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SPATIOTEMPORAL DYNAMICS OF A PREDATOR-PREY MODEL INCORPORATING A PREY REFUGE

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Abstract In this paper, we investigate the spatiotemporal dynamics of a ratio-dependent predator-prey model with cross diffusion incorporating proportion of prey refuge. First we get the critical lines of Hopf and Turing bifurcations in a spatial domain by using mathematical theory. More specifically, the exact Turing region is given in a two parameter space. Also we perform a series of numerical simulations. The obtained results reveal that this system has rich dynamics, such as spotted, stripe and labyrinth patterns which show that it is useful to use the predator-prey model to reveal the spatial dynamics in the real world.

Keywords Cross-diffusion, turing bifurcation, prey refuge, pattern formation.

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1. Introduction

The dynamic relationships between species and their complex properties are at the heart of many ecological and biological processes. One such relationship is the dynamical relationship between a predator and their prey which has long been and will continue to be one of the dominant themes in both ecology and mathematical ecology due to its universal existence and importance. The first model to describe the size (density) dynamics of two populations interacting as a predator-prey system was developed independently by A. Lotka (1925) and V. Volterra (1931). Since the classical Lotka-Volterra models suffer from some unavoidable limitations in describing precisely many realistic phenomena in biology, in some cases, they should make way to some more sophisticated models from both mathematical and biological points of view.

All the beings, including different kinds of populations, live in a spatial world and it is a natural phenomenon that a substance goes from high-density regions to low-density regions. As a result, more and more scholars use spatial model to study the interaction of the prey and predator [12]. Recently considerable interest has been shown to investigate the stability behavior of a system of interacting populations by taking into account the effect of self as well as cross-diffusion [14]. The term self-diffusion implies the movement of individuals from a higher to lower concentration region. Cross-diffusion expresses the population fluxes of one species due to the presence of the other species. The value of the cross-diffusion coefficient

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may be positive, negative or zero. The positive cross-diffusion coefficient denotes the movement of the species in the direction of lower concentration of another species and negative cross-diffusion coefficient denotes that one species tends to diffuse in the direction of higher concentration of another species [9].

In 1952, A.M. Turing first proposed the reaction-diffusion theory for pattern formation in his seminal work on the chemical basis of morphogenesis [23]. A situation in which a non-linear system is asymptotically stable in the absence of self and cross-diffusions but unstable in the presence of self and cross-diffusions is known as Turing instability. This concept has been playing significant roles in theoretical ecology, embryology and other branches of science. Similarly structured systems of ordinary differential equations govern the spatiotemporal dynamics of ecological population models; yet most of the simple models predict spatially homogeneous population distributions. One notable exception to this rule was demonstrated by Bartumeus et al. [1,4] who reported that intra-predator interaction or interference may facilitate spatial pattern formation in a variation of the DeAngelis model [8,15].

Recently many authors have performed various kinds of spatial patterns and Hopf bifurcation anaylsis of the predator-prey models have been reported (see [2,3,5,10,13,17–21,24]). Few papers have appeared on resulting patterns exhibited by spatiotemporal prey-predator model with ratio-dependent functional response. Banerjee [3] performed the linear stability analysis for a diffusive predator-prey model with ratio-dependent functional response for the predator and reported the diffusion driven instability behaviour and resulting Turing structures with heterogeneous environment. Martin Baurmann et al. [5] studied the dynamics of generalized predator-prey models with spatial interactions. The formulation and subsequent normalization of the generalized model allows us to perform a qualitative analysis of a whole class of predator-prey models without specifying the predator-prey functional response. Gui-Quan Sun et al. [18] analyze the spatial pattern formation of a Holling-Tanner predator-prey model with cross diffusion. Liu and Jin [13] analyze spatial pattern formation of a ratio-dependent predator-prey system with self diffusion. In addition, M. Sambath and K. Balachandran [19] studied the pattern formation of a ratio-dependent predator-prey system with cross diffusion and Y. Wang and J. Wang [24] analyze spatial pattern formation of prey refuge on ratio-dependent predator-prey system with self diffusion. The aim of this paper is to study the effect of cross diffusion of the Turing pattern formation of prey refuge on predator-prey model with ratio-dependent functional response.

The remainder of this paper is as follows. In Section 2, we analyze the predator-prey model with cross diffusion and derive the mathematical expressions for the Hopf and Turing bifurcation critical lines. In Section 3, we present the result of pattern formation via numerical simulation. Finally we present some conclusion and discussion in Section 4.

2. The model and Hopf bifurcation analysis

The dynamics of ratio-dependent predator-prey system incorporating a constants proportion of prey refuge with Michaelis-Menten-Holling type functional response [11] in homogeneous environment is governed by the following system of non-linear ordinary differential equations

$$\begin{cases} \dfrac{du}{d\tau} = Ru\left(1 - \dfrac{u}{K}\right) - \dfrac{Au(1-M)v}{u(1-M)+kv}, \\ \dfrac{dv}{d\tau} = -Dv + \dfrac{ABu(1-M)v}{u(1-M)+kv}, \\ u(0) = u_0 > 0, \quad v(0) = v_0 > 0, \end{cases} \tag{2.1}$$

where u and v represent prey and predators densities, respectively. Here R represents intrinsic growth rate of the prey and carrying capacity K in the absence of predation, B conversion efficiency, A capture rate, D death rate of the predator, k predators benefit from cofeeding and $M \in [0, 1)$ a constant rate of the prey using refuges. From the biological point of view all parameters are assumed positive.

In order to minimize the number of parameters involved in the model, it is extremely useful to write the system in non-dimensionalized form. Thus by taking $U = u/K,\ V = kv/K,\ b = A/kR,\ d = D/R,\ e = Bk$ and considering the dimensionless time $t = R\tau$, we arrive at the following equations containing dimensionless quantities:

$$\begin{cases} \dfrac{dU}{dt} = U(1-U) - \dfrac{bU(1-M)V}{U(1-M)+V}, \\ \dfrac{dV}{dt} = -dV + \dfrac{ebU(1-M)V}{U(1-M)+V}. \end{cases} \tag{2.2}$$

Thus the model with cross diffusion becomes

$$\begin{cases} \dfrac{\partial U}{\partial t} = d_{11}\Delta U + d_{12}\Delta V + U(1-U) - \dfrac{bU(1-M)V}{U(1-M)+V}, \\ \dfrac{\partial V}{\partial t} = d_{21}\Delta U + d_{22}\Delta V - dV + \dfrac{ebU(1-M)V}{U(1-M)+V}. \end{cases} \tag{2.3}$$

In the above, Δ is the Laplacian operator in two-dimensional space, $d_{11},\ d_{22}$ are self diffusion coefficients of prey and predator, $d_{12},\ d_{21}$ are the cross diffusion coefficients of prey and predator respectively.

The model (2.3) is analyzed with the initial populations $U(0) > 0,\ \ V(0) > 0$. We also assume that no external input is imposed from outside. Hence the boundary conditions are taken as

$$\left.\frac{\partial U}{\partial \nu}\right|_{(x,y)} = \left.\frac{\partial V}{\partial \nu}\right|_{(x,y)} = 0, \qquad (x, y) \in \partial\Omega,$$

where ν is the outward unit normal vector on $\partial\Omega$ and Ω is the two-dimensional spatial domain.

We are interested (from biological point of view) mostly in the positive equilibrium point $E^* = (U^*, V^*)$ which corresponds to co-existence of prey and predator and is given by

$$U^* = \frac{beM - dM + d + e - be}{e}, \qquad V^* = -\frac{U^*(beM - eb + d - dM)}{d}. \tag{2.4}$$

It is easy to obtain the condition ensuring the existence of E^* is that $eb > d$ and $M > (eb - e - d)/(eb - d)$.

We are interested in studying the stability behavior of the positive equilibrium point E^*. The Jacobian evaluated at the coexistence equilibrium $E^* = (u^*, v^*)$ is

$$J = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}, \tag{2.5}$$

where $a_{11} = \frac{d^2(M-1)+be^2(b-1-bM)}{be^2}$, $a_{12} = -\frac{d^2}{be^2}$, $a_{21} = \frac{(M-1)(be-d)^2}{be}$, $a_{22} = \frac{d(d-be)}{be}$. We linearize the predator-prey system (2.3) around the spatially homogeneous fixed point (u^*, v^*) as follows:

$$\begin{pmatrix} U(\vec{\eta}, t) \\ V(\vec{\eta}, t) \end{pmatrix} = \begin{pmatrix} U^* \\ V^* \end{pmatrix} + \begin{pmatrix} \hat{U}(\eta, t) \\ \hat{V}(\eta, t) \end{pmatrix}, \tag{2.6}$$

where $\left|\hat{U}(\eta, t)\right| << U^*$, $\left|\hat{V}(\eta, t)\right| << V^*$ and $\vec{\eta}$ is in two-dimensional space. By setting

$$\begin{pmatrix} U(\vec{\eta}, t) \\ V(\vec{\eta}, t) \end{pmatrix} = \begin{pmatrix} U_0 e^{\lambda t} e^{i\vec{k}, \hat{\eta}} \\ V_0 e^{\lambda t} e^{i\vec{k}, \hat{\eta}} \end{pmatrix}, \tag{2.7}$$

we obtain the characteristic equation

$$\left| J - \lambda I - k^2 D \right| = 0, \tag{2.8}$$

where

$$D = \begin{pmatrix} d_{11} & d_{12} \\ d_{21} & d_{22} \end{pmatrix}. \tag{2.9}$$

Now we obtain the characteristic polynomial from (2.8) as follows

$$\lambda^2 + T_k \lambda + D_k = 0, \tag{2.10}$$

where

$$T_k = (d_{11} + d_{22})k^2 - (a_{11} + a_{22}),$$

$$D_k = (d_{11}d_{22} - d_{12}d_{21})k^4 - (d_{11}a_{22} + d_{22}a_{11} - d_{12}a_{21} - d_{21}a_{12})k^2 + (a_{11}a_{22} - a_{12}a_{21}).$$

The roots of (2.10) are given by

$$\lambda_k = \frac{-T_k \pm \sqrt{T_k^2 - 4D_k}}{2}. \tag{2.11}$$

At the bifurcation point, two equilibrium points of the model intersect and exchange their stability. Biologically speaking, this bifurcation point corresponds to a smooth transition between equilibrium states. The Hopf bifurcation is space-independent and breaks the temporal symmetry of the system. This gives rise to oscillations that are uniform in space and periodic in time. The Turing bifurcation breaks the spatial symmetry leading to the formation of patterns that are stationary in time and oscillatory in space.

Now we give the expressions of the bifurcation critical line. The onset of Hopf instability corresponds to the case when a pair of imaginary eigenvalues cross the real axis from the negative to positive side and this situation occurs only when the diffusion vanishes. Mathematically speaking, the Hopf bifurcation occurs when

$$Im(\lambda(k)) \neq 0, \quad Re(\lambda(k)) = 0 \ \text{ at } \ k = 0.$$

Then we get the critical value of the Hopf bifurcation parameter$-M$ as $M_{_H}$ where

$$M_{_H} = \frac{d^2(e-1) + e^2(b^2 - b - bd)}{b^2e^2 - d^2}.$$

The positive equilibrium point (u^*, v^*) will be unstable if at least one of the roots of (2.10) is positive. By straight forward analysis, we find that D_k is a quadratic polynomial with respect to k^2. Its extremum is a minimum at some k^2 [16,22]. From D_k, elementary differentiation with respect to k^2 shows that

$$k^2_{min} = \frac{d_{11}a_{22} + d_{22}a_{11} - d_{12}a_{21} - d_{21}a_{12}}{2 \ det(D)}.$$

At the critical point, we have $D_k = 0$ when $k = k_{cr}$ [22]. For fixed kinetic parameters, this defines the critical cross diffusion coefficient d_{12} as the root of equation

$$(d_{11}a_{22} + d_{22}a_{11} - d_{12}a_{21} - d_{21}a_{12})^2 - 4 \ det(J) \ det(D) = 0.$$

The critical wavenumber k_{cr} is given by

$$k_{cr} = \sqrt{\frac{det(J)}{det(D)}}. \tag{2.12}$$

A general linear analysis [1, 6, 7] shows that the necessary conditions for yielding Turing patterns are given by

$$\begin{aligned}
&a_{11} + a_{22} < 0,\\
&a_{11}a_{22} - a_{12}a_{21} > 0,\\
&(d_{11}a_{22} + d_{22}a_{11} - d_{12}a_{21} - d_{21}a_{12}) > 0,\\
&(d_{11}a_{22} + d_{22}a_{11} - d_{12}a_{21} - d_{21}a_{12})^2 - 4 \ det(J) \ det(D) > 0,
\end{aligned}$$

where $det(J) = a_{11}a_{22} - a_{12}a_{21}$ and $det(D) = d_{11}d_{22} - d_{12}d_{21}$. Mathematically speaking, the Turing bifurcation occurs when

$$Im(\lambda(k)) = 0, \quad Re(\lambda(k)) = 0 \ \text{ at } \ k = k_{cr} \neq 0,$$

and the wave number k_{cr} is the same as in (2.12). By direct calculation, we obtain the critical value of bifurcation parameter M as $M_{_T}$ where

$$\begin{aligned}
M_{_T} = \ & \Big[b^4e^4(d_{22} - d_{12}e)^2 + bd^2(3dd_{11} - 4dd_{12} + d_{22})e^2(d_{22} + d_{12}e)\\
& + d^4(d_{22} - d_{12} + (d_{12} - d_{11})e)(d_{22} + d_{12}e) + b^2e^2d(d(d_{21} - 2d_{22})d_{22}\\
& + 3d(d_{12}d_{21} - d_{11}d_{22})e + d_{12}(6dd_{12} - 3dd_{11} - 2d_{22})e^2) + 2\sqrt{\Theta}\\
& + b^3e^4(d_{22}(d_{12}e - d_{22}) + d(d_{11}d_{22}(4d_{22} + ed_{11} - 2d_{21} - 4ed_{12})))\Big]\Big/\\
& \left[(d - be)^2(be(d_{22} - d_{12}e) + d(d_{22} + d_{12}e))^2\right],
\end{aligned}$$

where

$$\begin{aligned}\Theta = \ & be^2d(d_{12}d_{21}-d_{11}d_{22})(d^2(d_{21}+2d_{11}e)+be^2(d_{22}-d_{12}e)\\ & +de(d_{22}+d_{12}e+b(d_{21}-d_{11}e)))(d-be)^3(d(d_{22}+d_{12}e)-be^2d_{12}).\end{aligned}$$

We fix the deterministic model values $b = 2$, $d = 0.6$, $e = 0.7$, $d_{11} = 1$, $d_{21} = 1$, $d_{22} = 9$ and vary d_{12} as a function of c which is the coefficient of the cross diffusion of the prey. Now we discuss the bifurcations represented by these formulas in the parameter space. The bifurcation lines divide the parameter space into three distinct regions (see Fig. 1 (A)). The upper part of the displayed parameter space (where it is marked as III) corresponds to systems with homogeneous unconditionally stable equilibria. In region I, both Hopf and Turing bifurcations occur. The equilibria that can be found in the area, marked II, are stable with respect to homogeneous perturbations but lose their stability to homogeneous perturbations of specific wave number k.

Fig.1 (B) shows the Turing space properly. The dispersion relation of the model (2.3) with several values of the one parameter is fixed $M = 0.25$. It can be seen from Fig. 1 (B) that when d_{12} increases, the available Turing models $[Re(\lambda) > 0]$ decrease and all available models are weakened.

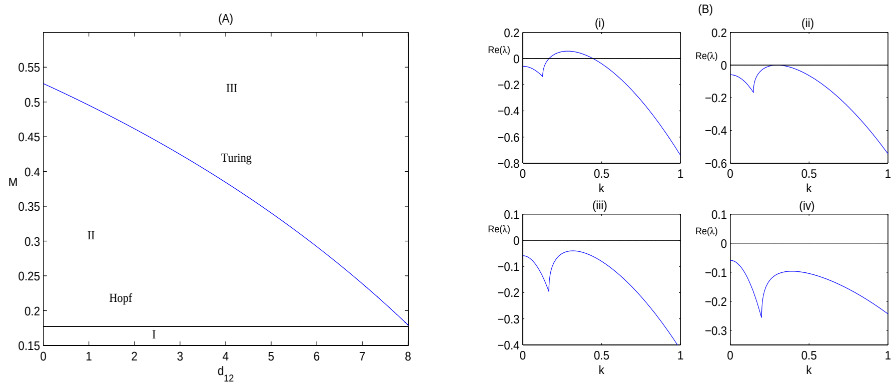

Figure 1. (A) The bifurcation diagram of model (2.3) with parameter values $b = 2$, $d = 0.6$, $e = 0.7$, $d_{11} = 1$, $d_{21} = 1$ and $d_{22} = 9$. The black and blue lines correspond to the Hopf (M_H) and Turing (M_T) bifurcation critical lines respectively. The figure shows the Turing space (it is marked by II) with the area bounded by the Turing bifurcation line and the Hopf bifurcation line.
(B) Variation of dispersion relation of the model (2.3) with the parameter values $b = 2$, $d = 0.6$, $e = 0.7$, $M = 0.25$, $d_{11} = 1$, $d_{21} = 1$ and $d_{22} = 9$. The values of d_{12} are: (i) $d_{12} = 0.1$, (ii) $d_{12} = 2.75$, (iii) $d_{12} = 4.5$, (iv) $d_{12} = 7$.

3. Main results

The dynamical behavior of the spatial predator-prey model cannot be studied by using analytical methods or normal forms. Thus we have to perform numerical simulations by computer. To solve the differential equation by computers, one has to discrete the space and time of the problem. In practice the continuous problem defined by the reaction-diffusion system in two-dimensional space domain is solved in a discrete domain with $M \times N$ ($M = N = 200$) lattice sites. The spacing in between the lattice points is defined by the lattice constants Δh. In the discrete system, the Laplacian describing diffusion is calculated using finite difference schemes, that is, the derivatives are approximated by differences over Δh. For $\Delta h \to 0$ the differences approach the derivatives. The time evolution is also discrete, that is, the time goes by steps of Δt and it can be solved by using Euler's method. The model (2.3) is solved by numerically approximating the spatial derivatives and an explicit Euler's method for the time integration with a time step size of $\Delta t = 0.01$ and space step size $\Delta h = 0.1$. All our numerical simulations employ the non-zero initial conditions and the Neumann boundary conditions.

Fig. 2 shows the evolution of the spatial pattern of the prey at $t = 0,\ 100,\ 300$ and 500 with small random perturbation of the stationary solution u^* and v^* of the spatially homogeneous system with $d_{12} = 0.1$. In this case, one see that for the system (2.3), the random initial distribution leads to formation of some stripe patterns. As the time is increased some spotted and stripes patterns prevail over the whole domain finally. The dynamics of the system does not undergo any further change.

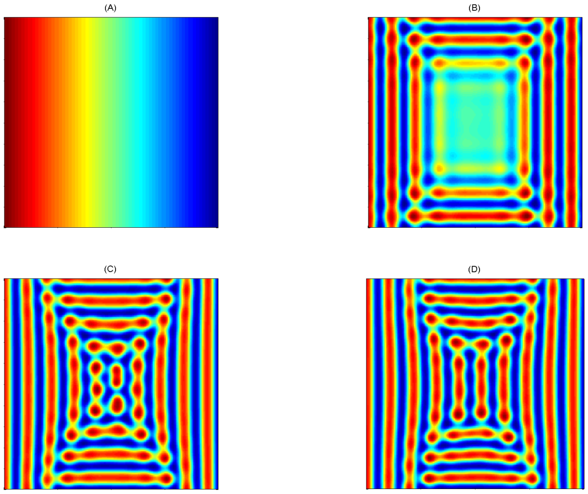

Figure 2. Snapshots of contour of the time evolution of the prey at different instants with $b = 2,\ d = 0.6,\ e = 0.7,\ M = 0.25,\ d_{11} = 1,\ d_{21} = 1\ d_{22} = 9$ and $d_{12} = 0.1$ and the parameter values in the Turing space. $(A)\ t = 0,\ (B)\ t = 100,\ (C)\ t = 300,\ (D)\ t = 500$.

Fig. 3 (A) shows the evolution of the spatial pattern of the prey at $t = 500$ with small random perturbation of the stationary solution u^* and v^* of the spatially homogeneous system with $d_{12} = 3$. We see from this figure that the labyrinth patterns prevail in the whole domain.

Fig. 3 (B) shows the evolution of the spatial pattern of the prey at $t = 500$ with small random perturbation of the stationary solution u^* and v^* of the spatially homogeneous system with $d_{12}=5$. We see from this figure that the spotted and labyrinth patterns prevail in the whole domain.

As d_{12} increases to 7, we show the spatial pattern of prey at $t=500$ in Fig. 3 (C). We see from the figure that the some spotted and striped patterns of spatial prevail in the whole domain.

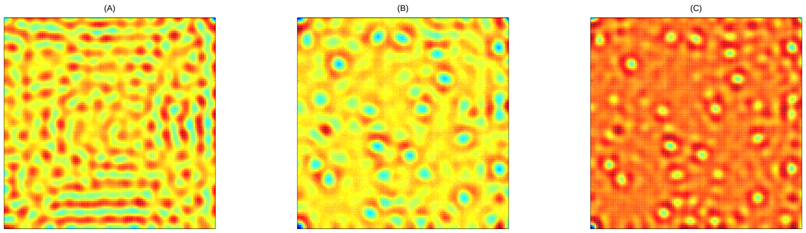

Figure 3. Snapshots of contour of the time evolution of the prey at $t=500$ with $b=2,\ d=0.6,\ e=0.7,\ M=0.25,\ d_{11}=1,\ d_{21}=1$ and $d_{22}=9$. The parameter values are chosen here in the Turing space. The values of d_{12} are: $(A)\ d_{12}=3,\ (B)\ d_{12}=5,\ (C)\ d_{12}=7$.

4. Conclusion

This paper has presented spatial patterns of a predator-prey model with self and cross diffusions. By using mathematical analysis and numerical simulations, we found that its spatial pattern includes the spotted, stripe and labyrinth patterns. That is to say, the interaction of self diffusion and cross diffusion can create stationary patterns.

From the biological point of view, our results have some clear meaning. The numerical simulation results indicated that the effect of the cross diffusion for pattern formation is remarkable. We assume that only one parameter is changing, such as d_{12}, others are remaining fixed. Increase of the cross diffusion coefficient of the predator plays an important role in the pattern formation. And different type of spatial patterns, such as spotted, stripe and labyrinth patterns (see. Figs. 2, 3) emerge, as d_{12} is being increased. This enriches the dynamics of the effect of the cross diffusion of the predator-prey model.

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