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Numerical Bifurcation And Stability Analysis Of An Predator-prey System With Generalized Holling Type III Functional Response

Z. Lajmiri, R. K. Ghaziani, M. Ghasemi

abstract: We perform a bifurcation analysis of a predator-prey model with Holling functional response. The analysis is carried out both analytically and numerically. We use dynamical toolbox MATCONT to perform numerical bifurcation analysis. Our bifurcation analysis of the model indicates that it exhibits numerous types of bifurcation phenomena, including fold, subcritical Hopf, cusp, Bogdanov-Takens. By starting from a Hopf bifurcation point, we approximate limit cycles which are obtained, step by step, using numerical continuation method and compute orbitally asymptotically stable periodic orbits.

Key Words: Hopf bifurcation, fold bifurcation, continuation method, Limit cycle.

Contents

1. Introduction

The dynamical relationship between predators and their preys is one of the dominant subjects in ecology and mathematical ecology due to its universal importance, see [3]. Mathematical modelling is an important and very useful tool in this field to get insight the dynamical behaviour of predator-prey systems. The key element in predator-prey interaction is "predator functional response on prey population", which is a function describing the number of prey consumed per predator per unit time for given quantities of prey and predator population. When there is no predator, the logistic equation models the behavior of the preys. For interactions between preys and predators, we use the generalized Holling response function of type III. These models with Holling functional response are further

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studied by many authors, see [10], [14], [15]. This response function which models the consumption of preys by predators is such that the predation rate of predators increases when the preys are few and decreases when they reach their satiety.
The main aim of this paper is to study the pattern of bifurcation that takes place as we vary some of the model parameters. We specially focus on the biological implications of the found bifurcations. Most importantly we show that the Hopf bifurcation plays, for various reasons, a crucial role. Ecological systems are complex because of the diversity of biological species as well as the complex nature of their interactions. In this work we will use the term complexity to describe the ecological complexity found in nature as well as the of dynamical complexity of the models. Although, only chaotic dynamics are called complex, we can say that periodic behavior is more complex than stationary behavior. Quasiperiodic behavior is more complex than periodic behavior but is less complex than chaotic behavior. It is interesting to note that the instability of steady-state for temporal models of predator-prey interaction leads to either oscillatory coexistence state or extinction of one or both the species [4], [6], [16]. This is actually done by studying the change in the eigenvalue of the Jacobian matrix and also following the continuation algorithm.
Numerical bifurcation analysis techniques are very powerful and efficient in physics, biology, engineering, and economics. The characteristics of Hopf point, the limit cycle and the general bifurcation may be explored using the software package MATCONT [5]. This package is a collection of numerical algorithms [1], implemented as a MATLAB toolbox for the detection, continuation and identification of limit cycles. In this package we use prediction-correction continuation algorithm based on the Moore-Penrose matrix pseudo inverse for computing the curves of equilibria, limit point (LP), along with fold bifurcation points of limit point (LP) and continuation of Hopf point (H), etc. In thise paper we rely heavily on advanced numerical methods, namely numerical continuation to obtain results that cannot be obtained analytically.

The paper is organized as follows: In Section 2, we introduce the model and discuss the stability and bifurcations of its equilibrium points. In Section 3, we numerically compute curves of codim-1 bifurcations and the critical normal form coefficients of codim-2 bifurcation points, using the MATLAB toolbox MTATCONT. In Section 4, we summarize our results.

2. The mathematical model and its stability analysis

Recently, the Leslie predator-prey model has received some interest, see [2], [7], [9], [12], [18]. We take the general form of Leslie predator-prey model as

$$\begin{cases} \dfrac{dx}{dt} = xg(x) - yp(x), \\ \dfrac{dy}{dt} = y\left[s(1-\dfrac{y}{K(x)})\right], \\ x(0)>0, \quad y(0)>0. \end{cases} \tag{2.1}$$

Table 1: summary of parameters used in Leslie model with generalized Holling type III functional response and their descriptions.

parameter	notation
x	prey density
y	predator density
K	environmental carrying capacity
r	logistic growth rate of prey
h	coefficient of competition for resources other than prey
s	growth rate of predator
a	attack coefficient
m	mutual interference constant
p	predator functional response

In this paper, we consider system (2.1) with response function of $p(x) = \dfrac{mx^2}{ax^2+bx+1}$ and functions, $g(x,K) = r(1-\dfrac{x}{K})$, $q(\dfrac{y}{x}) = s(1-\dfrac{y}{hx})$. Then the sysyem takes the following form:

$$\begin{cases} \dot{x} = rx(1-\dfrac{x}{K}) - \dfrac{x^2y}{ax^2+bx+1}, \\ \dot{y} = sy(1-\dfrac{y}{hx}). \end{cases} \tag{2.2}$$

where the parameters r, K, m, a, s and h are all positive constants, and b is negative and $b > -2\sqrt{a}$. Before going into details, we make the following rescaling:

$$\overline{x} = \frac{x}{K},\ \overline{y} = \frac{mKy}{r},\ \overline{a} = aK^2,$$
$$\overline{b} = bK,\ \delta = \frac{s}{r},\ \beta = \frac{s}{mhK^2},$$

$$\begin{cases} \dot{x} = x(1-x) - \dfrac{x^2y}{ax^2+bx+1}, \\ \dot{y} = y(\delta - \dfrac{\beta y}{x}). \end{cases} \tag{2.3}$$

This system first was studied in [11], in which some local bifurcations were studied analytically.
We further study this system to reveal more dynamical behaviors by employing numerical continuation method. System (2.3) has Three positive equilibrium $E_1 = (1-\delta, \dfrac{\delta}{\beta}(1-\delta))$, $E_2 = (\dfrac{3}{1-b}, \dfrac{\delta}{\beta}\dfrac{3}{1-b})$, $E_3 = (\dfrac{\beta\delta}{\beta\delta+(1-\delta)^2}, \dfrac{\delta^2}{\beta\delta+(1-\delta)^2})$, together with the following condition: $b > -2\sqrt{a}$ and $0 < \delta < 1$, [11], [15] .

From the biological point of view, we focus on the dynamics of the stationary state E_2 corresponding to the coexistence of prey and predator. Linearizing the model (2.3) about the equilibrium point $E_3 = (x_3, y_3)$ we have the Jacobian matrix J as

$$\mathbf{J(E_3)} = \begin{pmatrix} 1 - 2x_3 - \dfrac{(bx_3^2 + 2x_3)y_3}{(ax_3^2 + bx_3 + 1)^2} & \dfrac{-x_3^2}{(ax_3^2 + bx_3 + 1)} \\ \dfrac{\beta y_3^2}{x_3^2} & -\delta \end{pmatrix}$$

Theorem 2.1. *Define* $\delta^* = 1 - 2x_3 - \dfrac{(bx_3^2 + 2x_3)y_3}{(ax_3^2 + bx_3 + 1)^2}$ *then the following statements hold:*
(a) If $\delta < \delta^*$, the positive equilibrium E_3 is locally asymptotically stable.
(b) If $\delta > \delta^*$, the positive equilibrium E_3 is unstable.
(c) If $\delta = \delta^*$, then a Hopf bifurcation occurs around the positive equilibrium E_3.

Proof. The characteristic equation is given by

$$\lambda^2 - \lambda tr(J_E) + det(J_E) = 0,$$

with

$$Det(J_{E_3}) = -\delta\left(1 - 2x_3 - \frac{(bx_3^2 + 2x_3)y_3}{(ax_3^2 + bx_3 + 1)^2}\right) + \frac{\beta y_3^2}{(ax_3^2 + bx_3 + 1)},$$

and

$$Tr(J_{E_3}) = \left(1 - 2x_3 - \frac{(bx_3^2 + 2x_3)y_3}{(ax_3^2 + bx_3 + 1)^2}\right) - \delta.$$

Then the solutions of the characteristic yields the dispersion relation as

$$\lambda = \frac{1}{2}tr(J_E) \pm \sqrt{(tr(J_E))^2 - 4det(J_E)}.$$

By analyzing the distribution of roots of characteristic equation, we obtain the following results. see that $det(J) > 0$ and therefore (x_3, y_3) is locally asymptotically stable if $tr(J) < 0$, that is, if

$$\delta > 1 - 2x_3 - \frac{(bx_3^2 + 2x_3)y_3}{(ax_3^2 + bx_3 + 1)^2},$$

and unstable if $tr(J) > 0$,

$$\delta < 1 - 2x_3 - \frac{(bx_3^2 + 2x_3)y_3}{(ax_3^2 + bx_3 + 1)^2}.$$

By defining $\delta^* = 1 - 2x_3 - \dfrac{(bx_3^2 + 2x_3)y_3}{(ax_3^2 + bx_3 + 1)^2}$ when $\delta = \delta^*$, $tr(J_{E_3}) = 0$ and the characteristic equation has a pair of imaginary eigenvalues $\lambda = \pm i\sqrt{det(J_{E_3})}$. Let $\lambda(\delta) = p(\delta) \pm iq(\delta)$ be the roots characteristic equation when δ is near δ^*, then $p(\delta) = \dfrac{1}{2}tr(J_{E_3})$ and

$$\frac{dp}{d\delta} = \frac{d}{d\delta}Re(\lambda(\delta))|_{\delta=\delta^*} = -1 < 0.$$

holds when $0 < \delta < 1$ and $b > -2\sqrt{a}$. From the Poincare-Andronov-Hopf bifurcation theorem (See [17], [19], [13]), the system (2.3) undergoes a Hopf bifurcation at (δ^*, E_3) when $\delta = \delta^*$.

As a numerical illustration, we consider the parameter values $a = 10, b = -5.5, \beta = 0.333333$ then the equilibrium $E_3 = (x_3, y_3) = (0.4, 0.6)$ lies in the feasible region given by $0 < \delta < 1$ and $\delta = 0.7$. Here, from the definition of δ, we see that $\delta^* = 0.5$ and hence $\delta > \delta^*$. For these parameters, the equilibrium point E_3 of the temporal model (2.3) is asymptotically stable. Graphical presentation is given in the left panel of Figs. 1,3. On the other hand, for $\delta = 0.4999 < \delta^*$, the equilibrium point E_3, loses its stability via a Hopf point and becomes unstable. Right panel of Fig. 1. describes a phenomenon of Hopf bifurcation surrounding the equilibrium state $E_3 = (0.4, 0.6)$.

In this section, we analyze the local stability for the positive equilibrium $E_1 = (1-\delta, \dfrac{\delta}{\beta}(1-\delta))$ of system (2.3).The Jacobian matrix of system (2.3) at E_1:

$$\mathbf{J(E_1)} = \begin{pmatrix} 2\delta - 1 - \dfrac{\delta[b(1-\delta)^3 + 2(1-\delta)^2]}{\beta[a(1-\delta)^2 + b(1-\delta) + 1]^2} & \dfrac{-(1-\delta)^2}{a(1-\delta)^2 + b(1-\delta) + 1} \\ \dfrac{\delta^2}{\beta} & -\delta \end{pmatrix}$$

It is easy to see that the determinant of J_{E_1} is

$d = [a(1-\delta)^2 + b(1-\delta) + 1]$,

$$det(J_{E_1}) = 2\delta - 1 - \frac{\delta[b(1-\delta)^3 + 2(1-\delta)^2]}{\beta d^2} + \frac{\delta^2(1-\delta)^2}{\beta d} > 0.$$

The trace of J_{E_1} is

$$tr(J_{E_1}) = \delta - 1 - \frac{\delta[b(1-\delta)^3 + 2(1-\delta)^2]}{\beta d^2} < 0.$$

If condition $tr(J_{E_1}) < 0$ holds, then the positive equilibrium E_1 of system (2.3) is a locally asymptotically stable node or focus; if condition $tr(J_{E_1}) > 0$ holds, and the positive equilibrium E_1 of system (2.3) is an unstable node or a focus. Hence, we have the following results.

Lemma 2.2. *Let the following mutually exclusive conditions hold:*
(a) $\beta(2\delta - 1)d^2 + \delta^2(1-\delta)^2 d > \delta[b(1-\delta)^3 + 2(1-\delta)^2]$,
(b) $\beta(\delta - 1)d^2 < \delta[b(1-\delta)^3 + 2(1-\delta)^2]$,

then the positive equilibrium $E_1(x_1, y_1)$ of system (2.3) is locally asymptotical stable, Figs.5,6.

Lemma 2.3. *Let us assume the following mutually exclusive conditions hold:*
(a) $\beta(2\delta - 1)d^2 + \delta^2(1-\delta)^2 d > \delta[b(1-\delta)^3 + 2(1-\delta)^2]$,
(b) $\beta(\delta - 1)d^2 > \delta[b(1-\delta)^3 + 2(1-\delta)^2]$,

then the positive equilibrium E_1 is an unstable focus Figs.5,6.

3. Numerical results

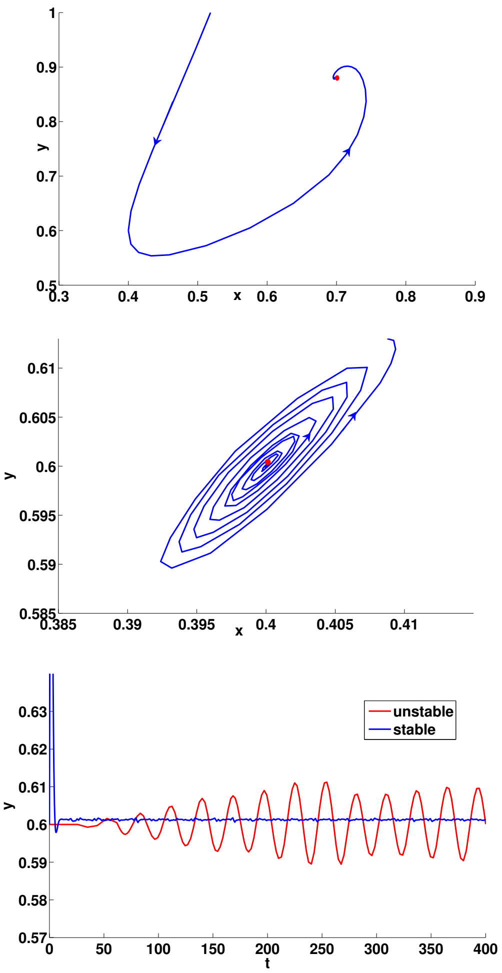
3.1. Continuation Curve of Equilibrium Points

The main aim of this section is to study the pattern of bifurcation that takes place as we vary the parameters δ, a and β. This is actually done by studying the change in the eigenvalue of the Jacobian matrix and also following the continuation algorithm. To start with, we consider a set of fixed point initial solution, $(x, y) = (0.39, 0.58)$, corresponding to a parameter set of values, $a = 10, b = -5.5, \beta = 0.333333, \delta = 0.5$. The characteristics of Hopf point, the limit cycle and the general bifurcation may be explored. To compute curve of equilibrium from the equilibrium point we take δ as the free parameter with fixed $a = 10, b = -5.5$ and $\beta = 0.333333$. From Fig.1, 2, it is evident that the system has a Hopf point (H) and two limit point (LP) at:

label = LP, x = (0.499996 0.749994 0.499999)
a=1.870593e+004
label = H , x = (0.499999 0.749999 0.499999)
Neutral saddle
label = LP, x = (0.430074 0.641692 0.497349)
a=-3.746749e+000
label = H , x = (0.400001 0.600001 0.499999)
First Lyapunov coefficient = 6.765879e+000

Table 2: One-parameter bifurcation points and eigenvalues.

lable	Eigenvalues
H_1	$\lambda_{1,2} = 1.08838e - 006 \pm i0.223604$
H_2	$\lambda_{1,2} = -3.59094e - 007 \pm i0.000589961$
LP_1	$\lambda_1 = -3.98652e - 005, \lambda_2 = 0.0726198$
LP_2	$\lambda_1 = -0.000824155, \lambda_2 = 0.00082704$



a

b

c

Figure 1: (a) The equilibrium $E_3 = (0.4, 0.6)$ is asymptotically stable for system (2.2) with $\delta = 0.7$, (b) , (c) bifurcating periodic solution for system (2.3) with $\delta = 0.4999$.

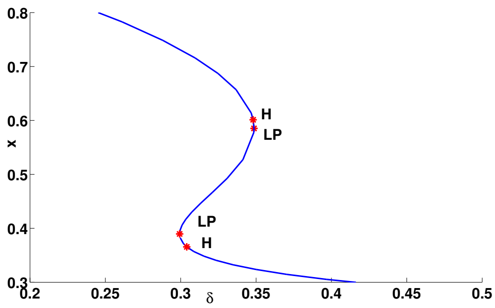


Figure 2: Bifurcation diagram of the equilibrium with the parameter δ undergoing a subcritical Hopf bifurcation for $\delta = 0.5$.

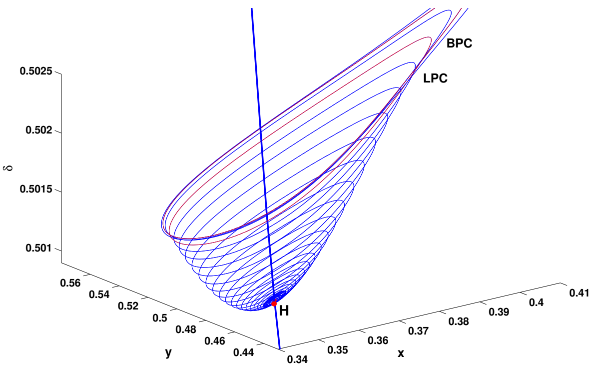
3.2. Cycle continuation starting from the Hopf-point

By selecting Hopf point in the one-parameter bifurcation diagram of the equilibrium as initial point, we can plot the limit cycle curve.

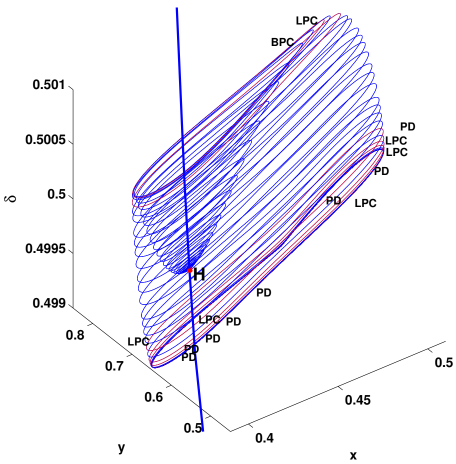
Limit point cycle (period = 1.122165e+002, parameter = 4.993620e-001)
Normal form coefficient = 2.376815e-002
Limit point cycle (period = 3.139456e+002, parameter = 4.993627e-001)
Normal form coefficient = -2.139121e-001
Limit point cycle (period = 4.570701e+002, parameter = 4.993627e-001)
Normal form coefficient = 4.031439e-001
Branch Point cycle(period = 2.809921e+001, parameter = 4.999995e-001)
Period Doubling (period = 2.594722e+002, parameter = 4.993627e-001)
Normal form coefficient = 1.255889e-011
Period Doubling (period = 3.690041e+002, parameter = 4.993627e-001)
Normal form coefficient = 6.370928e-011
Period Doubling (period = 4.298500e+002, parameter = 4.993627e-001)
Normal form coefficient = -1.697503e-011

Table 3: Bifurcations of limit cycles and eigenvalues, the family of limit cycles bifurcating from the Hopf point.

lable	Eigenvalues
LPC_1	$\mu_{1,2} = 1.00002 \pm i0.991333$
LPC_2	$\mu_{1,2} = 1 \pm i2.268191e-007$
LPC_3	$\mu_{1,2} = 1 \pm i0.019695$
BP	$\mu_{1,2} = 1 \pm i3.86191e-005$
PD_1	$\mu_1 = 2.11007e-007, \mu_2 = 108.314$
PD_2	$\mu_{1,2} = 491.755$
PD_3	$\mu_1 = 2.3363e+010, \mu_2 = 2.35772e+010 \pm i180$



a



b

Figure 3: (a) Limit cycles starting from the Hopf point, (b) Limit cycles and bifurcations of limit cycles.

3.3. Continuation of the Hopf bifurcation

The Bogdanov-Takens are common points for the limit pont curves and corresponding to equilibria with eigen values $\lambda_1 + \lambda_2 = 0$. Actually, at each BT point, the Hopf bifurcation curve (with $\lambda_{1,2} = \pm i\omega_0, \omega_0 \neq 0$) turns into the neutral saddle curve (with real $\lambda_1 = -\lambda_2$). Thus, we can start a Hopf curve from a Bogdanov-Takens point Fig 6.

label = BT, x = (0.500000 0.750000 0.333333 0.500000 0.000000)
(a,b)=(-1.849000e-001, -1.294300e+000)

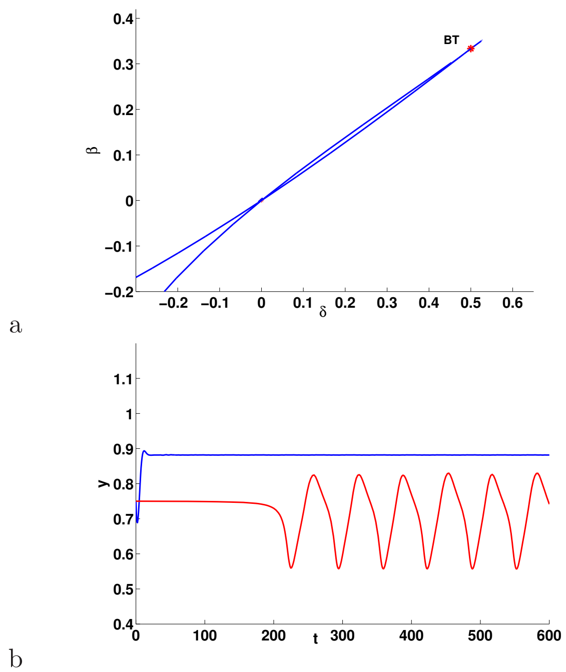


Figure 4: (a) , (b) Hopf curve in model (2.2), BT_1: Bogdanov-Takens, two-parameter bifurcation diagram.

3.4. Continuation of the fold bifurcation

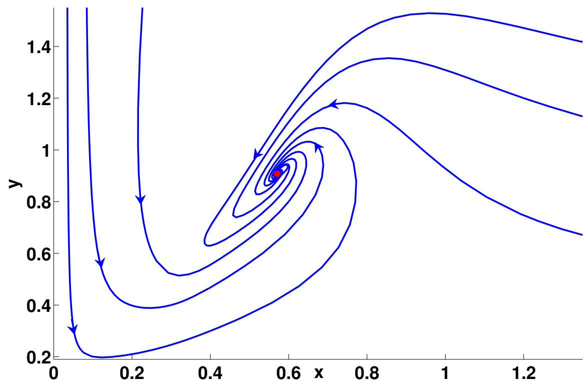
By selecting fold point in the one-parameter bifurcation diagram of the equilibrium as initial point, we can plot the one-parameter bifurcation curve of fold.

label = BT , x = (0.499998 0.750001 10.000012 0.500002)
(a,b)=(-1.848943e-001, -1.294274e+000)
label = BT , x = (0.474818 0.748102 10.147874 0.525185)
(a,b)=(-7.564260e-002, -8.239353e-001)

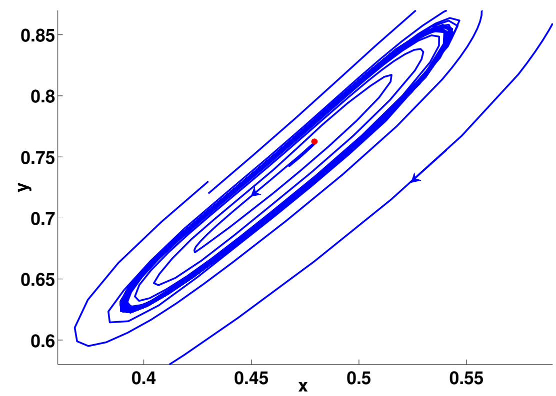
label = CP , x = (0.461538 0.732906 10.171296 0.529320)
c=1.228738e+002

Table 4: two-parameter bifurcation points and eigenvalues

label	eigenvalue
BT_1	$\lambda_1 = -7.81752e-006, \lambda_2 = 4.038e-008$
BT_2	$\lambda_{1,2} = 3.6331e-008 \pm i9.45239e-007$
CP	$\lambda_1 = 7.54952e-015, \lambda_2 = 0.00914109$



a



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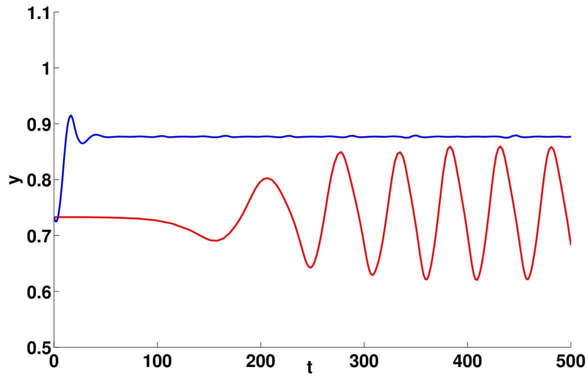

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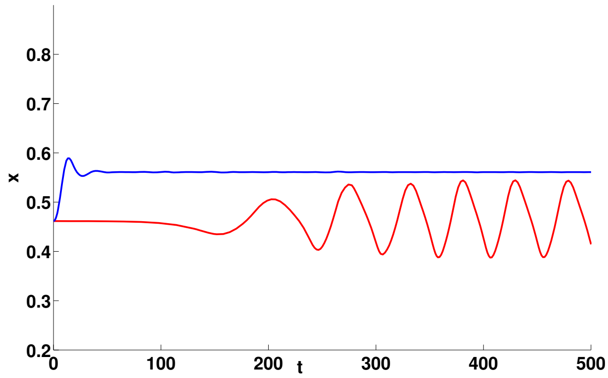
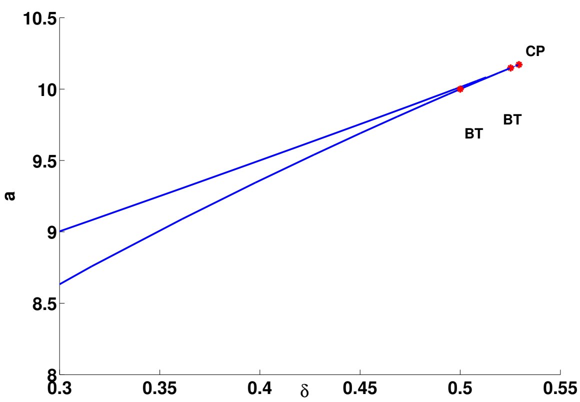
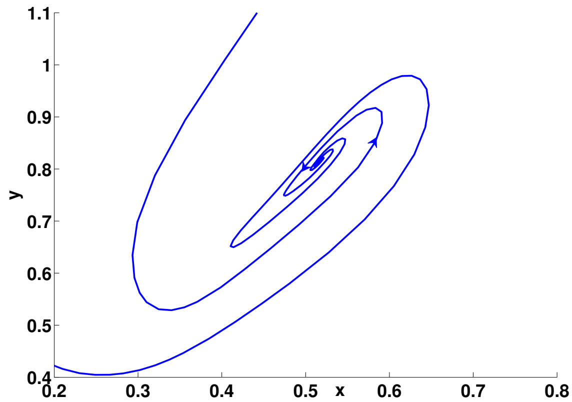


d

Figure 5: (a) The equilibrium $E_1 = (0.5, 0.75)$ is asymptotically stable for system (2.2) with $a = 10.2$, (b) The equilibrium $E_1 = (0.5, 0.75)$ is unstable for system (2.2) with $a = 10.1$.



a



b

Figure 6: (a) Dynamics of the model (2.2) with the emphasis on fold and cusp bifurcations. A bifurcation diagram in the (δ, a) parameter space with the cusp point at $\delta = 0.529320$, $a = 10.171296$. (b) BT_2: codimension2 Bogdanov–Takens,$a = 10.158874$, $\delta = 0.52518484$.

4. Concluding remarks

In this paper, we studied a planar system that models a predator-prey interaction with generalized Holling type III functional response. We derived analytically a complete description of the stability regions of the equilibrium points of the system, namely, E_3, and E_1. We showed that the system undergoes fold, Hopf, cusp and Bogdanov-Takens bifurcations. To support the analytical results and reveal the further complex behaviours of the system, we employed numerical continuation methods to compute curves of codimension 1 and 2 bifurcation points. We have shown that the ustable point equilibrium of the system undergoes a subcritical hopf bifurcation and becomes stable, while stable population cycles emerge.

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Z. Lajmiri, R. K. Ghaziani, M. Ghasemi,
Department of Applied Mathematics and Computer Sciences, Shahrekord University,
P. O. Box 115, Shahrekord, Iran.
E-mail address: `lajmiri.zb@gmail.com`
E-mail address: `khoshsiar@sci.sku.ac.ir`
E-mail address: `meh_ghasemi@yahoo.com`