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Analysis of a Predator–Prey System with Predator Switching

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In this paper, we consider an interaction of prey and predator species where prey species have the ability of group defence. Thresholds, equilibria and stabilities are determined for the system of ordinary differential equations. Taking carrying capacity as a bifurcation parameter, it is shown that a Hopf bifurcation can occur implying that if the carrying capacity is made sufficiently large by enrichment of the environment, the model predicts the eventual extinction of the predator providing strong support for the so-called 'paradox of enrichment'.

1. INTRODUCTION

The formulation of the model considered in this paper is motivated by the 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 supports tall, highly lignified grasses (Braun, 1973; McNaughton, 1979, 1985). Rainfall is a key factor influencing primary productivity in both grassland types (Braun, 1973; Sinclair, 1975; McNaughton, 1979, 1985). Each year, some 1 million wildebeest migrate across the serengeti mara ecosystem (Kreulen, 1979). The crude cost of this movement, relative to the neighbouring resident population of wildebeest, is a 3% increment in mortality per year (Sinclair, 1983). The overall migratory pattern is thought to be related to food supply, which is itself dependent on an uneven

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distribution of rainfall (Grzimek and Grzimek, 1960; Talbot and Talbot, 1963; Anderson and Talbot, 1965; Pennywick, 1975; Maddock, 1979). In the dry season, they need to drink (Jarman, 1972) and most home ranges include some river-bank habitat which is preferentially used during that season. At the start of the 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 (1975) noted that Serengeti wildebeest on their wet season preferred a short grass over a long grass habitat, and that calcium concentrations were higher on the short grassland. Migration has also been attributed to the wildebeest's dislike of wet and sticky ground (Talbot and Talbot, 1963; Anderson and Talbot, 1965). In this way herbivores maximize the growth potential of the vegetation through rotational grazing where movements are called seasonal migrations.

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 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. Here defended territory means the area where small prey species live and do not leave for feeding because they do not have defending capability with predators. 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 direction 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. Hence, doubling the local density of herbivores while predator density remains unchanged could lead to a halving of the mortality risk (Hamilton, 1971; Bertram, 1978). Of course, this assumes that predators do not seek out areas with very large prey density (Schaller, 1972). Pairs of musk-oxen can be successfully attacked by wolves but groups are rarely attacked (Tener, 1965). There are many examples of group defence—Yang and Humphrey (1975), May and Robinson (1985) and Holmes and Bethel (1972). 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, 1984). Cheetah prefer to hunt single animals. Coursing predators select less healthy, old, sick and young prey and those who have lost their herds during migration due to various reasons. Animals in poor condition and without group may reduce vigilance rates (Sinclair and Nortan-Griffths, 1979).

In a 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, a 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 greater 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 (1934), Lawton *et al*. (1974) and Murdoch (1969). 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 (1961), Takahashi (1964), May (1974), Murdoch and Oaten (1975), Roughgarden and Feldman (1975), Tansky (1976, 1978), Prajneshu and Holgate (1987) and Teramoto *et al*. (1979). In these papers switching has been found from protozen to birds. We presume this is a generic feature.

Freedman and Wolkowicz (1986) 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. Ruan and Freedman (1991) analyzed group defence in Gauss-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 Ruan (1992) have discussed a three species food chain model with group defence. They have shown that the model undergoes a sequence of Hopf bifurcations, using the carrying capacity of the environment as a bifurcation parameter.

   We consider a system having a predator species interacting with the 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 species is large. The predator will be attracted towards that habitat where prey species are less in number. A simple model is described here and some preliminary analysis is presented. This has provided an opportunity to determine a threshold parameter A and to show that prey–predator population can persist if and only if $A \leq 1$. If $A > 1$ then there will be Hopf bifurcation and population will survive undergoing regular fluctuations.

   Tansky (1978) investigated a mathematical model of a two prey and one predator system which has the switching property of predation of the following form:

$$\frac{dx}{dt} = \left(E_1 - \frac{az}{1 + (\frac{y}{x})^n} \right) x$$

$$\frac{dy}{dt} = \left(E_2 - \frac{bz}{1 + (\frac{x}{y})^n} \right) y$$

$$\frac{dz}{dt} = -E_3 + \frac{axz}{1 + (\frac{y}{x})^n} + \frac{byz}{1 + (\frac{x}{y})^n}, \qquad n = 1, 2, 3, \ldots$$

where x, y and z, denote the abundances of two kind of the prey species and a predator species respectively. The function $\frac{a}{1 + \left(\frac{y}{x}\right)^n}$ and $\frac{b}{1 + \left(\frac{x}{y}\right)^n}$ have a characteristic property of a switching mechanism. For instance, the intertidal snail Nucella lapillus preferably feeds barnacels when these are abundant but when mussels dominate, the latter are preferred (Fisher-Piette, 1934). This preferential phenomenon from a rare species to a most abundant one is known as switching. Lawton *et al.* (1974) have reported switching by two species of aquatic invertebrate predators, Notonecta and Ischnura, under laboratory conditions. They also established that switching is a normal feature of predator behaviour. More examples on switching can be found in Murdoch (1969). 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. For $n = 1$ these functions represent a simple multiplicative effect (Tansky, 1978) whereas for $n > 1$, these represent an effect that is stronger than the simple multiplicative effect (Prajneshu and Holgate, 1987). In the model below, we effectively assume $n = 1$ for simplicity. The case when $n > 1$ will be studied in a later paper.

2. THE MODEL

Let $x_1(t)$, $x_2(t)$ be the prey species at time t in the first and second habitats respectively and $y(t)$ at time t denotes predator species which feed upon x_1 and x_2. These are the state variables of our model. We are assuming that prey lives in two different habitats and predators live together away from prey species. Only at the time of attack they interact with each other. We are also assuming that predator species that disperses between two habitats have no barriers. We further assume that each prey species obeys logistic growth. Prey species are able to disperse among two different habitats at some cost to the population. Prey species have the ability of group defence, so predator will go towards the habitats where prey population is less numerically. This situation is described as given below:

$$\frac{dx_1}{dt} = x_1 g_1 \left(1 - \frac{x_1}{k_1}\right) + e_2 p_{21} x_2 - \frac{\beta_1 x_1 x_2 y}{x_1 + x_2}$$

$$\frac{dx_2}{dt} = x_2 g_2 \left(1 - \frac{x_2}{k_2}\right) + e_1 p_{12} x_1 - \frac{\beta_2 x_1 x_2 y}{x_1 + x_2} \qquad (2.1)$$

$$\frac{dy}{dt} = \left(-\mu + \frac{\delta_1 \beta_1 x_1 x_2}{x_1 + x_2} + \frac{\delta_2 \beta_2 x_1 x_2}{x_1 + x_2}\right) y$$

where

g_i the net effect or birth rate, death rate and the emigration rate.
k_i represents carrying capacities for prey species.
e_i inverse barrier strength in going out of the first habitat and the second habitat.
p_{ij} the probability of successful transition from ith habitat to jth habitat.
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.
μ per capita death rate of predator.

We have neglected dispersion since the spatially distribution is fairly uniform over the given habitats and, in order to investigate the possibility of the switching effects giving rise to oscillatory behaviour, we have assumed the dispersion coefficient is infinite. If it is infinite the effect demonstrated here will be preserved and even greater enriched behaviour will ensue. This will parallel the outcome for spatially distributed and uniform reacting/dispersing systems, that is 'spatial structure always enhances complexity and never decreases it'.

We assume that $\beta_i, \delta_i, e_i, p_{ij}, g_i, k_i$ and μ are positive constants. In order to avoid the mathematical complexity and to reduce the number of parameters, we consider here a considerably simplified case of the system (2.1), in which we assume the symmetrical relations $e_1 p_{12} = e_2 p_{21} = e$, $\beta_1 = \beta_2 = \beta$, $g_1 = g_2 = g$, $\delta_1 = \delta_2 = \delta$, $k_1 = k_2 = k$. Furthermore, if we transform $et = \tau$, we obtain

the equations

$$\frac{dx_1}{d\tau} = x_1 p_1 \left(1 - \frac{x_1}{k}\right) + x_2 - \frac{\beta' x_1 x_2 y}{x_1 + x_2}$$

$$\frac{dx_2}{d\tau} = x_2 p_1 \left(1 - \frac{x_2}{k}\right) + x_1 - \frac{\beta' x_1 x_2 y}{x_1 + x_2} \tag{2.2}$$

$$\frac{dy}{d\tau} = \left(-\mu_1 + \frac{\delta' \beta' x_1 x_2}{x_1 + x_2}\right) y$$

where $\frac{g}{e} = p_1$, $\frac{\beta}{e} = \beta'$, $\frac{\mu}{e} = \mu_1$, $2\delta = \delta'$.

3. STEADY STATES

We find the steady states of equation (2.2) by equating the derivatives on the left-hand sides to zero and solving the resulting algebraic equations. This gives two possible steady states

(i) $\bar{x}_1 = \bar{x}_2 = \bar{y} = 0$, i.e., the population is extinct and this always exists.
(ii)

$$\bar{x}_1 = \frac{\mu_1(\bar{x} + 1)}{\delta' \beta'}, \qquad \bar{x}_2 = \frac{\mu_1(\bar{x} + 1)}{\delta' \beta' \bar{x}}$$

$$\bar{y} = \frac{1 + \bar{x}}{\beta'} \left(p_1 - \frac{p_1}{k}\bar{x}_1 + \frac{1}{\bar{x}}\right) \qquad \text{or equivalently} \qquad (3.1)$$

$$\bar{y} = \frac{1 + \bar{x}}{\beta' \bar{x}} \left(p_1 - \frac{p_1 \bar{x}_2}{k} + \bar{x}\right).$$

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

$$p_1 \mu_1 \bar{x}^3 + (\delta' \beta' k - \delta' \beta' k p_1 + p_1 \mu_1)\bar{x}^2 + (\delta' \beta' k p_1 - p_1 \mu_1 - \delta' \beta' k)\bar{x} - p_1 \mu_1 = 0. \tag{3.2}$$

Obviously $\bar{x} = 1$ is the one real positive root of equation (3.2). The other two values of $\bar{x}$ will be real and positive if

$$\frac{\delta' \beta' k}{\delta' \beta' k - 2\mu_1} < p_1 \leq \frac{\delta' \beta' k}{\delta' \beta' k - 4\mu_1}. \tag{3.3}$$

When $x_1 = x_2$ there is one real positive root independent of k (carrying capacity). The other two roots will depend on k. The existence of Hopf bifurcation for those roots which satisfy equation (3.3) will be studied at a later stage. We note that the equation (3.3) implies that the net specific growth rate of the prey species should be greater than inverse barrier strength in going out of the first habitat and the second habitat.

4. STABILITY ANALYSIS

Consider small disturbances from the steady state and linearizing the resulting equation, we obtain the stability matrix from $(\bar{x}_1, \bar{x}_2, \bar{y}) = (0, 0, 0)$ (the extinct steady state) as follows:

$$\begin{pmatrix} p_1 & 1 & 0 \\ 1 & p_1 & 0 \\ 0 & 0 & -\mu_1 \end{pmatrix}. \tag{4.1}$$

The characteristic equation of this matrix is

$$(\mu_1 + \lambda)[(p_1 - \lambda)^2 - 1] = 0. \tag{4.2}$$

One eigenvalue will always be positive so the steady state $\bar{x}_1 = \bar{x}_2 = \bar{y} = 0$ is unstable.

Following the same procedure the stability matrix for the nonzero steady state $(\bar{x}_1, \bar{x}_2, \bar{y})$ becomes

$$\begin{pmatrix} \frac{-p_1\bar{x}_1}{k} - \frac{1}{\bar{x}} + \frac{\beta'\bar{x}\bar{y}}{(1+\bar{x})^2} & 1 - \frac{\beta'\bar{x}^2\bar{y}}{(1+\bar{x})^2} & \frac{-\beta'\bar{x}_1}{1+\bar{x}} \\ 1 - \frac{\beta'\bar{y}}{(1+\bar{x})^2} & \frac{-p_1\bar{x}_2}{k} - \bar{x} + \frac{\beta'\bar{x}\bar{y}}{(1+\bar{x})^2} & \frac{-\beta'\bar{x}_1}{1+\bar{x}} \\ \frac{\delta'\beta'\bar{y}}{(1+\bar{x})^2} & \frac{\delta'\beta'\bar{x}^2\bar{y}}{(1+\bar{x})^2} & 0 \end{pmatrix}. \tag{4.3}$$

The stability matrix equation (4.3) leads to the characteristic equation

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0, \tag{4.4}$$

where

$$a_1 = -L - M$$

$$a_2 = ML + Q\bar{x}^2 - (A-1)(A\bar{x}^2 - 1) + Q$$

$$a_3 = -MQ\bar{x}^2 + Q(1 - A\bar{x}^2) + Q(1-A)\bar{x}^2 - QL$$

$$L = \frac{-p_1\bar{x}_2}{k} - \bar{x} + A\bar{x}, \qquad M = \frac{-p_1\bar{x}_1}{k} - \frac{1}{\bar{x}} + A\bar{x}$$

$$Q = \frac{\delta'\beta'A\bar{x}_1}{1+\bar{x}} \qquad \text{and} \qquad A = \frac{\beta'\bar{y}}{(1+\bar{x})^2}. \tag{4.5}$$

By the Routh–Hurwitz criterion, it follows that all eigenvalues of equation (4.4) have negative real parts if and only if

$$a_1 > 0, \qquad a_3 > 0, \qquad a_1 a_2 > a_3.$$

Using $\bar{x} = 1$ a real positive root of equation (3.2) and assuming $A \leq 1$ gives
$L = M = \frac{-p_1\bar{x}_1}{k} - (1 - A) < 0$. Hence $a_1 > 0$.

Now $a_3 = -MQ + 2Q(1 - A) - QL > 0$.

To show that $a_1a_2 > a_3$

i.e., $-(L + M)(ML + Q - (A - 1)^2 + Q) > -MQ + 2Q(1 - A) - QL$

or $(L + M)(-ML + (A - 1)^2) - Q(L + M + 2 - 2A) > 0$.

Since $ML = L^2 = \frac{p_1^2\bar{x}_1^2}{k^2} - 2\frac{p_1\bar{x}_1}{k}(A - 1) + (A - 1)^2$, hence $-ML + (A - 1)^2 < 0$,
and $L + M + 2 - 2A = \frac{-2p_1\bar{x}_1}{k} < 0$.

Therefore $a_1a_2 > a_3$. Hence we have the following result.

THEOREM 1. *If $A \leq 1$ then the nonzero steady state $(\bar{x}_1, \bar{x}_2, \bar{y})$ is locally asymptotically stable.*

The above theorem discussed the case for $A \leq 1$. $A > 1$ implies $g > e$ where g is the specific growth rates of prey and e is the inverse barrier strength. This gives $\bar{y} > \frac{4e}{\beta}$. Hence $\beta < 4e$ since $\bar{y} > 1$. This means the predator response rates towards prey can be greater than the inverse barrier strength.

5. HOPF BIFURCATION ANALYSIS

We study the Hopf bifurcation for the system (2.2) when $\bar{y} > \frac{4}{\beta'}$, using carrying capacity k as the bifurcation parameter. The characteristic equation (4.4) has two purely imaginary roots if and only if $a_1a_2 = a_3$ for some value of k (say $k = \bar{k}$). At $k = \bar{k}$ the equation $a_1a_2 = a_3$ leads to $(A - 1 - L)[Q_1A + 2L(A - 1 + L)] = 0$ where $Q_1 = \delta'\beta'\bar{x}_1$ and $A - 1 - L \neq 0$. Hence

$$Q_1A + 2L(A - 1 + L) = 0 \qquad \text{at } k = \bar{k}. \tag{5.1}$$

On substitution this becomes

$$k^2\{\mu_1(p_1 + 1) + (p_1 - 1)^2\} + k\{-\mu_1p_1\bar{X}_2 - 5p_1(p_1 - 1)\bar{X}_2\} + 6p_1^2\bar{X}_2^2 = 0.$$

Therefore there will be at least one value of $k = \bar{k}$ provided that

$$\mu_1 + 5p_1 > 5 \qquad \text{and} \qquad \mu_1(14p_1 + 34) < \mu_1^2 + (p_1 - 1)^2,$$

at which we have Hopf bifurcation. For some $\epsilon > 0$ for which $\bar{k} - \epsilon > 0$, there is a neighbourhood of $\bar{k}$, say $(\bar{k} - \epsilon, \bar{k} + \epsilon)$ in which the characteristic equation cannot have real positive roots. For $k = \bar{k}$, we have

$$(\lambda^2 + a_2)(\lambda + a_1) = 0 \tag{5.2}$$

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

$$\lambda_1(k) = p(k) + iq(k)$$

$$\lambda_2(k) = p(k) - iq(k)$$

$$\lambda_3(k) = -a_1(k).$$

To apply the Hopf bifurcation theorem as stated in Marsden and McKracken (1976) we need to verify the transversality condition

$$\left.\frac{dp}{dk}\right|_{k=\bar{k}} \neq 0. \tag{5.3}$$

Substituting $\lambda_i(k) = p(k) + iq(k)$ into equation (4.4) and differentiating the resulting equation with respect to k and setting $p(\bar{k}) = 0$ and $q(\bar{k}) = \bar{q}_1$, we obtain

$$\frac{dp}{dk}(-3\bar{q}_1^2 + a_2) + \frac{dq}{dk}(-2a_1\bar{q}_1) = a_1'\bar{q}^2 - a_3'$$

$$\frac{dp}{dk}(2a_1\bar{q}_1) + \frac{dp}{dk}(-3\bar{q}_1^2 + a_2) = -a_2'\bar{q}_1 \tag{5.4}$$

where a_1, a_2 and a_3 are functions of k. Hence

$$\frac{da_1}{dk} = a_1', \qquad \frac{da_2}{dk} = a_2', \qquad \text{and} \qquad \frac{da_3}{dk} = a_3'.$$

Solving dp/dk and dq/dk, we have

$$\left.\frac{dp}{dk}\right|_{k=\bar{k}} = -\frac{a_2(a_1a_2' - a_3' + a_1'a_2)}{2(a_2^2 + a_1^2 a_2)}. \tag{5.5}$$

To establish Hopf bifurcation at $k = \bar{k}$, we need to show that

$$\left.\frac{dp}{dk}\right|_{k=\bar{k}} \neq 0 \qquad \text{i.e., } a_1a_2' - a_3' + a_1'a_2 \neq 0. \tag{5.6}$$

Substituting the values of a_1, a_2' and a_3' and using the equation (4.1), we get

$$a_1a_2' - a_3' = \frac{p_1\bar{x}_1}{k^2}[-11L^2 - 3L(A-1) - Q_1(L+1)] < 0$$

since $A > 1$, $L + 1 = A - \frac{p_1\bar{x}_1}{k} > 0$ because $\frac{p_1\bar{x}_1}{k} < 1$ for the growth rate to be positive for all values of x and $a_1'a_2 < 0$ we have $\left.\frac{dp}{dk}\right|_{k=\bar{k}} > 0$ and $\lambda_3(\bar{k}) = -a_1(\bar{k}) \neq 0$. We summarize the details in the following:
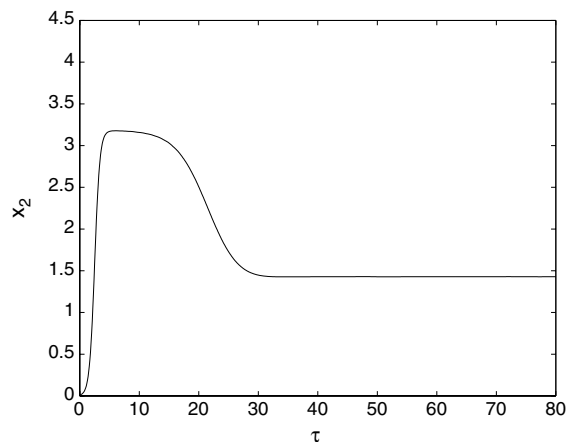
Figure 1. The graph of x_2 vs. τ for the parameter values $p_1 = 1.3, \beta' = 0.6, \mu_1 = 0.3, \delta' = 0.7$ and $k = 1.8$. These values give $A = 0.63$ implying stable behaviour for $A \leq 1$.

THEOREM 2. *There exists a value $\bar{k}$ such that the system* (2.2) *exhibits Hopf bifurcation in the first octant for $k > \bar{k}$ provided $A > 1$.*

The above theorem implies sufficiently increasing the prey carrying capacity can cause destabilization. That is predation is decreased or eliminated due to the ability of prey to defend or disguise themselves as their number increase.

6. NUMERICAL RESULTS

The set of equations given in (2.2) have been numerically integrated using the routine 'rk45' available in Matlab for three different cases. The initial conditions used are the corresponding equilibrium values in each case with slight perturbations. The results indicating the variation of prey species x_1, x_2 against time τ and the variation of predator species against time τ are given in Figs. 1–6 with the corresponding parameter and A values. Figures 1 and 2 give the behaviour of x_2 (same for x_1) and y with respect to τ when $A \leq 1$ and as expected, we get stable behaviour. Figures 3–6 give the effect of the parameter k on the stability when $A > 1$. We find that for $k > \bar{k}$ the equilibrium destabilizes and limit cycles arise by Hopf bifurcation while for $k < \bar{k}$ the equilibrium is stable.

7. SUMMARY AND CONCLUSIONS

We have formulated a simple model to describe the interaction of predator species with large size of prey species. The prey species live in two different habitats and exhibit group defence against the predator population. The group defence will be
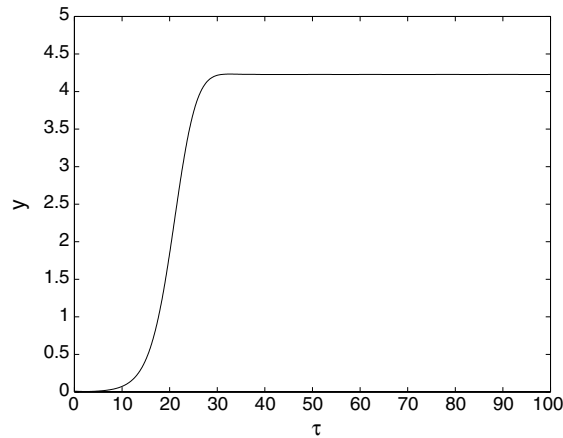
Figure 2. The graph of y vs. τ for the parameter values $p_1 = 1.3$, $\beta' = 0.6$, $\mu_1 = 0.3$, $\delta' = 0.7$ and $k = 1.8$. These values give $A = 0.63$ implying stable behaviour for $A \leq 1$.
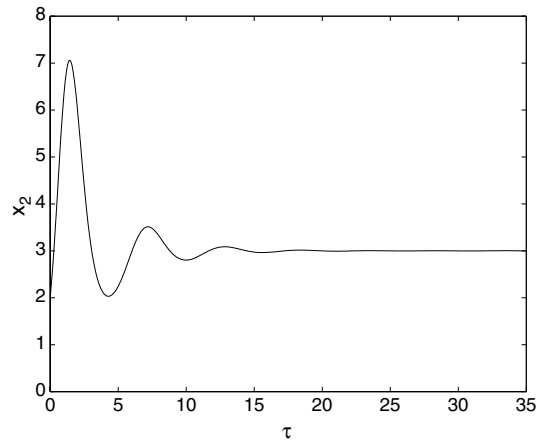

Figure 3. The graph of x_2 vs. τ for the parameter values $p_1 = 1.8$, $\beta' = 0.8$, $\mu_1 = 0.06$, $\delta' = 0.5$ and $k = 9$. These values give $A = 1.1$ implying stable behaviour for $A > 1$ and $k < \bar{k}$.

effective in the habitat where the population of prey species is large. The predator can feed on either habitats but it will be attracted towards that habitats where prey species are less numerically. Due to seasonal changes, prey species move from one habitat to other at the cost of mortality. We are assuming that predator species that disperse between two habitats in a heterogeneous environment and all the predators lump together and live away from prey species. At the time of attack they interact with prey and go back to their place. A number of authors have studied several mathematical models of prey–predator with predator switching, but to our knowledge all the models are based on insect, bird or fish systems. We are investigating in this model the prey–predator system as a mammal system. We have
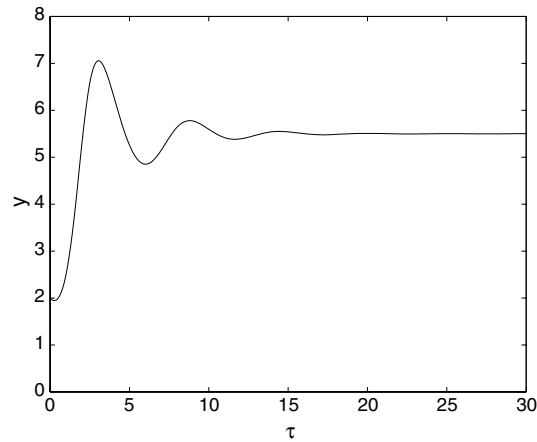
Figure 4. The graph of y vs. τ for the parameter values $p_1 = 1.8$, $\beta' = 0.8$, $\mu_1 = 0.06$, $\delta' = 0.5$ and $k = 9$. These values give $A = 1.1$ implying stable behaviour for $A > 1$ and $k < \bar{k}$.
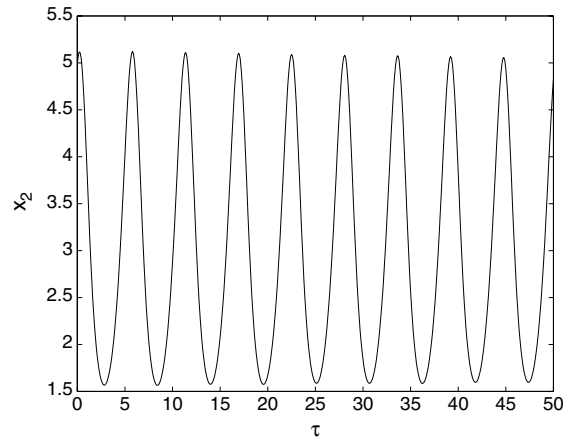

Figure 5. The graph of x_2 vs. τ for the parameter values $p_1 = 1.2$, $\beta' = 0.8$, $\mu_1 = 0.6$, $\delta' = 0.5$ and $k = 10^5$. These values give $A = 1.1$ implying limit cycles for $A > 1$ and $k > \bar{k}$.

been able to carry out a stability analysis for both zero and non-zero equilibrium points. The zero equilibrium $(0, 0, 0)$ will always be unstable. For non-zero equilibrium $(\bar{x}_1, \bar{x}_2, \bar{y})$ we have found a threshold condition, on the predator response rates towards prey. If this is sufficiently high in comparison to the inverse barrier strength, then there is a stability switch in the equilibrium solution leading to a supercritical Hopf bifurcation. This is at $A = 1$ in the above analysis (see the note after Theorem 1). If $A \leq 1$ then the system evolves towards a stable prey–predator state. If $A > 1$ and $k > \bar{k}$ the equilibrium destabilizes and stable limit cycles arise by Hopf bifurcations. In the region $A > 1$, we used the carrying capacity of
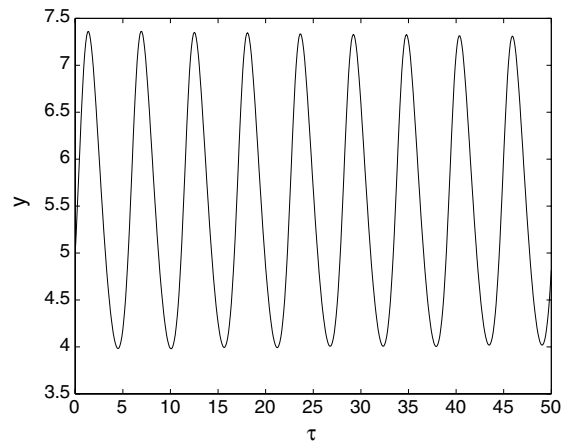
Figure 6. The graph of y vs. τ for the parameter values $p_1 = 1.2$, $\beta' = 0.8$, $\mu_1 = 0.6$, $\delta' = 0.5$ and $k = 10^5$. These values give $A = 1.1$ implying limit cycles for $A > 1$ and $k > \bar{k}$.

the environment as the bifurcations parameter and we were able to show that there may be a stable region in the neighbourhoods of the interior steady state where the steady state may be stable or unstable. In this way Hopf bifurcation has helped us in finding a region of instability in the neighbourhoods of nonzero equilibrium where the population will survive undergoing regular fluctuations.

We have shown numerically that if we increase the prey carrying capacity sufficiently large by enrichment of the environment it could lead to extinction of the predator population. The predator cannot survive on the prey species because their population is large and where group defence prevents the predator population increasing at any level. Our paper is another example supporting the warning that 'man must be careful in attempting to enrich the ecosystem in order to increase their food yield. There is a real chance that such activity may result in a decimation of the food species that are wanted in greater abundance'. This is the so-called paradox of enrichment.

The results and methodological framework outlined here will provide a useful tool to investigate the consequences for particular real systems to future work. We are assuming that predator species that disperse between two habitats in a heterogeneous environment do not involve a barrier. There could be mechanisms for predator survival such as the introduction of time delays or the introduction of a third population which interacts with the predator–prey system.

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