Cross-diffusion-driven Instability and Pattern Formation in a Nonlinear Predator-prey System

Wenbin Yang, Yimamu Maimaiti

Abstract—In this paper, a spatial predator-prey model with an alternative food source and cross-diffusion is studied. We show that the self-diffusion cannot induce a Turing Instability theoretically, but the cross-diffusion can. Moreover, the one-dimensional morphological spatial pattern is characterized, and the effects of parameter $\mu$ or $\rho$ on pattern formation are discussed numerically.

Index Terms—reaction-diffusion equations, predator-prey model, pattern dynamics, cross-diffusion.

I. INTRODUCTION

MANY of the most interesting dynamics in biology are related to the interactions between species, and the spatio-temporal dynamics of a predator-prey system has been investigated by many researchers [1]–[4]. For the predator population without any alternative source, the general Lotka-Volterra predator-prey system can be described as follows:

$$
\begin{align*}
\frac{du}{dt} &= \gamma u(1 - \frac{u}{K}) - \alpha uv, \\
\frac{dv}{dt} &= \rho uv - \beta v,
\end{align*}
$$

(1)

where $u$ and $v$ are the biomass of the prey and predator at any time $t$, respectively; $\gamma$ is the intrinsic growth rate; $K$ is the environmental carrying capacity of the prey species; $\alpha$ is the predation rate; $\rho(\leq 1)$ is called the conversion rate of prey to predator biomass; and $\beta$ is the natural death rate of the predator.

Ghosh and Kar [5] have considered a predator-prey ODE model having some alternative source to predator, as follows:

$$
\begin{align*}
\frac{du}{dt} &= \gamma u(1 - \frac{u}{K}) - \alpha uv, \\
\frac{dv}{dt} &= \mu v(1 - \frac{u}{K}) + \rho uv - \beta v, \\
\end{align*}
$$

(2)

where $\mu$ is the maximum growth rate due to alternative source for food. The term $(1 - u/K)$ adds a density-dependent effect to the focal prey, and it is observed that as the focal prey population $u$ increases, the predator uses less amount of alternative source and the consumption of alternative source tends to zero when $u$ approaches $K$. [5] showed that alternative source of food to the predator hurts the growth of the prey species.

Recently, much attention has been focused on the Turing instability of the predator-prey model by taking into account the effect of cross-diffusion [6], [7]. Cross-diffusion, the phenomenon in which a gradient in the concentration of one species induces a flux of another chemical species, has generally been neglected in the study of reaction-diffusion systems [8]–[14]. Now, we consider the Lotka-Volterra predator-prey model (2) with cross-diffusion and an alternative source of food for the predator:

$$
\begin{align*}
\frac{du}{dt} &= d_{11} \frac{\partial^2 u}{\partial x^2} + \gamma u(1 - \frac{u}{K}) - \alpha uv, \\
\frac{dv}{dt} &= d_{21} \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} + \mu v(1 - \frac{u}{K}) + \rho uv - \beta v, \\
\end{align*}
$$

(3)

where $x \in (0, l)$, $d_{11}$ and $d_{21}$ are diffusion coefficients of the prey and predator population, $d_{21}$ is cross-diffusion coefficient of the predator population, and $l > 0$ is a positive constant.

The paper is organized as follows. In section II, we will derive the sufficient conditions of the asymptotic stability and Turing Instability of our proposed models. The one-dimensional morphological spatial pattern will be characterized, and the effects of parameter $\mu$ or $\rho$ on pattern formation will be discussed in section III.

II. MATHEMATICAL ANALYSIS

In this section, we will consider the asymptotic stability and Turing instability of our proposed models. First, it is obvious that system (1) has the following nonnegative constant solutions:

1) $e_1 = (0, 0)$;
2) $e_2 = (K, 0)$;
3) $e_3 = (u_*, v_*) = (\frac{\beta}{\rho}, \frac{\gamma(K - \beta)}{\mu \rho K})$, if $\rho K > \beta$.

Accordingly, system (2), and thus system (3) has the following nonnegative constant solutions:

1) $U_1 = (0, 0)$;
2) $U_2 = (K, 0)$;
3) $U_3 = (0, c)$, where $c$ is an arbitrary positive constant, if $\mu \neq \beta$;
4) $U_4 = (u^*, v^*)$, where

$$
\begin{align*}
u^* &= v(u) = K\left(\frac{\beta - \mu}{\rho K - \mu}\right), \\
u^* &= v(u) = \frac{\gamma(K - \beta)}{\mu \rho K - \mu},
\end{align*}
$$

if either $\mu > \beta > \rho K$ or $\mu < \beta < \rho K$ holds.

Theorem 1. i) For system (1):

1. $e_3$ is an unstable saddle point.
2. If $\beta > \rho K$, then $e_2$ is a asymptotically stable node (a unstable saddle point).
3. Assume the $\rho K > \beta$. If $\frac{\beta^2}{\rho^2 K} > 4(\rho K - \beta)$, then $e_3$ is a asymptotically stable node; if $\frac{\beta^2}{\rho^2 K} < 4(\rho K - \beta)$, then $e_3$ is a asymptotically stable spiral point.

ii) For system (2):

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• If $\mu > \beta$ ($\mu < \beta$), then $U_1$ is an unstable node (a unstable saddle point).
• If $\beta > \rho K$ ($\beta < \rho K$), then $U_2$ is a asymptotically stable node (a unstable saddle point).
• If $\gamma < \alpha c$ and $\mu < \beta$, then $U_3$ is a asymptotically stable node (unstable); if $(\gamma - \alpha c)(\mu - \beta) < 0$, then $U_3$ is a unstable saddle point.
• If $\mu > \beta > \rho K$, then $U_4$ is unstable. Therefore, variation of the growth rate $\mu$ due to alternative source never stabilizes the system (2). If $\mu < \beta < \rho K$, $U_4$ is stable.

iii) For system (3):
• If $\mu < \beta < \rho K$ and $d_{21} = 0$, then $U_4$ is still stable.
• If $\mu < \beta < \rho K$, then a necessary condition for the emergence of cross-diffusion instability is $d_{21} \geq (2^{\alpha_11} - 1) - \sqrt{1 + 8(2\text{Det}(J) + \sqrt{\text{Det}(J)})}$.

The results show that, self-diffusion can not induce Turing instability, but cross-diffusion may lead to Turing instability.

Proof: We only consider cases ii) and iii), since a similar proof of case i) can be made in more straightforward way.

ii) For System (2), the Jacobian matrix at some an equilibrium is

$$J(U) = \begin{pmatrix} 0 & -\alpha \\ -\alpha u & \gamma - \alpha \end{pmatrix}.$$ (4)

At the equilibria $U_1, U_2$ and $U_3$, the corresponding Jacobian matrix can be respectively, calculated as

$$J(U_1) = \begin{pmatrix} 0 & -\alpha \\ -\alpha K & \gamma - \alpha \end{pmatrix}, \quad J(U_2) = \begin{pmatrix} 0 & -\alpha K \\ \gamma - \alpha & -\alpha \end{pmatrix},$$

$$J(U_3) = \begin{pmatrix} -\alpha & \gamma - \alpha \\ \gamma - \alpha & -\alpha \end{pmatrix}.$$ (5)

By the linear stability theory, we obtain that

• If $\mu > \beta$, then $U_1$ is an unstable node; if $\mu < \beta$, then $U_1$ is a unstable saddle point.
• If $\beta > \rho K$, then $U_2$ is a asymptotically stable node; if $\beta < \rho K$, then $U_2$ is an unstable saddle point.
• If $\gamma < \alpha c$ and $\mu < \beta$, then $U_3$ is a asymptotically stable node; if $\gamma > \alpha c$ and $\mu > \beta$, then $U_3$ is unstable; if $(\gamma - \alpha c)(\mu - \beta) < 0$, then $U_3$ is an unstable saddle point.

At the equilibrium $U_4$, the Jacobian matrix is

$$J \equiv J(U_4) = \begin{pmatrix} -\alpha u^* \\ 0 \end{pmatrix}.$$ (6)

Since $\gamma(1 - \frac{2\mu}{K}) - \alpha p = [\gamma(1 - \frac{1}{K}) - \alpha p] - \frac{\gamma u}{\mu} = -\frac{\gamma u}{\mu}$ and $\mu(1 - \frac{\mu}{K}) + \mu p - \beta = 0$ at the equilibrium $U_4$, we find

$$a_{11} < 0, \quad a_{12} < 0, \quad a_{21} > 0, \quad a_{22} = 0.$$ (7)

Now the first principle diagonal minor is $-\frac{\gamma u}{\mu} < 0$, the second principle diagonal minor is

$$\text{Det} \begin{pmatrix} -\frac{\gamma u}{\mu} \\ 0 \end{pmatrix} = \alpha u^* (\rho - \frac{\mu}{K}).$$

The second principle diagonal minor would be positive if and only if $\rho K > \mu$. Hence both the eigenvalues of the Jacobian matrix have negative real part. Now we can demand that the system is stable if $\rho K > \mu$, and unstable if $\rho K < \mu$.
To sum up, we have

$$\gamma d_{22} \frac{ak}{\alpha k} < d_{21} < \sqrt{4d_{11}d_{22} (\frac{\rho - \mu}{\alpha k} v_\ast) + \gamma d_{22}}$$

By the necessary conditions for instability above, let $(k^-)^2$ and $(k^+)^2$ be the two roots of $\text{Det}(M_k)$. They can be calculated as

$$(k^\pm)^2 = \frac{d_{22}a_{11} - d_{21}a_{12} \pm \Lambda_1}{2d_{11}d_{22}}, \quad (7)$$

where $\Lambda_1 = \sqrt{(d_{22}a_{11} - d_{21}a_{12})^2 - 4d_{11}d_{22} \text{Det}(J)}$. From (6), we deduce that

$$0 < (k^-)^2 < (k^+)^2.$$  

Thus, in order to get the instability of $(u_\ast, v_\ast)$, we must have $(k^-)^2 < k^2 < (k^+)^2$ for some positive integer $k$, and a necessary condition is $k^+ - k^- > 1$, which results in

$$2[(d_{22}a_{11} - d_{21}a_{12})^2 - 4d_{11}d_{22} \text{Det}(J)]$$

$$\geq 2d_{11}d_{22} \ast (d_{22}a_{11} - d_{21}a_{12} + \sqrt{\Lambda_2})$$

$$= 2d_{11}d_{22} \ast (d_{22}a_{11} - d_{21}a_{12} + 2\sqrt{d_{11}d_{22} \text{Det}(J)},$$

where $\Lambda_2 = (d_{22}a_{11} - d_{21}a_{12})^2 - [(d_{22}a_{11} - d_{21}a_{12})^2 - 4d_{11}d_{22} \text{Det}(J)]$. Let $d_{22} = d_{21} = 1$. Then $2[(a_{11} - d_{21}a_{12})^2 - 4\text{Det}(J)] \geq 2(a_{11} - d_{21}a_{12} + 2\sqrt{\text{Det}(J)},$ and we have

$$(a_{11} - d_{21}a_{12})^2 - 4\text{Det}(J)$$

$$\geq a_{11} - d_{21}a_{12} + 2\sqrt{\text{Det}(J)}$$

$$\Rightarrow (a_{11}^2 - d_{21}a_{12})^2 + (2\sqrt{\text{Det}(J)} - 2\sqrt{\text{Det}(J)}) \geq 0$$

$$\Rightarrow d_{21} \geq \frac{a_{11}^2 - d_{21}a_{12} - 2\sqrt{\text{Det}(J)}}{2\sqrt{\text{Det}(J)}}$$

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where $\Lambda_3 = \frac{a_{11}^2 - d_{21}a_{12} - 2\sqrt{\text{Det}(J)}}{2\sqrt{\text{Det}(J)}}$. This concludes the proof of the theorem.

III. NUMERICAL SIMULATION

In this section, we use numerical simulations methods to illustrate to verify our theoretical findings. To illustrate the results given by Theorem 2.1, we choose parameters $K = 2$, $\gamma = 1$, $\alpha = 1$ and $N = 1$.

We plot the phase portraits of system (1) for different $\beta$ in Fig.1. The equilibrium $e_1$ is unstable saddle point and the equilibrium $e_2$ is a asymptotically stable node when $\beta = 2.5$ (see Fig.1(a)). The equilibrium $e_3$ is a asymptotically stable node and $e_1$, $e_2$ are unstable saddle points when $\beta = 1.5$ (see Fig.1(b)). The equilibrium $e_3$ is a asymptotically stable spiral point and $e_1$, $e_2$ are unstable saddle points when $\beta = 1.5$ (see Fig.1(c)).

In Fig.2, we plot the phase portraits of system (2). The equilibrium point $U_1$ is unstable node when $\mu > \beta$ (see Fig.2(a, c)) or unstable saddle point when $\mu < \beta$ (see Fig.2(b, d)). The equilibrium $U_2$ is a asymptotically stable node when $\beta > 2$ (see Fig.2(a, d)) and unstable saddle point when $\beta < 2$ (see Fig.2(b, c)). Black and green rectangular line represent equilibrium $U_3 = (0, c)$ (where $c$ is an arbitrary positive constant) and asymptotically stable node when $c > 1$, $\beta > \mu$ (see Fig.2(b, d) black rectangular line) and unstable when $c < 1$, $\beta < \mu$ (see Fig.2(a, c) green rectangular line). The equilibrium $U_4$ is unstable when $\beta > 2$ (see Fig.2(a)) and stable when $2 < \beta > \mu$ (see Fig.2(b)), the positive equilibrium $U_4$ does not exist when $2 > \mu > \beta$ and $\beta > \mu > 2$ (see Fig.2(c, d)).

Here, we use parameters as $\gamma = 1$, $K = 2$, $\alpha = 1$, $N = 0.5$, $\rho = 1$, $\beta = 1.5$, $d_{11} = 1$ and $d_{22} = 1$. By Theorem 2.1, we have $d_{22}^\prime = 1.36$. According to Theorem 2.1 there exists an unbounded region $d_{22} > d_{22}^\prime$ in which Turing instability occurs. Taking cross-diffusion coefficient $d_{21} = 1.066$, a value less than the critical diffusion coefficient $d_{21}^\prime$, we observe that $Re(\lambda) < 0$ and $\text{Det}(M_k) > 0$ (red curve in Fig.3) for all $k$. If we take $d_{21} = 1.866$, a value that is greater
Fig. 2. The phase portraits of system (2) with fixed $K = 2, \gamma = 1, \alpha = 1$ and $\rho = 1$. $U_i$ ($i = 1, 2, 4$) represents the constant equilibrium. (a): $\beta = 3, \mu = 4$; (b): $\beta = 1.5, \mu = 1$; (c): $\beta = 1, \mu = 1.5$; (d): $\beta = 4, \mu = 3$.

Fig. 3. Plots of $Det(M(k))$ and $Re(\lambda)$ with fixed reaction parameter values $\gamma = 1, K = 2, \alpha = 1, \mu = 0.5, \rho = 1, \beta = 1.5, d_{11} = 1$ and $d_{22} = 1$.

1, $\mu = 0.5, \beta = 1.5, d_{11} = 1$ and $d_{22} = 1$, and consider the effect of $\rho$ on system (3). According to the Fig 4(b), it is easy to deduce that positive equilibrium exist when $\rho > 1$ and does not exist when $\rho < 1$. The system (3) admits patterns when $d_{21}(\rho) > d_{21}(\rho)$ (see red curve in Fig .4(b)), and stable when $d_{21}(\rho) < d_{21}(\rho)$, where $d_{21}(\rho)$ is given by Theorem 2.1. We consider the effect of $\rho$ on system (3). To be more precise, pattern formation occurs in black solid lines and does not emerge in black dashed lines when $d_{21} = 0.3, 1.366, 2.366$.

Fig. 4. The effects of parameter $\mu$ or $\rho$ on pattern formation for the model (3). (a): The parameter $\mu$ is vary and other parameters: $\gamma = 1, K = 2, \alpha = 1, \rho = 1, \beta = 1.5, d_{11} = 1$ and $d_{22} = 1$. (b): The parameter $\rho$ is vary and other parameters: $\gamma = 1, K = 2, \alpha = 1, \mu = 0.5, \beta = 1.5, d_{11} = 1$ and $d_{22} = 1$.

To investigate the impact of cross-diffusion on Turing
pattern, we fixed $\gamma = 1, K = 2, \alpha = 1, \mu = 0.5, \rho = 1, \beta = 1.5, d_{11} = 1$ and $d_{22} = 1$ in system 3, which means the equilibrium $U_4$ of the corresponding kinetic and diffusion systems is asymptotically stable (see Fig.5(a,b)). We illustrate the change in the pattern form as $d_{21} = 0, 1.066, 1.866$ and 2.366. By Fig.6(a,b), when the cross-diffusion rate $d_{21} = 0, 1.066$, the equilibrium $U_4$ is stable, which is did not occurs Turing instability. When cross-diffusion rate $d_{21} = 1.866$ and $d_{22} = 2.366$, the equilibrium $U_4$ is unstable (Fig.6(c-f)), which occurs Turing pattern state. It is easy to see that small values of the time $t$, the system resides in a stable homogeneously state (Fig.6(c)). As time increases to a value great, the homogeneous state becomes Turing unstable (Fig.6(c-f)). In Fig.6, we observe that the system (3) may generates pattern formation for large diffusivity $d_{21}$.

Fig. 5. Numerical solutions of the system (3) for $d_{21} = 0$ in the region $0 \leq x \leq 10$, and initial data $U_4, \gamma = 1, K = 2, \alpha = 1, \mu = 0.5, \rho = 1, \beta = 1, d_{11} = 1$ and $d_{22} = 1$.

**Fig. 6.** One dimensional numerical solutions of the system (1.3) for different $d_{21}$ in the region $0 \leq x \leq 10$, and initial data $U_4$, the green curve for $u$ and the red curve is $v$. The parameter $d_{21}$ is vary and other parameter: $\gamma = 1, K = 2, \alpha = 1, \mu = 0.5, \rho = 1, \beta = 1.5, d_{11} = 1$ and $d_{22} = 1$. (a): $d_{21} = 0$; (b): $d_{21} = 1.066$; (c,d,e): $d_{21} = 1.866$; (f): $d_{21} = 2.866$.

**REFERENCES**


