

## Research Article

# Cross-Diffusion-Driven Instability in a Reaction-Diffusion Harrison Predator-Prey Model

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We present a theoretical analysis of processes of pattern formation that involves organisms distribution and their interaction of spatially distributed population with cross-diffusion in a Harrison-type predator-prey model. We analyze the global behaviour of the model by establishing a Lyapunov function. We carry out the analytical study in detail and find out the certain conditions for Turing's instability induced by cross-diffusion. And the numerical results reveal that, on increasing the value of the half capturing saturation constant, the sequences "spots  $\rightarrow$  spot-stripe mixtures  $\rightarrow$  stripes  $\rightarrow$  hole-stripe mixtures  $\rightarrow$  holes" are observed. The results show that the model dynamics exhibits complex pattern replication controlled by the cross-diffusion.

## 1. Introduction

Understanding of spatial and temporal behaviors of interacting species in ecological systems is one of the central scientific problems in population ecology [1–15], since the pioneering work of Turing [16]. Throughout the history of theoretical ecology, reaction-diffusion equations have been intensively used to describe spatiotemporal dynamics [15, 17].

In recent years, the effect of cross-diffusion in reaction-diffusion systems has received much attention by both ecologists and mathematicians, for example, see [18–25] and the references therein. Kerner [18] was the first to examine that cross-diffusion can induce pattern forming instability in an ecological situation. Cross-diffusion expresses the population fluxes of one species due to the presence of the other species. And Gurtin [19] developed some mathematical models for population dynamics with the inclusion of cross-diffusion as well as self-diffusion and showed that the effect of cross-diffusion may give rise to the segregation of two species.

In this paper, we are attempting to study the effect of cross-diffusion in a predator-prey model with Harrison-type functional response [26]. The model can be written as

$$\begin{aligned} \frac{\partial u}{\partial t} = & ru \left( 1 - \frac{u}{K} \right) - \frac{c_1 uv}{m_1 v + 1} \\ & + D_{11} \Delta u + D_{12} \Delta v, \quad x = (\xi, \eta) \in \Omega, \quad t > 0, \end{aligned}$$

$$\begin{aligned} \frac{\partial v}{\partial t} = & v \left( -h_1 + \frac{b_1 u}{m_1 v + 1} \right) \\ & + D_{21} \Delta u + D_{22} \Delta v, \quad x = (\xi, \eta) \in \Omega, \quad t > 0, \\ u(x, 0) = & u_0(x), \quad v(x, 0) = v_0(x), \\ & x = (\xi, \eta) \in \Omega, \end{aligned} \quad (1)$$

where  $u$  and  $v$  represent population density of prey and predator at time  $t$ , respectively.  $r$  is the intrinsic growth rate of prey,  $K$  is the prey carrying capacity,  $c_1$  is the capture rate,  $m_1$  the half capturing saturation constant,  $h_1$  is the death rate of predator, and  $b_1$  is conversion rate.  $D_{11}$  and  $D_{22}$  are the self-diffusion coefficients of  $u$  and  $v$ , respectively,  $D_{12}$  and  $D_{21}$  are the cross-diffusion coefficients of  $u$  and  $v$ , respectively. We always assume that  $D_{11} > 0$ ,  $D_{22} > 0$  and  $D_{11}D_{22} - D_{12}D_{21} > 0$ . The value of the cross-diffusion coefficient may be positive, negative, or zero. Positive cross-diffusion coefficient denotes, that one species tends to move in the direction of lower concentration of another species, while negative cross-diffusion expresses the population fluxes of one species in the direction of higher concentration of the other species [27].  $\Delta = \partial^2/\partial x^2 = \partial^2/\partial \xi^2 + \partial^2/\partial \eta^2$  is the usual Laplacian operator in 2-dimensional space.  $\Omega \subset \mathbb{R}^2$  is a

bounded domain with smooth boundary  $\partial\Omega$ . The initial data  $u_0(x)$  and  $v_0(x)$  are continuous functions on  $\overline{\Omega}$ .

We make a change of variables:

$$(u, v, t) = \left( K\tilde{u}, K\tilde{v}, \frac{\tilde{t}}{r} \right). \quad (2)$$

For the sake of convenience, we still use variables  $u, v$  instead of  $\tilde{u}, \tilde{v}$ . Thus, considering zero-flux boundary conditions, model (1) is converted into

$$\begin{aligned} \frac{\partial u}{\partial t} &= u(1-u) - \frac{cuv}{mv+1} \\ &\quad + d_{11}\Delta u + d_{12}\Delta v, \quad x = (\xi, \eta) \in \Omega, \quad t > 0, \\ \frac{\partial v}{\partial t} &= v \left( -h + \frac{bu}{mv+1} \right) \\ &\quad + d_{21}\Delta u + d_{22}\Delta v, \quad x = (\xi, \eta) \in \Omega, \quad t > 0, \end{aligned} \quad (3)$$

$$\frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, \quad x = (\xi, \eta) \in \partial\Omega, \quad t > 0,$$

$$u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, \\ x = (\xi, \eta) \in \Omega,$$

where the new parameters are

$$\begin{aligned} c &= \frac{Kc_1}{r}, \quad m = Km_1, \quad h = \frac{h_1}{r}, \quad b = \frac{b_1K}{r}, \\ d_{11} &= \frac{D_{11}}{r}, \quad d_{12} = \frac{D_{12}}{r}, \quad d_{21} = \frac{D_{21}}{r}, \quad d_{22} = \frac{D_{22}}{r}. \end{aligned} \quad (4)$$

$D = \begin{pmatrix} d_{11} & d_{12} \\ d_{21} & d_{22} \end{pmatrix}$  is the diffusion matrix,  $d_{11} > 0$ ,  $d_{22} > 0$ , and  $\det(D) = d_{11}d_{22} - d_{12}d_{21} > 0$ .  $\nu$  is the outward unit normal vector on  $\partial\Omega$  and the zero-flux boundary conditions mean that model (3) is self-contained and has no population flux across the boundary  $\partial\Omega$  [28, 29].

In particular, when  $d_{12} = d_{21} = 0$ , that is, the cross-diffusion coefficients are equal 0, we can obtain the following model:

$$\begin{aligned} \frac{\partial u}{\partial t} &= u(1-u) - \frac{cuv}{mv+1} \\ &\quad + d_{11}\Delta u, \quad x = (\xi, \eta) \in \Omega, \quad t > 0, \\ \frac{\partial v}{\partial t} &= v \left( -h + \frac{bu}{mv+1} \right) \\ &\quad + d_{22}\Delta v, \quad x = (\xi, \eta) \in \Omega, \quad t > 0, \\ \frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu} = 0, \quad x = (\xi, \eta) \in \partial\Omega, \quad t > 0, \\ u(x, 0) &= u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, \\ x &= (\xi, \eta) \in \Omega. \end{aligned} \quad (5)$$

We call model (5) as self-diffusion model, while we call model (3) cross-diffusion model.

The corresponding kinetic equation to models (3) and (5) is:

$$\begin{aligned} \dot{u} &= u(1-u) - \frac{cuv}{mv+1} \triangleq f(u, v), \\ \dot{v} &= v \left( -h + \frac{bu}{mv+1} \right) \triangleq g(u, v). \end{aligned} \quad (6)$$

In recent years, there has been considerable interest to investigate the stability behavior of a predator-prey system by taking into account the effect of self- as well as cross-diffusion [3, 6, 8–10, 12–15]. But in the studies on the spatiotemporal dynamics of predator-prey system with functional response, little attention has been paid to study on the effect of cross-diffusion.

Mathematically speaking, an equilibrium in Turing's instability (diffusion-driven instability) means that it is an asymptotically stable equilibrium  $E^*$  of model (6) but is unstable with respect to the solutions of reaction-diffusion model (3) or (5). Especially, if  $E^*$  is also stable with respect to the solutions of the self-diffusion model (3), that is,  $d_{12} = d_{21} = 0$  in the cross-diffusion model (5), then there is nonexistence of Turing's instability in this situation.

And there comes a question: if there is nonexistence of Turing's instability in the case of self-diffusion (i.e.,  $d_{12} = d_{21} = 0$ ), does model (5) exhibit Turing's instability induced by cross-diffusion?

The main purpose of this paper is to focus on the effect of cross-diffusion on the spatiotemporal dynamics of the reaction-diffusion predation model. The paper is organized as follows. In Section 2, we give some properties of the solutions of the model. In Section 3, we give the linearized stability analysis to show (i.e., no cross-diffusion), deduce the conditions of Turing's instability induced by cross-diffusion, and illustrate the different Turing patterns by using the numerical simulations. Finally, in Section 4, some conclusions and discussions are given.

## 2. Dynamics Analysis

In this section, we present some preliminary results, including dissipativeness, boundedness, permanence of the solutions, and the equilibria stability analysis of the models.

### 2.1. Dissipativeness

**Theorem 1.** For any solution  $(u, v)$  of model (6),

$$\limsup_{t \rightarrow \infty} u(t) \leq 1, \quad \limsup_{t \rightarrow \infty} v(t) \leq \max \left\{ 0, \frac{b-h}{hm} \right\}. \quad (7)$$

Hence, model (6) is dissipative.

*Proof.* From the first equation of model (6), it can be easily shown that

$$\limsup_{t \rightarrow \infty} u(t) \leq 1. \quad (8)$$

If  $b > h$ , from the second equation of model (6), one has:

$$\dot{v} \leq v(b - h - hmv). \quad (9)$$

A standard comparison argument shows that

$$\limsup_{t \rightarrow \infty} v(t) \leq \frac{b-h}{hm} \triangleq \alpha. \quad (10)$$

If  $b \leq h$ , we have the following differential inequality:

$$\dot{v} \leq \frac{-hmv^2}{mv+1}, \quad (11)$$

and the same argument above yields

$$\limsup_{t \rightarrow \infty} v(t) \leq 0. \quad (12)$$

In either case, the second inequality of (7) holds.  $\square$

## 2.2. Boundedness

**Theorem 2.** All the solutions of model (6) which initiate in  $\mathbb{R}_2^+$  are uniformly bounded within the region  $\Gamma$ , where

$$\Gamma = \left\{ (u, v) : 0 \leq u + \frac{c}{b}v \leq 1 + \frac{1}{4h} \right\}. \quad (13)$$

*Proof.* Let us define the function:

$$w(t) = u(t) + \frac{c}{b}v(t). \quad (14)$$

Calculating the time derivative of  $w(t)$  along the trajectories of model (6), we get

$$\dot{w}(t) = \dot{u} + \dot{v} = u(1-u) - \frac{ch}{b}v. \quad (15)$$

Then,

$$\dot{w}(t) + hw(t) = u(1-u) + hu < \frac{1}{4} + h. \quad (16)$$

Using the theory of differential inequality, for all  $t \geq T \geq 0$ , we have

$$0 \leq w(t) \leq 1 + \frac{1}{4h} - \left(1 + \frac{1}{4h} - w(T)\right)e^{-(t-T)}. \quad (17)$$

Hence, we have

$$\limsup_{t \rightarrow \infty} w(t) \leq 1 + \frac{1}{4h}. \quad (18)$$

Hence, all the solutions of model (6) that initiate in  $\mathbb{R}_2^+$  are confined in the region  $\Gamma$ .  $\square$

## 2.3. Permanence

**Theorem 3.** If  $c < m$  and  $h < (b/2)(1 - c/m)$ , then model (6) has the permanence property.

*Proof.* By the first equation of model (6), we have

$$\begin{aligned} \dot{u} &= u(1-u) - \frac{cu}{mv+1} \\ &= u(1-u) - cu \frac{(1/m)(mv+1) - (1/m)}{mv+1} \\ &\geq u(1 - c/m - u). \end{aligned} \quad (19)$$

Since  $c < m$ , by the famous comparison theorem, we have

$$\liminf_{t \rightarrow \infty} u(t) \geq 1 - \frac{c}{m} > 0. \quad (20)$$

Hence, for large  $t$ ,  $u(t) > (1/2)(1 - c/m) \triangleq \eta$ .

As a result, for large  $t$ ,  $v$  satisfies

$$\dot{v} \geq v \left( -h + \frac{b\eta}{mv+1} \right) = \frac{v(b\eta - h - hmv)}{mv+1}. \quad (21)$$

Since  $h < (b/2)(1 - c/m)$ , by the famous comparison theorem, we can get

$$\liminf_{t \rightarrow \infty} v(t) \geq \frac{b(m-c) - 2hm}{2hm^2} \triangleq \beta > 0. \quad (22)$$

The proof is complete.  $\square$

**2.4. Stability Analysis of the Equilibria.** The nonspatial model (6) has three equilibria, which correspond to spatially homogeneous equilibria of model (3) and model (5), in the positive quadrant:

- (i)  $E_0 = (0, 0)$  (total extinct) is a saddle point;
- (ii)  $E_1 = (1, 0)$  (extinct of the predator, or prey only) is a saddle when  $b > h$ , or stable node when  $b < h$ ;
- (iii)  $E_3 = (u^*, v^*)$  (coexistence of prey and predator), where  $u^* = h(mv^* + 1)/b$ , and  $v^*$  satisfies

$$hm^2v^2 - (m(b-h) - hm - bc)v + h - b = 0. \quad (23)$$

It is easy to verify that it has a unique positive equilibrium if  $b > h$ .

The Jacobian matrix for the positive equilibrium  $E_3 = (u^*, v^*)$  is given by

$$J = \begin{pmatrix} -\frac{h(mv^*+1)}{b} & -\frac{ch}{b(mv^*+1)} \\ \frac{bv^*}{mv^*+1} & -\frac{hmv^*}{mv^*+1} \end{pmatrix} \triangleq \begin{pmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{pmatrix}. \quad (24)$$

Obviously,

$$\begin{aligned} \det(J) &= \frac{hv^*(hm^3v^{*2} + 2hm^2v^* + hm + bc)}{b(mv^*+1)^2} > 0, \\ \text{tr}(J) &= -\frac{h(m^2v^{*2} + m(2+b)v^* + 1)}{b(mv^*+1)} < 0. \end{aligned} \quad (25)$$

Therefore, we can obtain the following.

**Theorem 4.** Assume that the positive equilibrium  $E_3 = (u^*, v^*)$  exists, then  $E_3 = (u^*, v^*)$  is locally stable for model (6).

In the following, we shall prove that the positive equilibrium  $E_3 = (u^*, v^*)$  of model (3) is globally asymptotically stable.

**Theorem 5.** Suppose that  $h < b$ ,  $c < m$ , and  $h < (b/2)(1 - c/m)$ . The positive equilibrium  $E_3 = (u^*, v^*)$  of model (3) is globally asymptotically stable, if,

- (a1)  $h(mv^* + 1)/b - c/m + \beta c/(mv^* + 1) > 0$ ;
- (a2)  $h(h(mv^* + 1)/b + \beta c/(mv^* + 1) - 1)(1 - 1/(\beta m + 1)) - h^2/4b^2 - \alpha b^2/4(mv^* + 1)^2 > 0$ ;
- (a3)  $4d_{11}d_{22} > (d_{12} + d_{21})^2$ ,

where  $\alpha = (b - h)/hm > 0$ ,  $\beta = (b(m - c) - 2hm)/2hm^2$ .

*Proof.* We adopt the Lyapunov function:

$$V(t) = \int_{\Omega} [V_1(u(x, t)) + V_2(v(x, t))] dx, \quad (26)$$

where  $V_1(u) = (1/2)(u - u^*)^2$ ,  $V_2(v) = (1/2)(v - v^*)^2$ .

Then,

$$\begin{aligned} \frac{dV}{dt} &= \int_{\Omega} \left( \frac{\partial u}{\partial t} (u - u^*) + \frac{\partial v}{\partial t} (v - v^*) \right) dx \\ &= \int_{\Omega} \left( (u - u^*) \left( u - u^2 - \frac{cu v}{mv + 1} \right) \right. \\ &\quad \left. + (v - v^*) \left( -hv + \frac{bu v}{mv + 1} \right) \right) dx \\ &\quad + \int_{\Omega} ((u - u^*)(d_{11}\Delta u + d_{12}\Delta v) \\ &\quad + (v - v^*)(d_{21}\Delta u + d_{22}\Delta v)) dx \\ &= I_1 + I_2, \end{aligned} \quad (27)$$

where

$$\begin{aligned} I_1 &= \int_{\Omega} (u - u^*) \\ &\quad \times \left( u - u^2 - \frac{cu v}{mv + 1} - u^* + u^{*2} + \frac{cu^* v^*}{mv^* + 1} \right) dx \\ &\quad + \int_{\Omega} (v - v^*) \left( -hv + \frac{bu v}{mv + 1} + hv^* - \frac{bu^* v^*}{mv^* + 1} \right) dx, \end{aligned}$$

$$\begin{aligned} I_2 &= \int_{\Omega} (u - u^*) (d_{11}\Delta u + d_{12}\Delta v - d_{11}\Delta u^* - d_{12}\Delta v^*) dx \\ &\quad + \int_{\Omega} (v - v^*) (d_{21}\Delta u + d_{22}\Delta v - d_{21}\Delta u^* - d_{22}\Delta v^*) dx. \end{aligned} \quad (28)$$

By some computational analysis, we obtain

$$\begin{aligned} I_1 &= - \int_{\Omega} (u - u^*)^2 \left( u + u^* + \frac{cu}{mv^* + 1} - 1 \right) dx \\ &\quad - \int_{\Omega} (v - v^*)^2 \left( h - \frac{h}{(mv + 1)} \right) dx \\ &\quad - \int_{\Omega} (u - u^*) (v - v^*) \frac{u^* - bv(mv + 1)}{(mv^* + 1)(mv + 1)} dx. \end{aligned} \quad (29)$$

Considering the zero-flux boundary conditions, we have

$$\begin{aligned} I_2 &= -d_{11} \int_{\Omega} |\nabla u|^2 dx - d_{12} \int_{\Omega} \nabla u \nabla v dx \\ &\quad + 2d_{11} \int_{\Omega} \nabla u \nabla u^* dx + d_{12} \int_{\Omega} \nabla u \nabla v^* dx \\ &\quad + d_{12} \int_{\Omega} \nabla v \nabla v^* dx - d_{11} \int_{\Omega} |\nabla u^*|^2 dx \\ &\quad - d_{12} \int_{\Omega} \nabla u^* \nabla v^* dx - d_{22} \int_{\Omega} |\nabla v|^2 dx \\ &\quad - d_{21} \int_{\Omega} \nabla u \nabla v dx + d_{21} \int_{\Omega} \nabla v \nabla u^* dx \\ &\quad + 2d_{22} \int_{\Omega} \nabla v \nabla v^* dx + d_{21} \int_{\Omega} \nabla u \nabla v^* dx \\ &\quad - d_{21} \int_{\Omega} \nabla u^* \nabla v^* dx - d_{22} \int_{\Omega} |\nabla v^*|^2 dx \\ &= -d_{11} \int_{\Omega} |\nabla u|^2 dx - (d_{12} + d_{21}) \int_{\Omega} \nabla u \nabla v dx \\ &\quad + 2d_{11} \int_{\Omega} \nabla u \nabla u^* dx - d_{11} \int_{\Omega} |\nabla u^*|^2 dx \\ &\quad + (d_{12} + d_{21}) \int_{\Omega} \nabla u \nabla v^* dx \\ &\quad - (d_{12} + d_{21}) \int_{\Omega} \nabla u^* \nabla v^* dx + d_{12} \int_{\Omega} \nabla v \nabla v^* dx \\ &\quad + 2d_{22} \int_{\Omega} \nabla v \nabla v^* dx - d_{22} \int_{\Omega} |\nabla v|^2 dx \\ &\quad - d_{22} \int_{\Omega} |\nabla v^*|^2 dx + d_{21} \int_{\Omega} \nabla v \nabla u^* dx. \end{aligned} \quad (30)$$

$I_1$  and  $I_2$  in the curly brackets can be expressed in the form  $-XAX^T$  and  $-YBY^T$ , respectively, where

$$X = (u - u^*, v - v^*),$$

$$Y = (\nabla u, \nabla v, \nabla u^*, \nabla v^*),$$

$$A = \begin{pmatrix} u + u^* + \frac{cv}{mv^* + 1} - 1 & \frac{u^* - bv(mv + 1)}{2(mv^* + 1)(mv + 1)} \\ \frac{u^* - bv(mv + 1)}{2(mv^* + 1)(mv + 1)} & h - \frac{h}{mv + 1} \end{pmatrix}$$

$$\triangleq \begin{pmatrix} \varphi_1 & \varphi_2 \\ \varphi_3 & \varphi_4 \end{pmatrix},$$

$$B = \begin{pmatrix} d_{11} & \frac{d_{12} + d_{21}}{2} & -d_{11} & \frac{d_{12} + d_{21}}{2} \\ \frac{d_{12} + d_{21}}{2} & d_{22} & \frac{d_{12} + d_{21}}{2} & -d_{22} \\ -d_{11} & \frac{d_{12} + d_{21}}{2} & d_{11} & \frac{d_{12} + d_{21}}{2} \\ \frac{d_{12} + d_{21}}{2} & -d_{22} & \frac{d_{12} + d_{21}}{2} & d_{22} \end{pmatrix}. \quad (31)$$

$dV/dt$  is negative definite if the symmetric matrices  $A$  and  $B$  are positive. It can be easily shown that the symmetric matrix  $B$  is positive definite if

$$4d_{11}d_{22} > (d_{12} + d_{21})^2. \quad (32)$$

The symmetric matrix  $A$  is positive definite if

$$\varphi_1 > 0, \quad \varphi_4 > 0, \quad \Phi(u, v) = \varphi_1\varphi_4 - \varphi_2\varphi_3 > 0. \quad (33)$$

Since

$$\varphi_1 = u + u^* + \frac{cv}{mv^* + 1} - 1 > \frac{h(mv^* + 1)}{b} - \frac{c}{m} + \frac{\beta c}{mv^* + 1}, \quad (34)$$

due to (a1),  $\varphi_1 > 0$  is true. It is easy to verify that  $\varphi_4 = h - (h/(mv + 1)) > 0$ .

Since

$$\Phi(u, v) = h \left( u + u^* + \frac{cv}{mv^* + 1} - 1 \right) \times \left( 1 - \frac{1}{mv + 1} \right) - \frac{1}{4} \left( \frac{u^* - bv(mv + 1)}{(mv^* + 1)(mv + 1)} \right)^2$$

$$= h \left( u + \frac{h(mv^* + 1)}{b} + \frac{cv}{mv^* + 1} - 1 \right) \times \left( 1 - \frac{1}{mv + 1} \right) - \frac{1}{4} \left( \frac{h}{b(mv + 1)} - \frac{bv}{mv^* + 1} \right)^2, \quad (35)$$

then

$$\frac{\partial \Phi(u, v)}{\partial u} = h \left( 1 - \frac{1}{mv + 1} \right) > 0. \quad (36)$$

Hence,  $\Phi(u, v)$  is strictly increasing in  $\mathbb{R}_+$ , with respect to  $u$ , and

$$\Phi(0, v) = h \left( \frac{h(mv^* + 1)}{b} + \frac{cv}{mv^* + 1} - 1 \right) \left( 1 - \frac{1}{mv + 1} \right) - \frac{1}{4} \left( \frac{h}{b(mv + 1)} - \frac{bv}{mv^* + 1} \right)^2$$

$$\geq h \left( \frac{h(mv^* + 1)}{b} + \frac{\beta c}{mv^* + 1} - 1 \right) \left( 1 - \frac{1}{\beta m + 1} \right) - \frac{h^2}{4b^2} - \frac{\alpha b^2}{4(mv^* + 1)^2}. \quad (37)$$

Consequently, if (a2) holds,  $\Phi(0, v) > 0$ . As a result,  $\Phi(u, v) > \Phi(0, v) > 0$ .

Hence,  $V$  is a Lyapunov function and the positive equilibrium  $E_3$  of model (3) is globally asymptotically stable. This completes the proof.  $\square$

**Remark 6.** When  $d_{12} = d_{21} = 0$ , Theorem 5 is true, too. That is, the positive equilibrium  $E_3$  of the self-diffusion model (5) is globally asymptotically stable.

### 3. Turing's Instability and Pattern Formation

**3.1. Nonexistence of Turing's Instability in the Self-Diffusion Model (5).** And in the presence of diffusion, we will introduce small perturbations  $U_1 = u - u^*$ ,  $U_2 = v - v^*$ , where  $|U_1|, |U_2| \ll 1$ . To study the effect of self-diffusion on model (5), we consider the linearized form of system about  $E^* = (u^*, v^*)$  as follows:

$$\frac{\partial U_1}{\partial t} = J_{11}U_1 + J_{12}U_2 + d_{11}\Delta U_1, \quad (38)$$

$$\frac{\partial U_2}{\partial t} = J_{21}U_1 + J_{22}U_2 + d_{22}\Delta U_2,$$

where  $J_{11}, J_{12}, J_{21}$ , and  $J_{22}$  are defined as (24).

Following Malchow et al. [11], we can know any solution of model (38) can be expanded into a Fourier series so that

$$U_1(x, t) = \sum_{n,m=0}^{\infty} u_{nm}(x, t) = \sum_{n,m=0}^{\infty} \alpha_{nm}(t) \sin \mathbf{k}x, \quad (39)$$

$$U_2(x, t) = \sum_{n,m=0}^{\infty} v_{nm}(x, t) = \sum_{n,m=0}^{\infty} \beta_{nm}(t) \sin \mathbf{k}x,$$

where  $x = (\xi, \eta)$ , and  $0 < \xi < Lx$ ,  $0 < \eta < Ly$ .  $\mathbf{k} = (k_n, k_m)$  and  $k_n = n\pi/Lx$ ,  $k_m = m\pi/Ly$  are the corresponding wavenumbers.

Substituting  $u_{nm}$  and  $v_{nm}$  into (38), we obtain

$$\begin{aligned}\frac{d\alpha_{nm}}{dt} &= (J_{11} - d_{11}k^2)\alpha_{nm} + J_{12}\beta_{nm}, \\ \frac{d\beta_{nm}}{dt} &= J_{21}\alpha_{nm} + (J_{22} - d_{22}k^2)\beta_{nm},\end{aligned}\quad (40)$$

where  $k^2 = k_n^2 + k_m^2$ .

A general solution of (40) has the form  $C_1 \exp(\lambda_1 t) + C_2 \exp(\lambda_2 t)$ , where the constants  $C_1$  and  $C_2$  are determined by the initial conditions and the exponents  $\lambda_1, \lambda_2$  are the eigenvalues of the following matrix:

$$\bar{D} = \begin{pmatrix} J_{11} - d_{11}k^2 & J_{12} \\ J_{21} & J_{22} - d_{22}k^2 \end{pmatrix}. \quad (41)$$

Correspondingly,  $\lambda_1, \lambda_2$  are the solution of the following characteristic equation:

$$\lambda^2 - \rho_1 \lambda + \rho_2 = 0, \quad (42)$$

where

$$\begin{aligned}\rho_1 &= -k^2 (d_{11} + d_{22}) + \text{tr}(J), \\ \rho_2 &= d_{11}d_{22}k^4 - (d_{22}J_{11} + d_{11}J_{22})k^2 + \det(J).\end{aligned}\quad (43)$$

From (24), one can easily obtain

$$\rho_1 < 0, \quad \rho_2 > 0. \quad (44)$$

Then, we can conclude that the equilibrium  $E^* = (u^*, v^*)$  is also stable for self-diffusion model (5). That is to say, there is nonexistence of Turing's instability in model (5).

**3.2. Turing's Instability in the Cross-Diffusion Model (3).** The linearized form of the cross-diffusion model (3) about  $E^* = (u^*, v^*)$  is as follows:

$$\begin{aligned}\frac{\partial U_1}{\partial t} &= J_{11}U_1 + J_{12}U_2 + d_{11}\Delta U_1 + d_{12}\Delta U_2, \\ \frac{\partial U_2}{\partial t} &= J_{21}U_1 + J_{22}U_2 + d_{21}\Delta U_1 + d_{22}\Delta U_2.\end{aligned}\quad (45)$$

The characteristic equation of the linearized model (3) is:

$$\lambda^2 - \sigma_1 \lambda + \sigma_2 = 0, \quad (46)$$

where

$$\begin{aligned}\sigma_1 &= -k^2 (d_{11} + d_{22}) + \text{tr}(J), \\ \sigma_2 &= \det(D)k^4 \\ &\quad - (d_{22}J_{11} + d_{11}J_{22} - d_{21}J_{12} - d_{12}J_{21})k^2 + \det(J).\end{aligned}\quad (47)$$

Diffusive instability occurs when at least one of the following conditions is violated [2]:

$$\sigma_1 < 0 \quad \text{or} \quad \sigma_2 < 0. \quad (48)$$

It is evident that the condition  $\sigma_1 > 0$  is not violated when the requirement  $J_{11} + J_{22} < 0$  is met because we assume  $d_{11} > 0$  and  $d_{22} > 0$ . Hence, only violation of the condition  $\sigma_2 > 0$  will give rise to diffusion instability, that is, Turing's instability. Then the condition for diffusive instability is given by

$$d_{22}J_{11} + d_{11}J_{22} - d_{21}J_{12} - d_{12}J_{21} > 0, \quad (49)$$

otherwise  $\sigma_2 > 0$  for all  $k > 0$  since  $\det(D) > 0$  and  $\det(J) > 0$ .

For Turing's instability, we must have  $\sigma_2 < 0$  for some  $k$ . And we notice that  $\sigma_2$  achieves its minimum:

$$\begin{aligned}\min_{\mu_i} \sigma_2 \\ = \frac{4 \det(D) \det(J) - (d_{22}J_{11} + d_{11}J_{22} - d_{21}J_{12} - d_{12}J_{21})^2}{4 \det(D)}\end{aligned}\quad (50)$$

at the critical value  $k_c^2 > 0$  when

$$k_c^2 = \frac{d_{22}J_{11} + d_{11}J_{22} - d_{21}J_{12} - d_{12}J_{21}}{2 \det(D)}. \quad (51)$$

As a consequence, if  $d_{22}J_{11} + d_{11}J_{22} - d_{21}J_{12} - d_{12}J_{21} > 0$  and  $\sigma_2 < 0$  hold, then  $E_3 = (u^*, v^*)$  is an unstable equilibrium with respect to model (3). In this case,  $\sigma_2 = 0$  has two positive roots  $k_1^2$  and  $k_2^2$  which satisfy

$$k_{1,2}^2 = \frac{d_{22}J_{11} + d_{11}J_{22} - d_{21}J_{12} - d_{12}J_{21} \pm \sqrt{\Lambda}}{2 \det(D)}, \quad (52)$$

where  $\Lambda = (d_{22}J_{11} + d_{11}J_{22} - d_{21}J_{12} - d_{12}J_{21})^2 - 4 \det(D) \det(J)$ . Therefore, if we can find some  $k^2$  such that  $k_1^2 < k^2 < k_2^2$ , then  $\sigma_2 < 0$ .

Summarizing the above calculation, we obtain the following.

**Theorem 7.** Assume that the positive equilibrium  $E_3 = (u^*, v^*)$  exists. If the following conditions are true:

(i)  $d_{22}J_{11} + d_{11}J_{22} > d_{21}J_{12} + d_{12}J_{21}$ , that is,

$$chd_{21} > d_{22}hv^{*2}m^2 + hv^*(bd_{11} + 2d_{22})m + b^2d_{12}v^* + hd_{22}; \quad (53)$$

(ii)  $d_{22}J_{11} + d_{11}J_{22} - d_{21}J_{12} - d_{12}J_{21} > 2\sqrt{\det(D)\det(J)}$ , that is,

$$\begin{aligned}chd_{21} - (d_{22}hv^{*2}m^2 + hv^*(bd_{11} + 2d_{22})m + b^2d_{12}v^* + hd_{22}) \\ > 2\sqrt{bhv^*(d_{11}d_{22} - d_{12}d_{21})(hm^3v^{*2} + 2hm^2v^* + hm + bc)},\end{aligned}\quad (54)$$

then the positive equilibrium  $E_3$  of model (3) is Turing unstable if  $0 < k_1^2 < k^2 < k_2^2$  for some  $k$ .



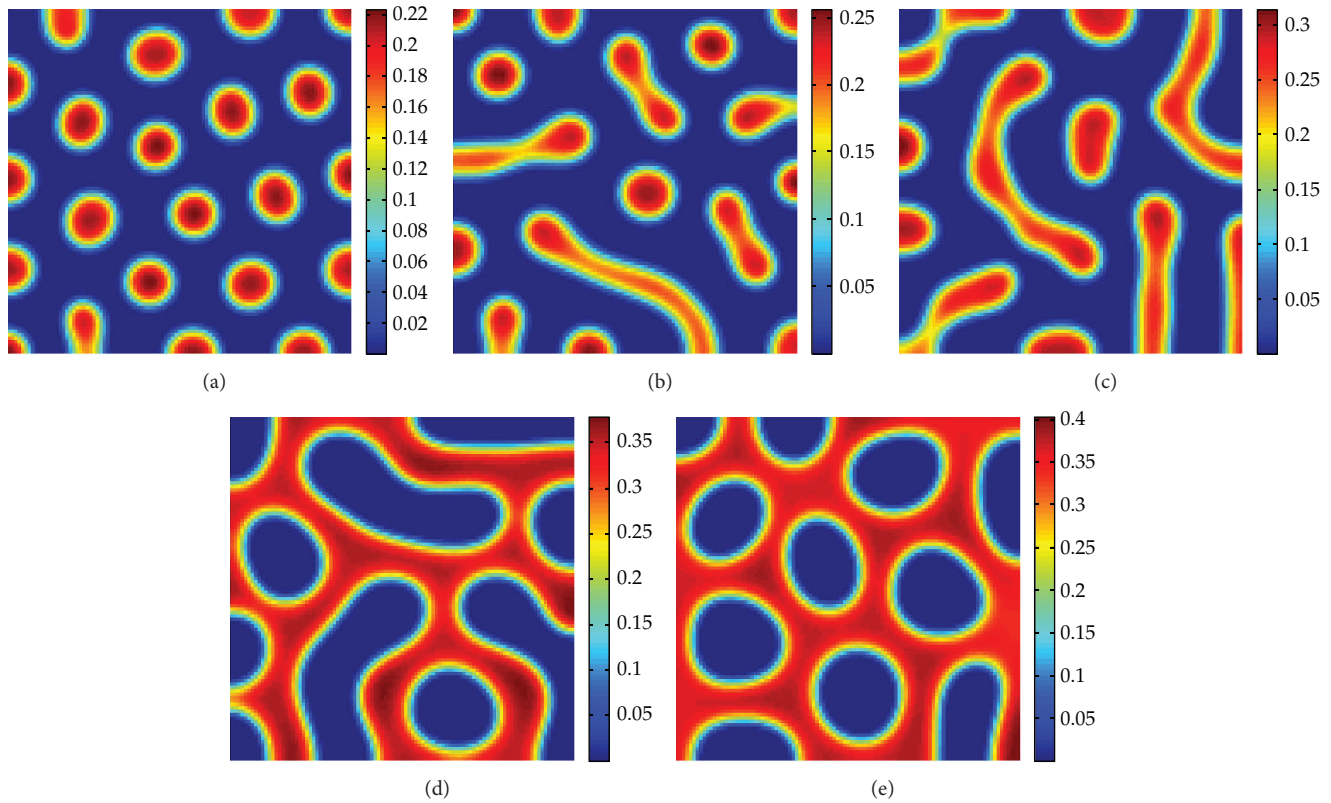


FIGURE 1: Five typical Turing's patterns of  $u$  in model (3) with fixed parameters  $b = 9$ ,  $c = 0.5$ ,  $d = 0.45$ ,  $d_{11} = 0.01$ ,  $d_{22} = 1$ ,  $d_{12} = -0.025$ , and  $d_{21} = 0.01$ . (a) Spots pattern,  $m = 0.05$ ; (b) spot-stripe mixtures pattern,  $m = 0.125$ ; (c) stripes pattern,  $m = 0.25$ ; (d) hole-stripe mixtures pattern,  $m = 0.45$ ; (e) holes pattern,  $m = 0.5$ . Iterations: pattern (a):  $5 \times 10^5$ , pattern (c):  $1 \times 10^5$ , and others:  $3 \times 10^5$ .

**3.3. Pattern Formation.** In this section, we perform extensive numerical simulations of the spatially extended model (3) in two-dimensional space, and the qualitative results are shown here. All our numerical simulations employ the zero-flux boundary conditions with a system size of  $100 \times 100$ . Other parameters are set as  $b = 9$ ,  $c = 0.5$ ,  $d = 0.45$ ,  $d_{11} = 0.01$ ,  $d_{22} = 1$ ,  $d_{12} = -0.025$ , and  $d_{21} = 0.01$ .

The numerical integration of model (3) is performed by using a finite difference approximation for the spatial derivatives and an explicit Euler method for the time integration [30, 31] with a time stepsize of  $1/1000$  and the space stepsize  $h = 1/10$ . The initial condition is always a small amplitude random perturbation around the positive equilibrium  $E_3 = (u^*, v^*)$ . After the initial period during which the perturbation spread, either the model goes into a time-dependent state or to an essentially steady-state solution (time independent).

In the numerical simulations, different types of dynamics are observed and it is found that the distributions of predator and prey are always of the same type. Consequently, we can restrict our analysis of pattern formation to one distribution. In this section, we show the distribution of prey  $u$ , for instance. We have taken some snapshots with red (blue) corresponding to the high (low) value of prey  $u$ .

Figure 1 shows five typical Turing's patterns of prey  $u$  in model (3) arising from random initial conditions for several values of the control parameter  $m$ .

In Figure 1(a)— $H_0$ -pattern,  $m = 0.05$ , consists of red (maximum density of  $u$ ) hexagons on a blue (minimum density of  $u$ ) background, that is, isolated zones with high population densities. In this paper, we call this pattern as "spots."

In Figure 1(b), when increasing  $m$  to 0.125, a few of stripes emerge, and the remainder of the spots pattern remains time independent. Pattern (b) is called  $H_0$ -hexagon-stripe mixtures pattern.

While increasing  $m$  to 0.25, model dynamics exhibits a transition from stripes-spots growth to stripes replication, that is, spots decay and the stripes pattern emerges (cf. Figure 1(c)).

In Figure 1(d),  $m = 0.45$ , on increasing of  $m$ , a few of blue hexagons (i.e., holes, named by Von Hardenberg et al. [32], associated with low population densities) fill in the stripes, that is, the stripes-holes pattern emerges. Pattern (d) is called  $H_\pi$ -hexagon-stripe mixtures pattern.

When increasing  $m$  to 0.5, model dynamics exhibits a transition from stripe-holes growth to spots replication, that is, stripes decay and the holes pattern ( $H_\pi$ -pattern) emerges (cf. Figure 1(e)).

From Figure 1, one can see that, on increasing the control parameter  $m$ , the sequences “spots  $\rightarrow$  spot-stripe mixtures  $\rightarrow$  stripes  $\rightarrow$  hole-stripe mixtures  $\rightarrow$  holes” are observed. Ecologically speaking, spots pattern shows that the prey population are driven by predators to a high level in those regions, while holes pattern shows that the prey population are driven by predators to a very low level in those regions. The final result is the formation of patches of high prey density surrounded by areas of low prey densities [3].

#### 4. Conclusions and Remarks

In this paper, we study the spatiotemporal dynamics of a Harrison predator-prey model with self- and cross-diffusions under the zero-flux boundary conditions. The value of this study lies in twofold. First, it gives the global stability of the positive equilibrium of the model by establishing a Lyapunov function. Second, it rigorously proves that the Turing instability can be induced by cross-diffusion, which shows that the model dynamics exhibits complex pattern replication controlled by the cross-diffusion.

The most important observation in this paper is that the cross-diffusion terms are necessary for the emergence of Turing's instability and pattern formation in the model. More precisely, with the help of the numerical simulations, the sequences “spots  $\rightarrow$  spot-stripe mixtures  $\rightarrow$  stripes  $\rightarrow$  hole-stripe mixtures  $\rightarrow$  holes” can be observed.

On the other hand, population dynamics in the real world is inevitably affected by environmental noise which is an important component in an ecosystem. The deterministic models, such as model (3) or (5), assume that parameters in the systems are all deterministic irrespective environmental fluctuations. It is well known that the fact that due to environmental noise, the birth rate, carrying capacity, competition coefficient, and other parameters involved in the system exhibit random fluctuation to a greater or lesser extent [33]. We think that there may be exist other noise-controlled self-replicating patterns in models (3) and (5). This is desirable in future studies.

It is believed that our results related to cross-diffusion in predator-prey interactions model would certainly be of some help to theoretical mathematicians and ecologists who are engaged in performing experimental work.

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