Research Article

Pattern Formation in a Cross-Diffusive Ratio-Dependent Predator-Prey Model

Xinze Lian, Yanhong Yue, and Hailing Wang

1 Chengdu Institute of Computer Application, Chinese Academy of Sciences, Chengdu 610041, China
2 School of Foreign Language, Wenzhou University, Wenzhou 325000, China
3 College of Mathematics and Physics, Chongqing University of Posts and Telecommunications, Chongqing 400065, China

Correspondence should be addressed to Xinze Lian, xinzelian@163.com

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Abstract

This paper presents a theoretical analysis of evolutionary process that involves organisms distribution and their interaction of spatial distribution of the species with self- and cross-diffusion in a Holling-III ratio-dependent predator-prey model. The diffusion instability of the positive equilibrium of the model with Neumann boundary conditions is discussed. Furthermore, we present novel numerical evidence of time evolution of patterns controlled by self- and cross-diffusion in the model and find that the model dynamics exhibits a cross-diffusion controlled formation growth to spots, stripes, and spiral wave pattern replication, which show that reaction-diffusion model is useful to reveal the spatial predation dynamics in the real world.

1. Introduction

Pattern formation is a topic in mathematical biology that studies how structures and patterns in nature evolve over time [1–12]. One of the mainstream topics in pattern formation involves the reaction-diffusion mechanisms of two chemicals, originally proposed by Turing [13] in 1952. In 1972, Segel and Jackson [14] called attention to the Turing’s ideas that would be also applicable in population dynamics. At the same time, Gierer and Meinhardt [15] gave a biologically justified formulation of a Turing model and studied its properties by numerical simulations. Levin and Segel [11] suggested that the scenario of spatial pattern formation is a possible origin of planktonic patchiness. A significant amount of work has been done using this idea in the field of mathematical biology by Cantrell and Cosner [2], Hoyle [5], Murray [8], Okubo and Levin [16], and others [17–19].

In recent years, many scientists have paid considerable attention to diffusive ratio-dependent predator-prey models, especially those with Holling III functional response
In [23], the author studied the spatial pattern formation of the following ratio-dependent predator-prey model:

\[
\begin{align*}
\frac{\partial u}{\partial t} &= ru\left(1 - \frac{u}{K}\right) - \frac{au^2v}{u^2 + m^2v^2} + D_{11} \nabla^2 u, \\
\frac{\partial v}{\partial t} &= bvu^2 - \frac{mv^2}{u^2 + m^2v^2} - dv + D_{22} \nabla^2 v,
\end{align*}
\]

where \(u\) and \(v\) are prey and predator density, respectively. \(r\) represents the intrinsic growth rate of the prey, \(K\) is the carrying capacity of the prey in the absence of predator, \(a\) is the maximum consumption, \(b\) is the conversion efficiency of food into offspring, \(m\) is the predator interference parameter, and \(d\) is the per capita predator death rate. \(\nabla^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}\) is the usual Laplacian operator in two-dimensional space. \(D_{11}\) and \(D_{22}\) are the self-diffusion coefficients that imply the movement of individuals from a higher to lower concentration region. In addition, the author showed that spots and stripes-spots patterns could be observed in pure Turing instability, and spiral pattern emerged in Hopf and Turing instability [23].

On the other hand, the predator-prey system models such a phenomenon: pursuit-evasion-predators pursuing prey and prey escaping the predators [18, 19, 24, 25]. In other words, in nature, there is a tendency that the preys would keep away from predators and the escape velocity of the preys may be taken as proportional to the dispersive velocity of the predators. In the same manner, there is a tendency that the predators would get closer to the preys, and the chase velocity of predators may be considered to be proportional to the dispersive velocity of the preys. Keeping these in view, cross-diffusion arises, which was proposed first by Kerner [26] and first applied in competitive population system by Shigesada et al. [27].

There has been a considerable interest in investigating the stability behavior of a predator-prey system by taking into account the effect of self- and cross-diffusion [17, 18, 28–35]. Cross-diffusion expresses the population fluxes of one species due to the presence of the other species. However, in the studies on spatiotemporal dynamics of the ratio-dependent predator-prey system with functional response, little attention has been paid to study on the effect of cross-diffusion.

In this paper, we mainly focus on the spatiotemporal dynamics of a cross-diffusion ratio-dependent predator-prey model with Holling III functional response. In the next section, we establish the cross-diffusion model and derive the sufficient conditions for Turing instability. Then, we present and discuss the results of pattern formation via numerical simulation in Section 3. Finally, some conclusions are drawn.

2. The Model and Analysis

2.1. The Model

We firstly pay attention to the spatially extended ratio-dependent predator-prey model with self- and cross-diffusion, which is as follows:

\[
\begin{align*}
\frac{\partial u}{\partial t} &= ru\left(1 - \frac{u}{K}\right) - \frac{au^2v}{u^2 + m^2v^2} + D_{11} \nabla^2 u + D_{12} \nabla^2 v, \\
\frac{\partial v}{\partial t} &= \frac{bvu^2}{u^2 + m^2v^2} - \frac{mv^2}{u^2 + m^2v^2} - dv + D_{21} \nabla^2 u + D_{22} \nabla^2 v,
\end{align*}
\]
where $D_{12}$ and $D_{21}$ are cross-diffusion coefficients that express population fluxes of the preys and predators resulting from the presence of the other species, respectively.

We consider the model on a square domain $\Omega$. We also add to the reaction-diffusion equation model positive initial conditions:

$$u(x, y, 0) > 0, \quad v(x, y, 0) > 0 \quad (x, y) \in \Omega = (0, L) \times (0, L).$$

(2.2)

It is natural to assume that nothing enters this model and nothing exits this model. Thus, we will take zero-flux boundary conditions for the flat domain:

$$\frac{\partial u}{\partial v} \bigg|_{\partial \Omega} = 0.$$

(2.3)

In the above, $L$ denotes the size of the system in square domain, and $v$ is the outward unit normal vector of the boundary $\partial \Omega$.

For simplicity, we nondimensionalize model (2.1) with the following scaling:

$$u \rightarrow \frac{u}{K}, \quad v \rightarrow \frac{mv}{K}, \quad t \rightarrow rt.$$

(2.4)

Then model (2.1) can be rewritten as

$$\frac{\partial u}{\partial t} = u(1 - u) - \frac{\alpha u^2 v}{u^2 + v^2} + d_{11} \nabla^2 u + d_{12} \nabla^2 v,$$

$$\frac{\partial v}{\partial t} = \frac{\beta u^2 v}{u^2 + v^2} - \gamma v + d_{21} \nabla^2 u + d_{22} \nabla^2 v,$$

(2.5)

where $\alpha = a/rm$, $\beta = b/r$, $\gamma = d/r$, $d_{11} = D_{11}/r$, $d_{12} = D_{12}/rm$, $d_{21} = D_{21}m/r$, $d_{22} = D_{22}/r$. In addition, we call

$$D = \begin{pmatrix} d_{11} & d_{12} \\ d_{21} & d_{22} \end{pmatrix}$$

(2.6)

the diffusive matrix.

### 2.2. Summary of the Noncross Diffusion Model

We first consider the case of spatially homogeneous solutions. In this case spatial model (2.5) is equivalent to the ordinary differential equation model

$$\frac{du}{dt} = u(1 - u) - \frac{\alpha u^2 v}{u^2 + v^2} \triangleq f(u, v),$$

$$\frac{dv}{dt} = \frac{\beta u^2 v}{u^2 + v^2} - \gamma v \triangleq g(u, v).$$

(2.7)
It can be seen that model (2.7) has two nonnegative real equilibria as follows.

(i) The equilibrium point \( E = (1,0) \) corresponding to extinction of the predator is a saddle point.

(ii) The equilibrium point \( E^* = (u^*, v^*) \) which is corresponding to a nontrivial stationary state coexistence of prey and predator, where

\[
\begin{align*}
  u^* &= \frac{\beta - \sqrt{\alpha^2 \beta \gamma - \alpha^2 \gamma^2}}{\beta}, \\
  v^* &= \frac{\sqrt{\alpha^2 \beta \gamma - \alpha^2 \gamma^2 N^*}}{\alpha \gamma}.
\end{align*}
\]  

(2.8)

It is easy to see that \( u^* > 0 \) and \( v^* > 0 \) when \( \beta - \gamma > 0 \) and \( \beta - \sqrt{\alpha^2 \beta \gamma - \alpha^2 \gamma^2} > 0 \) hold.

Besides, Turing instability at the coexistence equilibrium \( E^* \) of the model (2.5) has been analysis without cross-diffusion. Here, we only give a summary [23]. The characteristic equation at the steady state \( E^* \) of model (2.5) without cross-diffusion is

\[
|J_k - \lambda I| = 0,
\]

(2.9)

where, \( J_k = J - \text{diag}(d_1, d_2)k^2 \), and \( J \) is given by

\[
J = \begin{pmatrix}
\frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\
\frac{\partial g}{\partial u} & \frac{\partial g}{\partial v}
\end{pmatrix}
\]

\[
\triangleq \begin{pmatrix}
f_u & f_v \\
g_u & g_v
\end{pmatrix}
\]

\[
E^* \approx \begin{pmatrix}
-\frac{\beta^2 + 2 \sqrt{-\alpha^2 \gamma^2 (\gamma - \beta)}}{\beta^2} & -\frac{\alpha \gamma (2 \gamma - \beta)}{\beta^2} \\
2 \sqrt{-\alpha^2 \gamma (\gamma - \beta)} & 2 \frac{\gamma (\gamma - \beta)}{\beta}
\end{pmatrix},
\]

(2.10)

and the trace and determinant of matrix \( J \) is as follows:

\[
\text{tr}(J) = f_u + f_v,
\]

(2.11)

\[
\text{det}(J) = f_u g_v - f_v g_u.
\]

Now (2.9) can be solved, yielding the so-called characteristic polynomial of the original model (2.5) without cross-diffusion:

\[
\lambda^2 - \text{tr}(J_k) \lambda + \text{det}(J_k) = 0,
\]

(2.12)

where

\[
\text{tr}(J_k) = \text{tr}(J) - (d_1 + d_2)k^2,
\]

(2.13)

\[
\text{det}(J_k) = d_1 d_2 k^4 - (d_2 f_u + d_1 g_v) k^2 + \text{det}(J).
\]
The roots of (2.12) yield the dispersion relation:

\[ \lambda_{1,2}(J_k) = \frac{1}{2} \left( \text{tr}(J_k) \pm \sqrt{\text{tr}(J_k)^2 - 4 \det(J_k)} \right). \] (2.14)

And an equilibrium is Turing instability means that it is an asymptotically stable equilibrium of nonspatial model (e.g., model (2.7)) but is unstable with respect to solutions of spatial model (e.g., model (2.5)). One can know that the stability of nonspatial model is guaranteed if the following conditions hold

\[ \text{tr}(J) = f_u + g_v < 0, \] (2.15)
\[ \det(J) = f_u g_v - f_v g_u > 0. \] (2.16)

Then, the Turing instability sets in when at least one of (2.15) or (2.16) the following conditions is violated. However, it is evident that the first condition \( \text{tr}(J_k) < 0 \) is not violated when the condition \( f_u + g_v < 0 \) is met. Hence, only the violation of condition \( \det(J_k) > 0 \) gives rise to diffusion-driven instability. Thus, the condition for Turing instability is given by

\[ \det(J_k) = d_1 d_2 k^4 - f_u d_2 k^2 - d_1 g_v k^2 + f_u g_v - f_v g_u < 0. \] (2.17)

In summary, a general linear analysis shows that the necessary conditions for yielding Turing patterns are given by

\[ f_u + g_v < 0, \] (2.18)
\[ f_u g_v - f_v g_u > 0, \]
\[ d_2 f_u + d_1 g_v > 0, \]
\[ (d_2 f_u + d_1 g_v)^2 > 4d_1 d_2 (f_u g_v - f_v g_u). \] (2.19)

In fact, condition (2.18) ensured, by the definition that the equilibrium \( (u^* , v^*) \) is stable for model (2.5) without diffusion model (2.7). \( (u^* , v^*) \) becomes unstable for model (2.5) with diffusion if \( \text{Re}(\lambda_{1,2}(J_k)) \) bifurcate from negative value to positive one. From (2.17), simple algebraic computations lead to (2.19).

### 2.3. Dynamic Analysis of the Spatial Model

To study the effect of cross-diffusion on the model system, set \( u = u^* + \tilde{u}, \ v = v^* + \tilde{v}(|\tilde{u}|, |\tilde{v}| \ll 1) \), we consider the linearized \( (\tilde{u}, \tilde{v}) \) form of system as follows:

\[ \frac{\partial \tilde{u}}{\partial t} = f_u \tilde{u} + f_v \tilde{v} + d_{11} \nabla^2 \tilde{u} + d_{12} \nabla^2 \tilde{v}, \]
\[ \frac{\partial \tilde{v}}{\partial t} = g_u \tilde{u} + g_v \tilde{v} + d_{21} \nabla^2 \tilde{u} + d_{22} \nabla^2 \tilde{v}. \] (2.20)
Following [18], the characteristic equation of the linearized system is given by

$$\lambda^2 - \text{tr}(\tilde{J}_k)\lambda + \det(\tilde{J}_k) = 0,$$

(2.21)

where $\tilde{J}_k = J - Dk^2$, and

$$\text{tr}(\tilde{J}_k) = \text{tr}(J) - k^2 \text{tr}(D),$$

$$\det(\tilde{J}_k) = \det(D)k^4 - (d_{11}g_v - d_{12}g_u - d_{21}f_v + d_{22}f_u)k^2 + \det(J).$$

(2.22)

The Turing instability sets in when at least one of the following conditions is violated:

$$\text{tr}(\tilde{J}_k) < 0, \quad \det(\tilde{J}_k) > 0.$$  

(2.23)

The first condition $\text{tr}(\tilde{J}_k) = \text{tr}(J_k)$, which is evident that $\text{tr}(J_k)$ is not violated when the condition $\text{tr}(J) = f_u + g_v < 0$ is met. Hence, only the violation of condition $\det(\tilde{J}_k) > 0$ gives rise to diffusion-driven instability. Thus, the condition for diffusion-driven instability occurs when

$$\det(\tilde{J}_k) = \det(D)k^4 - (d_{11}g_v - d_{12}g_u - d_{21}f_v + d_{22}f_u)k^2 + \det(J) < 0.$$  

(2.24)

Based on the above discussions, we can get the following theorem.

**Theorem 2.1.** If the following conditions are true:

$$f_u + g_v < 0,$$

$$d_{11}g_v + d_{22}f_u < 0,$$

$$d_{11}g_v - d_{12}g_u - d_{21}f_v + d_{22}f_u > 0,$$

$$\left(d_{11}g_v - d_{12}g_u - d_{21}f_v + d_{22}f_u\right)^2 > 4(d_{11}d_{12} - d_{21}d_{12})(f_u g_v - f_v g_u),$$

(2.25)

then the positive equilibrium $E^*$ of model (2.5) is cross-diffusion-driven instability (i.e., Turing instability).

**Proof.** In view of $f_u + g_v < 0$ and $d_{11}g_v + d_{22}f_u < 0$, it follows that

$$\text{tr}(\tilde{J}_k) < 0, \quad \det(\tilde{J}_k) > 0$$  

(2.26)

when $d_{12} = 0$ and $d_{21} = 0$. This implies the positive equilibrium $E^*$ is asymptotic stable in the absent of cross-diffusion.
In this section, we perform extensive numerical simulations of the spatially extended model (2.5) in 2-dimensional (2D) spaces, and the qualitative results are shown here. Our numerical simulations employ the nonzero initial step and the grid width used in the simulations are \( \tau = 0.01 \) and \( \Delta h = 0.25 \), respectively. The parameters are fixed as

\[
\alpha = 2.5, \quad \beta = 1.1, \quad \gamma = 1.05, \quad d_{11} = 0.2, \quad d_{22} = 0.2.
\]  

Initially, the entire system is placed in the steady state \( (u^*, v^*) \), and the propagation velocity of the initial perturbation is thus on the order of \( 5 \times 10^{-4} \) space units per time unit. And the system is then integrated for 1000000 time steps, and the last images are saved. After the initial period during which the perturbation spreads, either the system goes into a time-dependent state, or to an essentially steady state (time independent).
Figure 1: The dispersal relation of $r$ with $\alpha$. Parameters: $\beta = 1.3$, $d_{11} = 0.2$, $d_{12} = 0.05$, $d_{21} = 0.35$, $d_{22} = 0.2$. The green, red, and blue curves represent Hopf, self-diffusion Turing, and self-cross-diffusion Turing bifurcation curve, respectively. They separate the parametric space into five domains, and domain (IV) is called Turing space.

With parameters (3.1), the positive equilibrium of model (2.5) is $(u^*, v^*) = (0.4793, 0.1046)$. Let $d_{12} = d_{21} = 0$, that is, we first consider Turing instability in the case of self-diffusion model. It is easy to conclude that $\text{tr}(J) < 0$, $\text{det}(J) > 0$, and for all $k$, $\text{tr}(J_k) < 0$ and $\text{det}(J_k) > 0$. Hence, in this case, there is nonexistence of Turing instability in the self-diffusion model (2.5).

Next, we consider the effect of the cross-diffusion in model (2.5), let $d_{21} = 0.05$, $d_{12} \in (0.2, 0.8)$, and other parameters are fixed as (3.1). It is easy to know that $\text{tr}(J_k) < 0$ for all $k$, and $\text{det}(J_k) < 0$ for some $k$. That is to say, in this case, Turing instability can occur. And in Figure 2, we show five typical Turing pattern of prey $u$ in model (2.5) with parameters set (3.1) and $d_{12}$ change from 0.4 to 0.76. From Figure 2, one can see that values for the concentration $u$ are represented in a color scale varying from blue to red. And on increasing the control cross-coefficient $d_{12}$, the sequences "spots patterns (Figure 2(a)) $\rightarrow$ spot-strips coexist patterns (Figure 2(b)) $\rightarrow$ strip patterns (c.f., Figure 2(c)) $\rightarrow$ hole-strips coexist patterns (Figure 2(d)) $\rightarrow$ holes patterns (Figure 2(e))" can be observed.

For the sake of learning the pattern formation in model (2.5) further, in the following, we select a special perturbed initial condition for investigating the evolutionary process of the infected spatial pattern, the initial condition is introduced as

\[
\begin{aligned}
  u(x, y, 0) &= u^*, \\
  v(x, y, 0) &= \begin{cases} 
  0.2, & \text{if } (x - 100)^2 + (y - 200)^2 < 200, \\
  0, & \text{otherwise},
\end{cases}
\end{aligned}
\]

(3.2)
The initial condition is given by

\[ u(x, y, 0) = u^* - \varepsilon_1 (x - 80)(x - 320), \]
\[ v(x, y, 0) = v^* - \varepsilon_2 (y - 100) - \varepsilon_2 (y - 300), \]

where \( \varepsilon_1 = 3 \times 10^{-7} \) and \( \varepsilon_2 = 1 \times 10^{-4} \).

The initial conditions are deliberately chosen to be unsymmetrical in order to make any influence of the corners of the domain more visible. Snapshots of the spatial distribution

which is a circle in \((x, y)\) plane. The parameters are taken the same as Figure 2(a). Then, we can observe that after the decay of target patterns, the spots pattern prevails over the whole domain finally (c.f. Figure 3(d)).

Besides Turing patterns (c.f., Figures 2 and 3), there exhibits spiral wave pattern self-replication in model (2.5). As an example, in Figure 4, we show spiral patterns with \( \alpha = 2.5, \beta = 1.3, \gamma = 1.1, d_{11} = 0.7, d_{12} = 0.05, d_{21} = 0.01, d_{22} = 1. \) In this case, the equilibrium is \((u^*, v^*) = (0.0980, 0.0418)\). In order to make the image more clearly, the system size is \(400 \times 400\) and the grid width \(\Delta h\) is 0.5. One can see the random initial distribution leads to the formation of macroscopic spiral patterns (c.f., Figure 4(a)). In other words, in this case, small random fluctuations will be strongly amplified by diffusion, leading to nonuniform population distributions. For the sake of learning the dynamics of this case further, we show time-series plots (c.f., Figure 4(b)). From Figure 4(b), one can see that the system gives rise to periodic oscillations in time, which is the reason why the spiral pattern emerges.

Thanks to the insightful works of Medvinsky et al. [36] and Upadhyay et al. [37], we have studied the spiral wave pattern for an initial condition discussed in the following equations. In this case, we employ \(\Delta h = 0.5\), and the system size is \(400 \times 400\). The parameters set are same as Figure 4. The initial condition is given by

\[ u(x, y, 0) = u^* - \varepsilon_1 (x - 80)(x - 320), \]
\[ v(x, y, 0) = v^* - \varepsilon_2 (y - 100) - \varepsilon_2 (y - 300), \]

where \( \varepsilon_1 = 3 \times 10^{-7} \) and \( \varepsilon_2 = 1 \times 10^{-4} \).
Figure 3: The process of spiral patterns of $u$ for parameters: $\alpha = 2.2, \beta = 1.1, \gamma = 1.05, d_{11} = 0.2, d_{12} = 0.05, d_{21} = 0.4, d_{22} = 0.2$. Time: (a) $t = 50$, (b) $t = 500$, (c) $t = 1000$, (d) $t = 2000$.

Figure 4: Dynamical behaviors of model (2.5) with the parameters: $\alpha = 2.5, \beta = 1.3, \gamma = 1.1, d_{11} = 0.7, d_{12} = 0.05, d_{21} = 0.01, d_{22} = 1$ at $t = 2000$. (a) Spiral pattern. (b) Time-series plots.

arising from (3.3) are shown in Figure 5 for $t = 0, 100, 250, 500$. Figure 5(a) shows that for the model (2.5) with initial conditions (3.3), the formation of the irregular patchy structure can be preceded by the evolution of a regular spiral spatial pattern. Note that the appearance of the spirals is not induced by the initial conditions. The center of each spiral is situated in a
critical point \((x_{cr}, y_{cr})\) are \((80, 200)\) and \((320, 200)\), where \(u(x_{cr}, y_{cr}) = u^*, \ v(x_{cr}, y_{cr}) = v^*\). The distribution (3.3) contains one point. After the spirals form (Figure 5(b)), they grow slightly for a certain time, their spatial structure becoming more distinct (Figures 5(c) and 5(d)).

4. Conclusions and Discussions

In this paper, we analyzed pattern formation of a cross-diffusion ratio-dependent predator-prey model within two-dimensional space and give the conditions of cross-diffusion-driven driven Turing instability. Then, we use numerical simulations to verify the correctness of the theoretical results and find that the model exhibits complex self-replication.

The results show that model (2.5) has rich spatiotemporal patterns (spots, stripes, holes, and spiral patterns); moreover, the existence of those patterns indicates that the cross-diffusion can induce more complex pattern formation than in the case of self-diffusion.

Compared to the paper of Lin [23], we present the condition of cross-diffusion Turing pattern, while in the case of self-diffusion the solution of the model is stable. We also show that the increasing speed of diffusion \(d_{12}\) will decrease the density of the prey. Similar, increasing speed of diffusion \(d_{21}\) will decrease density of the predator.

Therefore, we hope that the results presented here will be useful in studying the dynamic complexity of ecosystems or physical systems.
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