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Dynamics of Stage-Structured Predator–Prey Model with Beddington–DeAngelis Functional Response and Harvesting

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Abstract: In this paper, we investigate the stability of equilibrium in the stage-structured and density-dependent predator–prey system with Beddington–DeAngelis functional response. First, by checking the sign of the real part for eigenvalue, local stability of origin equilibrium and boundary equilibrium are studied. Second, we explore the local stability of the positive equilibrium for $\tau = 0$ and $\tau \neq 0$ (time delay τ is the time taken from immaturity to maturity predator), which shows that local stability of the positive equilibrium is dependent on parameter τ. Third, we qualitatively analyze global asymptotical stability of the positive equilibrium. Based on stability theory of periodic solutions, global asymptotical stability of the positive equilibrium is obtained when $\tau = 0$; by constructing Lyapunov functions, we conclude that the positive equilibrium is also globally asymptotically stable when $\tau \neq 0$. Finally, examples with numerical simulations are given to illustrate the obtained results.

Keywords: density-dependent predation; stage-structure; harvesting; Beddington–DeAngelis functional response

1. Introduction

The dynamical behavior of the predator–prey system is one of the main research topics in mathematical ecology and theoretical biology [1–9]. Functional response is the core component of the community and food web model, and their mathematical form strongly affects the dynamics and stability of the ecosystem [10–14]. Beddington [15] and DeAngelis [16] originally proposed the predator–prey model as follows:

$$\begin{cases} \frac{dx(t)}{dt} = x(t)\left(a - bx(t) - \frac{cy(t)}{m_1+m_2x(t)+m_3y(t)}\right), \\ \frac{dy(t)}{dt} = y(t)\left(-d + \frac{fx(t)}{m_1+m_2x(t)+m_3y(t)}\right), \end{cases} \qquad (1)$$

where $x(t)$ is the prey density, $y(t)$ is the predator density, a is the intrinsic growth rate of the prey, b represents the intensity of intraspecific competition of the prey, and d represents the predator's death rate. The Beddington–DeAngelis functional response is similar to the well-known Holling II type [17,18] functional response, but it has an extra term m_3y in the denominator modeling mutual interference among predators.

The functional response of consumers is a function of resource density [17,19,20]. However, it has been shown that other species and other predators can alter the predation process directly or indirectly [21]. In addition, Kratina [21] showed that predator dependence is very important not only when the predator density on per capita predation rate is very high, but also when the predator density is low. Therefore, we need to consider the realistic level of predator density when we study the predator–prey system.

Moreover, in nature, many species undergo two stages [22,23]: immature and mature, and species at these two stages may have different behaviors. The model of single-species stage-structured dynamics [22] was described as

$$
\begin{aligned}
\frac{dx_1(t)}{dt} &= dx_2(t) - d_i x_1(t) - de^{-d_i\tau} x_2(t-\tau), \\
\frac{dx_2(t)}{dt} &= de^{-d_i\tau} x_2(t-\tau) - r x_2^2(t),
\end{aligned}
\tag{2}
$$

where $x_1(t)$ and $x_2(t)$ represent the immature and mature populations densities, respectively, and τ represents a constant time to maturity. Therefore, in order to be in accord with the natural phenomenon, the system with the stage structure recently has been extensively studied [24–30]. Liu and Beretta [27] studied time delay τ in the response term $\frac{x(t)}{m_1+m_2 x(t)+m_3 y(t)}$ of (1) in the predator equation, that is,

$$
\begin{cases}
\frac{dx(t)}{dt} = rx(t)\left(1 - \frac{x(t)}{K}\right) - \frac{gx(t)y(t)}{1+k_1 x(t)+k_2 y(t)}, \\
\frac{dy(t)}{dt} = -dy(t) + \frac{nge^{-d_j\tau} x(t-\tau)y(t-\tau)}{1+k_1 x(t-\tau)+k_2 y(t-\tau)}, \\
\frac{dy_i(t)}{dt} = \frac{ngx(t)y(t)}{1+k_1 x(t)+k_2 y(t)} - \frac{nge^{-d_j\tau} x(t-\tau)y(t-\tau)}{1+k_1 x(t-\tau)+k_2 y(t-\tau)} - d_j y_j(t),
\end{cases}
\tag{3}
$$

where $g > 0$ (units: 1/time) and $k_1 > 0$ (units: 1/prey) stand the effects of capture rate and handling time, respectively, on the feeding rate; n is the birth rate of the predator; and $k_2 \geq 0$ (units: 1/predator) stands the magnitude of interference among predators. Liu and Beretta [27] pointed out the difference between Beddington–DeAngelis functional response and Holling type II, and the effect of $k_2 y$ (describing mutual interference by predators) on the dynamic of the system (3).

On the basis of the system (1) and the system (2), She and Li [29] investigated a predator–prey system with density-dependence for predator and stage structure for prey

$$
\begin{cases}
x_i'(t) = a'x(t) - d_i x_i(t) - a'e^{-d_i\tau} x(t-\tau), \\
x'(t) = a'e^{-d_i\tau} x(t-\tau) - bx^2(t) - \frac{cx(t)y(t)}{m_1+m_2 x(t)+m_3 y(t)}, \\
y'(t) = -dy(t) - py^2(t) + \frac{cx(t)y(t)}{m_1+m_2 x(t)+m_3 y(t)},
\end{cases}
\tag{4}
$$

where p stands for predator density-dependent mortality rate, the predator consumes prey with functional response of Beddington-DeAngelis type $\frac{cx(t)y(t)}{m_1+m_2 x(t)+m_3 y(t)}$ and contributes to its growth with rate $\frac{fx(t)y(t)}{m_1+m_2 x(t)+m_3 y(t)}$. Note that compared with the system (1), the system (4) contains not only $bx^2(t)$ (which stands for intraspecific competition of prey species), but also $py^2(t)$ (which stands for intraspecific competition of predator species). That is, they consider both the prey density dependence and the predator density dependence in the predator–prey model (4). She and Li [29] studied the dynamics of the system (4) and pointed out the impact of the predator density-dependent mortality rate p on the global attraction and permanence of the system (4).

The development of biological resources, the management of renewable resources, and the harvest of populations are universal human purposes for realizing the economic benefits of fishery, forestry and wildlife management [31,32]. Many researchers [28,30,33,34] have extensively studied the predator–prey model with harvesting and the role of harvesting in renewable resource management. Brauer [35] introduced the predator–prey system with constant-rate prey harvesting

$$
x' = xf(x,y) - F, \quad y' = yg(x,y),
\tag{5}
$$

where prey is harvested at a constant time rate F. May [36] put forward two types of harvesting regimes: constant-yield harvesting (representing harvested biomass independent of the size of the population) and constant-effort harvesting (representing harvested biomass proportional to the size of the population).

Based on the system (3), we construct a density-dependent and constant-effort harvesting predator–prey model:

$$
\begin{cases}
\frac{dx(t)}{dt} = x(t)\left(a - bx(t) - \frac{cy(t)}{m_1 + m_2 x(t) + m_3 y(t)}\right) - E_1 x(t), \\
\frac{dy(t)}{dt} = -dy(t) - py^2(t) + \frac{fe^{-d_i\tau}x(t-\tau)y(t-\tau)}{m_1 + m_2 x(t-\tau) + m_3 y(t-\tau)} - E_2 y(t), \\
\frac{dy_i(t)}{dt} = -d_i y_i(t) - py^2(t) + \frac{fx(t)y(t)}{m_1 + m_2 x(t) + m_3 y(t)} + pe^{-d_i\tau}y^2(t-\tau) \\
\qquad\qquad - \frac{fe^{-d_i\tau}x(t-\tau)y(t-\tau)}{m_1 + m_2 x(t-\tau) + m_3 y(t-\tau)},
\end{cases}
\tag{6}
$$

where $y_i(t)$ denotes the immature or juvenile predator density, juveniles suffer a mortality rate d_i and take τ units of time to be mature and $e^{-d_i\tau}$ is the surviving rate of each immature predator to reach maturity. E_1 and E_2 denote the harvesting effort of the mature population of prey and predator, respectively. Further, all the parameters a, d_i, b, c, d, f, m_1, m_2, m_3, p, E_1, E_2, and τ are positive.

In the system (6), as $y_i(t)$ does not intervene in the dynamics of $x(t)$ and $y(t)$, system (6) is equal to the following system:

$$
\begin{cases}
\frac{dx(t)}{dt} = x(t)\left(a - bx(t) - \frac{cy(t)}{m_1 + m_2 x(t) + m_3 y(t)}\right) - E_1 x(t), \\
\frac{dy(t)}{dt} = -dy(t) - py^2(t) + \frac{fe^{-d_i\tau}x(t-\tau)y(t-\tau)}{m_1 + m_2 x(t-\tau) + m_3 y(t-\tau)} - E_2 y(t).
\end{cases}
\tag{7}
$$

The initial conditions of the system (7) is

$$
x_0(\theta) = \phi_1(\theta) \geq 0, \quad y_0(\theta) = \phi_2(\theta) \geq 0, \quad \theta \in [-\tau, 0], \quad x(0) > 0, \quad y(0) > 0,
\tag{8}
$$

where $\phi = (\phi_1, \phi_2) \in C([-\tau, 0], R_+^2)$, $R_+^2 = \{(x,y) : x \geq 0, y \geq 0\}$, $\|\phi\| = max\{|\phi(\theta)| : \theta \in [-\tau, 0]\}$, and $|\phi|$ is the modulus in R_+^2. Normally, we use notation $x_t(\theta) = x(t+\theta), \theta \in [-\tau, 0]$.

This paper mainly investigates the local and global stability of positive equilibrium in the system (7) on parameter τ, which is organized as follows. In Section 2, we study local stability of origin equilibrium and boundary equilibrium. In Section 3, we derive local stability of the positive equilibrium for $\tau = 0$ and $\tau \neq 0$, respectively. In Section 4, we obtain the global asymptotical stability of the positive equilibrium for $\tau = 0$ and $\tau \neq 0$, respectively. Last, we conclude the paper.

2. Local Stability of Origin Equilibrium and Boundary Equilibrium

For any value of all parameters, system (7) has the equilibria $E_0(0,0)$ and $E_1\left(\frac{a-E_1}{b}, 0\right)$, denoted as the origin and the boundary equilibrium, respectively. In the following, we determine the local stability of two equilibria by the sign of eigenvalue for the corresponding characteristic matrix.

First, for origin equilibrium E_0, the corresponding characteristic matrix is

$$
J_{(0,0)} = \begin{bmatrix} \lambda - a + E_1 & 0 \\ 0 & \lambda + d + E_2 \end{bmatrix},
$$

and the eigenvalues are

$$
\lambda_1 = a - E_1 > 0, \quad \lambda_2 = -(d + E_2) < 0.
$$

Clearly, $E_0(0,0)$ is hyperbolic saddle and is unstable.

Next, for boundary equilibrium E_1, the corresponding characteristic matrix is

$$
J_{\left(\frac{a-E_1}{b}, 0\right)} = \begin{bmatrix} \lambda + a - E_1 & \frac{c(a-E_1)}{bm_1 + m_2(a-E_1)} \\ 0 & \lambda + d + E_2 - \frac{(a-E_1)fe^{-(\lambda+d_i)\tau}}{bm_1 + m_2(a-E_1)} \end{bmatrix}.
$$

We can obtain one eigenvalue $\lambda_1 = -(a - E_1) < 0$, the second eigenvalue is determined by the following equation:

$$\lambda_2 + d + E_2 - \frac{(a - E_1)fe^{-(\lambda_2 + d_i)\tau}}{bm_1 + m_2(a - E_1)} = 0.$$

Let n be the independent variable and g be the dependent variable; then, the straight line $g = n + (d + E_2)$ and the curve $g = \frac{(a-E_1)fe^{-d_i\tau}}{bm_1 + m_2(a-E_1)}e^{-n\tau}$ must intersect at a unique point (λ_2, g). Further, we can get the following:

(i) if $d + E_2 > \frac{(a-E_1)fe^{-d_i\tau}}{bm_1 + m_2(a-E_1)}$, then $\lambda_2 < 0$;

(ii) if $d + E_2 < \frac{(a-E_1)fe^{-d_i\tau}}{bm_1 + m_2(a-E_1)}$, then $\lambda_2 > 0$;

(iii) if $d + E_2 = \frac{(a-E_1)fe^{-d_i\tau}}{bm_1 + m_2(a-E_1)}$, then $\lambda_2 = 0$.

Therefore, we have the following conclusion about local stability of boundary equilibrium.

Theorem 1.
(1) If $(a - E_1)\left[fe^{-d_i\tau} - (d + E_2)m_2\right] < bm_1(d + E_2)$, boundary equilibrium $\left(\frac{a-E_1}{b}, 0\right)$ is locally asymptotically stable;

(2) If $(a - E_1)\left[fe^{-d_i\tau} - (d + E_2)m_2\right] > bm_1(d + E_2)$, boundary equilibrium $\left(\frac{a-E_1}{b}, 0\right)$ is unstable;

(3) If $(a - E_1)\left[fe^{-d_i\tau} - (d + E_2)m_2\right] = bm_1(d + E_2)$, boundary equilibrium $\left(\frac{a-E_1}{b}, 0\right)$ is linearly neutrally stable.

Remark 1. *By Theorem 1, when $\tau > \tau^*$, $\left(\frac{a-E_1}{b}, 0\right)$ is locally asymptotically stable; when $\tau < \tau^*$, $\left(\frac{a-E_1}{b}, 0\right)$ is unstable; when $\tau = \tau^*$, $\left(\frac{a-E_1}{b}, 0\right)$ is linearly neutrally stable, where*

$$\tau^* = \frac{1}{d_i} \log \frac{f(a - E_1)}{(d + E_2)[bm_1 + m_2(a - E_1)]}.$$

That is, τ^* is a threshold for the stability of the boundary equilibrium.

3. Local Stability of the Positive Equilibrium

We denote (x^*, y^*) as equilibrium other than the origin equilibrium and boundary equilibrium for the system (7) and satisfying the algebraic equations

$$\begin{cases} a - bx^* - \frac{cy^*}{m_1 + m_2 x^* + m_3 y^*} - E_1 = 0, \\ -d - py^* + \frac{fe^{-d_i\tau}x^*}{m_1 + m_2 x^* + m_3 y^*} - E_2 = 0. \end{cases} \quad (9)$$

From $a - bx - \frac{cy}{m_1 + m_2 x + m_3 y} - E_1 = 0$, we have the curve

$$y = \frac{bm_2 x^2 + [bm_1 - (a - E_1)m_2]x - (a - E_1)m_1}{(a - E_1)m_3 - c - bm_3 x} = F(x);$$

by $-d - py + \frac{fe^{-d_i\tau}x}{m_1 + m_2 x + m_3 y} - E_2 = 0$, we have another curve

$$x = \frac{pm_3 y^2 + [pm_1 + (d + E_2)m_3]y + (d + E_2)m_1}{fe^{-d_i\tau} - (d + E_2)m_2 - pm_2 y} = H(y).$$

By considering the intersection of curves $y = F(x)$ and $x = H(y)$ in the first quadrant, we can obtain if the condition

$$(a - E_1)\left[fe^{-d_i\tau} - (d + E_2)m_2\right] > bm_1(d + E_2) \tag{10}$$

holds, (x^*, y^*) is a positive equilibrium of system (7).

By the condition (10), we can directly obtain the following result.

Remark 2. *The positive equilibrium (x^*, y^*) exists for any predation maturation time τ in the interval $[0, \tau^*)$.*

The Jacobian matrix [37] of differential system (7) with delay coefficients at (x^*, y^*) is

$$J_{(x^*, y^*)} = \begin{bmatrix} a - E_1 - 2bx^* - \frac{cy^*(m_1 + m_3 y^*)}{(m_1 + m_2 x^* + m_3 y^*)^2} & -\frac{cx^*(m_1 + m_2 x^*)}{(m_1 + m_2 x^* + m_3 y^*)^2} \\ \frac{fe^{-d_i\tau}y^*(m_1 + m_3 y^*)}{(m_1 + m_2 x^* + m_3 y^*)^2}e^{-\lambda\tau} & -(d + E_2) - 2py^* + \frac{fe^{-d_i\tau}x^*(m_1 + m_2 x^*)}{(m_1 + m_2 x^* + m_3 y^*)^2}e^{-\lambda\tau} \end{bmatrix}.$$

Therefore, the characteristic equation is

$$\lambda^2 + a_1(\tau)\lambda + a_2(\tau)\lambda e^{-\lambda\tau} + a_3(\tau)e^{-\lambda\tau} + a_4(\tau) = 0, \tag{11}$$

where

$$a_1(\tau) = d + 2py^* + E_2 + (E_1 - a) + 2bx^* + \frac{cy^*(m_1 + m_3 y^*)}{(m_1 + m_2 x^* + m_3 y^*)^2},$$

$$a_2(\tau) = -\frac{fe^{-d_i\tau}x^*(m_1 + m_2 x^*)}{(m_1 + m_2 x^* + m_3 y^*)^2}, \quad a_3(\tau) = (a - 2bx^* - E_1)\frac{fe^{-d_i\tau}x^*(m_1 + m_2 x^*)}{(m_1 + m_2 x^* + m_3 y^*)^2},$$

$$a_4(\tau) = (d + 2py^* + E_2)\left(E_1 - a + 2bx^* + \frac{cy^*(m_1 + m_3 y^*)}{(m_1 + m_2 x^* + m_3 y^*)^2}\right).$$

We noticed that if $x^* > \frac{a - E_1}{2b}$, then $a_3(\tau) + a_4(\tau) > 0$. Therefore, when $x^* > \frac{a - E_1}{2b}$, $\lambda = 0$ cannot be a characteristic root of Equation (11).

The parameter τ is the time from immature to mature predator. Time delay $\tau \neq 0$, it shows the predator population is divided into immature and mature; time delay $\tau = 0$, it shows the model does not consider the immature predators. In the following, we discuss the local stability of positive equilibrium (x^*, y^*) for $\tau = 0$ and $\tau \neq 0$, respectively.

3.1. Local Stability of the Positive Equilibrium for $\tau = 0$

When $\tau = 0$, characteristic Equation (11) becomes

$$\lambda^2 + [a_1(0) + a_2(0)]\lambda + a_3(0) + a_4(0) = 0. \tag{12}$$

Obviously, when $\begin{cases} a_1(0) + a_2(0) > 0 \\ a_3(0) + a_4(0) > 0 \end{cases}$, all roots of characteristic Equation (12) have negative real part. Therefore, $(x^*(0), y^*(0))$ is locally asymptotically stable.

Further, by

$$a_1(0) + a_2(0) = bx^*(0) + py^*(0) + \frac{(fm_3 - cm_2)x^*(0)y^*(0)}{(m_1 + m_2 x^*(0) + m_3 y^*(0))^2},$$

we can obtain that if $fm_3 \geq cm_2$, then $a_1(0) + a_2(0) > 0$. According to the previous analysis, we also have if $x^* > \frac{a - E_1}{2b}$, $a_3(0) + a_4(0) > 0$. Therefore, we get the following conclusion.

Theorem 2. *Let (x^*, y^*) is a positive equilibrium of system (7), if the inequality (10) and the following inequalities*

$$\begin{cases} x^* > \frac{a - E_1}{2b} \\ cm_2 \leq fm_3 \end{cases} \tag{13}$$

hold, the positive equilibrium (x^*, y^*) of system (7) is locally asymptotically stable for $\tau = 0$.

Example 1. *Let $a = 3$, $b = 2$, $c = 2$, $d = 0.1$, $p = 10$, $f = 12$, $m_1 = \frac{1}{8}$, $m_2 = 4$, $m_3 = 2$, $E_1 = 0.5$, $E_2 = 0.05$, and $\tau = 0$, the system (7) becomes*

$$
\begin{cases}
\frac{dx(t)}{dt} = x\left(3 - 2x - \frac{2y}{\frac{1}{8} + 4x + 2y}\right) - 0.5x, \\
\frac{dy(t)}{dt} = -0.1y - 10y^2 + \frac{12xy}{\frac{1}{8} + 4x + 2y} - 0.05y.
\end{cases}
\tag{14}
$$

Clearly, $(a - E_1)(fe^{-d_i\tau} - (d + E_2)m_2) - b(d + E_2)m_1 = 28.4625 > 0$. Therefore, the system (14) exists a positive equilibrium. Moreover, we obtain the positive equilibrium $(1.2040, 0.2505)$ of system (14). As $\frac{a - E_1}{2b} = 0.625 < 1.2040$ and $cm_2 - fm_3 = -16 < 0$, the equilibrium $(1.2040, 0.2505)$ is locally asymptotically stable by Theorem 2.

3.2. Local Stability of the Positive Equilibrium for $\tau \neq 0$

In this subsection, we further discuss the sign of the real part of the characteristic root for the characteristic Equation (11) with the change of parameter τ, and determine stability switch.

First, assume that characteristic Equation (11) has a characteristic root with zero real part, and let it be $\lambda = i\omega (\omega \in R$ and $\omega \neq 0)$. Putting it into the characteristic Equation (11), we have

$$
\begin{cases}
a_2\omega \sin \omega\tau + a_3 \cos \omega\tau = \omega^2 - a_4, \\
a_2\omega \cos \omega\tau - a_3 \sin \omega\tau = -a_1\omega.
\end{cases}
\tag{15}
$$

Here, $a_1(\tau)$, $a_2(\tau)$, $a_3(\tau)$ and $a_4(\tau)$ are abbreviated as a_1, a_2, a_3 and a_4, respectively. From Equation (15), we can get

$$
\omega^4 + (a_1^2 - a_2^2 - 2a_4)\omega^2 + a_4^2 - a_3^2 = 0.
\tag{16}
$$

Regarding ω^2 as an invariant, by the quadratic root formula, we have

$$
\omega_\pm^2 = \frac{(a_2^2 + 2a_4 - a_1^2) \pm \sqrt{(a_1^2 - a_2^2 - 2a_4)^2 - 4(a_4^2 - a_3^2)}}{2}.
\tag{17}
$$

We discuss the case of roots for the Equation (16):
(I) If

$$
\begin{cases}
a_1^2 - a_2^2 - 2a_4 > 0, \\
a_4^2 - a_3^2 > 0, \\
(a_1^2 - a_2^2 - 2a_4)^2 - 4(a_4^2 - a_3^2) > 0
\end{cases}
\tag{18}
$$

ω_+^2 and ω_-^2 are negative, which obviously contradicts with $\omega \in R$. Therefore, Equation (16) does not have real roots, that is, characteristic Equation (11) does not have purely imaginary roots. Moreover, if the conditions (10) and (13) hold, all roots of the characteristic Equation (12) have negative real part for $\tau = 0$. Therefore, by Rouche's theorem, it follows that the roots of the characteristic Equation (11) also have negative real part.
(II) If

$$
\begin{cases}
a_4^2 - a_3^2 < 0, \\
or \\
a_1^2 - a_2^2 - 2a_4 < 0, \ (a_1^2 - a_2^2 - 2a_4)^2 - 4(a_4^2 - a_3^2) = 0,
\end{cases}
\tag{19}
$$

Equation (16) has a positive root ω_0^2. Furthermore, putting ω_0^2 into Equations (15), we have

$$
\tau_n = \frac{1}{\omega_0} \arcsin\left\{\frac{a_2\omega_0(\omega_0^2 - a_4) + a_1 a_3\omega_0}{a_2^2\omega_0^2 + a_3^2}\right\} + \frac{2n\pi}{\omega_0}, \quad n = 0, 1, 2, \cdots.
\tag{20}
$$

(III) If

$$\begin{cases} a_4^2 - a_3^2 > 0, \\ a_1^2 - a_2^2 - 2a_4 < 0, \\ (a_1^2 - a_2^2 - 2a_4)^2 - 4(a_4^2 - a_3^2) > 0, \end{cases} \tag{21}$$

Equation (16) has two positive roots $\omega_\pm^2$. Putting $\omega_\pm^2$ into Equations (15), we obtain

$$\tau_j^\pm = \frac{1}{\omega_\pm} \arcsin \left\{ \frac{a_2\omega_\pm(\omega_\pm^2 - a_4) + a_1 a_3\omega_\pm}{a_2^2\omega_\pm^2 + a_3^2} \right\} + \frac{2j\pi}{\omega_\pm}, \ j = 0, 1, 2, \cdots. \tag{22}$$

From the above analysis, we have the following conclusion.

Theorem 3.
   (i) If conditions (10) and (19) hold and $\tau = \tau_n$, then characteristic Equation (11) has a pair of purely imaginary roots $\pm i\omega_0$.
   (ii) If conditions (10) and (21) hold and $\tau = \tau_j^+(\tau = \tau_j^-)$, then characteristic Equation (11) has a pair of purely imaginary roots $\pm i\omega_+(\pm i\omega_-)$.

Second, we have that when $\tau > \tau_0$, $\tau > \tau_j^+$, and $\tau < \tau_j^-$, there are roots with positive real part in the characteristic Equation (11). Let these characteristic roots with positive real part be

$$\lambda_0 = \alpha_0(\tau) + i\omega_0(\tau), \ \lambda_j^\pm = \alpha_j^\pm(\tau) + i\omega_j^\pm(\tau), \ \ j = 0, 1, 2, \cdots,$$

and

$$\alpha_0(\tau_0) = 0, \ \omega_0(\tau_0) = \omega_0, \ \ \alpha_j^\pm(\tau_j^\pm) = 0, \ \omega_j^\pm(\tau_j^\pm) = \omega_\pm,$$

where

$$\tau_0 = \frac{1}{\omega_0} \arcsin \left\{ \frac{a_2\omega_0(\omega_0^2 - a_4) + a_1 a_3\omega_0}{a_2^2\omega_0^2 + a_3^2} \right\}.$$

According to the characteristic Equation (11), we get

$$\frac{d\lambda}{d\tau} = -\frac{\lambda(\lambda^2 + a_1\lambda + a_4)}{2\lambda + a_1 + a_2 e^{-\lambda\tau} + \tau(\lambda^2 + a_1\lambda + a_4)}. \tag{23}$$

Obviously, $sign\left\{ \frac{d}{d\tau} Re\lambda(\tau) \right\} = sign\left\{ Re(\frac{d\lambda(\tau)}{d\tau})^{-1} \right\}$. Therefore, in order to judge the sign of $\frac{d}{d\tau} Re\lambda(\tau)$, we only need to judge the sign of $Re\left(\frac{d\lambda(\tau)}{d\tau} \right)^{-1}$. According to (23), we can get

$$\left\{ Re\left(\frac{d\lambda}{d\tau} \right)^{-1} \right\}_{\lambda=i\omega} = \frac{a_2^2\omega^4 + 2a_3^2\omega^2 + a_3^2(a_1^2 - 2a_4) - a_2^2 a_4^2}{(a_2^2\omega^2 + a_3^2)[a_1^2\omega^2 + (a_4 - \omega^2)^2]}. \tag{24}$$

Last, we can easily prove that λ_0 and $\tau_j^\pm$ satisfy the following transversality conditions:

$$\frac{d}{d\tau} Re\lambda_0(\tau_0) > 0, \ \ \ \frac{d}{d\tau} Re\lambda_j^+(\tau_j^+) > 0, \ \ \ \frac{d}{d\tau} Re\lambda_j^-(\tau_j^-) < 0.$$

It follows that λ_0 and $\tau_j^\pm$ are bifurcation values. Thus, we have the following theorem about the distribution of the characteristic roots of Equation (11).

Theorem 4.

(i) If conditions (10), (13), and (18) hold, then all roots of Equation (11) have negative real parts for all $\tau \geq 0$. Therefore, the positive equilibrium (x^*, y^*) of system (7) is locally asymptotically stable.

(ii) If conditions (10) and (19) hold, when $\tau \in [0, \tau_0)$, all roots of Equation (11) have negative real parts, and the positive equilibrium (x^*, y^*) of system (7) is locally asymptotically stable; when $\tau = \tau_0$, Equation (11) has a pair of purely imaginary roots $\pm i\omega_0$, and when $\tau > \tau_0$, Equation (11) has at least one root with positive real part, and the positive equilibrium (x^*, y^*) of system (7) is unstable, that is, when τ keeps increasing and passes τ_0, the positive equilibrium (x^*, y^*) bifurcates into two periodic solutions with small amplitudes.

(iii) If conditions (10) and (21) hold, there is a positive integer k such that the positive equilibrium (x^*, y^*) of system (7) has k stability switches from stability to instability to stability. That is, when

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

all roots of Equation (11) have negative real parts, and the positive equilibrium (x^*, y^*) of system (7) is locally asymptotically stable. When

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

Equation (11) has at least one root with positive real part, the positive equilibrium (x^*, y^*) of system (7) is unstable. Furthermore, it shows when time delay τ passes the critical value $\tau_j^+, j = 0, 1, 2, ..., k - 1$, the positive equilibrium (x^*, y^*) of the system (7) loses its stability and Hopf bifurcation occurs.

4. Global Asymptotic Stability of Positive Equilibrium

In order to maintain healthy and sustainable ecosystem, the relevant departments need to plan harvesting. From the perspective of ecological managers, the positive equilibrium is best to be globally asymptotically stable. Therefore, we will investigate the global asymptotic stability of the positive equilibrium (x^*, y^*) for $\tau = 0$ and $\tau \neq 0$, respectively.

4.1. Global Asymptotic Stability of Positive Equilibrium for $\tau = 0$

In this subsection, when $\tau = 0$, our aim is to show that the positive equilibrium (x^*, y^*) is globally asymptotically stable.

When $\tau = 0$, then system (7) becomes

$$\begin{cases} \frac{dx}{dt} = x\left(a - E_1 - bx - \frac{cy}{m_1 + m_2 x + m_3 y}\right), \\ \frac{dy}{dt} = y\left(-d - E_2 - py + \frac{fx}{m_1 + m_2 x + m_3 y}\right). \end{cases} \tag{25}$$

The variational matrix of the system (25) is given by

$$J_{(x,y)} = \begin{bmatrix} a - E_1 - 2bx - \frac{cy(m_1 + m_3 y)}{(m_1 + m_2 x + m_3 y)^2} & \frac{-cx(m_1 + m_2 x)}{(m_1 + m_2 x + m_3 y)^2} \\ \frac{fy(m_1 + m_3 y)}{(m_1 + m_2 x + m_3 y)^2} & -d - E_2 - 2py + \frac{fx(m_1 + m_2 x)}{(m_1 + m_2 x + m_3 y)^2} \end{bmatrix} \tag{26}$$

and the trace of variational matrix is

$$tr(J_{(x,y)}) = a - E_1 - 2bx - \frac{cy(m_1 + m_3 y)}{(m_1 + m_2 x + m_3 y)^2} - d - E_2 - 2py + \frac{fx(m_1 + m_2 x)}{(m_1 + m_2 x + m_3 y)^2}$$

$$= a - E_1 - bx - \frac{cy}{m_1 + m_2 x + m_3 y} + x\left(-b + \frac{cm_2 y}{(m_1 + m_2 x + m_3 y)^2}\right)$$

$$-d - E_2 - py + \frac{fx}{m_1 + m_2 x + m_3 y} - y\left(p + \frac{fm_3 x}{(m_1 + m_2 x + m_3 y)^2}\right).$$

Let $\Gamma(t) = (x(t), y(t))$ be any nontrivial periodic orbit of system (25) with period $T > 0$. Next, following the proof of Theorem 2.1 in [38], we prove $\int_0^T tr(J)dt < 0$ and obtain the positive equilibrium (x^*, y^*) of system (7) is globally asymptotically stable.

As

$$\int_0^T \left[a - E_1 - bx - \frac{cy}{m_1 + m_2x + m_3y} \right] dt = \int_0^T \frac{x'(t)}{x(t)} dt = 0$$

and

$$\int_0^T \left[-d - E_2 - py + \frac{fx}{m_1 + m_2x + m_3y} \right] dt = \int_0^T \frac{y'(t)}{y(t)} dt = 0,$$

so we have

$$\int_0^T tr(J)dt = \int_0^T \left[-bx - py + \frac{(cm_2 - fm_3)xy}{(m_1 + m_2x + m_3y)^2} \right] dt. \tag{27}$$

Obviously, if $cm_2 \leq fm_3$, we have $tr(J) < 0$ for all $t \geq 0$. Therefore, $\int_0^T tr(J)dt < 0$. By Lemma 3.1 (P224) in [39], we can obtain that any non-trivial periodic orbit $\Gamma(t) = (x(t), y(t))$ with period $T(T > 0)$ is orbitally stable. However, it is impossible because the equilibrium (x^*, y^*) is inside the periodic orbit $\Gamma(t)$, $\Gamma(t)$ is orbitally stable, and (x^*, y^*) is locally asymptotically stable, there must exist an unstable periodic orbit between (x^*, y^*) and $\Gamma(t)$. This leads to a contradiction, and the assumption of nontrivial periodic orbit $\Gamma(t)$ is not true. Therefore, the system (25) does not have periodic orbits in R_+^2. In the system (25), (x^*, y^*) is locally asymptotically stable, equilibria $(0,0)$ and $\left(\frac{a-E_1}{b}, 0 \right)$ are all hyperbolic saddles, and there is not other attractors, then the other trajectories tend to (x^*, y^*). Therefore, (x^*, y^*) is globally asymptotically stable.

Theorem 5. *For $\tau = 0$, if system (7) satisfies conditions (10) and (13), then the positive equilibrium (x^*, y^*) of system (7) is globally asymptotically stable.*

Example 2 (Example 1 continued). *For system (14), the positive equilibrium $(1.2040, 0.2505)$ is globally asymptotically stable, which can be seen from Figure 1. Note that in Figure 1, four trajectories start from initial points $(0.5, 0.5)$, $(0.1, 0.1)$, $(1.5, 0.1)$, and $(1.5, 0.5)$, respectively, and all converge $(1.2040, 0.2505)$ as t tends to $+\infty$.*
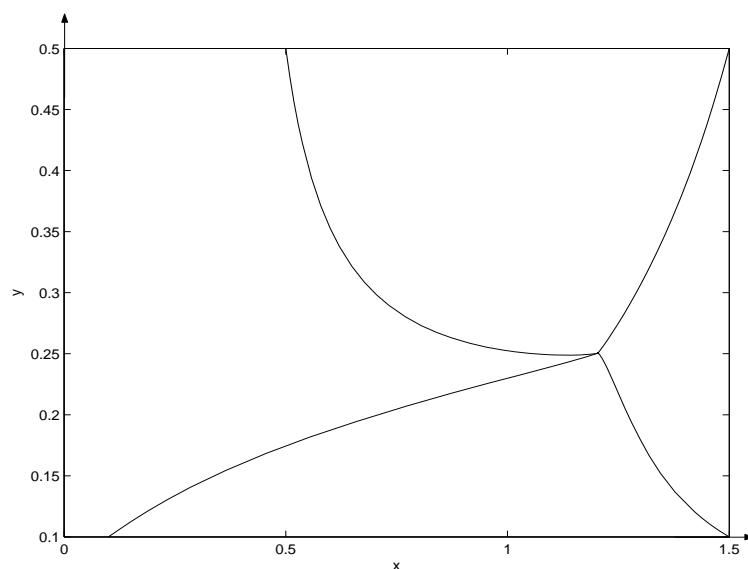

Figure 1. Four trajectories for system (14) when $\tau = 0$.

Remark 3. *Generally speaking, the exploited population should be mature population, which is more in line with the economic and biological views of renewable resource management. If*

$$(a - E_1)[f - (d + E_2)m_2] > bm_1(d + E_2), \quad x^* > \frac{a - E_1}{2b}, \quad cm_2 \le fm_3,$$

then the positive equilibrium (x^*, y^*) of system (7) is globally asymptotically stable for $\tau = 0$. From the perspective of eco-managers, in order to plan harvest strategies and maintain the sustainable development of the ecosystem, a positive equilibrium that is asymptotically stable may be required [28].

4.2. Global Asymptotic Stability of Positive Equilibrium for $\tau \ne 0$

In this subsection, we will study the global asymptotical stability of positive equilibrium (x^*, y^*) for system (7) by constructing Lyapunov function.

Let $x(t) = x^* + u(t), y(t) = y^* + v(t)$, linearized system of system (7) is

$$\begin{cases} u' = A_1 u(t) - A_2 v(t), \\ v' = A_3 u(t - \tau) - A_4 v(t) + A_5 v(t - \tau), \end{cases} \tag{28}$$

where

$$\begin{cases} A_1 = a - 2bx^* - \frac{cy^*(m_1 + m_3 y^*)}{(m_1 + m_2 x^* + m_3 y^*)^2} - E_1, \quad A_2 = \frac{cx^*(m_1 + m_2 x^*)}{(m_1 + m_2 x^* + m_3 y^*)^2}, \\ A_3 = \frac{fe^{-d_i \tau} y^*(m_1 + m_3 y^*)}{(m_1 + m_2 x^* + m_3 y^*)^2}, \quad A_4 = d + 2py^* + E_2, \quad A_5 = \frac{fe^{-d_i \tau} x^*(m_1 + m_2 x^*)}{(m_1 + m_2 x^* + m_3 y^*)^2}. \end{cases} \tag{29}$$

Rewrite the system (28) as follows:

$$\begin{cases} u' = A_1 u(t) - A_2 v(t), \\ v' = A_3 u(t) + (A_5 - A_4)v(t) - A_3 \int_{t-\tau}^t u'(s)ds - A_5 \int_{t-\tau}^t v'(s)ds. \end{cases} \tag{30}$$

In the following, we will construct a positive definite Lyapunov function $V(t)$ and prove that $V'(t) < 0$. Thus, if the global asymptotic stability of origin equilibrium $(0,0)$ for system (30) is obtained, we can have the global asymptotic stability of positive equilibrium (x^*, y^*) for system (7).

First, let $V_{11}(t) = v^2(t)$, then

$$V_{11}'(t) = 2v(t) \left[A_3 u(t) + (A_5 - A_4)v(t) - A_3 \int_{t-\tau}^t u'(s)ds - A_5 \int_{t-\tau}^t v'(s)ds \right]$$

$$= 2A_3 u(t)v(t) + 2(A_5 - A_4)v^2(t) - A_3 \int_{t-\tau}^t [2A_1 u(s)v(t) - 2A_2 v(s)v(t)]ds$$

$$- A_5 \int_{t-\tau}^t [2A_3 u(s - \tau)v(t) - 2A_4 v(s)v(t) + 2A_5 v(t)v(s - \tau)]ds.$$

By the inequality $2ab \le a^2 + b^2$, we have

$$V_{11}'(t) \le A_3(u^2(t) + v^2(t)) + (A_2 A_3 + A_4 A_5 + |A_1|A_3 + A_3 A_5 + A_5^2)v^2(t)\tau$$

$$+ 2(A_5 - A_4)v^2(t) + (A_2 A_3 + A_4 A_5) \int_{t-\tau}^t v^2(s)ds + |A_1|A_3 \int_{t-\tau}^t u^2(s)ds$$

$$+ A_3 A_5 \int_{t-\tau}^t u^2(s - \tau)ds + A_5^2 \int_{t-\tau}^t v^2(s - \tau)ds.$$

Second, let

$$V_{12}(t) = (A_2 A_3 + A_4 A_5) \int_{t-\tau}^t \int_z^t v^2(s)dsdz + |A_1|A_3 \int_{t-\tau}^t \int_z^t u^2(s)dsdz$$

$$+A_3A_5 \int_{t-\tau}^{t} \int_{z}^{t} u^2(s-\tau)dsdz + A_5^2 \int_{t-\tau}^{t} \int_{z}^{t} v^2(s-\tau)dsdz,$$

then

$$V_{12}'(t) = (A_2A_3 + A_4A_5)\left[\tau v^2(t) - \int_{t-\tau}^{t} v^2(s)ds\right] + |A_1|A_3\left[\tau u^2(t) - \int_{t-\tau}^{t} u^2(s)ds\right]$$

$$+A_3A_5\left[\tau u^2(t-\tau) - \int_{t-\tau}^{t} u^2(s-\tau)ds\right] + A_5^2\left[\tau u^2(t-\tau) - \int_{t-\tau}^{t} u^2(s-\tau)ds\right].$$

Therefore,

$$V_{11}'(t) + V_{12}'(t) \le 2A_3u(t)v(t) + (2A_2A_3 + 2A_4A_5 + A_5^2 + |A_1|A_3 + A_3A_5)\tau v^2(t)$$

$$+2(A_5 - A_4)v^2(t) + |A_1|A_3\tau u^2(t) + A_5^2\tau v^2(t-\tau) + A_3A_5\tau u^2(t-\tau).$$

Third, let

$$V_{13}(t) = A_5^2\tau \int_{t-\tau}^{t} v^2(s)ds + A_3A_5\tau \int_{t-\tau}^{t} u^2(s)ds,$$

then

$$V_{13}'(t) = A_5^2\tau[v^2(t) - v^2(t-\tau)] + A_3A_5\tau[u^2(t) - u^2(t-\tau)].$$

If $V_1(t) = V_{11}(t) + V_{12}(t) + V_{13}(t)$, we have

$$V_1'(t) \le v^2(t)\left[2(A_5 - A_4) + (2A_2A_3 + 2A_4A_5 + A_5^2 + |A_1|A_3 + A_3A_5)\tau\right]$$

$$+u^2(t)\tau(|A_1|A_3 + A_3A_5) + 2A_3u(t)v(t).$$

Assume $V_2(t) = u^2(t)$, then

$$V_2'(t) = 2A_1u^2(t) - 2A_2u(t)v(t).$$

Last, let $V(t) = V_1(t) + V_2(t)$, therefore,

$$V'(t) \le v^2(t)\left[2(A_5 - A_4) + (2A_2A_3 + 2A_4A_5 + A_5^2 + |A_1|A_3 + A_3A_5)\tau\right]$$

$$+2(A_3 - A_2)u(t)v(t) + u^2(t)[(2A_1 + (|A_1|A_3 + A_3A_5)\tau]$$

$$\le v^2(t)\left[2(A_5 - A_4) + |A_3 - A_2| + (2A_2A_3 + 2A_4A_5 + A_5^2 + |A_1|A_3 + A_3A_5)\tau\right]$$

$$+u^2(t)[(2A_1 + |A_3 - A_2| + (|A_1|A_3 + A_3A_5)\tau].$$

According to the definition of A_4 and A_5, we have $A_4 > A_5$. Obviously, if

$$\begin{cases} |A_3 - A_2| < \min\{-2A_1, 2(A_4 - A_5)\}, A_1 < 0 \\ \tau < \min\left\{\dfrac{2(A_4-A_5)-|A_3-A_2|}{2A_2A_3+2A_4A_5+2A_5^2+|A_1|A_3+A_3A_5}, \dfrac{-2A_1-|A_3-A_2|}{|A_1|A_3+A_3A_5}\right\} \end{cases} \quad (31)$$

holds, then $V'(t) < 0$. Through the above analysis, $V(t)$ is a positive definite function and $V'(t)$ is negative definite when the conditions (10) and (31) hold. Thus, $(0,0)$ of the system (30) is globally asymptotically stable. That is, the positive equilibrium (x^*, y^*) for system (7) is globally asymptotically stable. We can get the following theorem.

Theorem 6. *If the conditions (10) and (31) hold, the positive equilibrium (x^*, y^*) of system (7) is globally asymptotically stable for $\tau \ne 0$.*

Remark 4. *From the condition* (31)*, we obtain the interval* $[0, \tau^{**})$*, where*

$$\tau^{**} = \min\left\{ \frac{2(A_4 - A_5) - |A_3 - A_2|}{2A_2A_3 + 2A_4A_5 + 2A_5^2 + |A_1|A_3 + A_3A_5}, \frac{-2A_1 - |A_3 - A_2|}{|A_1|A_3 + A_3A_5} \right\};$$

from the condition (10) *and Remark* 2*, we have the interval* $[0, \tau^{*})$*. Therefore, when* $\tau <$ $\min\{\tau^{*}, \tau^{**}\}$*, Theorem* 6 *holds. This implies that the value of time delay determines the global asymptotic stability of the positive equilibrium.*

Example 3. *Let* $a = 1$, $b = 0.6$, $c = 0.15$, $d = 0.02$, $p = 0.9$, $f = 0.1$, $m_1 = 0.1$, $m_2 = 0.2$, $m_3 = 0.3$, $E_1 = 0.1$, $E_2 = 0.05$, $d_i = 0.01$*, and* $\tau = 0.2$*, the system* (7) *becomes*

$$\begin{cases} x'(t) = x\left(1 - 0.6x - \frac{0.15y}{0.1 + 0.2x + 0.3y}\right) - 0.1x, \\ y'(t) = -0.02y - 0.9y^2 + \frac{0.1e^{-0.002}x(t-0.2)y(t-0.2)}{0.1 + 0.2x(t-0.2) + 0.3y(t-0.2)} - 0.05y. \end{cases} \tag{32}$$

Clearly, $(a - E_1)(fe^{-d_i\tau} - (d + E_2)m_2) - b(d + E_2)m_1 = 0.073$ *and from the Equation* (29)*,* $A_1 = -0.7618$, $A_2 = 0.3755$, $A_3 = 0.023$, $A_4 = 0.5337$, $A_5 = 0.2498$, $-2A_1 = 1.5237$, $A_3 - A_2 = -0.3528$, $2(A_4 - A_5) = 0.5678$, $\frac{-2A_1 - |A_3 - A_2|}{|A_1|A_3 + A_3A_5} = 51.1008$, $\frac{2(A_4 - A_5) - |A_3 - A_2|}{2A_2A_3 + 2A_4A_5 + 2A_5^2 + |A_1|A_3 + A_3A_5}$ $= 0.4983$*. That is, conditions* (10) *and* (31) *hold. Due to Theorem* 6*, the positive equilibrium* $(1.3565, 0.2576)$ *of system* (32) *is globally asymptotically stable, which can also be seen from Figures* 2 *and* 3*. Note that in Figures* 2 *and* 3*, three trajectories start from initial points* $(1.6, 1.0)$*,* $(0.1, 0.1)$*, and* $(0.3, 0.3)$*, respectively, and all converge* $(1.3565, 0.2576)$ *as t tends to* $+\infty$*.*
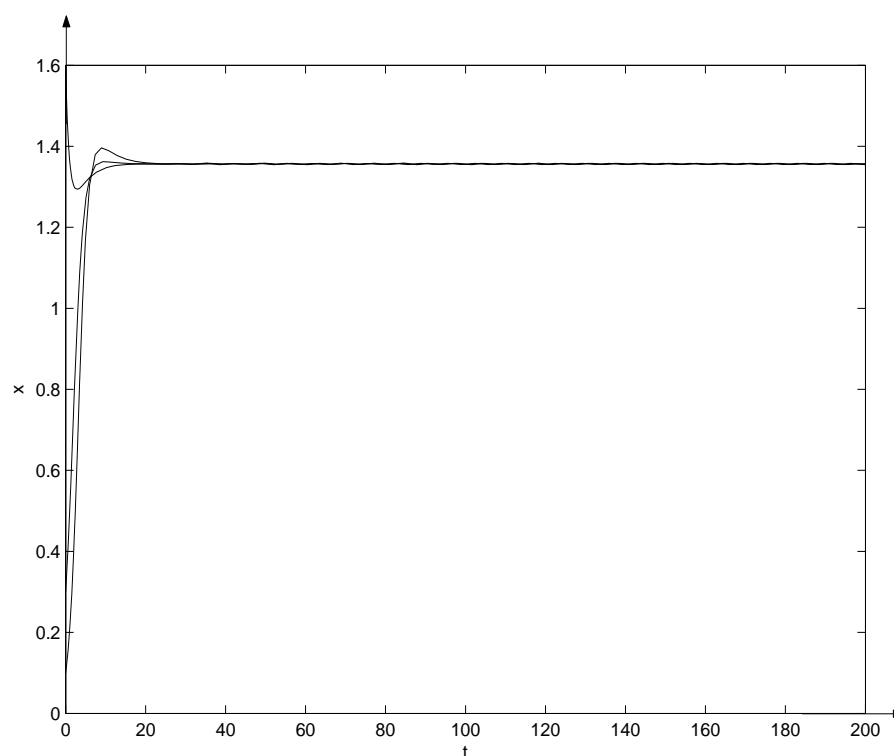

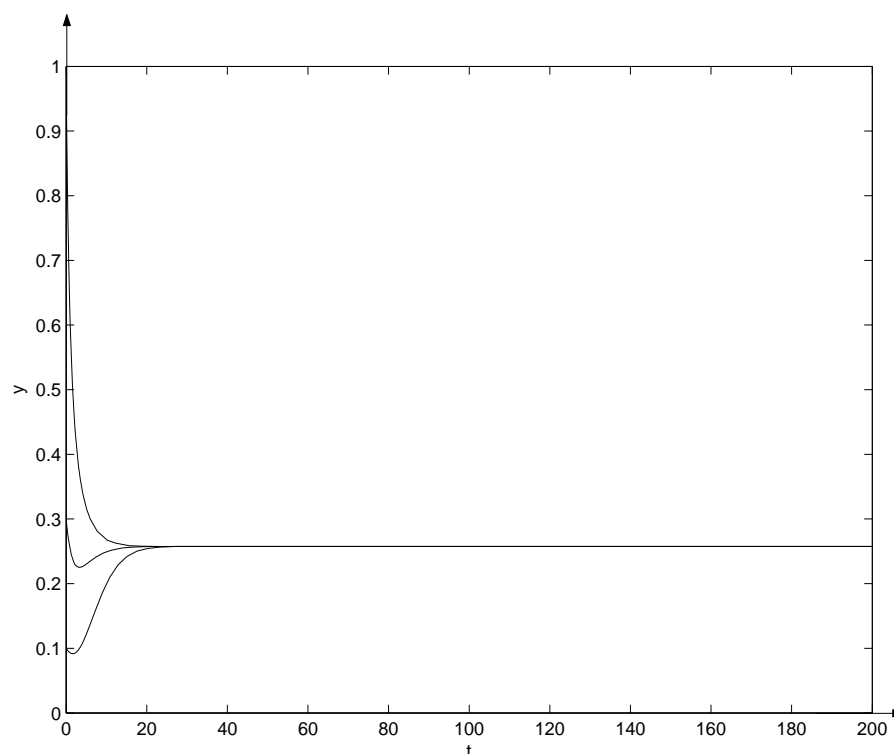**Figure 2.** Evolutions $x(t)$ of system (32).

Figure 3. Evolutions $y(t)$ of system (32).

5. Conclusions

In this paper, we investigate dynamics of a stage-structured density-dependent predator–prey system with Beddington–DeAngelis functional response and harvesting.

First, according to the sign for real part of eigenvalue, the local stability of the origin equilibrium $(0,0)$ and the boundary equilibrium $\left(\frac{a-E_1}{b},0\right)$ is determined.

In addition, we discuss local stability of positive equilibrium (x^*,y^*) for the case of $\tau = 0$ and $\tau \neq 0$, respectively. When $\tau = 0$, the positive equilibrium (x^*,y^*) of system (7) is locally asymptotically stable. However, when $\tau \neq 0$, the local stability of positive equilibrium (x^*,y^*) of the system (7) includes the following three cases:

(i) If (10), (13), and (18) hold, the positive equilibrium (x^*,y^*) of system (7) is locally asymptotically stable for any $\tau \geq 0$;

(ii) If (10) and (19) hold, when τ increases and passes τ_0, the stability of positive equilibrium (x^*,y^*) for system (7) switches from local asymptotical stability to instability and bifurcates into two periodic solutions with small amplitudes;

(iii) If (10) and (21) hold, there is a positive integer k such that the positive equilibrium (x^*,y^*) of system (7) has k switches from stability to instability to stability, which shows when the delay τ passes the critical value $\tau_j^+, j = 0,1,2,...,k-1$, the positive equilibrium (x^*,y^*) of system (7) loses its stability and Hopf bifurcation occurs.

Last, we consider the global asymptotical stability of the positive equilibrium (x^*,y^*) for system (7). When $\tau = 0$, stability theory of the periodic solution is used to prove that the positive equilibrium (x^*,y^*) is globally asymptotically stable by contradiction; when $\tau \neq 0$, by constructing Lyapunov functions we prove the positive equilibrium (x^*,y^*) for system (7) is globally asymptotically stable. Moreover, examples are given to illustrate the obtained results.

The predator–prey model studied in this paper, where not only the prey density dependence but also the predator density dependence are considered such that the system conforms to real biological environment. In Remarks 1, 2, and 4, we explain the effect of time delay on the stability of boundary equilibrium, the existence of the positive equilibrium, and the global asymptotic stability of the positive equilibrium, respectively. Moreover, we study the effect of harvesting on the global asymptotic stability of the posi-

tive equilibrium in Remark 3. Simultaneously, regarding the predator density-dependent mortality rate p, by Theorem 1 and the condition 10, the parameter p does not affect the stability of boundary equilibrium, the existence of the positive equilibrium, respectively. As $x^*, y^*, a_i(i = 1, 2, \cdots, 4), A_j(j = 1, 2, \cdots, 5)$ all contain parameter p, the predator density-dependent mortality rate p not only affects the local asymptotic stability of the positive equilibrium by Theorems 2 and 4, but also the global asymptotic stability of the positive equilibrium by Theorems 5 and 6. However, we cannot describe exactly how the predator density-dependent mortality rate affects the stability of the positive equilibrium. In our future work, we will further study the influence of parameter p on the predator–prey system.

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