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DYNAMICS OF A MODIFIED HOLLING-TANNER PREDATOR-PREY MODEL WITH DIFFUSION

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ABSTRACT. In this paper, we study the asymptotic behavior and Hopf bifurcation of the modified Holling-Tanner models for the predator-prey interactions in the absence of diffusion. Further the direction of Hopf bifurcation and stability of bifurcating periodic solutions are investigated. Diffusion driven instability of the positive equilibrium solutions and Turing instability region regarding the parameters are established. Finally we illustrate the theoretical results with some numerical examples.

1. INTRODUCTION

Reaction-diffusion mechanisms form the most widely studied class of biological models and have been successfully applied to a wide range of ecological systems. The predator-prey interactions play the most important role in the functioning of ecosystems. The ecological interaction between the species such as spider mite and mite, lynx and hare, sparrow and sparrow hark etc. is modeled through the predator-prey system by Tanner [1] and Wollkind et al. [2]. Robert May developed a model, known as the Holling-Tanner prey-predator model [3], in which he incorporated the Holling rate [4, 5]. The Holling-Tanner system is regarded as one of the prototypical predator-prey models in several classical mathematical biology books, see, for example, May [6] and Murray [7]. The dynamics of the models have been of interest to both applied mathematicians and ecologists. Here we focus our attention on the modified

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Holling-Tanner model in which is incorporated Beddington-DeAngelis functional response in the following form

$$\begin{cases} \dot{u}(t) = ru\left(1 - \dfrac{u}{K}\right) - \dfrac{kvu}{(a + bu + cv)}, \\ \dot{v}(t) = sv\left(1 - \dfrac{ev}{u}\right), \\ u(0) = u_0 > 0, \quad v(0) = v_0 > 0, \end{cases} \tag{1.1}$$

where the parameters $a,\ b,\ c,\ e,\ k,\ r,\ s$ and K are positive constants, u and v denote respectively the population densities of the prey and predator at time t. The prey population grows logistically with intrinsic growth rate r and carrying capacity K in the absence of predation. The rate at which predators consume the prey, $kvu/(a + bu + cv)$, is known as a Beddington-DeAnglis functional response and the predator population grows logistically with intrinsic growth rate s and carrying capacity proportional to the population size of the prey. The parameter e is the number of prey required to support one predator at equilibrium when v equals u/e.

The Beddington-DeAngelis functional response was introduced by Beddington [8] and DeAngelis et al. [9]. It is similar to the well-known Holling type-II functional response but has an extra term cv in the denominator which reflects the mutual interference among predators. Hence this kind of functional response is affected by both prey and predator and called the predator dependence [10].

For simplicity, we nondimensionalize (1.1) with the following scaling:

$$u \mapsto u/K, \quad v \mapsto v, \quad t \mapsto rt$$

and obtain the form

$$\begin{cases} \dot{u}(t) = u\,(1 - u) - \dfrac{muv}{(\alpha + u + \beta v)}, \\ \dot{v}(t) = \delta v\left(1 - \dfrac{\gamma v}{u}\right), \\ u(0) = u_0 > 0, \quad v(0) = v_0 > 0, \end{cases} \tag{1.2}$$

where $m = \dfrac{kr}{bK},\ \alpha = \dfrac{a}{bK},\ \beta = \dfrac{c}{bK},\ \delta = \dfrac{s}{r},\ \gamma = \dfrac{e}{K}.$

Now, from (1.2), the predator-prey with their density are confined to a fixed open bounded domain Ω in R^N with smooth boundary at any given time and have natural tendency of each species to diffuse to ares of smaller population concentration. We are led to consider the following reaction-diffusion system

$$\begin{cases} u_t = d_1 \Delta u + u\,(1-u) - \dfrac{muv}{(\alpha + u + \beta v)},\ x \in \Omega, \\ v_t = d_2 \Delta v + \delta v \left(1 - \dfrac{\gamma v}{u}\right),\ x \in \Omega, \\ \partial_\nu u = \partial_\nu v = 0,\ x \in \partial\Omega \ \text{and}\ t > 0, \\ u(x,0) = u_0(x) \geq 0, \quad v(x,0) = v_0(x) \geq 0,\ x \in \Omega. \end{cases} \tag{1.3}$$

In the above, Δ is the Laplaican operator on Ω, where d_1 and d_2 denoting respectively diffusivity of prey and predator are kept independent of space and time. The no-flux boundary condition means that the statical environment Ω is isolated and ν is the outward unit normal to $\partial\Omega$. The initial values $u_0(x),\ v_0(x)$ are assumed to be positive and bounded in Ω.

It has been observed that the Holling-Tanner predator-prey model, the studies of stability and Hopf bifurcation for the predator-prey model have been investigated extensively by many authors, see [11–23]. Hus and Huang [14] analyze the global stability of the positive equilibrium of Holling-Tanner predator-prey system without diffusivity along with certain conditions on the parameters and the existence/nonexistence of non-constant positive steady state solutions with cross diffusion and global stability of the positive constant steady state solution in [16,17]. Chen and Shi [12] prove that the unique constant equilibrium is globally asymptotically stable under a new simpler parameter condition. Li et al. [24] studied the Hopf bifurcation and Turing instability of the Holling-Tanner predator-prey model with diffusion. However, the prey-dependent functional responses mentioned [14, 15, 24] fail to model the interference among predators and have been facing challenges from the biology and physiology communities. The predator-dependent functional responses can provide better descriptions of predator feeding over a range of predator-prey abundances, as is supported by much significant laboratory and field evidence [25]. Shi [26] studied the existence and nonexistence of nonconstant positive steady state of the system (1.3). To the best of the authors knowledge, there is no work exists in the direction of Turing instability, Hopf bifurcation and bifurcated periodic solution for the modified Holling-Tanner predator-prey model.

The rest of the article is organized as follows: In Section 2, Hopf bifurcation, direction of Hopf bifurcation and the stability of bifurcating periodic solution of the system (1.2) are established. In Section 3, we study diffusion-driven instability of the equilibrium solutions of the system (1.3). The direction of the Hopf bifurcation and the stability of the bifurcating periodic solutions for the corresponding diffusion system are discussed in Section 4. In Section 5, we illustrate our theoretical results with some numerical examples and make concluding comments.

2. Local stability and Hopf bifurcation

In this section, we study mainly the local stability of the positive equilibrium of (1.2) and the existence of the Hopf bifurcation of constant periodic solutions surrounding the positive equilibrium in (1.2).

There are three equilibrium solutions of the system (1.2)

(i) $E^0 = (0, 0)$ is a saddle point (extinct of both prey and predator).
(ii) $E^1 = (1, 0)$ is a saddle point (extinct of the predator or only prey).
(iii) $E^* = (u^*, v^*)$ is a non-trivial stationary state (coexistence of prey and predator) where

$$u^* = \frac{-\Gamma + \sqrt{\Gamma^2 + 4\alpha\gamma(\gamma+\beta)}}{2(\gamma+\beta)} > 0,\ v^* = \frac{u^*}{\gamma} > 0,\ \text{where } \Gamma = (m + \alpha\gamma - \beta - \gamma).$$

From the biological point of view, it is more interesting to study the dynamical behavior of the positive equilibrium point $E^* = (u^*, v^*)$. The Jacobian matrix of the system (1.2) at the positive equilibrium point $E^* = (u^*, v^*)$ is

$$J = \begin{pmatrix} 1 - 2u^* - \dfrac{m(\alpha+\beta v^*)}{(\alpha+u^*+\beta v^*)^2} & -\dfrac{mu^*(\alpha+u^*)}{(\alpha+u^*+\beta v^*)^2} \\ \delta/\gamma & -\delta \end{pmatrix}.$$

Let $h_0 = 1 - 2u^* - \dfrac{m(\alpha+\beta v^*)}{(\alpha+u^*+\beta v^*)^2}$ and $h = \delta$. In the following, we use h as a parameter. In fact δ is the parameter representing predation efficiency and we analyze the Hopf bifurcation occurring at (u^*, v^*) by choosing h as the bifurcation parameter. Thus,

$$trJ = 1 - 2u^* - \frac{m(\alpha+\beta v^*)}{(\alpha+u^*+\beta v^*)^2} - \delta = h_0 - h$$

and

$$detJ = \frac{\delta}{\gamma(\alpha+u^*+\beta v^*)^2}\left[m(u^*(\alpha+u^*) + \gamma(\alpha+\beta v^*)) - \gamma(1-2u^*)(\alpha+u^*+\beta v^*)^2\right].$$

Assume

(H) $m(u^*(\alpha+u^*) + \gamma(\alpha+\beta v^*)) > \gamma(1-2u^*)(\alpha+u^*+\beta v^*)^2$.

Therefore the characteristic equation of the linearized system of (1.2) at the positive equilibrium $E^* = (u^*, v^*)$ is

$$\lambda^2 - trJ\lambda + detJ = 0. \tag{2.1}$$

The two roots are given by

$$\lambda_{1,2} = \frac{trJ \pm \sqrt{(trJ)^2 - 4detJ}}{2}.$$

If the roots of the characteristic equation (2.1) have negative real part, then the positive equilibrium E^* is asymptotically stable, that is, $h > h_0$ $(trJ > 0)$. Therefore $h = h_0$ is a bifurcation point of (1.2) about the positive equilibrium E^*. We analyze the existence of periodic solutions of the system (1.2) about the positive equilibrium E^* when the parameter h passes through the value of the bifurcation point h_0. The characteristic equation (2.1) has a pair of purely imaginary roots, when $h = h_0$. Therefore, by Hopf bifurcation theorem the system (1.2) can bifurcate to a small amplitude non-constant periodic solution from the equilibrium point E^* when h crosses through h_0 if the transversality condition is satisfied.

Now we verify the transversality condition. Let $\lambda = x+iy$ $(x, y \in R)$ be one of the roots of (2.1) when $|h - h_0|$ is sufficiently small and $\lambda = i\rho$ $(\rho = \sqrt{detJ})$ when $h = h_0$. Substituting λ into (2.1) and separating real and imaginary parts, we have

$$\begin{aligned} &x^2 - y^2 - x\, trJ + detJ = 0, \\ &2xy - y\, trJ = 0. \end{aligned} \tag{2.2}$$

Differentiating (2.2) with respect to h and noticing that $x = 0$ when $h = h_0$, we get

$$sgn\left[\frac{dx}{dh}\right]_{h=h_0} = -\frac{1}{2} < 0.$$

This shows that the transversality condition holds. Therefore the system (1.2) will undergo a Hopf bifurcation about the positive equilibrium $E^* = (u^*, v^*)$ as h passes through the value h_0. Therefore we have the following conclusion.

Theorem: 2.1. *Assume that the condition (H) holds.*
Then the positive equilibrium (u^*, v^*) of the system (1.2) is locally asymptotically stable when $h > h_0$ and unstable when $h < h_0$; the system (1.2) undergoes a Hopf bifurcation at the positive equilibrium (u^*, v^*) when $h = h_0$.

2.1. **Stability of bifurcating periodic solutions.** Next we will investigate the direction of Hopf bifurcation and stability of bifurcated periodic solutions arising through Hopf bifurcation. Now we translate the positive equilibrium $E^* = (u^*, v^*)$ to the origin by the translation $\hat{u} = u - u^*$, $\hat{v} = v - v^*$. For convenience, we denote $\hat{u}$ and $\hat{v}$ by u and v respectively. Thus the local system (1.2) becomes

$$\begin{cases} \dfrac{du}{dt} = (u+u^*)(1-(u+u^*)) - \dfrac{m(u+u^*)(v+v^*)}{\alpha + (u+u^*) + \beta(v+v^*)}, \\ \dfrac{dv}{dt} = \delta(v+v^*)\left(1 - \dfrac{\gamma(v+v^*)}{(u+u^*)}\right). \end{cases} \tag{2.3}$$

Rewrite (2.3) as

$$\begin{pmatrix} u_t \\ v_t \end{pmatrix} = J\begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} f(u,v,h) \\ g(u,v,h) \end{pmatrix}, \tag{2.4}$$

where J is defined in (2.1)

$$\begin{aligned} f(u,v,h) &= \left(\frac{mv^*(\alpha+\beta v^*)}{(\alpha+u^*+\beta v^*)^3}-1\right)u^2-\left(\frac{m\alpha}{(\alpha+u^*+\beta v^*)^2}+\frac{2m\beta u^*v^*}{(\alpha+u^*+\beta v^*)^3}\right)uv \\ &\quad +\left(\frac{m(\alpha-\beta v^*)}{(\alpha+u^*+\beta v^*)^3}+\frac{3m\beta u^*v^*}{(\alpha+u^*+\beta v^*)^4}\right)u^2v-\frac{mv^*(\alpha+\beta v^*)}{(\alpha+u^*+\beta v^*)^4}u^3+\dots, \\ g(u,v,h) &= -\frac{\delta}{\gamma u^*}u^2+\frac{2\delta}{u^*}uv-\frac{2\delta}{u^{*2}}u^2v+\frac{\delta}{\gamma u^{*2}}u^3+\dots . \end{aligned}$$

Therefore the characteristic roots of J are $\lambda_{1,2}=\eta(h)\pm i\omega(h)$, where

$$\eta(h)=\frac{1}{2}(trJ), \quad \omega(h)=\sqrt{(detJ)-(\eta(h))^2}.$$

The characteristic roots $\lambda_1,\ \lambda_2$ are a pair of complex conjugates, when $\left(detJ-(\eta(h))^2\right)>0$ and $\lambda_1,\ \lambda_2$ imaginary when $h=h_0$, that is, $\eta(h_0)=0$ and we get $\lambda_{1,2}=\pm\omega(h_0)i$.
Set the following matrix

$$B=\begin{pmatrix} 1 & 0 \\ M & N \end{pmatrix},$$

where

$$\begin{pmatrix} 1 \\ M-iN \end{pmatrix},$$

is the eigenvector corresponding to $\lambda=\eta(h)\pm i\omega(h)$ and

$$M=\frac{\left(1-2u^*-\dfrac{m(\alpha+\beta v^*)}{(\alpha+u^*+\beta v^*)^2}-\eta(h)\right)}{\left(\dfrac{mu^*(\alpha+u^*)}{(\alpha+u^*+\beta v^*)}\right)}, \quad N=\frac{\omega(h)}{\left(\dfrac{mu^*(\alpha+u^*)}{(\alpha+u^*+\beta v^*)}\right)}.$$

Clearly

$$B^{-1}=\begin{pmatrix} 1 & 0 \\ \frac{-M}{N} & \frac{1}{N} \end{pmatrix}.$$

By the transformation

$$\begin{pmatrix} u \\ v \end{pmatrix}=B\begin{pmatrix} x \\ y \end{pmatrix},$$

the system (2.3) becomes

$$\begin{pmatrix} \dot{x}(t) \\ \dot{y}(t) \end{pmatrix}=J(h)\begin{pmatrix} x \\ y \end{pmatrix}+\begin{pmatrix} F(x,y,h) \\ G(x,y,h) \end{pmatrix}, \tag{2.5}$$

where

$$J(h) = \begin{pmatrix} \eta(h) & -\omega(h) \\ \omega(h) & \eta(h) \end{pmatrix},$$

with

$$\begin{aligned} F(x,y,h) &= \left(\frac{mv^*(\alpha+\beta v^*)}{(\alpha+u^*+\beta v^*)^3} - \frac{\alpha m M}{(\alpha+u^*+\beta v^*)^2} - 1\right)x^2 + \frac{3m\beta u^* v^* N}{(\alpha+u^*+\beta v^*)^4}x^2 y \\ &\quad + \left(\frac{mM(\alpha+\beta v^*)}{(\alpha+u^*+\beta v^*)^3} - \frac{mv^*(\alpha+\beta v^*)}{(\alpha+u^*+\beta v^*)^4}\right)x^3 \\ &\quad - \left(\frac{\alpha m}{(\alpha+u^*+\beta v^*)^2} + \frac{2m\beta u^* v^*}{(\alpha+u^*+\beta v^*)^2}\right)Nxy\ldots, \end{aligned}$$

$$G(x,y,h) = \frac{-M}{N}F(x,y,h) + \frac{1}{N}g'(x,y,h)$$

and

$$g'(x,y,h) = \left(\frac{\delta(2\gamma M-1)}{\gamma u^*}\right)x^2 + \left(\frac{2\delta N}{u^*}\right)xy - \frac{2\delta N}{u^{*2}}x^2 y + \left(\frac{\delta(1-2\gamma M^2)}{\gamma u^{*2}}\right)x^3 + \ldots .$$

Rewrite (2.5) in the polar coordinates as

$$\begin{cases} \dot{r} = \eta(h)r + a(h)r^3 + \ldots, \\ \dot{\theta} = \omega(h) + c(h)r^2 + \ldots . \end{cases} \tag{2.6}$$

Then the Taylor expansion of (2.6) at $h = h_0$ yields

$$\begin{cases} \dot{r} = \eta'(h_0)(h-h_0)r + a(h_0)r^3 + \ldots, \\ \dot{\theta} = \omega(h_0) + \omega'(h_0)(h-h_0) + c(h_0)r^2 + \ldots . \end{cases}$$

To determine the stability of Hopf bifurcation periodic solution, we need to calculate the sign of the coefficient $a(h_0)$ given by

$$\begin{aligned} a(h_0) &= \frac{1}{16}\left[F_{xxx} + F_{xyy} + G_{xxy} + G_{yyy}\right]|_{(0,0,h_0)} + \frac{1}{16\omega(h_0)}\left[F_{xy}(F_{xx}+F_{yy})\right. \\ &\quad \left. -G_{xy}(G_{xx}+G_{yy}) - F_{xx}G_{xx} + F_{yy}G_{yy}\right]|_{(0,0,h_0)}, \end{aligned}$$

where

$$F_{xxx} = 6\left(\frac{mM(\alpha+\beta v^*)}{(\alpha+u^*+\beta v^*)^3} - \frac{mv^*(\alpha+\beta v^*)}{(\alpha+u^*+\beta v^*)^4}\right),\ F_{xxy} = \frac{6m\beta u^* v^* N}{(\alpha+u^*+\beta v^*)^4},$$

$$F_{xy} = -\left(\frac{\alpha m}{(\alpha+u^*+\beta v^*)^2} + \frac{2m\beta u^* v^*}{(\alpha+u^*+\beta v^*)^2}\right)N,\ g'_{xxx} = 6\left(\frac{\delta(1-2\gamma M^2)}{\gamma u^{*2}}\right)$$

$$F_{xx} = 2\left(\frac{mv^*(\alpha+\beta v^*)}{(\alpha+u^*+\beta v^*)^3} - \frac{\alpha m M}{(\alpha+u^*+\beta v^*)^2} - 1\right),\ g'_{xxy} = -\frac{4\delta N}{u^{*2}}$$

$$F_{xyy} = G_{xxy} = G_{yyy} = F_{yy} = 0,\ g'_{xx} = 2\left(\frac{\delta(2\gamma M - 1)}{\gamma u^*}\right)$$

$$G_{xxx} = -\tfrac{M}{N}F_{xxx} + \tfrac{1}{N}g'_{xxx},\ G_{xxy} = -\frac{M}{N}F_{xxy} + \frac{1}{N}g'_{xxy},$$

$$G_{xx} = -\frac{M}{N}F_{xx} + \frac{1}{N}g'_{xx},\ \ G_{xy} = -\frac{M}{N}F_{xy} + \frac{1}{N}g'_{xy},\ g'_{xy} = \left(\frac{2\delta N}{u^*}\right).$$

Thus we obtain

$$\mu_2 = -\frac{a(h_0)}{\eta'(h_0)}.$$

Now, from the Poincare-Andronov Hopf bifurcation theorem, $\eta'(h)|_{h=h_0} = -\frac{1}{2} < 0$ and from the above calculations of $a(h_0)$, we have the following conclusion:

Theorem: 2.2. *Assume that the condition (H) holds.*

(i) *If $a(h_0) < 0$, the bifurcated periodic solutions are stable and the direction of Hopf bifurcation is supercritical.*
(ii) *If $a(h_0) > 0$, the bifurcated periodic solutions are unstable and the direction of Hopf bifurcation is subcritical.*

3. Diffusion-driven instability of the equilibrium solution

In this section, we study the Turing instability (diffusion driven instability) under diffusion effect, that is, the stability of the positive equilibrium E^* changing from stability for the ODE system (1.2), to instability for the system (1.3).

In the previous section, we observed that the system (1.2) is locally asymptotically stable about the positive equilibrium E^*, when $h > h_0$. Now we consider the effects of diffusion on the stability of the positive equilibrium solution of (1.3) under the assumption $h > h_0$.

Now we consider the one-dimensional spatial domain $\Omega = (0, \pi)$. While our calculations can be carried to higher-dimensional spatial domain, we restrict ourselves to the case of spatial domain $(0, \pi)$ for which the structure of the eigenvalues is known. We know that each equilibrium of (1.2) is spatially uniform solution of (1.3) and also equilibrium solution of (1.3). We say that an equilibrium solution of system (1.3) is Turing unstable if it is stable without diffusion effect and it becomes unstable with diffusion effect.

We consider a reaction diffusion system with Neumann boundary condition in one-dimensional spatial domain $\Omega = (0, \pi)$ described by

$$\begin{cases} u_t = d_1 u_{xx} + u\,(1-u) - \dfrac{muv}{(\alpha + u + \beta v)},\ x \in (0, \pi), \\ v_t = d_2 v_{xx} + \delta v\left(1 - \dfrac{\gamma v}{u}\right),\ x \in (0, \pi), \\ \partial_\nu u = \partial_\nu v = 0, \quad x = 0,\ \pi \text{ and } t > 0, \\ u(x, 0) = u_0(x) \geq 0,\ v(x, 0) = v_0(x) \geq 0,\ x \in (0, \pi). \end{cases} \tag{3.1}$$

It is well known that the operator $u \to -u_{xx}$ with Neumann boundary condition has eigenvalues and normalized eigenfunctions as follows

$$\xi_0 = 0,\ \phi_0(x) = \sqrt{\frac{1}{\pi}},\ \xi_k = k^2,\ \phi_k(x) = \sqrt{\frac{2}{\pi}} cos(kx),$$

for $k = 1, 2, 3, \dots$.

The linearized system (3.1) at (u^*, v^*) has the form

$$\begin{pmatrix} u_t \\ v_t \end{pmatrix} = L \begin{pmatrix} u \\ v \end{pmatrix} = D \begin{pmatrix} u_{xx} \\ v_{xx} \end{pmatrix} + J \begin{pmatrix} u \\ v \end{pmatrix},$$

where J is the Jacobian matrix defined in Section 2 and $D = diag(d_1, d_2)$. L is a linear operator with domain

$$D_L = X_{\mathbb{C}} := X \oplus iX = \{u1 + iu2 : u1, u2 \in X\},\ \text{where}$$

$$X := \left\{(u, v) \in H^2[(0, \pi)] \times H^2[(0, \pi)] : u_x(0, t) = u_x(\pi, t) = 0, v_x(0, t) = v_x(\pi, t) = 0\right\}$$

is a real-valued Sobolev space.

From the standard linear operator theory, it is known that if all the eigenvalues of the operator L have negative real parts, then (u^*, v^*) is asymptotically stable and if some eigenvalues have positive real parts, then (u^*, v^*) is unstable.
Consider the characteristic equation $L(\phi, \psi)^T = \xi(\phi, \psi)^T$ and let $(\phi, \psi)^T = \sum_{k=0}^{\infty} (a_k, b_k)^T\ cos(kx)$. Then we obtain $\sum_{k=0}^{\infty} (J_k - \xi I)(a_k, b_k)^T\ cos(kx) = 0$, where $J_k = J - k^2 D$.
It is clear that all the eigenvalues of L are given by the eigenvalues of J_k for $k = 0, 1, 2, 3, \dots$.
Note that the characteristic equation of J_k is

$$\xi^2 - T_k \xi + D_k = 0, \quad k = 0, 1, 2, 3, \dots, \tag{3.2}$$

where

$$\begin{aligned} &T_k = trJ_k = trJ - (d_1 + d_2)k^2, \\ &D_k = detJ_k = d_1 d_2 k^4 + (d_1 h - d_2 h_0)k^2 - h(h_0 + \Theta/\gamma), \\ &\text{and } \Theta = -\frac{mu^*(\alpha + u^*)}{(\alpha + u^* + \beta v^*)^2}. \end{aligned}$$

Therefore we obtain the following result:

Theorem: 3.1. *Assume that the condition (H) holds. The equilibrium $E^*(u^*, v^*)$ of the system (1.2) is locally asymptotically stable when $h > h_0$. The equilibrium $E^*(u^*, v^*)$ is locally asymptotically stable of the system (3.1) if and only if the following is satisfied*

$(H1)$ $d_1 \geq h_0$,

$(H2)$ $d_1 \geq \dfrac{d_2 h_0}{h}$,

$(H3)$ $d_1 < min\left\{h_0, \dfrac{d_2 h_0}{h}\right\}$ *and* $h > \dfrac{k^2 d_2(h_0 - d1k^2)}{d1k^2 - (h_0 + \Theta/\gamma)}$,*for all* $k \geq 1$ *satisfying* $k < \sqrt{\dfrac{h_0}{d_1}}$,

and $E^*(u^*, v^*)$ is an unstable equilibrium solution of (14) if

$(H4)$ $d_1 < min\left\{h_0, \dfrac{d_2 h_0}{h}\right\}$ *and* $h < \dfrac{k_1^2 d_2(h_0 - d1k_1^2)}{d1k_1^2 - (h_0 + \Theta/\gamma)}$,*for some* $k_1 \in \mathbb{N}$ *satisfying* $k_1 < \sqrt{\dfrac{h_0}{d_1}}$.

Thus the equilibrium (u^*, v^*) is Turing unstable if s belongs to the interval

$$I_{k_1} = \left\{h : h_0 < h < \frac{k_1^2 d_2(h_0 - d1k_1^2)}{d1k_1^2 - (h_0 + \Theta/\gamma)}\right\}.$$

That is, if $h \in I_{k_1}$, then (u^*, v^*) is locally asymptotically stable with respect to (1.2) and it is unstable with respect to (1.3).

Proof. For convince, we write D_k as a quadratic function in k^2, $D_k = d_1 d_2 k^4 + (d_1 h - d_2 h_0)k^2 + det\ J$.
From the definition, T_k, for every $k \geq 0$, satisfies the condition $T_{k+1} < T_k$. So $T_k < 0$ for all $k \geq 0$. Hence the signs of the real parts of roots of (3.2) are determined by the signs of D_k respectively. The symmetric axis of the graph $(k^2, D(k^2))$ is $l(h) = (d_2 h_0 - d_1 h)/2d_1 d_2$.

(H1) implies that $d_1 k^2 - h_0 \geq 0$ for all $k \geq 0$, that means, $D_k > 0$ for all $k \geq 0$ (H2) implying that $l(h) < 0$. Then we conclude that $D_k > 0$ for all $k \geq 0$ since $D_0 > 0$. Clearly (H3) implies that $D_k > 0$ for all $k \geq 0$. So all roots of (3.2) have negative real parts under any one of the assumptions (H1), (H2) and (H3).

When (H4) holds, $D(k_1^2) < 0$, (3.2) has at least one positive real part. Hence $E^*(u^*, v^*)$ is an unstable equilibrium solution of the system (3.1). This completes the proof. □

4. Direction of Hopf bifurcation and the stability of the bifurcating periodic Solution

In this section, we study the direction of Hopf bifurcations and stability of bifurcating periodic solutions arising through Hopf bifurcation by applying the normal form theory and center manifold theorem introduced by Hassard et al. [27]. Let L^* be the conjugate operator of L defined in section 3. Then

$$L^* \begin{pmatrix} u \\ v \end{pmatrix} = D \begin{pmatrix} u_{xx} \\ v_{xx} \end{pmatrix} + J^* \begin{pmatrix} u \\ v \end{pmatrix},$$

where

$$J^* = \begin{pmatrix} 1 - 2u^* - \dfrac{m(\alpha + \beta v^*)}{(\alpha + u^* + \beta v^*)^2} & \dfrac{\delta}{\gamma} \\ -\dfrac{mu^*(\alpha + u^*)}{(\alpha + u^* + \beta v^*)^2} & -\delta \end{pmatrix},$$

with domain $D_{L^*} = X_{\mathbb{C}}$.
Let

$$q = \begin{pmatrix} 1 \\ A - i(1/2B) \end{pmatrix}, \quad q^* = \frac{B}{\pi} \begin{pmatrix} (1/2B) + iA \\ -i \end{pmatrix}, \text{ where}$$

$$A = \frac{(1-2u^*)(\alpha + u^* + \beta v^*)^2 - m(\alpha + \beta v^*)}{mu^*(\alpha + u^*)}, \; B = \frac{mu^*(a + bu^*)}{2\omega(h_0)(\alpha + u^* + \beta v^*)^2}.$$

It is easy to see that $\langle L^* a, b\rangle = \langle a, Lb\rangle$ for any $a \in D_{L^*}, \; b \in D_L$ and $L^* q^* = -i\omega_0 q^*, \; Lq = i\omega_0 q, \; \langle q^*, q\rangle = 1, \; \langle q^*, \overline{q}\rangle = 0$. Here $\langle a, b\rangle = \int_0^\pi \overline{a}^T b dx$ denotes the inner product in $L^2[(0,\pi)] \times L^2[(0,\pi)]$.
According to [27], we decompose $X = X^C \oplus X^S$ with $X^C = \{zq + \overline{z}\,\overline{q} : z \in \mathbb{C}\}, \; X^S = \{w \in X : \langle q^*, w\rangle = 0\}$. For any $(u,v) \in X$, there exist $z \in \mathbb{C}$ and $w = (w_1, w_2) \in X^S$ such that

$$(u,v)^T \quad zq + \overline{zq} + w; \;\; z = \left\langle q^*, (u,v)^T \right\rangle.$$

Thus

$$u = z + \overline{z} + w_1 \text{ and } v = z\,(A - i(1/2B)) + \overline{z}\,(A + i(1/2B)) + w_2.$$

From the above discussion, our system in (z, w) coordinates becomes

$$\begin{cases} \dot{u}(t) = i\omega_0 z + \left\langle q^*, \hat{f} \right\rangle, \\ \dot{w}(t) = Lw + \left[\hat{f} - \left\langle q^*, \hat{f}\right\rangle q - \left\langle q^*, \hat{f}\right\rangle \overline{q}\right], \end{cases}$$

with $\hat{f} = (f, g)^T$. Straightforward computation shows that, with f and g as defined in (2.4),

$$\left\langle q^*, \hat{f}\right\rangle = B\left(\tfrac{1}{2B} f - iAf + ig\right), \;\; \left\langle \overline{q}^*, \hat{f}\right\rangle = B\left(\tfrac{1}{2B} f + iAf - ig\right),$$

$$\left\langle q^*, \hat{f}\right\rangle q = \begin{pmatrix} \left\langle q^*, \hat{f}\right\rangle \\ \left\langle q^*, \hat{f}\right\rangle \left(A - \dfrac{i}{2B}\right) \end{pmatrix}, \;\; \left\langle \overline{q}^*, \hat{f}\right\rangle \overline{q} = \begin{pmatrix} \left\langle \overline{q}^*, \hat{f}\right\rangle \\ \left\langle \overline{q}^*, \hat{f}\right\rangle \left(A + \dfrac{i}{2B}\right) \end{pmatrix},$$

$$\left\langle q^*, \hat{f}\right\rangle q + \left\langle \overline{q}^*, \hat{f}\right\rangle \overline{q} = \begin{pmatrix} f \\ g \end{pmatrix}, \;\; H(z, \overline{z}, w) = \hat{f} - \left\langle q^*, \hat{f}\right\rangle q + \left\langle \overline{q}^*, \hat{f}\right\rangle \overline{q} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}.$$

Writing $w = \frac{w_{20}}{2}z^2 + w_{11}z\overline{z} + \frac{w_{02}}{2}\overline{z}^2 + o\left(|z|\right)^3$ for the equation of the center manifold, we can obtain:

$$(2\omega_0 - L) = w_{20} = 0, \quad (-L)w_{11} = 0, \text{ and } w_{02} = \overline{w_{20}}.$$

This implies that $w_{20} = w_{02} = w_{11} = 0$. Thus the equation on the center manifold in $z, \overline{z}$ coordinates now is

$$\frac{dz}{dt} = i\omega_0 z + \frac{1}{2}g_{20}z^2 + g_{11}z\overline{z} + \frac{1}{2}g_{02}\overline{z}^2 + \frac{1}{2}g_{21}z^2\overline{z} + o(|z|^4),$$

where

$$\begin{aligned} g_{20} &= \frac{1}{2}[B_{20} + 2B_{11}q_2], \quad g_{11} = \frac{1}{2}[B_{20} + B_{11}q_2 + B_{11}\overline{q}_2], \\ g_{02} &= \frac{1}{2}[B_{20} + 2B_{11}\overline{q}_2], \quad g_{21} = \frac{1}{2}[B_{30} + B_{21}q_2 + B_{21}\overline{q}_2], \end{aligned}$$

and

$$\begin{aligned} &B_{20} = \left(\frac{mv^*(\alpha + \beta v^*)}{(\alpha + u^* + \beta v^*)^3} - 1\right), \; B_{11} = -\left(\frac{m\alpha}{(\alpha + u^* + \beta v^*)^2} + \frac{2m\beta u^* v^*}{(\alpha + u^* + \beta v^*)^3}\right), \\ &B_{30} = -\frac{mv^*(\alpha + \beta v^*)}{(\alpha + u^* + \beta v^*)^4}, \; B_{21} = \left(\frac{m(\alpha - \beta v^*)}{(\alpha + u^* + \beta v^*)^3} + \frac{3m\beta u^* v^*}{(\alpha + u^* + \beta v^*)^4}\right), \\ &q_2 = A - i(1/2B), \; \overline{q}_2 = A + i(1/2B). \end{aligned}$$

From to [27], we have

$$C_1(0) = \frac{i}{2\omega_0}\left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2\right), \; \Lambda = -\frac{Re\{C_1(0)\}}{Re\{\lambda'(h_0)\}}, \; \beta_2 = 2Re\{C_1(0)\}.$$

The above calculation leads to the following theorem:

Theorem: 4.1. *Assume that (H) satisfied. The system (3.1) undergoes a Hopf bifurcation at (u^*, v^*) when $h = h_0$. The direction of Hopf bifurcation of the system (3.1) is the same as that of the system (1.2).*

(i) Λ *determines the directions of Hopf bifurcation. If* $\Lambda > 0 (< 0)$*, then the Hopf bifurcation is supercritical (subcritical).*
(ii) β_2 *determines the stability of bifurcating periodic solution. If* $\beta_2 < 0 (> 0)$*, then the bifurcating periodic solutions are stable (unstable).*

5. Numerical Studies

In this section, we present some numerical simulation by using finite difference method to verify our theoretical analysis proved in the previous section by using MATLAB. We consider the system (1.2) with $m = 0.6, \; \alpha = 0.15, \; \beta = 0.25, \; \gamma = 0.2$. We only change the predation

efficiency δ.
We know that the local system (1.2) has the following form:

$$\begin{cases} \dot{u}(t) = u\,(1-u) - \dfrac{0.6uv}{(0.15+u+0.25v)}, \\ \dot{v}(t) = \delta v\left(1 - \dfrac{0.2v}{u}\right), \\ u(0) = 0.1, \quad v(0) = 0.5. \end{cases} \tag{5.1}$$

The system (5.1) has a unique positive equilibrium
$E^*(u^*, v^*) = (0.1265, 0.6329)$. Under the set of parameters in (5.1), we have the critical point $h_0 = 0.127$ and it follows from Theorem 2.1 that $E^* = (0.1265, 0.6329)$ is asymptotically stable when $h > h_0 = 0.127$ and unstable when $h < h_0 = 0.127$. Also, when h passes through h_0 from the right side of $h_0, E^*(0.1265, 0.6329)$ will lose its stability and a Hopf bifurcation occurs, that is, a family of periodic solutions bifurcate from the interior equilibrium $E^*(0.1265, 0.6329)$. From Theorem 2.2, the Hopf bifurcation at $h = h_0$ is subcritical, and the bifurcating periodic solutions are local asymptotically stable. These facts are shown by the numerical simulations, see Figure 1-3 with time step size $t = 1000$.

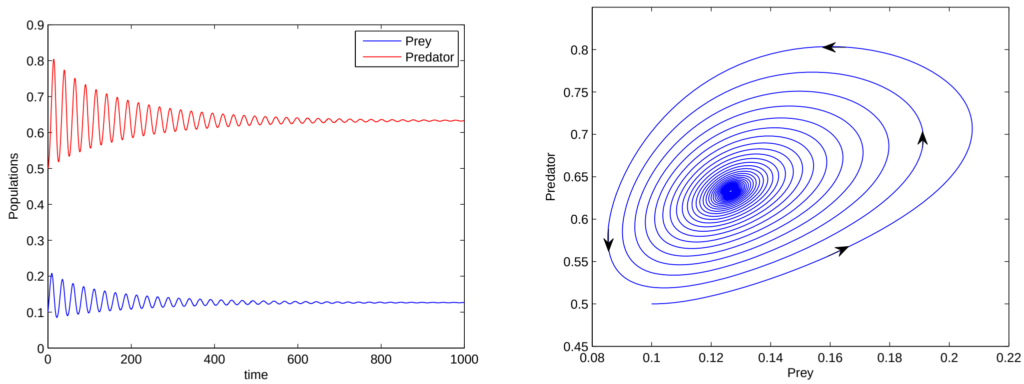

FIGURE 1. The trajectory graphs and phase portrait of the system (5.1) with $h = 0.143 > h_0 = 0.127, \ \delta = 0.143$ and initial data $(u_0, v_0) = (0.1, 0.5)$.

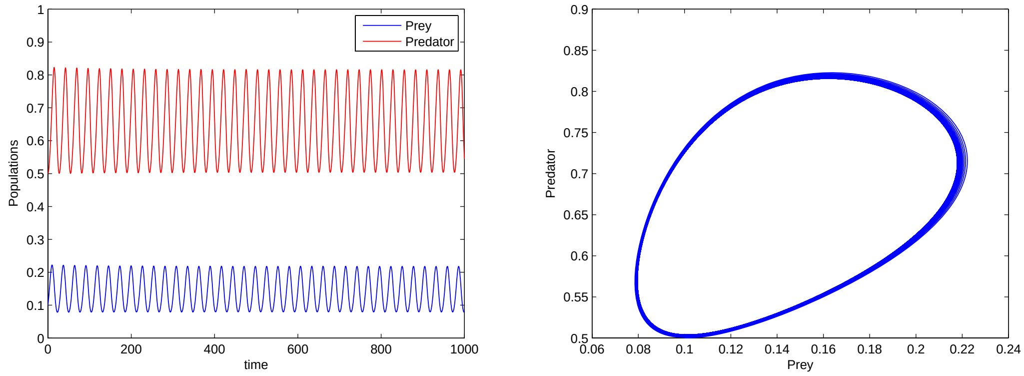

FIGURE 2. The trajectory graphs and phase portrait of the system (5.1) with $h = 0.127 = h_0 = 0.127,\ \delta = 0.127$ and initial data $(u_0, v_0) = (0.1, 0.5)$.

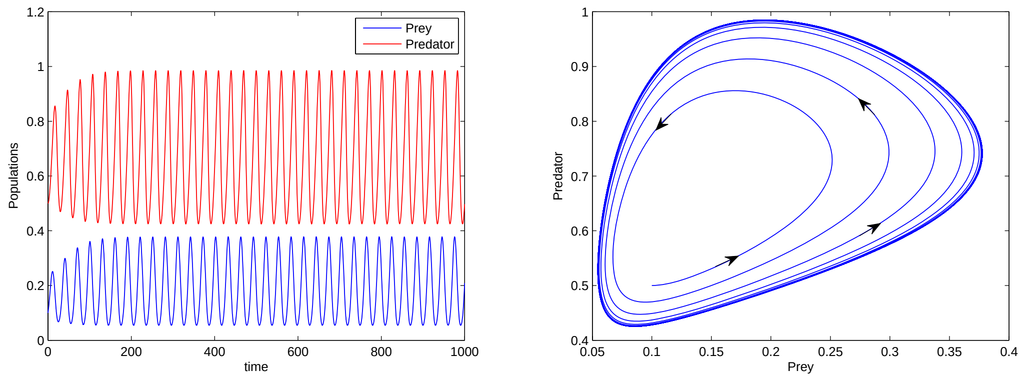

FIGURE 3. The trajectory graphs and phase portrait of the system (5.1) with $h = 0.105 < h_0 = 0.127,\ \delta = 0.105$ and initial data $(u_0, v_0) = (0.1, 0.5)$.

Consider the reaction-diffusion system with Neumann boundary condition on one dimensional spatial domain $\Omega = (0, 100)$. We only change the diffusion co-efficients d_1 and d_2.

$$\begin{cases} u_t = d_1 \Delta u + u\,(1-u) - \dfrac{0.6uv}{(0.15 + u + 0.25v)},\ x \in \Omega, \\ v_t = d_2 \Delta v + \delta v \left(1 - \dfrac{0.2v}{u}\right),\ x \in \Omega, \\ \partial_\nu u = \partial_\nu v = 0,\ \ x \in \partial\Omega \ \text{ and } \ t > 0, \\ u(x,0) = u_0(x) \geq 0, \quad v(x,0) = v_0(x) \geq 0,\ x \in \Omega. \end{cases} \tag{5.2}$$

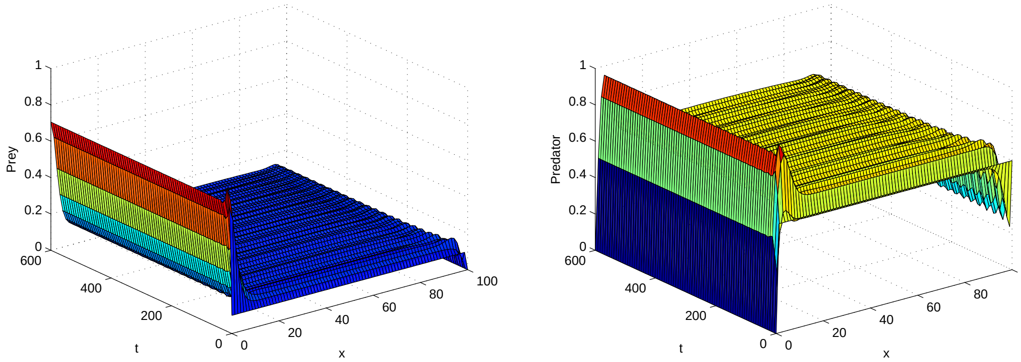

FIGURE 4. Numerical simulations of the system (5.2) showing the prey and predator for the parameter restriction $\delta = 0.105,\ 0.105 = h > h_0 = 0.127,\ d_1 = 1$ and $d_2 = 0.5$.

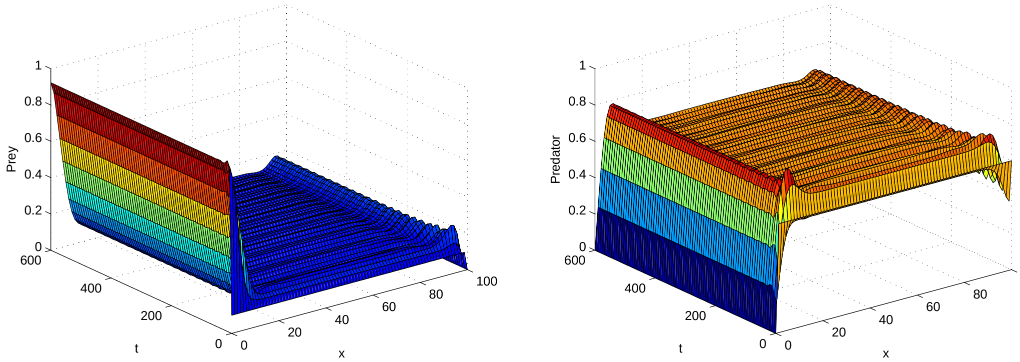

FIGURE 5. Numerical simulations of the system (5.2) showing the prey and predator for the parameter restriction $\delta = 0.105,\ 0.105 = h > h_0 = 0.127,\ d_1 = 0.5$ and $d_2 = 2$.

Under the parameters $d_1 = 1,\ d_2 = 0.5$ and $h = 0.127$, that is, $(H2)$ holds. By theorem (3), the homogeneous equilibrium (u^*, v^*) of system (5.2) is locally asymptotically stable (see Figure 4).

Under the parameters $d_1 = 0.5,\ d_2 = 2$ and $h = 0.127$, that is, $(H3)$ holds. By theorem (3), the homogeneous equilibrium (u^*, v^*) of system (5.2) is locally asymptotically stable (see Figure 5).

Under the parameters $d_1 = 0.1,\ d_2 = 5$ and $h = 0.127$, that is, $(H4)$ holds. By theorem (3), the homogeneous equilibrium (u^*, v^*) of system (5.2) is unstable (see Figure 6).

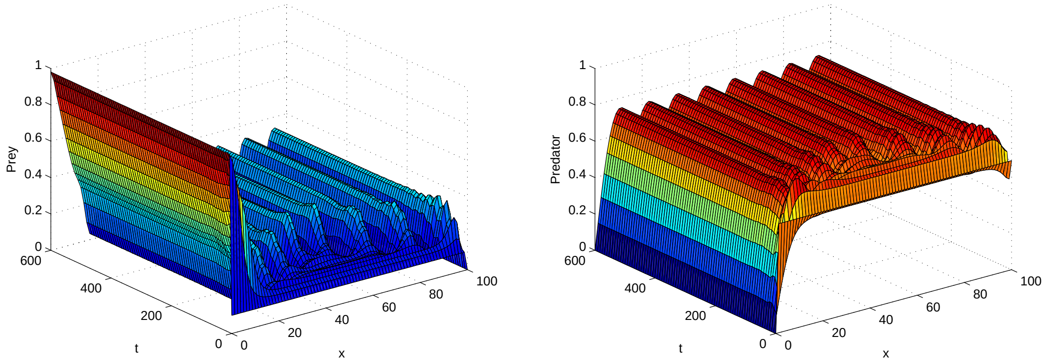

FIGURE 6. Numerical simulations of the system (5.2) showing the prey and predator for the parameter restriction $\delta = 0.105,\ 0.105 = h > h_0 = 0.127,\ d_1 = 0.1$ and $d_2 = 5$.

6. CONCLUSION

A rigorous investigation of the diffusive Holling-Tanner predator-prey system is attempted and the main purpose of this article is to study the stability and Hopf bifurcation of the system (1.2), as well as diffusion driven instability of the positive equilibrium $E^*(u^*, v^*)$ of the system (1.3).

For the local system (1.2), the positive equilibrium $E^*(u^*, v^*)$ is asymptotically stable when $h > h_0$ and unstable when $h < h_0$ and system (1.2) can undergo Hopf bifurcation of the positive equilibrium $E^*(u^*, v^*)$ when $h = h_0$ (see Figure 1-3). Moreover we obtain that when the direction of the Hopf bifurcation is supercritical then the bifurcating periodic solutions are stable and when the direction of the Hopf bifurcation is subcritical then the bifurcating periodic solutions are unstable. Diffusion driven instability of the system (1.3) occur due to the effect of diffusion, that is, Turing instability occurs (see Figure 4-6). The main results are presented in Theorem 3.1. From Theorem 4.1, the direction of the Hopf bifurcation and the stability of the bifurcating periodic solutions of the system (1.3) are same as of the local system (1.2).

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