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Bifurcation and Stability of Prey-Predator Model with Beddington-DeAngelis Functional Response

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Abstract

In this paper we discuss the harvesting of the prey species making a fraction of them to be accessed by the predator while both the prey and predator are being subjected to Beddington-DeAngelis functional response. It is observed that a Hopf-bifurcation may occur around the interior equilibrium taking the environmental carrying capacity of the prey species as the parameter. Some numerical examples and the corresponding curves are studied using Maple to explain the results of the proposed model.

Keywords: Catchability coefficient; Stability; Effort; Harvesting; Functional Response; Carrying capacity; Equilibrium point

MSC 2010: 92B05

1. Introduction

The central goal in ecology is to understand the dynamical relationship between predator and prey, Clark (1976) and Kot (2001). The most significant factor of the prey predator relationship is the predator's rate of feeding upon prey, known as predator's functional response, which is the average number of prey killed per individual predator per unit of time.

In 1965, Holling gave three different types of functional response for different kinds of species to model the phenomena of predation, making the standard Lotka-Volterra system, Lotka (1925) and Volterra (1926) more realistic.

Beddington (1975) and DeAngelis et al. (1975) independently proposed a functional response which is similar to Holling type II which contained an extra term describing mutual interference by predators. Thus, a predator prey model with Beddington-DeAngelis response is of the form,

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 \left(1 - \frac{x_1}{l}\right) - \frac{m_1 x_1 x_2}{A + Bx_1 + Cx_2}, \\ \frac{dx_2}{dt} &= -kx_2 + \frac{m_1 \alpha x_1 x_2}{A + Bx_1 + Cx_2}. \end{aligned} \tag{1.1}$$

Here, x_1 and x_2 are the population density of the prey species and the predator species respectively, r_1 is the intrinsic growth rate of the prey, l is the carrying capacity of the prey population, m_1 is the catching rate of the predator species, α is the efficiency with which resources are converted to new consumers, A is the saturation constant, C scales the impact of predator's mutual interference, k is the mortality rate of the predator. B (Units: 1/prey) describes the effort of handling time on the feeding rate.

In 2004, Fan and Kuang (2004) used the model to study the dynamics of a non-autonomous prey predator system. Wei and Chen (2012) modeled the periodic solution of Prey-Predator system using form (1.1)

Later on, Mehta et al. (2012) modified the response to study prey predator model with reserved and unreserved transmission function.

In the present paper, along with the above mentioned conditions, we further assume that the prey species is subjected to a harvesting effort, which is of major interest to researchers, Sharma and Samanta (2015), Daga et al. (2014), Mehta et al. (2012), Kar and Chakraborty (2010), Chaudhuri (1988), Kar and Chaudhuri (2003, 2003), Das et al. (2009, 2009, 2009), Mukherjee (2012), Chattopadhyay et al. (1999) and we consider the universally prevalent intra-specific competition among the predator species. This intra-specific competition is assumed to bring in an additional instantaneous death rate only to the predator population and is proportional to the square of the said population which further modifies the model suggested in (1.1).

Although some similar kind of models have appeared in recent literature, the main distinctive feature in the proposed model is the inclusion of prey species being harvested while the predator prey model is being subjected to Beddington-DeAngelis functional response. Incorporation of prey species under harvesting leaves a fraction of them to be accessible to the predators. Under this additional effect, the model becomes more ecologically realistic than the existing models.

The construction and model assumptions are discussed in Section 2. In Section 3, positivity and existence of the solutions of the equilibrium points are discussed using Cardan's Method and Descartes' rule of signs along with their existence and stability analysis. In the next section, our analysis shows the existence of Hopf Bifurcation around the interior equilibrium. All our important findings are numerically verified using Maple in Section 5. Finally, Section 6 contains the general discussions of the paper and the implications of our findings.

2. Formulation of the problem

Let us consider a prey and predator population whose growth obeys the given dynamical system:

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1\left(1-\frac{x_1}{l}\right)-\frac{m_1 x_1 x_2}{A+Bx_1+Cx_2}-c_1 E x_1 , \\ \frac{dx_2}{dt} &= r_2 x_2 - r_{22}x_2^2+\frac{m_1 \alpha x_1 x_2}{A+Bx_1+Cx_2}-k x_2 , \end{aligned} \tag{2.1}$$

with initial conditions

$$x_1(0)\geq 0,\ x_2(0)\geq 0. \tag{2.2}$$

Here $x_1(t)$ and $x_2(t)$ are the density of the prey and predator species; c_1 is the catchability coefficient; E is the effort; $r_1, l,\ k, m_1, \alpha, A, B$ and C are positive constants and have usual meanings as discussed in Section1; r_2 is the growth rate of the predator species and r_{22} defines the intra specific competition rate among predators.

3. Equilibrium points: their existence and stability

In this section we will discuss the dynamical behavior of the possible equilibrium points of the system (2.1) which are:

1. Trivial equilibrium: $E_0(0,0)$.
2. Axial equilibrium: $E_1(\bar{x}_1,0)$, where

$$\bar{x}_1 = \frac{l(r_1 - c_1 E)}{r_1}.$$

3. Interior equilibrium: $E_2\left(x_1^*, x_2^*\right)$.

3.1. Local stability analysis

Analyzing the existence of the non trivial interior equilibrium of the model system (2.1), i.e., on solving

$$\frac{dx_1}{dt} = 0, \qquad \frac{dx_2}{dt} = 0,$$

we find

$$Mx_1^3 + Nx_1^2 + Ox_1 + P = 0, \tag{3.1}$$

where

$$M = \frac{C}{l}\left(r_{22}B^2 r_1 - \frac{C^2 \alpha r_1^{\,2}}{l}\right),$$

$$N = \frac{r_2 C^2 B r_1}{l} + \frac{r_{22} 2ABCr_1}{l} + \frac{r_{22}B^2 Cc_1}{E} - r_{22}B^2 Cr_1 + \frac{C^3 \alpha 2r_1^2}{l} - \frac{C^3 \alpha 2r}{l}\left(c_1 E + \frac{m_1}{C}\right) - \frac{kC^2 Br_1}{l},$$

$$\begin{aligned} O = {} & r_2 C^2 B\left(c_1 E + \frac{m_1}{C}\right) + \frac{r_2 C^2 Ar_1}{l} - r_2 C^2 Br_1 + \frac{r_{22}A^2 Cr_1}{l} - r_{22} 2ABm_1 + \frac{r_{22} 2ABCc_1}{E} \\ & + r_{22} 2ABm_1 - r_{22} 2ABCr_1 - C^3 \alpha\left(c_1 E + \frac{m_1}{C}\right)^2 - C^3 \alpha r_1^2 + C^3 \alpha 2r_1\left(c_1 E + \frac{m_1}{C}\right) \\ & - kC^2\left(\frac{Ar_1}{l} + Bc_1 E + \frac{Bm_1}{C} - Br_1\right), \end{aligned}$$

$$P = r_2 C^2 A\left(c_1 E + \frac{m_1}{C}\right) - r_2 C^2 Ar_1 + \frac{r_{22}A^2 Cc_1}{E} r_1 - r_{22}A^2 Cr_1 - kC^2 Ac_1 E - kCAm_1 + kC^2 A.$$

The variational matrix corresponding to the system (2.1) is

$$V=\begin{bmatrix} r_1-\dfrac{2r_1x_1}{l}-\dfrac{(A+Cx_2)m_1x_2}{(A+Bx_1+Cx_2)^2}-c_1E & -\dfrac{(A+Bx_1)m_1x_1}{(A+Bx_1+Cx_2)^2} \\ \dfrac{(A+Cx_2)m_1\alpha x_2}{(A+Bx_1+Cx_2)^2} & r_2-2r_{22}x_2+\dfrac{(A+Bx_1)m_1\alpha x_1}{(A+Bx_1+Cx_2)^2}-k \end{bmatrix}.$$

3.1.1. Trivial equilibrium E_0

The variational matrix of the system (2.1) at $E_0(0,0)$ is given by

$$V(E_0)=\begin{bmatrix} r_1-c_1E & 0 \\ 0 & r_2-k \end{bmatrix}.$$

The roots of the corresponding characteristic equation are given by

$$\lambda_1=r_1-c_1E,\ \ \lambda_2=r_2-k.$$

Here,

1. $\lambda_1<0$ if $\dfrac{r_1}{c_1}<E$ (i.e., effort exceeds the BTP of the x_1 species) and
2. $\lambda_2<0$ if $r_2<k$ (i.e., the mortality rate exceeds the growth rate of the x_2 species).

Hence, we arrive at the following theorem.

Theorem 3.1.1.

The trivial equilibrium $E_0(0,0)$ exists and is a stable node provided $E>\dfrac{r_1}{c_1}$ and $k>r_2$.

3.1.2. Axial equilibrium E_1

The variational matrix of the system (2.1) at $E_1(\bar{x}_1,0)$, $\bar{x}_1=\dfrac{l(r_1-c_1E)}{r_1}$ is given by

$$V(E_1)=\begin{bmatrix} r_1-\dfrac{2r_1\bar{x}_1}{l}-c_1E & -\dfrac{\bar{x}_1m_1}{(A+B\bar{x}_1)} \\ 0 & r_2+\dfrac{m_1\alpha\bar{x}_1}{(A+B\bar{x}_1)}-k \end{bmatrix}.$$

The roots of the corresponding characteristic equation are

$$\lambda_1 = -r_1 + c_1 E$$

and

$$\lambda_2 = r_2 + \frac{m_1 \alpha l (r_1 - c_1 E)}{A r_1 + B l r_1 - B l c_1 E} - k .$$

$\lambda_1 < 0$ provided $E < \frac{r_1}{c_1}$ (thereby violating the existence of a stable node at $E_0(0,0)$)

and

$$\lambda_2 < 0 \ ,$$

if

$$r_2 + \frac{m_1 \alpha l (r_1 - c_1 E)}{r_1 + B l r_1 - B l c_1 E} < k.$$

Hence, we arrive at the following theorem.

Theorem 3.1.2.

The axial equilibrium E_1 of the system (2.1) is a stable node provided

$$E < \frac{r_1}{c_1}$$

and

$$r_2 + \frac{m_1 \alpha l (r_1 - c_1 E)}{r_1 + B l r_1 - B l c_1 E} < k.$$

Under this circumstance the trivial equilibrium at $E_0(0,0)$ becomes an unstable saddle point.

3.1.3. Interior equilibrium E_2

The variational matrix of the system (2.1) at $E_2(x_1^*, x_2^*)$ is given by

$$V = \begin{bmatrix} r_1 - \frac{2 r_1 x_1^*}{l} - \frac{(A + C x_2^*) m_1 x_2^*}{(A + B x_1^* + C x_2^*)^2} - c_1 E & -\frac{(A + B x_1^*) m_1 x_1^*}{(A + B x_1^* + C x_2^*)^2} \\ \frac{(A + C x_2^*) m_1 \alpha x_2^*}{(A + B x_1^* + C x_2^*)^2} & r_2 - 2 r_{22} x_2^* + \frac{(A + B x_1^*) m_1 \alpha x_1}{(A + B x_1^* + C x_2^*)^2} - k \end{bmatrix}.$$

The corresponding characteristic equation is given by

$$\lambda^2 + a_1\lambda + a_2 = 0, \tag{3.2}$$

where

$$a_1 = -\left[r_1 - \frac{2r_1x_1^*}{l} - \frac{\left(A + Cx_2^*\right)m_1x_2^*}{\left(A + Bx_1^* + Cx_2^*\right)^2} - c_1E + r_2 - 2r_{22}x_2^* + \frac{\left(A + Bx_1^*\right)m_1\alpha x_1}{\left(A + Bx_1^* + Cx_2^*\right)^2} - k \right],$$

$$a_2 = \left\{ r_1 - \frac{2r_1x_1^*}{l} - \frac{\left(A + Cx_2^*\right)m_1x_2^*}{\left(A + Bx_1^* + Cx_2^*\right)^2} - c_1E \right\} \left\{ r_2 - 2r_{22}x_2^* + \frac{\left(A + Bx_1^*\right)m_1\alpha x_1}{\left(A + Bx_1^* + Cx_2^*\right)^2} - k \right\}$$
$$+ \frac{\left(A + Cx_2^*\right)m_1\alpha x_2^* \times \left(A + Bx_1^*\right)m_1x_1^*}{\left(A + Bx_1^* + Cx_2^*\right)^4}.$$

It follows from Routh Hurwitz criterion; all eigenvalues of equation (3.2) have negative real parts if and only if

$$a_1 > 0,\ a_2 > 0. \tag{3.3}$$

Hence, we arrive at the following theorem.

Theorem 3.1.3.

The interior equilibrium is locally asymptotically stable if and only if inequalities (3.3) are satisfied.

3.2. Global stability analysis

Here, we will analyze the global stability behavior of the interior equilibrium point $E_2\left(x_1^*, x_2^*\right)$ of the system (2.1) by constructing a suitable Lyapunov function:

$$V\left(x_1, x_2\right) = \left[x_1 - x_1^* - x_1^* \ln \frac{x_1}{x_1^*} \right] + k_1 \left[x_2 - x_2^* - x_2^* \ln \frac{x_2}{x_2^*} \right],$$

where k_1 is a constant, whose value is to be determined in the subsequent steps. It can be easily shown that the function V is zero at the equilibrium point $\left(x_1^*, x_2^*\right)$ and is positive for all other values of x_1, x_2. Differentiating V with respect to t we get

$$\begin{aligned}\frac{dV}{dt} &= \frac{x_1 - x_1^*}{x_1}\frac{dx_1}{dt} + k_1\frac{x_2 - x_2^*}{x_2}\frac{dx_2}{dt} \\ &= \left(x_1 - x_1^*\right)\left[r_1\left(1 - \frac{x_1}{l}\right) - \frac{m_1 x_2}{A + Bx_1 + Cx_2} - c_1 E\right] \\ &\quad + k_1\left(x_2 - x_2^*\right)\left[r_2 - r_{22}x_2 + \frac{m_1 \alpha x_1}{A + Bx_1 + Cx_2} - k\right]. \end{aligned} \tag{3.4}$$

Also, we have set the equilibrium equations

$$r_1\left(1 - \frac{x_1^*}{l}\right) - \frac{m_1 x_2^*}{A + Bx_1^* + Cx_2^*} - c_1 E = 0,$$

$$r_2 - r_{22}x_2^* + \frac{m_1 \alpha x_1^*}{A + Bx_1^* + Cx_2^*} - k = 0. \tag{3.5}$$

$\frac{dV}{dt}$ is negative semidefinite in some neighborhood of $\left(x_1^*, x_2^*\right)$ provided

$$A + Bx_1^* + Cx_2^* > A + Bx_1 + Cx_2. \tag{3.6}$$

Hence, we arrive at the following theorem.

Theorem 3.2.

The interior equilibrium point E_3 of the system (2.1) is globally asymptotically stable if inequality (3.6) is fulfilled.

4. Hopf bifurcation at $E_2\left(x_1^*, x_2^*\right)$

The characteristic equation of the system (2.1) at E_2 is given by

$$\lambda^2 + a_1(l)\lambda + a_2(l) = 0, \tag{4.1}$$

where

$$a_1(l) = -[r_1 - 2\frac{r_1 x_1^*}{l} - \frac{\left(A + Cx_2^*\right)m_1 x_2^*}{\left(A + Bx_1^* + Cx_2^*\right)^2} - c_1 E + r_2 - 2r_{22}x_2^* + \frac{\left(A + Bx_1^*\right)m_1 \alpha x_1^*}{\left(A + Bx_1^* + Cx_2^*\right)^2} - k]$$

and

$$a_2(l)=\left\{r_1-\frac{2r_1x_1^*}{l}-\frac{\left(A+Cx_2^*\right)m_1x_2^*}{\left(A+Bx_1^*+Cx_2^*\right)^2}-c_1E\right\}\times\left\{r_2-2r_{22}x_2^*+\frac{\left(A+Bx_1^*\right)m_1\alpha x_1}{\left(A+Bx_1^*+Cx_2^*\right)^2}-k\right\}$$

$$+\frac{\left(A+Cx_2^*\right)m_1\alpha x_2^*\times\left(A+Bx_1^*\right)m_1x_1^*}{\left(A+Bx_1^*+Cx_2^*\right)^4}.$$

To check whether the system (2.1) is stable or not, let us consider l as the bifurcation parameter. For this purpose, let us state the following theorem.

Theorem 4.1. (Hopf bifurcation theorem Murray (1989)**)**

If $a_i(l), i=1,2$ are smooth functions of l in an open interval about $l_c\in R$ such that the characteristic equation (4.1) has a pair of complex eigenvalues

$$\lambda=b_1(l)\pm ib_2(l)\,(with\ b_1(l), b_2(l)\in R)$$

so that they become purely imaginary at

$$l=l_c$$

and

$$\frac{db_1}{dl}_{l=l_c}\neq 0,$$

then a Hopf Bifurcation occurs around E_2 at $l=l_c$ (i.e. a stability change of E_2 will be accompanied by the creation of a limit cycle at $l=l_c$).

Theorem 4.2.

The system (2.1) possesses Hopf Bifurcation around E_2 when l passes through l_c provided $a_2(l)>0,\ a_1(l)=0.$

Proof:

At $l=l_c$, the characteristic equation of (2.1) for E_2 becomes $\lambda^2+a_2=0$, giving roots

$$\lambda_1=i\sqrt{a_2},\ \lambda_2=-i\sqrt{a_2}.$$

Hence, there exists a pair of purely imaginary eigenvalues. Also $a_i's(i=1,2)$ are smooth functions of l. Taking l in a neighborhood of l_c, the roots are

$$\lambda_1 = b_1(l) + ib_2(l),\ \lambda_2 = b_1(l) - ib_2(l)$$

where

$$b_i(l),\ i=1,2 \text{ are real.}$$

We are going to verify the condition

$$\frac{d}{dl}(\mathrm{Re}(\lambda_i(l)))|_{l=l_c} \neq 0,\ i=1,2.$$

Substituting $\lambda(l) = b_1(l) + ib_2(l)$ in (4.1) we get

$$(b_1(l) + ib_2(l))^2 + a_1(b_1(l) + ib_2(l)) + a_2 = 0. \tag{4.2}$$

Taking derivative of both sides of (4.2) w.r.t l, we have

$$2(b_1(l) + ib_2(l))\left(b_1'(l) + ib_2'(l)\right) + a_1'(b_1(l) + ib_2(l)) + a_1\left(b_1'(l) + ib_2'(l)\right) + a_2' = 0. \tag{4.3}$$

Comparing real and imaginary parts of (4.3), we have

$$\left(2b_1b_1' - 2b_2b_2' + a_1'b_1 + a_1b_1' + a_2'\right) = 0,$$
$$\left(2b_2b_1' + 2b_1b_2' + a_1b_2' + a_1'b_2\right) = 0.$$

That is,

$$D_1b_1' - D_2b_2' + D_3 = 0, \tag{4.4}$$
$$D_2b_1' + D_1b_2' + D_4 = 0, \tag{4.5}$$

where

$$D_1 = 2b_1 + a_1,$$
$$D_2 = 2b_2,$$
$$D_3 = a_1'b_1 + a_2',$$
$$D_4 = a_1'b_2.$$

Now, from (4.4) and (4.5), we have,

$$b_1' = -\frac{D_1 D_3 + D_2 D_4}{D_1^2 + D_2^2}, \tag{4.6}$$

at $l = l_c$,

Case I:

At $b_1 = 0, b_2 = \sqrt{a_2}$,

$$D_1 = a_1,\ D_2 = 2\sqrt{a_2},\ D_3 = a_2',\ D_4 = a_1'\sqrt{a_2}.$$

So,

$$D_1 D_3 + D_2 D_4 = a_1 a_2' + 2a_1' a_2 \neq 0 \text{ at } l = l_c.$$

Case II:

At $b_1 = 0, b_2 = -\sqrt{a_2}$,

$$D_1 = a_1,\ D_2 = -2\sqrt{a_2},\ D_3 = a_2',\ D_4 = -a_1'\sqrt{a_2},$$

So

$$D_1 D_3 + D_2 D_4 = a_1 a_2' + 2a_1' a_2 \neq 0 \text{ at } l = l_c.$$

Therefore,

$$\frac{d}{dl}\left(\mathrm{Re}(\lambda_i(l))\right)|_{l=l_c} = -\frac{D_1 D_3 + D_2 D_4}{D_1^2 + D_2^2}|_{l=l_c}$$
$$\neq 0.$$

Hence, by theorem (4.1), the result follows.

5. Numerical results

Analytical studies remain incomplete without verification of the derived results. So, in this section, we consider two numerical examples:

Example 1.

We take the parameter values as

$$r_1 = 14.0,\ r_2 = 13.0,\ l = 1000,\ m_1 = 0.1,\ A = 12.0,\ B = 12.0,$$
$$C = 12.0,\ c_1 = 0.01,\ E = 1.0,\ r_{22} = 0.50, \alpha = 0.006$$

in appropriate units. For the above values we find that the equilibrium points are

$$x_1 = 999.2706342,\ x_2 = 27.00009727\,.$$

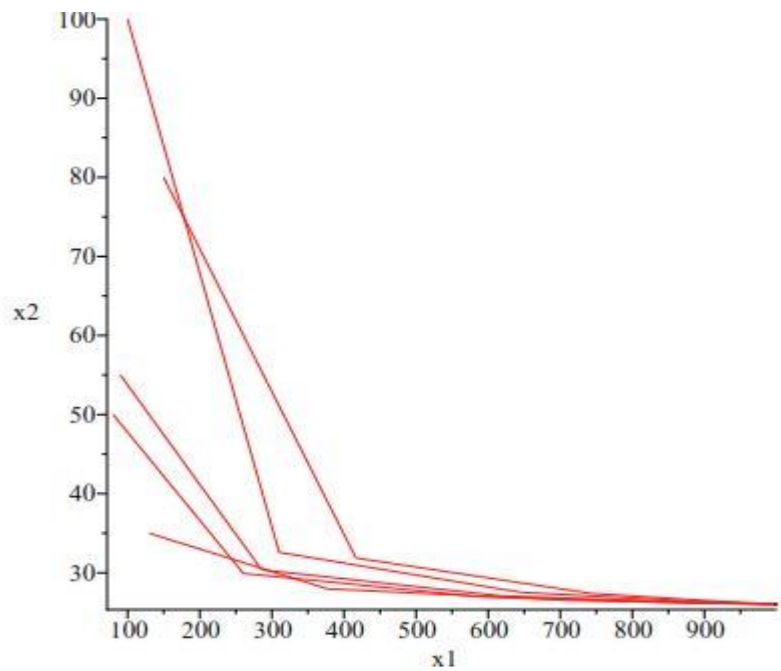

Figure 1. Phase plane trajectories of the prey predator system with different initial values corresponding to data set, Example1

Example 2.

On taking the parameter values as

$$r_1 = 3.0,\ l = 110,\ m_1 = 2.5,\ A = 12.0,\ B = 12.0,\ c_1 = 0.1,$$
$$E = 1.0,\ r_2 = 0.4,\ r_{22} = 0.01,\ \alpha = 0.006,\ C = 1.0$$

in appropriate units and find the equilibrium points

$$x_1 = 103.4912777,$$
$$x_2 = 40.11996529\,.$$

Further, the phase plane trajectory is given by

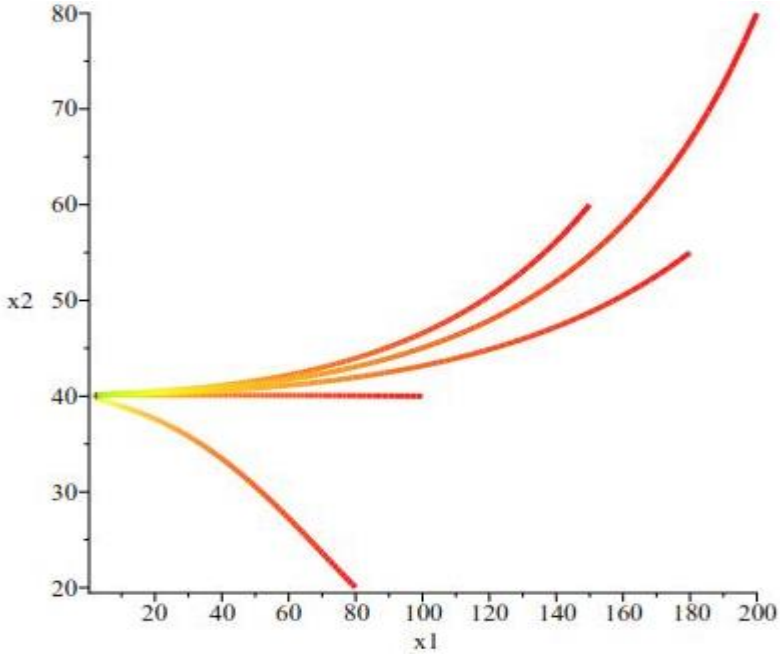

Figure 2. Phase plane trajectories of the prey predator system with different initial values corresponding to data set, Example 2

Plotting the prey and predator population w.r.t time t we find the curve

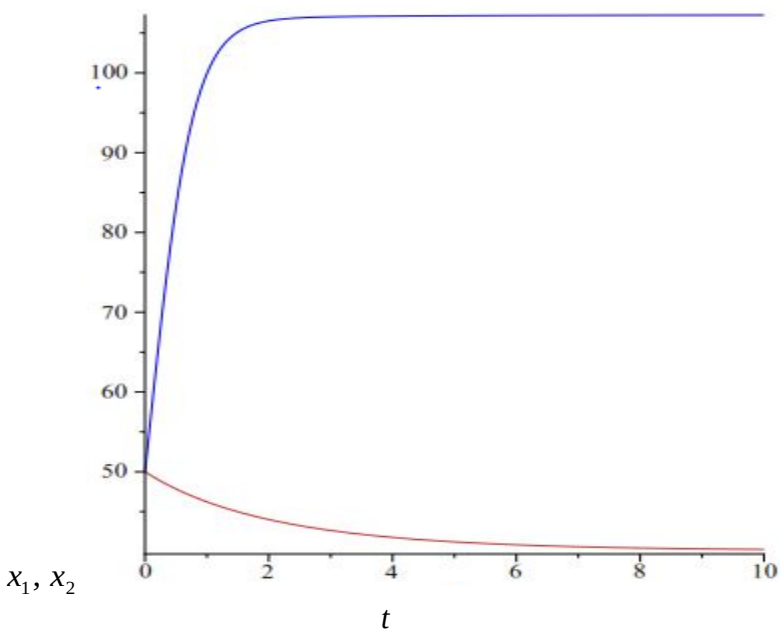

Figure 3. Solution curve of the prey-predator population for a period of $t = 0$ to 10 units

6. Conclusion

In the paper, we have developed a prey-predator model where only the prey population is being subjected to harvesting and the predator species is subjected to intra specific competition while both are under the effect of Beddington-DeAngelis functional response. Then we have discussed the dynamical behaviors of the system at various equilibrium points and their stability which are very similar to those of some recent research works. In our system there are three equilibrium points, E_0 the trivial one, E_1 the axial one and E_2 the interior one. Here, E_0 is a stable node provided

$$E > \frac{r_1}{c_1},\ k > r_2 .$$

The axial equilibrium E_1 exists but is either a saddle point or an unstable node. The interior equilibrium E_2 exists provided inequality (3.3) holds true. The global stability analysis is done by constructing a suitable Lyapunov function.

The major difference between our work and the other recent work done is the incorporation of Beddington-DeAngelis functional response on a harvested prey species and a predator species under the effect of intra specific competition thereby enriching the dynamics of the system. We have further investigated the condition for limit cycle to arise by Hopf bifurcation. The carrying capacity of the prey species l plays a vital role to control the stability of the population and a Hopf bifurcation may occur at the interior equilibrium point keeping it as a bifurcation parameter. If the carrying capacity of the prey species, l, remains below a threshold value, the stability of the prey species will be affected.

Since theorems remain incomplete without numerical verifications of analytical results. We consider some hypothetical data set and verify them using Maple. Growth curves and phase plane trajectories are also discussed.

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Appendix

1. Since the signs of $M, N, O\ P$ are not obvious, applying Descartes' Rule of sign on equation (3.1) we find that at least one positive root exists provided the following conditions are fulfilled:

$$\begin{aligned}
&M > 0,\ N > 0,\ O > 0,\ P < 0.\\
&M > 0,\ N > 0,\ O < 0,\ P < 0.\\
&M > 0,\ N < 0,\ O > 0,\ P < 0.\\
&M > 0,\ N < 0,\ O < 0,\ P < 0.\\
&M < 0,\ N > 0,\ O > 0,\ P > 0.\\
&M < 0,\ N > 0,\ O < 0,\ P > 0.\\
&M < 0,\ N < 0,\ O > 0,\ P > 0.\\
&M < 0,\ N < 0,\ O < 0,\ P > 0.
\end{aligned}$$

Further, by Cardan's method, roots of equation (3.1) is given by

$$x_1 = \left[\frac{1}{2}\left(-G + \sqrt{G^2 + 4H^3}\right)\right]^{1/3} + \left[\frac{1}{2}\left(-G - \sqrt{G^2 + 4H^3}\right)\right]^{1/3} - \frac{N}{3M},$$

where

$$H = \frac{O}{3M} - \frac{N^2}{9M^2} \text{ and } G = \frac{2N^3}{27M^2} - \frac{ON}{3M} + P,$$

which are real provided $\sqrt{G^2 + 4H^3} \geq 0$ and positive provided

$$\left[\frac{1}{2}\left(-G + \sqrt{G^2 + 4H^3}\right)\right]^{1/3} + \left[\frac{1}{2}\left(-G - \sqrt{G^2 + 4H^3}\right)\right]^{1/3} - \frac{N}{3M} > 0.$$

2. Corresponding to the equilibrium point $E_2\left(x_1^*, x_2^*\right)$.

We can write (3.4) together with (3.5) as:

$$\begin{aligned}
\frac{dV}{dt} = &\left(x_1 - x_1^*\right)\left[r_1\left(1 - \frac{x_1}{l}\right) - \frac{m_1 x_2}{A + Bx_1 + Cx_2} - r_1\left(1 - \frac{x_1^*}{l}\right) + \frac{m_1 x_2^*}{A + Bx_1^* + Cx_2^*}\right]\\
&+ k_1\left(x_2 - x_2^*\right)\left[r_2 - r_{22}x_2 + \frac{m_1 \alpha x_1}{A + Bx_1 + Cx_2} - r_2 + r_{22}x_2^* - \frac{m_1 \alpha x_1^*}{A + Bx_1^* + Cx_2^*}\right]
\end{aligned}$$

$$= -\frac{r_1}{l}\left(x_1 - x_1^*\right)^2 - k_1 r_{22}\left(x_2 - x_2^*\right)^2 - \frac{m_1}{A + Bx_1 + Cx_2} \times \left\{x_2\left(x_1 - x_1^*\right) - k_1 \alpha x_1\left(x_2 - x_2^*\right)\right\}$$

$$+ \frac{m_1}{A + Bx_1^* + Cx_2^*}\left\{x_2^*\left(x_1 - x_1^*\right) - k_1 \alpha x_1^*\left(x_2 - x_2^*\right)\right\}$$

$$= -\frac{r_1}{l}\left(x_1 - x_1^*\right)^2 - \frac{1}{\alpha} r_{22}\left(x_2 - x_2^*\right)^2 - m_1\left(x_1 x_2^* - x_2 x_1^*\right)\left[\frac{1}{A + Bx_1 + Cx_2} - \frac{1}{A + Bx_1^* + Cx_2^*}\right]$$

(On choosing $k_1 = \frac{1}{\alpha}$).

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