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Switching Effect Of Predation On Prey Species Living In Two Habitats Exhibiting Group Defense

BAL BHATT [1] , QAMAR KHAN [2] and RAMESHWAR JAJU [3]

[1] Department Of Mathematics & Computer Science
The University Of The West Indies,
St. Augustine,
TRINIDAD (W. I.)
Email: bbhatt@fans.uwi.tt

[2] Department Of Mathematics & Statistics
Sultan Qaboos University,
P.O.Box 36, Alkhod 123, Muscat
SULTANATE OF OMAN
Email: qjalil@squ.edu.om

[3] Department of Computer Science
University of Swaziland,
P/B 4, Kwaluseni,
SWAZILAND, (AFRICA)
Email: jajurp@science.uniswa.sz

Abstract: - Mathematical model with one prey species living in two different habitats and a predator where a prey exhibits group defense has been studied. The preys are able to migrate between two different habitats due to change in seasonal conditions. The stability analysis of non zero equilibrium values (where both prey and predator species co-exist) has been carried out. Hopf bifurcation points have been determined using rate of conversion of the prey to predator as bifurcation parameter. It has been shown that for one predatory rate, the Hopf bifurcation does not occur whereas for another predatory rate, the Hopf bifurcation does occur.

Keywords: - Prey, predator, switching, group defense, stability, differential equations, Bifurcation Point.

1 Introduction

In predator-prey system, it is of interest to see how a predator feeds upon preys. Predator prefers to feed itself in a habitat for some time and changes its preference to another habitat. This preferential phenomenon of change of habitats is called switching. Two types of problems have been studied in the past by various authors, namely, (i) when the predator attacks the preys in a habitat where they are in abundance and (ii) when the preys have ability to defend themselves, therefore the predator attacks the preys in the habitat where they are less in number. Khan et. al. (1998) [1] and Bhatt et.al.(1999) [2] have given a good account of the literature, particularly where preys show a group defense property (group defense is a term used to describe a phenomenon whereby predation is decreased or even prevented altogether by the ability of the prey population to better defend themselves when their number is large). They have considered the following model.

$$\begin{aligned}
\frac{dx_1}{dt} &= (\alpha_1 x_1 - \epsilon_1 x_1) + \epsilon_2 p_{21} x_2 - \frac{\beta_1 x_2 y}{1+\left(\frac{x_1}{x_2}\right)^n}, \\
\frac{dx_2}{dt} &= (\alpha_2 x_2 - \epsilon_2 x_2) + \epsilon_1 p_{12} x_1 - \frac{\beta_2 x_1 y}{1+\left(\frac{x_2}{x_1}\right)^n}, \\
\frac{dy}{dt} &= \left[-\mu + \frac{\delta_1 \beta_1 {x_2}^{n+1}}{{x_1}^n + {x_2}^n} + \frac{\delta_2 \beta_2 {x_1}^{n+1}}{{x_1}^n + {x_2}^n} \right] y
\end{aligned} \qquad (1)$$

for $n = 1$ and 2, with $x_1(0) > 0,\ x_2(0) > 0$ and $y(0) > 0$.

Where

x_i : represents the population of the prey species in two different habitats,

y :represents population of the predator species,

β_i : measure the feeding rates of the predator on the prey species in habitat 1 and habitat 2,

δ_i : conversion rate of the prey to the predator

ϵ_i : inverse barrier strength in going out of the i^{th} habitat,

p_{ij} : the probability of successful transition from i^{th} habitat to j^{th} habitat (where $i \neq j$),

α_i : per capita birth rate of the prey species in two different habitats and

μ : death rate of predator.

The third term in the first two equations of (1) represents the interaction of predator with preys in habitats 1 and 2 respectively, giving the predation rate as

$$k_1 = \frac{\beta_1 \left(\frac{x_2}{x_1}\right)}{1+\left(\frac{x_1}{x_2}\right)^n} \text{ and } k_2 = \frac{\beta_2 \left(\frac{x_1}{x_2}\right)}{1+\left(\frac{x_2}{x_1}\right)^n} \qquad (2).$$

For

$$x_1 \gg x_2,\ k_1 \to 0,\ k_2 \to \beta_2 \left(\frac{x_1}{x_2}\right) \gg \beta_2 \qquad (3)$$

and

$$x_2 \gg x_1,\ k_1 \to \beta_1 \left(\frac{x_2}{x_1}\right) \gg \beta_1,\ k_2 \to 0 \qquad (4)$$

(3) and (4) show a switching behavior of predators which attack the preys in the habitat where they are less in number.

The object of present study is to replace (2) by

$$k_1 = \frac{\beta_1}{1+\left(\frac{x_1}{x_2}\right)^n} \text{ and } k_2 = \frac{\beta_2}{1+\left(\frac{x_2}{x_1}\right)^n} \qquad (5)$$

so that, for

$$x_1 \gg x_2,\ k_1 \to 0,\ k_2 \to \beta_2 \text{ and} \qquad (6)$$

$$x_2 \gg x_1,\ k_1 \to \beta_1,\ k_2 \to 0 \qquad (7)$$

which seems more plausible. The reason being that the terms representing the interaction of prey and predator must be $k_1 x_1 y$ and $k_2 x_2 y$ respectively with proper k_1 and k_2 which give the switching behaviour such that predators attack the habitat where number of preys are less. We consider both the models corresponding to $n = 1$ and 2. The stability analysis of the non zero equilibrium values has been carried out. The Hopf bifurcation points have been obtained taking the conversion rate from prey to predator as bifurcation parameter.

It is interesting to note that for $n = 1$ the Hopf bifurcation does not occur (i.e. the system remains stable or unstable for $0 \le \delta_1 \le 1$ and $0 \le \delta_2 \le 1$.), whereas for $n = 2$, we do get Hopf bifurcation.

2 The Model

One - predator two - prey system where the prey species exhibit group defense is given by :

$$\frac{dx_1}{dt} = (\alpha_1 x_1 - \epsilon_1 x_1) + \epsilon_2 p_{21} x_2 - \frac{\beta_1 x_1 y}{1 + \left(\frac{x_1}{x_2}\right)^n},$$

$$\frac{dx_2}{dt} = (\alpha_2 x_2 - \epsilon_2 x_2) + \epsilon_1 p_{12} x_1 - \frac{\beta_2 x_2 y}{1 + \left(\frac{x_2}{x_1}\right)^n},$$

$$\frac{dy}{dt} = \left[-\mu + \frac{\delta_1 \beta_1 x_1 {x_2}^n}{{x_1}^n + {x_2}^n} + \frac{\delta_2 \beta_2 x_2 {x_1}^n}{{x_1}^n + {x_2}^n} \right] y \qquad (8)$$

with $x_1(0) > 0$, $x_2(0) > 0$ and $y(0) > 0$; $n = 1, 2, 3, \ldots$.

We have carried out the analysis for $n = 1$ and $n = 2$ and also compared the results with Bhatt et. al. (1999) [2].

3 Stability of Equilibria

For $n = 1$**:** The non-zero equilibrium point of the system (8) is given by:

$$\bar{x_1} = \frac{\mu(\bar{x} + 1)}{\delta_1 \beta_1 + \delta_2 \beta_2}, \quad \bar{x_2} = \frac{\mu(1 + \bar{x})}{\bar{x}(\delta_1 \beta_1 + \delta_2 \beta_2)}$$

$$\bar{y} = \frac{((\alpha_1 - \epsilon_1)\bar{x} + \epsilon_2 p_{21})(1 + \bar{x})}{\beta_1 \bar{x}} \quad \text{or}$$

$$\bar{y} = \frac{((\alpha_2 - \epsilon_2) + \bar{x}\epsilon_1 p_{12})(1 + \bar{x})}{\beta_2 \bar{x}} \qquad (9)$$

where $\bar{x} = \dfrac{\bar{x_1}}{\bar{x_2}}$ satisfies the equation

$$\bar{x} = \frac{\beta_1(\alpha_2 - \epsilon_2) - \beta_2 \epsilon_2 p_{21}}{\beta_2(\alpha_1 - \epsilon_1) - \beta_1 \epsilon_1 p_{12}} > 0 \qquad (10)$$

The equilibrium values ($\bar{x_1}$, $\bar{x_2}$, $\bar{y}$) have to be positive, therefore,

$$\frac{\epsilon_2 - \alpha_2}{\epsilon_1 \, p_{12}} < \bar{x} < \frac{\epsilon_2 \, p_{21}}{\epsilon_1 - \alpha_1} \qquad (11)$$

Let $\bar{E} = (\bar{x_1}, \bar{x_2}, \bar{y})$ denotes the non zero equilibrium point where $\bar{x_1}$, $\bar{x_2}$ and $\bar{y} > 0$. We investigate the stability of $\bar{E}$ and the bifurcation structure, particularly Hopf bifurcation, for the system (8) using δ_i (conversion rates of the prey to the predator) as the bifurcation parameter. We first obtain the characteristic equation for the linearization of the system (8) near the equilibrium. We consider a small perturbation about the equilibrium value i.e. $x_1 = \bar{x_1} + u$, $x_2 = \bar{x_2} + v$ and $y = \bar{y} + w$. Substituting these into the system (8) and neglecting the terms of second order in small quantities, we obtain the stability equation

$$\begin{vmatrix} a - \lambda & -a\bar{x} & \dfrac{-\beta_1 \bar{x_1}}{1 + \bar{x}} \\ b & -b\bar{x} - \lambda & \dfrac{-\beta_2 \bar{x_1}}{1 + \bar{x}} \\ p & p\bar{x}^2 & -\lambda \end{vmatrix} = 0, \qquad (12)$$

which leads to the eigenvalue equation

$$\lambda^3 + b_1 \lambda^2 + b_2 \lambda + b_3 = 0 \qquad (13)$$

where $b_1 = b\bar{x} - 1$,

$$b_2 = \frac{p\bar{x_1}(\beta_2 \bar{x}^2 + \beta_1)}{1 + \bar{x}}$$

and

$$b_3 = -p\bar{x}_1\bar{x}(a\beta_2 - b\beta_1)$$

.

Also

$$a = \alpha_1 - \epsilon_1 - \frac{\beta_1\bar{y}}{(1+\bar{x})^2} ,$$

$$b = -\left(\frac{\alpha_2 - \epsilon_2}{\bar{x}}\right) + \frac{\beta_2\bar{x}\bar{y}}{(1+\bar{x})^2} \quad \text{and}$$

$$p = \frac{\bar{y}(\delta_1\beta_1 + \delta_2\beta_2)}{(1+\bar{x})^2}$$

The Routh-Hurwitz stability criteria for the third order system is $b_1 > 0$, $b_3 > 0$ and $b_1 b_2 > b_3$. Hence the equilibrium $\bar{E}$ will be locally stable to small perturbations if it satisfies the following conditions:

$$\bar{x} > \frac{a}{b} , \tag{14}$$

$$b\beta_1 > a\beta_2 \quad \text{and} \tag{15}$$

$$(b\bar{x}^2 + a)(\beta_2\bar{x} - \beta_1) > 0 \tag{16}$$

Stability of the equilibrium point depends upon the conditions (11), (14), (15) and (16) together with various parameters.

For $n = 2$:

The non-zero equilibrium point is given by :

$$\bar{X}_1 = \frac{\mu(\bar{X}^2 + 1)}{\delta_1\beta_1 + \delta_2\beta_2\bar{X}} ,$$

$$\bar{X}_2 = \frac{\mu(1 + \bar{X}^2)}{\bar{X}(\delta_1\beta_1 + \delta_2\beta_2\bar{X})} ,$$

$$\bar{Y} = \frac{((\alpha_1 - \epsilon_1)\bar{X} + \epsilon_2 p_{21})(1 + \bar{X}^2)}{\beta_1\bar{X}} \quad \text{or}$$

$$\bar{Y} = \frac{((\alpha_2 - \epsilon_2) + \bar{X}\epsilon_1 p_{12})(1 + \bar{X}^2)}{\beta_2\bar{X}^2} \tag{17}$$

where $\bar{X} = \dfrac{\bar{X}_1}{\bar{X}_2}$ is the real positive root of the following equation:

$$\beta_2(\alpha_1 - \epsilon_1)\bar{X}^2 + (\beta_2\epsilon_2 p_{21} - \beta_1\epsilon_1 p_{12})\bar{X} - \beta_1(\alpha_2 - \epsilon_2) = 0 \tag{18}$$

and $\alpha_1 > \epsilon_1$, $\alpha_2 > \epsilon_2$ otherwise in the model $\dfrac{dX_1}{dt} < 0$ and $\dfrac{dX_2}{dt} < 0$ if there is no migration, (11) is still to be satisfied.
Let $\bar{E}_1 = (\bar{X}_1, \bar{X}_2, \bar{y})$ denotes the non-zero equilibrium point where $\bar{X}_1, \bar{X}_2, \bar{y} > 0$. We investigate the stability of $\bar{E}_1$ and the bifurcation structure, particularly Hopf bifurcation, for the system (8) using δ_i (conversion rates of the prey to the predator) as the bifurcation parameter. Following the procedure of the case $n = 1$, in this case we get the stability conditions as:

$$A + B < 0 , \tag{19}$$

$$(M + L\bar{X})(A\beta_2\bar{X}^2 + B\beta_1) < 0 \tag{20}$$

and

$$\left(\frac{BM}{\bar{X}} - LA\right)(\beta_1 - \beta_2\bar{X}^2) > 0 \tag{21}$$

where

$$A = \alpha_1 - \epsilon_1 - \frac{\beta_1\bar{Y}(1 - \bar{X}^2)}{(1 + \bar{X}^2)^2} ,$$

$$B = \alpha_2 - \epsilon_2 + \frac{\beta_2\bar{Y}\bar{X}^2(1 - \bar{X}^2)}{(1 + \bar{X}^2)^2} ,$$

$$L = \frac{\bar{Y}}{(1 + \bar{X}^2)^2}\Big[\delta_1\beta_1(1 - \bar{X}^2) + 2\delta_2\beta_2\bar{X}\Big] ,$$

$$M = \frac{\bar{Y}\bar{X}^2}{(1 + \bar{X}^2)^2}\Big[2\delta_1\beta_1\bar{X} - \delta_2\beta_2\bar{X}(1 - \bar{X}^2)\Big]$$

Stability of the equilibrium point depends upon the conditions (11), (19), (20) and (21) together with various parameters.

4 Hopf Bifurcation Analysis

For $n = 1$:

We study the Hopf bifurcation for the system (8) when $n = 1$, using δ_1 (rate of conversion of the prey in habitat 1 to the predator) as the bifurcation parameter. The eigenvalue equation (13) has two purely imaginary roots if and only if $b_1 b_2 = b_3$ for some value of δ_1 (say $\delta_1 = {\delta_1}^*$). For $a < 0, b < 0$ and $p > 0$ b_1, b_2 and b_3 are positive. There exists ${\delta_1}^*$ such that $b_1 b_2 = b_3$. Therefore there is only one value of δ_1 at which we have a bifurcation. For some $\epsilon > 0$ for which ${\delta_1}^* - \epsilon > 0$, there is a neighbourhood of ${\delta_1}^*$, say $({\delta_1}^* - \epsilon,\ {\delta_1}^* + \epsilon)$ in which the eigenvalue equation (13) cannot have real positive roots. For $\delta_1 = {\delta_1}^*$, we have

$$(\lambda^2 + b_2)(\lambda + b_1) = 0 \tag{22}$$

which has three roots,
$\lambda_1 = i\sqrt{b_2}$, $\lambda_2 = -i\sqrt{b_2}$ and $\lambda_3 = -b_1$. The roots are in general of the form

$$\begin{aligned} \lambda_1(\delta_1) &= u(\delta_1) + iv(\delta_1) \\ \lambda_2(\delta_1) &= u(\delta_1) - iv(\delta_1) \\ \lambda_3(\delta_1) &= -b_1(\delta_1) \end{aligned} \tag{23}$$

To apply the Hopf bifurcation theorem as stated in [3] (Marsden and McCracken (1976)), we need to verify the transversality condition

$$\left.\frac{du}{d\delta_1}\right|_{\delta_1 = {\delta_1}^*} \neq 0 \tag{24}$$

Substituting $\lambda_k(\delta_1) = u(\delta_1) + iv(\delta_1)$ into the equation (13) and differentiating the resulting equations with respect to δ_1 and setting $u = 0$ and $v(\delta_1) = \bar{v_1}$, we get

$$\begin{aligned} &\frac{du}{d\delta_1}(-3\bar{v_1}^2 + b_2) + \frac{dv}{d\delta_1}(-2b_1\bar{v_1}) = \\ &\qquad {b_1}'\ \bar{v_1}^2 - {b_3}' \quad , \\ &\frac{du}{d\delta_1}(2b_1\bar{v_1}) + \frac{dv}{d\delta_1}(-3\bar{v_1}^2 + b_2) = \\ &\qquad -\ {b_2}'\ \bar{v_1} \end{aligned} \tag{25}$$

where

$${b_1}' = \frac{db_1}{d\delta_1} = 0,\ {b_2}' = \frac{db_2}{d\delta_1}$$

$$\text{and} \quad {b_3}' = \frac{db_3}{d\delta_1}$$

.

$\bar{x}$ is a real positive root of the equation (10) which is independent of δ_1 .

Solving for $\frac{du}{d\delta_1}$ and $\frac{dv}{d\delta_1}$, we have

$$\left.\frac{du}{d\delta_1}\right|_{\delta_1 = {\delta_1}^*} = -\frac{2b_2(b_1{b_2}' - {b_3}')}{4{b_2}^2 + 4{b_1}^2 b_2} \tag{26}$$

To establish Hopf bifurcation at $\delta_1 = {\delta_1}^*$, we need to show that

$$\left.\frac{du}{d\delta_1}\right|_{\delta_1 = {\delta_1}^*} \neq 0 \quad i.e. \quad b_1{b_2}' - {b_3}' \neq 0. \tag{27}$$

At $\delta_1 = {\delta_1}^*$; $b_1 b_2 = b_3$, gives

$$\bar{x}^2 = \frac{a}{b}. \tag{28}$$

Substituting the values of $b_1, {b_2}'$ and ${b_3}'$ in the equation (27) and using equation (28), we get

$$\begin{aligned} b_1{b_2}' - {b_3}' &= \frac{1}{1 + \bar{x}}(\beta_2\bar{x} - \beta_1)(b\bar{x}^2 + a) \\ &\quad \left(\frac{dp}{d\delta_1}\bar{x_1} - \frac{d\bar{x_1}}{d\delta_1}p\right) \\ &= 0 \text{ at } \delta_1 = {\delta_1}^*, \end{aligned} \tag{29}$$

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due to (28). Therefore there will be no bifurcation.
We summarize the above results in the following theorem -

THEOREM-1 : Suppose $\bar{E} = (x_1, x_2, y)$ exists and ${\delta_1}^*$ be a positive root of the equation $b_1 b_2 = b_3$, then a Hopf bifurcation does not occur as δ_1 passes through ${\delta_1}^*$.

Similar analysis can be carried out by varying δ_2 (rate of conversion of the prey in second habitat to the predator) and we shall get a similar result.

$n = 2$:

We can follow similar steps for $n = 2$ as above and obtain the following theorem:

THEOREM-2 : Suppose $\bar{E_1} = (\bar{X_1}, \bar{X_2}, \bar{Y})$ exists, $A < 0, B < 0, M > 0, L > 0$ and ${\delta_1}^*$ be a positive root of the equation $b_1 b_2 = b_3$, then a Hopf bifurcation occurs as δ_1 passes through ${\delta_1}^*$ provided $\dfrac{\beta_1}{\beta_2} \neq \bar{X}^2$.

Similar analysis can be carried out varying δ_2 (rate of conversion of the prey in second habitat to the predator) and we shall get a similar result.

5 Numerical Solutions

Here we see the effect of various parameters on the stability. Table 1 gives the behaviour of stability with respect to β's and δ's.

In Table 1 we have taken:

$\mu = 0.01, \alpha_1 = 0.015, \alpha_2 = 0.025, \epsilon_1 = 0.02, \epsilon_2 = 0.03, p_{12} = 0.3, p_{21} = 0.2$ and we see the effect of δ_1 and δ_2 on the stability for $n = 2$.

In the case of $n = 1$, the system remains stable for all the data in Table 1 and we have no bifurcation points.

In Table 2 we see the effect of ϵ's and δ's and we take:

$\mu = 0.01, \beta_1 = 0.01, \beta_2 = 0.02$ and $n = 2$.
SET (1). $p_{12} = 0.2, p_{21} = 0.7, \epsilon_1 = 0.04, \epsilon_2 = 0.03, \alpha_1 = 0.015, \alpha_2 = 0.025$
SET (2). $p_{12} = 0.2, p_{21} = 0.7, \epsilon_1 = 0.1, \epsilon_2 = 0.3, \alpha_1 = 0.05, \alpha_2 = 0.25$
SET (3). $p_{12} = 0.5, p_{21} = 0.2, \epsilon_1 = 0.1, \epsilon_2 = 0.3, \alpha_1 = 0.05, \alpha_2 = 0.25$

In Table 1 and Table 2 the bifurcation points are in fact the Hopf bifurcation points (where the model is stable, below / above these values the model is unstable/stable).

Using the four cases and values of parameters in Table 1, The set of equations given in (8) have been integrated numerically for $n = 1$ and 2. The behaviour of (8) is given in Table 3.

These sets were picked up while doing the computations of the analytical results in the previous section. The initial conditions used are the corresponding equilibrium values in each case with slight perturbations.

Table 1

β_1	β_2	δ_1 / δ_2	STABLE	UNSTABLE	Bifurcation Point ($n = 2$)
0.01	0.02	$\delta_1 = 0.1$	$0 \leq \delta_2 \leq 0.062671$	$\delta_2 \geq 0.062672$	$\delta_2 = 0.062671$
0.02	0.01	$\delta_1 = 0.1$	$\delta_2 \geq 0.159563$	$0 \leq \delta_2 \leq 0.159562$	$\delta_2 = 0.159563$
0.01	0.02	$\delta_2 = 0.3$	$\delta_1 \geq 0.478678$	$0 \leq \delta_1 \leq 0.478687$	$\delta_1 = 0.478678$
0.02	0.01	$\delta_2 = 0.3$	$0 \leq \delta_1 \leq 0.188014$	$\delta_1 \geq 0.188015$	$\delta_1 = 0.188014$

Table 2

SET	δ_1 / δ_2	STABLE	UNSTABLE	Bifurcation Point ($n = 2$)
(1)	$\delta_1 = 0.1$	$-$	$0 \leq \delta_2 \leq 1$	$-$
	$\delta_2 = 0.3$	$-$	$0 \leq \delta_1 \leq 1$	$-$
(2)	$\delta_1 = 0.1$	$0 \leq \delta_2 \leq 1$	$-$	$-$
	$\delta_2 = 0.3$	$0 \leq \delta_1 \leq 1$	$-$	$-$
(3)	$\delta_1 = 0.1$	$0 \leq \delta_2 \leq 0.076571$	$\delta_2 \geq 0.076572$	$\delta_2 = 0.075671$
	$\delta_2 = 0.3$	$\delta_1 \geq 0.391793$	$0 \leq \delta_1 \leq 0.391792$	$\delta_1 = 0.391793$

Table 3

n	β_1	$\beta 2$	δ_1	δ_2	Behaviour
1	0.01	0.02	0.5	0.3	STABLE
1	0.01	0.02	0.1	0.3	STABLE
1	0.02	0.01	0.1	0.3	STABLE
1	0.02	0.01	0.3	0.3	STABLE
2	0.01	0.02	0.5	0.3	STABLE
2	0.01	0.02	0.1	0.3	UNSTABLE
2	0.02	0.01	0.1	0.3	STABLE
2	0.02	0.01	0.3	0.3	UNSTABLE

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