Dynamical systems in medicine, biology, ecology, and chemistry

Switching Effect Of Predation On Large Size Prey Species Exhibiting Group Defense

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Abstract

A Mathematical model with one prey species living in two different habitats and a predator where a prey exhibits group defense is studied. The prey species

is able to migrate between two different habitats due to change in seasonal conditions. The stability analysis is carried out for a critical point of the system where all species co-exist. Using rate of conversion of the prey to predator as bifurcation parameter, conditions for a Hopf bifurcation to occur are derived. It is shown numerically that predatory rate increases at low population density of prey species, has not always stabilizing effect for the prey-predator system.

1. Introduction

In predator-prey environment, the predator prefers to feed itself in a habitat for some duration and changes its preference to another habitat. This preferential phenomenon of change of habitats from one to other is called switching. The mathematical models that have generally been proposed with switching are those involving interaction of one predator with two prey species (Holling [1], Takahashi [2], May [3], Murdoch and Oaten [4], Roughgarden and Feldman [5], Tansky [6,7], Prajneshu and Holgate [8], Khan et.al. [9,10]).

When the prey species is relatively small in size with little or insignificant defense capability with respect to predator, like small antelope, the predator prefers to catch prey species in a habitat where they are in abundance. Small size prey species lives in less cohesive and coordinated feeding groups since they have to search for scarce, scattered food items of high quality like new leaves, seeds, fruits and are also unable to communicate in vegetation. When the prey population in habitat starts declining due to heavy predation the predator switches over to other habitat where the prey species is in large number due to light predation.

Large prey species like wildbeest, zebra, Thomson's gazelle feed upon abundant, evenly dispersed, easily found food items. Food items of low quality (nature leaves, stems) are much more in abundant than those of high quality within selected habitats and so they form huge and cohesive groups. Seasonal condition of heavy rain storms, dry season and other harsh environment force wildlife to migrate to other habitats for better conditions, food and surface water. Usually wildlife animal concentrate near permanent water during dry periods and disperse into neighbouring dry habitat during wet periods (Dasman and Mossman [11], Lamprey [12], Jarman [13], Stanley Price [14], Afolayen and Ajayi [15], Sinclair [16]). With the advent of dry weather the wildbeest return to their dry seasons range because grass growth on the wet seasons rage stops after a few days without rain, and there remains almost no standing crop as a food reservoir Mc Nayghton [17]. Free standing water is also largely absent

from this area. Wildbeests are thus forced to return to their dry season range which maintain green leaf for a long period and retains a substantial reservoir of grass swards due to light grazing pressure in the wet season. Free standing water is also available there in pools among major river systems. In this way herbivores maximize the growth potential of the vegetation through rotational grazing. Where the two concentration areas are sufficiently far apart the movements are called seasonal migration. Sinclair [16] reported 3 % increment in mortality per year for wildbeest due to this migration.

Large herd farmers are more likely dependent upon self defense and group defense, to avoid being killed by predators. 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. The predators do not seek out areas with very large prey density (Schaller [18]). Pairs of musk- oxen can be successfully attacked by wolves but groups are rarely attacked (Tener [19]). There are many examples of group defense (Yang and Humphrey [20], May and Robinson [21], Holmes and Bethel [22]). Herds remain well coordinated even under attack and individuals may benefit from the alertness and communication. Individuals tend to conform with their neighbour activities and many hundreds even thousands of wildbeest can coordinate rapidly in response to an alarm. Large groups also benefit from increased probability of detection of predators. The hunting success of lions decline if the group size of prey is large (Van Orsdol [23]). Cheetah prefers to hunt single animals.

Freedman and Wolkowicz [24], Ruan and Freedman [25] and Freedman and Raun [26] have studied mathematical models for the prey-predator system in which the prey population exhibits group defense. Khan et al [27] have analyzed a switching model with two habitats and a predator involving group defense.

In this paper we have considered a system having a predator species interacting with some prey species living in two habitats separated by a barrier. The prey species is able to migrate among two different habitats at some cost to the population in the sense that the probability of survival during a change of habitat may be less than one. The predator can feed on either habitat. The prey species in both the habitats have the ability of group defense but it will be effective in the habitat where the population of the prey species is large. The predator will be attracted towards that habitat where the prey species is less in number. Due to seasonal migration of the prey species, none of the habitat population will extinct.

Tansky [7] investigated a mathematical model of two prey and one predator system which has the switching property of predation of the following form

$$\frac{dx}{dt} = \left\{ r_1 - \frac{az}{1 + (y/x)^n} \right\} x,$$

$$\frac{dy}{dt} = \left\{ r_2 - \frac{bz}{1 + (x/y)^n} \right\} y,$$

$$\frac{dz}{dt} = -r_3 + \frac{a_1 xz}{1 + (y/x)^n} + \frac{a_2 yz}{1 + (x/y)^n}, \qquad n = 1, 2, 3, ...$$

where x, y and z denote the abundance of two kind of the prey species and a predator species respectively. The functions $\dfrac{a}{1 + (y/x)^n}$ and $\dfrac{b}{1 + (x/y)^n}$ have a characteristic property of switching mechanism. The predatory rate that an individual of the prey species is attacked by a predator decreases when the population of that species becomes rare compared with the population of another prey species. This property is much amplified for large value of n. He studied the model with simplest form of the function for $n = 1$.

2. The Model: The prey-predator model where the prey species exhibits group defense is of the form:

$$\frac{dx_1}{dt} = \alpha_1 x_1 - \varepsilon_1 x_1 + \varepsilon_2 p_{21} x_2 - \frac{\beta_1 x_2 y}{1 + \left(\dfrac{x_1}{x_2}\right)^n},$$

$$\frac{dx_2}{dt} = \alpha_2 x_2 - \varepsilon_2 x_2 + \varepsilon_1 p_{12} x_1 - \frac{\beta_2 x_1 y}{1 + \left(\dfrac{x_2}{x_1}\right)^n}, \qquad (2.1)$$

$$\frac{dy}{dt} = \left[-\mu + \frac{\delta_1 \beta_1 x_2{}^{n+1}}{x_1{}^n + x_2{}^n} + \frac{\delta_2 \beta_2 x_1{}^{n+1}}{x_1{}^n + x_2{}^n} \right] y$$

with $n = 2$, the equations become

$$\frac{dx_1}{dt} = \alpha_1 x_1 - \varepsilon_1 x_1 + \varepsilon_2 p_{21} x_2 - \frac{\beta_1 x_2^3 y}{x_1^2 + x_2^2},$$

$$\frac{dx_2}{dt} = \alpha_2 x_2 - \varepsilon_2 x_2 + \varepsilon_1 p_{12} x_1 - \frac{\beta_2 x_1^3 y}{x_1^2 + x_2^2}, \qquad (2.2)$$

$$\frac{dy}{dt} = \left[-\mu + \frac{\delta_1 \beta_1 x_2^3}{x_1^2 + x_2^2} + \frac{\delta_2 \beta_2 x_1^3}{x_1^2 + x_2^2} \right] y$$

with $x_1(0) > 0, \quad x_2(0) > 0, \quad y(0) > 0.$

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

y : represents population of 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 prey to predator

ε_i : inverse barrier strength in going out of the first habitat

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

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

μ : the death rate of the predator

For $n = 1$, the case has been studied by Khan et. al. [27] where the relative abundance of the prey species has a simple multiplicative effect. Here we have studied the same model with $n = 2$ where the effect of relative density is stronger than the simple multiplicative.

3. Stability of Equilibria: The non-zero equilibrium point of the system (2.2) is given by :

$$\bar{x}_1 = \frac{\mu \bar{x}(\bar{x}^2 + 1)}{\delta_1 \beta_1 + \delta_2 \beta_2 \bar{x}^3}, \qquad\qquad \bar{x}_2 = \frac{\mu(\bar{x}^2 + 1)}{\delta_1 \beta_1 + \delta_2 \beta_2 \bar{x}^3},$$

$$\bar{y} = \frac{((\alpha_1 - \varepsilon_1)\bar{x} + \varepsilon_2 p_{21})(1 + \bar{x}^2)}{\beta_1} \quad \text{or} \quad \bar{y} = \frac{((\alpha_2 - \varepsilon_2) + \bar{x}\varepsilon_1 p_{12})(1 + \bar{x}^2)}{\bar{x}^3 \beta_2}.$$

$$(3.1)$$

Where $\bar{x} = \bar{x}_1/\bar{x}_2$, is real positive root of the following fourth order equation

$$\beta_2(\alpha_1 - \varepsilon_1)\bar{x}^4 + \beta_2\,\varepsilon_2\,p_{21}\,\bar{x}^3 - \beta_1\,\varepsilon_1\,p_{12}\,\bar{x} - \beta_1(\alpha_2 - \varepsilon_2) = 0. \qquad (3.2)$$

For equilibrium values $(\bar{x}_1,\ \bar{x}_2,\ \bar{y})$ to be positive, a positive real root of the equation (3.2) must be bounded, therefore

$$\frac{\varepsilon_2 - \alpha_2}{\varepsilon_1\,p_{12}} \quad < \quad \bar{x} \quad < \quad \frac{\varepsilon_2\,p_{21}}{\varepsilon_1 - \alpha_1}. \qquad (3.3)$$

Let $\bar{E} = (\bar{x}_1, \bar{x}_2, \bar{y})$ denote the non-zero equilibrium point where $\bar{x}_1, \bar{x}_2, \bar{y} > 0$. We investigate the stability of $\bar{E}$ and the bifurcation structure, particularly Hopf bifurcation, for the system (2.2) 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 (2.2) 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 (2.2) and neglecting the terms of second order in small quantities, we obtain the stability matrix equation

$$\begin{pmatrix} A - \lambda & \dfrac{-A\bar{x}_1}{\bar{x}_2} & \dfrac{-\beta_1\bar{x}_2^{\,3}}{\bar{x}_1^{\,2} + \bar{x}_2^{\,2}} \\[4mm] \dfrac{-D\bar{x}_2}{\bar{x}_1} & D - \lambda & \dfrac{-\beta_2\bar{x}_1^{\,3}}{\bar{x}_1^{\,2} + \bar{x}_2^{\,2}} \\[4mm] E & F & -\lambda \end{pmatrix} = 0, \qquad (3.4)$$

which leads to the eigenvalue equation

$$\lambda^3 + b_1\lambda^2 + b_2\lambda + b_3 = 0, \qquad (3.5)$$

where:

$$b_1 = -(A + D),$$

$$b_2 = \frac{F\beta_2\bar{x}_1^{\,3}}{\bar{x}_1^{\,2} + \bar{x}_2^{\,2}} + \frac{E\beta_1\bar{x}_2^{\,3}}{\bar{x}_1^{\,2} + \bar{x}_2^{\,2}},$$

$$b_3 = -\left(\frac{DF\beta_1\bar{x}_2^4}{\bar{x}_1(\bar{x}_1^2 + \bar{x}_2^2)} + \frac{DE\beta_1\bar{x}_2^3}{\bar{x}_1^2 + \bar{x}_2^2} + \frac{AF\beta_2\bar{x}_1^3}{\bar{x}_1^2 + \bar{x}_2^2} + \frac{AE\beta_2\bar{x}_1^4}{\bar{x}_2(\bar{x}_1^2 + \bar{x}_2^2)}\right),$$

$$A = (\alpha_1 - \varepsilon_1) + \frac{2\bar{y}\beta_1\bar{x}_1\bar{x}_2^3}{(\bar{x}_1^2 + \bar{x}_2^2)^2},$$

$$B = \varepsilon_2 p_{21} + \frac{2\bar{y}\beta_1\bar{x}_2^4}{(\bar{x}_1^2 + \bar{x}_2^2)^2} - \frac{3\bar{y}\beta_1\bar{x}_2^2}{\bar{x}_1^2 + \bar{x}_2^2},$$

$$C = \varepsilon_1 p_{12} + \frac{2\bar{y}\beta_2\bar{x}_1^4}{(\bar{x}_1^2 + \bar{x}_2^2)^2} - \frac{3\bar{y}\beta_2\bar{x}_1^2}{\bar{x}_1^2 + \bar{x}_2^2}, \tag{3.6}$$

$$D = (\alpha_2 - \varepsilon_2) + \frac{2\bar{y}\beta_2\bar{x}_1^3\bar{x}_2}{(\bar{x}_1^2 + \bar{x}_2^2)^2},$$

$$E = \frac{3\delta_2\beta_2\bar{x}_1^2\bar{y}}{\bar{x}_1^2 + \bar{x}_2^2} - \frac{2\delta_1\beta_1\bar{x}_1\bar{x}_2^3\bar{y}}{(\bar{x}_1^2 + \bar{x}_2^2)^2} - \frac{2\delta_2\beta_2\bar{x}_1^4\bar{y}}{(\bar{x}_1^2 + \bar{x}_2^2)^2},$$

$$F = \frac{3\delta_1\beta_1\bar{x}_2^2\bar{y}}{\bar{x}_1^2 + \bar{x}_2^2} - \frac{2\delta_1\beta_1\bar{x}_2^4\bar{y}}{(\bar{x}_1^2 + \bar{x}_2^2)^2} - \frac{2\delta_2\beta_2\bar{x}_1^3\bar{x}_2\bar{y}}{(\bar{x}_1^2 + \bar{x}_2^2)^2}.$$

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:

$$\alpha_1 + \alpha_2 + \frac{2\bar{x}_1\bar{x}_2^3\bar{y}\beta_1}{\bar{x}_1^2 + \bar{x}_2^2} + \frac{2\bar{x}_1^3\bar{x}_2\bar{y}\beta_2}{(\bar{x}_1^2 + \bar{x}_2^2)^2} > \varepsilon_1 + \varepsilon_2,$$

$$AF\beta_2\bar{x}_1^3 + DE\beta_1\bar{x}_2^3 + \frac{DF\beta_1\bar{x}_2^4}{\bar{x}_1} + \frac{AE\beta_2\bar{x}_1^4}{\bar{x}_2} < 0$$

and

$$(AE\bar{x}_1 - DF\bar{x}_2)(\beta_1\bar{x}_2^4 - \beta_2\bar{x}_1^4) < 0. \tag{3.7}$$

Stability of the equilibrium point depends upon the conditions (3.3) and (3.7) together with various parameters.

4. Hopf Bifurcation Analysis: We study the Hopf bifurcation for the system (2.2) using δ_1 (rate of conversion of the prey in habitat 1 to the predator)

as the bifurcation parameter. The eigenvalue equation (3.5) has two purely imaginary roots if and only if $b_1 b_2 = b_3$ for some value of δ_1 (say $\delta_1 = \delta_1{}^\star$). For $A < 0, D < 0, E > 0$ and $F > 0$; b_1, b_2, b_3 are positive. There exists $\delta_1{}^\star$ 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 $\varepsilon > 0$ for which $\delta_1{}^\star - \varepsilon > 0$, there is a neighbourhood of $\delta_1{}^\star$, say $(\delta_1{}^\star - \varepsilon, \delta_1{}^\star + \varepsilon)$ in which the eigenvalue equation (3.5) cannot have real positive roots. For $\delta_1 = \delta_1{}^\star$, we have

$$(\lambda^2 + b_2)(\lambda + b_1) = 0, \tag{4.1}$$

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

$$\begin{aligned}
\lambda_1(\delta_1) &= u(\delta_1) + iv(\delta_1), \\
\lambda_2(\delta_1) &= u(\delta_1) - iv(\delta_1), \\
\lambda_3(\delta_1) &= -b_1(\delta_1).
\end{aligned} \tag{4.2}$$

To apply the Hopf bifurcation theorem as stated in (Marsden and McCracken [28]), we need to verify the transversality condition

$$\left. \frac{du}{d\delta_1} \right|_{\delta_1 = \delta_1{}^\star} \neq 0. \tag{4.3}$$

Substituting $\lambda_k(\delta_1) = u(\delta_1) + iv(\delta_1)$ into the equation (3.5) and differentiating the resulting equations with respect to δ_1 and setting $u = 0$ and $v(\delta_1) = \bar{v}_1$, we get

$$\frac{du}{d\delta_1}(-3\bar{v}_1{}^2 + b_2) + \frac{dv}{d\delta_1}(-2b_1\bar{v}_1) = b_1'\bar{v}_1{}^2 - b_3',$$

$$\frac{du}{d\delta_1}(-2b_1\bar{v}_1) + \frac{dv}{d\delta_1}(-3\bar{v}_1{}^2 + b_2) = -b_1'\bar{v}_1, \tag{4.4}$$

where

$$b_1' = \frac{db_1}{d\delta_1} = 0, \quad b_2' = \frac{db_2}{d\delta_1} \quad \text{and} \quad b_3' = \frac{db_3}{d\delta_1},$$

$\bar{x}$ is a real positive root of the equation (3.2) which is independent of δ_1.

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

$$\frac{du}{d\delta_1}\bigg|_{\delta_1=\delta_1{}^\star} = -\frac{2b_2(b_1b_2{}' - b_3{}')}{4b_2{}^2 + 4b_1{}^2b_2}. \tag{4.5}$$

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

$$\frac{du}{d\delta_1}\bigg|_{\delta_1=\delta_1{}^\star} \neq 0, \quad i.e. \quad b_1b_2{}' - b_3{}' \neq 0 \tag{4.6}$$

At $\delta_1 = \delta_1{}^\star$; $b_1b_2 = b_3$, gives

$$(\beta_1\bar{x}_2{}^4 - \beta_2\bar{x}_1{}^4)(AE\bar{x}_1 - DF\bar{x}_2) = 0,$$

i.e.

$$\bar{x} = \frac{DF}{AE} \tag{4.7}$$

Substituting the values of $b_1, b_2{}'$ and $b_3{}'$ in the equation (4.6) and using the equation (4.7), we get

$$b_1b_2{}' - b_3{}' = \frac{1}{1 + \bar{x}^2}\left(\beta_1\bar{x}_2 - \beta_2\bar{x}_1\bar{x}^3\right)\left(\frac{D}{\bar{x}}\frac{dF}{d\delta_1} - A\frac{dE}{d\delta_1},\right)$$

where

$$\frac{D}{\bar{x}}\frac{dF}{d\delta_1} - A\frac{dE}{d\delta_1} < 0, \quad i.e. \quad \frac{du}{d\delta_1}\bigg|_{\delta_1=\delta_1{}^\star} > 0$$

provided

$$\bar{x}^4 \neq \frac{\beta_1}{\beta_2} \quad \text{and} \quad \lambda_3(\delta_1) = -b_1(\delta_1) \neq 0.$$

We summarize the above results in the following theorem -

THEOREM : Suppose $\bar{E} = (\bar{x}_1, \bar{x}_2, \bar{y})$ exists, $A < 0, D < 0, E > 0, F > 0$ and $\delta_1{}^\star$ be a positive root of the equation $b_1b_2 = b_3$, then a Hopf bifurcation occurs as δ_1 passes through $\delta_1{}^\star$ provided $\dfrac{\beta_1}{\beta_2} \neq \bar{x}^4$.

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 the similar results.

5. Numerical Solutions : Here we see the effect of various parameters on the stability. Table-I gives the behaviour of stability with respect to β's and δ's. In Table $-$ I we have taken:

$\mu = 0.01, \alpha_1 = 0.05, \alpha_2 = 0.25, \varepsilon_1 = 0.1, \varepsilon_2 = 0.3, p_{12} = 0.5, p_{21} = 0.2$

and see the effect of δ_1 and δ_2 on the stability for $n = 2$. We also compare the bifurcation points when $n = 1$ and $n = 2$

Table - I

				Bifurcation Points	
β_1	$\beta2$	δ_1/δ_2	Stable	$n = 1$	$n = 2$
0.01	0.02	$\delta_2 = 0.3$	$0.78142 \le \delta_1 \le 1$	$\delta_2 = 0.75123$	$\delta_2 = 0.78142$
0.01	0.02	$\delta_1 = 0.5$	$0 \le \delta_2 \le 0.19196$	$\delta_1 = 0.19968$	$\delta_1 = 0.19196$
0.02	0.01	$\delta_2 = 0.3$	$0 \le \delta_1 \le 0.16651$	$\delta_2 = 0.16448$	$\delta_2 = 0.16651$
0.02	0.01	$\delta_1 = 0.5$	$0.90083 \le \delta_2 \le 1$	$\delta_1 = 0.91196$	$\delta_1 = 0.90083$
0.01	0.01	$\delta_1 = 0.5$	$0 \le \delta_2 \le 41291$	$\delta_1 = 0.42507$	$\delta_1 = 0.41291$

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

$\mu = 0.01, \alpha_1 = 0.05, \alpha_2 = 0.25, \beta_1 = 0.01, \beta_2 = 0.02, p_{12} = 0.5, p_{21} = 0.2$

Table - II

				Bifurcation Point
ε_1	ε_2	δ_1/δ_2	Stable	$n = 2$
0.04	0.03	$\delta_1 = 0.1$	$0.04331 \le \delta_2 \le 1$	$\delta_2 = 0.04331$
0.04	0.03	$\delta_2 = 0.3$	$0 \le \delta_1 \le 0.69273$	$\delta_1 = 0.69273$
0.1	0.3	$\delta_1 = 0.1$	$0 \le \delta_2 \le 0.00256$	$\delta_2 = 0.00256$
0.1	0.3	$\delta_2 = 0.003$	$0.11682 \le \delta_1 \le 1$	$\delta_1 = 0..11682$

In Tables I and II the bifurcation points are in fact the Hopf bifurcation points (where the model is stable, below / above these values the model is unstable / stable). The set of equations given in (2.2) for $n = 2$ have been integrated numerically for four cases given in Table-III with other variables as taken in the Table-I.

Table-III

Case	β_1	$\beta2$	δ_1	δ_2	Stable / Unstable
(i)	0.01	0.02	0.5	0.15	stable
(ii)	0.01	0.02	0.5	0.25	unstable
(iii)	0.02	0.01	0.5	0.95	stable
(iv)	0.02	0.01	0.5	0.75	unstable

Fig. 1

GROUP DEFENSE n = 2 ($\beta 1 < \beta 2$)
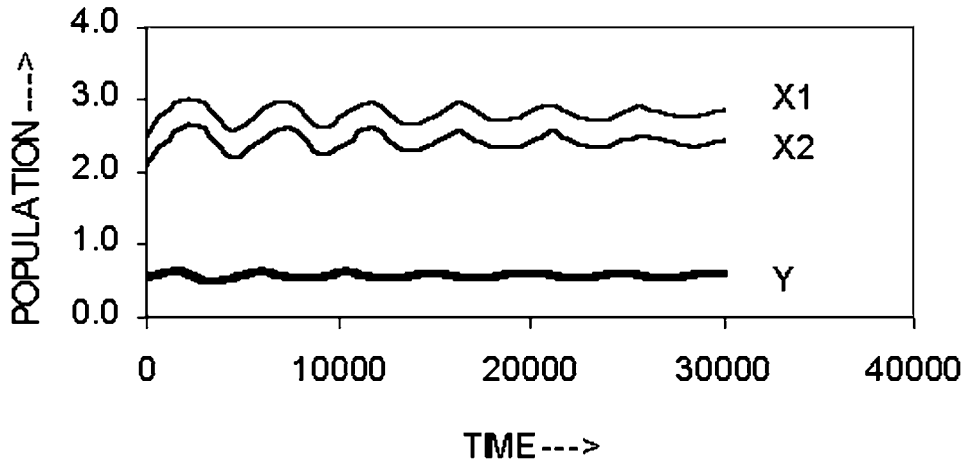
Fig. 2

GROUP DEFENSE n = 2 ($\beta 1 < \beta 2$)

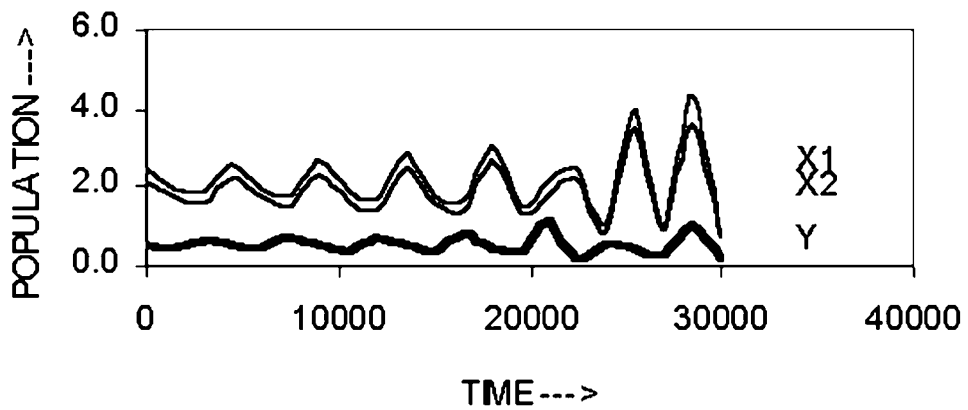**Fig. 3**

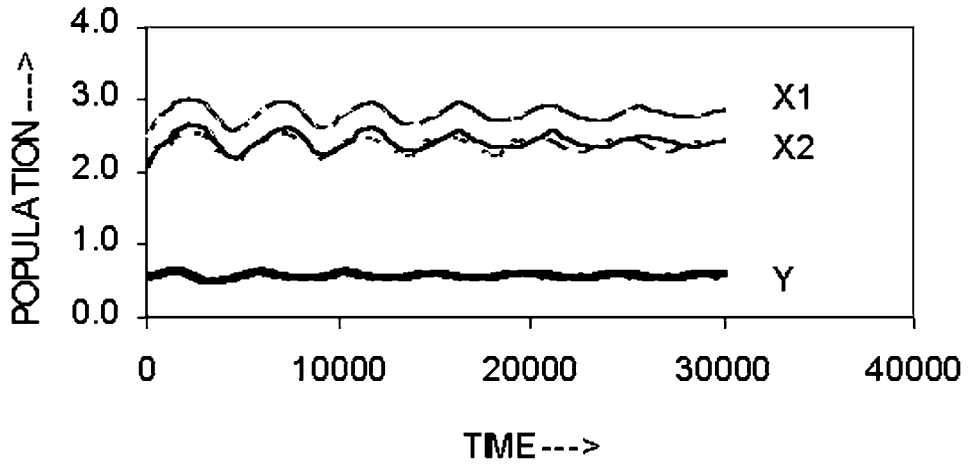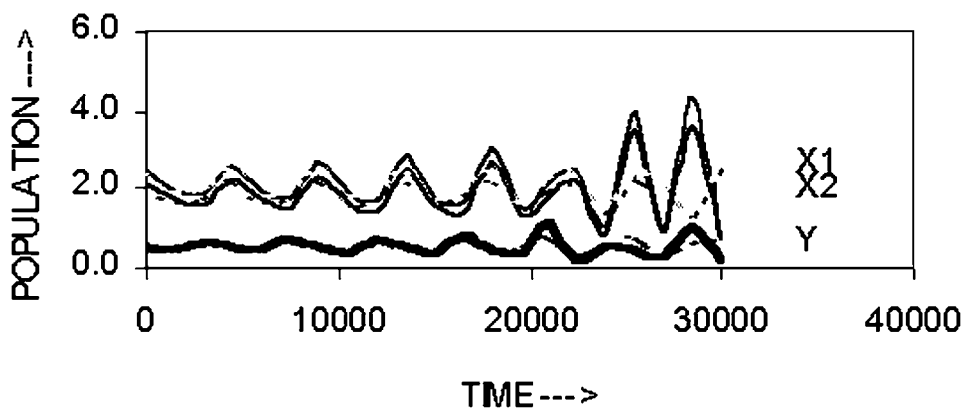GROUP DEFENSE (β1 > β2) n = 1 (---), n = 2 (___)

Fig. 4

GROUP DEFENSE (β1 > β2) n = 1 (---), n = 2 (___)

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 small perturbations. Figures 1 to 4 give the behaviour of x_1, x_2, y with respect to t in above four cases and as expected we get stable behavior in the figures 1 and 3 and unstable behavior in the figures 2 and 4. In figures 3 and 4 we have compared the results with $n = 1$ also.

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