

ASYMPTOTIC DYNAMICS AND SPATIAL PATTERNS OF A RATIO-DEPENDENT PREDATOR-PREY SYSTEM WITH PREY-TAXIS

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ABSTRACT. This paper is concerned with the global dynamics of a ratio-dependent predator-prey system with prey-taxis. We establish the global existence and uniform-in-time boundedness of solutions in any dimensional bounded domain with Neumann boundary conditions, and furthermore prove the global stability of homogeneous steady states under certain conditions. Finally we perform numerical simulations to show that the pattern formation may arise and prey-taxis is a factor driving the evolution of spatial inhomogeneity into homogeneity.

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1. INTRODUCTION

Prey-taxis plays important roles in ecological system, such as regulating prey (pest) population to avoid incipient outbreaks, forming large-scale aggregation for survival and so on [13, 25, 30]. The mathematical model of prey-taxis reads as (cf. [18])

$$\begin{cases} u_t = \Delta u - \nabla \cdot (\chi u \nabla v) + \beta u F(u, v) - \theta u, \\ v_t = d \Delta v - u F(u, v) + v f(v), \end{cases} \quad (1.1)$$

where $u = u(x, t)$ and $v = v(x, t)$ denote the predator density and prey density at position x and time $t > 0$, respectively; the term $-\nabla \cdot (\chi u \nabla v)$ accounts for the prey-taxis with prey-tactic coefficient χ . $F(u, v)$ is the so-called functional response (intake rate of the predator as a function of prey density), and β is the harvesting rate, $\theta > 0$ denotes predator's natural death rate, d is the prey diffusion rate. The function $f(v)$ denotes the per capita growth rate of prey which is assumed to be negative for large $v > 0$ due to the limitation of resources. The most typical forms of $f(v)$ include the following two types:

$$\begin{aligned} (a) \quad & f(v) = r \left(1 - \frac{v}{K}\right) \quad (\text{Logistic type}), \\ (b) \quad & f(v) = r \left(1 - \frac{v}{K}\right) \left(\frac{v}{A} - 1\right) \quad (\text{Bistable type}), \end{aligned} \quad (1.2)$$

where $r > 0$ is the intrinsic growth rate of prey and $K > 0$ is called the carrying capacity with $0 < A < K$.

An important class of functional response function $F(u, v)$ is $F(v, v) := F(v)$, namely $F(u, v)$ depends on prey density only, where the widely used forms in the literature are:

$$\begin{aligned} F(v) = v \quad & (\text{Holling type I}), \quad F(v) = \frac{v}{m + v} \quad (\text{Holling type II}), \\ F(v) = \frac{v^h}{m^h + v^h} \quad & (\text{Holling type III}), \end{aligned} \quad (1.3)$$

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where $m > 0$ and $h > 1$. Some other functional response functions can be found in books [26, 37].

Without prey-taxis (i.e., $\chi = 0$), model (1.1) becomes the diffusive predator-prey system which has been widely studied in the literature and a large body of results have been available (cf. see [38] and references therein). When prey-taxis comes in ($\chi > 0$), the model structure changes drastically and the results on the predator-prey system with prey-taxis ($\chi > 0$) are much less compared to the one without prey-taxis. First Lee *et al.* [22] investigated the traveling wave solutions of system (1.1) in \mathbb{R} , and later exploited the pattern formation of (1.1) in a bounded interval with zero Neumann boundary condition [23]. It was further numerically explored in [10] that initial conditions and the form of functional response function play important roles in the pattern formation. When $F(u, v) = F(v)$ is prey-dependent only, Wu *et al.* [44] recently obtained the global existence of classical solutions of (1.1) in any dimensions for small $\chi > 0$. Subsequently Jin and Wang [16] established the global existence of classical solutions of (1.1) in two dimensions for any $\chi > 0$ and proved the global stability of the homogeneous steady states. When the prey-taxis term $-\nabla \cdot (\chi u \nabla v)$ is replaced by $-\nabla \cdot (\rho(u) u \nabla v)$ with some truncation conditions on $\rho(u)$, the global existence of solutions of (1.1) was established in [1, 14, 34]. When $\chi < 0$, the existence of non-constant steady states of (1.1) was studied in [24, 41] by global/Hopf bifurcation theorem and index degree theory. In [40], the authors studied nonconstant positive steady states of (1.1) in one dimension for a Holling-Tanner type predator-prey population dynamics. Recently the predator-prey system with density-dependent diffusion and prey-taxis has been studied in [17].

Apart from the afore-mentioned prey-dependent functional response, it has been argued by some biologists with evidences from field and laboratory experiments (cf. [2, 3, 7, 8, 11]) that in some situations, especially when predators have to search for food (and therefore have to share or compete for food), a ratio-dependent theory should be more suitable for the predator-prey dynamics, namely the per capita predator growth rate should be a function of the ratio of prey to predator abundance. Based on the Holling type II function, Arditi and Ginzburg [7] proposed the following ratio-dependent functional response function:

$$F(u, v) := F(v/u) = \frac{\frac{v}{u}}{m + \frac{v}{u}} = \frac{v}{mu + v}, \quad (1.4)$$

where $m > 0$ is a constant. Then the ratio-dependent predator-prey model with prey-taxis reads

$$\begin{cases} u_t = \Delta u - \nabla \cdot (\chi u \nabla v) + \frac{\beta uv}{mu + v} - \theta u, & x \in \Omega, t > 0, \\ v_t = d \Delta v - \frac{uv}{mu + v} + v f(v), & x \in \Omega, t > 0, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x), \quad v(x, 0) = v_0(x), & x \in \Omega, \end{cases} \quad (1.5)$$

where we have assumed the population live in a bounded habitat $\Omega \subset \mathbb{R}^N$ ($N \geq 1$) with smooth boundary and ν denotes the outward normal vector of $\partial\Omega$ with $\partial_\nu = \frac{\partial}{\partial \nu}$. For the convenience of presentation, we shall use the notation $F(w) = \frac{w}{m+w}$ with $w = \frac{v}{u}$ from time to time in the sequel.

Without spatial structure (namely both diffusion and prey-taxis are not considered), the system (1.5) becomes the ratio-dependent predator-prey ODE system whose dynamics have been well understood (see [19, 15, 45] and references therein). If diffusion is included and prey-taxis is ignored ($\chi = 0$), the following results have been obtained for (1.5) when $f(v)$ is of logistic type. Pang and Wang [27] established the (local) stability of both constant and non-constant steady states for system (1.5) and showed that the diffusion is a factor inducing pattern formations. Later, Fan and Li [12] obtained the global stability of homogeneous steady states by the method of upper-lower solutions combined with the monotone iteration and construction of suitable Lyapunov functions. The finite difference solution and its asymptotic behavior were studied in [42]. Pattern formation and Hopf-Turing bifurcation were investigated in [39, 9, 33, 32]. When

$f(v)$ is of bistable type, the existence of non-constant positive steady states and spatial patterns of (1.5) with $\chi = 0$ were established in [29].

To the best of our knowledge, when prey-taxis is considered (i.e., $\chi > 0$), no results have been available to the system (1.5). The main objective of this paper is to establish global existence and stability of solutions to (1.5), show that nonconstant steady states exist in some range of parameters and identify the role that the prey-taxis plays. For the function $f(v)$, we shall consider the logistic type only in this paper. Hence in the sequel, we assume $f(v)$ satisfies the following conditions:

(H1) The function $f : [0, \infty) \rightarrow \mathbb{R}$ is continuously differentiable satisfying $f'(v) \leq -\delta$ for some constant $\delta > 0$ and for all $v \geq 0$, and there exist two constants $r, K > 0$ such that $f(0) > 0$, $f(K) = 0$ and $f(v) < 0$ for all $v > K$.

The rest of this paper is organized as follows: In Section 2, we prove the global existence of classical solutions of (1.5). In Section 3, we show the global stability of the homogenous steady states by using the method of Lyapunov functional along with the LaSalle's invariant principle. In Section 4, we study the pattern formation of (1.5), numerically illustrate pattern formation and exploit the role of prey-taxis in the predator-prey dynamics.

2. GLOBAL EXISTENCE OF SOLUTIONS

In this section, we are concerned with the global existence of classical solutions to the system (1.5). When the functional response function $F(v/u)$ is prey-dependent only, namely with $F(v/u) = F(v)$, the global existence of classical solutions of (1.5) was established in two dimensions for any $\chi > 0$ in [16] and in any dimensions for small $\chi > 0$ in [44]. In this paper, we shall prove that if $F(v/u)$ is ratio-dependent, the system (1.5) admits the global classical solutions in any dimension ($N \geq 1$) for all $\chi \geq 0$, as asserted in the following theorem.

Theorem 2.1 (Global existence of solutions). *Let Ω be a bounded domain in \mathbb{R}^N ($N \geq 1$) with smooth boundary and hypothesis (H1) hold. Assume $(u_0, v_0) \in [W^{1,\infty}(\Omega)]^2$ with $u_0, v_0 \geq 0$ ($\neq 0$). Then system (1.5) has a unique global classical solution $(u, v) \in [C([0, \infty) \times \bar{\Omega}) \cap C^{2,1}((0, \infty) \times \bar{\Omega})]^2$ satisfying $u, v \geq 0$ for all $t > 0$ and*

$$\|u(\cdot, t)\|_{L^\infty(\Omega)} + \|v(\cdot, t)\|_{W^{1,\infty}(\Omega)} \leq C,$$

where $C > 0$ is a constant independent of t . In particular, $0 < v(x, t) \leq K_0 := \max\{\|v_0\|_{L^\infty}, K\}$.

The proof of Theorem 2.1 consists of local existence of solutions and the *a priori* estimates of solutions. Treating (1.5) as a triangular system, the local existence of classical solutions can be obtained directly from Amann's theorem [5, 6]. Below we only state the local existence result and omit the proof for brevity (we refer to [17] for details).

Lemma 2.1 (Local existence with extension criterion). *Let the conditions in Theorem 2.1 hold. Then the system (1.5) has a unique local-in-time non-negative classical solution $(u, v) \in C(\bar{\Omega} \times T_{max}) \cap C^{2,1}(\bar{\Omega} \times T_{max})$ satisfying $u, v \geq 0$ for all $t > 0$, where T_{max} denotes the maximal existence time. Moreover, if $T_{max} < \infty$ then*

$$\lim_{t \rightarrow T_{max}} \|u(\cdot, t)\|_{L^\infty(\Omega)} = \infty.$$

Now to prove theorem 2.1, it remains to derive the *a priori* estimates for the local solutions obtained in Lemma 2.1, which involves a few technical details. Below we shall derive some basic results first. Hereafter we shall use C_i ($i \geq 1$) or c_i ($i \geq 1$) to denote a generic positive constant which may vary in the context.

Lemma 2.2. *Let the hypotheses (H1) hold. Then the solution (u, v) of system (1.5) satisfies*

$$0 < v(x, t) \leq K_0 := \max\{\|v_0\|_{L^\infty}, K\}, \quad \limsup_{t \rightarrow \infty} v(x, t) \leq K, \quad (2.1)$$

$$\|u(\cdot, t)\|_{L^1(\Omega)} \leq K_1 := \max\left\{\|u_0\|_{L^1(\Omega)}, \frac{1}{\theta m} \beta K_0 |\Omega|\right\}, \quad (2.2)$$

$$\|\nabla v(\cdot, t)\|_{L^\infty} \leq C_0 \quad (2.3)$$

where C_0 is a constant independent of t .

Proof. Using the fact that u, v and $F(v/u)$ are non-negative, we have

$$\begin{cases} v_t - d\Delta v = -F(v/u)u + vf(v) \leq vf(v), & x \in \Omega, t > 0, \\ \partial_\nu v = 0, & x \in \partial\Omega, t > 0, \\ v(x, 0) = v_0(x), & x \in \Omega. \end{cases} \quad (2.4)$$

Let $v^*(t)$ be a solution of the following ODE problem

$$\begin{cases} \frac{dv^*(t)}{dt} = v^*(t)f(v^*(t)), & t > 0, \\ v^*(0) = \|v_0\|_{L^\infty}. \end{cases} \quad (2.5)$$

Then the hypothesis (H1) gives $v^*(t) \leq K_0 = \max\{\|v_0\|_{L^\infty}, K\}$, and furthermore $v^*(t)$ is a super-solution of the following PDE problem

$$\begin{cases} V_t - d\Delta V = Vf(V), & x \in \Omega, t > 0, \\ \partial_\nu V = 0, & x \in \partial\Omega, t > 0, \\ V(x, 0) = v_0(x), & x \in \Omega. \end{cases} \quad (2.6)$$

Therefore we have

$$0 < V(x, t) \leq v^*(t), \text{ for all } (x, t) \in \bar{\Omega} \times (0, \infty). \quad (2.7)$$

From (2.4)-(2.7), we have by the comparison principle that

$$0 < v(x, t) \leq V(x, t) \leq v^*(t) \leq K_0, \text{ for all } (x, t) \in \bar{\Omega} \times (0, \infty). \quad (2.8)$$

Since $f(v) < 0$ for all $v > K$ by the hypothesis (H1), we have from (2.5) that $\limsup_{t \rightarrow \infty} v^*(x, t) \leq K$, which along with (2.8) gives (2.1).

Next we show (2.2). Indeed with the fact that $0 < v \leq K_0$ and $\frac{F(v/u)}{v/u} \leq \frac{1}{m}$, we integrate the first equation of (1.5) and get

$$\frac{d}{dt} \int_{\Omega} u dx = \int_{\Omega} (\beta u F(v/u) - \theta u) \leq \frac{\beta}{m} \int_{\Omega} v - \theta \int_{\Omega} u \leq \frac{\beta}{m} K_0 |\Omega| - \theta \int_{\Omega} u$$

which yields (2.2) with the help of Gronwall's inequality.

Finally we prove (2.3). To this end, we denote by $(e^{td\Delta})_{t \geq 0}$ the Neumann heat semigroup generated by $-d\Delta$ on Ω . Then by the variation of constant formula, the solution v of the second equation of (1.5) can be written as

$$v(x, t) = e^{dt\Delta} v_0(x) + \int_0^t e^{d(t-s)\Delta} (vf(v) - uF(v/u))(x, s) ds$$

which gives

$$\|\nabla v(\cdot, t)\|_{L^\infty(\Omega)} \leq \|\nabla e^{dt\Delta} v_0\|_{L^\infty(\Omega)} + \int_0^t \|\nabla e^{d(t-s)\Delta} (vf(v) - uF(v/u))(x, s)\|_{L^\infty(\Omega)} ds.$$

Note that

$$vf(v) - uF(v/u) = vf(v) - v \frac{F(v/u)}{v/u} \leq v \left(f(v) + \frac{1}{m} \right) \leq K_0 \left(r + \frac{1}{m} \right) := c_0.$$

Then by the L^p - L^q estimates of Neumann heat semigroup (cf. [43, Lemma 1.3]), we find some constants $c_1, c_2 > 0$ such that

$$\|\nabla v(\cdot, t)\|_{L^\infty(\Omega)} \leq c_1 \|\nabla v_0\|_{L^\infty(\Omega)} + c_2 \int_0^t c_0 (1 + (t-s)^{-1/2}) e^{-\lambda_1(t-s)} ds$$

which hence gives (2.3) and completes the proof. \square

Next we will prove the following useful boundedness result by the Moser iteration method. The result is not only useful in this paper but also useful for other purposes. Hence we shall present a brief proof.

Lemma 2.3. *Let $u \geq 0$ solve the following reaction-diffusion-advection equation with Neumann boundary condition in $\Omega \times (0, T)$ for some $T > 0$:*

$$\begin{cases} u_t = \Delta u - \chi \nabla \cdot (u \vec{w}) + f(u), & \text{in } \Omega \times (0, T) \\ \partial_\nu u = \vec{w} \cdot \nu = 0, & \text{on } \partial\Omega \\ u(x, t) = u_0(x) \end{cases} \quad (2.9)$$

where $\chi \in \mathbb{R}$ is a constant, \vec{w} is a vector uniformly bounded in $\Omega \times (0, T)$ and $f(u)$ satisfies that $f(u) \leq bu$ for all $u \geq 0$ and some constant $b > 0$. If $u_0 \in L^\infty(\Omega)$, then the solution of (2.9) satisfies

$$\|u\|_{L^\infty(\Omega)} \leq C$$

provided that $u \in L^1(\Omega)$, where $C > 0$ is a constant independent of t .

Proof. Multiply the first equation of (2.9) by u^{p-1} and integrate the resulting equation with Neumann boundary conditions to get

$$\begin{aligned} & \frac{1}{p} \frac{d}{dt} \int_{\Omega} u^p + (p-1) \int_{\Omega} u^{p-2} |\nabla u|^2 \\ &= \chi(p-1) \int_{\Omega} u^{p-1} \nabla u \vec{w} + b \int_{\Omega} u^{p-1} f(u) \\ &\leq c_1(p-1) \int_{\Omega} u^{p-1} \nabla u + b \int_{\Omega} u^p \\ &\leq \frac{p-1}{2} \int_{\Omega} u^{p-2} |\nabla u|^2 + c_2(p-1) \int_{\Omega} u^p, \end{aligned}$$

which gives

$$\frac{d}{dt} \int_{\Omega} u^p + p(p-1) \int_{\Omega} u^p + \frac{p(p-1)}{2} \int_{\Omega} u^{p-2} |\nabla u|^2 \leq (1+c_3)p(p-1) \int_{\Omega} u^p. \quad (2.10)$$

Then we follow the exact Moser iteration procedure of (see [35, Proof of Theorem 2.1]) to conclude that

$$\|u\|_{L^\infty(\Omega)} \leq c$$

where c is a constant depending only the space dimension, $\|u_0\|_{L^\infty(\Omega)}$ and $\|u_0\|_{L^1(\Omega)}$. \square

Based on Lemma 2.3, we get the L^∞ estimate for u -component of the solution of (1.5) directly.

Lemma 2.4. *Let the conditions in Theorem 2.1 hold. Then there is a constant $C > 0$ independent of time such that the solution of (1.5) satisfies*

$$\|u\|_{L^\infty(\Omega)} < C. \quad (2.11)$$

Proof. Notice that $F(v/u) = \frac{v}{mu+v}$ is bounded for any $u, v > 0$. This yields a constant c_0 such that $\frac{\beta uv}{mu+v} - \theta u < c_0 u$. Then Lemma 2.4 is a direct consequence of the result of Lemma 2.3 with (2.2)-(2.3). \square

Proof of Theorem 2.1: With Lemma 2.1, Theorem 2.1 follows from the *a priori* estimates in Lemma 2.4.

3. GLOBAL STABILITY OF HOMOGENEOUS STEADY STATES

The mostly concerned question in population system is whether the population can reach the coexistence steady state or otherwise competition exclusion/extinction. This usually amounts to exploit the global stability of homogeneous/nonhomogeneous steady states. We first look at the homogeneous steady states (u_s, v_s) of system (1.5) which satisfies

$$(u_s, v_s) = \begin{cases} (0, K), & \text{if } \beta \leq \theta, \\ (0, K) \text{ and } (u_*, v_*), & \text{if } \beta > \theta \text{ and } f(0) > \frac{1}{m} \end{cases}$$

where the condition $f(0) > \frac{1}{m}$ warrants the positivity of steady state (u_*, v_*) which satisfies

$$\theta = \beta F(v_*/u_*), \quad f(v_*) = \frac{u_*}{mu_* + v_*}. \quad (3.1)$$

The steady state $(0, K)$ is referred to as the prey-only steady state and (u_*, v_*) the coexistence steady state. With the definition of $F(v/u)$ given in (1.4), one can explicitly find (u_*, v_*) from (3.1) as

$$u_* = \frac{v_*(\beta - \theta)}{m\theta}, \quad v_* = f^{-1}\left(\frac{\beta - \theta}{\beta m}\right). \quad (3.2)$$

In particular, if $f(v) = r(1 - v/K)$, then it has that $u_* = \frac{K(\beta - \theta)}{m\theta}(1 - \frac{\beta - \theta}{r\beta m})$, $v_* = K(1 - \frac{\beta - \theta}{r\beta m})$.

We remark that the extinction (trivial) steady state $(0, 0)$ is not well-defined in our considered system and hence will not be considered in this paper. Indeed by extending the definition of the system at $(0, 0)$, the system (1.5) without spatial variable (i.e., ODEs corresponding to (1.5)) possesses very rich dynamics near the trivial steady state $(0, 0)$, see [19, 46].

It can be easily checked that $(0, K)$ is linearly stable if $\theta > \beta$ and unstable if $\theta < \beta$. By the hypothesis (H1), the following result can be easily verified.

Lemma 3.1. *If $f(0) > \frac{1}{m}$, then there exists a constant $\tilde{v} > 0$ such that $f(\tilde{v}) = \frac{1}{m}$ and $f(v) > \frac{1}{m}$ when $0 \leq v < \tilde{v}$.*

When $f(v) = r(1 - v/K)$, one can calculate that $\tilde{v} = \frac{1}{K}(1 - \frac{1}{rm})$ where $rm > 1$ since $r = f(0) > \frac{1}{m}$.

Then our global stability results are stated as follows.

Theorem 3.2 (Global stability). *Assume $f(0) > \frac{1}{m}$, hypothesis (H1) and assumptions of Theorem 2.1 hold. Let (u, v) be the solution obtained in Theorem 2.1. Then the following convergence results hold.*

- (1) *If $\theta > \beta$, then the prey-only steady state $(0, K)$ is globally exponentially stable.*
- (2) *If $\theta < \beta$, then the co-existence steady state (u_*, v_*) is globally exponentially stable if*

$$\frac{d}{\chi^2} \geq \frac{K^2}{4m\beta} \quad (\text{"=" holds if } \|v_0\|_{L^\infty} \leq K) \quad \text{and} \quad \frac{\beta - \theta}{m\beta} < \delta\tilde{v}.$$

Before giving the proof of Theorem 3.2, we present some preliminary results.

Lemma 3.3. *Under the conditions in Theorem 2.1, if $f(0) > \frac{1}{m}$ and hypothesis (H1) hold, then there exist positive constants $\varrho > 0$ and $t_0 > 0$ such that the solution (u, v) of (1.5) satisfies*

$$v(x, t) \geq \varrho \quad \text{for all } (x, t) \in \bar{\Omega} \times (t_0, \infty), \quad (3.3)$$

and

$$\liminf_{t \rightarrow \infty} v(x, t) \geq \tilde{v} \quad \text{for all } x \in \bar{\Omega}, \quad (3.4)$$

where $\tilde{v} = f^{-1}(\frac{1}{m})$.

Proof. First notice that $\frac{F(w)}{w} = \frac{1}{m+w} \leq \frac{1}{m}$ for all $w \geq 0$. By the maximum principle applied to the second equation of (1.5), we can find a $0 < t_0 < \infty$ such that $\min_{x \in \Omega} v(x, t_0) = \bar{v} > 0$ for all $x \in \Omega$. Then we consider the following problem

$$\begin{cases} v_t - d\Delta v = v \left(f(v) - \frac{F(v/u)}{v/u} \right) \geq v \left(f(v) - \frac{1}{m} \right), & x \in \Omega, t > t_0, \\ \partial_\nu v = 0, & x \in \partial\Omega, t > t_0, \\ v(x, t_0) = \bar{v}, & x \in \Omega. \end{cases} \quad (3.5)$$

Let $v_*(t)$ be the solution of the following ODE problem

$$\begin{cases} \frac{dv_*(t)}{dt} = v_*(t) \left(f(v_*(t)) - \frac{1}{m} \right), & t > t_0, \\ v_*(t_0) = \bar{v} > 0. \end{cases} \quad (3.6)$$

Then the hypothesis (H1) yields that $v_*(t) \geq \min\{\bar{v}, \tilde{v}\} =: \varrho$ for all $t \geq t_0$. It is obvious that $v_*(t)$ is a lower solution of the following PDE problem

$$\begin{cases} V_t^0 - d\Delta V^0 = V^0 \left(f(V^0) - \frac{1}{m} \right), & x \in \Omega, t > t_0, \\ \partial_\nu V^0 = 0, & x \in \partial\Omega, t > t_0, \\ V^0(x, t_0) = v(x, t_0), & x \in \Omega. \end{cases} \quad (3.7)$$

Then we have

$$v_*(t) \leq V^0(x, t) \text{ for all } (x, t) \in \bar{\Omega} \times (t_0, \infty). \quad (3.8)$$

Combining (3.5), (3.7) and (3.8), and using the comparison principle, one has

$$\varrho \leq v_*(t) \leq V^0(x, t) \leq v(x, t) \text{ for all } (x, t) \in \bar{\Omega} \times (t_0, \infty), \quad (3.9)$$

which gives (3.3). By Lemma 3.1, we note that $v(f(v) - \frac{1}{m}) > 0$ for all $0 < v < \tilde{v}$. Therefore from (3.6), we have

$$\liminf_{t \rightarrow \infty} v_*(t) \geq \tilde{v},$$

which along with (3.9) gives (3.4). \square

To prove Theorem 3.2, we present a basic result which is an application of [16, Lemma 4.1].

Lemma 3.4. *For some constant $\omega > 0$, we define*

$$\zeta(v) = \int_\omega^v \frac{s - \omega}{s} ds,$$

which is a convex function such that $\zeta(v) \geq 0$. If $v \rightarrow \omega$ as $t \rightarrow \infty$, then there exists a constant $T_0 > 0$ such that

$$\frac{1}{4\omega}(v - \omega)^2 \leq \zeta(v) = \int_\omega^v \frac{s - \omega}{s} ds \leq \frac{1}{\omega}(v - \omega)^2 \text{ for all } t \geq T_0. \quad (3.10)$$

Now we come to a position to prove Theorem 3.2.

Proof of Theorem 3.2. For initial data $\mathbf{w}_0 = (u_0, v_0)$, we denote the unique global classical solution of (1.5) by $\mathbf{w}(t; \mathbf{w}_0) = (u, v)(t)$ for all $t \geq 0$, which defines a semi-flow (or trajectory) on $X = [W^{1,\infty}(\bar{\Omega})]^2$ (e.g. see [4]). We proceed with two separate cases. Since are only concerned with the asymptotic behavior of solutions, we always assume $t \geq t_0$ below in order to use Lemma 3.3 unless otherwise stated, where t_0 is given in Lemma 3.3.

Case 1: $\theta > \beta$. We define the following energy functional:

$$E(\mathbf{w}) = E(u(t), v(t)) =: E(t) = \sigma_0 \int_\Omega u(x, t) + \int_\Omega \left(\int_K^v \frac{s - K}{s} ds \right), \quad (3.11)$$

where $\sigma_0 = \frac{3K}{2\rho(\theta - \beta)} > 0$ with ρ defined in (3.3). It is clear from Lemma 3.4 that $E(\mathbf{w}) = 0$ iff $\mathbf{w} = (0, K)$ and $E(\mathbf{w}) > 0$ for all $\mathbf{w} \neq (0, K)$, which implies that $E(\mathbf{w})$ is a positive definite function. Moreover, by the definition of $E(\mathbf{w})$ and Theorem 2.1, we have $E(\mathbf{w}) \leq C$, where $C > 0$ is a constant independent of $t > 0$ for any solution $\mathbf{w} = (u, v) \in X$.

Next, we prove $\frac{d}{dt}E(\mathbf{w}) = \frac{d}{dt}E(t) \leq 0$ for all $\mathbf{w} \in X$, where “=” holds iff $\mathbf{w} = (0, K)$. Differentiating the functional (3.11) with respect to t and using the equations in (1.5), one has

$$\begin{aligned} \frac{dE(t)}{dt} &= \int_{\Omega} \left[\sigma_0 u_t + \left(\frac{v-K}{v} \right) v_t \right] dx \\ &= \int_{\Omega} \sigma_0 u (\beta F(v/u) - \theta) dx + \int_{\Omega} (v-K) \left(f(v) - \frac{F(v/u)}{v/u} \right) dx - dK \int_{\Omega} \frac{|\nabla v|^2}{v^2} dx \\ &= \int_{\Omega} u \left(\frac{\sigma_0 \beta v}{mu+v} - \sigma_0 \theta - \frac{v-K}{mu+v} \right) dx + \int_{\Omega} f(v)(v-K) dx - dK \int_{\Omega} \frac{|\nabla v|^2}{v^2} dx \\ &= \int_{\Omega} u \left(\frac{\sigma_0 \beta v}{mu+v} - \sigma_0 \theta - \frac{v-K}{mu+v} \right) dx + \int_{\Omega} f'(\xi)(v-K)^2 dx - dK \int_{\Omega} \frac{|\nabla v|^2}{v^2} dx \\ &=: I_1 + I_2 + I_3, \end{aligned} \tag{3.12}$$

where ξ is between v and K . Clearly $I_2 \leq 0$ from the hypothesis (H1) and $I_3 \leq 0$. Moreover, since $\sigma_0 = \frac{3K}{2\rho(\theta - \beta)} > 0$ for $\theta > \beta$, we may write I_1 as

$$I_1 = \int_{\Omega} \frac{u}{mu+v} \left(\frac{K(2\rho - 3v)}{2\rho} - \sigma_0 m \theta u - v \right) dx.$$

Lemma 3.3 directly implies that $I_1 \leq 0$. Hence $\frac{dE(t)}{dt} \leq 0$ for all $\mathbf{w} \in X$, where $\frac{dE(t)}{dt} = 0$ holds if and only if $\mathbf{w} = (0, K)$. Then, by the LaSalle's invariant principle (e.g. see [31, Theorem 5.24] or [21, Theorem 3]), $\mathbf{w}(t; \mathbf{w}_0) = (u, v) \rightarrow (0, K)$ as $t \rightarrow \infty$ for any $\mathbf{w}_0 \in X$, which implies that $(0, K)$ is globally asymptotically stable.

We now derive the convergence rate of solutions. To this end, we define

$$W(t) := \int_{\Omega} u dx + \int_{\Omega} (v-K)^2 dx + \int_{\Omega} \frac{|\nabla v|^2}{v^2} dx.$$

Then, by (3.12), Lemma 2.2, Lemma 3.3 and Theorem 2.1, we can find a constant c_1 and $T_1 > 0$ such that

$$\frac{dE(t)}{dt} \leq -c_1 W(t) \text{ for all } t \geq T_1. \tag{3.13}$$

Applying Lemma 3.4 with $\omega = K$, we can find a constant $T_2 > 0$ such that

$$\frac{1}{4K}(v-K)^2 \leq \int_K^v \frac{s-K}{s} ds \leq \frac{1}{K}(v-K)^2 \text{ for all } t \geq T_2. \tag{3.14}$$

Using the definitions of $E(t)$ and $W(t)$ with (3.14), we can find a constant $c_2 > 0$ such that $c_2 E(t) \leq W(t)$ for all $t \geq T_2$. Then from (3.13) and the nonnegativity of $E(t)$, it follows that

$$\frac{dE(t)}{dt} \leq -c_1 W(t) \leq -c_1 c_2 E(t) \text{ for all } t \geq T_3 := \max\{T_1, T_2\},$$

which leads to $E(t) \leq c_3 e^{-c_4 t}$ for all $t \geq T_3$ and some constants $c_3, c_4 > 0$. This, along with the definition of $E(t)$ and (3.14), yields

$$\|u\|_{L^1} + \|v-K\|_{L^2} \leq c_5 e^{-c_4 t} \text{ for all } t \geq T_3. \tag{3.15}$$

Next, we proceed to investigate the decay rate of L^∞ -norm. By Theorem 2.1, we have $\chi u \nabla v$ and $\frac{\beta uv}{mu+v} - \theta u$ are bounded in $L^\infty(\Omega \times (0, \infty))$. Then, by the standard parabolic regularity

theory (e.g. see [28, Theorem 1.3]) and [36, Lemma 3.2]) applied to the first equation of (1.5), there exists a constant $\beta \in (0, 1)$ such that

$$\|u\|_{C^{\beta, \frac{\beta}{2}}(\bar{\Omega} \times [t, t+1])} \leq c_6 \text{ for all } t > 1. \quad (3.16)$$

Furthermore, by the parabolic Schauder theory [20] applied to the second equation of (1.5), we obtain

$$\|v\|_{C^{2+\beta, 1+\frac{\beta}{2}}(\bar{\Omega} \times [t, t+1])} \leq c_7 \text{ for all } t > 1. \quad (3.17)$$

By conditions (3.16) and (3.17), we can find a constant $c_8 > 0$ (e.g. see [36, Lemma 3.14]) such that

$$\|u\|_{W^{1, \infty}} \leq c_8 \text{ for all } t > 1.$$

Then with (3.15) and the Gagliardo-Nirenberg inequality, we have

$$\|u\|_{L^\infty} \leq c_9(\|\nabla u\|_{L^\infty}^{\frac{2}{3}}\|u\|_{L^1}^{\frac{1}{3}} + \|u\|_{L^1}) \leq c_{10}(\|u\|_{L^1}^{\frac{1}{3}} + \|u\|_{L^1}) \leq c_{11}e^{-c_{12}t} \quad (3.18)$$

for all $t \geq T_3$. Moreover, by Theorem 2.1 and Gagliardo-Nirenberg inequality, we have from (3.15) that

$$\|v - K\|_{L^\infty} \leq c_{13}(\|\nabla(v - K)\|_{L^\infty}^{\frac{1}{2}}\|v - K\|_{L^2}^{\frac{1}{2}} + \|v - K\|_{L^2}) \leq c_{14}e^{-c_{15}t} \text{ for all } t \geq T_c. \quad (3.19)$$

Then, by (3.18) and (3.19), we get

$$\|u\|_{L^\infty} + \|v - K\|_{L^\infty} \leq c_{16}e^{-\lambda_1 t} \text{ for all } t \geq T_3, \lambda_1 = \min\{c_{12}, c_{15}\}.$$

Case 2: $\theta < \beta$. Note that in this scenario, we have from (3.2) that $w_* =: \frac{v_*}{u_*} = \frac{m\theta}{\beta - \theta}$. Then we define the Lyapunov functional

$$V(u(t), v(t)) =: V(t) = \alpha \int_{\Omega} \int_{u_*}^u \frac{s - u_*}{s} ds dx + \int_{\Omega} \int_{v_*}^v \frac{s - v_*}{s} ds dx \quad (3.20)$$

with

$$\alpha = \frac{v_*}{m\beta u_*} = \frac{w_*}{m\beta} = \frac{\theta}{\beta(\beta - \theta)}. \quad (3.21)$$

It follows from Lemma 3.4 that $V(t) = 0$ if $(u(t), v(t)) = (u_*, v_*)$ and $V(t) > 0$ for all $(u(t), v(t)) \neq (u_*, v_*)$.

Next, differentiating the functional (3.20) with respect to t , we have

$$\begin{aligned} \frac{d}{dt}V(t) &= \alpha \int_{\Omega} \left(1 - \frac{u_*}{u}\right) u_t dx + \int_{\Omega} \left(1 - \frac{v_*}{v}\right) v_t dx \\ &= \underbrace{-\alpha u_* \int_{\Omega} \left|\frac{\nabla u}{u}\right|^2 dx - v_* d \int_{\Omega} \left|\frac{\nabla v}{v}\right|^2 dx + \chi u_* \alpha \int_{\Omega} \frac{\nabla u \nabla v}{u} dx}_{J_1} \\ &\quad + \underbrace{\alpha \int_{\Omega} \left(1 - \frac{u_*}{u}\right) (\beta u F(v/u) - \theta u) dx + \int_{\Omega} \left(1 - \frac{v_*}{v}\right) (-F(v/u)u + v f(v)) dx}_{J_2}. \end{aligned} \quad (3.22)$$

Now we rewrite J_1 as

$$J_1 = - \int_{\Omega} \Theta^T A \Theta, \quad \Theta = \begin{pmatrix} \nabla u \\ \nabla v \end{pmatrix}, \quad A = \begin{pmatrix} \frac{\alpha u_*}{u^2} & -\frac{\alpha \chi u_*}{2u} \\ -\frac{\alpha \chi u_*}{2u} & \frac{dv_*}{v^2} \end{pmatrix},$$

where Θ^T denotes the transpose of Θ . Then $J_1 \leq 0$ if and only if the matrix A is non-negative definite. From (3.21), we have $w_* = \alpha\beta m$. Since $\frac{\alpha u_*}{u^2} > 0$ due to $u > 0$ for all $t > 0$, then by the Sylvester's criterion, it can be easily checked that A is non-negative definite if and only if

$$\frac{d}{\chi^2} \geq \frac{v^2}{4\beta m}. \quad (3.23)$$

Now we claim that (3.23) holds true for large $t > 0$ if

$$\frac{d}{\chi^2} \geq \frac{K^2}{4\beta m}, \text{ where " = " holds if } \|v_0\|_{L^\infty} \leq K. \quad (3.24)$$

Indeed if $\|v_0\|_{L^\infty} \leq K$, then $0 < v(x, t) \leq K$ from Lemma 2.2 and as a consequence the condition (3.24) gives rise to (3.23). If $\|v_0\|_{L^\infty} > K$, we therefore consider $\frac{d}{\chi^2} > \frac{K^2}{4\beta m}$, which means that there exists a constant $0 < \epsilon_0 \ll 1$ such that

$$\frac{d}{\chi^2} \geq \frac{K^2}{4\beta m} + \epsilon_0. \quad (3.25)$$

By (2.1), we derive

$$\limsup_{t \rightarrow \infty} \frac{v^2}{4\beta m} = \frac{1}{4\beta m} \limsup_{t \rightarrow \infty} v^2 \leq \frac{K^2}{4\beta m}. \quad (3.26)$$

Hence, for the $\epsilon_0 > 0$ given above, there exists $T_1^* > 0$ such that

$$\frac{v^2}{4\beta m} \leq \frac{K^2}{4\beta m} + \epsilon_0 \quad \text{for } (x, t) \in \bar{\Omega} \times [T_1^*, \infty). \quad (3.27)$$

The combination of (3.25) and (3.27) yields

$$\frac{v^2}{4\beta m} \leq \frac{d}{\chi^2} \quad \text{for } (x, t) \in \bar{\Omega} \times [T_1^*, \infty).$$

In summary, if $t \geq T_1^*$, (3.24) holds and hence $J_1 \leq 0$.

Next, we examine J_2 . Using the facts $\theta = \beta F(w_*)$ and $f(v_*) = \frac{F(w_*)}{w_*}$, J_2 can be reformulated as

$$\begin{aligned} J_2 &= \alpha \int_{\Omega} (u - u_*) (\beta F(w) - \theta) dx + \int_{\Omega} (v - v_*) (f(v) - F(w)/w) dx \\ &= \alpha \beta \int_{\Omega} (u - u_*) (F(w) - F(w_*)) dx + \int_{\Omega} (v - v_*) [f(v) - f(v_*) + F(w_*)/w_* - F(w)/w] dx \\ &= \alpha \beta m \int_{\Omega} (u - u_*) \frac{u_* (v - v_*) + v_* (u_* - u)}{(mu + v)(mu_* + v_*)} dx + \int_{\Omega} f'(\xi) (v - v_*)^2 dx \\ &\quad + \int_{\Omega} (v - v_*) \frac{u_* (v - v_*) + v_c (u_* - u)}{(mu + v)(mu_* + v_*)} dx \\ &= -\frac{\alpha \beta m v_*}{m u_* + v_*} \int_{\Omega} \frac{(u - u_*)^2}{mu + v} dx + \frac{u_*}{m u_* + v_*} \int_{\Omega} \frac{(v - v_*)^2}{mu + v} dx \\ &\quad + \left(\frac{\alpha \beta m u_*}{m u_* + v_*} - \frac{v_*}{m u_* + v_*} \right) \int_{\Omega} \frac{(u - u_*)(v - v_*)}{mu + v} dx + \int_{\Omega} f'(\xi) (v - v_*)^2 dx, \end{aligned}$$

where ξ is between v and v_* . Noticing $\alpha = \frac{w_*}{m\beta}$, we have

$$J_2 = -\frac{\alpha \beta m v_*}{m u_* + v_*} \int_{\Omega} \frac{(u - u_*)^2}{mu + v} dx + \int_{\Omega} \left(f'(\xi) + \frac{u_*}{(mu + v)(mu_* + v_*)} \right) (v - v_*)^2 dx =: M_1 + M_2.$$

Clearly $M_1 \leq 0$ ("=" holds iff $u = u_*$). By the fact $u > 0$ for any $t > 0$, $f'(\xi) \leq -\delta$ from (H1) and Lemma 3.3, we see that $M_2 \leq 0$ ("=" holds iff $v = v_*$) provided that

$$-\delta + \frac{u_*}{v(mu_* + v_*)} \leq 0 \quad (\text{i.e., } 1 \leq v\delta(m + w_*)) \quad (3.28)$$

We proceed to show that (3.28) holds true for large $t > 0$ if

$$1 < \tilde{v}\delta(m + w_*) = \frac{m\beta\delta\tilde{v}}{\beta - \theta}. \quad (3.29)$$

In fact, if $1 < \frac{m\beta\delta\tilde{v}}{\beta - \theta}$, then there exists a small $0 < \epsilon_0 \ll 1$ such that

$$1 \leq \frac{m\beta\delta\tilde{v}}{\beta - \theta} - \epsilon_0. \quad (3.30)$$

By (3.4), we derive

$$\liminf_{t \rightarrow \infty} \frac{m\beta\delta v}{\beta - \theta} = \frac{m\beta\delta}{\beta - \theta} \liminf_{t \rightarrow \infty} v \geq \frac{m\beta\delta\tilde{v}}{\beta - \theta}. \quad (3.31)$$

Hence, for the $\epsilon_0 > 0$ given above, there exists a $T_2^* > 0$ such that

$$\frac{m\beta\delta v}{\beta - \theta} \geq \frac{m\beta\delta\tilde{v}}{\beta - \theta} - \epsilon_0 \quad \text{for } (x, t) \in \bar{\Omega} \times [T_2^*, \infty). \quad (3.32)$$

The combination of (3.30) and (3.32) yields

$$v\delta(m + w_*) = \frac{m\beta\delta v}{\beta - \theta} \geq 1 \quad \text{for } (x, t) \in \bar{\Omega} \times [T_2^*, \infty)$$

which gives rise to (3.28) for $t \geq T_2^*$. Therefore we conclude that $I_2 \leq 0$ for all $t \geq T_2^*$ under the condition (3.29). Hence with (3.29), we have $\frac{d}{dt}V(t) \leq 0$ for all $t \geq \max\{T_1^*, T_2^*\}$ and $\frac{d}{dt}V(t) = 0$ iff $(u, v) = (u_*, v_*)$. By the LaSalle's invariant principle, we conclude (u_*, v_*) is globally asymptotically stable in $W^{1,\infty}(\bar{\Omega})$.

Finally we derive the exponential rate of convergence. In the above proof, we have shown that if (3.29) and (3.24) hold, there exists a constant $c_1 > 0$ and $t_1 > 0$ such that

$$\frac{d}{dt}V(t) \leq -c_1 \int_{\Omega} [(u - u_*)^2 + (v - v_*)^2] \quad \text{for all } t > t_1. \quad (3.33)$$

Since $(u, v) \rightarrow (u_*, v_*)$ as $t \rightarrow \infty$, by Lemma 3.4, we can find constants $c_2, c_3 > 0$ and t_2 such that for all $t > t_2$

$$c_2(\|u - u_*\|_{L^2}^2 + \|v - v_*\|_{L^2}^2) \leq V(t) \leq c_3(\|u - u_*\|_{L^2}^2 + \|v - v_*\|_{L^2}^2).$$

Then, by (3.33), there exists a constant $c_4 > 0$ such that

$$\frac{d}{dt}V(t) \leq -c_4V(t) \quad \text{for all } t > t_0 = \max\{t_1, t_2\},$$

which, by Gronwall's inequality, gives rise to the following exponential decay

$$\|u - u_*\|_{L^2}^2 + \|v - v_*\|_{L^2}^2 \leq c_5 e^{-c_6 t}$$

for some constants $c_5, c_6 > 0$. Then by the same arguments as deriving (3.18) and (3.19), we readily get the exponential convergence rate and hence completes the proof of Theorem 3.2.

4. SPATIAL PATTERNS AND ROLE OF PREY-TAXIS

In previous sections, we have established the global existence of classical solutions (see Theorem 2.1) and global stability of homogenous steady states (see Theorem 3.2) for the ratio-dependent predator-prey system (1.5). In this section, we shall investigate whether the system (1.5) admits pattern formation (non-homogenous steady states). Compared to the existing works on the ratio-dependent predator-prey system without prey-taxis, the difficulty of analyzing the current system (1.5) lies in the prey-taxis term which makes conventional methods, such as the maximum principle or monotone method, inapplicable. In this section, we shall find conditions for the pattern formation and numerically illustrate the spatio-temporal patterns to find the role

that the prey-taxis plays in the dynamics. To this end, we investigate the stability/instability of constant equilibria $(0, K)$ and (u_*, v_*) of (1.5) where (u_*, v_*) is positive if $0 < \frac{\beta - \theta}{m\beta} < r$.

4.1. Linear stability analysis. We start with the ODE system corresponding to the system (1.5):

$$\mathbf{u}_t = G(\mathbf{u}) \quad (4.1)$$

where for convenience we denote $\mathbf{u} = (u, v)$ and

$$G(\mathbf{u}) = \begin{pmatrix} \frac{\beta uv}{mu + v} - \theta u \\ vf(v) - \frac{uv}{mu + v} \end{pmatrix}.$$

The linearized operator of $G(\mathbf{u})$ at equilibrium (u_s, v_s) is given by

$$G_{\mathbf{u}}(u_s, v_s) = \begin{pmatrix} A & B \\ C & D \end{pmatrix}, \quad (4.2)$$

where

$$A = \frac{\beta v_s^2}{(mu_s + v_s)^2} - \theta, \quad B = \frac{m\beta u_s^2}{(mu_s + v_s)^2}, \quad C = \frac{-v_s^2}{(mu_s + v_s)^2}, \quad D = f(v_s) + v_s f'(v_s) - \frac{mu_s^2}{(mu_s + v_s)^2}.$$

Hence we obtain

$$G_{\mathbf{u}}(0, K) = \begin{pmatrix} A(0, K) & B(0, K) \\ C(0, K) & D(0, K) \end{pmatrix} = \begin{pmatrix} \beta - \theta & 0 \\ -1 & K f'(K) \end{pmatrix} \quad (4.3)$$

and

$$G_{\mathbf{u}}(u_*, v_*) = \begin{pmatrix} A(u_*, v_*) & B(u_*, v_*) \\ C(u_*, v_*) & D(u_*, v_*) \end{pmatrix} = \begin{pmatrix} \frac{\theta(\theta - \beta)}{\beta} & \frac{(\beta - \theta)^2}{m\beta} \\ -\theta^2 & \frac{\theta(\beta - \theta)}{m\beta^2} + v_* f'(v_*) \end{pmatrix}. \quad (4.4)$$

Clearly, we have

$$\text{trace}(G_{\mathbf{u}}(0, K)) = \beta - \theta + K f'(K), \quad \det(G_{\mathbf{u}}(0, K)) = K f'(K)(\beta - \theta)$$

and

$$\text{trace}(G_{\mathbf{u}}(u_*, v_*)) = \frac{-\theta(\beta - \theta)}{\beta} v_* f'(v_*), \quad \det(G_{\mathbf{u}}(u_*, v_*)) = \frac{\theta(\beta - \theta)(1 - m\beta)}{\beta} + v_* f'(v_*).$$

Then by the direct calculations, we have the following results concerning the asymptotic stability of equilibria $(0, K)$ and (u_*, v_*) for (4.1).

Lemma 4.1. *For the ODE system (4.1), the following results hold.*

- (1) *The equilibrium $(0, K)$ is linearly unstable (resp. stable) if $\beta > \theta$ (resp. $\beta < \theta$).*
- (2) *For $0 < \frac{\beta - \theta}{m\beta} < r$, we have the following results for the equilibrium (u_*, v_*) :*
 - (a) *If $m\beta < 1$ and $0 < -v_* f'(v_*) < \frac{\theta(\beta - \theta)(1 - m\beta)}{m\beta^2}$, then (u_*, v_*) is unstable;*
 - (b) *If $m\beta \geq 1$ or $m\beta < 1$ and $-v_* f'(v_*) > \frac{\theta(\beta - \theta)(1 - m\beta)}{m\beta^2}$, then (u_*, v_*) is asymptotically stable.*

Next we consider under what conditions, the stable equilibrium of the ODE system will become unstable in the presence of spatial variables. For this, we introduce some notations as follows. Let $0 = \lambda_0 < \lambda_1 < \lambda_2 < \dots < \lambda_j < \dots$ be the eigenvalues of the operator $-\Delta$ in Ω subject to no-flux boundary conditions and m_j be the algebraic multiplicity of λ_j . Let $\{\phi_{jk}\}_{k=1}^{m_j}$ be an orthonormal basis of the subspace generated by the eigenfunctions corresponding to λ_j in $L^2(\Omega)$.

The linearized operator, denoted by L , of the system (1.5) at the equilibria (u_*, v_*) and $(0, K)$ are respectively given by

$$L_1 := L|_{(0,K)} = \begin{pmatrix} \Delta + \beta - \theta & 0 \\ -1 & d\Delta + Kf'(K) \end{pmatrix}.$$

and

$$L_2 := L|_{(u_*, v_*)} = \begin{pmatrix} \Delta + \frac{\theta(\theta - \beta)}{\beta} & -\chi u_* \Delta + \frac{(\beta - \theta)^2}{m\beta} \\ \frac{-\theta^2}{\beta^2} & d\Delta + \frac{\theta(\beta - \theta)}{m\beta^2} + v_* f'(v_*) \end{pmatrix}.$$

Suppose that $(\Phi_i(x), \Psi_i(x))$ is an eigenfunction of L_i corresponding to eigenvalue μ_i ($i = 1, 2$). Then we derive

$$(L_i - \mu_i I) \begin{pmatrix} \Phi_i \\ \Psi_i \end{pmatrix} = 0, \quad i = 1, 2.$$

By the Fourier expansion, there exist $\{a_{jk}\}$, $\{b_{jk}\}$, $\{c_{jk}\}$ and $\{d_{jk}\}$ such that

$$\begin{aligned} \Phi_1 &= \sum_{0 \leq j \leq \infty, 1 \leq k \leq m_j} a_{jk} \phi_{jk} \quad \text{and} \quad \Psi_1 = \sum_{0 \leq j \leq \infty, 1 \leq k \leq m_j} b_{jk} \phi_{jk}, \\ \Phi_2 &= \sum_{0 \leq j \leq \infty, 1 \leq k \leq m_j} c_{jk} \phi_{jk} \quad \text{and} \quad \Psi_2 = \sum_{0 \leq j \leq \infty, 1 \leq k \leq m_j} d_{jk} \phi_{jk}. \end{aligned}$$

Therefore we obtain

$$\sum_{0 \leq j \leq \infty, 1 \leq k \leq m_j} \underbrace{\begin{pmatrix} -\lambda_j + \beta - \theta - \mu_2 & 0 \\ -1 & -d\lambda_j + Kf'(K) - \mu_2 \end{pmatrix}}_{M_2} \begin{pmatrix} a_{jk} \\ b_{jk} \end{pmatrix} \phi_{jk} = 0$$

and

$$\sum_{0 \leq j \leq \infty, 1 \leq k \leq m_j} \underbrace{\begin{pmatrix} -\lambda_j + \frac{\theta(\theta - \beta)}{\beta} - \mu_1 & \chi u_* \lambda_j + \frac{(\beta - \theta)^2}{m\beta} \\ \frac{-\theta^2}{\beta^2} & -d\lambda_j + \frac{\theta(\beta - \theta)}{m\beta^2} + v_* f'(v_*) - \mu_1 \end{pmatrix}}_{M_1} \begin{pmatrix} c_{jk} \\ d_{jk} \end{pmatrix} \phi_{jk} = 0.$$

It is easy to check that μ_i is an eigenvalue of L_i ($i = 1, 2$) if and only if the determinant of the corresponding coefficient matrix M_i is equal to zero for some $j \geq 0$.

By the result of Lemma 4.1, for the equilibrium $(0, K)$, we are concerned with whether $\det(M_1) = 0$ has a positive eigenvalue μ_1 in the case of $\beta < \theta$. Indeed, we can directly find that $\mu_1 < 0$ if $\beta < \theta$ and hence no bifurcation (i.e., no pattern formation) will arise from the equilibrium $(0, K)$. Next we turn to examine the instability of (u_*, v_*) in the case of $0 < \frac{\beta - \theta}{m\beta} < r$ under the condition (b) in Lemma 4.1(2). Clearly $\det(M_2) = 0$ gives

$$\mu_2^2 + a(\lambda_j)\mu_2 + b(\lambda_j) = 0, \quad (4.5)$$

where

$$\begin{aligned} a(\lambda_j) &= (1 + d)\lambda_j - \left(\frac{\theta(\theta - \beta)}{\beta} + \frac{\theta(\beta - \theta)}{m\beta^2} + v_* f'(v_*) \right), \\ b(\lambda_j) &= d\lambda_j^2 - \lambda_j \left(\frac{d\theta(\theta - \beta)}{\beta} + \frac{\theta(\beta - \theta)}{m\beta^2} + v_* f'(v_*) - \chi u_* \frac{\theta^2}{\beta^2} \right) + \frac{\theta v_* f'(v_*)(\theta - \beta)}{\beta}. \end{aligned}$$

To see whether there is a non-trivial solution bifurcating from (u_*, v_*) , it suffices to determine whether there is a $\mu_2 > 0$ for some $j \geq 1$. By some tedious computations (omitted here for brevity), we arrive at the following results.

Lemma 4.2. *Assume $0 < \frac{\beta - \theta}{m\beta} < r$. Let $m\beta \geq 1$ or $m\beta < 1$ and $-v_* f'(v_*) > \frac{\theta(\beta - \theta)(1 - m\beta)}{m\beta^2}$. Then the following results hold.*

- (1) (u_*, v_*) is linearly stable and hence the system (1.5) has no pattern formation if $d \geq 1$ or $d < 1$ and one of the following conditions hold

(a1): $d\beta m \geq 1$;

(a2): $d\beta m < 1$, $-v_* f'(v_*) \geq \frac{\theta(\beta - \theta)(1 - m\beta d)}{m\beta^2}$;

(a3): $d\beta m < 1$, $-v_* f'(v_*) < \frac{\theta(\beta - \theta)(1 - m\beta d)}{m\beta^2}$ and $\chi > \chi_c$, where

$$\chi_c = \frac{v_* f'(v_*) + \frac{F^2(w_*)}{w_*}(1 - d\beta m) - 2\sqrt{-d\beta w_* v_* f'(v_*) F'(w_*)}}{u_* F^2(w_*)}. \quad (4.6)$$

- (2) For $d < 1$, $dm\beta < 1$ and $-v_* f'(v_*) < \frac{\theta(\beta - \theta)(1 - m\beta d)}{m\beta^2}$, if $0 < \chi < \chi_c$ holds, then (u_*, v_*) is linearly unstable and pattern formation can be expected if there is a j such that

$$0 < \frac{\eta - \sqrt{\eta^2 + 4d \frac{\theta(\beta - \theta)}{\beta} v_* f'(v_*)}}{2d} < \lambda_j < \frac{\eta + \sqrt{\eta^2 + 4d \frac{\theta(\beta - \theta)}{\beta} v_* f'(v_*)}}{2d}, \quad (4.7)$$

where $\eta = v_* f'(v_*) + \frac{\theta(\beta - \theta)}{\beta} \left(\frac{1}{m\beta} - d \right) - \chi u_* \frac{\theta^2}{\beta^2} > 0$.

Remark 4.3. Theorem 3.2(2) gives the sufficient conditions for the global stability of (u_*, v_*) , while Lemma 4.2(2) gives sufficient conditions for the instability of (u_*, v_*) . It can be seen that if $0 < d \ll 1$, then the conditions in Lemma 4.2(2) are satisfied while the conditions in Theorem 3.2(2) are violated. In other words, the conditions in Lemma 4.2(2) violate the conditions in Theorem 3.2(2) if $d > 0$ is small.

4.2. Numerical patterns and role of prey-taxis. In this section, we shall perform numerical simulations in an interval $\Omega = [0, l]$ to illustrate the pattern formation of the system (1.5) arising from the homogeneous steady state (u_*, v_*) , where for definiteness we choose

$$f(v) = r \left(1 - \frac{v}{K} \right).$$

That is we consider the following ratio-dependent predator-prey model with prey-taxis

$$\begin{cases} u_t = \Delta u - \nabla \cdot (\chi u \nabla v) + \frac{\beta u v}{m u + v} - \theta u, & x \in \Omega, t > 0, \\ v_t = d \Delta v - \frac{u v}{m u + v} + r v \left(1 - \frac{v}{K} \right), & x \in \Omega, t > 0, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x), \quad v(x, 0) = v_0(x), & x \in \Omega. \end{cases} \quad (4.8)$$

The above system is solved by the MATLAB pde solver based on the finite difference scheme. We choose the initial value (u_0, v_0) as a small perturbation of the homogeneous steady state (equilibrium) (u_*, v_*) . Without loss of generality, we set

$$u_0 = u_* + 0.01 \cos(\pi x/2), \quad v_0 = v_* + 0.01 \cos(\pi x/2).$$

We set $l = 20$ and system parameters are chosen as follows

$$r = 0.84, K = 1, m = 1, \theta = 0.1, \beta = 0.3, d = 0.001 \quad (4.9)$$

to satisfy the conditions in Lemma 4.2(2).

Then it can be easily verified that the system (4.8) has a unique positive equilibrium $(u_*, v_*) = (0.412698, 0.20635)$. According to (4.6), we can find that

$$\chi_c = 0.9164362070.$$

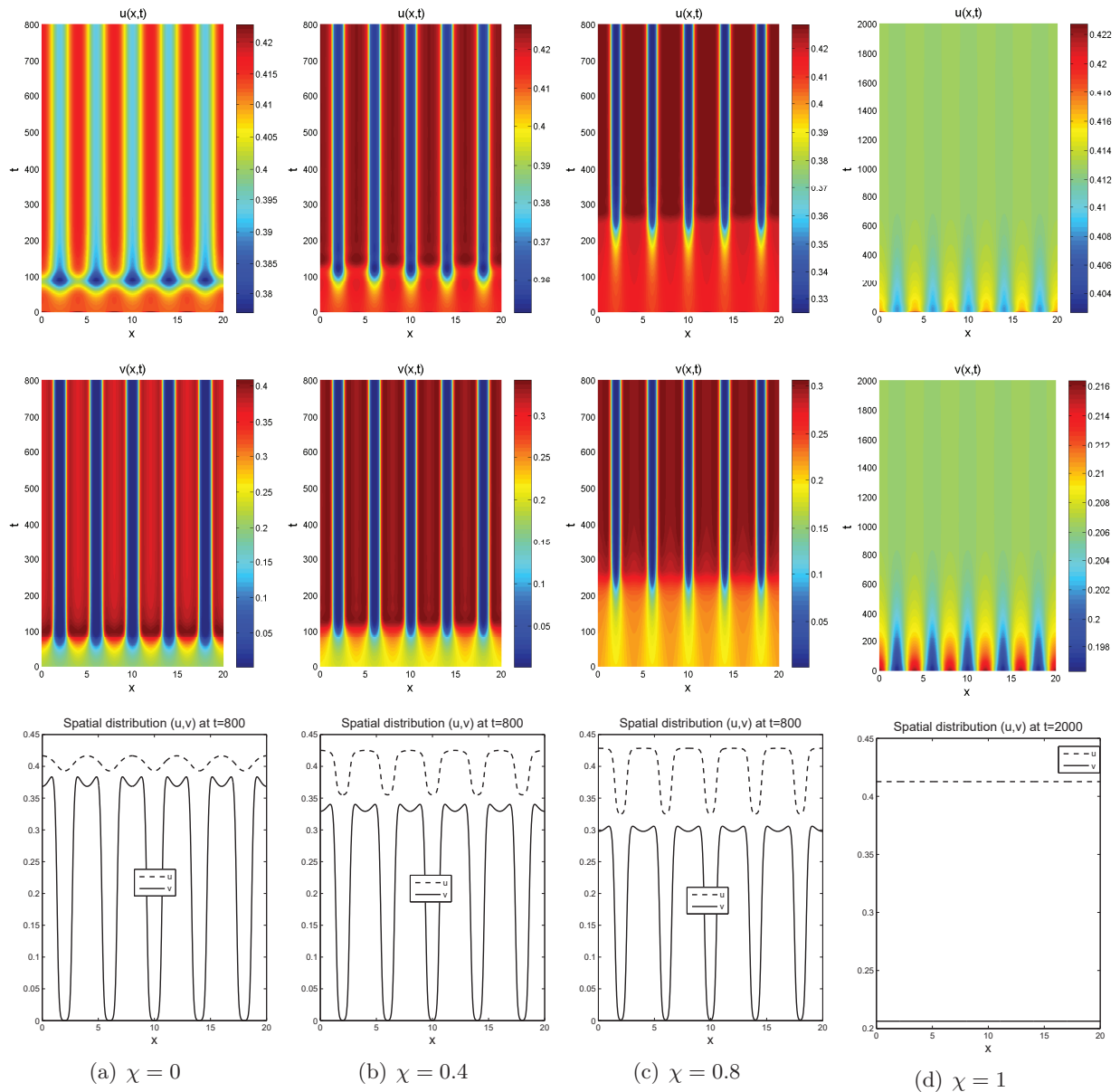


FIGURE 1. Spatio-temporal patterns generated by the system (1.1) in the interval $[0, 20]$. Top: Spatio-temporal pattern of the predator; Middle: Spatio-temporal pattern of the prey; Bottom: Spatial profile of the predator and the prey. System parameters are the same as those in (4.9) and $u_0 = 0.412698 + 0.01 \cos(\pi x/2)$, $v_0 = 0.20635 + 0.01 \cos(\pi x/2)$.

Therefore by Lemma 4.2(2), spatial patterns may arise when the value of χ is less than χ_c . This is indeed verified by our numerical simulations shown in Fig.1 where we choose several different values of $\chi > 0$. From the simulations, we find that when $\chi < \chi_c$, the system (4.8) produces spatially inhomogeneous patterns (see Fig. 1(a)-(c)) as expected from Lemma 4.2(2). As χ increases to be larger than the critical value χ_c , the spatially inhomogeneous patterns will gradually evolve to the spatially homogeneous patterns. These simulation results are well consistent with the results of Lemma 4.2.

From the numerical simulations shown in Fig.1, we find that the prey-taxis is a stabilizing factor driving the population to reach the spatially homogeneous co-existence steady state. This is very different from the usual chemotaxis models where chemotaxis is a destabilizing

TABLE 1. A summary for the (total) population of the predator and the prey.

Value of χ	u_m	v_m	$u_m + v_m$
$\chi = 0$	8.1157	4.9753	13.0910
$\chi = 0.4$	8.0301	4.6479	12.6780
$\chi = 0.8$	7.9726	4.4185	12.3911
$\chi = 1$	8.2457	4.1229	12.3686

factor inducing the pattern formation. However it is hard to determine whether the prey-taxis plays a positive or negative role in the predator-prey dynamics based on this distinctive feature since which of homogeneity or inhomogeneity is more favorable to the ecological system is a controversial topic. Below we shall discuss this briefly by calculating how the total population of predators and/or prey supported changes with respect to the prey-taxis coefficient χ . To this end, we plot the profiles of u (predator) and v (prey) at the third panel (bottom) of Fig. 1 at the final time step. Then we calculate the total population (mass) of u and v over the interval $[0, 20]$, denoted by u_m and v_m , respectively. The values of (u_m, v_m) are recorded in the Table 1 for different values of χ shown in Fig.1. We find that within the instability regime (i.e. $0 \leq \chi < \chi_c$), the total population of the predator will decrease with respect to the prey-taxis coefficient χ , and so does for the prey. However, as long as the value of χ jumps over the critical value χ_c , the inhomogeneous co-existence steady states will evolve into stable homogeneous co-existence steady states, and we find the total population of the predator will immediately increases to a fixed number (since u_* is unique) which is larger than the one in the instability regime, while the total population of the prey decreases to a fixed number (since v_* is unique) when χ crosses the critical value χ_c . These numerical findings imply that in the predator-prey evolution, the attainment of co-existence steady states does not depend on the value of $\chi \geq 0$, but its homogeneity and inhomogeneity is divided at the critical value χ_c . Within the weak prey-taxis regime (i.e. $0 \leq \chi < \chi_c$), prey-taxis is disadvantageous to both predators and prey in terms of the number of their total population supported. However once the prey-taxis coefficient exceeds its critical value (i.e. $\chi > \chi_c$), it appears that prey-taxis is beneficial for the predator while harmful to the prey (see Table 1) but the asymptotic dynamics will be irrespective of the strength of prey-taxis anymore since the total population of both predators and prey will remain the same asymptotically due to the convergence to the constant steady state (u_*, v_*) .

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