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Switching Model with Two Habitats and a Predator Involving Group Defence

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Abstract

Switching model with one predator and two prey species is considered. The prey species have the ability of group defence. Therefore, the predator will be attracted towards that habitat where prey are less in number. The stability analysis is carried out for two equilibrium values. The theoretical results are compared with the numerical results for a set of values. The Hopf bifuracation analysis is done to support the stability results.

1. Introduction

Among related herbivore species, individuals of smaller species like Dik-dik will be vulnerable to a greater range of predator species and are less likely than larger to be able to defend themselves against, or to out run, predators. All small species avoid being detected by predators. Smaller species are likely to have to seek carefully their scare, scattered food item of high quality and form less cohesive and coordinated feeding groups. They live singly or in pairs and find their resources within a defended territory. Because they are small and vulnerable, they move and feed cautiously and slowly and never move far from cover. The size of the territory is presumably determined by the area that a pair can defend and by the availability of suitable food at the season of greatest scarcity. These species characteristically remain in one vegetation type in all seasons.

Larger species individuals feeding upon abundant, evenly dispersed, easily found items, are likely to be tolerating low quality food. They form enormous, rather formless, feeding aggregations of many thousands of animals. Major predators of zebra, buffalo, kongoni, toki and Thomson's gazelle are hyena, wild dog, lion, leopard and cheetas. They form groups for defence against predators and more likely depend upon self-defence, group defence, group alertness within a group and speed, to avoid being killed by a predator. Dense vegetation and broken terrain disrupt visual communication, and flat open country favour it. So such groups are more likely to be found where visual communication is favoured and where individuals can conform to the group, speed, and direction of movement. Unless the group remains cohesive and coordinated, the individual risks becoming an outstanding target. At all times individuals in groups must remain in communication and their speeds and directions when moving must vary little between individuals. Group defence 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 or disguise themselves when their number is large. Aggregation tends to reduce the risk of predation through simple dilution. Hence, doubling the local density of herbivores while predator density remains unchanged could lead to a halving of the mortality risk Hamilton [1], Bertram [2]. Of course, this assumes that predators do not seek out areas with very large prey density Schaller [3]. Pairs of musk-oxen can be successfully attacked by wolves but groups are rarely attacked Tener [4]. There are many examples of group defence – Yang and Humphrey [5], May and Robinson [6], Holmes and Bethel [7]. Herds remain well coordinated even under attack and individuals may benefit from the alertness and communication within the herd. Individuals tend to conform with their neighbour activities, and many hundreds, even thousands of wildebeest 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 [8]. Cheetah prefer to hunt single animals. Coursing predators select less healthy, old, sick and young prey and those who have lost their herds during migrations due to various reasons. Animals in poor condition and without group may reduce vigilance rates.

Each year, some one million wildebeest migrate across the Serengeti mara ecosystem D. Kreulen [9]. The crude cost of this movement, relative to neighbouring resident populations of wildebeest, is a 3% increment in mortality per year Sinclair [10]. The overall migratory pattern is thought to be related to food supply, which is itself dependent on an uneven distribution of rainfall Grzimek and Grzimek [11], Talbot and Talbot [12], Anderson and Talbot [13], Pennywick [14], Maddock [15]. In the dry season, they need to drink Jarman [16] and most home ranges include some riverbank habitat, which is preferentially used during that season. At the start of wet season, they move away from the rivers to occupy the woodlands where they feed predominantly on new green grass leaves, with some herbs, many of these plants may be annuals. As grasses mature and rains cease, their diet starts to include progressively more browse and they move into plant communities where browse is more. Movements could also be influenced by change in requirements for specific nutrients. Kreulen [17] noted that Serengeti wildebeest on their wet season range preferred a short-grass over a long grass habitat, and that calcium concentration were higher on the short grassland. Migration has also been attributed to the wildebeest's dislike of wet and sticky ground Talbot and Talbot [12], Anderson and Talbot [13]. 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 migrations.

In predator-prey environment, the predator prefers to feed itself in a habitat for some duration and then changes its preference to another habitat. This preferential phenomenon of change of habitat by the predator is called switching. There may be several reasons of switching of predators. For example – predator prefers to catch prey species in a habitat where they are in abundance but after some duration of heavy predation, when the prey species population starts declining, the predator changes its preference to another habitat. In this habitat prey species are more in number due to less predation i.e. the predator feeds preferentially on the most numerous prey species habitat. This is found to be the case when prey species is relatively smaller in size with little or insignificant defence capability with respect to predator, like small antelope and cruising predators to locate prey. Many examples may be cited where a predator prefers to prey species that is most abundant at any time, see Fisher-Piette [18], Lawton et al. [19] and Murdoch [20]. The mathematical models which have been generally proposed with such type of predator switching are those involving one predator with two prey species, e.g., Holling [21], Takashi [22], May [23], Murdoch and Oaten [24], and Raughgarden and Feldman [25], Tanskey [26, 27], Prajneshu and Holgate [28], Teramoto et al [29].

We are motivated by Serengeti ecosystem which can be divided into two habitats for wild life – (a) open southern grasslands with low rainfall that support a relatively low biomass of short-growing grasses and (b) wooded northern grasslands with higher rainfall that support tall, highly lignified grasses Braun [30], McNaughton [31, 32]. Rainfall is a key factor influencing primary productivity in both grassland types Braun [30] Sinclair [33]. McNaughton [31, 32] . All of the migratory species (wildebeest, zebra, and Thomson's gazelle) show similar seasonal shifts in habitats, using short grassland in the south during wet season and tall grasslands in the north during dry season Pennywick [14] and Maddock [15]. Their long range movements roughly correspond to seasonal transitions. We have considered a system having a predator species interacting with same prey species in two habitats. Prey 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 habitats. The prey species in both habitats have the ability of group defence but it will be effective in the habitat where the population of prey is large. The predator will be attracted toward s that habitat where prey are less in number.

Freedman and Walkowicz [34] considered a predator-prey system in which the prey population exhibits group defence. They described that if the carrying capacity of the prey population is sufficiently large and there is no mutual interference among predators then the predator population always goes to extinction. Freedman and Quan [35] studied predator-prey system with third population extinction. Shigui Ruan and Freedman [36] analyzed group defence in Gause-type models for three species. They gave criteria for persistence when there is no mutual interference and when there is mutual interference of predators. Freedman and Shigui Ruan [37] have discussed a three species food chain model with group defence. They have shown that model undergoes a sequence of Hopf bifurcations, using the carrying capacity of the environment as a bifurcation parameter.

This paper is organized as follows – Model formulation is in Section 2 and equilibrium and stability is discussed in Section 3. Section 4 includes Hopf bifurcation analysis with respect to δ (conversion rates of prey to predator) and ν (death rate of the predator). Bifurcation points and effect on stability for selected numerical data values are in Section 5. Final discussion and results are summarized in Section 6.

2. Prey-Predator model with group defence

We consider a class of Voltera predator prey model with group defence exhibition by the the prey of the form

$$\begin{aligned}
\dot{X}_1 &= (\alpha_1 - \epsilon_1)X_1 + \epsilon_2 p_{21} X_2 - \frac{\beta_1 X_2^2 Y}{(X_1 + X_2)}, \quad X_1(0) \geq 0,\\
\dot{X}_2 &= (\alpha_2 - \epsilon_2)X_2 + \epsilon_1 p_{12} X_1 - \frac{\beta_2 X_1^2 Y}{(X_1 + X_2)}, \quad X_2(0) \geq 0, \qquad (2.1)\\
\dot{Y} &= \left(-\nu + \frac{\delta_1 \beta_1 X_2^2}{(X_1 + X_2)} + \frac{\delta_2 \beta_2 X_1^2}{(X_1 + X_2)}\right) Y, \qquad Y(0) \geq 0,
\end{aligned}$$

where $\left(\cdot = \frac{d}{dt}\right)$, and $X_1(t), X_2(t)$ are prey species in the first and second habitats respectively and $Y(t)$ denote predator species which feed upon X_1 and X_2. Prey species are able to disperse among 2 different habitats at some cost to the population. Prey have the ability of group defence, so predator will go towards the habitats where prey population is less numerically. We consider that in the beginning, prey species are less in habitat 1 and so predator will be attracted towards them. For giving protection to their mates the prey species of the habitat 2 will rush towards habitat 1. In this way their strength in the habitat 2 will fall short and the predators will be attracted towards them. So to protect them prey start coming from hibitats 1 to 2. This implies a kind of switching from one habitat source of food to another habitat as the prey fall short alternately. Due to seasonal migration of prey species, none of the habitat population will be extinct. This situation is described by the above model where

β_i : Predator response rates towards the two prey X_1 and X_2 respectively.

δ_i : The rate of conversion of prey to predator.

ϵ_i : Inverse barrier strength in going out of the first habitat and the second habitat.

p_{ij} : The probability of successful transition from i^{th} habitat to j^{th} habitat.

α_i : Specific growth rate of the prey in the absence of predation.

ν : Per capita death rate of predator.

We assume that β_i, δ_i, ϵ_i, p_{ij}, α_i, and ν are positive constants and $\epsilon_1 p_{12} > \beta_2 Y(0)$, $\epsilon_2 p_{21} > \beta_1 Y(0)$, so that the X_1 and X_2 are not negative.

3. Analytical Solution

In this section, we proceed to analyze the system (2.1). We examine the equilibrium of this system. We obtain equilibrium solutions by setting time derivatives to zero. If in equations (2.1) $\bar{X}_1, \bar{X}_2, \bar{Y}$ are the equilibrium values of X_1, X_2, Y respectively, there are two possible equilibria, namely,

(i) $\bar{X}_1 = \bar{X}_2 = \bar{Y} = 0$, i.e., population is extinct and this always exists.

$$\text{(ii)}\quad \bar{X}_1 = \frac{\nu(\bar{X}+1)\bar{X}}{(\delta_1\beta_1+\delta_2\beta_2\bar{X}^2)}, \qquad \bar{X}_2 = \frac{\nu(1+\bar{X})}{(\delta_1\beta_1+\delta_2\beta_2\bar{X}^2)},$$

$$\bar{Y} = \frac{(1+\bar{X})\left\{(\alpha_2-\epsilon_2)+\epsilon_1 p_{12}\bar{X}\right\}}{\beta_2\bar{X}^2} \qquad \text{or equivalently}$$

$$\bar{Y} = \frac{(1+\bar{X})\left\{(\alpha_1-\epsilon_1)\bar{X}+\epsilon_2 p_{21}\right\}}{\beta_1}.$$

Here, $\bar{X} = \left(\bar{X}_1/\bar{X}_2\right)$ is a real positive root of the cubic equation,

$$\beta_2(\alpha_1-\epsilon_1)\bar{X}^3+\beta_2\epsilon_2 p_{21}\bar{X}^2-\beta_1\epsilon_1 p_{12}\bar{X}-\beta_1(\alpha_2-\epsilon_2)=0. \tag{3.1}$$

For equilibrium values $\left(\bar{X}_1,\bar{X}_2,\bar{Y}\right)$ to be positive, a positive real root of (3.1) must be bounded as

$$\frac{\epsilon_2-\alpha_2}{\epsilon_1 p_{12}} < \bar{X} < \frac{\epsilon_2 p_{21}}{\epsilon_1-\alpha_1}, \tag{3.2}$$

Since in the absence of the predator $\dfrac{dX_1}{dt} > 0$ and $\dfrac{dX_2}{dt} > 0$.

From Descarte's sign rule the equation (3.1) has unique positive root and hence the unique positive equilibrium solution of model (2.1).

(a) Stability Analysis of Equilibirum (i). Consider a small perturbation about the equilibrium level $X_1 = \bar{X}_1 + u$, $X_2 = \bar{X}_2 + v$, $Y = \bar{Y} + w$. Substituting these into the differentiale equation (2.1) and neglecting products of small quantities, we obtain stability matrix

$$\begin{pmatrix} \alpha_1-\epsilon_1 & \epsilon_2 p_{21} & 0 \\ \epsilon_1 p_{12} & \alpha_2-\epsilon_2 & 0 \\ 0 & 0 & -\nu \end{pmatrix}. \tag{3.3}$$

The characteristic equation of this matrix is

$$(\nu+\alpha)\left[\lambda^2-\lambda\{\alpha_1-\epsilon_1)+(\alpha_2-\epsilon_2)\}+(\alpha_1-\epsilon_1)(\alpha_2-\epsilon_2)-\epsilon_1\epsilon_2 p_{12}p_{21}\right]=0. \tag{3.4}$$

If $\alpha_1 < \epsilon_1$ and $\alpha_2 < \epsilon_2$ and $(\alpha_1-\epsilon_1)(\alpha_2-\epsilon_2) > \epsilon_1\epsilon_2 p_{12}\, p_{21}$, the equilibrium $\bar{X}_1 = \bar{X}_2 = \bar{Y} = 0$ is locally stable otherwise unstable.

(b) Stability Analysis of Equilibrium (ii). Following the above procedure as in (a) the stability matrix becomes:

$$\begin{pmatrix} A & -\dfrac{\bar{X}_1}{\bar{X}_2}A & -\dfrac{\beta_1\bar{X}_2^2}{(\bar{X}_1+\bar{X}_2)} \\ -\dfrac{\bar{X}_2}{\bar{X}_1}B & B & -\dfrac{\beta_2\bar{X}_1^2}{(\bar{X}_1+\bar{X}_2)} \\ C\bar{Y} & D\bar{Y} & 0 \end{pmatrix}. \tag{3.5}$$

The characteristic equation associated with the positive equilibrium $(\bar{X}_1, \bar{X}_2, \bar{Y})$ of this model is

$$\begin{aligned} &\lambda^3 - \lambda^2(A+B) + \lambda\left(\frac{C\beta_1\bar{Y}\bar{X}_2^2}{(\bar{X}_1+\bar{X}_2)} + \frac{D\bar{Y}\beta_2\bar{X}_1^2}{(\bar{X}_1+\bar{X}_2)}\right) \\ &\quad - \left(\frac{AC\beta_2\bar{Y}\bar{X}_1^3}{\bar{X}_2(\bar{X}_1+\bar{X}_2)} + \frac{BC\beta_1\bar{Y}\bar{X}_2^2}{(\bar{X}_1+\bar{X}_2)} + \frac{AD\bar{Y}\beta_2\bar{X}_1^2}{(\bar{X}_1+\bar{X}_2)} + \frac{BD\bar{Y}\beta_1\bar{X}_2^3}{\bar{X}_1(\bar{X}_1+\bar{X}_2)}\right) = 0, \end{aligned} \tag{3.6}$$

where

$$\begin{aligned} &A = (\alpha_1 - \epsilon_1) + \frac{\beta_1\bar{X}_2^2\bar{Y}}{(\bar{X}_1+\bar{X}_2)^2}, \qquad B = (\alpha_2 - \epsilon_2) + \frac{\beta_2\bar{X}_1^2\bar{Y}}{(\bar{X}_1+\bar{X}_2)^2}, \\ &C = \frac{(-\nu + 2\bar{X}_1\delta_2\beta_2)\bar{Y}}{(\bar{X}_1+\bar{X}_2)}, \qquad D = \frac{(-\nu + 2\bar{X}_2\delta_1\beta_1)\bar{Y}}{\bar{X}_1+\bar{X}_2}. \end{aligned}$$

Equation (3.6) can be written in the form

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0, \tag{3.7}$$

where

$$\begin{aligned} &a_1 = -(A+B), \qquad a_2 = \frac{C\beta_1\bar{Y}\bar{X}_2^2}{(\bar{X}_1+\bar{X}_2)} + \frac{D\bar{Y}\beta_2\bar{X}_1^2}{(\bar{X}_1+\bar{X}_2)}, \\ &a_3 = -\left(\frac{AC\beta_2\bar{Y}\bar{X}_1^3}{\bar{X}_2(\bar{X}_1+\bar{X}_2)} + \frac{BC\beta_1\bar{Y}\bar{X}_2^2}{(\bar{X}_1+\bar{X}_2)} + \frac{AD\bar{Y}\beta_2\bar{X}_1^2}{(\bar{X}_1+\bar{X}_2)} + \frac{BD\bar{Y}\beta_1\bar{X}_2^3}{\bar{X}_1(\bar{X}_1+\bar{X}_2)}\right). \end{aligned} \tag{3.8}$$

The Routh-Hurwitz stability criteria for the third order system is

(a) $a_1 > 0,\ a_3 > 0,$

(b) $a_1 a_2 > a_3.$

Hence, the equilibrium (ii) will be locally stable to small perturbations if it satisfies the following conditions

$$\begin{aligned} &A + B < 0, \\ &\left(C\bar{X}_1 + D\bar{X}_2\right)\left(A\beta_2\bar{X}_1^3 + B\beta_1\bar{X}_2^3\right) < 0, \\ &\left(\beta_1\bar{X}_2^3 - \beta_2\bar{X}_1^3\right)\left(BD\bar{X}_2 - AC\bar{X}_1\right) > 0. \end{aligned} \tag{3.9}$$

Here we observe that the stability of the model depends upon the conditions (3.2) and (3.9) together with various parameters.

4. Hopf Bifurcation Analysis

We investigate the Hopf bifurcation for the system (2.1) taking δ_1, δ_2 and ν as the bifurcation parameters.

First, we determine the criteria for Hopf bifurcation using δ_1 (rate of conversion of prey in the habitat 1 to predator) as the bifurcation parameter. For non zero equilibrium we look at the characteristic equation (3.7).

For $\quad A < 0, B < 0, C > 0, \quad$ and $\quad D > 0;$

a_1, a_2 and a_3 are positive in (3.8), clearly (3.7) has two purely imaginary roots iff $a_1a_2 = a_3$ for some value of δ_1 (say $\delta_1 = \bar{\delta}_1$). There exists a unique $\bar{\delta}_1$ such that $a_1a_2 = a_3$. Therefore there is only one value of δ_1 at which we have a Hopf bifurcation. Thus in the neighbourhood of $\bar{\delta}_1$ the characteristic equation (3.7) cannot have real positive roots. For $\delta_1 = \bar{\delta}_1$, we have

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

which has three roots

$$\lambda_1 = i\sqrt{a_2}, \qquad \lambda_2 = -i\sqrt{a_2}, \qquad \lambda_3 = -a_1.$$

The roots are in general of the form

$$\lambda_1(\delta_1) = p(\delta_1) + iq(\delta_1), \qquad \lambda_2(\delta_1) = p(\delta_1) - iq(\delta_1), \qquad \lambda_3(\delta_1) = -a_1(\delta_1). \tag{4.2}$$

To apply Hopf's bifurcation Theorem [38] to (2.1), we have to verify the transverality condition

$$Re\left(\frac{d\lambda_k}{d\delta_1}\right)_{\delta_1=\bar{\delta}_1} \neq 0, \qquad k = 1, 2. \tag{4.3}$$

Substituting $\lambda_k(\delta_1) = p(\delta_1) + iq(\delta_1)$ into (3.7) and calculating the derivative, we get

$$\begin{aligned} &R(\delta_1)p'(\delta_1) - S(\delta_1)q'(\delta_1) + T(\delta_1) = 0, \\ &S(\delta_1)p'(\delta_1) + R(\delta_1)q'(\delta_1) + U(\delta_1) = 0, \end{aligned} \tag{4.4}$$

where

$$\begin{aligned} &R(\delta_1) = 3p^2(\delta_1) + 2a_1(\delta_1)p(\delta_1) + a_2(\delta_1) - 3q^2(\delta_1), \\ &S(\delta_1) = 6p(\delta_1)q(\delta_1) + 2a_1(\delta_1)q(\delta_1), \\ &T(\delta_1) = p^2(\delta_1)a_1'(\delta_1) + a_2'(\delta_1)p(\delta_1) + a_3'(\delta_1) - a_1'(\delta_1)q^2(\delta_1), \\ &U(\delta_1) = 2p(\delta_1)q(\delta_1)a_1'(\delta_1) + a_2'(\delta_1)q(\delta_1). \end{aligned} \tag{4.5}$$

If $SU + RT \neq 0$ at $\delta_1 = \bar{\delta}_1$, then

$$Re\left(\frac{d\lambda_k}{d\delta_1}\right)_{\delta_1=\bar{\delta}_1} = -\frac{(SU + RT)}{2(R^2 + S^2)}\bigg|_{\delta_1=\bar{\delta}_1} \neq 0. \tag{4.6}$$

Now from equation (4.5)

$$SU + RT = a_1a_2' - a_3' \quad \text{at} \quad \delta_1 = \bar{\delta}_1, \tag{4.7}$$

where $a_2' = \dfrac{da_2}{d\delta_1}$ and $a_3' = \dfrac{da_3}{d\delta_1}$. $\bar{X}$ is a real positive root of equation (3.1) and independent of $\delta_1 \;\Rightarrow\; \dfrac{d\bar{X}}{d\delta_1} = 0$.

Substituting the values of a_1, a_2' and a_3' in equation (4.7), and using $a_1a_2 = a_3$ at $\delta_1 = \bar{\delta}_1$ which gives

$$\left(\beta_2\bar{X}^2 - \frac{\beta_1}{\bar{X}}\right)\left(\frac{BD}{\bar{X}} - AC\right) = 0 \quad \text{at} \quad \delta_1 = \bar{\delta}_1,$$

i.e., $\dfrac{BD}{AC} = \bar{X}$, at $\delta_1 = \bar{\delta}_1$ and value of $\dfrac{d\bar{X}_1}{d\delta_1}$, we obtain,

$$\begin{aligned}(SU+RT) &= \frac{2\bar{Y}^2}{(1+\bar{X})^2}\left(\frac{\beta_1}{\bar{X}} - \beta_2\bar{X}^2\right) B\beta_1\bar{X}_2 \\ &\times\left[\frac{\bar{X}_2\delta_1\beta_1 - \nu + \bar{X}_1\delta_2\beta_2 + \bar{X}(-\nu + 2\bar{X}_1\delta_2\beta_2}{-\nu + 2\bar{X}_1\delta_2\beta_2}\right].\end{aligned} \tag{4.8}$$

Since C and D are positive, the terms in square bracket are positive. Hence

$$Re\left(\frac{d\lambda_k}{d\delta_1}\right)_{\delta_1=\bar{\delta}_1} \neq 0 \quad \text{if} \quad \frac{\beta_1}{\beta_2} \neq \bar{X}^3, \quad k = 1, 2.$$

and $\lambda_3(\delta_1) = -a_1(\delta_1) \neq 0$.

We summarize the above results in the following:

Theorem. *Suppose $\bar{E}(\bar{X}_1, \bar{X}_2, \bar{Y})$ exists and $A < 0, B < 0, C > 0$ and $D > 0$. The system (2.1) exhibits a Hopf's bifurcation in the first octant leading to a family of periodic solutions that bifurcates $\bar{E}$ for a suitable value of δ_1 in a neighbourhood of $\bar{\delta}_1$ if $\dfrac{\beta_1}{\beta_2} \neq \bar{X}^3$.*

We can get a similar result when δ_2 is taken as a bifurcation parameter. Therefore the bifurcation points that we obtain in Table I of section 5 are the Hopf's bifurcation points.

Now we analyze the dynamics of (2.1) with respect to ν (per capita death rate of predator).

Similar to (4.3) we need to verify

$$Re\left(\frac{d\lambda_k}{d\nu}\right)_{\nu=\bar{\nu}} = -\frac{SU+RT}{2(R^2+S^2)} \neq 0, \qquad k = 1, 2, \tag{4.9}$$

where S, U, R, T have the similar expression as given in (4.4) but now these are functions of ν (instead of δ_1).

$$SU + RT = a_1 a_2' - a_3', \quad \text{where} \quad a_2' = \frac{da_2}{d\nu} \quad \text{and} \quad a_3' = \frac{da_3}{d\nu}.$$

Using the relation

$$\frac{d\bar{X}_1}{d\nu} = \frac{(\bar{X}+1)\bar{X}}{(\delta_1\beta_1 + \delta_2\beta_2\bar{X}^2)}, \tag{4.10}$$

we can show that

$$\frac{dC}{d\nu} = \frac{dD}{d\nu} = 0. \tag{4.11}$$

For purely imaginary roots of (3.7), $a_1 a_2 = a_3$ at $\nu = \bar{\nu}$, we get

$$(A+B)\left(\frac{C\beta_1}{\bar{X}} + D\beta_2\bar{X}\right) = AC\beta_2\bar{X}^2 + \frac{BC\beta_1}{\bar{X}} + AD\bar{X}. \tag{4.12}$$

Now using (4.10)–(4.12) we obtain the value of

$$a_1 a_2' - a_3' = 0. \tag{4.13}$$

Therefore, from (4.9), we get

$$Re\left(\frac{d\lambda_k}{d\nu}\right)_{\nu=\bar{\nu}} = 0, \qquad k = 1, 2,$$

i.e., if ν is a bifurcation parameter, there is no Hopf's bifurcation. Hence with respect ν the system (2.1) is either stable or unstable, the result which we obtain in Section 2.

5. Numerical Solutions

For illustration we have seen the effects of β's, δ's. The behaviour of stability with respect to β's and δ's is given in Table I.

Table I

$\nu = 0.01$, $\alpha_1 = 0.05$, $\alpha_2 = 0.25$, $\epsilon_1 = 0.1$, $\epsilon_2 = 0.3$, $p_{12} = 0.5$, $p_{21} = 0.2$

β_1	β_2	δ_1/δ_2	Bifurcation point	stable
0.01	0.02	$\delta_2 = 0.3$	$\delta_1 = 0.75123$	$0.75124 \leq \delta_1 \leq 1$
0.01	0.02	$\delta_1 = 0.5$	$\delta_2 = 0.19968$	$0 \leq \delta_2 \leq 0.19967$
0.01	0.03	$\delta_1 = 0.5$	$\delta_2 = 0.12949$	$0 \leq \delta_2 \leq 0.12948$
0.02	0.01	$\delta_2 = 0.3$	$\delta_1 = 0.16448$	$0 \leq \delta_1 \leq 0.16447$
0.01	0.01	$\delta_1 = 0.5$	$\delta_2 = 0.42507$	$0 \leq \delta_2 < 0.42506$
0.015	0.01	$\delta_1 = 0.5$	$\delta_2 = 0.66456$	$0.66457 \leq \delta_2 \leq 1$
0.02	0.01	$\delta_1 = 0.5$	$\delta_2 = 0.91196$	$0.91197 \leq \delta_2 \leq 1$

The last 2 columns give the values of δ_1/δ_2 at which the model is stable or unstable. In fact fourth column gives the bifurcation point (where the model is stable, below/above that value the model is unstable/stable). In the appendix we show that these bifurcation points are in fact Hopf bifurcation points. We have also done computations to see the effect of ν on the stability when $\beta_1 > \beta_2$. It is interesting to find that the model is either stable or unstable with respect to $\delta's.$ and Hopf bifurcation does not exist with respect to ν.

One can try similar analysis with respect to other parameters also.

The set of equations given in (2.1) have been numerically integrated for four cases given in Table II with other parameters as given in Table I.

Table II

Case	β_1	β_2	δ_1	δ_2	Stable/unstable
(i)	0.01	0.02	0.95	0.3	stable
(ii)	0.02	0.01	0.5	0.3	stable
(iii)	0.01	0.02	0.15	0.3	unstable
(iv)	0.02	0.01	0.6	0.3	unstable

These sets were picked up while doing the computations of analytical results in previous section where the behaviour of the model is shown in the last column. The initial conditions used are the corresponding equilibrium values in each case with slight perturbations. Figures 1 to 4 give the behaviour of X_1, X_2 and Y with respect to t in above four cases and as expected we get stable behaviour in the figures 1 and 2 and unstable behaviour in the figures 3 and 4. Figures 5 to 8 give the prey-predator dynamics when the model is stable whereas figures 9 to 12 represent the prey-predator dynamics when the model is unstable. These contours also support the predictions of Table II.

6. Summary and Discussion

We have considered a system having a predator species interacting with prey species in two habitats. Prey is of large size and migrate between two different habitats at some cost to its population in the sense that the probability of survival during a change of habitat is less than one. The predator can feed on either habitats. The prey species in both habitats have the ability of group defence but it will be effective in the habitat where the population of prey is large. Due to group defence ability of the prey, predator will select the habitat where prey might have insufficient defending capability (i.e. numerically less, old, sick, some youngs and those who might have lost their group during migration due to various reasons). The stability analysis has been carried out for both zero and nonzero equilibrium values. Nonzero equilibrium $\bar{X_1}$ and $\bar{X_2}$ for prey in first and second habitats depends on the death rate of predators i.e. if the death rate of the predator is high then values of $\bar{X_1}$ and $\bar{X_2}$ will increase or vice versa. $\bar{X_1}$ and $\bar{X_2}$ values will decrease if the predator response towards both habitats increases respectively. Nonzero equilibrium will be stable if it satisfies all three conditions of equation (3.9). Consider first the limit where $\epsilon_1 \to 0$ and $\epsilon_2 \to 0$, there is no movement of prey in or out of both habitat and so values of A and B in $(3.9)_1$, will be positive and nonzero equilibrium will become unstable. Hence, increasing the values of ϵ_1 and ϵ_2 always stabilizes. We can conclude from $(3.9)_2$ that stability increases for increasing values of conversion rate of prey species by predator. From $(3.9)_3$ we see that if $\bar{X_2} > \bar{X_1}$ then for stability it is more likely $\beta_1 > \beta_2$ provided $\dfrac{BD}{AC} > \bar{X}$ or vice versa i.e. if the equilibrium value of prey species in second habitat is more than first habitat then predator will attract towards first habitat because prey exhibits group defence and our model predicts this behaviour.

Hopf bifurcation analysis has been carried out for both models with respect to λ (conversion rate of prey to predator) as a parameter. In the sense of ecology, Hopf bifurcation has helped us in finding the existence of a region of instability in the neighbourhood of nonzero equilibrium, where prey species in both the habitats and predator will survive undergoing regular fluctuations. However, the conditions of Hopf bifurcation might not be satisfied due to changes in other parameters and change the steady state or otherwise.

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