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DYNAMICS AND PATTERN FORMATION IN DIFFUSIVE PREDATOR-PREY MODELS WITH PREDATOR-TAXIS

ZHONGYUAN SUN, JINFENG WANG

Abstract. We consider a three-species predator-prey system in which the predator has a stage structure and the prey moves to avoid the mature predator, which is called the predator-taxis. We obtain the existence and uniform-in-time boundedness of classical global solutions for the model in any dimensional bounded domain with the Neumann boundary conditions. If the attractive predator-taxis coefficient is under a critical value, the homogenerous positive steady state maintains its stability. Otherwise, the system may generate Hopf bifurcation solutions. Our results suggest that the predator-taxis amplifies the spatial heterogeneity of the three-species predator-prey system, which is different from the effect of that in two-species predator-prey systems.

1. Introduction

Predator-prey interaction is common in ecological systems. The relatively simple models which describe the behaviors of one predator and one prey have been extensively studied. Some problems of stage structures were proposed since there are always two stages in the growing process of the majority of species, such as immature and mature stages [6, 8, 26, 27, 32, 33]. A reaction diffusion model with stage structure for the predator was proposed in [8],

$$
\begin{gathered}
\frac{\partial u}{\partial t} - d\Delta u = bv - mu, \quad x \in \Omega, t > 0, \\
\frac{\partial v}{\partial t} - d\Delta v = ruw - v, \quad x \in \Omega, t > 0, \\
\frac{\partial w}{\partial t} - d_1\Delta w = (a-w)w - \epsilon vw - uw, \quad x \in \Omega, t > 0, \\
\frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = \frac{\partial w}{\partial \nu} = 0, \quad x \in \partial\Omega, \\
u(x,0) \ge 0, v(x,0) \ge 0, w(x,0) \ge 0, \quad x \in \Omega,
\end{gathered}
\tag{1.1}
$$

where $u(x,t), v(x,t)$ and $w(x,t)$ represent the densities of mature predator, immature predator and prey respectively at position x and time t; Ω is a bounded domain in $\mathbb{R}^N$, $N \ge 1$ with smooth boundary $\partial\Omega$ and unit outer normal ν; the homogeneous Neumann boundary condition indicates that the predator-prey system is self-contained with zero population flux across the boundary. It can deem that

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the diffusion rates of immature and mature organisms are identical since the immature predator always follows the mature one for the same species, the constants d, d_1(diffusion rates) and b, m, r, a, ϵ are all positive.

The pursuit and evasion between predators and prey (predators chasing prey and prey evading from predators) have a strong impact on the movement pattern of predators and prey [14, 22, 34]. Such movement is not random but directed: predators move toward the gradient direction of prey distribution, and prey moves in the negative gradient direction of predator distribution. It is important to study such movement that describes an ecological interesting phenomenon and provides new insights into the effects of dispersal on predators and prey.

Besides the fact that predators forage prey, prey may avoid predators actively as well. Because of the great gap between the ability of the mature and immature predators to capture prey, the reality of the interaction among the prey, the mature predators and their young is that the prey tends to avoid the mature predators. We model this by the cross diffusion term $\alpha\nabla\cdot(\beta(w)w\nabla u)$ for the predator-taxis with predator-tactic coefficient $\alpha > 0$, which implies that the prey w moves to the opposite direction of the increasing mature predators gradient u, and $\beta(w)$ is the sensitivity of prey to predation risk (i.e. predator-taxis). Combined with (self-)diffusion, the prey thus diffuses with flux $d_1\nabla w + \alpha(\beta(w)w\nabla u)$. Thus, the cross diffusion system that we shall study is the following,

$$\begin{gathered}
\frac{\partial u}{\partial t} - d\Delta u = bv - mu, \quad x \in \Omega, t > 0, \\
\frac{\partial v}{\partial t} - d\Delta v = ruw - v, \quad x \in \Omega, t > 0, \\
\frac{\partial w}{\partial t} - d_1\Delta w - \alpha\nabla\cdot(\beta(w)w\nabla u) = (a-w)w - \epsilon vw - uw, \quad x \in \Omega, t > 0, \\
\frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = \frac{\partial w}{\partial \nu} = 0, \quad x \in \partial\Omega, \\
u(x,0) = u_0(x) \ge 0, v(x,0) = v_0(x) \ge 0, w(x,0) = w_0(x) \ge 0, \quad x \in \Omega.
\end{gathered} \tag{1.2}$$

Taking into account the volume filling effect for $\beta(w)$, we adopt $\beta(w)$ as (e.g. see [29]):

$$\beta(w) = \begin{cases} 1 - \frac{w}{M}, & 0 \le w \le M, \\ 0, & w > M, \end{cases} \tag{1.3}$$

where M measures the maximum number of prey that one unit volume can be filled. Referring to [19, 29], we can assume that $M > a$, where a represents the carrying capacity of prey. The parameters ϵ, r are both restricted in the interval $(0, 1)$ and $abr > m$ is set to warrant the existence of non-trivial steady states. The initial data u_0, v_0, w_0 are continuous functions.

It is noticed that volume filling is also common in chemotaxis models. For example, Hillen and Painter in [12] considered the prevention of overcrowding in the chemotaxis model, namely there is no chemo-tactic response when the cell density is high. This phenomenon also exists in other two-species predator-prey systems (e.g. see [1, 11, 21, 29]): so many prey occur that the volume can not accommodate, prey will not move towards the area around them which leads to nothingness of the predator-taxis term [29].

In two-species predator prey systems with prey-taxis, a large body of outcomes have been obtained. The traveling wave solutions, the pattern formation in a bounded domain under zero Neummann boundary conditions and the global existence of classical solutions were successively studied in [1, 4, 11, 13, 15, 16, 17, 21, 28, 30]. These results show that prey-taxis plays a stabilization role in the dynamical behavior. Compared with prey-taxis system, predator-taxis ($\alpha > 0$) systems are much less common. The global existence of positive classical solutions and stability of positive equilibria in three-species predator-prey systems with prey-taxis were studied (see [10, 23, 24]). As a result, they found that attractive predator-taxis ($\alpha > 0$) inhibits spatial pattern formation, instead of generating that. Without predator taxis (i.e. $\alpha = 0$), model (1.1) was proposed in [8], based on the classical Lotka-Volterra interaction, the authors studied the stability of nonnegative steady states of the system (1.1) and the reduced ODE system. In addition, the dynamics of the cross diffusion system were also analyzed.

Our main result in this paper is further to investigate the effect of repulsive predator-taxis on the dynamics of three-species system (1.2). It found that a strong predator-taxis can promote the spatial pattern, while the constant equilibrium regains its stability for weak predator-taxis. Moreover, attractive predator-taxis can drive the generation of spatial pattern. This provides another mechanism for spatial pattern formation: introducing an attractive predator-taxis into a reaction-diffusion system with three-species predator-prey interaction. We also obtain the existence of non-constant equilibrium of (1.2) rigorously by using the bifurcation theory. The results here differ from earlier partial results for prey-taxis systems [16, 25, 28] and predator-taxis systems [31] with two species.

The remainder of this paper is organized as follows: In Section 2, the global existence of the classical solutions of (1.2) is investigated; In Section 3, the effect of predator-taxis coefficient α on pattern formation is explored. Pattern formation is numerically illustrated in Section 4. We use $\|\cdot\|_p$ as the norm of $L^p(\Omega)$, $1 \le p \le \infty$ through the paper.

2. Existence of global classical solution

In this section, the existence of global classical solutions to (1.2) will be established. First, we shall ensure that the solutions to (1.2) are classical. However, it is obvious that $\beta(w)$ is not differentiable. To overcome this problem, referring to [29], we make a smooth extension of $\beta(w)$ by

$$\tilde{\beta}(w) \begin{cases} > 1, & w < 0, \\ = \beta(w), & 0 \le w \le M, \\ < 0, & w > M. \end{cases} \tag{2.1}$$

Replacing $\beta(w)$ with $\tilde{\beta}(w)$ in (1.2), we obtain

$$\begin{gathered} \frac{\partial u}{\partial t} - d\Delta u = bv - mu, \quad x \in \Omega, t > 0, \\ \frac{\partial v}{\partial t} - d\Delta v = ruw - v, \quad x \in \Omega, t > 0, \\ \frac{\partial w}{\partial t} - d_1\Delta w - \alpha\nabla\cdot(\tilde{\beta}(w)w\nabla u) = (a-w)w - \epsilon vw - uw, \quad x \in \Omega, t > 0, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = \frac{\partial w}{\partial \nu} = 0, \quad x \in \partial\Omega, \\ u(x,0) \ge 0, v(x,0) \ge 0, w(x,0) \ge 0, \quad x \in \Omega. \end{gathered} \tag{2.2}$$

If $0 \le w \le M$, we can see $\beta(w) = \tilde{\beta}(w)$ in which case system (1.2) is equivalent to (2.2). Indeed, it is a fact that $0 \le w \le M$ (we will explain it later). Let $p \in (n, \infty)$, then $W^{1,p}(\bar{\Omega}, R^3)$ is continuously embedded in $C(\Omega, R^3)$. Define

$$X := \{\omega \in W^{1,\rho}(\Omega, R^3) \mid \frac{\partial \omega}{\partial \nu} = 0 \text{ on } \partial\Omega\}. \tag{2.3}$$

It is easy to see that (2.2) can be written as a triangular system, then we obtain the existence of local solutions with the help of Amann's theorem [3].

Lemma 2.1. *(1) System (2.2) has a unique solution $(u(x,t), v(x,t), w(x,t)) \in X$ defined on $\Omega \times (0,T)$ satisfying $(u,v,w) \in C((0,T), X) \cap C^{2,1}((0,T) \times \bar{\Omega}, R^3)$, where T depends on the initial data $(u_0, v_0, w_0) \in X$.*

(2) Define $X_1 = \{(u,v,w) \in R^3 \mid u \ge 0, v \ge 0, 0 \le w \le M\}$ at $G \subset R^3$ such that $X_1 \subset G$. If for every $G \subset R^3$ containing X_1, (u,v,w) is bounded away from the boundary of G in $L^\infty(\Omega)$ norm for $t \in (0,T)$, then $T = \infty$, this means that the solution (u,v,w) exists globally.

Based on the second part of Lemma 2.1, it remains to derive the L^∞-bound of u, v, w to prove the global existence of solutions.

Theorem 2.2. *Assume that $u_0 \ge 0, v_0 \ge 0, 0 \le w_0 \le M$, and $M > a$. Then the solution $(u(x,t), v(x,t), w(x,t))$ of (2.2) satisfies $0 \le u(x,t) \le K^*, 0 \le v(x,t) \le K^*$ and $0 \le w(x,t) \le M$, where K^* depends on $|\Omega|$, M and $\|bv_0(x) + u_0(x)\|_\infty$, and it exists globally in time.*

Proof. Firstly, we show that $w \in [0, M]$. We define an operator

$$\mathcal{L}w = w_t - d_2 \Delta w - \alpha \nabla(\tilde{\beta}(w) w \nabla u). \tag{2.4}$$

From $w_0 \ge 0$, $w = 0$ is a lower solution of the equation. Plugging $w = M$ into (2.4), we obtain

$$\mathcal{L}M = 0 \ge (a - M)M - \epsilon M v - M u \tag{2.5}$$

since $M > a$. It is noticed that (2.5) satisfies the boundary condition and initial value:

$$\frac{\partial M}{\partial \nu} = 0, \quad M \ge w_0. \tag{2.6}$$

Thus we have that $w = M$ is an upper solution of the w equation from (2.5) and (2.6), which implies

$$0 \le w \le M \tag{2.7}$$

from the comparison principle of parabolic equations [20]. Now we prove that the L^∞ norm of u, v are bounded. Integrating the second equation of (1.2), we obtain

$$\begin{aligned}
\int_\Omega v_t dx &= \int_\Omega \nabla \cdot (d \nabla v) dx + \int_\Omega (ruw - v) dx \\
&= \int_{\partial\Omega} (d \nabla v) \cdot n dS + \int_\Omega (ruw - v) dx \\
&= \int_\Omega (ruw - v) dx.
\end{aligned} \tag{2.8}$$

Similarly, integrating the first equation and the third equation of (1.2), respectively, we have

$$\int_\Omega u_t dx = \int_\Omega (bv - mu) dx, \tag{2.9}$$

$$\int_\Omega w_t dx = \int_\Omega ((a-w)w - \epsilon vw - uw)dx. \tag{2.10}$$

Multiplying (2.10) by r and adding the resulting equation to (2.8), we obtain

$$\begin{aligned} \frac{d}{dt}\int_\Omega (rw+v)dx &= \int_\Omega (r(a-w)w - \epsilon rvw - v)dx \\ &= r\int_\Omega (a-w-\epsilon v+1)wdx - \int_\Omega (rw+v)dx \\ &\le r\int_\Omega (a+1)wdx - \int_\Omega (rw+v)dx \\ &\le r|\Omega|(a+1)M - \int_\Omega (rw+v)dx. \end{aligned} \tag{2.11}$$

In view of (2.11), it can be shown that

$$\frac{d}{dt}\|rw+v\|_1 \le r|\Omega|(a+1)M - \|rw+v\|_1. \tag{2.12}$$

From (2.12), we have

$$\lim_{t\to\infty} \sup \|rw+v\|_1 \le r|\Omega|(a+1)M,$$

which indicate that $\|rw+v\|_1$ is bounded. Hence

$$\|v\|_1 \le r|\Omega|(a+1)M. \tag{2.13}$$

Referring to (2.9) and (2.13), we obtain

$$\begin{aligned} \frac{d}{dt}\int_\Omega udx &= \int_\Omega (bv-mu)dx \\ &= b\int_\Omega vdx - m\int_\Omega udx \\ &\le br|\Omega|(a+1)M - m\int_\Omega udx, \end{aligned} \tag{2.14}$$

which implies that

$$\|u\|_1 \le \frac{br|\Omega|(a+1)M}{m}. \tag{2.15}$$

From (2.13) and (2.15), we obtain $\|bv+u\|_1 \le \frac{(m+1)br|\Omega|(a+1)M}{m} =: K$ (a finite positive constant) and $\sup_{t\ge 0}\int_\Omega (bv+u)dx < K+1$. Below we will illustrate that $\|bv+u\|_\infty$ is bounded. Clearly,

$$\begin{aligned} \frac{\partial(u+bv)}{\partial t} &= d\Delta(u+bv) + (bruw - mu) \\ &\le d\Delta(u+bv) + brMu \\ &\le d\Delta(u+bv) + brM(u+bv). \end{aligned}$$

Therefore, by [2, Theorem 3.1], we conclude that $\sup_{t\ge 0}\|bv+u\|_\infty \le K^*$, where K^* is a constant which depends on K and $\|bv_0(x)+u_0(x)\|_\infty$. The desired results are proved. $\square$

Theorem 2.2 indicates that the taxis terms can not give rise to blow up of solution, which is consistent with the results of many models with taxis terms introduced in volume filling effect (see [12, 19, 29]).

Furthermore, we can obtain the boundedness of steady state solutions, which solve the elliptic system

$$
\begin{gathered}
d\Delta u + bv - mu = 0, \quad x \in \Omega, \\
d\Delta v + ruw - v = 0, \quad x \in \Omega, \\
d_1 \Delta w + \alpha \nabla \cdot (\beta(w) w \nabla u) + (a - w)w - \epsilon vw - uw = 0, \quad x \in \Omega, \\
\frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = \frac{\partial w}{\partial \nu} = 0, \quad x \in \partial\Omega.
\end{gathered}
\tag{2.16}
$$

Theorem 2.3. *Let (u, v, w) be a positive solution of (2.16) and $d^* > 0$ be a fixed positive constant. Then there exists a positive constant $C(d^*) > 0$ such that*

$$
\|u, v, w\|_{C^{2+\alpha}(\bar{\Omega})} \le C(d^*), \tag{2.17}
$$

where $d, d_1 \ge d^*$.

Proof. We define the operator

$$
\mathcal{L}w = -d_1 \Delta w - \alpha \nabla \cdot (\beta(w) w \nabla u) - ((a - w)w - \epsilon vw - uw). \tag{2.18}
$$

Inserting $w = M$ into (2.18), we obtain

$$
\mathcal{L}M = -M(a - M - \epsilon v - u) \ge 0.
$$

Then we know that $w = M$ is an upper solution in the w equation. Therefore $w \le M$ by the comparison principle of elliptic equations [9], which also shows $\max_{\bar{\Omega}} w \le M$. Suppose that

$$
\max_{\bar{\Omega}} u, \max_{\bar{\Omega}} v, \max_{\bar{\Omega}} w \le C(d^*) \tag{2.19}
$$

is not true, then there exists (d_n, d_{1n}) satisfying $d_n, d_{1n} \ge d^*$, and a corresponding positive solution (u_n, v_n, w_n) of (2.16) with $(d, d_1) = (d_n, d_{1n})$, such that

$$
\max_{\bar{\Omega}} u_n + \max_{\bar{\Omega}} v_n \to \infty \quad \text{as } n \to \infty. \tag{2.20}
$$

Assume that $u_n(x_0) = \max_{x \in \bar{\Omega}} u_n(x)$, then we obtain $bv(x_0) - mu(x_0) \ge 0$ with the help of the maximum principle in the equation of u_n, which implies that

$$
\max_{\bar{\Omega}} u_n \le b \max_{\bar{\Omega}} v_n. \tag{2.21}
$$

Similarly, let $v_n(x_1) = \max_{x \in \bar{\Omega}} v_n(x)$. Again the maximum principle to the equation of v_n, we have $v_n(x_1) \le ru_n(x_1)w_n(x_1) \le rMu_n(x_1) \le rMu_n(x_0)$, which indicates that

$$
\max_{\bar{\Omega}} v_n \le rM \max_{\bar{\Omega}} u_n. \tag{2.22}
$$

Based on (2.20)-(2.22), we have

$$
\lim_{n \to \infty} \max_{\bar{\Omega}} u_n = \lim_{n \to \infty} \max_{\bar{\Omega}} v_n = \infty.
$$

Set $\tilde u_n = \frac{u_n}{\|u_n\|_\infty}$ and $\tilde v_n = \frac{v_n}{\|v_n\|_\infty}$, then $(\tilde u_n, \tilde v_n, w_n)$ satisfies

$$\begin{aligned} -\Delta \tilde u_n &= \frac{1}{d_n}\Big(b\frac{\|v_n\|_\infty}{\|u_n\|_\infty}\tilde v_n - m\tilde u_n\Big), \quad x\in\Omega,\\ -d_n\Delta \tilde v_n &= r\frac{\|u_n\|_\infty}{\|v_n\|_\infty}\tilde u_n w_n - \tilde v_n, \quad x\in\Omega,\\ -d_{1n}\Delta w_n &= \alpha\|u_n\|_\infty \nabla\cdot(\beta(w_n)w_n\nabla\tilde u_n) + (a-w_n)w_n\\ &\quad - \epsilon\tilde v_n\|v_n\|_\infty w_n - \tilde u_n\|u_n\|_\infty w_n, \quad x\in\Omega,\\ \frac{\partial\tilde u_n}{\partial\nu} = \frac{\partial \tilde v_n}{\partial\nu} &= \frac{\partial\tilde w_n}{\partial\nu} = 0, \quad \|\tilde u_n\|_\infty = \|\tilde v_n\|_\infty = 1, \quad x\in\partial\Omega. \end{aligned} \tag{2.23}$$

In view of (2.21) and (2.22), we have $A\|v_n\|_\infty \le \|u_n\|_\infty \le B\|v_n\|_\infty$, where both A and B are positive constants. Notice that $0\le w_n\le M$ and $0\le \tilde u_n, \tilde v_n\le 1$, we can suppose that

$$\frac{\|v_n\|_\infty}{\|u_n\|_\infty} \to \gamma \quad (\gamma>0), \tag{2.24}$$

and $d_n\to d$, $d_{1n}\to d_1$ with $d, d_1 \ge d^*$, $\tilde v_n \to \tilde v$ strongly in $L^p(\Omega)$, $w_n\to w$ weakly in $L^p(\Omega)$, $\tilde u_n\to\tilde u$ weakly in $W^{2,p}(\Omega)$, and $\|\tilde u\|_\infty = 1$, where $p>N$. These yield $\tilde u\in C^{1+\alpha}(\bar\Omega)$ for some $\alpha>0$, and $\tilde u_n\to\tilde u$ in $C^{1+\alpha}(\bar\Omega)$.

If $d_1=\infty$, then $\tilde u$ satisfies

$$\begin{aligned} -\Delta\tilde u &= 0, \quad x\in\Omega,\\ \frac{\partial\tilde u}{\partial\nu} &= 0, \quad x\in\partial\Omega, \end{aligned}$$

which implies that $\tilde u = 1$ along with $\|\tilde u\|_\infty = 1$. If $d<\infty$, then $\tilde u$ satisfies $\|\tilde u_n\|_\infty = 1$ and

$$\begin{aligned} -d\Delta\tilde u &= b\gamma\tilde v - m\tilde u, \quad x\in\Omega,\\ \frac{\partial\tilde u}{\partial\nu} &= 0, \quad x\in\partial\Omega, \end{aligned} \tag{2.25}$$

which gives $\tilde u>0$ on $\bar\Omega$ by the strong maximum principle and the Hopf boundary lemma for the $W^{2,p}(\Omega)$ solution (see [9] and [7]).

Clearly, we have $\tilde u>0$ on $\bar\Omega$. Hence, there exists $\delta>0$ such that $\tilde u\ge\delta$ on $\bar\Omega$ (we might as well suppose $\delta = \frac{2\gamma b}{m}+1$). Accordingly, $\tilde u_n \ge \delta/2$ on $\bar\Omega$ for all large n. From (2.24), we can see $\frac{\|v_n\|_\infty}{\|u_n\|_\infty} < \epsilon_0+\gamma$ for n large sufficiently, where ϵ_0 can be restricted as $\epsilon_0 < \frac{m\delta}{2b} - \gamma$. Consequently, for large n, we have

$$\begin{aligned} -d_n\Delta\tilde u_n = b\frac{\|v_n\|_\infty}{\|u_n\|_\infty}\tilde v_n - m\tilde u_n &< b(\gamma+\epsilon_0) - m(\delta/2) < 0, \quad x\in\Omega,\\ \frac{\partial\tilde u_n}{\partial\nu} &= 0, \quad x\in\partial\Omega, \end{aligned} \tag{2.26}$$

which contradicts $\int_\Omega \Delta\tilde u_n dx = 0$. Finally we have estimate (2.17) from the regularity of elliptic equations. $\square$

3. Effect of predator-taxis on dynamical behaviors

In this section, we shall study the role that the predator-taxis plays in the dynamical behavior of (1.2). Obviously, system (1.2) has two trivial solutions $(0,0,0)$,

$(0,0,a)$, and a positive constant steady state $(\bar{u},\bar{v},\bar{w})$ under the condition $abr>m$, where

$$\bar{u}=\frac{abr-m}{r(b+m\epsilon)},\quad \bar{v}=\frac{m(abr-m)}{br(b+m\epsilon)},\quad \bar{w}=\frac{m}{br}. \tag{3.1}$$

Firstly, we consider the stability of the positive steady state $(\bar{u},\bar{v},\bar{w})$. For that purpose, we make a linearization of the reaction-diffusion-taxis system (1.2) at $(\bar{u},\bar{v},\bar{w})$,

$$\begin{pmatrix}\frac{\partial u}{\partial t}\\ \frac{\partial v}{\partial t}\\ \frac{\partial w}{\partial t}\end{pmatrix}=D\begin{pmatrix}\Delta u\\ \Delta v\\ \Delta w\end{pmatrix}+J\begin{pmatrix}u\\ v\\ w\end{pmatrix},$$

with

$$D=\begin{pmatrix}d&0&0\\ 0&d&0\\ \alpha\beta(\bar{w})\bar{w}&0&d_1\end{pmatrix},\quad J=\begin{pmatrix}a_{11}&a_{12}&a_{13}\\ a_{21}&a_{22}&a_{23}\\ a_{31}&a_{32}&a_{33}\end{pmatrix},$$

where

$$\begin{gathered}a_{11}=-m,\quad a_{12}=b,\quad a_{13}=0,\\ a_{21}=r\bar{w},\quad a_{22}=-1,\quad a_{23}=r\bar{u},\\ a_{31}=-\bar{w},\quad a_{32}=-\epsilon\bar{w},\quad a_{33}=-\bar{w}.\end{gathered}$$

We denote the eigenvalue of $-\Delta$ under Neumann boundary conditions and the corresponding eigenfunction by μ_k and ϕ_k $(k\geq 0)$. Then the stability of $(\bar{u},\bar{v},\bar{w})$ is determined by the eigenvalue problem

$$(D\Delta+J)\begin{pmatrix}\phi_1\\ \phi_2\\ \phi_3\end{pmatrix}=\lambda\begin{pmatrix}\phi_1\\ \phi_2\\ \phi_3\end{pmatrix},$$

where λ is an eigenvalue of $D\Delta+J$ (i.e. $-\mu_k D+J$) for each $k\geq 0$. The characteristic equation for the eigenvalue λ is

$$\lambda^3+A_k\lambda^2+B_k\lambda+C_k=0, \tag{3.2}$$

where

$$\begin{aligned}A_k&=(2d+d_1)\mu_k-(a_{11}+a_{22}+a_{33})>0,\\ B_k&=(d^2+2dd_1){\mu_k}^2-(2da_{33}+(d+d_1)(a_{11}+a_{22}))\mu_k\\ &\quad+a_{11}a_{22}+a_{11}a_{33}+a_{22}a_{33}-a_{12}a_{21}-a_{23}a_{32}>0,\\ C_k&=(d^2d_1){\mu_k}^3-(d^2a_{33}+dd_1(a_{11}+a_{22})){\mu_k}^2\\ &\quad+(d(a_{22}a_{33}+a_{11}a_{33}+a_{23}a_{32})+d_1(a_{11}a_{22}-a_{12}a_{21}))\mu_k\\ &\quad+a_{11}a_{23}a_{32}-a_{12}a_{23}a_{31}-a_{11}a_{22}a_{33}+a_{12}a_{21}a_{33}\\ &\quad+a_{12}a_{23}\alpha\beta(\bar{w})\bar{w}\mu_k>0.\end{aligned}$$

Therefore,

$$H_k=A_kB_k-C_k=h_1{\mu_k}^6+h_2{\mu_k}^4+h_3{\mu_k}^2+h_4+f_1{\mu_k}^2, \tag{3.3}$$

where

$$\begin{aligned}h_1&=(2d+d_1)(d^2+2dd_1)-d^2d_1,\\ h_2&=-((4d^2+4dd_1)a_{33}+(3d^2+{d_1}^2+4dd_1)a_{22}\\ &\quad+(3d^2+{d_1}^2+4dd_1)a_{11}),\end{aligned}$$

$$
\begin{aligned}
h_3 &= 2(2d+d_1)(a_{11}a_{22}+a_{11}a_{33}+a_{22}a_{33}) + 2da_{33}^2 + (d+d_1)(a_{11}^2+a_{22}^2) \\
&\quad - 2da_{12}a_{21} - (d+d_1)a_{23}a_{32}, \\
h_4 &= -2a_{11}a_{22}a_{33} - a_{11}^2(a_{22}+a_{33}) - a_{22}^2(a_{11}+a_{33}) - a_{33}^2(a_{11}+a_{22}) \\
&\quad + a_{11}a_{12}a_{21} + a_{23}a_{32}a_{33} + a_{12}a_{23}a_{31} + a_{22}a_{12}a_{21} + a_{22}a_{23}a_{32}, \\
f_1 &= -a_{12}a_{23}\alpha\beta(\bar{w})\bar{w}.
\end{aligned}
$$

Lemma 3.1. *Suppose that $b \le \epsilon(1+\frac{m}{br})$, $\beta(w) > 0$, then α_k has the minimum value $\tilde{\alpha}$ for some $k \in \mathbb{N}_+$, i.e. $\tilde{\alpha} = \min_{k\in\mathbb{N}_+} \alpha_k$, where*

$$
\alpha_k = \frac{h_1{\mu_k}^3 + h_2{\mu_k}^2 + h_3\mu_k + h_4}{br\bar{u}\beta(\bar{w})\bar{w}\mu_k}. \tag{3.4}
$$

Proof. It is easy to see that α_k can be reformulated as

$$
\alpha_k = \frac{h_1{\mu_k}^2}{br\bar{u}\beta(\bar{w})\bar{w}} + \frac{h_2\mu_k}{br\bar{u}\beta(\bar{w})\bar{w}} + \frac{h_3}{br\bar{u}\beta(\bar{w})\bar{w}} + \frac{h_4}{br\beta(\bar{w})\bar{w}\mu_k}. \tag{3.5}
$$

Taking the derivative of α_k with respect to μ_k, we obtain

$$
\alpha_k' = \frac{2h_1\mu_k}{br\bar{u}\beta(\bar{w})\bar{w}} + \frac{h_2}{br\bar{u}\beta(\bar{w})\bar{w}} - \frac{h_4}{br\bar{u}\beta(\bar{w})\bar{w}{\mu_k}^2}, \tag{3.6}
$$

$$
\alpha_k'' = \frac{2h_1}{br\bar{u}\beta(\bar{w})\bar{w}} + \frac{2h_4}{br\bar{u}\beta(\bar{w})\bar{w}{\mu_k}^3} > 0, \tag{3.7}
$$

which indicate that α_k can achieve its minimum value $\tilde{\alpha}$ at some k. □

Theorem 3.2. *Assume $\beta(w) > 0$, $b \le \epsilon(1+\frac{m}{br})$ and the condition $m < abr$ holds. Let $(\bar{u},\bar{v},\bar{w})$ be the unique positive constant steady state of (1.2).*

1. *If $\alpha < \tilde{\alpha}$, then $(\bar{u},\bar{v},\bar{w})$ is locally asymptotically stable; If $\alpha > \tilde{\alpha}$, then $(\bar{u},\bar{v},\bar{w})$ is unstable.*
2. *Assume that $\alpha_j \ne \alpha_k$ for any $j \ne k$, then α_k can derive the occurrence of periodic solutions bifurcating from $(\bar{u},\bar{v},\bar{w})$, where $k, j \in \mathbb{N}_+$.*

Proof. According to the Routh-Hurwitz criterion [5], or [18, Corollary 2.2], we know that the constant steady state $(\bar{u},\bar{v},\bar{w})$ is asymptotically stable if and only if the following conditions hold:

$$
A_k > 0, \quad C_k > 0, \quad H_k > 0, \quad \text{for all } k \in \mathbb{N}_+,
$$

while $(\bar{u},\bar{v},\bar{w})$ is unstable provided that $A_k \le 0$, or $C_k \le 0$, or $H_k \le 0$ for some $k \in \mathbb{N}_+$. Note that we always have $A_k > 0, C_k > 0$ for each $k \in \mathbb{N}_+$, thereby the stability/instability of $(\bar{u},\bar{v},\bar{w})$ is subject to consider the sign of H_k. Setting $H_k = 0$ and choosing α as the bifurcation point, we obtain (3.4). It is easy to check that $H_k > 0$ as $\alpha < \tilde{\alpha}$ and $H_k < 0$ as $\alpha > \tilde{\alpha}$.

Next we demonstrate that Hopf bifurcation occurs at every $\alpha_k (k \in \mathbb{N}_+)$. It is known that $H_k = A_kB_k - C_k = 0$ at α_k, and direct calculations show that (3.2) has one negative real root and two pure imaginary roots, i.e. $\lambda_1 = -A_k$, $\lambda_{2,3} = \pm\sqrt{B_k}i$. This indicates the possibility of Hopf bifurcation and the existence of a branch of periodic solutions bifurcating from $(\bar{u},\bar{v},\bar{w})$ at $\alpha = \alpha_k$. Denote $\lambda_1 = \xi + \eta i$, $\lambda_2 = \xi - \eta i$, then it remains to verify $\frac{d\xi}{d\alpha}\,|_{\alpha=\alpha_k} \ne 0$ to ensure the occurrence of Hopf bifurcation at α_k. We notice that $A_kB_k - C_k = -2\xi((\xi+\lambda_1)^2+\eta^2)$, which along with (3.3) gives

$$
F(\alpha,\xi) = -2\xi((\xi+\lambda_1)^2+\eta^2) - (h_1{\mu_k}^3 + h_2\mu^2 + h_3\mu_k + h_4) + br\bar{u}\alpha\beta(\bar{w})\bar{w}\mu_k = 0.
$$

By the implicit function differentiability theorem, we have

$$\frac{d\xi}{d\alpha}\Big|_{\alpha=\alpha_k} = -\frac{F_\alpha}{F_\xi} = \frac{br\bar{u}\beta(\bar{w})\bar{w}}{2({\lambda_1}^2+\eta^2)} > 0\,. \tag{3.8}$$

The proof is complete. □

Remark 3.3. It can not expect the steady state bifurcation occurring at $(\bar{u},\bar{v},\bar{w})$ since there is no zero root for the characteristic equation (3.2).

Remark 3.4. The second part in Theorem 3.2 implies that the Hopf bifurcation can not occur at α_0. In fact, we can claim that $(\bar{u},\bar{v},\bar{w})$ is asymptotically stable under the condition $b \le \epsilon(1+\frac{m}{br})$ for $k=0$. It is noticed that

$$\begin{gathered} A_0 = -(a_{11}+a_{22}+a_{33}) > 0, \\ B_0 = a_{11}a_{22}+a_{11}a_{33}+a_{22}a_{33}-a_{12}a_{21}-a_{23}a_{32} > 0, \\ C_0 = a_{11}a_{23}a_{32}-a_{12}a_{23}a_{31}-a_{11}a_{22}a_{33}+a_{12}a_{21}a_{33} > 0. \end{gathered} \tag{3.9}$$

Moreover, it can be derived that

$$\begin{aligned} H_0 = &-2a_{11}a_{22}a_{33} - a_{11}^2(a_{22}+a_{33}) - a_{22}^2(a_{11}+a_{33}) - a_{33}^2(a_{11}+a_{22}) \\ &+ a_{11}a_{12}a_{21} + a_{23}a_{32}a_{33} + a_{12}a_{23}a_{31} + a_{22}a_{12}a_{21} + a_{22}a_{23}a_{32} > 0 \end{aligned} \tag{3.10}$$

under the condition $b \le \epsilon(1+\frac{m}{br})$. Combining (3.9) and (3.10) implies the desired results.

Now, we investigate the stability of steady state $(0,0,a)$ of system (1.2).

Theorem 3.5. *(1) If $m > abr$, then $(0,0,a)$ is asymptotically stable; if $m < abr$, then $(0,0,a)$ is unstable.*
(2) If $m > Mbr$, then $(0,0,a)$ is globally attractive.

Proof. (1) Linearizing system (1.2) at $(0,0,a)$ leads to the characteristic equation

$$(\lambda+\mu_k d_1 + a)((\lambda+\mu_k d + m)(\lambda+\mu_k d+1) - rab) = 0, \tag{3.11}$$

then

$$\lambda + \mu_k d + a = 0, \tag{3.12}$$

or

$$(\lambda+\mu_k d+m)(\lambda+\mu_k d+1) - rab = 0. \tag{3.13}$$

We denote the roots of (3.11) by $\lambda_i (i=1,2,3)$, we readily get $\lambda_1 = -\mu_k d_1 - a < 0$ by (3.12). Moreover, it follows from (3.13) that

$$\begin{gathered} \lambda_2+\lambda_3 = -(2\mu_k d + 1 + m) < 0, \\ \lambda_2\lambda_3 = {\mu_k}^2 d^2 + \mu_k d + \mu_k m d + m - rab. \end{gathered} \tag{3.14}$$

Therefore, the condition $m > abr$ indicates that $\lambda_i < 0, (i=1,2,3)$, thus $(0,0,a)$ is asymptotically stable. And $m < abr$ shows that $\lambda_2\lambda_3 < 0$ for $k=0$, thus (3.11) has a positive real root and $(0,0,a)$ is unstable.

(2) We claim that $\lim_{t\to\infty}(u,v,w) = (0,0,M)$, where (u,v,w) represents the nonnegative solution of (1.2) and $w \ne 0$. As $w \le M$, we have $\limsup_{t\to\infty} w(x,t) \le$

M uniformly in $x \in \bar{\Omega}$. It is clear to see that there exists $T > 0$ such that $w(x,t) \leq M + \delta_0$ for sufficiently small $\delta_0 > 0$. Suppose that (u^*, v^*) satisfies

$$\begin{gathered} \frac{du^*}{dt} = bv^* - mu^*, \quad t > T, \\ \frac{dv^*}{dt} = r(M+\delta_0)u^* - v^*, \quad t > T, \\ u^*(T) = \max_{x\in\bar{\Omega}} u(x,T), \quad v^*(T) = \max_{x\in\bar{\Omega}} v(x,T). \end{gathered} \tag{3.15}$$

Then, $u(x,t) \leq u^*(t)$ and $v(x,t) \leq v^*(t)$ for all $t \geq T$ and $x \in \bar{\Omega}$. Notice the condition $m > Mbr$, we have $(M+\delta_0)br < m$, thus $\lim_{t\to\infty}(u^*(t), v^*(t)) = (0,0)$, which implies that $\lim_{t\to\infty}(u(x,t), v(x,t)) = (0,0)$ uniformly in $x \in \bar{\Omega}$. This, along with the fact $\lim_{t\to\infty} w(x,t) = M$, yields $\lim_{t\to\infty}(u,v,w) = (0,0,M)$. Moreover, the equation of w in (1.2) can be written as

$$\begin{gathered} \frac{\partial w}{\partial t} - d_1\Delta w = (a-w)w, \quad x \in \Omega, t > 0, \\ \frac{\partial w}{\partial \nu} = 0, \quad x \in \partial\Omega, \\ w(x,0) = w_0(x) \geq 0, \quad x \in \Omega \end{gathered} \tag{3.16}$$

when $(u,v) = (0,0)$. It is well known that the solution $w(x,t)$ of (3.16) eventually tends to a for any non-negative initial value $w_0(x)$. According the above analysis, we conclude that $(0,0,a)$ is globally attractive. □

4. Conclusions and numerical simulations

In this paper, we propose a three species predator-prey model with stage structure for the predators. Predators are assumed to move randomly in their habitats, and prey mobiles to avoid the mature predators. Our analysis shows that the addition of repulsive predator-taxis does destroy the stability of constant steady states and induce the occurrence of spatial patterns, see Theorem 3.2. Contrast to the results, the predator-taxis induced instability can not occur for two species predator-prey systems as shown in [24, 31], where both predator-taxis and prey-taxis may annihilate the spatial patterns.

Some numerical simulations of (1.2) are shown in Figures 2–5, where we use $d = d_1 = 1$, $a = 2$, $b = 0.7$, $r = 3$, $\epsilon = 0.5$, $m = 1.2$, $M = 10$ defined in (1.3) and $\Omega = (0, 20\pi)$ (one-dimensional space). We can calculate that $(\bar{u}, \bar{v}, \bar{w}) = (0.7692, 1.3187, 0.5714)$ is the unique positive constant steady state solution. Without loss of generality, the initial value is always chosen as

$$(u_0, v_0, w_0) = (0.7692 + 0.02\sin(2x), 1.3187 + 0.02\sin(2x), 0.5714 + 0.02\cos(2x)).$$

From (3.4), we can find that

$$\alpha_k = \frac{8(\frac{k}{20})^6 + 22.1712(\frac{k}{20})^4 + 19.1942(\frac{k}{20})^2 + 3.5970}{0.8703(\frac{k}{20})^2}, \quad k \in \mathbb{N}_+, \tag{4.1}$$

whose picture can be plotted with respect to varying $k (k \in \mathbb{N})$, see Figure 1. We can calculate that $\tilde{\alpha} = 43.8978$ for $k = 11$ as defined in Lemma 3.1. As $\alpha = 0$, $(\bar{u}, \bar{v}, \bar{w})$ is asymptotically stable, see Figure 2, which is consistent with the consequence in [8]. As shown in Theorem 3.2, the value of α which is less than $\tilde{\alpha}$ may inhibit spatial patterns since $(\bar{u}, \bar{v}, \bar{w})$ still keeps its local stability, see Figure 3. However, when α

increases to be larger than the critical value $\tilde{\alpha}$, the system (1.2) produces spatially inhomogeneous periodic solutions bifurcating from $(\bar{u}, \bar{v}, \bar{w})$, as shown in Figure 4 (corresponds to the Hopf bifurcation value α_{16}), and Figure 5 (corresponds to the Hopf bifurcation value α_{32}).

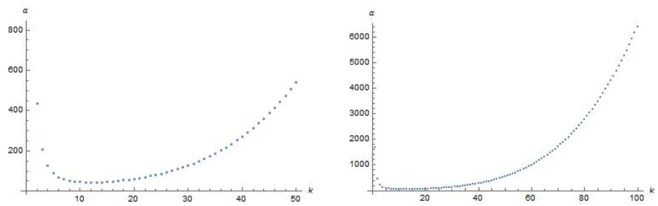

FIGURE 1. Change of α_k with nonnegative integer k. Left: k varies from 1 to 50. Right: k varies from 1 to 100.

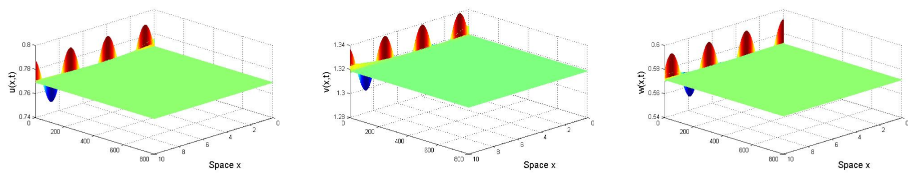

FIGURE 2. $(\bar{u}, \bar{v}, \bar{w})$ is asymptotically stable for (1.2) when $\alpha = 0$.

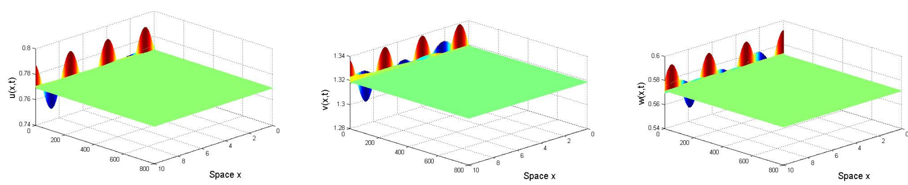

FIGURE 3. $(\bar{u}, \bar{v}, \bar{w})$ remains stable for (1.2) when $\alpha = 10 < \tilde{\alpha}$.

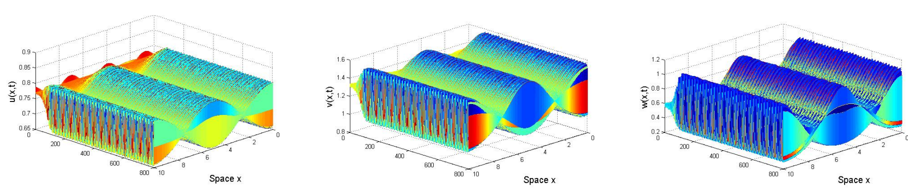

FIGURE 4. Spatial heterogenous and time-periodic patterns in system (1.2) when $\alpha = 48.582 (k = 16)$.

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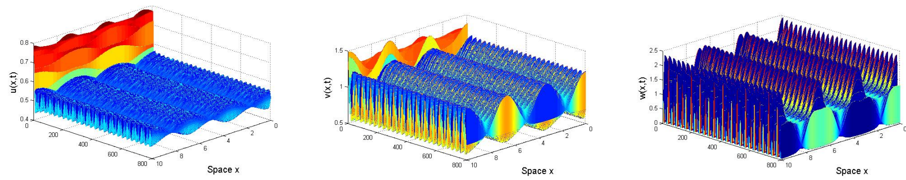

Figure 5. Spatial heterogenous and time-periodic patterns in system (1.2) when $\alpha = 149.128 (k = 32)$.

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Zhongyuan Sun
School of Mathematics Sciences and Y. Y. Tseng Functional Analysis Research Center, Harbin Normal University, Harbin, Heilongjiang, 150001, China
Email address: zhongyuansunmath@163.com

Jinfeng Wang (corresponding author)
School of Mathematics Sciences and Y. Y. Tseng Functional Analysis Research Center, Harbin Normal University, Harbin, Heilongjiang, 150001, China
Email address: jinfengwangmath@163.com