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Hopf Bifurcation of a Predator-Prey Model with Time Delay

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Abstract

We consider the predator-prey model studied in [1] by adding a time lag, τ for the delay in the growth response of the predators. Using τ as a bifurcation parameter, we show that the positive equilibrium loses its stability and exhibits Hopf bifurcation. Numerical simulations are presented to illustrate the results.

Keywords: Hopf bifurcation, predator-prey model, time delay
Mathematics Subject Classification: 34D20, 35B32

1 Introduction

Many studies have been done on predator-prey model with time delay, differing on the growth rates of preys, functional response of the predators and the time delays used. Time delays may be due to maturation and gestation, hunting, and conversion of food to growth. Some examples are in [2, 3, 5, 8].

Time delays affect the dynamics of the system such as bifurcation, oscillations, and induce periodic solutions. Hopf bifurcation is a bifurcation from a branch of equilibria to a branch of periodic oscillations [9]. The occurrence of these periodic solutions can also be observed in nature, for instance, Hopf bifrucation has been observed in the predator-prey relationships of *Didinium* and *Paramecium*, *Paramecium bursaria* and *Schizoccharomyces pombe* [10], and lynx and hare [11].

The model studied in [1] is given by

$$\begin{aligned}\frac{dx}{dt} &= x(1-k_1x-k_2x^2)-y\frac{x}{1+ax},\\ \frac{dy}{dt} &= y\left(-\delta_0-\delta_1 y+\gamma\frac{x}{1+ax}\right),\end{aligned} \tag{1.1}$$

where x and y represent the prey and predator densities, respectively, and all the parameters, $k_1, k_2, a, \delta_0, \delta_1, \gamma$, are positive. There exists a real number $K>0$, such that $1-k_1K-k_2K^2=0$ and $\big(1-k_1x(t)-k_2(x(t))^2\big)\big(x(t)-K\big)<0$. That is, in the absence of predators, the growth of the prey population is bounded. The parameter δ_0 represents the natural death rate of the predator and δ_1 is the death rate due to intraspecies competition. The functional response is bounded by $1/a$, and γ is the proportion of the contribution of prey to predator growth.

The contribution of prey consumption to the growth rate of the predator density is delayed by some time allotted for gestation, that is, the time from conception to birth. Thus the addition of time lag in (1.1) makes it more realistic to model the rate of change of the predator density. There has not been a Hopf Bifurcation analysis done to a predator-prey model of this specific form, where time-delay is added to this type of functional response in the growth rate of the predator. We modify model (1.1) by adding a time delay $\tau>0$, which is the delay due to gestation. Gestation is the time from conception to birth. The modified model is given by

$$\begin{cases}\dfrac{dx(t)}{dt} = x(t)\left[1-k_1x(t)-k_2(x(t))^2\right]-y(t)\dfrac{x(t)}{1+ax(t)}\\ \dfrac{dy(t)}{dt} = y(t)\left[-\delta_0-\delta_1y(t)+\gamma\dfrac{x(t-\tau)}{1+ax(t-\tau)}\right],\end{cases} \tag{1.2}$$

with initial conditions

$$\begin{gathered}\big(x(\theta),y(\theta)\big)=\big(\Phi_1(\theta),\Phi_2(\theta)\big),\\ x(0)>0, y(0)>0,\end{gathered} \tag{1.3}$$

where $\big(\Phi_1(\theta),\Phi_2(\theta)\big)\in C\big([-\tau,0],\mathbb{R}_+^2\big)$. Here $C\big([-\tau,0],\mathbb{R}_+^2\big)$ is the space of continuous functions from $[-\tau,0]$ to $\mathbb{R}_+^2$, and $\mathbb{R}_+^2=\{(x,y)|\ x>0,\ y>0\}$. That is, $x(t)$ and $y(t)$ are predefined as functions on the negative time interval $[-\tau,0]$ so that for $0\le t\le\tau$, $x(t-\tau)$ will already have values.

2 Existence, Positivity, and Boundedness of Solutions

In this section prove the existence, uniqueness and boundedness of solutions of (1.2). First, we present published theorems to support our proof.

Let $\mathbb{R}^n$ be the $n-$dimensional Euclidean space with the Euclidean norm $|\cdot|$. For $\alpha<\beta$, we denote $C\big([\alpha,\beta],\mathbb{R}^n\big)$ the Banach space of continuous functions mapping the interval $[\alpha,\beta]$ into $\mathbb{R}^n$. For $\phi\in C\big([\alpha,\beta],\mathbb{R}^n\big)$, the norm is defined as $\|\phi\|=\sup_{\alpha\le\theta\le\beta}\big|\phi(\theta)\big|$, where $|\cdot|$ is the Euclidean norm.

Let $\sigma,b,r\in\mathbb{R}$ with $b\ge 0, r>0$, and $\chi\in C\big([\sigma-r,\sigma+b],\mathbb{R}^n\big)$. For $t\in[\sigma,\sigma+b]$, we define χ_t as a function on the interval $[-r,0]$ and $\chi_t(s)=\chi(t+s)$.

Suppose $B\subset\mathbb{R}\times\mathbb{R}^{np}$ and $\chi\in C\big([\sigma-r,\sigma+b],\mathbb{R}^n\big)$. Let f be a function from B to $\mathbb{R}^n$, and consider the delay differential equation with finite number p of delays $\tau_1,\tau_2,...,\tau_p$:

$$\frac{d\chi(t)}{dt}=f\Big(t,\chi\big(t-\tau_1\big),...,\chi\big(t-\tau_p\big)\Big), \tag{2.1}$$

where $0 \leq \tau_j \leq r$, for $j = 1, 2, ..., p$.

Let Ω be a subset of $\mathbb{R} \times C([-r, 0], \mathbb{R}^n)$. By the definition of $\chi_t(s)$, Equation (2.1) can be written as

$$\frac{d\chi(t)}{dt} = f\Big(t, \chi_t\big(-\tau_1\big), ..., \chi_t\big(-\tau_p\big)\Big), \tag{2.2}$$

which can also be expressed as just $f(t, x_t)$, which is a function on Ω. Equation (2.2) is called a *retarded functional differential equation.* We say (2.2) is *autonomous* if f does not depend on the independent variable t.

Let us first consider equation (2.1). Suppose I is an interval in $\mathbb{R}$ and D an open set in $\mathbb{R}^n$. Let $f : I \times D^p \to \mathbb{R}^n$. For $t \in [\sigma, \beta)$, with $\beta > 0$, consider equation (2.1) with initial condition

$$\chi(t) = \Phi(t) \quad \text{for } \Phi \in C\big([\sigma - r, \sigma], \mathbb{R}^n\big). \tag{2.3}$$

Definition 2.1 ([4]). *A* solution *of equations (2.1) and (2.3) is a continuous function,* $\chi : [\sigma - r, \beta_1) \to D$ *for some* $\beta_1 \in (\sigma, \beta]$ *such that*

i. $\chi(t) = \Phi(t)$ *for* $t \in [\sigma - r, \sigma]$*, and*

ii. $\dfrac{d\chi(t)}{dt} = f\Big(t, \chi\big(t - \tau_1\big), ..., \chi\big(t - \tau_p\big)\Big)$ *for* $t \in [\sigma, \beta_1)$*.*

To establish uniqueness of the solution to (2.1) and (2.3), we assume that f is locally Lipschitz.

Definition 2.2 ([4]). *We say that* f *is* Lipschitz *with Lipschitz constant* K *on a set* $G \subset I \times D^p$ *if*

$$\big|f(t, \eta_{(1)}, ..., \eta_{(p)}) - f(t, \tilde{\eta}_{(1)}, ..., \tilde{\eta}_{(p)})\big| \leq K \max_{j=1,...,p} |\eta_{(j)} - \tilde{\eta}_{(j)}|$$

for all $(t, \eta_{(1)}, ..., \eta_{(p)})$ *and* $(t, \tilde{\eta}_{(1)}, ..., \tilde{\eta}_{(p)})$ *in* G*. We shall also say* f *is* Lipschitzian *on* G*.*

Definition 2.3 ([4]). *Let* D *be an open subset of* $\mathbb{R}^n$ *and* I *an interval in* $\mathbb{R}$*. We say that* $f : I \times D^p \to \mathbb{R}^n$ *is* locally Lipschitzian *if for each point* $(t_1, \eta_{(1)}, ..., \eta_{(p)}) \in I \times D^p$ *there exist numbers* $a > 0$ *and* $b > 0$ *such that each*

$$A_j \equiv \{\xi \in \mathbb{R}^n \ : \ |\xi - \eta_{(j)}| \leq b\}, \quad j = 1, ..., p$$

is a subset of D *and* f *is Lipschitzian on the set*

$$\big([t_1 - a, t_1 + a] \cap I\big) \times A_1 \times \cdots \times A_p.$$

Lemma 2.4 ([4]). *Let* D *be an open subset of* $\mathbb{R}^n$*. If* $f : [\sigma, \beta) \times D^p \to \mathbb{R}^n$*, where* $\beta \leq \infty$*, has continuous first partial derivatives with respect to all but its first argument, then* f *is locally Lipschitzian.*

Theorem 2.5 ([4]). *In Equation (2.1), let* f *be continuous and locally Lipschitzian on* $[\sigma, \beta) \times D^p$*, let each delay* τ_j *be continuous with* $-r \leq t - \tau_j \leq t$ *on* $[\sigma, \beta)$ *for* $j = 1, .., p$*, and let* Φ *be continuous on* $[\sigma - r, \sigma]$*. Then equations (2.1) and (2.3) have at most one solution on any interval* $[\sigma - r, \beta')$ *for some* β' *on* $(\sigma, \beta]$*.*

Theorem 2.5 gives conditions for a solution to (2.1) and (2.3) to be unique if it exists. Next we consider (2.2) with initial condition

$$\chi_\sigma(s) = \phi(s), \quad \text{for } s \in [\sigma - r, \sigma], \tag{2.4}$$

where $\phi(s) = \Phi(\sigma + s)$, and $\phi \in C\big([\sigma - r, \sigma], \mathbb{R}^n\big)$.

The next theorem is on the existence of solutions to equations (2.2) and (2.4).

Theorem 2.6 ([6]). *Let Ω be an open subset of $\mathbb{R}\times C([-r,0],\mathbb{R}^n)$. Suppose that the function $f:\Omega\to\mathbb{R}^n$ in Equation (2.2) is continuous. If $(\sigma,\phi)\in\Omega$, then there is a solution of (2.2) passing through (σ,ϕ).*

We now apply these to prove that the solution to system (1.2) with initial conditions (1.3) exists and is unique.

Theorem 2.7. *For each $\Phi=(\Phi_1,\Phi_2)\in C\big([-\tau,0],\mathbb{R}^2_+\big)$, the solution to Equations (1.2) and (1.3) exists and is unique.*

Proof: Let $\Omega=\mathbb{R}\times C([-\tau,0],\mathbb{R}^2_+)$ and $\chi=(x,y)$. We have

$$\frac{d\chi(t)}{dt}=\begin{bmatrix}\dfrac{dx(t)}{dt}\\ \dfrac{dy(t)}{dt}\end{bmatrix}=\begin{bmatrix}x(t)\left[1-k_1x(t)-k_2(x(t))^2\right]-y(t)\dfrac{x(t)}{1+ax(t)}\\ y(t)\left(-\delta_0-\delta_1y(t)+\gamma\dfrac{x(t-\tau)}{1+ax(t-\tau)}\right)\end{bmatrix}=g(t,\chi(t),\chi(t-\tau)),\tag{2.5}$$

with initial conditions

$$\begin{gathered}\big(x(\theta),y(\theta)\big)=\big(\Phi_1(\theta),\Phi_2(\theta)\big)\in C([-\tau,0],\mathbb{R}^2_+)\\ x(0)>0,\quad y(0)>0.\end{gathered}\tag{2.6}$$

Note that g is a function on $\mathbb{R}\times\mathbb{R}^4_+$ and can be written as $g\big(t,\chi_t(0),\chi_t(-\tau)\big)=g(t,\chi_t)$, which is a function on Ω.

Clearly, g is continuous on Ω and $\Phi\in C\big([-\tau,0],\mathbb{R}^2_+\big)$. Therefore by Theorem 2.6, with $\sigma=0$, there exists a solution to (1.2) passing through $(0,\Phi)$. Also note that g has continuous partial derivatives with respect to all but its first argument. It follows from Lemma 2.4 that g is locally Lipschitzian and thus, by Theorem 2.5, the solution is unique. □

For the model to be biologically meaningful, we would like the population densities to be nonnegative. Indeed, if the initial population is positive, they will remain positive.

Theorem 2.8. *Any solution of system (1.2) that satisfies the initial conditions (1.3) is positive for $t\geq 0$.*

Proof: Observe that (1.2) can be written as

$$\begin{aligned}\frac{dx(t)}{dt}&=x(t)\left[1-k_1x(t)-k_2(x(t))^2-\frac{y(t)}{1+ax(t)}\right]\\ \frac{dy(t)}{dt}&=y(t)\left[-\delta_0-\delta_1y(t)+\gamma\frac{x(t-\tau)}{1+ax(t-\tau)}\right],\end{aligned}$$

whose solution is of the form

$$\begin{aligned}x(t)&=x(0)\exp\left[\int_0^t\left(1-k_1x(s)-k_2(x(s))^2-\frac{y(s)}{1+ax(s)}\right)ds\right]\\ y(t)&=y(0)\exp\left[\int_0^t\left(-\delta_0-\delta_1y(s)+\gamma\frac{x(s-\tau)}{1+ax(s-\tau)}\right)ds\right].\end{aligned}$$

Since we assumed $x(0)>0$ and $y(0)>0$, the solution to (1.2) is positive for $t>0$. □

To prove the boundedness of the solution, we will use this lemma from [3].

Lemma 2.9 ([3])**.** *Suppose $a > 0$, $b > 0$ and $\frac{dx}{dt} \leq x(t)(a - bx(t))$. If $x(0) > 0$, then*

$$x(t) \leq \left(\frac{a}{b}\right)\left[1 + \left(\frac{a}{bx(0)} - 1\right)e^{-at}\right]^{-1}, \text{ for } t \geq 0.$$

Let us simplify the inequality in Lemma 2.9. If $x(0) \geq \frac{a}{b}$, then $\frac{a}{bx(0)} - 1 \leq 0$. Since $a > 0$ and $t \geq 0$, then $e^{-at} \leq 1$. Thus,

$$\left[\frac{a}{bx(0)} - 1\right]e^{-at} \geq \frac{a}{bx(0)} - 1,$$

which implies that

$$\left(\frac{a}{b}\right)\left[1 + \left(\frac{a}{bx(0)} - 1\right)e^{-at}\right]^{-1} \leq x(0).$$

On the other hand, if $x(0) \leq \frac{a}{b}$, then $\frac{a}{bx(0)} \geq 1$. Since $e^{-at} > 0$, we obtain

$$\left(\frac{a}{b}\right)\left[1 + \left(\frac{a}{bx(0)} - 1\right)e^{-at}\right]^{-1} \leq \frac{a}{b}.$$

Thus, the result of Lemma 2.9 is equivalent to

$$x(t) \leq \max\left\{x(0), \frac{a}{b}\right\}. \tag{2.7}$$

We will be using this last inequality in our proof to show that the solution to (1.2) and (1.3) is bounded.

Theorem 2.10. *The solutions of system (1.2) with initial condition (1.3) are bounded.*

Proof: From the first equation of (1.2), we see that

$$\frac{dx(t)}{dt} \leq x(t)\big(1 - k_1 x(t)\big).$$

Thus by (2.7), if $M_1 = \max\{x(0), \frac{1}{k_1}\}$ then $0 < x(t) \leq M_1$. Using this M_1 in the second equation of (1.2), we get

$$\frac{dy(t)}{dt} \leq y(t)\big(\gamma M_1 - \delta_1 y(t)\big).$$

Again by (2.7), if we set $M_2 = \max\{y(0), \frac{\gamma M_1}{\delta_1}\}$, then $0 < y(t) \leq M_2$. Hence the solutions of system (1.2) are bounded. □

3 Local Stability Analysis

Time delay does not affect the equilibrium points of a system. Thus the equilibrium points of system (1.2) are the same as that of (1.1). From [1], the three equilibrium points of system (1.2) are $E_0 = (0, 0)$, $E_K = (K, 0)$, and $E^* = (x^*, y^*)$, where E^* is unique if any one of the following is satisfied:

1. $0 < a < \min\left\{k_1 + \sqrt{k_1^2 + k_2}, \frac{\delta_1 k_1 + \gamma}{\delta_0 + 2\delta_1}\right\}$,

2. $a > \max\left\{k_1 + \sqrt{k_1^2 + k_2}, \dfrac{\delta_1 k_1 + \gamma}{\delta_0 + 2\delta_1}\right\}$,

3. $\dfrac{\delta_1 k_1 + \gamma}{\delta_0 + 2\delta_1} < a < k_1 + \sqrt{k_1^2 + k_2}$.

To analyze the local stability of the equilibrium points of system (1.2), first we rewrite it using the following transformations. Let $E = (\bar{x}, \bar{y})$ be any equilibrium point. Define

$$n = x - \bar{x} \quad \text{and} \quad p = y - \bar{y},$$

where $n \ll 1$ and $p \ll 1$. With these transformations, system (1.2) becomes

$$\begin{aligned} \frac{dn(t)}{dt} &= (n(t) + \bar{x})\left[1 - k_1(n(t) + \bar{x}) - k_2((n(t) + \bar{x}))^2\right] - (p(t) + \bar{y})\frac{(n(t) + \bar{x})}{1 + a(n(t) + \bar{x})} \\ \frac{dp(t)}{dt} &= (p(t) + \bar{y})\left[-\delta_0 - \delta_1(p(t) + \bar{y}) + \gamma\frac{n(t-\tau) + \bar{x}}{1 + a(n(t-\tau) + \bar{x})}\right]. \end{aligned} \tag{3.1}$$

Next, we linearize system (3.1) about $(n, p) = (0, 0)$. Let $\dfrac{dn}{dt} = f_1$ and $\dfrac{dp}{dt} = f_2$. We get the partial derivatives of f_1 and f_2 at $n(t)$, $p(t)$ and $n(t - \tau)$.

$$\begin{aligned} \frac{df_1(t)}{dn(t)} &= (n(t) + \bar{x})\Big[-k_1 - 2k_2(n(t) + \bar{x}) + \frac{a(p(t) + \bar{y})}{(1 + a(n(t) + \bar{x}))^2}\Big] \\ &\quad +1 - k_1(n(t) + \bar{x}) - k_2((n(t) + \bar{x}))^2 - \frac{(p(t) + \bar{y})}{1 + a(n(t) + \bar{x})}, \\ \frac{df_1(t)}{dp(t)} &= -\frac{n(t) + \bar{x}}{1 + a(n(t) + \bar{x})}, \\ \frac{df_2(t)}{dn(t-\tau)} &= \frac{\gamma(p(t) + \bar{y})}{(1 + a(n(t) + \bar{x}))^2}, \\ \frac{df_2(t)}{dp(t)} &= -\delta_1(p(t) + \bar{y}) - \delta_0 - \delta_1(p(t) + \bar{y}) + \gamma\frac{n(t-\tau) + \bar{x}}{1 + a(n(t-\tau) + \bar{x})}. \end{aligned}$$

Evaluating these at $(0, 0)$, we get the linearized form of (3.1):

$$\begin{bmatrix} \dfrac{dn(t)}{dt} \\ \dfrac{dp(t)}{dt} \end{bmatrix} = \begin{bmatrix} b_{11} & b_{12} \\ 0 & b_{22} \end{bmatrix}\begin{bmatrix} n(t) \\ p(t) \end{bmatrix} + \begin{bmatrix} 0 & 0 \\ c_{21} & 0 \end{bmatrix}\begin{bmatrix} n(t-\tau) \\ p(t-\tau) \end{bmatrix}, \tag{3.2}$$

where

$$\begin{aligned} b_{11} &= \bar{x}\Big[-k_1 - 2k_2\bar{x} + \frac{a\bar{y}}{(1 + a\bar{x})^2}\Big] + \Big[1 - k_1\bar{x} - k_2(\bar{x})^2 - \frac{\bar{y}}{1 + a\bar{x}}\Big], \\ b_{22} &= -\delta_1\bar{y} + \Big[-\delta_0 - \delta_1\bar{y} + \gamma\frac{\bar{x}}{1 + a\bar{x}}\Big], \\ b_{12} &= -\frac{\bar{x}}{1 + a\bar{x}}, \\ c_{21} &= \frac{\gamma\bar{y}}{(1 + a\bar{x})^2}. \end{aligned}$$

The characteristic equation of (3.2) about any equilibrium point $(\bar{x}, \bar{y})$ is given by

$$\det\left(\begin{bmatrix} b_{11} & b_{12} \\ 0 & b_{22} \end{bmatrix} + \begin{bmatrix} 0 & 0 \\ c_{21} & 0 \end{bmatrix} e^{-\lambda\tau} - \lambda \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}\right) = 0,$$

or

$$\lambda^2 - (b_{11} + b_{22})\lambda + b_{11}b_{22} - b_{12}c_{21}e^{-\lambda\tau} = 0. \tag{3.3}$$

At the trivial equilibrium point, E_0, the characteristic equation is $(1-\lambda)(-\delta_0 - \lambda) = 0$. The eigenvalues are $\lambda_1 = 1$ and $\lambda_2 = -\delta_0$. Thus, $(0,0)$ is a saddle point.

At E_K, the characteristic equation is $\big(-K(k_1 + 2k_2K) - \lambda\big)\left(-\delta_0 + \dfrac{\gamma K}{1+aK} - \lambda\right) = 0$. The eigenvalues are

$$\lambda_1 = -K(k_1 + 2k_2K) \quad \text{and} \quad \lambda_2 = -\delta_0 + \frac{\gamma K}{1+aK}.$$

Since the K, k_1, k_2 are positive, we see that $\lambda_1 < 0$. Thus, $(K, 0)$ is stable if $\delta_0 > \dfrac{\gamma K}{1+aK}$ and a saddle point if $\delta_0 < \dfrac{\gamma K}{1+aK}$.

For the positive equilibrium E^*, note that $1 - k_1x^* - k_2x^{*2} - \dfrac{y^*}{1+ax^*} = 0$ and $-\delta_0 - \delta_1 y^* + \dfrac{\gamma x^*}{1+ax^*} = 0$. The characteristic equation is given by

$$\lambda^2 - b\lambda + c_1 - c_2e^{-\lambda\tau} = 0, \tag{3.4}$$

where

$$\begin{aligned} b &= -k_1x^* - 2k_2x^{*2} - \delta_1y^* + \frac{ax^*y^*}{(1+ax^*)^2}, \\ c_1 &= \delta_1k_1x^*y^* + 2\delta_1k_2x^{*2}y^* - \frac{a\delta_1x^*y^{*2}}{(1+ax*)^2}, \\ c_2 &= -\frac{\gamma x^*y^*}{(1+ax^*)^3}. \end{aligned}$$

If there is no delay, i.e., $\tau = 0$, then the characteristic equation is just

$$\lambda^2 - b\lambda + c_1 - c_2 = 0. \tag{3.5}$$

The eigenvalues are

$$\lambda = \frac{b \pm \sqrt{b^2 - 4(c_1 - c_2)}}{2}.$$

Both will have negative real parts if $b < 0$ and $c_1 - c_2 > 0$. The real parts will both be positive if $b > 0$ and $c_1 - c_2 > 0$, and will have opposite in signs if $c_1 - c_2 < 0$.

We will explore the stability of E^* for $\tau > 0$ in the next section. The results of the local stability analysis of system (1.2) are given in the following theorem.

Theorem 3.1. *In (1.2), for any value of τ,*

(i) the trivial equilibrium point E_0 is a saddle point, and

(ii) the equilibrium point E_K is locally stable if $\delta_0 > \dfrac{\gamma K}{1+aK}$ and a saddle point if $\delta_0 < \dfrac{\gamma K}{1+aK}$.

In the absence of delay, the positive equilibrium point E^* is

(a) locally stable if $b < 0$ and $c_1 - c_2 > 0$,

(b) unstable if $b > 0$ and $c_1 - c_2 > 0$, and

(c) a saddle point if $c_1 - c_2 < 0$.

The stability results of E_0 and E_K is the same in both systems (1.1) and (1.2). For E^* we explore more of its stability for $\tau > 0$ in the next section.

4 Hopf Bifurcation

In this section, by choosing τ as the bifurcation parameter, we show that system (1.2) undergoes a Hopf bifurcation at some critical value $\tau_c > 0$. This type of bifurcation is associated with the appearance of a pair of purely imaginary eigenvalues [7].

We formally state the conditions needed for Hopf Bifurcation to occur, as stated in [6]. We first consider a retarded functional differential equation dependent on a parameter μ,

$$\frac{d\chi(t)}{dt} = L(\mu, \chi_t) + f(\mu, \chi_t), \quad \mu \in \mathbb{R}, \tag{4.1}$$

where L and f are continuously differentiable in μ and χ_t, $f(\mu, 0) = 0$ and $\partial f(\mu, 0)/\partial \chi_t = 0$. The function L is linear in χ_t, and

$$L(\mu, \chi_t) = \sum_{k=0}^{\infty} B_k(\mu)\chi(t - \tau_k(\mu)) + \int_{-r}^{0} B(\mu, \theta)\chi(t+\theta)d\theta,$$

for $\chi_t \in C\big([-r, 0], \mathbb{R}^2_+\big)$, $\mu \in \mathbb{R}$. Here, $\tau_0(\mu) = 0$ and $\tau_k(\mu) \in (0, r]$, and $B_k(\mu)$ and $B(\mu, \theta)$ satisfy

$$\sum_{k=0}^{\infty} |B_k(\mu)| + \int_{-r}^{0} |B(\mu, \theta)| d\theta < \infty.$$

where $|\cdot|$ is the determinant of the matrices $B_k(\mu)$ and $B(\mu, \theta)$.

The characteristic equation is given by $\det \Delta(\mu, \lambda) = 0$, where

$$\Delta(\mu, \lambda) = \lambda I - \sum_{k=0}^{\infty} B_k(\mu) e^{-\lambda \tau_k(\mu)} I,$$

and I is the identity matrix.

For Hopf bifurcation to occur, the following must be satisfied:

(H1) For $\mu = \mu_0$, the charactersitic equation, $\det \Delta(\mu, \lambda) = 0$ has a purely imaginary simple root $\lambda_0 = i\omega_0$, with $\omega_0 > 0$, and no root of $\det \Delta(\mu, \lambda) = 0$ other than $\pm i\omega_0$ is an integral multiple of λ_0.

(H2) $\operatorname{Re} \dfrac{\partial \lambda(\mu_0)}{\partial \mu} \neq 0$.

To start our analysis, we first rewrite system (1.2) by applying the following transformations.

$$n = x - x^*, \quad p = y - y^*,$$

where $E^* = (x^*, y^*)$ is the positive equilibrium of (1.2). After applying the above transformations, we get

$$\begin{aligned} \frac{dn(t)}{dt} &= (n(t) + x^*)\left[1 - k_1(n(t) + x^*) - k_2(n(t) + x^*)^2 - \frac{(p(t) + y^*)}{1 + a(n(t) + x^*)}\right], \\ \frac{dp(t)}{dt} &= (p(t) + y^*)\left[-\delta_0 - \delta_1(p(t) + y^*) + \gamma\frac{n(t-\tau) + x^*}{1 + a(n(t-\tau) + x^*)}\right]. \end{aligned} \tag{4.2}$$

We now have a system dependent on the parameter τ and have $(0, 0)$ as an equilibrium point. For $s \in [-\tau, 0]$, we let $n(t + s) = n_t(s)$ and $p(t + s) = p_t(s)$. Then by getting the Taylor expansion of (4.2) at $(0, 0)$ up to the second degree, it can be written as functional differential equation in $C\big([-\tau, 0], \mathbb{R}^2_+\big)$ of the form

$$\begin{bmatrix} \dfrac{dn(t)}{dt} \\ \dfrac{dp(t)}{dt} \end{bmatrix} = B_0 \begin{bmatrix} n_t(0) \\ p_t(0) \end{bmatrix} + B_1 \begin{bmatrix} n_t(-\tau) \\ p_t(-\tau) \end{bmatrix} + \tau \begin{bmatrix} f_{11} \\ f_{12} \end{bmatrix}, \tag{4.3}$$

where

$$B_0 = \begin{bmatrix} b_{11} & b_{12} \\ 0 & b_{22} \end{bmatrix} \quad B_1 = \begin{bmatrix} 0 & 0 \\ b_{21} & 0 \end{bmatrix},$$

with

$$\begin{aligned} b_{11} &= (-k_1x^* - 2k_2(x^*)^2) + \frac{ax^*y^*}{(1 + ax^*)^2} \\ b_{12} &= -\frac{x^*}{1 + ax^*} \\ b_{21} &= \frac{\gamma y^*}{(1 + ax^*)^2} \\ b_{22} &= -\delta_1 y^* \end{aligned}$$

and

$$\begin{aligned} f_{11} = &\left(-k_1 - 3k_2x^* + \frac{ay^*}{(1 + ax^*)^2} - \frac{a^2x^*y^*}{(1 + ax^*)^3}\right)(n_t(0))^2 \\ &+ \left(\frac{ax^*}{(1 + ax^*)^2} - \frac{1}{(1 + ax^*)}\right) n_t(0)p_t(0), \end{aligned}$$

$$f_{12} = -\frac{y^*\gamma a}{(1 + ax^*)^3}(n_t(-\tau))^2 + \frac{\gamma}{(1 + ax^*)^2} n_t(-\tau)p_t(0) - \delta_1(p_t(0))^2.$$

Clearly, (4.3) satisfies the conditions stated for equation (4.1). Next, we show that equation (4.3) satisfies (H1) and (H2). The characteristic equation for (4.3) is given by

$$\lambda^2 - b\lambda + c_1 - c_2 e^{-\lambda\tau} = 0, \tag{4.4}$$

where $b = b_{11} + b_{22}$, $c_1 = b_{11}b_{22}$, and $c_2 = b_{21}b_{12}$.

First, we show that the characteristic equation will have a purely imaginary solution.

Lemma 4.1. *If* $c_1^2 - c_2^2 < 0$ *and*

$$\left|\frac{c_1 - \omega_0^2}{c_2}\right| \leq 1 \quad \text{and} \quad \left|\frac{b\omega_0}{c_2}\right| \leq 1,$$

then the characteristic equation (4.4) has a pair of purely imaginary solutions $\pm i\omega_0$*, with*

$$\omega_0 = \sqrt{\frac{-(b^2 - 2c_1) + \sqrt{(b^2 - 2c_1)^2 - 4(c_1^2 - c_2^2)}}{2}}$$

for $\tau = \tau^{(k)}$*, where we define for* $k \in \{0, 1, 2, ...\}$*,*

$$\tau^{(k)} := \frac{\cos^{-1}(\frac{c_1 - \omega_0^2}{c_2}) + 2k\pi}{\omega_0}.$$

Proof: Let $\omega > 0$. Then $i\omega$ is a root of (4.4) if and only if

$$(i\omega)^2 - bi\omega + c_1 - c_2 e^{-i\omega\tau} = 0. \tag{4.5}$$

Replacing $e^{-i\omega\tau}$ in (4.5) by $\cos(\omega\tau) - i\sin(\omega\tau)$, and equating the real and imaginary parts to zero, we then have the system of equations

$$c_2 \cos(\omega\tau) = c_1 - \omega^2, \qquad c_2 \sin(\omega\tau) = b\omega. \tag{4.6}$$

Applying the Pythagorean identity to (4.6), gives

$$\omega^4 + (b^2 - 2c_1)\omega^2 + (c_1^2 - c_2^2) = 0, \tag{4.7}$$

whose solutions are given by

$$\omega = \pm\sqrt{\frac{-(b^2 - 2c_1) \pm \sqrt{(b^2 - 2c_1)^2 - 4(c_1^2 - c_2^2)}}{2}}.$$

If $c_1^2 - c_2^2 < 0$, we will have a unique positive value for ω. If $c_1^2 - c_2^2 > 0$, then ω will have two positive values if in addition we have $b^2 - 2c_1 < 0$. However, from the definition of b and c_1, c_1 can be written as $c_1 = b_{22}(b - b_{22}) = b_{22}b - b_{22}^2$, and so we see that

$$b^2 - 2c_1 = b^2 - 2(b_{22}b - b_{22}^2) = (b - b_{22})^2 + b_{22}^2$$

is always positive. Thus the solution to (4.7) is real, positive and unique if and only if $c_1^2 - c_2^2 < 0$. This unique solution is

$$\omega_0 = \sqrt{\frac{-(b^2 - 2c_1) + \sqrt{(b^2 - 2c_1)^2 - 4(c_1^2 - c_2^2)}}{2}}.$$

Substituting this to (4.6), we get

$$\cos(\omega_0\tau) = \frac{c_1 - \omega_0^2}{c_2}, \qquad \sin(\omega_0\tau) = \frac{b\omega_0}{c_2}, \tag{4.8}$$

which are well-defined if the corresponding right-hand sides have moduli of at most 1.

Therefore, we have the following as solutions for the critical values $\tau = \tau^{(k)}$:

$$\tau^{(k)} = \frac{1}{\omega_0}\cos^{-1}\left(\frac{c_1 - \omega_0^2}{c_2}\right) + \frac{2k\pi}{\omega_0}, \qquad k \in \{0, 1, 2, ...\}.$$

□

Next, we determine the conditions when the roots of (4.4) cross the imaginary axis. For each $k \in \{0, 1, 2, ...\}$, let $\lambda_k(\tau) = \alpha_k(\tau) + i\omega_k(\tau)$ denote the roots of (4.4) for τ-values close to $\tau^{(k)}$, satisfying

$$\omega_k(\tau^{(k)}) = \omega_0 \text{ and } \alpha_k(\tau^{(k)}) = 0.$$

Lemma 4.2. $\dfrac{d}{d\tau}\left[\text{Re } \lambda_k(\tau^{(k)})\right] > 0$, *for* $k \in \{0, 1, 2, ...\}$.

Proof: Differentiating (4.4) with respect to τ, and solving for $d\lambda/d\tau$, we get

$$\frac{d\lambda}{d\tau} = \frac{\lambda c_2 e^{-\lambda\tau}}{-2\lambda + b - \tau c_2 e^{-\lambda\tau}}.$$

To simplify our computations, we instead use the reciprocal of $\dfrac{d\lambda}{d\tau}$. Evaluating this at $\tau = \tau^{(k)}$ and only taking the real part, we get

$$\begin{aligned} \text{Re}\left(\frac{d\lambda_k}{d\tau}\right)^{-1}\Bigg|_{\tau=\tau^{(k)}} &= \frac{-2\cos(\omega_0\tau^{(k)})}{c_2} + \frac{b\sin(\omega_0\tau^{(k)})}{\omega_0 c_2} \\ &= \frac{\sqrt{(b^2 - 2c_1)^2 - 4(c_1^2 - c_2^2)}}{c_2^2} > 0. \end{aligned}$$

It follows that $\text{Re}\,(d\lambda_k/d\tau)$ is positive at $\tau = \tau^{(k)}$. Note that we have also made use of the fact that $\text{sgn}\Big(\dfrac{d}{d\tau}\text{Re}\,\lambda_k(\tau^{(k)})\Big) = \text{sgn}\Big(\text{Re}\dfrac{d\lambda_k(\tau^{(k)})}{d\tau}\Big)$. □

Lemmas 4.1 and 4.2 have proven that system (4.3) satisfies (H1) and (H2). Our main result is given by the theorem below.

Theorem 4.3. *For system (1.2), if* $c_1^2 - c_2^2 < 0$, *and*

$$\left|\frac{c_1 - \omega_0^2}{c_2}\right| \leq 1 \quad \textit{and} \quad \left|\frac{b\omega_0}{c_2}\right| \leq 1,$$

then, E^* *undergoes Hopf Bifurcation at* $\tau = \tau^{(k)}$, $k = 0, 1, 2, ...$

5 Numerical Simulations

We perform simulations using MATLAB DDE23 to show the change in stability as the value of τ changes from less than $\tau^{(0)}$ to a value greater than $\tau^{(0)}$. We use the same parameter values used in [1]:

$$a = 2.9, \quad k_1 = 0.03, \quad k_2 = 0.1, \quad \gamma = 5, \quad \delta_0 = 0.05, \quad \delta_1 = 0.1.$$

With these parameter values, the positive equilibrium is $E^* = (0.03529, 1.1011)$, and we compute $b = -0.01866$ and $c_1 = -0.01007$. This implies that for $\tau = 0$, i.e., without delay, E^* is stable. The characteristic equation has a purely imaginary pair of eigenvalues $i\omega_0$ at $\tau = \tau^{(0)}$, where $\omega_0 = 0.3672$ and $\tau^{(0)} = 0.1287$. We keep the values of the above parameters fixed and run simulations for varying values of τ.

Simulation 1: $\tau < \tau^{(0)}$. We take $\tau = 0.05$, which is less than $\tau^{(0)}$ and initial point at $(0.03, 0.6)$. As shown in Figure 1 the solution is moving towards E^*. Figure 2 shows the

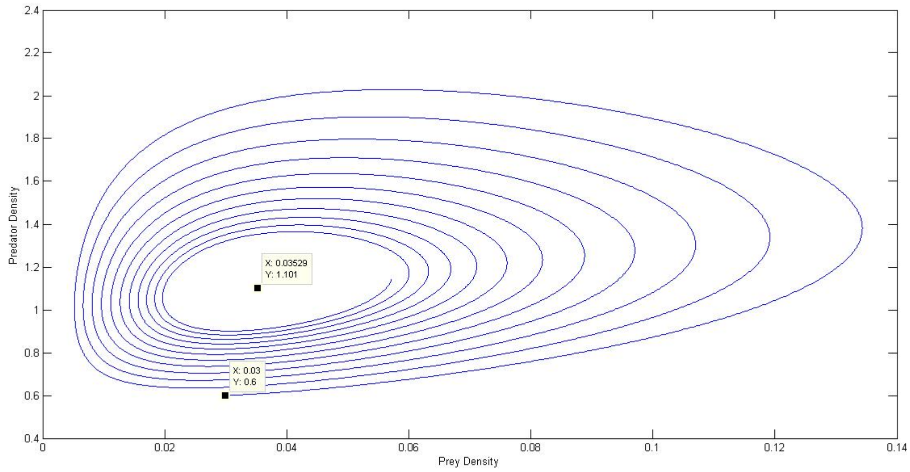

Figure 1: Phase space for $\tau < \tau^{(0)}$.

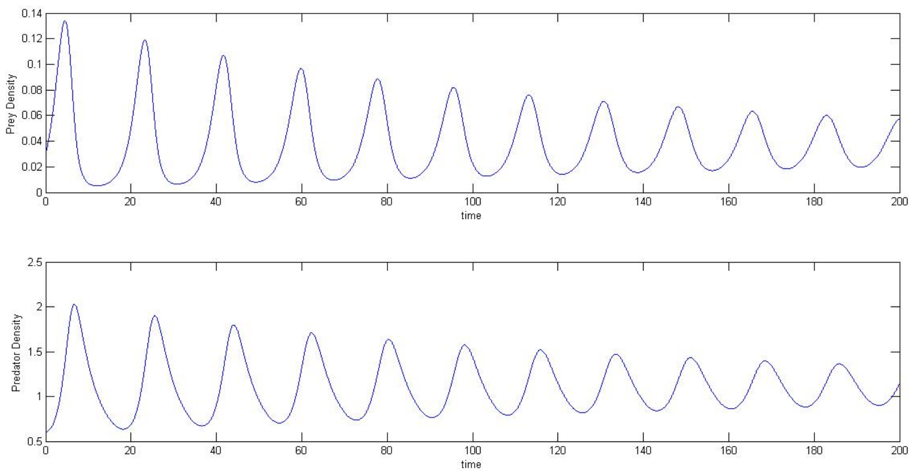

Figure 2: Time evolution of densities for $\tau < \tau^{(0)}$.

decreasing amplitude in the oscillations of the densities and getting closer to the equilibrium value. For $\tau < \tau^{(0)}$, E^* remained stable.

Simulation 2: $\tau > \tau^{(0)}$. This time, we take $\tau = 0.5$, which is greater than $\tau^{(0)}$ and the same initial point as in the first simulation. Notice that E^* became unstable. The solution moved away from the equilibrium point E^* as shown in Figures 3 and 4. Observe also that the trajectory seems to be approaching a limit cycle.

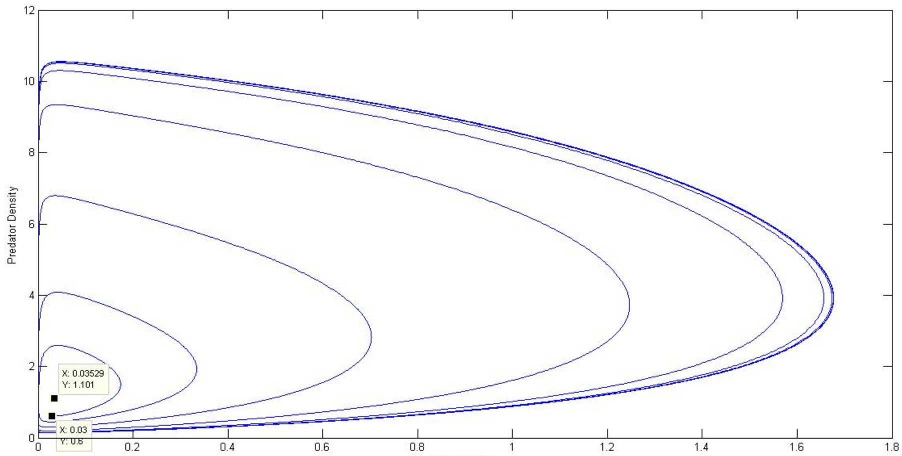

Figure 3: Phase space for $\tau > \tau^{(0)}$.

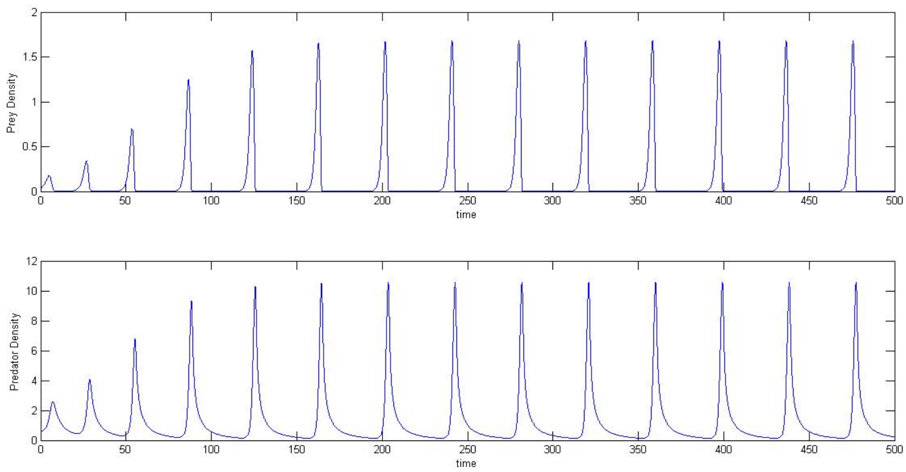

Figure 4: Time evolution of densities for $\tau > \tau^{(0)}$.

Simulation 3: We use the same value of τ as in Simulation 2 and pick an initial point outside the limit approached by the graph in Figure 3. The graph in Figure 5 shows two trajectories with $\tau > \tau^{(0)}$. The one in blue has initial point $(0.03, 0.6)$ and is moving away from E^* and approaching a limit cycle, while the one in green has initial point $(0.6, 12)$ and is moving in towards the limit cycle.

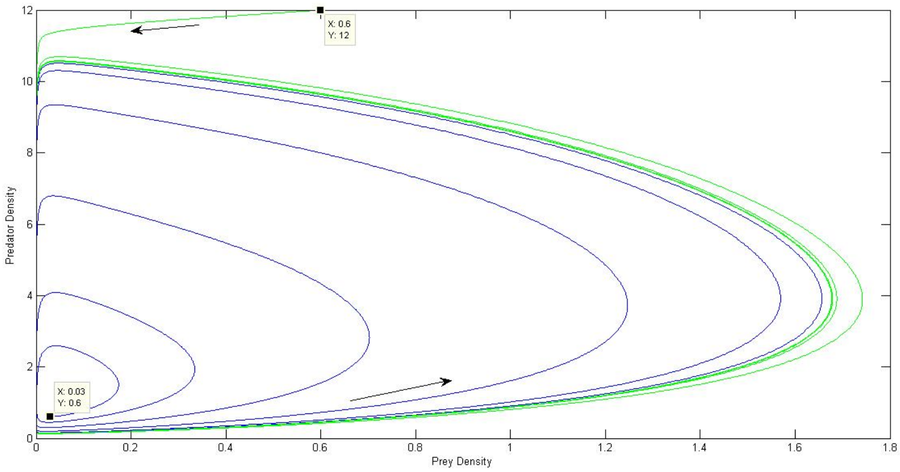

Figure 5: Trajectories approaching the limit cycle from the inside and out at $\tau > \tau^{(0)}$.

6 Discussion

We have shown that system (1.2) with initial conditions (1.3) has a unique and bounded solution. Also, we have proven that even with the addition of time delay to system (1.1), the stability results for the equilibrium points E_0 and E_K would still be the same.

In [1], they analyzed the Hopf bifurcation of the system with a as the bifurcation parameter while in our case, we used the time delay τ. For the three equilibrium points of system (1.2), only the characteristic equation at E^* is dependent on the bifurcation parameter τ. For this reason, the second half of this paper is focused only on E^*. We have shown that under some conditions, Hopf bifurcation occurs. The occurence of Hopf bifurcation is dependent of the behavior of the system near E^* for τ values near $\tau^{(k)}$. We have obtained infinitely many critical values $\tau^{(k)}$ but note that the change in stability occurs only when $\tau = \tau^{(k)}$, and from Lemma 4.2, the change is from stable to unstable. In our numerical simulations we have shown that a stable positive equilibrium point at $\tau < \tau^{(0)}$ becomes unstable when $\tau > \tau^{(0)}$. Figure 5 shows that at $\tau > \tau^{(0)}$, the solution approaches a stable periodic orbit.

If the positive equilibrium point is stable, the amplitude of the oscillating solution is decreasing and in the long run, the rise and fall in their population density will be closer to the equilibrium value. On the other hand, if it is unstable for τ greater than the critical value, the densities would approach a periodic orbit. In a periodic solution, the peak density of each population could be much higher than the equilibrium value. As the period of the periodic solution increase, the higher the value of these peaks will be. But the time when the densities stay at very low values would be longer. In reality, it could lead to the population dying out. Thus one must also consider the rate at which a certain species reproduce while they are at a very low density. If the goal is to have a stable periodic solution, then the time for gestation must be greater than the critical value but not too big that the population would be too low for a long time interval. However, for most species, gestation time is fixed. Thus there is a need to lower the critical value of the time delay by adjusting other factors like the loss through intraspecific competion by providing more resources for the species; or change the death rate by limiting other harmful factors for the population.

Further analysis could be done like determining the direction of bifurcation and the stability of the periodic solution, global stability of the equilibrium points, and global existence of periodic solutions.

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