PHYSICAL REVIEW E **90**, 052908 (2014)

Delay-induced Turing instability in reaction-diffusion equations

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(Received 25 May 2014; published 10 November 2014)

Time delays have been commonly used in modeling biological systems and can significantly change the dynamics of these systems. Quite a few works have been focused on analyzing the effect of small delays on the pattern formation of biological systems. In this paper, we investigate the effect of any delay on the formation of Turing patterns of reaction-diffusion equations. First, for a delay system in a general form, we propose a technique calculating the critical value of the time delay, above which a Turing instability occurs. Then we apply the technique to a predator-prey model and study the pattern formation of the model due to the delay. For the model in question, we find that when the time delay is small it has a uniform steady state or irregular patterns, which are not of Turing type; however, in the presence of a large delay we find spiral patterns of Turing type. For such a model, we also find that the critical delay is a decreasing function of the ratio of carrying capacity to half saturation of the prey density.

DOI: 10.1103/PhysRevE.90.052908 PACS number(s): 89.75.Kd, 82.40.Ck, 47.54.−r

I. INTRODUCTION

Time delays, also known as time lags, are becoming common in mathematical models describing biological [1,2], chemical [2], engineering, and physical processes [3]. In ecology, time delay is commonly used to measure a maturation, gestation period, or reaction time of a predator population [1,4,5], and mathematically it may result in a much richer dynamics for a system, such as inducing the instability of an equilibrium so that Hopf bifurcation occurs [6–12]. Therefore, systems with time delays have received wide attention over the past years. For example, a few of works have recently focused on the investigation of reaction-diffusion equations with small time delays [2,3,9], where the authors reported that small time delays might result in a Turing instability of such systems so that spatial patterns were formed. The Turing instability is a mechanism used to explain how a biological pattern forms and was proposed by the pioneer Turing in Ref. [13], where the author discussed the instability of the equilibrium of a nonlinear system induced by diffusions [14–17]. Only most recently have some authors reported a Turing instability induced by time delays [2,3,9], where the authors assumed all time delays were small so that a Taylor series expansion could be employed to reduce systems with time delays to those without time delays. Then the conventional Turing technique can be applied. In these studies, the authors did not give answers to dealing with cases with larger time delays because, for the latter cases, a Taylor series expansion cannot applied. However, in practice, time delays in biological systems may be large— see Refs. [7,8,18,19], for example. For a model described by reaction-diffusion equations, could a large time delay induce a Turing instability? If so, how can one analyze the effect of delay on this instability? Bearing this in mind, we next propose a method to answer these questions by using a biological model with time delay. More precisely, we consider

$$\begin{aligned}\frac{\partial u}{\partial t} &= au\left(1-\frac{u}{k}\right)-\frac{buv}{c+u}+D_u\Delta u,\\ \frac{\partial v}{\partial t} &= \frac{mu(t-\tau)v}{c+u(t-\tau)}-nv+D_v\Delta v,\\ \frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu}=0,\\ u(\mathbf{r},0)>0,&\quad v(\mathbf{r},0)>0,\quad \mathbf{r}\in\Omega,\end{aligned}\tag{1}$$

where $\Delta=\frac{\partial^2}{\partial x^2}+\frac{\partial^2}{\partial y^2}$ is the Laplacian, $\mathbf{r}=(x,y)$ is a spatial vector, Ω is an open set in $\mathbf{R}^2$, and ν is the unit outward normal vector of the boundary $\partial\Omega$. $u=u(\mathbf{r},t)$ and $v=v(\mathbf{r},t)$ are the population densities of prey and predator at time t and position $\mathbf{r}$, respectively, D_u and D_v are diffusive coefficients, $\tau\geqslant 0$ is a time delay measuring the reaction time of the predator population, and we refer explanations of all other parameters to Ref. [20]. Without time delay and diffusion, namely, $\tau=D_u=D_v=0$, model (1) is the well-known population model due to Rosenzweig and MacArthur [20]. With diffusion and when $\tau=0$, the authors of Ref. [20] investigated the patterns of system (1), which, however, are not due to a Turing instability since the positive equilibrium is originally unstable. In the present paper, we aim to investigate if patterns, due to the Turing instability, exist in the presence of a time delay.

To this end, we briefly, in the context of system (1), revisit the Turing instability, which is a mechanism used to explain how biological patterns form [13–16]. Assume $\tau=0$ and the linearization of (1) at its equilibrium is

$$\begin{aligned}\frac{\partial u}{\partial t} &= a_{11}u+a_{12}v+d_1\Delta u,\\ \frac{\partial v}{\partial t} &= a_{21}u+a_{22}v+d_2\Delta v,\end{aligned}\tag{2}$$

where $d_i,i=1,2$ are diffusive coefficients. Considering a solution of (2) in the form $ce^{\lambda t+i\mathbf{kr}}$ and using Refs. [16] or [17], system (2) has an associated characteristic equation

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$\lambda_k^2 - \mathrm{tr}_k\,\lambda_k + \Delta_k = 0$, where k is known as a wave number defined by $k^2 = \mathbf{k}\cdot\mathbf{k}$, $\mathrm{tr}_k = [a_{11} + a_{22} - (d_1 + d_2)k^2]$, and $\Delta_k = d_1 d_2 k^4 - (d_1 a_{22} + d_2 a_{11})k^2 + a_{11}a_{22} - a_{12}a_{21}$. In his pioneering work [13], Turing assumed that the equilibrium was originally stable, but became unstable under the influence of diffusion so that biological patterns formed. When $d_i = 0$, following Turing's idea, we require that $\mathrm{tr}_0 = a_{11} + a_{22} < 0$, $\Delta_0 = a_{11}a_{22} - a_{12}a_{21} > 0$ (see also Refs. [15,17]). Notice that $\mathrm{tr}_k < \mathrm{tr}_0 < 0$ for $k \neq 0$. Then, the origin in the nonhomogeneous case changes its stability only when Δ_k changes sign from positive to negative. Further, notice that Δ_k is a quadratic equation of k^2 and $\Delta_0 > 0$. There exists some $k > 0$ at which $\Delta_k < 0$ if and only if $\Delta_{k_c} = \Delta_0 - \frac{(d_1 a_{22}+d_2 a_{11})^2}{4 d_1 d_2} < 0$, where the critical wave number k_c is given by $k_c^2 = \frac{d_1 a_{22}+d_2 a_{11}}{2 d_1 d_2} > 0$. Hence, the necessary conditions of Turing instability are (A) $a_{11}a_{22} < 0$ and (B) $a_{11} > 0(<0)$ implies $d_2 > (<)d_1$, which are independent of the wave number and are always true in the absence of time delay. In the presence of time delay, we ask the following: Can patterns still form, even if neither (A) nor (B) is satisfied? How does a time delay affect the formation of patterns?

To answer these questions, some attempts have been made. For example, the authors of Refs. [2,3,18,21,22] proposed to use a Taylor series expansion to approximate the delayed variable as follows: $u(t-\tau,x) = u(t,x) - \tau\frac{\partial u(t,x)}{\partial t} + O(\tau^2)$. Note that the approximation holds only when τ is small as it is the Taylor series expansion for $u(t-\tau,u)$ at $\tau = 0$. However, in practice, the delay may be large [7,8,18,19] or, as will be seen in this paper below, the above proposed technique is no longer valid. Reference [9] also made an attempt to find a critical delay and they proposed $\omega_c\tau_c = \arccos(\frac{\omega_c^2 - B}{C})$, in which, as seen from Ref. [9], B and C are functions that are dependent on the wave number. Apart from the dependence on the wave number, it is easy to see that the above formula cannot give τ_c so that $\omega_c\tau_c \geqslant \pi$.

Therefore, in our paper here, we first propose a uniform way of finding the critical time delay τ_c, which will be discussed in Sec. II. We then apply this result to a predator-prey model in Sec. III. Our study shows that when $\tau < \tau_c$, the steady state is stable so there is no pattern to form, while for $\tau > \tau_c$ the steady state loses its stability and a spatial pattern forms. Furthermore, we find in the presence of time delay that most of the patterns discovered in Ref. [20] can be recovered via a Turing instability.

II. A METHOD OF CALCULATING THE CRITICAL TIME DELAY

In this section, we aim at developing a method for finding the critical time delay for a general system of reaction-diffusion equations with a time delay. Consider

$$\frac{\partial u_i}{\partial t} = f_i(u_1,\ldots,u_n,u_{1\tau},\ldots,u_{n\tau}) + D_i\Delta u_i, \qquad (3)$$

where $u_{i\tau} = u_i(t-\tau), i = 1,\ldots,n$ are delayed variables. Assume system (3) has an equilibrium $E^* = (u_i^*)$, at which we define $a_{ij} = \frac{\partial f_i}{\partial u_j}$ and $b_{ij} = \frac{\partial f_i}{\partial u_{j\tau}}$. Then the linearization of (3) at E^* has an associated characteristic equation [7,8,10],

$$\det(\lambda_k I - A - B^{-\lambda_k\tau} + k^2 D) = 0, \qquad (4)$$

where I is an identity matrix, $A = (a_{ij})$, $B = (b_{ij})$, $D = \mathrm{diag}(D_i)$, and k is the wave number. For simplicity, we assume $n = 2$ in the rest of this section, although our method works for any $n \in \mathbf{N}$, and we also assume $b_{12}b_{21} = 0$. Then the characteristic equation (4) reads

$$\lambda_k^2 - P_k\lambda_k + Q_k - (\lambda_k R_k + S_k)e^{\lambda_k\tau} = 0, \qquad (5)$$

where $P_k = a_{11} + a_{22} - (d_1 + d_2)k^2$, $Q_k = d_1 d_2 k^4 - (d_1 a_{22} + d_2 a_{11})k^2 + a_{11}a_{22} - a_{12}a_{21}$, $R_k = b_{11} + b_{22}$, and $S_k = (d_1 b_{22} + d_2 b_{11})k^2 + b_{12}a_{21} + b_{21}a_{12} - a_{11}b_{22} - a_{22}b_{11}$. As λ, the root of (5), especially the real part of such a root, is dependent on τ [6,10], we know the stability of E^* changes only when the real part of λ changes its sign, which happens when $\tau = \tau_c$ at which $\lambda = \pm i\omega_k$, $\omega_k > 0$ [7,8,10]. Next we find such a τ_c. Assuming (5) has a pure imaginary root $i\omega_k$, substituting into it, and separating the real and imaginary parts yields

$$\tau_j^k = \begin{cases} \frac{1}{\omega_k}\arctan\left(\frac{T_1^k}{T_2^k}\right) + \frac{j2\pi}{\omega_k}, & \text{if } T_i^k > 0,\\ \frac{1}{\omega_k}\left[\pi + \arctan\left(\frac{T_1^k}{T_2^k}\right)\right] + \frac{j2\pi}{\omega_k}, & \text{if } T_2^k < 0,\\ \frac{1}{\omega_k}\left[2\pi + \arctan\left(\frac{T_1^k}{T_2^k}\right)\right] + \frac{j2\pi}{\omega_k}, & \text{if } T_1^k < 0,\ T_2^k > 0, \end{cases} \qquad (6)$$

where $j = 0,1,\ldots$, $T_1^k = P_k S_k\omega_k + Q_k R_k\omega_k - R_k\omega_k^3$, and $T_2^k = S_k Q_k - S_k\omega_k^2 - P_k R_k\omega_k^2$. Here $\omega_k > 0$ are determined by the positive solution of $(T_1^k)^2 + (T_2^k)^2 = (S_k^2 + R_k^2\omega_k^2)^2$. Then from Ref. [11] we know the critical time delay is given by $\tau_c = \min_k\{\tau_0^k\}$. Furthermore, from Refs. [11,12] we conclude that, if E^* is stable when $\tau = 0$, then for τ_c given above (a) the equilibrium E^* is stable for all $0 \leqslant \tau < \tau_c$, (b) E^* is unstable for all $\tau > \tau_c$, and (c) if $\mathrm{Re}(\frac{d\lambda_k}{d\tau})|_{\tau=\tau_c} > 0$, Hopf bifurcation occurs at $\tau = \tau_c$.

III. APPLICATION TO THE EXTENDED ROSENZWEIG AND MACARTHUR MODEL

In this section, we apply the result obtained in Sec. II to the extended Rosenzweig and MacArthur model (1) with a zero flux boundary condition. First, we apply transformations in Ref. [20] to system (1) so that we can reduce the number of parameters. We then reach the following dimensionless model,

$$\begin{aligned} \frac{du}{dt} &= \alpha u\left(1 - u - \frac{v}{1+\beta u}\right) + d_1\Delta u,\\ \frac{dv}{dt} &= v\left(\frac{\beta u(t-\tau)}{1+\beta u(t-\tau)} - \gamma\right) + d_2\Delta v, \qquad (7)\\ \frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu} = 0, \end{aligned}$$

where all parameters are positive, according to their physical meaning. It is easy to check that system (7) has three equilibria, $E_0(0,0)$, $E_1(1,0)$, and $E_2(u^*,v^*)$, with $u^* = \frac{\gamma}{\beta(1-\gamma)}$, $v^* = (1-u^*)(1+\beta u^*)$, which implies that a positive equilibrium exists if and only if $\beta > \beta_0 = \frac{\gamma}{1-\gamma}$ and $0 < \gamma < 1$. Since we are only interested in the dynamical behavior of the positive equilibrium, in the rest of this paper we assume this condition holds.

A. Linear stability analysis of (7)

Linearizing (7) at E_2 gives

$$\begin{pmatrix}\dot u\\ \dot v\end{pmatrix}=\begin{pmatrix}J_{11} & J_{12}\\ 0 & 0\end{pmatrix}\begin{pmatrix}u\\ v\end{pmatrix}+\begin{pmatrix}0 & 0\\ J_{21} & 0\end{pmatrix}\begin{pmatrix}u_\tau\\ v_\tau\end{pmatrix}+\begin{pmatrix}d_1 & 0\\ 0 & d_2\end{pmatrix}\begin{pmatrix}\Delta u\\ \Delta v\end{pmatrix}, \tag{8}$$

where $J_{11}=\alpha u^*\frac{-(1+\beta u^*)^2+\beta v^*}{(1+\beta u^*)^2}=\frac{\alpha\gamma(\beta-\beta_1)}{\beta}$, $J_{12}=\frac{-\alpha u^*}{1+\beta u^*}=-\frac{\alpha\gamma}{\beta}<0$, $J_{21}=\frac{\beta v^*}{(1+\beta u^*)^2}=(1-\gamma)(\beta-\beta_0)>0$, and $\beta_1=\frac{1+\gamma}{1-\gamma}>1$. The characteristic equation associated with (8) is

$$\begin{aligned}&\lambda_k^2+[(d_1+d_2)k^2-J_{11}]\lambda_k\\ &\quad+d_1d_2k^4-d_2J_{11}k^2-J_{12}J_{21}e^{-\lambda_k\tau}\\ &=\lambda_k^2+p_k\lambda_k+q_k+s_ke^{-\lambda_k\tau}=0,\end{aligned} \tag{9}$$

the roots of which determine the stability of E_2 [6–8,10]. So, we next investigate the distribution of such roots.

1. The case without diffusion

In this case we have $d_1=d_2=0$. Then the characteristic equation (9) becomes

$$\lambda_0^2-J_{11}\lambda_0-J_{12}J_{21}e^{-\lambda_0\tau}=0. \tag{10}$$

Assuming (10) has a pure imaginary root $i\omega$, substituting it into (10), and separating the real and imaginary parts yields

$$\begin{aligned}\omega^2+J_{12}J_{21}\cos(\omega\tau)&=0,\\ J_{11}\omega-J_{12}J_{21}\sin(\omega\tau)&=0.\end{aligned} \tag{11}$$

It implies

$$\omega^4+J_{11}^2\omega^2-J_{12}^2J_{21}^2=0. \tag{12}$$

Obviously, Eq. (12) has a unique positive solution ω_0 given by $\omega_0^2=\frac{-J_{11}^2+\sqrt{J_{11}^4+4J_{12}^2J_{21}^2}}{2}$ and at which we have

$$\tau_j=\begin{cases}\frac{1}{\omega_0}\arctan\left(-\frac{J_{11}}{\omega_0}\right)+\frac{2\pi j}{\omega_0}, j=0,1,\ldots, & \text{if}\quad J_{11}<0,\\ \frac{1}{\omega_0}\arctan\left(-\frac{J_{11}}{\omega_0}\right)+\frac{2\pi j}{\omega_0}, j=1,\ldots, & \text{if}\quad J_{11}>0.\end{cases} \tag{13}$$

Clearly, $0<\tau_0<\tau_1<\cdots<\tau_j<\cdots$, and when $\tau=\tau_j$, $\lambda_0=\pm i\omega_0$ are a pair of pure imaginary roots. From (10), we have $(\frac{d\lambda}{d\tau})^{-1}=\frac{J_{11}-2\lambda}{\lambda(\lambda^2-J_{11}\lambda)}-\frac{\tau}{\lambda}$. Then at $\tau=\tau_j$, we have

$$\begin{aligned}\operatorname{sgn}\operatorname{Re}\left(\frac{d\lambda}{d\tau}\right)&=\operatorname{sgn}\operatorname{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}\\ &=\operatorname{sgn}\left(\frac{J_{11}^2+2\omega_0^2}{\omega_0^2(J_{11}^2+\omega_0^2)}\right)>0,\end{aligned} \tag{14}$$

which is known as the transversality condition. Notice that when $\tau=0$, the equilibrium E_2 is stable if and only if $\beta<\beta_1$. From Refs. [7,8,10], transversality condition (14) implies the following: (1) If $\beta\geqslant\beta_1$, E_2 is unstable for all $\tau\geqslant 0$; (2) if $\beta<\beta_1$, there $\tau_0>0$ given by (13) such that E_2 is stable for all $0\leqslant\tau<\tau_0$, and unstable for $\tau>\tau_0$; and (3) when $\tau=\tau_0$, Hopf bifurcation occurs.

More precisely, Hopf bifurcation happens with a stable bifurcated periodic solution on the center manifold due to the stability of the equilibrium changes from stable to unstable when τ crosses τ_0 from the left to the right. In full phase space, however, the stability of the periodic solution needs to be determined by the normal form [7,10].

Note that, from the above conclusions, the positive equilibrium E_2 exists when $\beta>\beta_0$ and $0<\gamma<1$; furthermore, it is stable when $\tau=0$, $\beta<\beta_1$, which agrees well with Ref. [20].

2. The case with diffusion

The existence of diffusion implies $d_1d_2\neq 0$. As what we did in the previous section, assume (9) has a pure imaginary root $i\omega_k$ ($\omega_k>0$), but is dependent on the wave number k. Then we have

$$\begin{aligned}-\omega_k^2+q_k+s_k\cos(\omega_k\tau)&=0,\\ p_k\omega_k-s_k\sin(\omega_k\tau)&=0,\end{aligned} \tag{15}$$

which implies

$$\omega_k^4+\left(p_k^2-2q_k\right)\omega_k^2+q_k^2-s_k^2=0. \tag{16}$$

Since $p_k^2-2q_k=(d_1^2+d_2^2)k^4-2J_{11}k^2+J_{11}^2>d_1^2k^4-2J_{11}k^2+J_{11}^2=(d_1k^2-J_{11})^2\geqslant 0$, Eq. (16) has a unique positive solution ω_k^2 if and only if

$$q_k^2-s_k^2<0. \tag{17}$$

Noticing that $J_{11}<0$ when $\beta<\beta_1$, and $J_{12}<0$, $J_{21}>0$ yields $p_k>0, q_k>0$, and $s_k>0$. Condition (17) is equivalent

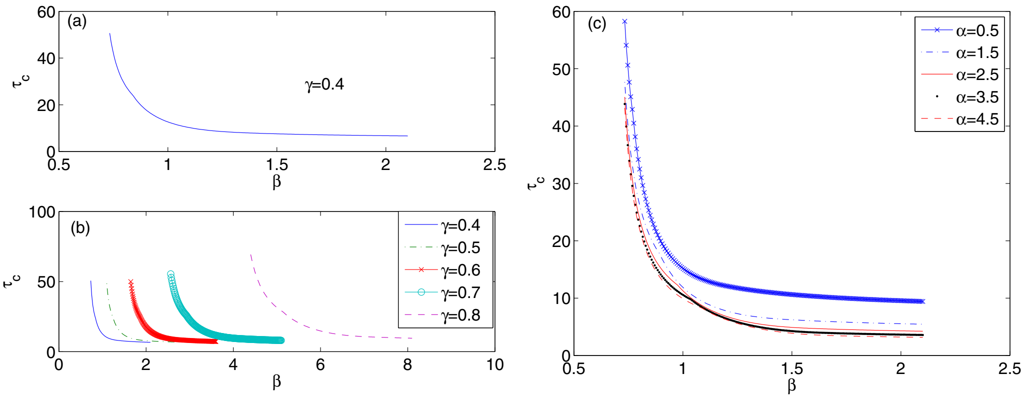

FIG. 1. (Color online) Values of the critical delay τ_c for (a), (b) $\alpha=1$ and (c) $\gamma=0.4$.

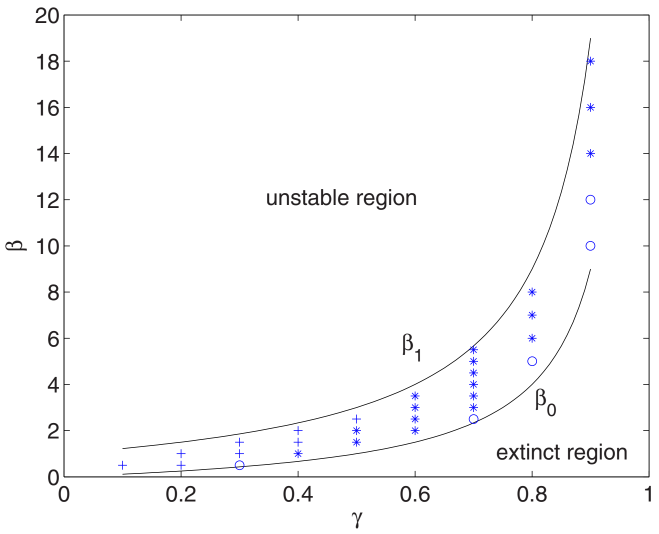

FIG. 2. (Color online) Pattern selection for $d_1 = 0.1$, $d_2 = 0.01$, and $\alpha = 1$ with + for spirals, ○ for targets, and * for microspirals.

to

$$d_1 d_2 k^4 - d_2 J_{11} k^2 + J_{12} J_{21} < 0, \tag{18}$$

under which, at each ω_k, we have the critical delay

$$\tau_j^k = \begin{cases} \frac{1}{\omega_k} \arctan\left(\frac{p_k \omega_k}{q_k - \omega_k^2}\right) + \frac{2\pi j}{\omega_k}, & \text{if} \quad q_k - \omega_k^2 > 0, \\ \frac{1}{\omega_k}\left[\arctan\left(\frac{p_k \omega_k}{q_k - \omega_k^2}\right) + \pi\right] + \frac{2\pi j}{\omega_k}, & \text{if} \quad q_k - \omega_k^2 < 0, \end{cases} \tag{19}$$

where $j = 0,1,\ldots$. From (9), we have $(\frac{d\lambda}{d\tau})^{-1} = \frac{2\lambda_k + p_k}{\lambda_k s_k e^{-\lambda_k \tau}} - \frac{\tau}{\lambda_k} = -\frac{2\lambda_k + p_k}{\lambda_k(\lambda_k^2 + p_k \lambda_k + q_k)} - \frac{\tau}{\lambda_k}$, which yields, at $\tau = \tau_j^k$, the following transversality condition:

$$\begin{aligned} \operatorname{sgn} \operatorname{Re}\left(\frac{d\lambda}{d\tau}\right) &= \operatorname{sgn} \operatorname{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1} \\ &= \operatorname{sgn}\left(\frac{p_k^2 - 2q_k + 2\omega_k^2}{\left(q_k - \omega_k^2\right)^2 + p_k^2 \omega_k^2)}\right) > 0. \end{aligned} \tag{20}$$

Notice that when $\tau = 0$ equilibrium E_2 is stable if and only if $p_k > 0$, namely,

$$(d_1 + d_2)k^2 > J_{11}, \tag{21}$$

which is automatically satisfied due to the assumption $\beta < \beta_1$, made in the previous section. Let $\tau_c = \min\{\tau_0^k, 0 \leqslant k \leqslant k_c\}$, where k_c is determined by (18). Then we make our conclusion as follows: (1) If $\beta \geqslant \beta_1$, E_2 is unstable for all $\tau \geqslant 0$; (2) if $\beta < \beta_1$, there is $\tau_c > 0$ given by (19) such that E_2 is stable for all $0 \leqslant \tau < \tau_c$, and unstable for $\tau > \tau_c$; and (3) when $\tau = \tau_c$, Hopf bifurcation occurs when τ crosses τ_0 from the left to the right.

The bifurcation direction can be determined by using the normal form [11]. If we choose the time delay as the control parameter, then from this conclusion, we obtain the so-called Turing space [15–17], $\alpha > 0$, $0 < \gamma < 1$, $\beta_0 < \beta < \beta_1$, and $\tau > \tau_c$ in which the Turing instability occurs.

Please note that when $\beta > \beta_1$, $\tau = 0$, the authors of Ref. [20] also investigated the formation of patterns of system (7). However, as seen from our discussion above, the patterns in Ref. [20] are not of Turing type, which was pointed out in the Introduction.

B. Pattern selection

In order to study the selection of patterns, we first discuss the relation between the critical delay and parameters appearing in the model equations. Using a numerical method, we found that the critical delay is a decreasing function of α, β and an increasing function of γ, as seen in Fig. 1, where we showed two cases in Figs. 1(a) and 1(a) for $\alpha = 1$ and Fig. 1(c) for $\gamma = 0.4$. In Fig. 1(a), where we set $\alpha = 1$ and $\gamma = 0.4$, the critical delay varies from 50 to 10 as β varies in the range from 0.67 to 2.3. In Fig. 1(b), we fixed $\alpha = 1$ only and varied both β and γ. Then for any given β the critical delay increases as γ increases. For example, for $\beta = 2$ we can see that the critical delay increases as γ changes from 0.4 to 0.8. In Fig. 1(c) we set $\gamma = 0.4$, and it shows that τ_c decreases as α increases.

Recalling the model equations (1) and (7) and Ref. [20], we know $\alpha = \frac{a}{m}$, $\beta = \frac{k}{c}$, $\gamma = \frac{n}{m}$, where a is the growth rate

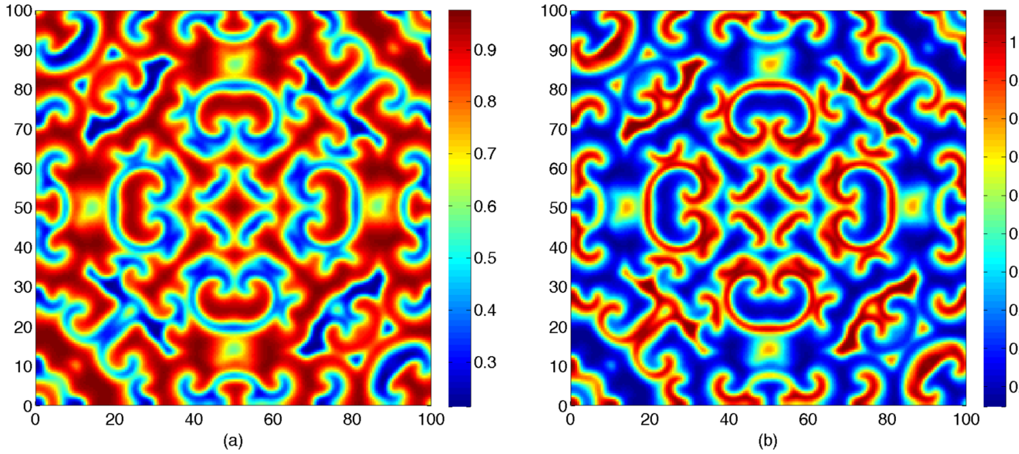

FIG. 3. (Color online) Micro spirals: (a) prey and (b) predator. The parameters are $d_1 = 0.1$, $d_2 = 0.01$, $\alpha = 1$, $\gamma = 0.4$, $\beta = 1$, $\tau = 12.7$, and time $t = 9100$.

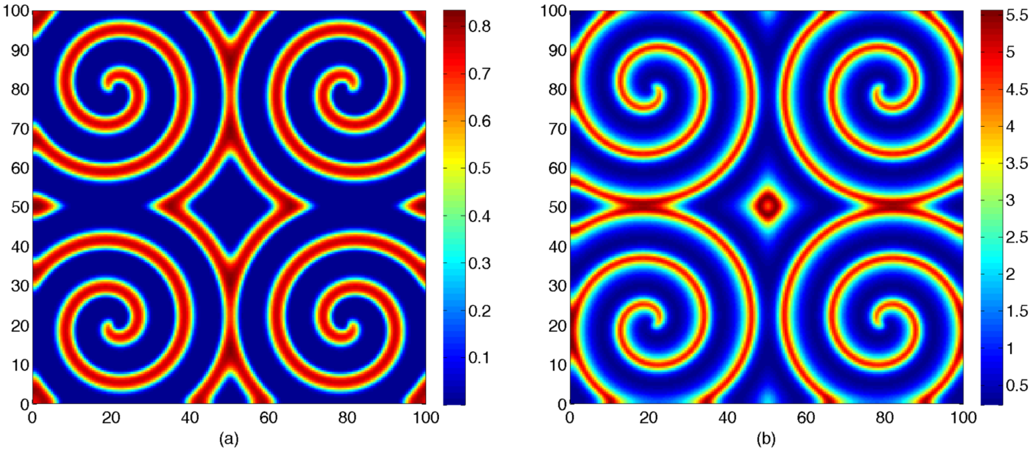

FIG. 4. (Color online) Four-head spirals: (a) prey and (b) predator. The parameters are $d_1 = 0.1$, $d_2 = 0.01$, $\alpha = 1$, $\gamma = 0.1$, $\beta = 0.5$, $\tau = 10.5$, and time $t = 1500$.

of prey, c the half saturation of prey density, k the carrying capacity defined as the maximum number of prey that the environment can sustain indefinitely, and m and n are the birth rate and death rate of the predator. Then, from an ecological point of view, if the prey grows faster than the predator or the net increase of the predator gets bigger, the steady state of system (1) becomes unstable at a small time delay, otherwise the stability of the steady state is more robust towards the effect of time delay. In other words, a large ratio of the prey's growth rate and the birth rate of the predators results in a small critical period of maturation or gestation of the predators; however, a large ratio of the birth rate and death rate of the predators implies a large critical maturation or gestation period of the predators. The latter says that the predator has a large critical period of maturation or gestation if the birth rate of the predator is larger than its death rate.

We know from a previous analysis that the Turing instability occurs in system (1) or (7) when the time delay crosses its critical value τ_c and all other parameters are in the Turing space. Now, we numerically investigate the effect of time delay on the formation of patterns, and we found three types of patterns (see Fig. 2), where we fixed $\alpha = 1$ and varied γ from 0 to 1 and β from β_0 to β_1.

We note that when γ is small, say, less than 0.5, the spirals dominate the dynamics of the system, while for large γ, say, greater than 0.5, microspirals or lattices dominate. Furthermore, when the parameters are close to curve β_0, we observed target patterns. Again, we would like to emphasize that all patterns observed are due to the Turing instability, which is different from the case investigated in Ref. [20], where all patterns are not due to the Turing instability and the time delay is zero.

To observe the patterns, in our simulations we set the parameters as follows: $d_1 = 0.1$, $d_2 = 0.01$, $\alpha = 1$, the spatial step size is 0.5, and the time step is 0.1. Furthermore, $\gamma = 0.4$, $\beta = 1$ for the microspirals; then we know the critical time delay is $\tau_c = 12.6818$. So we use $\tau = 12.7$. See Fig. 3, which shows the microspiral patterns in both the predator and prey populations.

To see spirals, we set $\gamma = 0.1$, $\beta = 0.5$, $\tau = 10.5$. Then $\tau_c = 10.4367$, and at times $t = 1500$ and $t = 1000$ we obtained Figs. 4 and 5, respectively. If we set $\gamma = 0.8$, $\beta = 5$,

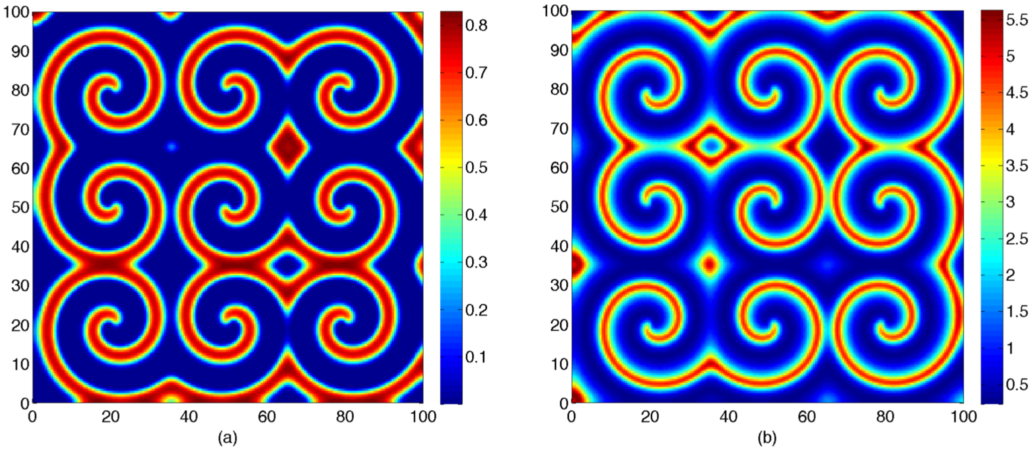

FIG. 5. (Color online) Nine-head spirals: (a) prey and (b) predator. The parameters are $d_1 = 0.1$, $d_2 = 0.01$, $\alpha = 1$, $\gamma = 0.1$, $\beta = 0.5$, $\tau = 10.5$, and time $t = 1000$.

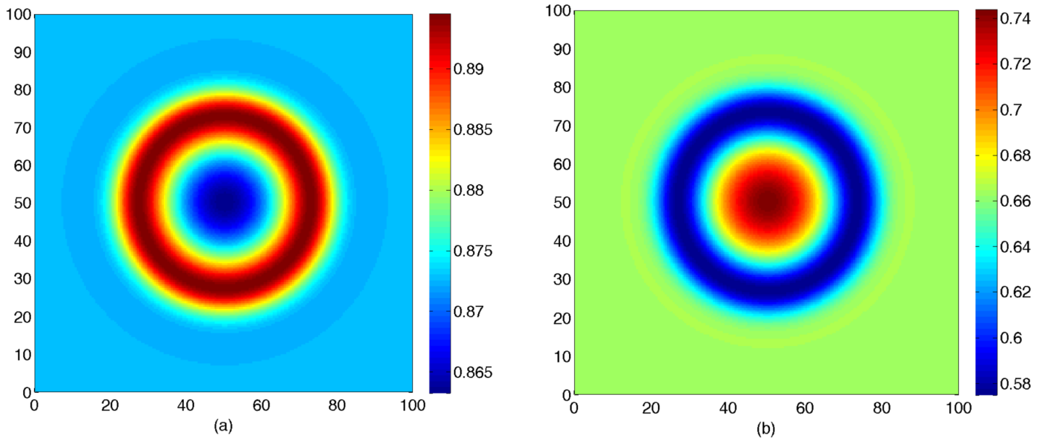

FIG. 6. (Color online) Targets: (a) prey and (b) predator. The parameters are $d_1 = 0.1$, $d_2 = 0.01$, $\alpha = 1$, $\gamma = 0.8$, $\beta = 5$, $\tau = 31.5$, and time $t = 10\,000$.

$\tau = 31.5$, then $\tau_c = 31.4859$, and at time $t = 10\,000$ we obtained Fig. 6.

For our simulation, we used the standard two-dimensional (2D) finite difference method with special settings for the initial values due to the delay, namely, we used $u(t) = u(0)$, $v(t) = v(0)$ for $-\tau \leqslant t < 0$. The initial value $[u(0), v(0)]$ is the perturbation of the equilibrium $E^*(u^*, v^*)$. For example, for Fig. 4 the initial values are $u(0) = u^* - 0.000\,001(x - 20)(x - 80)$ and $v(0) = v^* - 0.000\,001(y - 20)(y - 80)$, and for Fig. 5 we used $u(0) = u^* - 0.000\,001(x - 20)(x - 50)(x - 80)$ and $v(0) = v^* - 0.000\,001(y - 20)(y - 50)(y - 80)$.

IV. CONCLUSION

Time delay is commonly used for providing more realistic models to describe biological and chemical processes, and it may significantly change the dynamics of systems. In this paper we have formulated a way of calculating the critical time delay, which can be used to investigate the Turing instability due to the time lag. Then we applied our result to a predator-prey model with time delay, which ecologically measures the maturation, gestation period, or reaction time of the predator population. Turing patterns have been observed from the predator-prey model in question under the influence of time delay.

ACKNOWLEDGMENTS

We gratefully thank the anonymous referees for their comments on improvement of the presentation of this work. H.Z. would also like to acknowledge the support from the National Natural Science Foundation of China (Grant No. 11101318).

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