Research Article

Allee-Effect-Induced Instability in a Reaction-Diffusion Predator-Prey Model

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We investigate the spatiotemporal dynamics induced by Allee effect in a reaction-diffusion predator-prey model. In the case without Allee effect, there is nonexistence of diffusion-driven instability for the model. And in the case with Allee effect, the positive equilibrium may be unstable under certain conditions. This instability is induced by Allee effect and diffusion together. Furthermore, via numerical simulations, the model dynamics exhibits both Allee effect and diffusion controlled pattern formation growth to holes, stripes-holes mixture, stripes, stripes-spots mixture, and spots replication, which shows that the dynamics of the model with Allee effect is not simple, but rich and complex.

1. Introduction

In 1952, Turing published one paper [1] on the subject called "pattern formation"—one of the central issues in ecology [2], putting forth the Turing hypothesis of diffusion-driven instability. Pattern formation in mathematics refers to the process that, by changing a bifurcation parameter, the spatially homogeneous steady states lose stability to spatially inhomogeneous perturbations, and stable inhomogeneous solutions arise [3]. Turing's revolutionary idea was that passive diffusion could interact with the chemical reaction in such a way that even if the reaction by itself has no symmetry-breaking capabilities, diffusion can destabilize the symmetry, so that the system with diffusion can have them [4]. From then on, pattern formation has become a very active area of research, motivated in part by the realization that there are many common aspects of patterns formed by diverse physical, chemical, and biological systems and by cellular automata and reaction-diffusion equations [5–7]. And the appearance and evolution of these patterns have been a focus of recent research activity across several disciplines [8–15].

Segel and Jackson [16] were the first to call attention to the Turing's ideas that would be also applicable in population dynamics. At the same time, Gierer and Meinhardt [17] gave a biologically justified formulation of a Turing model and studied its properties by employing numerical simulation. Levin and Segel [18, 19] suggested this scenario of spatial pattern formation as a possible origin of planktonic patchiness.

The understanding of patterns and mechanisms of spatial dispersal of interacting species is an issue of significant current interest in conservation biology, ecology, and biochemical reactions [20–22]. The spatial component of ecological interaction has been identified as an important factor in how ecological communities are shaped. Empirical evidence suggests that the spatial scale and structure of environment can influence population interactions [23]. A significant amount of work has been done by using this idea in the field of mathematical biology by Murray [20], Okubo and Levin [21], Cantrell and Cosner [23], and others [3, 24–27].

In general, assume that the species prey and predator move randomly on spatial domain, and the spatial movement of the individuals is modeled by diffusion with diffusion coefficients $d_1 > 0$, $d_2 > 0$ for the prey u and predator v, respectively. As an example, a prototypical predator-prey

interaction model with logistic growth rate of the prey in the absence of predation is of the following form [28, 29]:

$$\frac{du}{dt} = u(\alpha - \beta u) - f(u)g(v) + d_1 \Delta u,$$

$$\frac{dv}{dt} = \sigma f(u)g(v) - z(v) + d_2 \Delta v,$$

(1)

where $u(t)$ and $v(t)$ are the densities of the prey and predator at time $t > 0$, respectively. And $\Delta = \partial^2/\partial x^2 + \partial^2/\partial y^2$ is the Laplacian operator in two-dimensional space.

In recent years, many studies, for example, [30–40] and the references therein, show that the reaction-diffusion predator-prey model (e.g., model (1)) is an appropriate tool for investigating the fundamental mechanism of complex spatiotemporal predation dynamics. Of them, Alonso et al. [30] studied how diffusion affects the stability of predator-prey coexistence equilibria and show a new difference between ratio- and prey-dependent models; that is, the prey-dependent models cannot give rise to spatial structures through diffusion-driven instabilities; however, predator-dependent models with the same degree of complexity can. Baurmann et al. [31] investigated the emergence of spatiotemporal patterns in a generalized predator-prey system, derived the conditions for Hopf and Turing instabilities without specifying the predator-prey functional responses discussed their biological implications, identified the codimension-2 Turing-Hopf bifurcation and the codimension-3 Turing-Takens-Bogdanov bifurcation, and found that these bifurcations give rise to complex pattern formation processes in their neighborhood. And Banerjee and Petrovskii [36] studied possible scenarios of pattern formation in a ratio-dependent predator-prey system and found that the emerging patterns are stationary in the large time limit and exhibit only an insignificant spatial irregularity, and spatiotemporal chaos can indeed be observed but only for parameters well inside the Turing-Hopf parameter domain, away from the bifurcation point. Rodrigues et al. [40] paid their attentions to system properties in a vicinity of the Turing-Hopf bifurcation of the predator-prey and found that the asymptotical stationary pattern arises as a sudden transition between two different patterns.

On the other hand, in the research of population dynamics, Allee effect in the population growth has been studied extensively. Allee effect, named after ecologist Allee [41], is a phenomenon in biology characterized by a positive correlation between population size or density and the mean individual fitness (often times measured as per capita population growth rate) of a population or species [42] and may occur under several mechanisms, such as difficulties in finding mates when population density is low, social dysfunction at small population sizes, and increased predation risk due to failing flocking or schooling behavior [43–45]. In an ecological point of view, Allee effect has been modeled into strong and weak cases. The strong Allee effect introduces a population threshold, and the population must surpass this threshold to grow. In contrast, a population with a weak Allee effect does not have a threshold. It has been attracting much more attention recently owing to its strong potential impact

on the population dynamics of many plants and animal species [46]. Detailed investigations relating to Allee effect may be found in [47–59].

In most predation models, it has been considered that Allee effect influences only the prey population. For instance, in model (1), corresponding to the function of prey growth rate of the prey $u(\alpha - \beta u)$, to express Allee effect, the most usual continuous growth of the equation that is given as:

$$G(u) = u\left(\alpha - \beta u - \frac{q}{u+b}\right),$$

(2)

is called additive Allee effect, which was first deduced in [43] and applied in [60–62]. Here, $qu/(u+b)$ is the term of additive Allee effect and $b \in (0,1)$ and $q \in (0,1)$ are Allee-effect constants. If $q < b\alpha$, then $G(0) = 0$, $G'(0) > 0$, and $G(u)$ is called weak Allee effect; if $q > b\alpha$, then $G(0) = 0$, $G'(0) < 0$, and $G(u)$ is strong Allee effect.

Corresponding to model (1), a prototypical predator-prey interaction model with Allee effect on the prey is given by

$$\frac{du}{dt} = u\left(\alpha - \beta u - \frac{q}{u+b}\right) - f(u)g(v) + d_1 \Delta u,$$

$$\frac{dv}{dt} = \sigma f(u)g(v) - z(v) + d_2 \Delta v.$$

(3)

According to Turing's idea [1], for model (1)—the special case of model (3) without Allee effect (i.e., $q = 0$)—if the positive equilibrium point $E^* = (u^*, v^*)$ is stable in the case $d_1 = d_2 = 0$ (the nonspatial model) but unstable with respect to solutions in the cases $d_1 > 0$ and $d_2 > 0$ (the spatial model), then E^* is called diffusion-driven instability (i.e., Turing instability or Turing bifurcation), and model (1) may exhibit Turing pattern formation. In contrast, if $E^* = (u^*, v^*)$ is stable in the cases $d_1 > 0$ and $d_2 > 0$, then there is nonexistence of diffusion-driven instability for model (1), and the model cannot exhibit any pattern formation. And in this situation, for model (3), with Allee effect on the prey, there comes a question: is there any instability of the positive equilibrium occurring? Or, is there any diffusion-driven instability of the positive equilibrium occurring? In addition, does model (3) exhibit any pattern formation controlled by Allee effect?

The goal of this paper is to make an insight into the instability induced by the Allee effect in model (3). Our main interest is to check whether the Allee effect is a plausible mechanism of developing spatiotemporal pattern in the model.

The paper is organized as follows. In the next section, we give the model and stability of the equilibria. In Section 3, we discuss the stability/instability of the spatial model with/without Allee effect, derive the conditions for the occurrence of Allee-diffusion-driven instability of the case with Allee effect, and illustrate typical Turing patterns via numerical simulations. Finally, conclusions and remarks are presented in Section 4.

2. The Model System

In model (1), the product $f(u)g(v)$ gives the rate at which prey is consumed. The prey consumed per predator, $f(u)g(v)/v$, was termed as the functional response by Solomon [63]. These functions can be defined in different ways. In this paper, following Lotka [64], we adopt

$$f(u) = cu, \tag{4}$$

which is a linear functional response without saturation, where $c > 0$ denotes the capture rate [65]. And following Harrison [28, 29], we set

$$g(v) = \frac{v}{mv + 1}, \tag{5}$$

where $m > 0$ represents a reduction in the predation rate at high predator densities due to mutual interference among the predators while searching for food.

The proportionality constant σ is the rate of prey consumption. And the function $z(v)$ is given by

$$z(v) = \gamma v + lv^2, \quad \gamma > 0, \ l \geq 0, \tag{6}$$

where γ denotes the natural death rate of the predator, and $l > 0$ can be used to model predator intraspecific competition that is not the direct competition for food, such as some type of territoriality [28]. In this paper, we will discuss the case $l = 0$, which is used in a much more traditional case.

Based on the previous discussions, we can establish the following predation model of two partial differential equations with additive Allee effect on prey:

$$\frac{\partial u}{\partial t} = u\left(\alpha - \beta u - \frac{q}{u + b}\right) - \frac{cuv}{mv + 1} + d_1 \Delta u,$$
$$\frac{\partial v}{\partial t} = v\left(-\gamma + \frac{su}{mv + 1}\right) + d_2 \Delta v, \tag{7}$$

with the positive initial conditions:

$$u(x, y, 0) > 0, \qquad v(x, y, 0) > 0,$$
$$(x, y) \in \Omega = (0, L) \times (0, L), \tag{8}$$

and the zero-flux boundary conditions:

$$\frac{\partial u}{\partial v} = \frac{\partial v}{\partial v} = 0, \quad (x, y) \in \partial \Omega, \tag{9}$$

where s denotes conversion rate, and Ω is a bounded open domain in $\mathbb{R}_+^2$ with boundary $\partial \Omega$. v is the outward unit normal vector on $\partial \Omega$, and zero-flux conditions reflect the situation where the population cannot move across the boundary of the domain.

The main purpose of this paper is to focus on the impacts of diffusion or/and Allee effect on the model system about the positive equilibrium, especially for the instability and pattern formation.

3. Stability Analysis

3.1. The Case without Allee Effect. We first consider the stability of the positive equilibria of model (7) without Allee effect; that is, $q = 0$, and the model is given by

$$\frac{\partial u}{\partial t} = u(\alpha - \beta u) - \frac{cuv}{mv + 1} + d_1 \Delta u,$$
$$\frac{\partial v}{\partial t} = v\left(-\gamma + \frac{su}{mv + 1}\right) + d_2 \Delta v. \tag{10}$$

Easy to know that model (10) has a unique positive equilibrium $E^* = (u^*, v^*)$ with $s\alpha > \beta\gamma$, where

$$u^* = \frac{ms\alpha - cs + \sqrt{s^2(m\alpha - c)^2 + 4cms\beta\gamma}}{2ms\beta},$$
$$v^* = \frac{su^* - \gamma}{m\gamma}, \tag{11}$$

which is locally asymptotically stable. Next, we will discuss the effect of diffusion on E^*.

Set $U_1 = u - u^*$, $V_1 = v - v^*$, and the linearized system (10) around $E^* = (u^*, v^*)$ is as follows:

$$\frac{\partial U_1}{\partial t} = d_1 \Delta U_1 - \beta u^* U_1 - \frac{cu^*}{(mv^* + 1)^2} U_2,$$
$$\frac{\partial U_2}{\partial t} = d_2 \Delta U_2 + \frac{sv^*}{mv^* + 1} U_1 - \frac{msu^* v^*}{(mv^* + 1)^2} U_2, \tag{12}$$
$$\left.\frac{\partial U_1}{\partial v}\right|_{\partial \Omega} = \left.\frac{\partial U_2}{\partial v}\right|_{\partial \Omega} = 0.$$

Following Malchow et al. [66], we know that any solution of system (12) can be expanded into a Fourier series as follows:

$$U_1(\mathbf{r}, t) = \sum_{n,m=0}^{\infty} u_{nm}(\mathbf{r}, t) = \sum_{n,m=0}^{\infty} \alpha_{nm}(t) \sin \mathbf{k r},$$
$$U_2(\mathbf{r}, t) = \sum_{n,m=0}^{\infty} v_{nm}(\mathbf{r}, t) = \sum_{n,m=0}^{\infty} \beta_{nm}(t) \sin \mathbf{k r}, \tag{13}$$

where $\mathbf{r} = (x, y)$ and $0 < x < L$, $0 < y < L$. $\mathbf{k} = (k_n, k_m)$ and $k_n = n\pi/L$, $k_m = m\pi/L$ are the corresponding wavenumbers.

Having substituted u_{nm} and v_{nm} into (12), we obtain

$$\frac{d\alpha_{nm}}{dt} = \left(-\beta u^* - d_1 k^2\right)\alpha_{nm} + -\frac{cu^*}{(mv^* + 1)^2}\beta_{nm},$$
$$\frac{d\beta_{nm}}{dt} = \frac{sv^*}{mv^* + 1}\alpha_{nm} + \left(-\frac{msu^* v^*}{(mv^* + 1)^2} - d_2 k^2\right)\beta_{nm}, \tag{14}$$

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

A general solution of (14) 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 (8) and the exponents λ_1, λ_2 are the eigenvalues of the following matrix:

$$J_{E^*} = \begin{pmatrix} -\beta u^* - d_1 k^2 & -\dfrac{cu^*}{(mv^* + 1)^2} \\ \dfrac{sv^*}{mv^* + 1} & -\dfrac{msu^* v^*}{(mv^* + 1)^2} - d_2 k^2 \end{pmatrix}. \quad (15)$$

Correspondingly, λ_i $(i = 1, 2)$ arises as the solution of following equation:

$$\lambda_i^2 - \mathrm{tr}\,(J_{E^*})\,\lambda_i + \det(J_{E^*}) = 0, \quad (16)$$

where the trace and determinant of J_{E^*} are, respectively,

$$\mathrm{tr}\,(J_{E^*}) = -(d_1 + d_2)\,k^2 - \beta u^* - \frac{msu^* v^*}{(mv^* + 1)^2},$$

$$\det(J_{E^*}) = d_1 d_2 k^4 + \left(d_2 \beta u^* + \frac{d_1 msu^* v^*}{(mv^* + 1)^2} \right) k^2 \quad (17)$$

$$+ \frac{bm\beta u^{*2} v^*}{(mv^* + 1)^2} + \frac{bcu^* v^*}{(mv^* + 1)^3}.$$

It is easy to know that $\mathrm{tr}(J_{E^*}) < 0$ and $\det(J_{E^*}) > 0$. Hence, the positive equilibrium E^* of model (10) is uniformly asymptotically stable.

Obviously, there is no effect on the stability of the positive equilibrium whether model (10) with diffusion or not. That is to say, there is nonexistence of diffusion-driven instability in model (10), which is the special case of model (7) without Allee effect.

3.2. The Case with Allee Effect

3.2.1. Allee-Diffusion-Driven Instability. In this subsection, we restrict ourselves to the stability analysis of spatial model (7), which is in the presence of Allee effect on prey.

For the sake of learning the effect of Allee effect on the positive equilibrium of model (7), we first give a definition called Allee-diffusion-driven instability as follows.

Definition 1. If a positive equilibrium is uniformly asymptotically stable in the reaction-diffusion model without Allee-effect (e.g., model (10)) but unstable with respect to solutions of the reaction-diffusion model with Allee effect (e.g., model (7)), then this instability is called Allee-diffusion-driven instability.

Next, we will only investigate the stability of the positive equilibrium of model (7). For simplicity, we take the weak Allee effect case $(0 < q < b\alpha)$ as an example, and the unique positive equilibrium is named $E_w = (u_w, v_w) = (u_w, (su_w - \gamma)/m\gamma)$. We first give the stability of E_w in the case without diffusion as follows that is, $d_1 = d_2 = 0$ in model (7):

$$\frac{du}{dt} = u\left(\alpha - \beta u - \frac{q}{u + b} \right) - \frac{cuv}{mv + 1} \triangleq f(u, v),$$

$$\frac{dv}{dt} = v\left(-\gamma + \frac{su}{mv + 1} \right) \triangleq g(u, v). \quad (18)$$

The Jacobian matrix of (18) evaluated in the positive equilibrium E_w takes the form:

$$J_{E_w} = \begin{pmatrix} -\beta u_w + \dfrac{qu_w}{(u_w + b)^2} & -\dfrac{c\gamma^2}{s^2 u_w} \\ \dfrac{su_w - \gamma}{mu_w} & \dfrac{(\gamma - su_w)\gamma}{su_w} \end{pmatrix}. \quad (19)$$

Suppose that $(u_w + b)^2(c\gamma + ms\beta u_w^2) - mqsu_w^2 > 0$, and set

$$q^{[u_w]} = \left(\beta u_w - \frac{(\gamma - su_w)\gamma}{su_w} \right) \frac{(u_w + b)^2}{u_w}. \quad (20)$$

By some computational analysis, we obtain $\mathrm{tr}(J_{E_w}) < 0$, $\det(J_{E_w}) > 0$. Hence $E_w = (u_w, (su_w - \gamma)/m\gamma)$ is locally asymptotically stable.

And the Jacobian matrix of model (7) at $E_w = (u_w, v_w)$ is given by

$$\widetilde{J}_{E_w}$$

$$= \begin{pmatrix} \left(-\beta + \dfrac{q}{(u_w + b)^2} \right) u_w - d_1 k^2 & -\dfrac{c\gamma^2}{s^2 u_w} \\ \dfrac{su_w - \gamma}{mu_w} & -\dfrac{\gamma(su_w - \gamma)}{su_w} - d_2 k^2 \end{pmatrix}$$

$$(21)$$

and the characteristic equation of $\widetilde{J}_{E_w}$ at E_w is

$$\lambda^2 - \mathrm{tr}\left(\widetilde{J}_{E_w} \right)\lambda + \det\left(\widetilde{J}_{E_w} \right) = 0, \quad (22)$$

where

$$\mathrm{tr}\left(\widetilde{J}_{E_w} \right) = \mathrm{tr}\left(J_{E_w} \right) - (d_1 + d_2)\,k^2,$$

$$\det\left(\widetilde{J}_{E_w} \right) = \det\left(J_{E_w} \right) + d_1 d_2 k^4$$

$$+ \left(\frac{d_1 \gamma(su_w - \gamma)}{su_w} \right. \quad (23)$$

$$\left. + \left(\beta - \frac{q}{(u_w + b)^2} \right) d_2 u_w \right) k^2.$$

And the instability sets in when at least $\mathrm{tr}(\widetilde{J}_{E_w}) > 0$ or $\det(\widetilde{J}_{E_w}) < 0$ is violated.

Since $\mathrm{tr}(J_{E_w}) < 0$,

$$\mathrm{tr}\left(\widetilde{J}_{E_w} \right) = \mathrm{tr}\left(J_{E_w} \right) - (d_1 + d_2)\,k^2 < 0 \quad (24)$$

is always true. Hence, only violation of $\det(\widetilde{J}_{E_w}) < 0$ gives rise to Allee-diffusion-driven instability, which leads to

$$\frac{d_1 \gamma(su_w - \gamma)}{su_w} + \left(\beta - \frac{q}{(u_w + b)^2} \right) d_2 u_w \triangleq \Theta < 0, \quad (25)$$

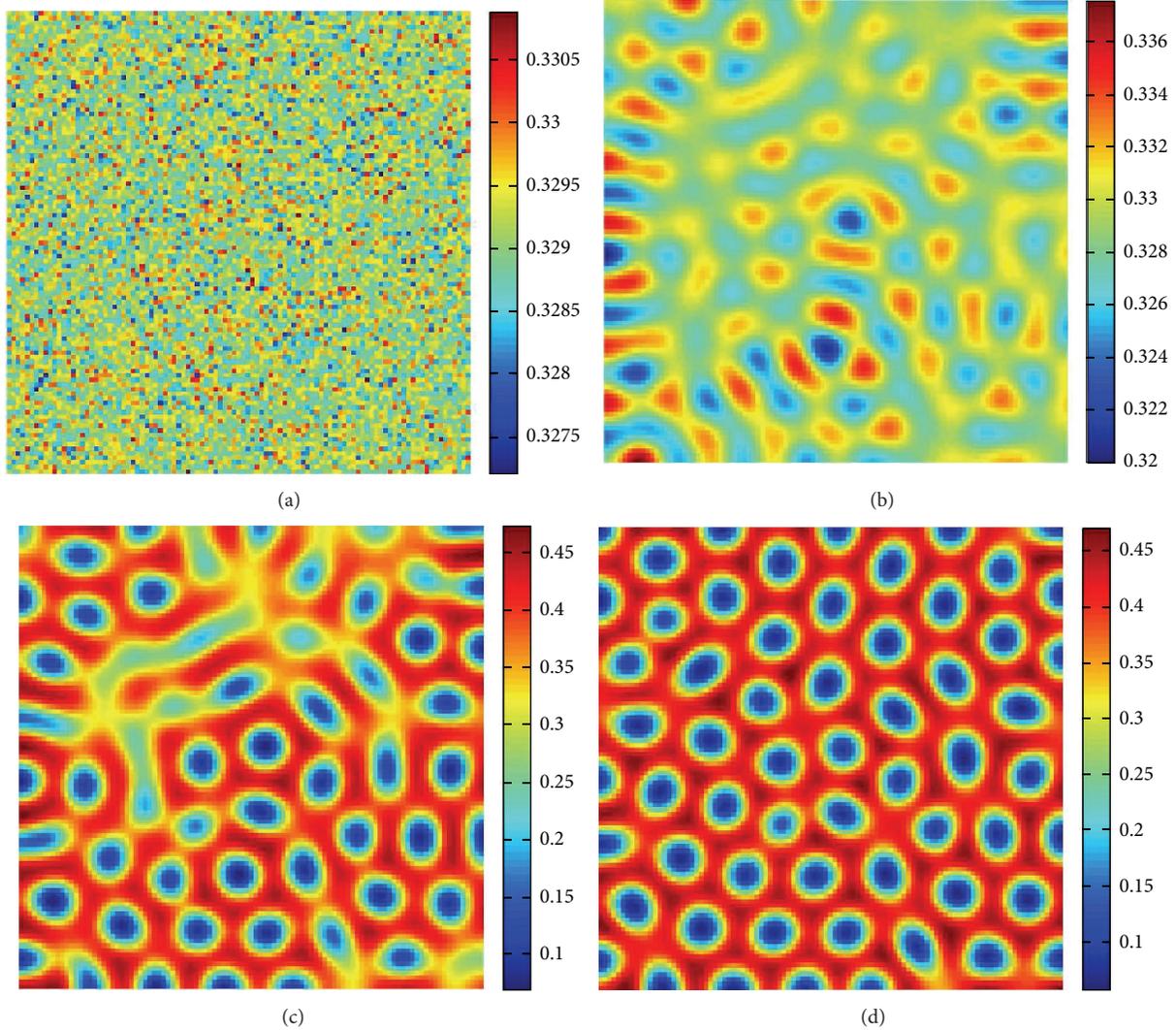otherwise, $\det(\widetilde{J}_{E_w}) > 0$ for all k if $\det(J_{E_w}) > 0$.

FIGURE 1: Typical Turing patterns of u in model (7) with parameters $\alpha = 1$, $\beta = 0.3$, $\gamma = 0.3$, $b = 0.5$, $c = 0.6$, $m = 0.6$, $q = 0.35$, $s = 1.75$, $d_1 = 0.015$, and $d_2 = 1$. Times: (a) 0; (b) 50; (c) 250; (d) 2500.

Notice that $\det(\widetilde{J}_{E_w})$ achieves its minimum

$$\min_k \det\left(\widetilde{J}_{E_w}\right) = \frac{4d_1d_2 \det\left(J_{E_w}\right) - \Theta^2}{4d_1d_2} \qquad (26)$$

at the critical value $k^{*2} > 0$ where

$$k^{*2} = -\frac{\Theta}{2d_1d_2}. \qquad (27)$$

And $\Theta < 0$ is equivalent to

$$\left(\frac{d_1\gamma\left(su_w - \gamma\right)}{d_2su_w^2} + \beta\right)(u_w + b)^2 < q < b\alpha, \qquad (28)$$

where $\min_k \det(\widetilde{J}_{E_w}) < 0$ is equivalent to $4d_1d_2 \det(J_{E_w}) - \Theta^2 < 0$, which is equivalent to

$$q > (u_w + b)^2 \left(\beta + \frac{d_1\gamma\left(su_w - \gamma\right)}{d_2su_w^2} + \frac{2\sqrt{d_1d_2 \det\left(J_{E_w}\right)}}{d_2u_w}\right). \qquad (29)$$

And from $\det(\widetilde{J}_{E_w}) = 0$, we can determine k_1 and k_2 as

$$k_1^2 = \frac{-\Theta + \sqrt{\Theta^2 - 4d_1d_1 \det\left(J_{E_w}\right)}}{2d_1d_2},$$

$$k_2^2 = \frac{-\Theta - \sqrt{\Theta^2 - 4d_1d_1 \det\left(J_{E_w}\right)}}{2d_1d_2}. \qquad (30)$$

In conclusion, if $k_1^2 < k^2 < k_2^2$, then $\det(\widetilde{J}_{E_w}) < 0$, and the positive equilibrium E_w of model (7) is unstable. That's to say,
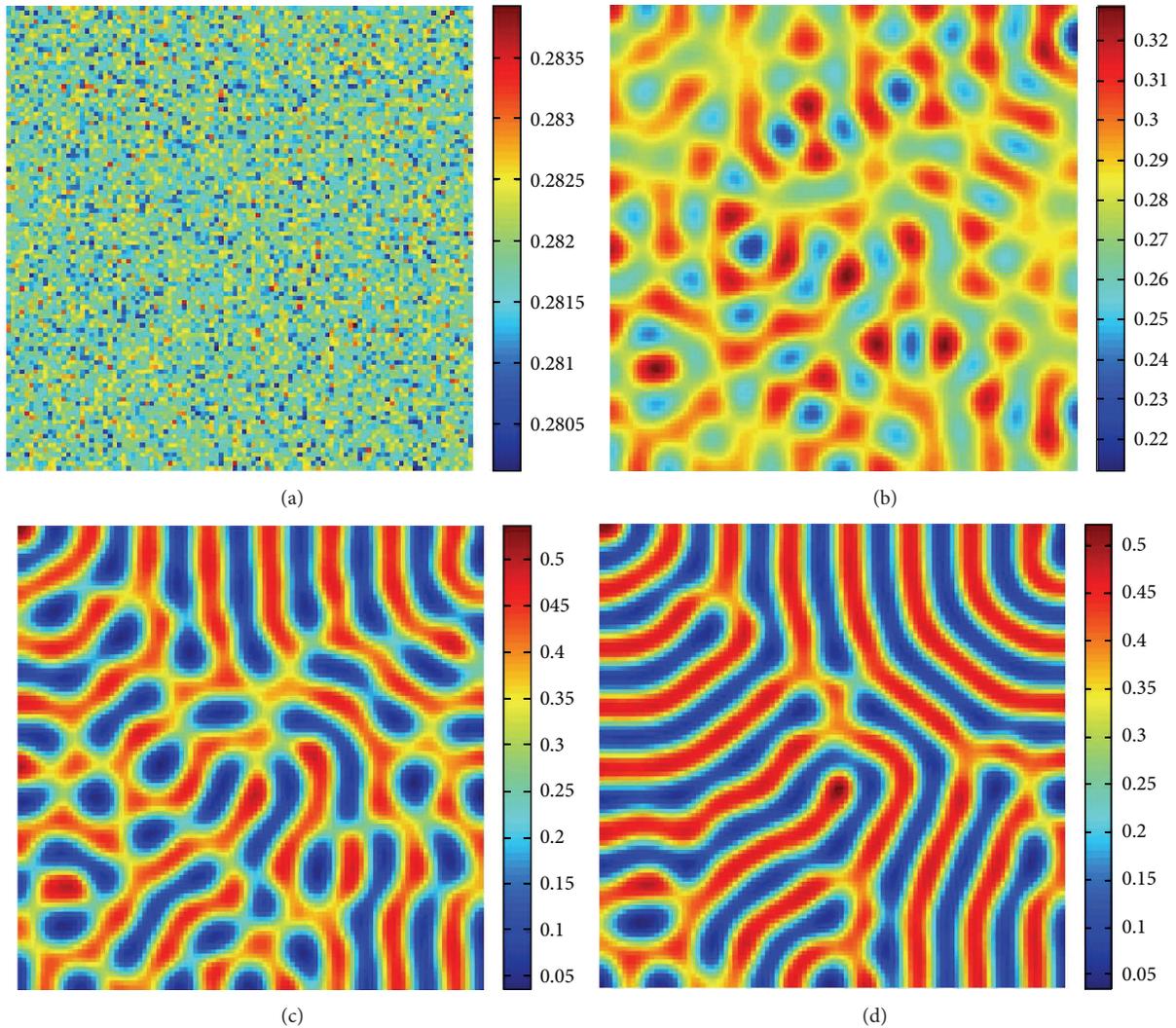
(a)

(b)

(c)

(d)

FIGURE 2: Typical Turing patterns of u in model (7) with parameters $\alpha = 1$, $\beta = 0.3$, $\gamma = 0.3$, $b = 0.5$, $c = 0.6$, $m = 0.6$, $q = 0.35$, $s = 2$, $d_1 = 0.015$, and $d_2 = 1$. Times: (a) 0; (b) 50; (c) 250; (d) 2500.

Allee-diffusion-driven instability occurs, and model (7) may exhibit Turing pattern formation.

3.2.2. Pattern Formation.

In this subsection, in two-dimensional space, we perform extensive numerical simulations of the spatially extended model (7) in the case with weak Allee effect and show qualitative results. All of the numerical simulations employ the zero-flux boundary conditions (9) with a system size of 200×200. Other parameters are fixed as $\alpha = 1$, $\beta = 0.3$, $\gamma = 0.3$, $b = 0.5$, $c = 0.6$, $m = 0.6$, $q = 0.35$, $d_1 = 0.015$, and $d_2 = 1$.

The numerical integration of model (7) is performed by using an explicit Euler method for the time integration [67] with a time step size $\Delta t = 1/100$ and the standard five-point approximation [68] for the 2D Laplacian with the zero-flux boundary conditions. The initial conditions are always a small amplitude random perturbation around the positive constant steady state solution E_w. After the initial period during which the perturbation spreads, the model goes into either a time-dependent state or an essentially steady state solution (time-independent state).

In the numerical simulations, different types of dynamics can be 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. We only show the distribution of prey u as an instance.

In Figure 1, with $s = 1.75$, there is a pattern consisting of blue hexagons (minimum density of u) in a red (maximum density of u) background, that is, isolated zones with low population densities. We call this pattern as "holes."

When increasing s to $s = 2$, the model dynamics exhibits a transition from stripes-holes growth to stripes replication; that is, holes decay and the stripes pattern emerges (c.f., Figure 2).
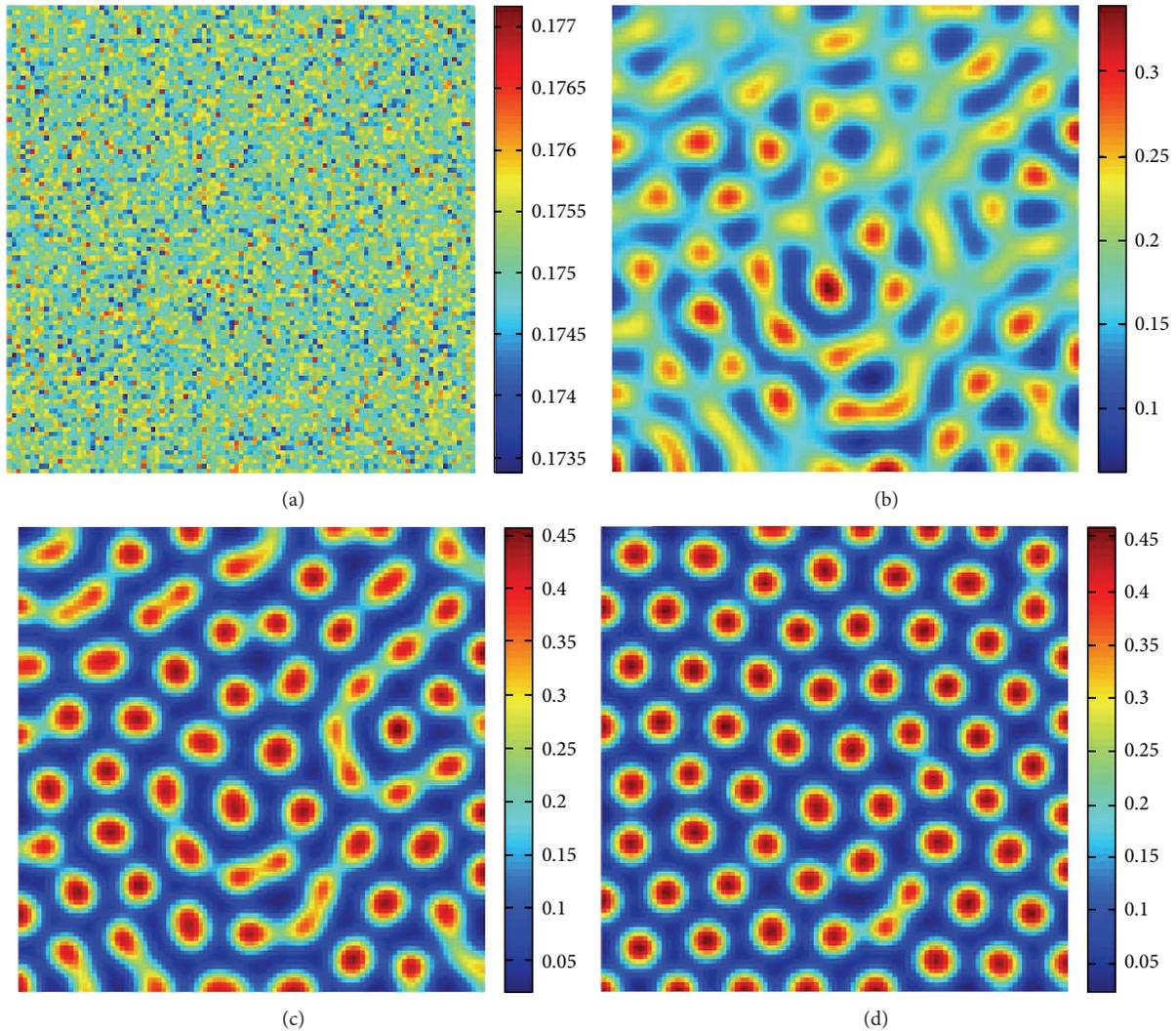
FIGURE 3: Typical Turing patterns of u in model (7) with parameters $\alpha = 1$, $\beta = 0.3$, $\gamma = 0.3$, $b = 0.5$, $c = 0.6$, $m = 0.6$, $q = 0.35$, $s = 3.0$, $d_1 = 0.015$, and $d_2 = 1$. Times: (a) 0; (b) 50; (c) 250; (d) 2500.

When s increasing to $s = 3.0$, the later random perturbations make these stripes decay, end with the time-independent regular spots (c.f., Figure 3), which is isolated zones with high prey densities.

In Figure 4, we show patterns of time-independent stripes-holes and stripes-spots mixture obtained with model (7). These two patterns are similar to each other. With $s = 1.9$ (c.f., Figure 4(a)), the stripes-holes mixture pattern is at relatively low prey densities, while $s = 2.45$ (c.f., Figure 4(b)), at high prey densities.

From Figures 1 to 4, one can see that, on increasing the control parameter s, the pattern sequence "holes $\rightarrow$ stripes-holes mixture $\rightarrow$ stripes $\rightarrow$ stripes-spots mixture $\rightarrow$ spots" is observed.

From the viewpoint of population dynamics, "spots" pattern (c.f., Figure 3) shows that the prey population is driven by predator 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 [30]. That is to say, under the

control of these parameters, the prey is predominant in the domain. In contrast, "holes" pattern (c.f., Figure 1) indicates that the predator is predominant in the domain.

4. Conclusions and Remarks

In summary, in this paper, we have investigated the spatiotemporal dynamics of a predator-prey model that involves Allee effect on prey analytically and numerically.

For model (7), in the case without Allee effect, there is no effect on the stability of the positive equilibrium whether with diffusion or not. That is to say, there is nonexistence of diffusion-driven instability in the model without Allee effect. More precisely, the distribution of species converge to a spatially homogeneous steady state which varies in time.

And in the case with Allee effect, the positive equilibrium may be unstable. This instability is induced by Allee effect and diffusion together, so we give a new definition called "Allee-diffusion-driven instability" and present the analysis of this
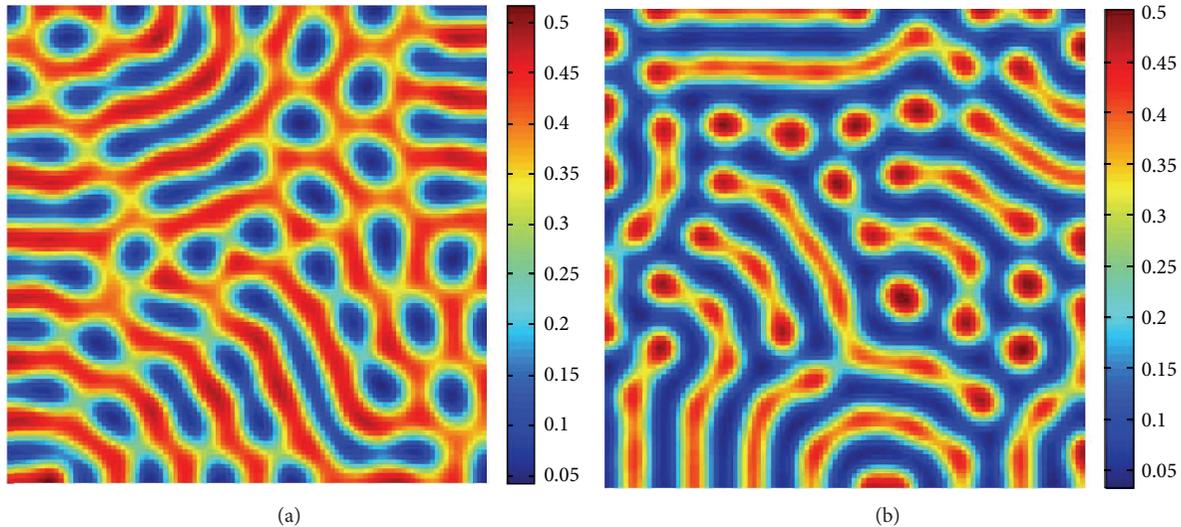
(a)

(b)

FIGURE 4: Typical Turing patterns of u in model (7) with parameters $\alpha = 1$, $\beta = 0.3$, $\gamma = 0.3$, $b = 0.5$, $c = 0.6$, $m = 0.6$, $q = 0.35$, $d_1 = 0.015$, and $d_2 = 1$. (a) $s = 1.9$; (b) $s = 2.45$.

instability of the model in details. To the best of our knowledge, this is the first reported case. Furthermore, via numerical simulations, it is found that the model dynamics exhibits both Allee effect and diffusion controlled pattern formation growth to holes, stripes-holes mixtures, stripes, stripes-spots mixtures, and spots replication. That is to say, the distribution of species is aggregation. This indicates that the pattern formation of the model with Allee effect is not simple, but rich and complex.

In fact, for a predator-prey system, Okubo and Levin [21] noted Allee effect on the functional response, and a density-dependent death rate of the predator is necessary to generate spatial patterns. And in this paper, we show that a predator-prey system with Allee effect on prey can generate complex Turing spatial patterns, which may be a supplementary to [21].

It is needed to note that, in this paper, we investigate the dynamics of localized patterns in model (7). Such patterns are characterized by a highly spatially heterogeneous solutions and are far from the spatially uniform state. These patterns occur in two-component systems when the ratio of the two diffusion coefficients are very large. In the numerical simulations, we take the diffusivity ratio as $1/0.015 \gg 1$, and so we are close to the regime of localized patterns. And the existence of these spatial patterns can be rigorously proved using tools from nonlinear functional analysis such as Liapunov-Schmidt reduction and fixed-point theorems [13, 14], this is desirable in future studies.
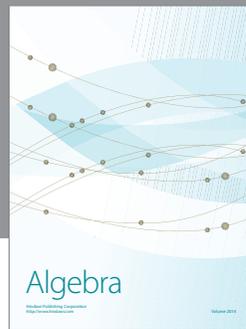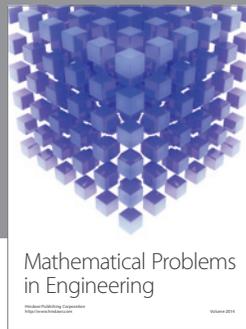
Acknowledgments

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