THE DYNAMICAL CHARACTERISTIC OF A FUNCTIONAL RESPONSE MODEL WITH CONSTANT HARVEST

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Abstract. The predator-prey model with a functional response has very complicated dynamic properties. Especially, under some constant harvest, this model displays various complicated dynamic features, including changes of the positive equilibrium and stability, as well as emergence of bifurcations, periodic solutions and limit cycles. In this paper, we mainly study the effect of constant harvest on the dynamical characteristic for such model, obtain various conditions for it to have stable positive equilibria, bifurcation, periodic solutions and cycles respectively.

Key Words. Functional response model, Equilibrium, Bifurcation, Limit cycle.

1. Introduction

Many ecological populations can be expressed by some predator-prey model. The harvest on this resource may be considered as a control on this model. There is a great deal of interest in the study of the dynamic properties of such systems. Murry [1] proposed the following predator-prey model with a functional response

\begin{align*}
\dot{N} &= rN(1 - N/k) - aNP(1 - e^{-bN}) \\
\dot{P} &= -dP + cP(1 - e^{-bN})
\end{align*}

with \(N(0) > 0\) and \(P(0) > 0\). Here \(N(T), P(T)\) represent the population density of the predator and the prey respectively at time \(T\). We assume that the prey grow with carrying capacity \(k\) and intrinsic growth rate \(r\) in the absence of predation. The predator consumes the prey according to the Holling type II functional response. \(a, b, c,\) and \(d\) are positive parameters, and \(c > d\). System (1) is commonly practiced in invertebrate animals, for example, shrimp, crab and other halobios. It can represent many reproducible resources. Therefore, the study of such population dynamics with harvesting is a very interesting subject in mathematical bioecology.

In this paper, we will do a sequence of analysis of model (2):

\begin{align*}
\dot{N} &= rN(1 - N/k) - aNP(1 - e^{-bN}) - u \\
\dot{P} &= -dP + cP(1 - e^{-bN}) - v
\end{align*}

where \(u, v\) are positive parameters, while their biological implications are harvesting rates. In this framework, we demonstrate that system (2) can exhibit qualitatively different dynamical behaviors, including changes of the positive equilibrium and...
stability, as well as emergence of the static bifurcation and the Hopf bifurcation, or even periodic solutions and limit cycles.

This paper is organized as follows. The general analysis is conducted in Section 2. In section 3 we give the condition for such model to have limit cycles. In section 4, we choose \( h \) as the bifurcation parameter for system (2) and show that system (2) exhibits the Hopf bifurcation and possesses limit cycles. Finally, a numerical simulation is given to illustrate the obtained results.

2. Preliminaries

With the introduction of the following nondimensional variables and constants

\[
N = kx, \quad P = \frac{r}{a}y, \quad \tau = rt, \quad \alpha = \frac{c}{r}, \quad \beta = bk, \quad \delta = \frac{d}{r}, \quad w_1 = \frac{u}{rk}, \quad w_2 = \frac{a}{r^2}y
\]

system (2) can be transformed to a non-dimensional form

\[
\begin{align*}
\frac{dx}{d\tau} &= x(1 - x) - xy(1 - e^{-\beta x}) - w_1 \\
\frac{dy}{d\tau} &= -\delta y + \alpha y(1 - e^{-\beta x}) - w_2
\end{align*}
\]

where \( \alpha, \beta \) and \( \delta \) are positive parameters, and \( \alpha > \delta \). To be biologically meaningful, we are only interested in the dynamics of system (3) in the first quadrant. We will discuss system (3) under \( w_1 = h, w_2 = 0 \). If we fix the parameters \( \alpha, \beta \) and \( \delta \), then we can easily see that the number of equilibria of points

\[
R_0 \left( \frac{1}{2}(1 - \sqrt{1 - 4h}), 0 \right), \quad R_1 \left( \frac{1}{2}(1 + \sqrt{1 - 4h}), 0 \right), \quad \text{and a unique positive equilibrium point } R_2(x^*, y^*)
\]

where

\[
x^* = -\frac{1}{\beta} \ln \left( 1 - \frac{\delta}{\alpha} \right) \quad \text{and} \quad y^* = \frac{\alpha}{\delta} \left[ 1 + \frac{1}{\beta} \ln \left( 1 - \frac{\delta}{\alpha} \right) + \frac{\beta h}{\ln (1 - \delta/\alpha)} \right]
\]

Let

\[
h_0 = \left[ \frac{1}{\beta} \ln \left( 1 - \frac{\delta}{\alpha} \right) \right]^2 \frac{\delta + \beta(\alpha - \delta)}{\delta - (\alpha - \delta) \ln (1 - \delta/\alpha)}
\]

\[
h_1 = -\frac{1}{\beta} \ln \left( 1 - \frac{\delta}{\alpha} \right) \left[ 1 + \frac{1}{\beta} \ln \left( 1 - \frac{\delta}{\alpha} \right) \right]
\]

and

\[
h_2 = \frac{1}{4}
\]

Simple linear stability analysis of system (3) yields that \( R_0, R_1 \) are saddle points, while the stability of the positive equilibrium point \( R_2 \) depends on the determinant and trace of the variable matrix \( A \) of system (3) which are given by

\[
\det(A) = \alpha \beta x^* y^* e^{-\beta x^*}(1 - e^{-\beta x^*})
\]

\[
\text{trace}(A) = h/x^* - x^*(1 + \beta y^* e^{-\beta x^*})
\]

since \( \det(A) > 0 \) for all \( x > 0, y > 0, \) \( R_2 \) is locally stable if \( \text{trace}(A) < 0 \) and unstable if \( \text{trace}(A) > 0 \).

The above results are summarized below

1. If \( h < h_0 < h_1 < h_2 \) then the equilibrium point \( R_2 \) is globally asymptotically stable in the interior of the first quadrant.

2. If \( h_0 < h < h_1 \) then the equilibrium point \( R_2 \) is unstable.
3. Limit Cycle

Theorem 1. If \( h_0 < h < h_1 \), then there exists at least one limit cycle for system (3).

Proof. By using \( h_0 < h_1 \), we know that \( \beta + 2 \ln (1 - \delta/\alpha) > 0 \), that is, \( x^* = -\frac{1}{\beta} \ln (1 - \delta/\alpha) < \frac{1}{2} \). We construct a Poincare-Bendixson loop region (Fig. 1):

\[
\begin{align*}
OA &: x = 0 \\
AB &: y = m \quad (m > y^*) \\
BC &: y = kx + n, \quad n = m - kx^*, \quad k < 0 \\
CD &: x = (1 + \sqrt{1 - 4h})/2 \\
DO &: y = 0
\end{align*}
\]

(1). \( \vec{n}_{AB} = (0, 1) \) denotes the outward normal to AB. We have

\[
\vec{n}_{AB} \cdot (dx/dt, dy/dt) = dy/dt < 0
\]

for all points on the boundary. It means that the ‘velocity’ vector \((dx/dt, dy/dt)\) points inward.

(2). \( \vec{n}_{BC} = (-k, 1) \) is the outward normal to BC. We have

\[
\vec{n}_{BC} \cdot (dx/dt, dy/dt) = -k(x - x^2 - xy + xye^{-\beta x} - h) + (\alpha - \delta - \alpha e^{-\beta x})
\]

Because BC is above \( L_1 \), \( x - x^2 - xy + xye^{-\beta x} - h < 0 \). If \(|k|\) is sufficiently large, there is \( \vec{n}_{BC} \cdot (dx/dt, dy/dt) < 0 \). This indicates that the ‘velocity’ vector \((dx/dt, dy/dt)\) points inward.

(3). \( \vec{n}_{CD} = (1, 0) \) denotes the outward normal to CD. We have

\[
\vec{n}_{CD} \cdot (dx/dt, dy/dt) = dx/dt < 0
\]

for all points on CD. Intuitively this means that no solution trajectories can leave the domain if once inside, since, if they indeed reach the boundary, their ‘velocity’ points inwards and so the trajectories move back into the domain.

(4). OA and DO are the parts of orbits, so there are no solution trajectories through them.

OABCD is a simple closed boundary curve in the positive quadrant of the \((x, y)\) phase plane. The phase trajectories always point into the enclosed domain and there is an unstable equilibrium \( R_2 \) in this region. According to the well-known Poincare-Bendixson theorem, there exists not less than one limit cycles in the region. \( \square \)
4. Bifurcation and Period Solution

Theorem 2. \( h_1 \) and \( h_2 \) are two static bifurcation values of system (3).

Theorem 3. System (3) undergoes a Hopf bifurcation at the positive equilibrium \( R_2 \) if \( h_0 < h_1 \). Moreover, if the parameter \( h \) varies in a small neighborhood of \( h_0 \), there exists a periodic solution near \( h = h_0 \), whose period is approximately \( 2\pi/\omega \), where

\[
\omega = \sqrt{-\alpha(1-\delta/\alpha)\ln(1-\delta/\alpha)[1 + \ln(1-\delta/\alpha)]/\beta + \beta h_0/\ln(1-\delta/\alpha)}
\]

Proof. Let \( h = h_0 < h_1 \), system (3) has a positive equilibrium \( R_2 \). It is also easy to show that \( \text{trace}(A(x^*, y^*, h_0)) = 0 \) and \( \text{det}(A(x^*, y^*, h_0)) > 0 \). We assume that

\[
A(x^*, y^*, h) = A(x^*, y^*, h_0) + (h - h_0)B(x^*, y^*, h)
\]

then

\[
\text{tr}B(x^*, y^*, h_0) = \lim_{h \to h_0} \text{tr}B(x^*, y^*, h) = \lim_{h \to h_0} \frac{(\text{tr}A(x^*, y^*, h) - A(x^*, y^*, h_0))/(h - h_0)}{h_0} = \frac{1/x^* + \alpha \beta e^{-\beta x^*}/\delta}{\beta(\alpha/\delta - 1 - 1/\ln(1-\delta/\alpha))}
\]

\[
> 0
\]

According to the theorems in [9], system (3) has a periodic solution near the positive equilibrium \( R_2 \) if \( h \) varies in a small neighborhood of \( h_0 \). Its period is about \( 2\pi/\omega \).

\[
\lambda = \frac{\pm \sqrt{-\alpha(1-\delta/\alpha)\ln(1-\delta/\alpha)[1 + \ln(1-\delta/\alpha)]/\beta + \beta h_0/\ln(1-\delta/\alpha)}}{\pi}
\]

so

\[
\omega = \sqrt{-\alpha(1-\delta/\alpha)\ln(1-\delta/\alpha)[1 + \ln(1-\delta/\alpha)]/\beta + \beta h_0/\ln(1-\delta/\alpha)}
\]

This completes the proof. \( \square \)

In the following theorem, we will show that the system can possess stable limit cycles in another way.

For the sake of convenience, we do transformation of variables in the following way,

\[
x = \xi + x^*, \quad y = \eta + y^*
\]

where

\[
x^* = -(1/\beta)\ln(1-\delta/\alpha), \quad y^* = (\alpha/\delta)[1 + (1/\beta)\ln(1-\delta/\alpha) + \beta h/\ln(1-\delta/\alpha)]
\]

then we can transform system (3) into the system

\[
\dot{\xi} = a_{11} \xi + a_{12} \eta + a_{13} \xi \eta + a_{14} \xi^2 + a_{15} \xi^2 \eta + a_{16} \xi^3 + \cdots
\]

\[
\dot{\eta} = a_{21} \xi + a_{22} \eta + a_{23} \xi \eta + a_{24} \xi^2 + a_{25} \xi^2 \eta + a_{26} \xi^3 + \cdots
\]

where

\[
a_{11} = 1 - 2x^* - y^*((1 + x^* \beta e^{-\beta x^*} - e^{-\beta x^*})), \quad a_{12} = -x^*(1 - e^{-\beta x^*})
\]

\[
a_{13} = -1 + (1 - \beta x^*)e^{-\beta x^*}, \quad a_{14} = -1 - (1 - \beta x^*/2)\beta y^* e^{-\beta x^*}
\]

\[
a_{15} = -(-1 + \beta x^*/2)\beta e^{-\beta x^*}, \quad a_{16} = (1 - \beta x^*/3)\beta^2 y^* e^{-\beta x^*}/2
\]

\[
a_{21} = \alpha \beta y^* e^{-\beta x^*}, \quad a_{22} = 0
\]

\[
a_{23} = \alpha \beta e^{-\beta x^*}, \quad a_{24} = -\alpha \beta^2 y^* e^{-\beta x^*}/2
\]

\[
a_{25} = -\alpha \beta^2 e^{-\beta x^*}/2, \quad a_{26} = \alpha \beta^2 y^* e^{-\beta x^*}/6
\]
It is observed that system (4) has equilibrium point \((0, 0)\), and the eigenvalue of the variable matrix of system (4) is \(\lambda_{1,2}(h_0) = \pm \omega\) if \(h = h_0\), where

\[
\omega = \sqrt{-\alpha(1 - \delta/\alpha)\ln(1 - \delta/\alpha)[1 + \ln(1 - \delta/\alpha)/\beta + \beta h_0/\ln(1 - \delta/\alpha)]}
\]

Changing variables again via \(\begin{pmatrix} \xi \\ \eta \end{pmatrix} = P \begin{pmatrix} u \\ v \end{pmatrix}\)

where

\[
P = \begin{pmatrix} 1 & 0 \\ 0 & \alpha \omega/\delta x^* \end{pmatrix}
\]

system (4) is converted accordingly to the following form

\[
(5) \quad \dot{u} = b_{11} u + b_{12} v + b_{13} uv + b_{14} u^2 + b_{15} u^2 v + b_{16} u^3 + \cdots = -\omega v + f(u, v)
\]

\[
\dot{v} = b_{21} u + b_{22} v + b_{23} uv + b_{24} u^2 + b_{25} u^2 v + b_{26} u^3 + \cdots = \omega u + g(u, v)
\]

where

\[
\begin{align*}
b_{11} &= 0, \\
b_{12} &= -\omega/x^* - \alpha \beta \omega e^{-\beta x^*/\delta}, \\
b_{13} &= -\omega/\beta x^* - (1 + \beta x^*/2)/\delta x^*, \\
b_{14} &= -1 - (1 + \beta x^*/2) \beta y^* e^{-\beta x^*}/2, \\
b_{15} &= (1 - \beta x^*/3) \beta^2 y^* e^{-2\beta x^*}/2, \\
b_{21} &= \omega, \\
b_{22} &= 0, \\
b_{23} &= \alpha \beta \omega e^{-\beta x^*}, \\
b_{24} &= -\beta \omega/2, \\
b_{25} &= -\alpha \beta^2 e^{-\beta x^*}/2, \\
b_{26} &= \beta^2 \omega/6
\end{align*}
\]

**Theorem 4.** Let \(c_0 + c_1 y^* < 2\). Then system (4) has not less than one limit cycles near \(R_2\) if \(h_0 < h_1, h > h_0\) and that \((h - h_0) > 0\) is sufficiently small. Moreover, if \(h\) is close enough to \(h_0\), then they will reach \(R_2\), where

\[
c_0 = -1/\ln(1 - \delta/\alpha) + \alpha/\delta - 3\beta(\alpha - \delta)
\]

\[
c_1 = -\beta(1 - \delta/\alpha)[1/\ln(1 - \delta/\alpha) + (1 - \alpha/\delta)\ln(1 - \delta/\alpha)/2 + (1 - \alpha/\delta)]
\]

\[
y^* = (\alpha/\delta)[1 + (1/\beta)\ln(1 - \delta/\alpha) + \beta h_0/\ln(1 - \delta/\alpha)]
\]

**Proof.** Firstly, we will show that \(R_2\) is a weak focus of system (4). Let \(t/T = \tau/2\pi\), where

\[
T = 2\pi(1 + \mu_2 \epsilon^2 + \mu_3 \epsilon^3 + \cdots)/\omega
\]

It is the time when the solution of the following equations rotates around a cycle and returns to the \(u\) axis.

\[
(6) \quad u(\tau) = u_1(\tau)c + u_2(\tau)c^2 + \cdots
\]

\[
v(\tau) = v_1(\tau)c + v_2(\tau)c^2 + \cdots
\]

where \(u(0) = c, v(0) = 0, \mu_2, \mu_3, \cdots\) are constants. Then system (5) is transformed into

\[
(7) \quad \begin{align*}
\frac{du}{d\tau} &= (-v + b_{13} uv + b_{14} u^2 + b_{15} u^2 v + b_{16} u^3 + \cdots)(1 + \mu_2 \epsilon^2 + \mu_3 \epsilon^3 + \cdots) \\
\frac{dv}{d\tau} &= (u + b_{23} uv + b_{24} u^2 + b_{25} u^2 v + b_{26} u^3 + \cdots)(1 + \mu_2 \epsilon^2 + \mu_3 \epsilon^3 + \cdots)
\end{align*}
\]

where

\[
u_1(0) = 1, u_2(0) = u_3(0) = \cdots = v_1(0) = v_2(0) = \cdots = 0
\]
From (6) and above equations, we obtain the following equations

\[
(I) \left\{ \begin{aligned}
\frac{du_1}{d\tau} &= -v_1 \\
\frac{dv_1}{d\tau} &= u_1
\end{aligned} \right.
\]

\[
(II) \left\{ \begin{aligned}
\frac{du_2}{d\tau} &= -v_2 + (b_{13}/\omega) \sin \tau \cos \tau + (b_{14}/\omega) \cos^2 \tau = -v_2 + P_2 \\
\frac{dv_2}{d\tau} &= u_2 + (b_{23}/\omega) \sin \tau \cos \tau + (b_{24}/\omega) \cos^2 \tau = u_2 + Q_2
\end{aligned} \right.
\]

\[
(III) \left\{ \begin{aligned}
\frac{du_3}{d\tau} &= -v_3 - \mu_2 v_1 + (2b_{14}/\omega) u_1 u_2 + (b_{13}/\omega)(u_1 v_2 + u_2 v_1) \\
&\quad + (b_{15}/\omega) u_1^3 v_1 + (b_{16}/\omega) u_1^3 = -v_3 - \mu_2 v_1 + P_3 \\
\frac{dv_3}{d\tau} &= u_3 + \mu_2 u_1 + (2b_{24}/\omega) u_1 u_2 + (b_{23}/\omega)(u_1 v_2 + u_2 v_1) \\
&\quad + (b_{25}/\omega) u_1^3 v_1 + (b_{26}/\omega) u_1^3 = u_3 + \mu_2 u_1 + Q_3
\end{aligned} \right.
\]

By using \( u_1(0) = 1, v_1(0) = 0 \) for (I), we have the following equation

\[
u_1(\tau) = \cos \tau, \quad v_1(\tau) = \sin \tau
\]

It’s obvious that \( u_1 \) and \( v_1 \) are functions with period \( 2\pi \). Furthermore, \( u_2 \) and \( v_2 \) are also functions with period \( 2\pi \) because

\[
\int_0^{2\pi} (P_2 \cos \tau + Q_2 \sin \tau) d\tau = 0
\]

where

\[
\begin{pmatrix}
  u_2 \\
  v_2
\end{pmatrix} = \begin{pmatrix}
  \frac{b_{13}-b_{24}}{3\omega} \sin^2 \tau - \frac{b_{13}+b_{24}}{3\omega} \cos^2 \tau + \frac{2b_{14}+b_{23}}{3\omega} \sin \tau \cos \tau + \frac{b_{14}-b_{23}}{3\omega} \sin \tau \\
  \frac{2b_{14}+b_{23}}{3\omega} \sin^2 \tau + \frac{b_{14}-b_{23}}{3\omega} \cos \tau + \frac{b_{14}-b_{23}}{3\omega} \sin \tau \cos \tau - \frac{b_{14}+b_{23}}{3\omega} \sin \tau
\end{pmatrix}
\]

By simple computation, we obtain that

\[
I_3 = \int_0^{2\pi} (P_3 \cos \tau + Q_3 \sin \tau) d\tau
\]

\[
= \int_0^{2\pi} \left[ \left( \frac{2b_{13}b_{14} + b_{23}b_{24}}{\omega^2} + \frac{b_{25}}{\omega} \right) \cos^2 \tau \\
+ \left( -\frac{7b_{13}b_{14} + 2b_{14}b_{24} + 5b_{23}b_{24}}{3\omega^2} + \frac{b_{16} + b_{25}}{\omega} \right) \cos \tau \right] d\tau
\]

\[
= \frac{1}{4\omega^2} (b_{13}b_{14} - 2b_{14}b_{24} - b_{23}b_{24} + 3b_{16} + 7b_{25})
\]

If follows from \( c_0 + c_1 y^* < 2 \) that \( b_{13}b_{14} - 2b_{14}b_{24} - b_{23}b_{24} + 3b_{16} + 7b_{25} < 0 \), namely, \( I_3 < 0 \). The above indicates that \((0, 0)\) is a weak focus, that is, \( R_2 (x^*, y^*, h_0) \) is a weak focus. Applying some theorems in [8, 9], we obtain that system (4) has a stable limit cycle nearly \((0, 0)\) if \((h - h_0) > 0\) is sufficiently small. This completes the proof. \(\square\)

5. Numerical Simulation

In this section, as an example we consider system (3) with fixed \( \alpha \), \( \beta \) and \( \delta \), that is, we consider the following model

\[
\begin{aligned}
\dot{x} &= x(1-x) - xy(1 - e^{-100x}) - h \\
\dot{y} &= -38y + 40y(1 - e^{-100x})
\end{aligned}
\]

By simple computation, we obtain that

\[
h_0 \approx 4.75 \times 10^{-3}, \quad h_1 = 0.0291, \quad h_2 = 0.25
\]

\[
R_0((1-\sqrt{1-4h})/2, 0), \quad R_1((1+\sqrt{1-4h})/2, 0), \quad R_2(3/100, (20/19)(97/100-100h/3))
\]
According to theorem 3, the system undergoes a Hopf bifurcation if the parameter $h$ varies in a small neighborhood of $h_0$ and has a periodic orbit of period $20\sqrt{11/5358}\pi$ around $R_2$. From Fig. 2, we can see that $x$, $y$ population do oscillate periodically around $R_2$. Furthermore, there exist limit cycles near $R_2$ as shown in Fig.3.

6. Conclusions

In this paper, we have studied the effect of constant harvest on the dynamical characteristics of the predator-prey model with a functional response. For $h$ is in a certain range, limit cycles will emerge in some enclosed domain. This model
system admits limit cycles, exhibits bifurcations properties as certain parameters vary. On crossing the bifurcation value the steady state becomes unstable and a periodic limit cycle solution appears: that is a uniform steady state bifurcations to an oscillatory solution.

Acknowledgments

The author thanks the anonymous authors whose work largely constitutes this paper. This research was supported by the National Natural Science Foundation of China.

References


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