi_1 + \phi_2 Q_i). \end{aligned}$$

Solving (4.22) leads to

$$\int_0^l p_1 \cos\frac{2i\pi x}{l}dx = \frac{D_1}{D_0}, \qquad \int_0^l q_1 \cos\frac{2i\pi x}{l} = \frac{D_2}{D_0}, \tag{4.23}$$

where

$$D_0 = \left(-d_1\left(\frac{2i\pi}{l}\right)^2 + f_1\right)\left(-d_2\left(\frac{2i\pi}{l}\right)^2 + g_2\right) - \left(\chi_i\phi^*\left(\frac{2i\pi}{l}\right)^2 + g_1\right)f_2,$$
$$D_1 = C_3\left(-d_2\left(\frac{2i\pi}{l}\right)^2 + g_2\right) - C_4 f_2,$$
$$D_2 = \left(-d_1\left(\frac{2i\pi}{l}\right)^2 + f_1\right)C_4 - \left(\chi_i\phi^*\left(\frac{2i\pi}{l}\right)^2 + g_1\right)C_3,$$

and D_0 is nonzero due to (3.15). Combining (4.19), (4.21) and (4.23), we can represent K_2 in (4.14) and the stability of the bifurcating solutions is asserted by the following theorem.

Theorem 4.2. *Assume that all conditions in Theorem 3.1 hold. Let K_2 be given in (4.14), $\Gamma_i(\epsilon)$ be the bifurcation branch of (3.1) obtained in Theorem 3.1.*

(i) If $\phi(u^*, v^*) > 0$, and $\chi_{i_0} = \max_{i\in\mathbb{N}^+}\{\chi_i\}$, then all positive integers $i \neq i_0$ and small constant $\epsilon > 0$, $\Gamma_i(\epsilon)$ is always unstable for $\epsilon \in (-\delta, \delta)$. Moreover, $\Gamma_{i_0}(\epsilon)$ is stable for $\epsilon \in (-\delta, \delta)$ if $K_2 < 0$ and it is unstable for $\epsilon \in (-\delta, \delta)$ if $K_2 > 0$.

(ii) If $\phi(u^*, v^*) < 0$, and $\chi_{i_0} = \min_{i\in\mathbb{N}^+}\{\chi_i\}$, then all positive integers $i \neq i_0$ and small constant $\epsilon > 0$, $\Gamma_i(\epsilon)$ is always unstable for $\epsilon \in (-\delta, \delta)$. Moreover, $\Gamma_{i_0}(\epsilon)$ is stable for $\epsilon \in (-\delta, \delta)$ if $K_2 > 0$ and it is unstable for $\epsilon \in (-\delta, \delta)$ if $K_2 < 0$.

Proof. We shall only prove case (i), case (ii) is treated similarly.

For each $i \in \mathbb{N}^+$, we linearize (3.1) around $(\chi_i(\epsilon); u_i(\epsilon, x), v_i(\epsilon, x))$ and obtain the following eigenvalue problem

$$F_{(u,v)}(\chi_i(\epsilon); u_i(\epsilon, x), v_i(\epsilon, x))(u, v) = \lambda(\epsilon)(u, v), \qquad (u, v) \in X \times X. \tag{4.24}$$

Then, $(\chi_i(\epsilon); u_i(\epsilon, x), v_i(\epsilon, x))$ is asymptotically stable if and only if the real part of any eigenvalue $\lambda(\epsilon)$ is negative for $\epsilon \in (-\delta, \delta)$.

Sending ϵ to 0, we know that $\lambda = \lambda(0)$ is a simple eigenvalue of the following eigenvalue problem

$$\begin{cases} d_1 u'' + f_1 u + f_2 v = \lambda u & \text{on } (0, l), \\ d_2 v'' - \chi_i\phi^* u'' + g_1 u + g_2 v = \lambda v & \text{on } (0, l), \\ u' = v' = 0 & \text{at } x = 0, l, \end{cases} \tag{4.25}$$

which has a one-dimensional eigenspace

$$\mathrm{Ker}(F_{(u,v)}(\chi_i; u^*, v^*)) = \left\{(1, Q_i)\cos\frac{i\pi x}{l}\right\}$$

and one can also prove that $(1, Q_i)\cos\frac{i\pi x}{l} \notin \mathrm{Range}(F_{(u,v)}(\chi_i; u^*, v^*))$, following the same analysis of Section 3 that leads to (3.16).

Multiplying (4.25) by $\cos\frac{i\pi x}{l}$ and integrating it over $(0, l)$, we have

$$\begin{pmatrix} -d_1\left(\frac{i\pi}{l}\right)^2 + f_1 - \lambda & f_2 \\ \chi_i\phi^*\left(\frac{i\pi}{l}\right)^2 + g_1 & -d_2\left(\frac{i\pi}{l}\right)^2 + g_2 - \lambda \end{pmatrix}\begin{pmatrix} \int_0^l u\cos\frac{i\pi x}{l}dx \\ \int_0^l v\cos\frac{i\pi x}{l}dx \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix},$$

where λ satisfies the following characteristic equation

$$\Theta_i(\lambda) = \lambda^2 + T_i\lambda + D_i$$

with

$$T_i = (d_1 + d_2)\left(\frac{i\pi}{l}\right)^2 - f_1 - g_2,$$

$$D_i = d_1 d_2\left(\frac{i\pi}{l}\right)^4 - (d_1 g_2 + d_2 f_1 + \phi^* f_2 \chi_i)\left(\frac{i\pi}{l}\right)^2 + f_1 g_2 - f_2 g_1.$$

If $\chi_i \neq \chi_{i_0} = \max_{i\in\mathbb{N}^+}\{\chi_i\}$, due to (3.8), then $\Theta_i(\lambda) = 0$ always has a positive root $\lambda(0)$ for all $i \neq i_0$. From the standard eigenvalue perturbation theory in [15], for ϵ being small, there exists an eigenvalue $\lambda(\epsilon)$ to (4.24) that has a positive root and therefore $\Gamma_i(\epsilon)$ is unstable for $\epsilon \in (-\delta, \delta)$.

To study the stability of $\Gamma_i(\epsilon)$ with $i = i_0$, we first see that $\Theta_{i_0}(\lambda) = 0$ has one being negative and the other being zero. Hence, we need to consider the asymptotic behavior of the zero eigenvalue as $\epsilon \approx, \neq 0$. According to Corollary 1.13 in [8], there exists an interval S with $\chi_{i_0} \in S$ and C^1-smooth functions (χ, ϵ): $S \times (-\delta, \delta) \to (\theta(\chi), \lambda(\epsilon))$ such that $(\theta(\chi_{i_0}), \lambda(0)) = (0, 0)$. Moreover, $\lambda(\epsilon)$ is the only eigenvalue in any fixed neighborhood of the complex plane origin and $\theta(\chi)$ is the only eigenvalue of the following eigenvalue problem

$$F_{(u,v)}(\chi; u^*, v^*)(u, v) = \theta(\chi)(u, v), \qquad (u, v) \in X \times X, \tag{4.26}$$

or equivalently

$$\begin{cases} d_1 u'' + f_1 u + f_2 v = \theta(\chi) u & \text{on } (0, l), \\ d_2 v'' - \chi\phi^* u'' + g_1 u + g_2 v = \theta(\chi) v & \text{on } (0, l), \\ u' = v' = 0 & \text{at } x = 0, l. \end{cases} \tag{4.27}$$

Furthermore, the eigenfunction of (4.26) can be represented by $(u(\chi, x), v(\chi, x))$ which depends on χ smoothly and is uniquely determined by

$$(u(\chi_{i_0}, x), v(\chi_{i_0}, x)) = (1, Q_{i_0}) \cos\frac{i_0\pi x}{l}$$

and

$$(u(\chi, x), v(\chi, x)) - (1, Q_{i_0}) \cos\frac{i_0\pi x}{l} \in Z.$$

Differentiating (4.27) with respect to χ and evaluated at $\chi = \chi_{i_0}$, we get

$$\begin{cases} d_1\dot{u}'' + f_1\dot{u} + f_2\dot{v} = \dot{\theta}(\chi_{i_0}) \cos\dfrac{i_0\pi x}{l}, & x \in (0, l), \\ d_2\dot{v}'' - \chi_{i_0}\phi^*\dot{u}'' - \phi^*\left(\cos\dfrac{i_0\pi x}{l}\right)'' + g_1\dot{u} + g_2\dot{v} = \dot{\theta}(\chi_{i_0}) Q_{i_0} \cos\dfrac{i_0\pi x}{l}, & x \in (0, l), \\ \dot{u}'(x) = \dot{v}'(x) = 0, & x = 0, l, \end{cases} \tag{4.28}$$

where $\cdot$ denotes the derivative taken with respect to χ.

Multiplying (4.28) by $\cos\frac{i_0\pi x}{l}$ and integrating it over $(0, l)$ yield

$$\begin{pmatrix} -d_1\left(\dfrac{i_0\pi}{l}\right)^2 + f_1 & f_2 \\ \chi_{i_0}\phi^*\left(\dfrac{i_0\pi}{l}\right)^2 + g_1 & -d_2\left(\dfrac{i_0\pi}{l}\right)^2 + g_2 \end{pmatrix} \begin{pmatrix} \int_0^l \dot{u}\cos\dfrac{i_0\pi x}{l}dx \\ \int_0^l \dot{v}\cos\dfrac{i_0\pi x}{l}dx \end{pmatrix} = \begin{pmatrix} \dfrac{l}{2}\dot{\theta}(\chi_{i_0}) \\ \dfrac{l}{2}\left(\dot{\theta}(\chi_{i_0})Q_{i_0} - \phi^*\left(\dfrac{i_0\pi}{l}\right)^2\right) \end{pmatrix}.$$

The coefficient matrix is singular thanks to (3.8), therefore if the algebraic system solvable, we must have

$$\frac{-d_1\left(\frac{i_0\pi}{l}\right)^2+f_1}{\chi_{i_0}\phi^*\left(\frac{i_0\pi}{l}\right)^2+g_1}=\frac{\dot\theta(\chi_{i_0})}{\dot\theta(\chi_{i_0})Q_{i_0}-\phi^*\left(\frac{i_0\pi}{l}\right)^2},$$

which together with (3.11) $(i=i_0)$ implies that

$$\dot\theta(\chi_{i_0})=\frac{\phi^*\left(\frac{i_0\pi}{l}\right)^2}{1+Q_{i_0}^2}>0.$$

According to Theorem 1.16 in [8], the functions $\lambda(\epsilon)$ and $-\epsilon\chi'(i_0,\epsilon)\dot\theta(\chi_{i_0})$ have the same zeros and signs near $\epsilon=0$. Moreover, for $\lambda(\epsilon)=0$, one has that

$$\lim_{\epsilon\to 0}\frac{-\epsilon\chi'(i_0,\epsilon)\dot\theta(\chi_{i_0})}{\lambda(\epsilon)}=1.$$

Therefore, $\operatorname{sgn}(\lambda(0))=\operatorname{sgn}(K_2)$ in terms of $K_1=0$. Following the standard perturbation theory, one can see that $\operatorname{sgn}(\lambda(\epsilon))=\operatorname{sgn}(K_2)$ for $\epsilon\in(-\delta,\delta)$, δ being small constant. This completes the proof. □

5 Discussions and concluding remarks

In this paper, our main purpose is to describe the existence and stability of nonconstant positive steady states to the ratio-dependent predator–prey model (1.1) with prey-taxis. It is worth noting that the method used in the paper does apply to a wide class of prey-taxis model with general functional responses.

The stability of the unique positive constant equilibrium is studied when the domain is a general dimensional (Theorem 2.1). The results show that both prey-taxis coefficient χ and sensitivity function ϕ determines the linearized stability of this equilibrium. It is found that contrary to the foraging behavior of predator that may transform heterogeneous environments into homogeneous environments, the retreating behavior of predator may transform homogeneous environments into heterogeneous environments. That is to say, prey-taxis can generate pattern formation if prey defenses are considered. These results indicate, to some extent, that the dynamics behavior of ratio-dependent model with prey-taxis are rich and interesting.

Under the assumption of Theorem 3.1, each $(\chi_i;u^*,v^*)$ is a bifurcation point with respect to the trivial branch $(\chi;u^*,v^*)$ and the number of such bifurcation points is infinite. However, Theorem 3.1 does not provide information about the bifurcation curve away from the bifurcation point, and the condition $\chi_i\neq\chi_j$ for any integer $i\neq j$ guarantees $\dim\operatorname{Ker}F_{(u,v)}(\chi_i;u^*,v^*)=1$, that is 0 is a simple eigenvalue of $F_{(u,v)}(\chi_i;u^*,v^*)$. Hence, we can apply global bifurcation theory to understand its global structure, it is our further study. In addition, $i\mapsto\chi_i$ is not a one-to-one and χ_i is not monotonous function. If $\chi_i=\chi_j$ for some integer $i\neq j$, then $\dim\operatorname{Ker}F_{(u,v)}(\chi_i;u^*,v^*)>1$. We also hope to discuss this case in the near future.

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