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A DELAYED PREDATOR-PREY MODEL WITH HOLLING IV FUNCTIONAL RESPONSE AND PREY REFUGE

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ABSTRACT: A delay-induced predator-prey model with Holling IV functional response and effect of prey refuge is proposed. The globally asymptotically stability of the coexist equilibrium and Hopf bifurcation are investigated by the theory of the differentially dynamical system. The results show that there exist stability switches and Hopf bifurcation occurs while the gestation delay cross a threshold value.

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1. INTRODUCTION

The predator-prey model has long been and will continue to be widely applied in understanding the dynamics of interacting populations since the pioneering work of Lotka and Volterra who first proposed two differential equations that describe the relationship between predators and prey in 1925 and 1926, respectively [1]. For over the last one hundred years, the rich and varied dynamics of Lotka-Volterra model has been researched from various fields such as mathematics, mathematical biology, ecology, economics, etc [2]. Therefore, it has been modified and improved in many ways. Such as modifying the functional response of predators to prey population which defined as the amount of prey catch per predator per unit of time to improve the realistic application of the proposed predator-prey models [2-13].

In fact, the dynamical consequences of the predator-prey model can be determined by much ecological effect, such as Allee effect, harvesting effect, Crowding effect, habitat complex, prey refuge, etc. Theoretical research and field observations on population dynamics of prey refuges lead to the conclusion that prey refuges have the stabilizing and/or destabilizing effect on the considered predator-prey systems [14-22]. Ruxton [18] proposed a predator-prey model based on the assumption that the rate of prey moving into refuges is proportional to predator density and the results showed that the effect of prey refuge has a stabilizing effect. The stabilizing effect was also observed in a Holling II type predator-prey model studied by Gonzalez-Olivares and Ramos-Jiliberto [21]. Ma et al. [22] formulated a predator-prey model with a class of functional response incorporating the effect of prey refuges and observed the stabilizing and destabilizing effect due to the increases in the prey refuges.

Predator-prey models with time delay were much more realistic since delay occurred in almost every biological situation and assumed to be one of the reasons of regular fluctuations in population density [23-28]. New reproduction of predators after consuming prey was not momentary and instantaneous, but mediated by some time lag required for gestation of predators [24]. Therefore, in order to make a predator-prey model biologically more realistic, Incorporating this gestation delay in predator-prey models was essential and interesting.

Motivated by these, the predator-prey model with Holling IV type response function and the effect of prey refuge is proposed as following form:

$$\begin{cases} \dot{x}(t) = rx(1-\dfrac{x}{K}) - \frac{c(1-\beta)^n x^n y}{1+ch(1-\beta)x^n}, \\ \dot{y}(t) = \frac{ec(1-\beta)^n x^n y}{1+ch(1-\beta)^n x^n} - dy, \\ x(0) = x_0 > 0, \quad y(0) = y_0 > 0. \end{cases} \tag{1}$$

where $x(t)$ and $y(t)$ are the density of prey and predator populations at time t, respectively, hence are all positive number. The other parameters have the following biological meanings: r is the intrinsic per capita growth rate of prey population, K is the prey environmental carrying capacity, c is the attack coefficient and h is the handing time; e $(0 < e < 1)$ is the conversion efficiency, measuring the number of newly born predators for each captured prey, d is the per capita death rate of predators.

Now, the gestation delay is incorporated into system (1), and it is obtained the following system with time delay:

$$\begin{cases} \dot{x}(t) = rx(1-\dfrac{x}{K}) - \frac{c(1-\beta)^n x^n y}{1+ch(1-\beta)x^n}, \\ \dot{y}(t) = \frac{ec(1-\beta)^n x^n (t-\tau) y(t-\tau)}{1+ch(1-\beta)^n x^n (t-\tau)} - dy, \\ x(\xi) = \varphi(\xi) > 0, \quad y(\xi) = \psi(\xi) > 0, \ \xi \in (-\tau, 0]. \end{cases} \tag{2}$$

in which τ ($\tau > 0$) is the gestation delay denoting the time lag from the predation of prey population to the birth of the new predators.

Throughout this paper, we assume that $h < e/d$ and $n \geq 1$.

2. EXISTENCE OF EQUILIBRIA

By solving the following equations

$$\begin{cases} rx(1-\dfrac{x}{K}) - \frac{c(1-\beta)^n x^n y}{1+ch(1-\beta)^n x^n} = 0, \\ (\frac{ec(1-\beta)^n x^n}{1+ch(1-\beta)^n x^n} - d)y = 0. \end{cases} \tag{3}$$

we can obtain all equilibrium points of system (2): $E_0(0,0)$, $E_K(K,0)$, $\tilde{E}(\tilde{x},\tilde{y})$, where

$$\tilde{x} = \frac{1}{1-\beta}\sqrt[n]{\frac{d}{c(e-dh)}}; \quad \tilde{y} = \frac{er\tilde{x}}{d}(1-\frac{\tilde{x}}{K}).$$

The equilibrium point $\tilde{E}(\tilde{x},\tilde{y})$ is positive if and only if $1-\dfrac{\tilde{x}}{K} > 0$, that is, $\beta < 1-\dfrac{1}{K}(\dfrac{d}{c(e-dh)})^{1/n}$.

3. POSITIVITY AND BOUNDEDNESS OF SYSTEM (1)

In order to study the positivity and boundedness for the solutions of system (1), we denote the function on the right hand of system(1) as $\mathbf{G} = (xg_1, yg_2)$ in which

$$g_1(x,y) = r(1-\frac{x}{K}) - \frac{c(1-\beta)^n x^{n-1} y}{1+ch(1-\beta)^n x^n},$$
$$g_2(x,y) = \frac{ec(1-\beta)^n x^n}{1+ch(1-\beta)^n x^n} - d.$$

Clearly, $G \in C^1(R_+^2)$. Thus $\mathbf{G}: R_+^2 \to R^2$ is locally lipschitz on $R_+^2 = \{(x,y)|x > 0, y > 0\}$. Hence the fundamental theorem of existence and uniqueness assures existence and uniqueness of solution of the system (1.1) with the given initial conditions. The state space of the system is the non-negative cone in R_+^2. In the theoretical ecology, positivity and boundedness of the system establishes the biological well behaved nature of system.

Theorem 1. *All the solutions of the system (1) with the given initial conditions are always positive and bounded.*

Proof. Firstly, we wish to prove that $(x(t), y(t)) \in R_+^2$ for all $t \in [0, +\infty]$. We show this by method of contradiction. Supposing this is not true. Hence, there must exists one $\bar{t} \in [0, +\infty]$, such that $x(\bar{t}) \leq 0$ and $y(\bar{t}) \leq 0$. From the system(1), we have

$$x(t) = x(0) \exp(\int_0^t g_1(x, y)dt),$$

$$y(t) = x(0) \exp(\int_0^t g_2(x, y)dt).$$

Since $(x(t), y(t))$ are well defined and continuous on $[0, \bar{t}]$, there must exist a $M > 0$ such that $\forall\ t \in [0, \bar{t}]$

$$x(t) = x(0) \exp(\int_0^t g_1(x, y)dt) \geq x(0) \exp(-M\bar{t}),$$

$$y(t) = x(0) \exp(\int_0^t g_2(x, y)dt) \geq y(0) \exp(-M\bar{t}).$$

It is clear that if limit $t \to \bar{t}$, we obtain

$$x(\bar{t}) \geq x(0) \exp(-M\bar{t}) > 0,$$

$$y(\bar{t}) \geq y(0) \exp(-M\bar{t}) > 0,$$

which is a contradiction.

Hence, all the solutions of the system (1) are always positive.

Secondly, we will prove the boundedness.

Letting $V(t) = x(t) + \frac{1}{e}y(t)$, then we obtain that

$$\dot{V}(t) = rx(1 - \frac{x}{K}) - \frac{c(1-\beta)^n x^n y}{1 + ch(1-\beta)^n x^n} + \frac{c(1-\beta)^n x^n y}{1 + ch(1-\beta)^n x^n} - \frac{d}{c}y \leq -dV(t) + (d+r)K.$$

Integrating both sides of above equation and applying the theorem of differential inequality, we have

$$0 < V(t) < \frac{(d+r)K}{d}(1 - e^{-dt}) + V(0)e^{-dt}, \quad V(0) = V(x(0), y(0)).$$

and $\lim_{t \to +\infty} V(t) \leq \frac{(d+r)K}{d}$.

Hence, all solutions of system (1) without delay are bounded. □

4. STABILITY AND BIFURCATION ANANLYSIS

In this paper, we mainly consider the stability of the positive equilibrium point and omit study the trivial equilibrium point $E_0(0, 0)$ and predator-extinction equilibrium point $E_K(K, 0)$. To do these, the characteristic equation of model (2) at the positive equilibrium point $\tilde{E}(\tilde{x}, \tilde{y})$ is given as following form

$$\lambda^2 - (A + de^{-\lambda\tau})\lambda + Be^{-\lambda\tau} - C = 0. \tag{4}$$

in which

$$A = \frac{r[(1-n)K + ch(1-\beta)^n K\tilde{x}^n - (2-n)\tilde{x} - 2ch(1-\beta)^n \tilde{x}^{n+1}]}{K(1+ch(1-\beta)^n \tilde{x}^n)} - d,$$

$$B = \frac{dr[(1-n)K + ch(1-\beta)^n K\tilde{x}^n - (2-n)\tilde{x} - 2ch(1-\beta)^n \tilde{x}^{n+1}]}{K(1+ch(1-\beta)^n \tilde{x}^n)} + \frac{nder(K-\tilde{x})}{K(1+ch(1-\beta)^n \tilde{x}^n)},$$

$$C = \frac{dr[(1-n)K + ch(1-\beta)^n K\tilde{x}^n - (2-n)\tilde{x} - 2ch(1-\beta)^n \tilde{x}^{n+1}]}{K(1+ch(1-\beta)\tilde{x}^n)} > 0.$$

When there is no delay, the corresponding characteristic equation (4) is given by

$$\lambda^2 - (A+d)\lambda + B - C = 0. \tag{5}$$

and the eigenvalues are

$$\lambda_{1,2} = \frac{(A+d) \pm \sqrt{(A+d)^2 - 4(B-C)}}{2}.$$

The standard qualitative analysis depicts that the locally asymptotic stability of equilibrium is determined by the sign of the $A+d$ at the corresponding equilibrium point. The following conclusions can be made on the locally asymptotic stability of boundary equilibria. Therefore, the positive equilibrium point $\tilde{E}(\tilde{x}, \tilde{y})$ is locally stable if and only if

$$\begin{aligned}
&A + d < 0\\
&\Leftrightarrow r(1-\frac{2\tilde{x}}{K}) - \frac{n}{1+ch(1-\beta)^n\tilde{x}^n}[r(1-\tfrac{\tilde{x}}{K})] < 0\\
&\Leftrightarrow r(1-\frac{2\tilde{x}}{K}) - \frac{n(e-dh)}{(e-dh)+d}[r(1-\frac{\tilde{x}}{K})] < 0\\
&\Leftrightarrow \frac{nr(e-dh)}{(e-dh)+d}[(1-n)(e-dh)+d-((2-n)(e-dh)+2d)\frac{\tilde{x}}{K}] < 0\\
&\Leftrightarrow [(1-n)(e-dh)+d] - [(2-n)(e-dh)+2d]\frac{1}{K(1-\beta)}\sqrt[n]{\frac{d}{c(e-dh)}} < 0.
\end{aligned} \tag{6}$$

Therefore, we can obtain the following theorem.

Theorem 2. *If* $[(1-n)(e-dh)+d] - [(2-n)(e-dh)+2d]\frac{1}{K(1-\beta)}\sqrt[n]{\frac{d}{c(e-dh)}} < 0$, $h < e/d$ *and* $n \geq 1$, *then system (2) is globally asymptotically stable without time delay around the equilibrium point* $\tilde{E}(\tilde{x}, \tilde{y})$.

Proof. Now, we will prove the global stability of the positive equilibrium point $\tilde{E}(\tilde{x}, \tilde{y})$.

We first choose a Lyapunov function defined as follows

$$W(x(t),y(t))=\int_{\tilde{x}}^{x}\frac{u-\tilde{x}}{u}du+p\int_{\tilde{y}}^{y}\frac{w-\tilde{y}}{w}dw\quad(p>0).$$

By simple computation on the region $\Sigma=\{(x,y)|x\in B(\tilde{x}),\ y>0\}$, we obtain that

$$\frac{dW}{dt}=\frac{x-\tilde{x}}{x}\frac{dx}{dt}+p\frac{y-\tilde{y}}{y}\frac{dy}{dt}$$

$$\begin{aligned}
&=(x-\tilde{x})[r(1-\frac{x}{K})-\frac{c(1-\beta)^n x^{n-1}y}{1+ch(1-\beta)^n x^n}]+p(y-\tilde{y})(\frac{ec(1-\beta)^n x^n}{1+ch(1-\beta)^n x^n}-d)\\
&=(x-\tilde{x})[r(1-\frac{x}{K})+\frac{c(1-\beta)^n \tilde{x}^{n-1}\tilde{y}}{1+ch(1-\beta)^n \tilde{x}^n}-r(1-\frac{\tilde{x}}{K})-\frac{c(1-\beta)^n x^{n-1}y}{1+ch(1-\beta)^n x^n}]\\
&\quad+p(y-\tilde{y})[\frac{ec(1-\beta)^n x^n}{1+ch(1-\beta)^n x^n}-\frac{ec(1-\beta)^n \tilde{x}^n}{1+ch(1-\beta)^n \tilde{x}^n}]\\
&=-\frac{r}{K}(x-\tilde{x})^2-y(x-\tilde{x})(\frac{c(1-\beta)^n \tilde{x}^{n-1}}{1+ch(1-\beta)^n \tilde{x}^n}-\frac{c(1-\beta)^n x^{n-1}}{1+ch(1-\beta)^n x^n})\\
&\quad+(x-\tilde{x})(y-\tilde{y})\frac{c(1-\beta)^n \tilde{x}^{n-1}}{1+ch(1-\beta)^n \tilde{x}^n}\\
&\quad+p(y-\tilde{y})[\frac{ec(1-\beta)^n x^n}{1+ch(1-\beta)^n x^n}-\frac{ec(1-\beta)^n \tilde{x}^n}{1+ch(1-\beta)^n \tilde{x}^n}]\\
&=-\frac{r}{K}(x-\tilde{x})^2-\frac{c(1-\beta)^n(n-1)\tilde{x}^{n-2}y}{1+ch(1-\beta)^n \tilde{x}^n}(x-\tilde{x})^2\\
&\quad+[\frac{c(nep-1)(1-\beta)^n \tilde{x}^{n-1}}{1+ch(1-\beta)^n \tilde{x}^n}](x-\tilde{x})(y-\tilde{y}).
\end{aligned}$$

Selecting $p=\frac{1}{ne}>0$, then we have

$$\frac{dW}{dt}=-\frac{r}{K}(x-\tilde{x})^2-c(1-\beta)^n(n-1)\tilde{x}^{n-2}y(x-\tilde{x})^2.$$

Hence, $\frac{dW}{dt}<0$ if $n\geq 1$. □

For the delay-induced system (2), the the equilibrium point $\tilde{E}(\tilde{x},\tilde{y})$ will be asymptotically stable if all the roots of the corresponding characteristic equation (4) have negative real parts. To determine the nature of the stability, we require the sign of the real parts of the roots of the equation (4). We start with the assumption that $\tilde{E}(\tilde{x},\tilde{y})$ is asymptotically stable in case of non-delayed system and then find conditions for which $\tilde{E}(\tilde{x},\tilde{y})$ is still stable for all delays [29]. By Rouche's Theorem [30] and the continuity, the transcendental equation (4) has roots with positive real parts if and only if it has purely imaginary roots. From this, we shall be able to find conditions for all eigenvalues to have negative real parts.

Let

$$\lambda(\tau) = \eta(\tau) + i\omega(\tau),$$

in which η and ω are real. As the positive equilibrium point $\tilde{E}(\tilde{x}, \tilde{y})$ of the non-delayed model is stable, we assume $\eta(0) < 0$. By continuity, if τ ($\tau > 0$) is sufficiently small, we still have $\eta(\tau) < 0$ ($\tau > 0$) and the positive equilibrium point $\tilde{E}(\tilde{x}, \tilde{y})$ is stable. The change of stability will occur at some values of τ for which $\eta(\tau) = 0$ and $\omega(\tau) \neq 0$, let $\overline{\tau}$ be such that $\eta(\overline{\tau}) = 0$ and $\omega(\overline{\tau}) = \overline{\omega} \neq 0$. Hence, the $\lambda(\overline{\tau}) = i\overline{\omega}$ is the purely imaginary root. Now, substituting $i\overline{\omega}$ into the characteristic equation (4), it is obtained

$$-\overline{\omega}^2 - i(A + de^{-i\overline{\omega}\,\overline{\tau}})\overline{\omega} + Be^{-i\overline{\omega}\,\overline{\tau}} - C = 0. \tag{7}$$

Separating the real and imaginary parts, we have

$$\begin{cases} -\overline{\omega}^2 - C = -d\overline{\omega}\sin(\overline{\omega}\,\overline{\tau}) - B\cos(\overline{\omega}\,\overline{\tau}), \\ A\overline{\omega} = B\sin(\overline{\omega}\,\overline{\tau}) - d\overline{\omega}\cos(\overline{\omega}\,\overline{\tau}). \end{cases} \tag{8}$$

From the above equations (8), we get

$$\overline{\omega}^4 + R\overline{\omega}^2 + S = 0. \tag{9}$$

in which

$$\begin{aligned} R &= A^2 + 2C - d^2 \\ &= \left(\frac{r[(1-n)K + ch(1-\beta)^n K\tilde{x}^n - (2-n)\tilde{x} - 2ch(1-\beta)^n \tilde{x}^{n+1}]}{K(1 + ch(1-\beta)^n \tilde{x}^n)}\right)^2 > 0, \\ S &= C^2 - B^2. \end{aligned}$$

Now, two cases are considered as follows

- if $S > 0$, then the positive equilibrium point $\tilde{E}(\tilde{x}, \tilde{y})$ is locally asymptotically stable since all roots of equation (9) have negative real parts for all delay,
- if if $S < 0$, then the positive equilibrium point $\tilde{E}(\tilde{x}, \tilde{y})$ is unstable since equation (9) has one positive root,

The secondary case implies that the characteristic equation (4) will have a pair of purely imaginary roots $\pm i\overline{\omega}$ such that $\eta(\overline{\tau}) = 0$ and $\omega(\overline{\tau}) = \overline{\omega}$. Solving $\overline{\tau}$ from the equations (9), we have

$$\overline{\tau}_j = \frac{1}{\overline{\omega}} \cos^{-1}\left[\frac{(B - dA)\overline{\omega}^2 + dC}{B^2 + (d\overline{\omega})^2}\right] + \frac{2j\pi}{\overline{\omega}} \quad j = 0, 1, 2, \ldots . \tag{10}$$

Next, we will verify the transversality condition, so differentiating the characteristic equation (4) with τ

$$2\lambda\frac{d\lambda}{d\tau} - (A + de^{-\lambda\tau})\frac{d\lambda}{d\tau} - d\lambda e^{-\lambda\tau}\left(-\lambda - \tau\frac{d\lambda}{d\tau}\right) + Be^{-\lambda\tau}\left(-\lambda - \tau\frac{d\lambda}{d\tau}\right) = 0,$$

and solving $(\frac{d\lambda}{d\tau})^{-1}$ associating the characteristic equation (4), we have

$$(\frac{d\lambda}{d\tau})^{-1}=\frac{2\lambda-A}{C\lambda+A\lambda^2-\lambda^3}-\frac{B}{B\lambda+d\lambda^2}-\frac{\tau}{\lambda}.$$

Thus, at $\tau=\overline{\tau}$ and $\lambda=i\overline{\omega}$, we can get

$$(\frac{d(Re\lambda(\tau)}{d\tau})^{-1}|_{\tau=\overline{\tau}}=\frac{A^2+d^2-2C+2\overline{\omega}^2}{B^2+(d\overline{\omega})^2}=\frac{R+2\overline{\omega}^2}{B^2+(d\overline{\omega})^2}>0\ since\ R>0.$$

According to Theorems 2 and the continuity, the real part of $\eta(\tau)$ will become positive when $\tau>\overline{\tau}$ and the positive equilibrium point $\tilde{E}(\tilde{x},\tilde{y})$ becomes globally stable to unstable and a Hopf bifurcation occurs while τ passes through the threshold value $\overline{\tau}$.

Therefore, we can obtain the following theorem

Theorem 3. *Assuming*

$$[(1-n)(e-dh)+d]-[(2-n)(e-dh)+2d]\frac{1}{K(1-\beta)}\sqrt[n]{\frac{d}{c(e-dh)}}<0,$$

$h<e/d$ and $n\geq 1$, we have

- *if $S\leq 0$, then the positive equilibrium point $\tilde{E}(\tilde{x},\tilde{y})$ is globally asymptotically stable for $\tau<\overline{\tau}$ and unstable for $\tau>\overline{\tau}$, a Hopf bifurcation occurs as τ passes through the threshold value $\overline{\tau}$, where $\overline{\tau}=\frac{1}{\overline{\omega}}\cos^{-1}[\frac{(B-dA)\overline{\omega}^2+dC}{B^2+(d\overline{\omega})^2}]$.*
- *if $S>0$, then the positive equilibrium point $\tilde{E}(\tilde{x},\tilde{y})$ is globally asymptotically stable for all $\tau>0$.*

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