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SPATIAL PATTERN OF A RATIO-DEPENDENT PREDATOR-PREY MODEL WITH CROSS-DIFFUSION

Zhi Ling and Jingjing Li

School of Mathematical Science
Yangzhou University
Yangzhou 225002, P. R. China
e-mail: zhling@yzu.edu.cn

Abstract

In this paper, a ratio-dependent predator-prey model with both self-diffusion and cross-diffusion is investigated. We consider the effects of cross-diffusion on pattern formation and obtain the conditions for cross-diffusion-driven instability. Our results show that under certain hypotheses, the positive cross-diffusion can trigger Turing patterns even though the corresponding model without cross-diffusion fails. Finally, the numerical simulations are carried out to provide a better understanding of the results.

1. Introduction

The formation and development of pattern and shape in biology is an interesting phenomenon known as morphogenesis. The most widely studied model for spatial pattern formation is the reaction-diffusion model that was

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proposed by Turing in 1952 [14], who showed that a system of reacting and diffusing chemicals could evolve from initial near-homogeneity into a spatial pattern of chemical concentration. Then the interest in the diffusion-driven instability has long expanded from chemical system to biological system [2]. On the other hand, ecological systems are characterized by the interaction between species and their natural environment. An important type of interaction that affects population dynamics of all species is predation. Thus, spatial predator-prey models have been in the focus of ecological science, since the early days of this discipline. A variety of theoretical approaches have been developed and considerable progress has been made during the last three decades, we refer to [1, 3, 4, 10, 11, 15, 17].

Recently, many authors considered the following ratio-dependent predator-prey system [8]:

$$\begin{cases} N_t - d_1\Delta N = \gamma N\left(1 - \dfrac{N}{K}\right) - \dfrac{\alpha N^2 P}{m^2P^2 + N^2}, & (x,\ y) \in \Omega,\ t > 0, \\ P_t - d_2\Delta P = -\mu P + \dfrac{\beta N^2 P}{m^2P^2 + N^2}, & (x,\ y) \in \Omega,\ t > 0, \\ \partial_\eta N = \partial_\eta P = 0, & (x,\ y) \in \partial\Omega,\ t > 0, \\ N(x,\ 0) = N_0 > 0,\ P(x,\ 0) = P_0 > 0, & (x,\ y) \in \Omega, \end{cases} \tag{1}$$

where α, β, γ, μ, m and K are all positive constants. $\Delta = \partial^2/\partial x^2 + \partial^2/\partial y^2$ denotes the usual Laplacian operator in space domain $\Omega \in \mathbb{R}^2$, Ω is bounded and connected. η is the outward unit normal vector on $\partial\Omega$. $N(x,\ y,\ t)$, $P(x,\ y,\ t)$ represent the population density of prey and predator at $(x,\ y)$ and at time t, respectively. The prey grows with intrinsic growth rate γ and carrying capacity K in the absence of predation. The constant μ is the death rate of predator, α is the capture rate. β/α presents the conversion efficiency. m is the half-saturation constant. Diffusion terms d_1

and d_2 are the self-diffusion coefficients for N and P, respectively. The homogeneous Neumann boundary condition means that model (1) is self-contained and has no population flux across the boundary $\partial\Omega$.

However, in population dynamics, one of the observed features is that different concentration levels of the prey direct the movements of the predator and vice versa. In other words, the movement of a predator at any particular location is influenced by the gradient of the concentration of the prey at that location, and the movement of the prey is affected by the gradient of the concentration of the predator at the same location. For such reason, we will investigate the following model with cross-diffusion:

$$\begin{cases} N_t - d_1 \Delta N = \gamma N\left(1 - \frac{N}{K}\right) - \frac{\alpha N^2 P}{m^2 P^2 + N^2}, & (x, y) \in \Omega,\ t > 0, \\ P_t - d_2 \Delta(1 + d_3 N)P = -\mu P + \frac{\beta N^2 P}{m^2 P^2 + N^2}, & (x, y) \in \Omega,\ t > 0, \\ \partial_\eta N = \partial_\eta P = 0, & (x, y) \in \partial\Omega,\ t > 0, \\ N(x, 0) = N_0 > 0,\ P(x, 0) = P_0 > 0, & (x, y) \in \Omega. \end{cases} \tag{2}$$

The constant $d_2 d_3$ could be referred to as cross-diffusion pressure, which describes a mutual interference between individuals. The system (2) means that, in addition to the dispersive force, the diffusion of P also depends on population pressure from N. We rewrite

$$-d_2 \Delta(1 + d_3 N)P = -d_2 div((1 + d_3 N)\nabla P + d_3 P \nabla N)$$

and regard $-d_2(1 + d_3 N)\nabla P - d_2 d_3 P \nabla N$ as the flux of the predator P. If $d_3 > 0,$ the term $-d_2 d_3 P$ of the flux of the predator is directed toward the decreasing population density of N. More details about the cross-diffusion can be found in [5-7, 9, 12, 13, 16].

The main aim of this paper is to study the effects of cross-diffusion in system (2) by using mathematical analysis and numerical simulations. The paper is organized as follows. In Section 2, we derive the conditions on the parameter values for cross-diffusion-driven instability and give the mathematical expression for the Hopf bifurcations and Turing bifurcation critical line. On the basis of these conditions, we locate the Turing bifurcation domain within the parameter space. In Section 3, by performing a series of simulations, we illustrate the emergence of different patterns. In the last section, some conclusions and discussions are given.

2. Mathematical Analysis

In order to minimize the number of parameters involved in the model, we can choose the scaling $u \to N/K,\ v \to mP/K,\ t \to \gamma t,$ then the model (2) can take the non-dimensionalized form as following:

$$\begin{cases} u_t - d_u \Delta u = u(1-u) - \dfrac{au^2 v}{u^2 + v^2}, & (x, y) \in \Omega,\ t > 0, \\ v_t - d_v \Delta(1 + du)v = -bv + \dfrac{cu^2 v}{u^2 + v^2}, & (x, y) \in \Omega,\ t > 0, \\ \partial_\eta u = \partial_\eta v = 0, & (x, y) \in \partial\Omega,\ t > 0, \\ u(x, 0) = u_0 > 0, & (x, y) \in \Omega, \end{cases} \tag{3}$$

where

$$a = \frac{\alpha}{m\gamma}, \quad b = \frac{\mu}{\gamma}, \quad c = \frac{\beta}{\gamma}, \quad d_u = \frac{d_1}{\gamma}, \quad d_v = \frac{d_2}{\gamma}, \quad d = d_3 K.$$

Simple calculations show that the system (3) has two equilibrium points:

(i) the semi-trivial equilibrium point $E_1 = (1, 0)$ corresponding to extinction of the predator or prey only;

(ii) the non-trivial equilibrium point $E^* = (u^*, v^*)$ corresponding to coexistence of prey and predator, where

$$u^* = \frac{c - ae}{c}, \quad v^* = \frac{e}{b} u^*$$

with $e = \sqrt{bc - b^2}$.

It is easy to obtain that the condition for ensuring that u^* and v^* are positive is that

$$0 < a < \frac{b}{\sqrt{bc - b^2}}. \tag{4}$$

From the biological point of view, we are interested in studying the stability behavior of the interior equilibrium point E^*. By direct calculations, we can obtain the Jacobian corresponding to the equilibrium point E^* is

$$\boldsymbol{J} = \begin{pmatrix} \frac{-c^2 + 2abe}{c^2} & \frac{ab(c - 2b)}{c^2} \\ \frac{2e(c - b)}{c} & -\frac{2b(c - b)}{c} \end{pmatrix} \triangleq \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}.$$

In order to linearize the reaction-diffusion equations (3) around the spatially homogeneous fixed point (u^*, v^*), we consider a perturbation

$$u(\boldsymbol{r}, t) = u^* + \hat{u}(\boldsymbol{r}, t),$$

$$v(\boldsymbol{r}, t) = v^* + \hat{v}(\boldsymbol{r}, t), \tag{5}$$

where $|\hat{u}(\boldsymbol{r}, t)| << u^*$, $|\hat{v}(\boldsymbol{r}, t)| << v^*$ and $\boldsymbol{r} = (x, y)$. Taking $\omega_1, \omega_2 > 0$ and setting

$$\hat{u}(\boldsymbol{r}, t) = \omega_1 \exp(\lambda t) \exp(i\vec{\boldsymbol{k}} \cdot \boldsymbol{r}),$$

$$\hat{v}(\boldsymbol{r}, t) = \omega_2 \exp(\lambda t) \exp(i\vec{\boldsymbol{k}} \cdot \boldsymbol{r}), \tag{6}$$

where $\vec{\boldsymbol{k}} \cdot \vec{\boldsymbol{k}} = k^2$, k and λ are wave-number and frequency, respectively. Then we obtain the characteristic equation

$$|\, \lambda \boldsymbol{I} + k^2 \boldsymbol{D} - \boldsymbol{J} \,| = 0, \tag{7}$$

where $\boldsymbol{I}$ is the unit tensor and

$$\boldsymbol{D} = \begin{pmatrix} d_u & 0 \\ d_v d v^* & d_v(1 + du^*) \end{pmatrix}.$$

It follows that $\lambda = \lambda(k^2)$ satisfies the dispersion relation

$$\lambda^2 + A(k^2)\lambda + B(k^2) = 0, \tag{8}$$

where

$$A(k^2) = (d_u + d_v(1 + du^*))k^2 - (a_{11} + a_{22}),$$

$$B(k^2) = d_u d_v (1 + du^*)k^4 - (d_v(1 + du^*)a_{11} + d_u a_{22} - d_v dv^* a_{12})k^2$$
$$+ a_{11}a_{22} - a_{12}a_{21}. \tag{9}$$

The roots of equation (8) can be obtained by the following form:

$$\lambda_{1,2}(k^2) = \frac{1}{2}[-A(k^2) \pm \sqrt{(A(k^2))^2 - 4B(k^2)}].$$

For diffusion-driven instability to occur, one of the roots of (8) must have $Re\lambda(k^2) > 0$ for some $k^2 > 0$. If $k = 0$ (corresponding to the case of no diffusion), then we require that the homogeneous steady state is stable, i.e., $Re\lambda(k^2) < 0$, which is guaranteed provided that

$$Tr(\boldsymbol{J}) = a_{11} + a_{22} < 0, \tag{10}$$

$$Det(\boldsymbol{J}) = a_{11}a_{22} - a_{12}a_{21} > 0. \tag{11}$$

The condition (10) implies that $A(k^2) > 0$ for all $k^2 > 0$. Therefore, $Re(k^2) > 0$ only when $B(k^2) < 0$ for some $k^2 > 0$. The equation for $B(k^2)$ is quadratic in terms of k^2, so it is easy to show that $B(k^2) < 0$ (for some $k^2 > 0$) if and only if

$$d_v(1 + du^*)a_{11} + d_u a_{22} - d_v dv^* a_{12} > 0,$$

and

$$[d_v(1 + du^*)a_{11} + d_u a_{22} - d_v dv^* a_{12}]^2 > 4d_u d_v(1 + du^*)(a_{11}a_{22} - a_{12}a_{21}).$$

Therefore, for the model in this paper, the conditions for cross-diffusion driven instability can be summarized as

$$a_{11} + a_{22} < 0, \tag{12}$$

$$a_{11}a_{22} - a_{12}a_{21} > 0, \tag{13}$$

$$d_v(1 + du^*)a_{11} + d_u a_{22} - d_v dv^* a_{12} > 0, \tag{14}$$

$$(d_v(1 + du^*)a_{11} + d_u a_{22} - d_v dv^* a_{12})^2$$

$$- 4d_u d_v(1 + du^*)(a_{11}a_{22} - a_{12}a_{21}) > 0. \tag{15}$$

The four inequalities in (12)-(15) define a domain in parameter space (A, B, d), known as the Turing space, wherein the uniform steady state (u^*, v^*) is linearly unstable. Note that, if $d = 0$, then these conditions are identical to those derived for the system without cross-diffusion.

Now we will give the critical line of Hopf and Turing bifurcations in a spatial domain. According to the above analysis, we know that the onset of Hopf instability corresponds to the case, when a pair of imaginary eigenvalues crosses the real axis from the negative to the positive side. This situation occurs only when the diffusion vanishes. Mathematically speaking, the Hopf bifurcation occurs when $\mathrm{Im}(\lambda(k^2)) \neq 0$, $Re(\lambda(k^2)) = 0$ at $k = 0$. Then we can obtain the critical value of the transition, the Hopf bifurcation parameter, i.e., a equal to

$$a_H = \frac{c^2 + 2bc(c - b)}{2be}.$$

The next task is to study the Turing bifurcation. As we know that the system (3) will be unstable if at least one of the roots of equation (8) is positive. By straightforward analysis, we find that $B(k^2)$ is a quadratic polynomial with respect to k^2. Its extremum is a minimum at some k^2. From (9), elementary differentiation with respect to k^2 shows

$$k_{\min}^2 = \frac{d_v(1+du^*)a_{11} + d_u a_{22} - d_v dv^* a_{12}}{2d_u d_v(1+du^*)}. \tag{16}$$

By substituting $k^2 = k_{\min}^2$ into equation (9), we have

$$B(k_{\min}^2) = d_u d_v(1+du^*)k_{\min}^4 - [d_v(1+du^*)a_{11} + d_u a_{22} - d_v dv^* a_{12}]k_{\min}^2 + a_{11}a_{22} - a_{12}a_{21}. \tag{17}$$

By setting $B(k_{\min}^2) = 0,$ we can obtain the critical value of Turing bifurcation parameter, d_T, equal to

$$d_T = bc(d_v c^2 - 2b^2 d_u c + 2d_u bc^2 + 8aeb^2 d_u d_v - 8abed_u d_v c - 2d_v bae - 8b^2 d_u d_v c + 8d_u bd_v c^2)/(-c+ae)d_v(-2aeb^2 + 8aed_u b^3 - 8aeb^2 d_u c - 2bcae + 2c^2 ae + bc^2 - 8b^3 d_u c + 8b^2 d_u c^2). \tag{18}$$

Note that the right side of equation (18) includes the parameter a. Thus, we can draw the bifurcation line in a-d plane.

At the critical point, we have $B(k^2) = 0$ when $k = k_c$. For fixed kinetics parameters, this defines a critical cross-diffusion coefficient d_c as the appropriate root of

$$[d_v(1+du^*)a_{11} + d_u a_{22} - d_v dv^* a_{12}]^2 - 4d_u d_v(1+du^*)(a_{11}a_{22} - a_{12}a_{21}) = 0. \tag{19}$$

Then critical wavenumber k_c is given by

$$k_c^2 = \frac{d_v(1+du^*)a_{11} + d_u a_{22} - d_v dv^* a_{12}}{2d_u d_v(1+du^*)} = \sqrt{\frac{a_{11}a_{22} - a_{12}a_{21}}{d_u d_v(1+du^*)}}, \tag{20}$$

which shows that the cross-diffusion has effect on the critical wavenumber.

In other words, the critical wavenumber of the cross-diffusion system is different from the system without cross-diffusion. Now, let us discuss the bifurcations represented by these formulas in the parameter space spanned by the parameters *a* and *d* which can be seen from Figure 1.

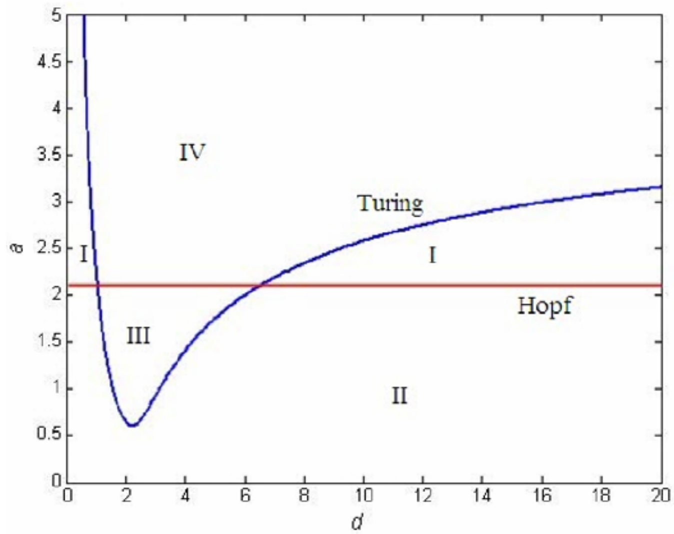

Figure 1. Bifurcation diagram for system (3). We set the parameter values $b = 0.7$, $c = 1.13$, $d_u = 1$, $d_v = 1$. The Turing space is marked by I, which is the area bounded by the Turing bifurcation line and Hopf bifurcation line.

The whole class of spatial model is included in this parameter space. The upper part of the displayed parameter space (where it is marked by IV) corresponds to systems with homogeneous equilibria, which is unconditionally stable. If this region is left via a bifurcation (Turing or Hopf), then the qualitative behaviour of such equilibria changes. If an equilibrium is represented by a point in the part of the parameter space (where it is marked by I), then it can be destabilized by a homogeneous oscillation. In domain II, both Hopf and Turing instabilities occur. The equilibria that can be found in the area (where it is marked by III) are stable with respect to homogeneous perturbations but loose their stability with respect to perturbations of specific wavenumbers *k*. In this region, stationary inhomogeneous patterns can be observed.

3. Numerical Simulation

In this section, we will perform numerical simulations by computer to illustrate the results obtained in previous section. We are interested in that how cross-diffusion has influence on the dynamics for fixed deterministic parameters. To this end, we fix the deterministic model parameters to the values $a = 2.3$, $b = 0.7$, $c = 1.13$, $d_u = 1$, $d_v = 1$ and vary the cross-diffusion coefficient d. Notice that for the no cross-diffusion system, there is no Turing pattern [14]. The values of these parameters can ensure the conditions (12) and (13) hold. Thus, we need to check the conditions (14) and (15) by varying d. From Figure 2, we can see that Turing pattern can emerge when d is more than the value corresponding to the point θ.

To solve differential equations by computers, one has to discretize the space and time of the problem. The continuous problem defined by the reaction-diffusion system in two-dimensional space is solved in a discrete domain with $M \times N$ lattice sites. The spacing between the lattice points is defined by the lattice constant Δh. In the discrete system, the Laplacian describing diffusion is calculated using finite differences. The time evolution is also discrete and can be solved by using the Euler method with time step Δt. We set $\Delta h = 1$, $\Delta t = 0.01$ and $M = N = 200$. And it is checked that a further decrease of the step values does not lead to any significant modification of the results.

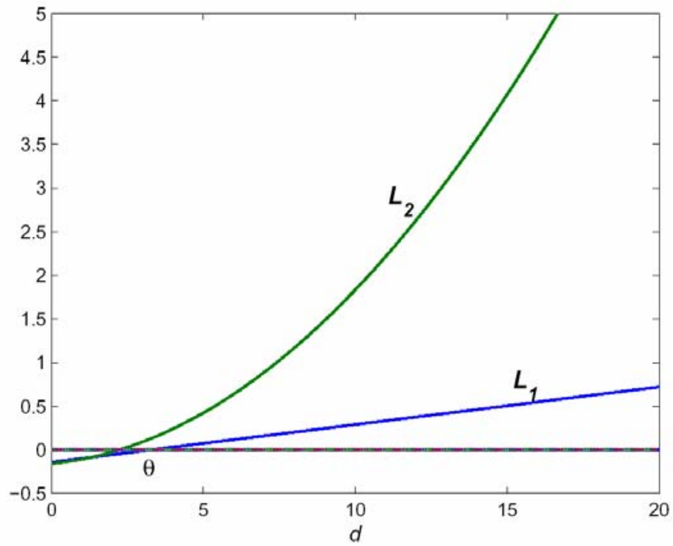

Figure 2. $L_1 = d_v(1 + du^*)a_{11} + d_u a_{22} - d_v dv^* a_{12}$, $L_2 = (d_v(1 + du^*)a_{11} + d_u a_{22} - d_v dv^* a_{12})^2 - 4d_u d_v(1 + du^*)(a_{11}a_{22} - a_{12}a_{21})$. The values of the other parameters are in the text.

Figure 3 shows the evolution of the spatial pattern of prey population with small random perturbation of stationary solutions u and v of the spatially homogeneous system when the parameter values are in the domain of Turing space. As d increases, stripes only, coexistence of stripes and spots, and spots only pattern emerge successively.

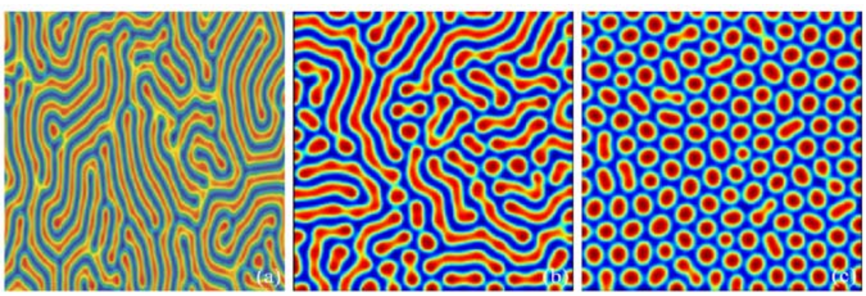

Figure 3. Spatial pattern of species u with system (3) for: (a) $d = 5$, (b) $d = 10$ and (c) $d = 15$. The other parameters are stated in the text. The step of the iteration for time is 100,000.

4. Conclusion and Discussion

In this paper, pattern formation of a ratio-dependent predator-prey model with both self-diffusion and cross-diffusion in two-dimensional space is investigated. We obtain the conditions for cross-diffusion-driven instability. Based on both mathematical analysis and numerical simulations, the different spatial patterns including stripes, stripe-spots and spots patterns can be obtained.

The influence of cross-diffusion on the pattern formation is revealed. More specifically, Turing pattern formation cannot occur for the equal self-diffusion coefficients. However, combining with cross-diffusion, we obtain Turing pattern as d increases. It means that cross-diffusion can violate the stability and trigger stable Turing patterns.

Although more work is needed, in principle, it seems that cross-diffusion is able to generate many different kinds of spatiotemporal patterns. For such reason, we can predict that the interaction of self-diffusion and cross-diffusion can be considered as an important mechanism for the appearance of complex spatiotemporal dynamics in predator-prey models.

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References

[1] M. Baurmann, T. Gross and U. Feudel, Instabilities in spatially extended predator-prey systems: spatio-temporal patterns in the neighborhood of Turing-Hopf bifurcation, J. Theoret. Biol. 245 (2007), 220-229.

[2] R. E. Baker, E. A. Gaffney and P. K. Maini, Partial differential equations for self-organization in cellular and developmental biology, Nonlinearity 251 (2008), 251-290.

[3] R. S. Cantrell and C. Cosner, Spatial Ecology via Reaction-diffusion Equations, Wiley Ser. Math. Comput. Biol., John Wiley & Sons, Ltd., 2003.

[4] J. H. P. Dawes, After 1952: the later development of Alan Turing's ideas on the mathematics of pattern formation, Historia Math. 43 (2016), 49-64.

[5] K. Kuto, Stability of steady-state solutions to a prey-predator system with cross-diffusion, J. Differential Equations 197 (2004), 293-314.

[6] K. Kuto and Y. Yamada, Multiple coexistence states for a prey-predator system with cross-diffusion, J. Differential Equations 197 (2004), 315-348.

[7] L. Li, Z. Jin and G. Q. Sun, Spatial pattern of an epidemic model with cross diffusion, Chin. Phys. Lett. 25 (2008), 3500-3503.

[8] X. X. Liu and L. H. Huang, Permanence and periodic solutions for a diffusive ratio-dependent predator-prey system, Appl. Math. Model. 33 (2009), 683-691.

[9] Y. Lou and W. M. Ni, Diffusion, self-diffusion and cross-diffusion, J. Differential Equations 131 (1996), 79-131.

[10] A. B. Medvinsky, S. V. Petrovskii, I. A. Tikhonova, H. Malchow and B. L. Li, Spatiotemporal complexity of plankton and fish dynamics, SIAM Rev. 44(3) (2002), 311-370.

[11] R. Peng, J. P. Shi and M. X. Wang, Stationary pattern of a ratio-dependent food chain model with diffusion, SIAM J. Appl. Math. 67(5) (2007), 1479-1503.

[12] R. Peng, M. X. Wang and G. Y. Yang, Stationary patterns of the Holling-Tanner prey-predator model with diffusion and cross-diffusion, Appl. Math. Comput. 196 (2008), 570-577.

[13] C. R. Tian, Z. Ling and Z. G. Lin, Turing pattern formation in a predator-prey-mutualist system, Nonlinear Anal. Real World Appl. 12 (2011), 3224-3237.

[14] A. Turing, The chemical basis of morphogenesis, Philos. Trans. Royal. Soc. B 237 (1952), 37-72.

[15] J. F. Wang, J. P. Shi and J. J. Wei, Dynamics and pattern formation in a diffusive predator-prey system with strong Allee effect in prey, J. Differential Equations 251 (2011), 1276-1304.

[16] Y. Wang, J. Z. Wang and L. Zhang, Cross diffusion-induced pattern in an SI model, Appl. Math. Comput. 217 (2010), 1965-1970.

[17] J. F. Zhang, W. T. Li and X. P. Yan, Hopf bifurcation and Turing instability in spatial homogeneous and inhomogeneous predator-prey models, Appl. Math. Comput. 218 (2011), 1883-1893.