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Predator-prey models with delay and prey harvesting

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Abstract. It is known that predator-prey systems with constant rate harvesting exhibit very rich dynamics. On the other hand, incorporating time delays into predator-prey models could induce instability and bifurcation. In this paper we are interested in studying the combined effects of the harvesting rate and the time delay on the dynamics of the generalized Gause-type predator-prey models and the Wangersky-Cunningham model. It is shown that in these models the time delay can cause a stable equilibrium to become unstable and even a switching of stabilities, while the harvesting rate has a stabilizing effect on the equilibrium if it is under the critical harvesting level. In particular, one of these models loses stability when the delay varies and then regains its stability when the harvesting rate is increased. Computer simulations are carried to explain the mathematical conclusions.

1. Introduction

Predator-prey models play a crucial role in bioeconomics, that is the management of renewable resources. When practiced, the management of renewable resources has been based on the MSY, abbreviation for maximum sustainable yields. The MSY is a simple way to manage resources taking into consideration that over-exploiting resources lead to a loss in productivity.

Based on a biological growth model, the MSY depends upon the environmental carrying capacity K. As the population approaches the value K, the surplus production approaches zero. Therefore, the aim is to determine how much we can harvest without altering dangerously the harvested population.

The MSY level is the level with maximized growth rate, that is where the surplus production is the greatest. According to Clark [6], the MSY level has been found to be situated between 40% and 60% of the carrying capacity in most population where the biological growth model applies. The main problem of the MSY is economical irrelevance. It is so since it takes into consideration the benefits of resource exploitation, but completely disregard the cost operation of resource exploitation. For example, it ignores the fact that if a species is harvested such that

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its population decreases to a certain level, then the cost of harvesting can become exorbitant because finding the desirable resource becomes more time consuming. This might lead to a situation where the cost of harvesting is higher than the benefit.

Confronted with the inadequacy of the MSY, people tried to replace it by the OSY, that is, the optimum sustainable yield, which is based on the standard cost-benefit criterion used to maximize the revenues. Historically, however, few real cases have been managed using the OSY. Actually, many population harvesting activities have not been managed at all. If it had been managed, it was mainly using the MSY, which often gave rise to critical situations.

Renewable resources management is complicated and constructing accurate mathematical models about the effect of harvesting on vegetable or animal populations is even more complicated. This is so because to have a perfect model we would have to take into account many factors having an effect on the cost-benefit criterion and on the survival of the harvested population. For each population we would need to consider its size, growth rate, carrying capacity, predators, competitors combined with the cost of harvesting and the price obtained for the harvested species. More informations can be found about these factors in Clark [6], but it is obvious that a perfect model cannot be achieved because even if we could put all these factors in a model, the model could never predict ecological catastrophes or Mother Nature caprice. Therefore, the best we can do is to look for analyzable models that describe as well as possible the reality or the effect of harvesting on populations.

The effect of constant-rate harvesting on the dynamics of predator-prey systems has been investigated by many authors, see, for example, Brauer and Soudack [4, 5], Dai and Tang [11], Myerscough et al. [24], Xiao and Ruan [28], very rich and interesting dynamical behaviors have been observed, such as the stability of the equilibria, existence of Hopf bifurcation, limit cycles, homoclinic loops, Bogdanov-Takens bifurcations, and even catastrophe. It is also observed that in some cases, before a catastrophic harvest rate is reached the effect of harvesting is to stabilize the equilibrium of the population system.

On the other hand, time delays of one type or another have been incorporated into biological models by many researchers, we refer to the monographs of Cushing [8], Gopalsamy [17], Kuang [21] and MacDonald [23] for general delayed biological systems and to Beretta and Kuang [2], Gopalsamy [15,16], Hastings [19], May [22], Ruan [26] and the references cited therein for studies on delayed predator-prey systems. In general, delay differential equations exhibit much more complicated dynamics than ordinary differential equations since a time delay could cause a stable equilibrium to become unstable and cause the populations to fluctuate.

There are many different kinds of delayed predator-prey models in the literature. Let $x(t)$ and $y(t)$ denote the prey and predators population densities at time t, respectively. For the generalized Gause-type predator-prey model of the following form

$$\begin{aligned} x'(t) &= x(t)g(x(t)) - y(t)p(x(t)), \\ y'(t) &= y(t)[-d + p(x(t))], \end{aligned} \tag{1.1}$$

basically a constant time delay can be incorporated into the model in three different ways. (a) A time delay τ in the prey specific growth term $g(x(t))$, that is,

$$\begin{aligned} x'(t) &= x(t)g(x(t-\tau)) - y(t)p(x(t)), \\ y'(t) &= y(t)[-d + p(x(t))]. \end{aligned} \tag{1.2}$$

System (1.2) is proposed based on the assumption that in the absence of predators the prey satisfies the Hutchinson's equation. We refer to May [22] for detailed discussion and analysis about (1.2) and its variants. (b) A time delay τ in the predator response term $p(x(t))$ in the predator equation, that is,

$$\begin{aligned} x'(t) &= x(t)g(x(t)) - y(t)p(x(t)), \\ y'(t) &= y(t)[-d + p(x(t-\tau))]. \end{aligned} \tag{1.3}$$

The delay in system (1.3) can be regarded as a gestation period or reaction time of the predators. System (1.3) has been studied extensively, we refer to Kuang [21], Beretta and Kuang [2] and the references therein. (c) A time delay τ in the interaction term $y(t)p(x(t))$ of the predator equation, that is,

$$\begin{aligned} x'(t) &= x(t)g(x(t)) - y(t)p(x(t)), \\ y'(t) &= -dy(t) + y(t-\tau)p(x(t-\tau)). \end{aligned} \tag{1.4}$$

System (1.4) assumes that the change rate of the predators depends on the number of prey and of predators present at some previous time. The well-known Wangersky and Cunningham model ([27]) is such a model.

The objective of this paper is to study the combined effects of constant-rate harvesting and delay on the dynamics of predator-prey systems. To do so we focus on three very well studied delayed predator-prey models (1.2), (1.3), and a special case of (1.4) and assume that the prey population is harvested at a constant rate. Namely, we first consider a generalized Gause-type predator-prey model with prey harvesting and a time delay in the prey specific growth term. Secondly, a generalized Gause-type predator-prey model with prey harvesting and a time delay in the predator response function is analyzed. Finally, we study the Wangersky and Cunningham ([27]) predator-prey model with prey harvesting.

The reasons for choosing the above delayed predator-prey models are two-folds. First, the dynamics of delayed systems (1.2) – (1.4) are well understood and are different. Secondly, since we know the dynamics of systems (1.2) – (1.4), it will be better for us to determine how the constant harvesting affects the dynamics of these models. In fact, it is shown that in the first and third models the time delay could cause not only instability and oscillations but also the switching of stabilities, while the constant harvesting changes only the equilibrium values but not the properties of solutions. In the second model, the time delay induces instability and bifurcation but there is no switching of stabilities; however, increasing the harvesting level will help the system to regain its stability. This indicates that the prey harvesting has a stabilizing effect on the dynamics of the model. Examples and computer simulations are presented to illustrate the obtained results.

2. Generalized Gause model with prey harvesting and delay in the prey specific growth

In this section, we consider the system

$$\begin{aligned} x'(t) &= x(t)[f(x(t-\tau)) - y(t)h(x(t))] - H, \\ y'(t) &= \mu y(t)[x(t)h(x(t)) - Jh(J)], \end{aligned} \tag{2.1}$$

where $\mu > 0$ is a constant, $f(x)$ is the specific growth rate of the prey in the absence of predators, $xh(x)$ is the response function, J is the minimum prey population required for the predator population to establish itself, and H is the constant-rate harvesting of the prey species x. Also, $f(0) \geq 0$ and $f(x)$ is continuous and decreasing in x. The delay $\tau \geq 0$ is a constant representing the assumption that in the absence of predators, the prey's growth is affected by population density only after a fixed period of time. $h(x)$ satisfies the conditions

$$h(x) > 0, \quad h'(x) \leq 0, \quad g'(x) = xh'(x) + h(x) > 0, \tag{2.2}$$

where $g(x) = xh(x)$ is the response function.

When $\tau = 0$, the ODE model was studied by Brauer and Soudack [4,5]; when $H = 0$, the delayed predator-prey model has been analyzed by May [22], Hassard et al. [18], Ruan [26], etc. The stability of system (2.1) was investigated by Brauer [3].

The equilibrium point is given by $x^* = J$ and

$$x^*[f(x^*) - y^*h(x^*)] - H = 0 \tag{2.3}$$

if (2.3) has non-negative real solution for y^*. We can see that as H increases, y^* decreases continuously until it reaches zero at $H = x^* f(x^*)$ which gives us the critical harvest rate

$$H = x^* f(x^*) = Jf(J).$$

To linearize the system about the equilibrium point (x^*, y^*), let $X = x - x^*$,$Y = y - y^*$. We then obtain the linearized system

$$\begin{aligned} X'(t) &= x^* f'(x^*)X(t-\tau) + (f(x^*) - y^*g'(x^*))X(t) - g(x^*)Y(t), \\ Y'(t) &= \mu y^* g'(x^*)X(t). \end{aligned} \tag{2.4}$$

From the linearized system we obtain the characteristic equation

$$\lambda^2 + p\lambda + q\lambda e^{-\lambda\tau} + \alpha = 0, \tag{2.5}$$

where

$$\begin{aligned} p &= -[f(x^*) - y^*g'(x^*)], \\ q &= -x^* f'(x^*), \\ \alpha &= \mu y^* g(x^*)g'(x^*). \end{aligned}$$

For $\tau = 0$ the characteristic equation becomes

$$\lambda^2 + (p+q)\lambda + \alpha = 0 \tag{2.6}$$

which has the roots

$$\lambda = \frac{-(p+q) \pm \sqrt{(p+q)^2 - 4\alpha}}{2}. \tag{2.7}$$

Looking at equation (2.7), we can see that (2.6) has negative real roots if and only if $p + q > 0$ and $\alpha > 0$ or equivalently,

$$y^* g'(x^*) - f(x^*) - x^* f'(x^*) > 0 \tag{2.8}$$

and

$$\mu y^* g(x^*) g'(x^*) > 0.$$

Since $\mu > 0$, $g'(x^*) > 0$, $g(x^*) > 0$, and $y^* > 0$, the last condition is always true and we are left with (2.8). Now for $\tau \neq 0$, if $\lambda = i\omega$ is a root of equation (2.5), then we have

$$-\omega^2 + iq\omega e^{-i\omega\tau} + pi\omega + \alpha = 0.$$

Separating the real and imaginary parts, we have

$$\begin{aligned} \alpha - \omega^2 - q\omega \sin(\omega\tau) &= 0, \\ p\omega + q\omega \cos(\omega\tau) &= 0. \end{aligned} \tag{2.9}$$

Squaring both sides gives

$$\begin{aligned} q^2\omega^2 \sin^2(\omega\tau) &= \omega^4 - 2\alpha\omega^2 + \alpha^2, \\ q^2\omega^2 \cos^2(\omega\tau) &= p^2\omega^2. \end{aligned}$$

Adding both equations and regrouping by powers of ω, we obtain the following fourth degree polynomial

$$\omega^4 + (p^2 - q^2 - 2\alpha)\omega^2 + \alpha^2 = 0, \tag{2.10}$$

from which we obtain

$$\omega_\pm^2 = \frac{q^2 - p^2 + 2\alpha \pm \sqrt{(q^2 - p^2 + 2\alpha)^2 - 4\alpha^2}}{2}. \tag{2.11}$$

It follows that if

$$p^2 - q^2 - 2\alpha > 0 \tag{2.12}$$

is satisfied, the equation (2.10) does not have positive solutions; that is, the characteristic equation (2.5) does not have purely imaginary roots. Equation (2.8), which is $p + q > 0$, guarantees that all roots of equation (2.6) have negative real parts. Using Rouch*é*'s theorem (see Dieudonné [12]), we have the following result.

Lemma 2.1. *If* $p+q>0, \alpha>0$ *and* $p^2-q^2-2\alpha>0$, *then all roots of equation (2.5) have negative real parts for all* $\tau \geq 0$; *that is, the equilibrium* (x^*, y^*) *is asymptotically stable for all* $\tau \geq 0$.

From (2.11) we can see that there is a unique positive solution ω_+^2 if

$$q^2 - p^2 + 2\alpha > 0 \text{ and } (q^2 - p^2 + 2\alpha)^2 = 4\alpha^2. \tag{2.13}$$

Also, if

$$q^2 - p^2 + 2\alpha > 0 \text{ and } (q^2 - p^2 + 2\alpha)^2 > 4\alpha^2, \tag{2.14}$$

then there are two positive solutions $\omega_\pm^2$. We can now find the value of $\tau_j^\pm$ by substituting $\omega_\pm^2$ into system (2.9) and solving for τ. We obtain

$$\tau_j^\pm = \frac{1}{\omega_\pm} \arctan\left(\frac{\omega_\pm^2-\alpha}{p\omega_\pm}\right) + \frac{2j\pi}{\omega_\pm}, \qquad j=0,1,2,... \tag{2.15}$$

From the above analysis, we have the following result.

Lemma 2.2. *Let* $p+q>0, \alpha>0$. *If* $q^2-p^2+2\alpha>0$ *and* $(q^2-p^2+2\alpha)^2=4\alpha^2$ *hold, then the equation (2.5) with* $\tau=\tau_j^+$ *has a pair of pure imaginary roots* $\pm i\omega_+$. *If* $q^2-p^2+2\alpha>0$ *and* $(q^2-p^2+2\alpha)^2>4\alpha^2$ *hold and* $\tau=\tau_j^+$ ($\tau=\tau_j^-$ *respectively), then the equation (2.5) has a pair of pure imaginary roots* $\pm i\omega_+$ ($\pm i\omega_-$ *respectively).*

To see if bifurcations occur, we need to verify the transversality conditions

$$\frac{d}{d\tau} Re\lambda_j^+(\tau_j^+) > 0, \qquad \frac{d}{d\tau} Re\lambda_j^-(\tau_j^-) < 0.$$

Differentiating equation (2.5) with respect to τ we obtain:

$$\left\{2\lambda + p + q(1-\tau\lambda)e^{-\lambda\tau}\right\}\frac{d\lambda}{d\tau} = \lambda^2 q e^{-\lambda\tau}. \tag{2.16}$$

Unless $p=q=0$, we can see that all purely imaginary roots are simple. Also,

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{(2\lambda+p)e^{\lambda\tau}+q}{\lambda^2 q} - \frac{\tau}{\lambda}, e^{\lambda\tau} = \frac{-q\lambda}{\lambda^2+p\lambda+\alpha}. \tag{2.17}$$

Following Cooke and Grossman [7], we therefore obtain (using equation (2.10) for the last step)

$$\begin{aligned} sign\left\{\frac{d(Re\lambda)}{d\tau}\right\}_{\lambda=i\omega} &= sign\left\{Re\left(\frac{d\lambda}{d\tau}\right)^{-1}\right\}_{\lambda=i\omega} \\ &= sign\left\{Re\left[\frac{-(2\lambda+p)}{\lambda(\lambda^2+p\lambda+\alpha)}\right]_{\lambda=i\omega} + Re\left[\frac{q}{\lambda^2 q}\right]_{\lambda=i\omega}\right\} \\ &= sign\left\{\frac{p^2-2(\alpha-\omega^2)}{p^2\omega^2+(\omega^2-\alpha^2)^2} - \frac{q^2}{q^2\omega^2}\right\} \\ &= sign\{p^2-q^2-2\alpha^2+2\omega^2\}. \end{aligned}$$

From (2.11), (2.14), and the last result, we can see that the transversality conditions are satisfied. Therefore, $\tau_j^{\pm}$ are bifurcation values. Regrouping our results we have the following theorem.

Theorem 2.3. *Let $\tau_j^{\pm}$ be defined by equation (2.15).*

(i) *If $p+q>0, \alpha>0$ and $p^2-q^2-2\alpha>0$, then the equilibrium (x^*, y^*) of system (2.1) is asymptotically stable for all $\tau \geq 0$.*

(ii) *If $p+q>0, \alpha>0, q^2-p^2+2\alpha>0$ and $(q^2-p^2+2\alpha)^2=4\alpha^2$, then the equilibrium (x^*, y^*) of system (2.1) is asymptotically stable for $\tau \in [0, \tau_0)$ and unstable for $\tau > \tau_0$. Hopf bifurcation occurs when $\tau=\tau_0$; that is, a family of periodic solutions bifurcates from (x^*, y^*) as τ passes through the critical value τ^*.*

(iii) *If $p+q>0, \alpha>0, q^2-p^2+2\alpha>0$ and $(q^2-p^2+2\alpha)^2>4\alpha^2$, then there exists a positive integer k such that there are k switches from stability to instability and to stability. In other words, when*

$$\tau \in [0, \tau_0^+), (\tau_0^-, \tau_1^+), ..., (\tau_{k-1}^-, \tau_k^+),$$

the equilibrium (x^*, y^*) of system (2.1) is stable, and when

$$\tau \in [\tau_0^+, \tau_0^-), (\tau_1^+, \tau_1^-), ..., (\tau_{k-1}^+, \tau_k^-),$$

(x^*, y^*) is unstable. Therefore, there are bifurcations at (x^*, y^*) for $\tau = \tau_j^{\pm}, j=0,1,2,...$

Remark 2.4. The characteristic equation (2.5) and the characteristic equations in the following sections are related to the one analyzed in Hethcote, Stech and van den Driessche [20] with Q a step function. Since we are concerned about not only the stability of the steady state but also the possible bifurcations at the steady state, we re-analyze these equations following the lines of Cooke and Grossman [7].

Remark 2.5. We would like to mention that switching of stabilities in delayed predator-prey models has been observed and studied in Cushing [9] and Cushing and Saleem [10]. The above theorem indicates that the phenomenon of switching of stabilities occurs in the model with prey harvesting as well. In the following example, we will see numerically how the harvesting constant changes the steady state values and the properties.

Example 2.6. As an example, let $f(x)$ be the logistic growth function and $g(x)$ be the Holling type-II response function; that is, let

$$f(x)=r(1-\frac{x}{K}), \quad g(x)=xh(x)=\frac{ax}{b+x}.$$

We consider the system

$$\begin{aligned} \frac{dx}{dt} &= x(t)\left\{2\left[1-\frac{x(t-\tau)}{40}\right]-\frac{y(t)}{x(t)+10}\right\}-10, \\ \frac{dy}{dt} &= y(t)\left[\frac{x(t)}{x(t)+10}-\frac{2}{3}\right]. \end{aligned} \tag{2.18}$$

There is a positive equilibrium $(x^*, y^*)=(20, 15)$.

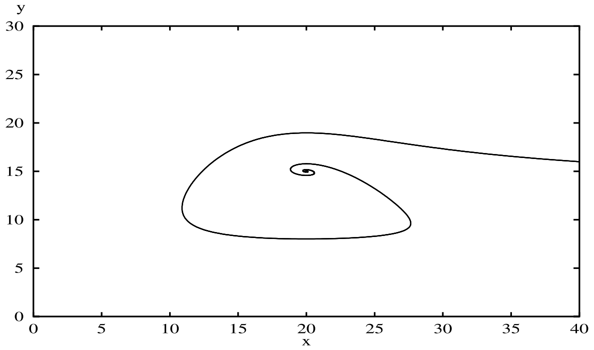

Fig. 2.1. The equilibrium $(x^*, y^*) = (20, 15)$ is asymptotically stable when $\tau = 0$. Here $x(0) = 40$, $y(0) = 16$.

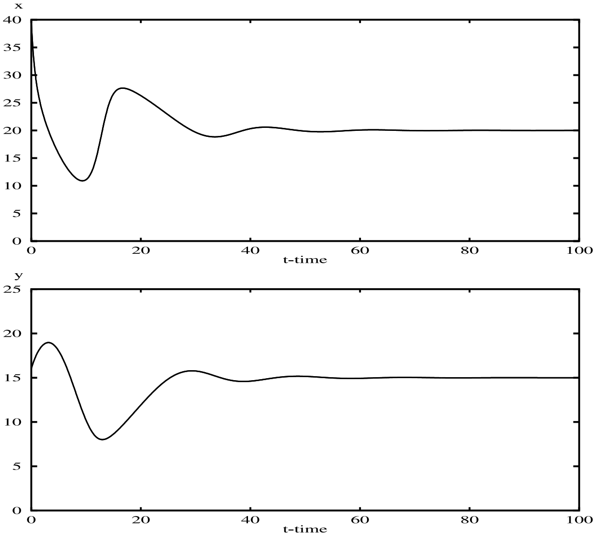

Fig. 2.2. Both the prey and predator populations converge to their equilibrium values.

Case I. $\tau = 0$. In this case, the numerical simulation (see Figure 2.1) shows that the predator and prey populations spiral toward the equilibrium (20,15). We can also look at predators and prey separately to study their behaviors in time. From Figure 2.2, we can see that both the prey and the predator populations converge in finite time to their equilibrium values $x^* = 20$ and $y^* = 15$, respectively.

We want to see how the harvesting constant H affects the dynamics. Since the equilibrium value y^* depends on H, the more a prey population is harvested, the lower is the number of predators at the equilibrium, and the less a prey population is harvested, the higher is the number of predators y^*. Recall that the critical harvest rate $H = Jf(J) = 20$ in this case. Therefore, for $H < 20$ the equilibrium is

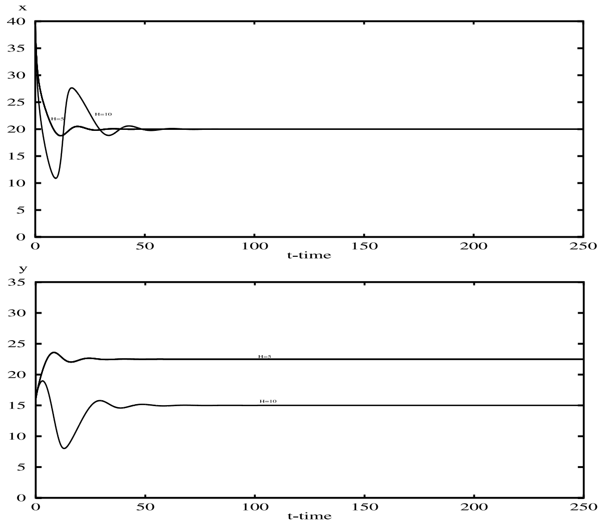

Fig. 2.3. Behaviors of the prey and predator populations in time for $H = 5$ and $H = 10$ when $\tau = 0$ with $x(0) = 40$, $y(0) = 16$.

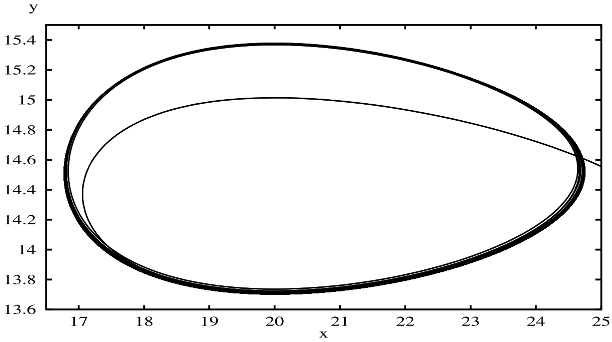

Fig. 2.4. There is a bifurcating periodic solution for $\tau = 0.826$.

positive and stable, but for $H \geq 20$ the predator species is driven to extinction and the system collapses. We also notice that the smaller H is the faster the prey and the predator populations go to the equilibrium (x^*, y^*). An example of these behaviors is shown in Figure 2.3.

Case II. $\tau \neq 0$. We are interested in studying the combined effect of the delay τ and the harvesting rate H on the dynamics of the model. By Theorem 2.3., there is a critical value $\tau_0 = 0.8256$, the equilibrium (x^*, y^*) is stable when $\tau < 0.8256$; Hopf bifurcation occurs when $\tau = 0.8256$; and the equilibrium becomes unstable and a bifurcating periodic solution exists when $\tau > 0.8256$ (see Figure 2.4). Figure 2.5 shows that both the prey and predator populations reach periodic oscillations around the equilibrium $(x^*, y^*) = (20, 15)$ in finite time.

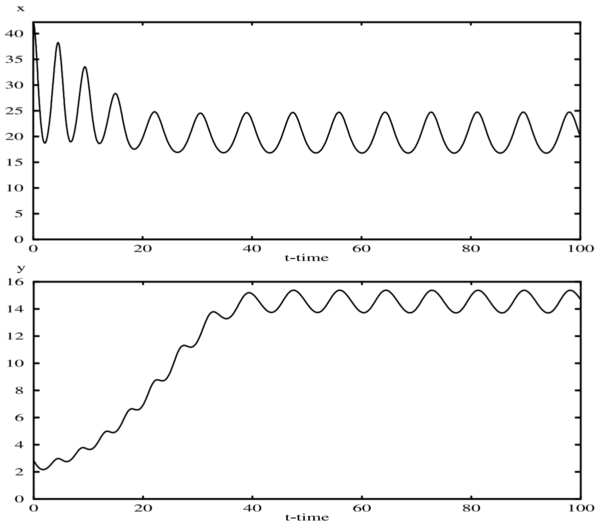

Fig. 2.5. The oscillations of the prey and predator populations in time for $\tau = 0.826$.

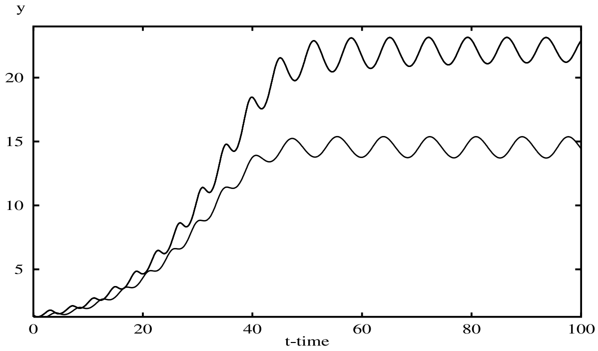

Fig. 2.6. Behavior of the predator population for different values of $H = 10$ (top) and $H = 15$ (bottom) for $\tau = 0.826$.

We would like to mention that the example (2.18) was studied by Brauer [3]. He showed that the equilibrium $(20, 15)$ is stable for $\tau < 0.826$. Our analysis coincides with his result (and slightly improves his estimate). Moreover, we have shown that Hopf Bifurcation indeed occurs when $\tau \geq 0.826$.

As in the case for $\tau = 0$, we can see that varying H will affect the dynamics of the model. For $\tau = 0.826$, varying the value of the harvesting constant H changes the y^* value of the equilibrium point (x^*, y^*) : increasing H decreases y^* and decreasing H increases y^* (see Figure 2.6). The graph of x in time has been omitted, but varying the value of H does not change its behavior in time. Unlike when $\tau = 0$, varying H for $\tau = 0.826$ does not change the frequencies of these oscillations.

3. Generalized Gause model with prey harvesting and delay in the predator response function

In this section, we consider the system

$$\begin{aligned} x'(t) &= x(t)[f(x(t)) - y(t)h(x(t))] - H, \\ y'(t) &= y(t)[-d + cx(t-\tau)h(x(t-\tau))], \end{aligned} \tag{3.1}$$

where $c > 0$ is the rate of conversion of consumed prey to predator, $d > 0$ is the death rate of the predator in the absence of the prey, H is the constant-rate harvesting of the prey species x. Also, $f(x)$ is the specific growth rate of the prey in the absence of predators where $f(0) \geq 0$ and $f(x)$ is continuous and decreasing in x. The capture rate of prey per predator, that is the functional response is given by $xh(x) = g(x)$ where $h(x) > 0$ and $h'(x) \leq 0$ and $g'(x) > 0$. The delay $\tau \geq 0$ is a constant.

When $H = 0$, the system has been studied by many researchers, see Beretta and Kuang [2], Ruan [26] and the references cited therein.

The equilibrium (x^*, y^*) is given by

$$y^* = \frac{x^* f(x^*) - H}{x^* h(x^*)}, \quad -d + cx^* h(x^*) = 0,$$

where x^* is a non-negative real value. The y^* value implies that $x^* f(x^*) > H$. Let $X = x - x^*$, $Y = y - y^*$. We then obtain the linearized system

$$\begin{aligned} X'(t) &= (f(x^*) - y^* g'(x^*) + x^* f'(x^*))X(t) - g(x^*)Y(t), \\ Y'(t) &= cy^* g'(x)X(t-\tau). \end{aligned} \tag{3.2}$$

From the linearized system we obtain the characteristic equation

$$\lambda^2 + p\lambda + re^{-\lambda\tau} = 0, \tag{3.3}$$

where

$$\begin{aligned} p &= -[f(x^*) + x^* f'(x^*) - y^* g'(x^*)], \\ r &= cx^* y^* g(x^*) g'(x^*). \end{aligned}$$

For $\tau = 0$ the characteristic equation becomes

$$\lambda^2 + p\lambda + r = 0 \tag{3.4}$$

which has the roots

$$\lambda = \frac{-p \pm \sqrt{p^2 - 4r}}{2}. \tag{3.5}$$

These roots are negative and real if and only if

$$p > 0 \quad \text{and} \quad r > 0, \tag{3.6}$$

but r is always positive so we only need $p > 0$. Now for $\tau \neq 0$, if $\lambda = i\omega$ is a root of equation (3.3), we then have

$$-\omega^2 + p\omega i + re^{-i\omega\tau} = 0.$$

Separating the real and imaginary parts, we have

$$\begin{aligned} -\omega^2 + r\cos(\omega\tau) &= 0, \\ p\omega - r\sin(\omega\tau) &= 0. \end{aligned} \tag{3.7}$$

Squaring both sides gives

$$\begin{aligned} r^2\cos^2\omega\tau &= \omega^4, \\ r^2\sin^2\omega\tau &= p^2\omega^2. \end{aligned}$$

Adding both equations and regrouping by the powers of ω, we obtain the following fourth degree polynomial

$$\omega^4 + p^2\omega^2 - r^2 = 0, \tag{3.8}$$

from which we obtain

$$\omega_\pm^2 = \frac{-p^2 \pm \sqrt{p^4 + 4r^2}}{2}. \tag{3.9}$$

From (3.9), since $p^4 + 4r^2 > p^2$, there is only one positive solution ω_+^2. Thus, equation (3.3) has one pair of purely imaginary roots $\pm i\omega_+$. We can find the value of τ_j^+ by substituting ω_+^2 into equations (3.7) and solving for τ. We obtain

$$\tau_j^+ = \frac{1}{\omega_+}\arctan\left(\frac{p}{\omega_+}\right) + \frac{2j\pi}{\omega_+}, \quad j = 0, 1, 2, \ldots \tag{3.10}$$

From the above analysis, we have the following result.

Lemma 3.1. *If $p > 0, r > 0$ and $\tau = \tau_0^+$, then equation (3.3) has a pair of pure imaginary roots $\pm i\omega_+$.*

Similarly as in section 2, we can verify the transversality conditions

$$\frac{d}{d\tau}Re\lambda_j^+(\tau_j^+) > 0.$$

Therefore, $\tau_j^\pm$ are bifurcation values. Regrouping our results we have the following theorem.

Theorem 3.2. *Let τ_j^+ be defined by equation (3.10). If $p > 0$ and $r > 0$, then the equilibrium (x^*, y^*) of system (3.1) is stable for $\tau < \tau_0^+$ and unstable for $\tau > \tau_0^+$. The system undergoes a bifurcation at τ_0^+.*

Looking at Theorem 2.3 and Theorem 3.2, we can see that delays have a major impact on the dynamics of models. Indeed, the systems (2.1) and (3.1) are the same except that the delay was in the logistic function for the first one and in the functional response of the predator equation for the second one. We have seen that the harvesting rate does not change the properties of the solutions to the first model. We will see that it changes the dynamics of the second model as the following example will show.

Example 3.3. As an example, we consider the system

$$\begin{aligned} \frac{dx}{dt} &= x(t)\left\{2\left[1-\frac{x(t)}{50}\right]-\frac{y(t)}{x(t)+40}\right\}-10, \\ \frac{dy}{dt} &= y(t)\left[-3+\frac{6x(t-\tau)}{x(t-\tau)+40}\right]. \end{aligned} \tag{3.11}$$

The equilibrium is $(x^*, y^*) = (40, 12)$. When $\tau = 0$, we can see in Figure 3.1 that the predator and prey populations do not spiral toward the equilibrium (40,12) as in the previous section, the equilibrium (40, 12) is a stable node.

We wish to study the effect of the delay τ on the dynamics of the model. By Theorem 3.2, there is a critical value $\tau_0 = 8.205$. The equilibrium $(x^*, y^*) = (40, 12)$ is asymptotically stable for $\tau < 8.205$, becomes unstable for $\tau > 8.205$, and there is a bifurcating periodic solution. Figure 3.2 shows that the equilibrium point (40, 12) is a stable focus for $\tau = 7$ and Figure 3.3 shows that for $\tau = 9$ a limit cycle is present.

We can also vary the harvesting constant H to see how it affects the dynamics. Notice that the equilibrium value y^* depends on H : the more a prey population is harvested, the lower is the number of predators at the equilibrium, and the less a prey population is harvested, the higher is the number of predators y^*. In this example, the critical harvesting rate is $H = xf(x) = 16$. Therefore, for $H < 16$ the equilibrium is positive and stable, but for $H \geq 16$ the prey species is driven to extinction and the system collapses. Unlike the example in the previous section, a variation in H can change the stability of the model (3.11). For example, choose

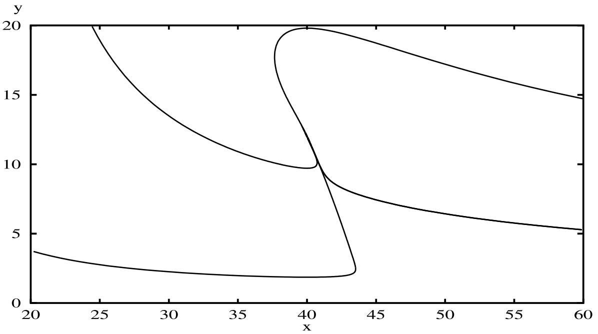

Fig. 3.1. The equilibrium $(x^*, y^*) = (40, 12)$ is an asymptotically stable node for $\tau = 0$.

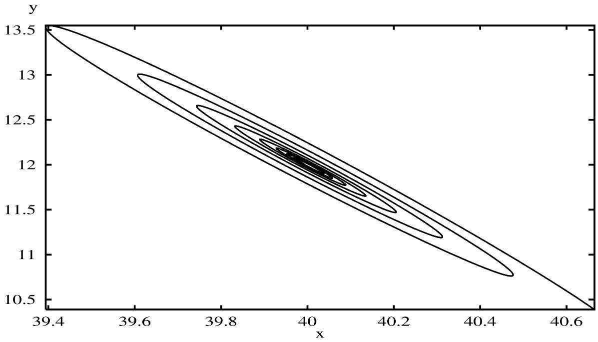

Fig. 3.2. The equilibrium $(x^*, y^*) = (40, 12)$ is an asymptotically stable focus for $\tau = 7$.

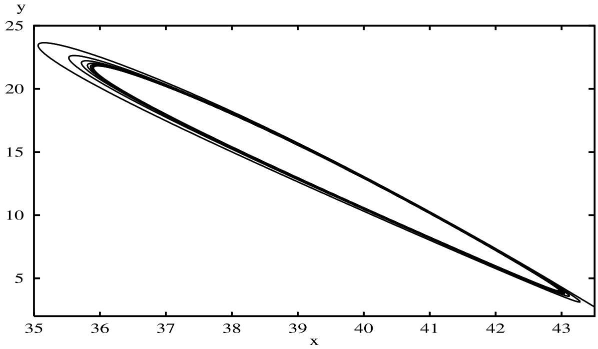

Fig. 3.3. There is a bifurcating periodic solution for $\tau = 9$.

$\tau = 9$ (a value at which the equilibrium is unstable), when $H = 10$ both the prey and predator populations oscillate about the equilibrium values; when $H = 15$ (a value close to the critical harvesting rate) both the prey and predator populations converge to the equilibrium values (see Figure 3.4). Therefore, the system regains its stability when the prey harvesting constant is increased but less than the critical harvesting. This indicates that the harvesting rate has an effect of stabilizing the equilibrium of the model.

4. Wangersky–Cunningham Model with Prey Harvesting

In this section, we consider the system:

$$\begin{aligned} x'(t) &= x(t)[r_1 - ax(t) - by(t)] - H, \\ y'(t) &= -r_2 y(t) + cx(t-\tau)y(t-\tau), \end{aligned} \tag{4.1}$$

where r_1 is the rate of increase of the prey population, r_2 is the death rate of the predator population, b is the coefficient of effect of predation on x, c is the coefficient of effect of predation on y, H is the constant-rate harvesting of the prey species x. Also, $a = r_1/K_x$ where K_x, a density-dependent term, represents the

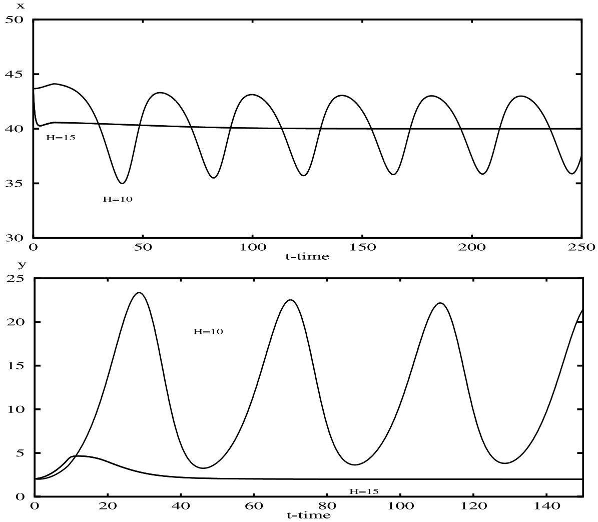

Fig. 3.4. Behavior of the prey and predator populations for different values of H for $\tau = 9$.

limitation upon the growth of the prey other than by predation. The delay $\tau \geq 0$ is a constant based on the assumption that the change rate of predators depends on the number of prey and of predators present at some previous time.

The model when $H = 0$ was proposed and analyzed by Wangersky and Cunningham [27] and their analysis was criticized by Goel et al. [14]. However, as pointed out by Nunney [25], the analysis of Goel et al. is incomplete either. Our results hold if $H = 0$.

The equilibrium (x^*, y^*) is given by

$$x^* = \frac{r_2}{c}, \quad y^* = \frac{cr_1r_2 - ar_2^2 - Hc^2}{bcr_2} \tag{4.2}$$

if $cr_1r_2 - ar_2^2 - Hc^2 \geq 0$. We can see that as H increases, y^* decreases continuously until it reaches zero at the critical harvest rate

$$H = x^*(x^*r_1 - ax^*).$$

Let $X = x - x^*$, $Y = y - y^*$. We then obtain the linearized system

$$\begin{aligned} X'(t) &= (r_1 - 2ax^* - by^*)X(t) - bx^*Y(t), \\ Y'(t) &= cy^*X(t-\tau) - r_2Y(t) + cx^*Y(t-\tau). \end{aligned} \tag{4.3}$$

From the linearized system we obtain the characteristic equation

$$\lambda^2 + p\lambda + r + (s\lambda + q)e^{-\lambda\tau} = 0, \tag{4.4}$$

where

$$\begin{aligned} p &= r_2 - r_1 + 2ax^* + by^*, \\ q &= cx^*(r_1 - 2ax^* - by^*) + bcx^*y^*, \\ r &= -r_2(r_1 - 2ax^* - by^*), \\ s &= -cx^*. \end{aligned}$$

For $\tau = 0$ the characteristic equation becomes

$$\lambda^2 + (p+s)\lambda + q + r = 0 \tag{4.5}$$

which has the roots

$$\lambda = \frac{-(p+s) \pm \sqrt{(p+s)^2 - 4(q+r)}}{2}. \tag{4.6}$$

Looking at equation (4.6), we can see that both roots are negative and real if and only if

$$p + s > 0 \quad \text{and} \quad q + r > 0. \tag{4.7}$$

Now for $\tau \neq 0$, if $\lambda = i\omega$ is a root of equation (4.4) we have

$$-\omega^2 + qe^{-i\omega\tau} + pi\omega + r + is\omega e^{-i\omega\tau} = 0,$$

which implies that

$$\begin{aligned} r - \omega^2 - s\omega\sin(\omega\tau) + q\cos(\omega\tau) &= 0, \\ p\omega + s\omega\cos(\omega\tau) + q\sin(\omega\tau) &= 0. \end{aligned} \tag{4.8}$$

Simplifying system (4.8), we obtain the fourth order polynomial

$$\omega^4 + (p^2 - s^2 - 2r)\omega^2 + r^2 - q^2 = 0, \tag{4.9}$$

from which we have

$$\omega_\pm^2 = \frac{s^2 - p^2 + 2r \pm \sqrt{(s^2 - p^2 + 2r)^2 - 4(r^2 - q^2)}}{2}. \tag{4.10}$$

It follows that if

$$p^2 - s^2 - 2r > 0 \quad \text{and} \quad r^2 - q^2 > 0 \tag{4.11}$$

are satisfied, then equation (4.9) does not have positive solutions; that is, the characteristic equation (4.4) does not have purely imaginary roots. Inequalities in (4.7) guarantee that all roots of equation (4.5) have negative real parts. Using Rouch*é*'s theorem, we can conclude the following:

Lemma 4.1. *If conditions (4.7) and (4.11) are satisfied, then all roots of equation (4.4) have negative real parts for all* $\tau \geq 0$*; that is, the equilibrium* (x^*, y^*) *is asymptotically stable for all* $\tau \geq 0$.

From (4.10) we can see that there is one positive solution ω_+^2 if

$$r^2 - q^2 < 0. \tag{4.12}$$

Also, if

$$r^2 - q^2 > 0, \quad s^2 - p^2 + 2r > 0 \ \text{ and } \ (s^2 - p^2 + 2r)^2 > 4(r^2 - q^2) \tag{4.13}$$

hold, then there are two positive solutions $\omega_\pm^2$. Substituting $\omega_\pm^2$ into system (4.8) and solving for τ, we obtain

$$\tau_j^\pm = \frac{1}{\omega_\pm} \arctan\left(\frac{\omega_\pm(pq - rs + s\omega_\pm^2)}{ps\omega_\pm^2 + (r - \omega_\pm^2)q}\right) + \frac{2j\pi}{\omega_\pm}, \quad j = 0, 1, 2, \ldots \tag{4.14}$$

From the above analysis, we have the following result.

Lemma 4.2. *If conditions (4.7) and (4.12) hold, then equation (4.4) with $\tau = \tau_j^+$ has a pair of pure imaginary roots $\pm i\omega_+$. If conditions (4.7) and (4.13) hold and $\tau = \tau_j^+$ ($\tau = \tau_j^-$ respectively), then equation (4.4) has a pair of pure imaginary roots $\pm i\omega_+$ ($\pm i\omega_-$ respectively).*

As in section 2, we can show that the transversality conditions

$$\frac{d}{d\tau} Re\lambda_j^+(\tau_j^+) > 0, \qquad \frac{d}{d\tau} Re\lambda_j^-(\tau_j^-) < 0$$

are satisfied. Therefore, $\tau_j^\pm$ are bifurcation values and we have the following theorem.

Theorem 4.3. *Let $\tau_j^\pm$ be defined by equation (4.14).*

(i) *If (4.7) and (4.11) hold, then the equilibrium (x^*, y^*) of system (4.1) is asymptotically stable for all $\tau \geq 0$.*
(ii) *If (4.7) and (4.12) hold, then the equilibrium (x^*, y^*) of system (4.1) is asymptotically stable for $\tau < \tau_0$ and unstable for $\tau > \tau_0$. Hopf bifurcation occurs when $\tau = \tau_0$.*
(iii) *If (4.7) and (4.13) hold, then there exists a positive integer k such that there are k switches from stability to instability and to stability. In other words, when*

$$\tau \in [0, \tau_0^+), (\tau_0^-, \tau_1^+), \ldots, (\tau_{k-1}^-, \tau_k^+),$$

the equilibrium (x^*, y^*) of system (4.1) is stable, and when

$$\tau \in [\tau_0^+, \tau_0^-), (\tau_1^+, \tau_1^-), \ldots, (\tau_{k-1}^+, \tau_k^-),$$

(x^*, y^*) is unstable. Therefore, there are bifurcations at (x^*, y^*) when $\tau = \tau_j^\pm, j = 0, 1, 2, \ldots$

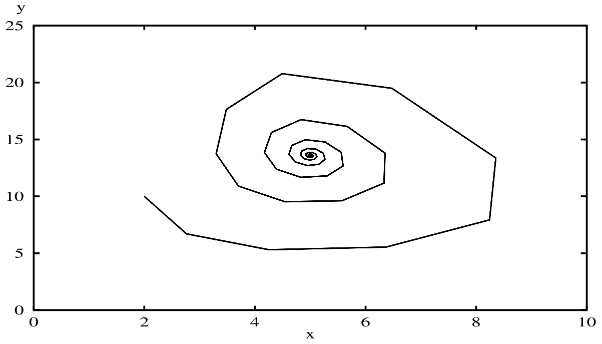

Fig. 4.1. The equilibrium $(x^*, y^*) = (5, 68/5)$ is asymptotically stable when $\tau = 0$. Here $x(0) = 2$, $y(0) = 10$.

Example 4.4. As an example, we consider the following system

$$\begin{aligned} \frac{dx}{dt} &= x(t)\,[20 - x(t) - y(t)] - 7, \\ \frac{dy}{dt} &= -15y(t) + 3x(t-\tau)y(t-\tau), \end{aligned} \tag{4.15}$$

which has a positive equilibrium $(x^*, y^*) = (5, 68/5)$.

When $\tau = 0$, we can see in Figure 4.1 that the predator and prey populations spiral toward the equilibrium (5,68/5).

We are interested in studying the effect of the delay τ on the dynamics of the model. From Theorem 4.3 there is a critical value $\tau_0 = 0.0385$, when $\tau < 0.0385$ the equilibrium (5,68/5) is asymptotically stable; when $\tau = 0.0385$ the equilibrium (5,68/5) loses its stability; and when $\tau > 0.0385$ the equilibrium (5,68/5) becomes unstable and there is a bifurcating periodic solution (see Figure 4.2).

To see whether varying H will affect the dynamics of the model, we calculate that for $H = 1$, $y^* = 74/5$, compared to $y^* = 68/5$ for $H = 7$. Therefore, varying H also varies y^* : increasing H decreases y^* and decreasing H increases

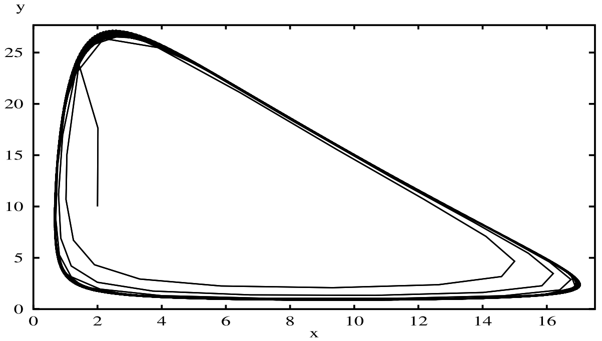

Fig. 4.2. There is a bifurcating periodic solution for $\tau = 0.05$.

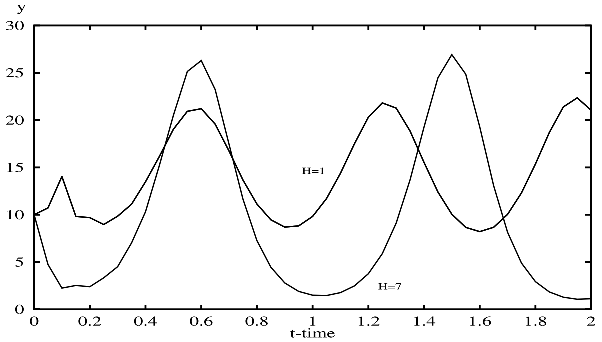

Fig. 4.3. Behavior of the predator population for different values of H for $\tau = 0.05$.

y^*. However, as Figure 4.3 shows, varying the value of H does not change the behavior of the solutions.

5. Discussion

We have studied three predator-prey systems with delay and constant-rate harvesting. In the first model a time delay appears in the prey specific growth term, in the second model there is a delay in the predator response function, while the third one is the well-known Wangersky-Cunningham model. In all three systems, it is assumed that the prey population is harvested at a constant rate.

It has been shown that the time delay can induce instability and oscillations via Hopf bifurcations in all three systems; moreover, switching of stability occurs in the first and third models. On the other hand, as long as the harvesting rate is below a critical harvesting rate H_c, it has the effect of stabilizing the equilibria; in particular, the second model regained its stability when the harvesting rate is increased.

There is still a tremendous amount of work to do in this area. For example, it would be interesting to see what the behavior of systems (2.1), (3.1) and (4.1) would be when the harvesting constant is in the predator equation. We could expect some differences from the examples seen in this paper, at least for systems (2.1) and (3.1) where Brauer and Soudack (see [4,5]) noticed different types of solutions whether the harvesting was in the prey or in the predator equation when the delay was nil. Ideally, we would be interested in studying systems (2.1), (3.1) and (4.1) with both predator and prey harvesting constants since we usually harvest, or would like to harvest, both populations. It would also be interesting to study, at least with computer simulations, the Wangersky-Cunningham model with delays in both the predator and prey equations as in the Bartlett's model (see Bartlett [1] and Hastings [19]). Finally, it would be interesting to study the effect of time delays on MSY and OSY. We leave these for future consideration.

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