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SWITCHING EFFECT IN PREY-PREDATOR SYSTEMS IN THREE AND FOUR SPECIES MODELS

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July, 1999

Dedicated to
My Bou and Bana



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CERTIFICATE

The research work embodied in this dissertation entitled "SWITCHING EFFECT IN PREY-PREDATOR SYSTEMS IN THREE AND FOUR SPECIES MODELS", has been carried out at the School of Environmental Sciences, Jawaharlal Nehru University, New Delhi. The work is original and has not been submitted in part or in full, for any other degree or diploma of the University.

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INTRODUCTION

There is much interest in studying the dynamics of interacting species in theoretical ecology. The theoretical modelling efforts have contributed to developing an understanding of the temporal evolution of some simple ecosystems using techniques used in the study of non-linear dynamics. Mathematical models for ecosystems generally consist of a set of differential equations and are required to describe the interaction of different species of population. The dynamics of a community comprising populations of various interacting species may, in general, be modeled by no-linear set of differential equations. The models, the mathematical structures of which have increasingly been guided by field and laboratory observations, incorporate a variety of forms for the stabilising density-dependent or resource-limitation effects in the prey birth rates, and the destabilizing functional and numerical responses on the predator's behalf (corresponding to saturation of their appetites and reproductive capacities, and like effects) (May, 1972).

The first objective in analysing the models is to know the stability of the system which depends upon whether the equations describing the system are linear or nonlinear. Stability can be of equilibrium type or of periodic type. If the equations are linear, then we get the linear type of stability. In non-linear type of equations both the linear and non-linear types of stability are possible. The analysis of stability is done by using Routh-Horwitch criteria.

There may be prey or predator species in the ecosystem and there should be a proper balance between the prey and predator species for the existence of the system. The predator takes the prey which is easily found, and diverts it's attention to other prey species if the abundance of the previous one become scarce. This mechanism is generally referred as "switching" of predator. The occurrence of switching is widespread irrespective of the predator's phylogenetic position; switching has been found from protozoa to birds, and the same predator or similar predators may not switch depending on circumstances. Co-existence can be perpetuated in situations where one species grows faster than the second when the environment is rich and / or the population density is low, but grows slower than the other when there is severe competition, if the species are subjected to periodic reduction in numbers.

In the present work we are basically interested to see the equilibrium or oscillatory state in which the predator depends on three prey species proportionately. So to investigate this, we have first reviewed the two-prey-one-predator model given by Tansky (1978) and Prajneshu &

Holgate, P. (1987) by introducing the switching terms given by Tansky (1978). It is observed that there exists a stable equilibrium among the three species in the system.

The main objective of the proposed work is to see whether it is possible to get either stable equilibrium or oscillatory type of solutions by introducing a third prey species in a two-prey one-predator system keeping switching in mind. There may arise two cases of predator switching in the system, leading to two different kinds of models. The two models are studied by the computer simulations to see the switching and coexisting state, if any. As an illustration of our solution, time series trajectories of three and four species system are shown. We find that unlike in case of the three-species system, in the four-species system, all the four populations can coexist in a state where they all continue to show stable oscillatory behaviour after initial adjustments. Such stable oscillatory behaviour is indicative of the switching property of the predator. Note that this desirable behaviour follows in the four species case only for the second kind of switching terms. For the first kind of switching terms, the four species case also leads only to stable equilibrium as in case of the three species system, and not to stable oscillations. This suggests that our switching terms of the second kind may be more profitable for multispecies models where switching effects are desirable.

Chapter- I

1.1 Switching Effect: some definitions and mathematical functions

In any ecosystem, there may be a number of predator or prey species. The ecological balance is disturbed if the population of either prey or predator increases continuously. In the ecosystem, predation is an important factor in enhancing the diversity of plant and animal communities. Suppose there are two prey species which are competing in the system and one of them may exclude the other in the absence of predation. The mechanism by which a predator can enable these competing prey species to coexist is by directing a disproportionately large amount of it's attention to the prey species that is most abundant in the system at any instant of time. This mechanism may be termed as switching of predator for the most locally abundant prey species (May, 1977). In otherwords, the process or mechanism by which the predator directs it's attention disproportionately to the prey which is abundant in the ecosystem is said to be the switching of predator. Switching is part of the behavioural repertoire of many predators (Cornell, 1976). There are some cases in which all general predators may not switch (e.g. Coccinellids, Murdoch, and Marks, 1973; Cyclops, Jamieson, 1980; Mites, Santos, 1976). Switching may stabilise prey dynamics (Murdoch and Oaten, 1975); result in frequency-dependent selection that can maintain genetic polymorphism (Ayala and Campbell, 1974); and enable competing prey species to coexist (Roughgarden and Feldman, 1975; May, 1977).

A predator which feeds on more than one prey species does not attack all types of prey indiscriminately. The predator may stop searching entirely the prey which is scarce in the environment and begin to hunt, instead another, more abundant prey type (Matsuda, 1985). Several authors have studied the relationship between prey preference and prey frequencies (or densities) (e.g., Ivlev, 1961; Tinbergen, 1960; Murdoch, 1969; Royama, 1970; Murdoch and Oaten, 1975; May, 1977; Jacobs, 1977; Steele, 1974; Vance, 1978; Holling, 1961). The potential importance of switching as an ecological factor has prompted a number of theoretical studies of predator-prey dynamics. Such mathematical models which describe relationships between the preference and the prey frequency have been presented by Comins & Hassell (1976), Tansky (1978), Teramoto, Kawasaki & Shigesada (1979) extended models of the Nicholson-Bailey type. These (and other) studies show that switching can stabilize the system as a whole and permit the

coexistence of competitors.

Now let us consider a two prey one predator system where the outcome of feeding is characterised by both the total amount of prey intake and the proportion of the two preys captured for such a predator. The predator can feed on either species of prey. However, instead of choosing individuals at random, so that the chance that a predator would catch a member of one or other prey species is proportional to the abundance of the prey species, the predators feed preferentially on the most numerous species (Prajneshu and Holgate, P. 1987).

Let X_i be density of prey i, and N_i be the number of prey i eaten by the predator per unit time. So the Risk Index introduced by Tinbergen (1960) is written as,

$$K_i = N_i / X_i$$
 (i=1,2).....1

If prey species "i" is present in large number than that of j ($j \neq i$) species, then K_i would be greater than K_i . K_i also varies with the prey densities X_1 and X_2 .

Murdoch (1977), defined the term "switching" to refer to the case in which the relative amount of prey in the predator's diet increases more than proportionally to the relative prey density. Mathematically, or in otherwords, a predator is subjected to switching, when the relative preference K_1/K_2 increases with relative prey density X_1/X_2 .

Tansky (1978), presented another notation of "switching" that the Risk index of one prey grows with increase in it's density and declines with increasing density of the other prey, i.e.,

Various functional forms satisfying both relations (1) and (2) have been discussed by several authors are as follows:

Commins and Hassell (1976), adopted the following function:

$$K_1 = a / 2[1+s(x_1-x_2)/(x_1+x_2)], K_2 = b / 2[1-s(x_1-x_2)/(x_1+x_2)], (0 < s \le 1)....3$$

Where a&b are searching efficiencies (Predation coefficients) on the first and second prey species, respectively, and s is called the degree of switching.

Tansky (1978), Teramoto et al (1979) have adopted the following functions

$$K_1 = a [x_1^n / (x_1^n + x_2^n)], \quad K_2 = b [x_2^n / (x_1^n + x_2^n)], \quad n > 0............4$$

Where, n is called the intensity of switching. Switching becomes sharper as n increases.

Vance (1978) adopted the following functions

$$K_1 = a [x_1 / (x_1 + x_2)]^n, K_1 + K_2 = 1, n > 0.$$

Jacobs (1977) adopted the following functions for switching,

Steele (1974) adopted the switching functions,

Murdoch and Oaten (1975) adopted the switching functions,

$$K_{1} = \lambda p_{12} (p_{11} x_{1} + p_{12} x_{2}) / [p_{21} x_{1} + p_{12} x_{2} + \lambda \{ p_{11} p_{21} h_{1} x_{1}^{2} + p_{12} p_{21} (h_{1+} h_{2}) x_{1} x_{2} + p_{12} p_{22} h_{1} x_{2}^{2} - \dots - 8$$

Murdoch (1977) proposed the following function for switching

Sub-models for φ₁ include (from Murdoch and Oaten 1975; Murdoch, 1977

i)
$$\phi_1 = x_1 / (x_1 + x_2)$$

ii)
$$\phi_1 = c + dx_1 + x_2$$
, $c < \phi_1 < d > 0$

iii)
$$\phi_1 = c + (1-2c)[1 - \exp(-dx_1)]$$
(10)

iv)
$$\phi_1 = c + (1-2c)[x_1^n / (x_1^n + x_2^n)], n \ge 1$$

A more general function to describe the switching (Elton & Greenwood, 1970; and Baum, 1974)

is,
$$K_1 = af(x_1, x_2)$$
, $K_2 = bg(x_1, x_2)$ (11.1)
Where $f(x_1, x_2) = u^n x_1^n / [u^n x_1^n + (1-u)^n x_2^n]$, $g(x_1, x_2) = (1-u)^n x_2^n / [u^n x_1^n + (1-u)^n x_2^n]$, $n > 0, 0 < u < 1, \dots$ (11.2)

Here f and g are switching functions, which represent the fractional allocations of searching efforts to each prey; u is a measure of bias in switching response. The functional forms given by equation

(11.2) involve a wide range of switching effects from no switching to a sharp switching, especially "probabity matching" (n=1, u=0.5) and an optimal foraging strategy ($n\to\infty$, u=a/(a+b), see Mastuda, 1985). Note that f>g when $ux_1>(1-u)x_2$ and vice versa.

1.2 Review of Two-prey one predator system with introduction of switching terms

Some polyphagous predators switch their preference to prey depending on the relative prey frequencies. To elucidate how the switching property can evolve under natural selection, dynamical behaviours of two-prey and one-predator systems are analysed. It is assumed that the switching property can be characterised by intensity of switching (n). Comins & Hassell (1979) and Teramoto et al (1979) studied systems consisting of one predator and two prey species with a competitive interaction between the prey species, and concluded that switching enbales the competing prey species to co-exit, and that it dampens population fluctuations. We can consider varieties of such systems in which the two prey have still different types of interactions such as predation and symbiosis.

Extending the one-prey one predator equation of volterrra:

$$dN_1 / dt = (\epsilon_1 - k_1 N_2) N_1$$

$$dN_2 / dt = (-\epsilon_2 - k_2 N_1) N_2 \qquad (1)$$

to three species system in which there are two-preys and one-predator system, the equations are represented as:

$$dN_{1}/dt = (\epsilon_{1} - k_{1}N_{3}) N_{1} = \epsilon_{1} N_{1} - k_{1}N_{3} N_{1}$$

$$dN_{2}/dt = (\epsilon_{2} - k_{2}N_{3})N_{2} = \epsilon_{2} N_{2} - k_{2}N_{3} N_{2} \qquad (2)$$

$$dN_{3}/dt = (-\epsilon_{3} + k_{1}N_{1} + K_{2}N_{2}) N_{3} = \epsilon_{3}N_{3} + k_{1}N_{1}N_{3} + K_{2}N_{2}N_{3}$$

where

 N_1 and N_2 represent the population of two kinds of prey species,

N₃ represents the population of predator species.

 ϵ_1 (>0), ϵ_2 (>0) represent the intrinsic growth rate of the of population of N_1 , N_2 respectively.

 $-\epsilon_3$ (< 0) represents the intrinsic death rate of predator species, N_3 . k_1 and k_2 represent the predatory rates of the two prey species.

The switching mechanism of the predation which tsabilises the coexisting state of the three species system is introduced. The predatory rates can be replaced by functions given by different authors. Here Tansky (1978) has introduced the following functions for the predatory rates, k_1 , k_2 and we have adopted the functions of this kind for our three-prey -one-predator model discussed in next chapter. The switching functions given by Tansky., 1978 are as follows:

$$k_1(N_1, N_2) = af_1(N_1, N_2) = a / \{1 + (N_2 / N_1)^n\} = aN_1^n / (N_1^n + N_2^n)$$

$$k_2(N_1, N_2) = bf_2(N_1, N_2) = b / \{1 + (N_1 / N_2)^n\} = bN_2^n / (N_1^n + N_2^n)......(3), which explains characteristic property of switching mechanism.$$

Here f_1 represents the relative abundance (or rtelative density) of prey one to the total population and $f_1 + f_2 = 1$. The equation (2) can lead to extinction of one of the prey species which has smaller value of ϵ_i / k_i .

Here in deriving the above equations, for two-prey one-predator, it is assumed that (i), there is no intra- or inter-specific competitive interactions, between the prey species and (ii) the predation rate for a prey is proportional to the relative abundace of that prey species. This property is much amplified for large value of n, as shwon in the figure 1.

Murdoch (1969) suggested that a mechanism of this kind can have a stabilising effect on a population Murdoch's criterian is dissuced in the Appendix-II and this represents that the predator catches the more abundant prey species disproportionately. This was also discussed by Holling (1961), Murdoch and Oaten (1978). This model which is to be reviewed is a deterministic mathematical model given by Tansky (1978) and by Prajneshu & Holgate, P., 1987 separately.

When n = 0, there is no switching. So the above system has no feasible (possible) equilibrium point. When n = 1, the relative abundance (or density) of the prey species has a simple mulplicative effect. When $n \to \infty$, the predator species feeds exclusively on the more abundant prey species. For values of n lying between 1 and ∞ , the effect of density is stronger than the simple mulplicative, but weaker than the exclusivity.

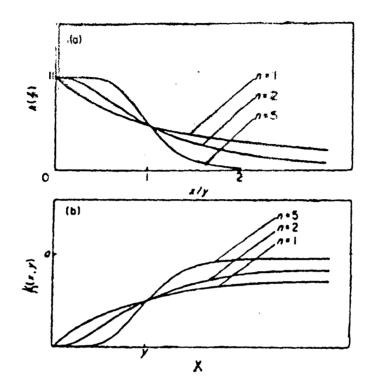


Figure-1 Predatory rate k(x,y): (a) function k(y/x) as a function of y/x, (b) function $k_1(x,y)$ as a function of x with a given value of y.

Stability of co-exiting state

Equation (2) cann't be solved explicitly. So we should proceed to a linear stability analysis. In calculating the equilibrium points let us take two cases: case - (i) where we have considered the simplest form of the function (3) with n = 1 (solved by Tansky, 1978); and case - (ii) where we have taken n > 0 (solved by Prajneshu & Holgate, P., 1987).

case (i):
$$n = 1$$

So the equations of (2) are rewritten as,

$$dN_1/dt = [\epsilon_1 - a N_3/\{1+(N_2/N_1)\}] N_1 = [\epsilon_1 - a N_3 N_1/(N_1+N_2)] N_1$$

$$dN_2/dt = [\epsilon_2 - bN_3/\{1+(N_1/N_2)\}] N_2 = [\epsilon_2 - bN_3 N_2/(N_2+N_1)] N_2 \qquad (4)$$

$$dN_3/dt = [-\epsilon_3 + a N_1/\{1+(N_2/N_1) + bN_2/\{1+(N_1/N_2)\}] N_3 = [-\epsilon_3 + (aN_1^2 + bN_2^2)/(N_1+N_2)/N_3]$$
let the feasible equilibrium point of the system be denoted by Q*, and is defined as:

$$Q^* = Q^* (N_1 N_2 N_3)$$
, where, $N_1 > 0$, $N_2 > 0$ and $N_3 > 0$.

Therefore four critical points at which the first order derivative is zero are:

- (i) the trivial point : (0, 0, 0)
- (ii) points at which one of the prey is absent and the other is in a standard Lotka Volterra equilibrium with predators: $(\epsilon_3/a, 0, \epsilon_1/a)$, $(0, \epsilon_3/b, \epsilon_3/b)$
- (iii) threee species coexistence point Q*

Calcutation of the point Q*

Case (i): n=1

For calculation of coexisting state or the equlibrium point, let us set the equation (4) to zero.

$$\Rightarrow \epsilon_{2} = b N_{3} N_{2} / \{ N_{1} + N_{2} \}$$

$$= \frac{dN_{3}}{dt} = 0$$

$$\Rightarrow [-\epsilon_{3} + a N_{1} / \{1 + (N_{2} / N_{1})\} + bN_{2} / \{1 + (N_{1} / N_{2})\}] N_{3} = 0$$

$$\Rightarrow -\epsilon_{3} + a N_{1} / \{1 + (N_{2} / N_{1})\} + bN_{2} / \{1 + (N_{1} / N_{2})\} = 0$$

$$\Rightarrow -\epsilon_{3} + a N_{1} N_{1} / (N_{1} + N_{2}) + b N_{2} N_{2} / (N_{1} + N_{2}) = 0$$

$$\Rightarrow \epsilon_{3} = (a N_{1}^{2} + b N_{2}^{2}) / (N_{1} + N_{2})$$

Now dividing equation (5) by equation (6), we have,

$$\epsilon_1/\epsilon_2 = a N_1/b N_2$$

$$\Rightarrow$$
 $N_1 = \epsilon_1 b N_2 / a \epsilon_2 \dots 8$

Here the bold letter represents the equilibrium points of the system.

Now substituing the value of N_1 from equation (8) in equation (7), we have,

$$\epsilon_{3} = (\mathbf{a} \, \mathbf{N}_{1}^{2} + \mathbf{b} \mathbf{N}_{2}^{2}) / (\mathbf{N}_{1} + \mathbf{N}_{2})$$

$$\Rightarrow \epsilon_{3} = [\mathbf{a}(\epsilon_{1} \, \mathbf{b} \, \mathbf{N}_{2} / \mathbf{a} \epsilon_{2})^{2} + \mathbf{b} \mathbf{N}_{2}^{2}] / [(\epsilon_{1} \, \mathbf{b} \, \mathbf{N}_{2} / \mathbf{a} \epsilon_{2}) + \mathbf{N}_{2}]$$

$$\Rightarrow \epsilon_{3} (\epsilon_{1} \, \mathbf{b} / \mathbf{a} \epsilon_{2} + \mathbf{1}) = \{ \epsilon_{1}^{2} \, \mathbf{b}^{2} / \mathbf{a} \epsilon_{2}^{2} + \mathbf{b} \} \, \mathbf{N}_{2}$$

$$\Rightarrow \mathbf{N}_{2} = \epsilon_{2} \epsilon_{2} (\epsilon_{1} \, \mathbf{b} + \mathbf{a} \epsilon_{2}) / \mathbf{b} * \{ \epsilon_{1}^{2} \, \mathbf{b} + \mathbf{a} \epsilon_{2}^{2} \}$$

Similarly the value of N_1 (from equation (8) is calculated to be

$$\begin{aligned} N_1 &= (\epsilon_1 \, b \, / \, a \epsilon_2) \, N_2 \\ \text{or,} \qquad N_1 &= (b \epsilon_1 \, / \, a \epsilon_2) \, (\epsilon_1 \, b \, + \, a \epsilon_2) \epsilon_3 \, \epsilon_2 \, / \, b \, * \, \{ \, \epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \} \\ \text{or,} \qquad N_1 &= \epsilon_1 \epsilon_3 \, (b \epsilon_1 \, + \, a \epsilon_2) \, / \, a \, * \{ \, \epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \} \, \dots \, 10 \\ \text{Now from equation (6),} \qquad N_3 &= (N_1 + N_2) \epsilon_2 \, / \, b N_2 \\ \text{or,} \qquad N_3 &= \epsilon_2 \big[\epsilon_3 \, \epsilon_2 \, \left(\epsilon_1 \, b \, + \, a \epsilon_2 \, \right) \, / \, b \, * \, \{ \, \epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \} \, + \epsilon_1 \epsilon_3 \, \left(b \epsilon_1 \, + \, a \epsilon_2 \, \right) \, / \, a \, * \{ \, \epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \} \, \big] \, / \, d \, + \, \left[\left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, \big] \, / \, d \, + \, \left[\left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, \big] \, / \, d \, + \, \left[\left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a \epsilon_2^{\, 2} \, \right) \, / \, a \, + \, \left(\epsilon_1^{\, 2} \, b \, + \, a$$

$$b[\ \epsilon_3 \epsilon_2 \ (\epsilon_1 \ b \ + a \epsilon_2 \) / \ b \ * \ \{\ \epsilon_1^2 \ b \ + a \epsilon_2^2 \ \}]$$
 or,
$$N_3 = \ (\epsilon_1 \ b \ + a \epsilon_2 \) / ab \(11)$$

Case (ii) : n > 0

Now setting equation (4) to zero, we have,

Now dividing equation (12) by equation (13), we have,

Now substituting the value of N₁ from equation (15) in equation (14), we have,

$$\Rightarrow \epsilon_3 = [a\{(\epsilon_1 b / a\epsilon_2)^{1/n} N_2\}^{1+n} + b N_2^{1+n}] / [\{(\epsilon_1 b / a\epsilon_2)^{1/n} N_2\}^n + N_2^n]$$

$$\Rightarrow N_2 = \{\epsilon_3 (a\epsilon_2)^{1/n} (\epsilon_1 b + a\epsilon_2) / ab\} / [\epsilon_2 (a\epsilon_2)^{1/n} + \epsilon_1 (b\epsilon_1)^{1/n}] \dots 16$$

Therefore, $N_1 = (\epsilon_1 b / a \epsilon_2)^{1/n} \{ \epsilon_3 (a \epsilon_2)^{1/n} (\epsilon_1 b + a \epsilon_2) / a b \} / [\epsilon_2 (a \epsilon_2)^{1/n} + \epsilon_1 (b \epsilon_1)^{1/n}]$

$$\Rightarrow N_1 = \{ \epsilon_3 (b\epsilon_1)^{1/n} (\epsilon_1 b + a\epsilon_2) / ab \} / [\epsilon_2 (a\epsilon_2)^{1/n} + \epsilon_1 (b\epsilon_1)^{1/n}] \dots 17$$

Now from equation (13), we have,

$$\mathbf{N_{3}} = \epsilon_{2} \{ \mathbf{N_{1}} + \mathbf{N_{2}} \}^{n} / (\mathbf{b} \mathbf{N_{2}}^{n})
\Rightarrow \mathbf{N_{3}} = \epsilon_{2} \{ \{ \epsilon_{3} (\mathbf{b} \epsilon_{1})^{1/n} (\epsilon_{1} \mathbf{b} + \mathbf{a} \epsilon_{2}) / \mathbf{a} \mathbf{b} \} / [\epsilon_{2} (\mathbf{a} \epsilon_{2})^{1/n} + \epsilon_{1} (\mathbf{b} \epsilon_{1})^{1/n}] + (\mathbf{a} \epsilon_{2})^{1/n} (\epsilon_{1} \mathbf{b} + \mathbf{a} \epsilon_{2}) / \mathbf{a} \mathbf{b} \} / [\epsilon_{2} (\mathbf{a} \epsilon_{2})^{1/n} + \epsilon_{1} (\mathbf{b} \epsilon_{1})^{1/n}] \}^{n} / \mathbf{b} (\{ \epsilon_{3} (\mathbf{a} \epsilon_{2})^{1/n} (\epsilon_{1} \mathbf{b} + \mathbf{a} \epsilon_{2}) / \mathbf{a} \mathbf{b} \} / [\epsilon_{2} (\mathbf{a} \epsilon_{2})^{1/n} + \epsilon_{1} (\mathbf{b} \epsilon_{1})^{1/n}])^{n}
\Rightarrow \mathbf{N_{3}} = \epsilon_{2} / \mathbf{b} + \epsilon_{1} / \mathbf{a} \qquad (18)$$

Analysis of the equilibrium points

The equilibrium points of the above system are given by the equations (10), (9) and (11) when n = 1, and by equations (17), (16) and (18) when n > 0 for N_1 , N_2 , N_3 respectively.

The equlibrium at (0, 0, 0) is trivially unstable.

Now let us discuss the stability of the point $(\epsilon_3/a, 0, \epsilon_1/a)$ for which y = 0 and n = 1. So the eigenvalue equation for this point is:

$$\begin{vmatrix} 0-\lambda & \epsilon_1 & -\epsilon_3 \\ 0 & -\lambda & 0 \\ \epsilon_1 & -\epsilon_1 & -\lambda \end{vmatrix} = 0$$

or,
$$-\lambda (\lambda^2 - 0) - \epsilon_1 (0 - 0) - \epsilon_3 (0 + \lambda \epsilon_1) = 0$$

or, $-\lambda^3 - \lambda \epsilon_1 \epsilon_3 = 0$
or, $-\lambda (\lambda^2 + \epsilon_1 \epsilon_3) = 0$
or, $-\lambda = 0$ or $\lambda^2 + \epsilon_1 \epsilon_3 = 0$
or, $\lambda = (-\epsilon_1 \epsilon_3)^{1/2} = i(\epsilon_1 \epsilon_3)^{1/2}$

The pair of purely imaginary roots here show that the existence of neutral equilibrium of the two species Lotka- Volterra Model in respect of perturbations in N_1 and N_3 From the above equilibrium point analysis, it corresponds the fact that if the predators maintain equilibrium with prey ,i.e., N_1 the population can be invaded by a small number of prey, N_2 with intrisic varible ϵ_2 . Same analysis can be applied to other two equilibrium point. It can also be seen that all the boundary equilibrium points, (0, 0, 0), $(\epsilon_3 / a, 0, \epsilon_1 / a)$ are unstable. In another process it can also

be seen that all the boundary equilibrium points (0, 0, 0), $(\epsilon_3 / a, 0, \epsilon_1 / a)$ and $(0, \epsilon_3 / b, \epsilon_2 / b)$ are unstable, because $k_1(x, 0) = k_2(0, y) = 0$. If the notations of Comins & Hassell (1978) is used then the boundary equilibrium points can be stable, because the predator still allocates it's searching effort to a scarce prey even when this prey is absent. Such a situation would correspond to "apparent competition" by Holt (1977).

Local stability analysis of the point Q*(see the appendix-I)

The eigenvalue equation for studying the stability of three species co-existing point is:

$$\begin{vmatrix} -a\{N_{1}N_{2}N_{3}/(N_{1}+N_{2})^{2}\}-\lambda & N_{1}^{2}N_{3}a/(N_{1}+N_{2})^{2} & -aN_{1}^{2}/(N_{1}+N_{2}) \\ bN_{2}^{2}N_{3}/(N_{1}+N_{2})^{2} & -b\{N_{1}N_{2}N_{3}/(N_{1}+N_{2})^{2}\}-\lambda & -bN_{2}^{2}/(N_{1}+N_{2}) \\ \{2aN_{1}(N_{1}+N_{2})-(aN_{1}^{2}+bN_{2}^{2})\}N_{3}/(N_{1}+N_{2})^{2} & \{2bN_{2}(N_{1}+N_{2})-(aN_{1}^{2}+bN_{2}^{2})\}N_{3}/(N_{1}+N_{2})^{2} & -\lambda \end{vmatrix}$$

20

The local stability analysis can be done by using the Routh-Hurwitch criteria. The polynomial equation corresponding to equation (20) is,

All eigen values have negative real parts if and only if the coefficient of equation (21) satisfy the following relations.

$$c_2 = \{N_3/(N_1 + N_2)^3\} * \{a^2 N_1^4 + 2 a^2 N_1^3 N_2 - 2ab N_1^2 N_2^2 + 2b^2 N_1 N_3^3 + b^2 N_2^4 \dots 23$$

$$c_3 = ab N_1 N_2 N_3^2 (a N_1^2 + b N_2^2)/(N_1 + N_2)^3 > 0$$

$$Now, c_1c_2 - c_3 = N_1N_2N_3^2\{a^3\ N_1^4 + 2\ a^3\ N_1^3\ N_2 - 3ab\ (a + b)N_1^2\ N_2^2 + 2b^3N_1\ N_3^3 + b^3N_2^4\}/(N_1 + N_2)^5$$

Now by replacing $aN_1 = n_1$ and $bN_2 = n_2$, the above equation ca be reduced to

$$c_1c_2-c_3=N_1\ N_2\ N_3^2\ (\ n_1-\ n_2)^2\{n_1N_1+2(n_1N_2+n_2\ N_1\)+\ n_2\ N_2\ \}\ /\ (N_1+N_2\)^5\ge\ 0\(24)$$

Thus it is proved that the system (4) has a locally stable coexisting equilibrium point (N_1, N_2, N_3) except the special case when $n_1 = n_2$ or $\epsilon_1 = \epsilon_2$ for n = 1.

The eigenvalue equation for studying the stability of the three species co-existing point can be found out from the Jacobian for n > 1 which is as follows:

$$\begin{pmatrix} (N_1^n + N_2^n)^{-2} \\ -an \ N_1^n \ N_2^n & an \ N_1^{n+1} \ N_2^{n-1} \ N_3 & -a \ N_1^{n+1} \ (N_1^n + N_2^n) \\ bn \ N_1^{n-1} \ N_2^{n+1} \ N_3 & -bn \ N_1^n \ N_2^n N_3 & -b \ N_2^{n+1} \ (N_1^n + N_2^n) \\ N_1^{n-1} \ N_3 \{a \ N_1 \ (N_1^n + N_2^n) & N_2^{n-1} \ N_3 \{b \ N_2 \ (N_1^n + N_2^n) & 0 \\ +n \ N_2^n \ (aN_1 - bN_2)\} & +n \ N_1^n \ (bN_2 - aN_1)\} \end{pmatrix}$$

The characteristic equation of (25) is $\lambda^3 + c_1 \lambda^2 + c_2 \lambda + c_3 = 0$, where $c_1 = n (a + b) N_1^n N_2^n N_3 (N_1^n + N_2^n)^{-2} > 0$

$$\begin{split} c_2 &= N_3 \; \{ (N_1^{\;n} \; + \; N_2^{\;n})^{\!-\!2} \, (a^2 \; N_1^{\;2n+1} \! + b^2 \, N_2^{\;\;2n+1}) \; + \\ & \qquad \qquad \qquad n \; N_1^{\;n} N_2^{\;n} \; (b \; N_2 - a \; N_1) (b N_2^{\;n} - a N_1^{\;n}) \} (N_1^{\;n} \; + \; N_2^{\;n})^{\!-\!3} \\ c_3 &= abn \; N_1^{\;n} \; N_2^{\;n} \; N_3^{\;2} \; (a N_1^{\;n+1} \! + b \; N_2^{\;n+1}) \; (N_1^{\;n} \; + \; N_2^{\;n})^{\!-\!3} > 0 \end{split}$$

Now
$$c_1 c_2 - c_3 = n N_1^n N_2^n N_3^2 (a N_1^n - b N_2^n) (N_1^n + N_2^n)^{-5 *}$$

$$\{ (N_1^n + N_2^n) (a^2 N_1^{n+1} - b^2 N_2^{n+1}) + n(a+b) N_1^n N_2^n (a N_1 - b N_2) \} \dots (26)$$

On substituing the values of N_1 , N_2 , N_3 from equations (17), (16), (18) respectively we obtain that $c_1 c_2 - c_3 = g((\epsilon_1 / \epsilon_2) - 1)\{(1 + b\epsilon_1 / (a\epsilon_2))[(b\epsilon_1 / (a\epsilon_2))^{1+1/n} - b^2 / a^2] +$

$$n (1 + b / a)[(b\epsilon_1 / (a\epsilon_2))^{1+1/n} - b^2\epsilon_1 / (a^2\epsilon_2)]$$
(27),

where g > 0.

Since $c_3 > 0$, the pruduct of the eigenvalues of (25) is negative. Thus if all the roots are real, one or all three must be negative. If two roots are complex conjugate their product is positive and the

third root must be real and negative. Thus in each case there is at least one real root. We consider three cases, depending on whether $c_1 c_2$ is greater than, or less than c_3 .

(i)
$$c_1 c_2 > c_3$$

This implies $c_2 > c_1^{-1} c_3 > 0$. Thus all the coefficients of the characteristic equation of (25) are positive, and none of its roots can have non-negative real part. Thus the system is stable.

(ii)
$$c_1 c_2 = c_3$$

The characteristic equation, $\lambda^3 + c_1 \lambda^2 + c_2 \lambda + c_1 c_2 = 0$ is reduced to

$$(\lambda + c_1) * (\lambda^2 + c_2) = 0.$$

As in the previous one, $c_2 > 0$ and the cubic has one real negative and two purely imaginary roots. Hence the system is oscillatory with period $2\Pi / (c_2)^{1/2}$.

(iii)
$$c_1 c_2 < c_3$$

At $\lambda = -c_1$, $\lambda^3 + c_1 \lambda^2 + c_2 \lambda + c_3 = c_3 - c_1 c_2 > 0$, while as $\lambda \to \infty$, the cubic approaches minus infinity. Hence there is one negative real root α in $(-\infty, c_1)$. The sum of the other two roots is therefore $-c_1 - \alpha > 0$, and their product is positive. Hence they are either real and positive, or complex conjugate pair with positive real part. Thus the system is unstable.

For n> 1, stability, divergence and oscullatory behaviour are possible at the three species equilibrium expression (27) is certainty if

either (i)
$$\epsilon_1/\epsilon_2 > 1$$
 and $\epsilon_1/\epsilon_2 \ge (b/a)^{n-1}$(28.1)

or (ii)
$$\epsilon_1/\epsilon_2 < 1$$
 and $\epsilon_1/\epsilon_2 \le (b/a)^{n-1}$(28.2)

In particular the system is stable if either (i) $\epsilon_1 > \epsilon_2$ and $a \ge b$, or (ii) $\epsilon_1 < \epsilon_2$ and $a \le b$.

A necessary condition for instability is that both parts of (28) should be violated. This occurs if

$$1 < \epsilon_1 / \epsilon_2 \le (b/a)^{n-1} \qquad (29)$$

or if similar inequalities hold with prey species interchanged. If (29) is true, it is necessary and sufficient that the factor in curly brackets in (27) should be negative, and this condition can be written $(a/b)^{1-1/n}(\epsilon_1/\epsilon_2)^{1+1/n} < \{1 + n(1+b/a)(\epsilon_1/\epsilon_2)\} / \{1 + n(1+b/a)\}$.

As $n \to \infty$, that is as we approach the situation where the predator feeds exclusively on the most abundant prey, the latter inequality approaches the limiting form a / b < 1.

Discussion

It is a known that the switching property of predation, which generally means that the predatory rate diminishes at low population of prey, has a stabilising effect for the prey predator system. Analysing the dyna mical system (4), it is observed that the predation pressure which has the switching property given by equation (3) has the effect to stabilise this three-species system and it always attains stable coexisting equilibrium state. This model does not exhibit the dynamical switching behaviour of predation. The stabilising effect is enhanced if the bias in switching resopnse is toward the prey with a lower intrinsic growth rate. The computer simulation shows that any trajectory starting from a point in the positive quadrant converges to Q* (i.e. the stable equilibrium point). The coexistence of the two prey species changesteh numerical value of the equilibrium point. The system is always stable if the prey species with the higher relative birth rate suffers the higher relative rate of consumption by the predators in the absence of the other. When the prey are present in the correct abundance and also the correct relative proportions, their tendency to grow through birth is balanced by predation.

The stable equilibrium state is shown in the figure -2 and figure -3 with different set of parameters and different coexisting point.

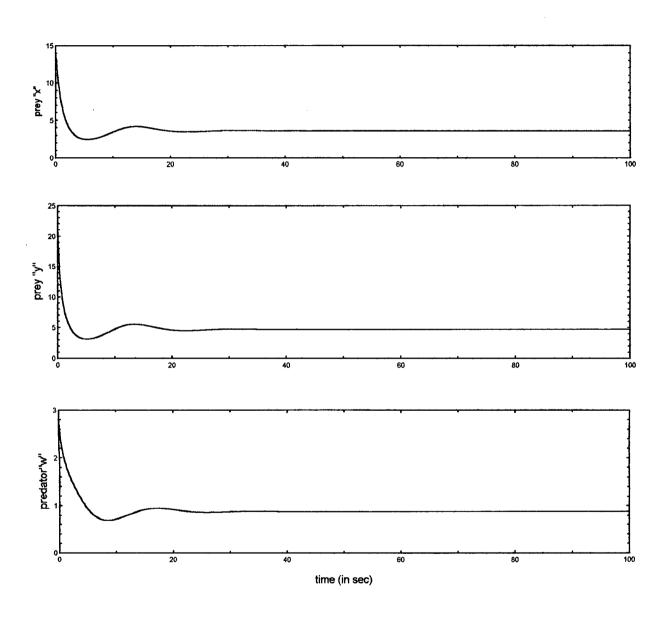


Figure 2: Variation of prey-predator population with time.

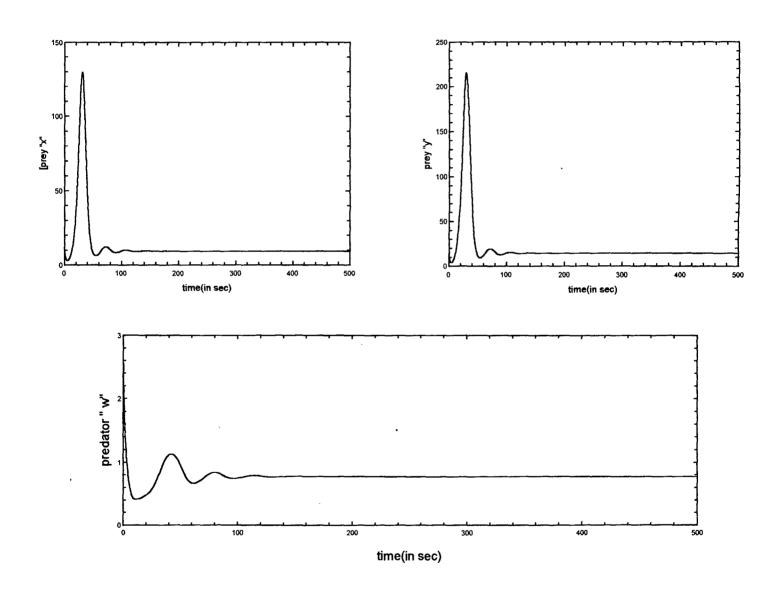


Figure 3: Variation of prey-predator population with time.

Chapter-II

ANALYSIS OF SWITCHING EFFECT IN THREE PREY ONE PREDATOR SYSTEM

In the last chapter, we have discussed the two-prey- one-predator system given by Tansky (1978) and Prajneshu & Holgate, P. (1986). In the present discussion, we have just extended to a three prey-one-predator system, keeping the switching terms in mind. Now the equations describing the system of prey-predator interaction are:

$$dN_{1}/dt = (\epsilon_{1} - k_{1}N_{4}) N_{1}$$

$$dN_{2}/dt = (\epsilon_{2} - k_{2}N_{4}) N_{2}$$

$$dN_{3}/dt = (\epsilon_{3} - k_{3}N_{4}) N_{3}$$

$$dN_{4}/dt = (-\epsilon_{4} + k_{1}N_{1} + K_{2}N_{2} + k_{3}N_{3}) N_{4}$$

Where

N₁, N₂, N₃ represent the population of three prey species and N₄ represent the population of predator species in the ecosystem.

 ϵ_1 (>0), ϵ_2 (>0), ϵ_3 (>0) represent the intrinsic growth rates of N_1 , N_2 , N_3 species respectively and ϵ_4 represents intrinsic death rate of N_4 species.

n represents the intensity of switching (switching becomes sharper as n increses).

 f_1 , f_2 , f_3 , are called the switching functions representing the fractional allocations of searching efforts to each prey.

a,b, c are the searching efficiencies or predation coefficients on the first, second, and third prey species respectively.

Here the predatory rates k_1 , k_2 , k_3 can be replaced by suitable switching terms. There may arise two cases of switching for each of predatory rates k_1 , k_2 , k_3 due to the presence of three prey species. In one case, i.e. case-A the switching terms or the predatory rates can be taken as follows:

$$k_1 = a f_1(N_1, N_2, N_3) = a / \{1 + (N_2/N_1)^n + (N_3/N_1)^n\} = aN_1^n/(N_1^n + N_2^n + N_3^n)$$

$$k_2 = bf_2(N_1, N_2, N_3) = b / \{1 + (N_1/N_2)^n + (N_3/N_2)^n\} = bN_2^n/(N_1^n + N_2^n + N_3^n)$$

In the other case, i.e. case-B the predatory rates can be substituted by the functions which are as follows:

$$k_1 = a f_1(N_1, N_2, N_3) = a / \{1 + (N_2 * N_3 / N_1)^n\} = a N_1^n / (N_1^n * N_3^n)$$

$$k_2 = bf_2(N_1, N_2, N_3) = b / \{1 + (N_1 * N_3 / N_2)^n\} = bN_2^n / (N_1^n * N_3^n)$$

Now let us analyse the case-A. The other case is discussed after this by the computer simulations. Thus by substituting equation(2) in equation(1), we get the following set of equations:

$$dN_1/dt = [\epsilon_1 - a N_4/\{1+(N_2/N_1)^n+(N_3/N_1)^n\}] N_1$$

$$dN_2/dt = [\epsilon_2 -bN_4/\{1 + (N_1/N_2)^n + (N_3/N_2)^n\}] N_2$$

$$dN_3/dt = [\epsilon_3 - cN_4/\{1+(N_1/N_3)^n+(N_2/N_3)^n\}]N_3$$

$$dN_4/dt = \left[-\epsilon_4 + a N_1 / \left\{ 1 + (N_2/N_1)^n + (N_3/N_1)^n \right\} + bN_2/ \left\{ 1 + (N_1/N_2)^n + (N_3/N_2)^n \right\}$$

$$+cN_3/\{1+(N_1/N_3)^n+(N_2/N_3)^n\}]N_4$$

Before going on to the further mathematical study of equations, it should be pointed out that we have built a model in which the predator can feed prey preferentially on one or the other prey according to circumstances. However, while a population is evolving under its interdynamics, there will be no point at which an actual switching in preferred prey occurs while the population evolves along a continuous trajectory. There will generally be an approach to a relative rate of

predation between the species that is, for a convergent trajectory, in balance. Actual switching would occur if the population were forced to a suitable path by external factors.

CALCULATION OF EQUILIBRIUM POINTS

For calculation of coexisting state or the equlibrium point, let us set the equations of equation (4) to zero. Now let us solve equation (4) for (i) case I: n = 1 and (ii) case II: n > 0

Case I: n=1

$$+cN_3/\{1+(N_1/N_3)+(N_2/N_3)\}=0$$

$$\Rightarrow -\epsilon_4 + a N_1 N_1 / (N_1 + N_2 + N_3) + bN_2 N_2 / (N_1 + N_2 + N_3) +$$

$$cN_3 N_3/(N_1+N_2+N_3)=0$$

Now dividing equation (5) by equation (6), we have,

$$\dot{\epsilon}_1/\epsilon_2 = a N_1/b N_2$$

$$\Rightarrow$$
 $N_1 = \epsilon_1 b N_2 / a \epsilon_2 \dots 9$

Here the bold letter represents the equilibrium points of the system.

Now again dividing equation (6) by equation (7), we have,

$$\epsilon_2 / \epsilon_3 = b N_2 / c N_3$$

$$\Rightarrow N_3 = \epsilon_3 b N_2 / c \epsilon_2 \dots 10$$

Now substituing the values of N_1 and N_3 from equations (9) and (10) in equation (8), we have,

$$\epsilon_4 = \mathbf{a}(\epsilon_1 \mathbf{b} \mathbf{N}_2 / \mathbf{a}\epsilon_2)^2 + \mathbf{b} \mathbf{N}_2^2 + \mathbf{c}(\epsilon_3 \mathbf{b} \mathbf{N}_2 / \mathbf{c}\epsilon_2)^2 / \left[(\epsilon_1 \mathbf{b} \mathbf{N}_2 / \mathbf{a}\epsilon_2) + \mathbf{N}_2 + (\epsilon_3 \mathbf{b} \mathbf{N}_2 / \mathbf{c}\epsilon_2) \right]$$

$$\implies \epsilon_4 (\epsilon_1 \mathbf{b} / \mathbf{a}\epsilon_2 + 1 + \epsilon_3 \mathbf{b} / \mathbf{c}\epsilon_3) = \{ \epsilon_1^2 \mathbf{b}^2 / \mathbf{a}\epsilon_2^2 + \mathbf{b} + \mathbf{b}^2 \epsilon_3^2 / \mathbf{c}\epsilon_3^2 \} \mathbf{N}_2$$

$$\Rightarrow N_2 = \epsilon_4 \epsilon_2 \left(\epsilon_1 b c + a c \epsilon_2 + \epsilon_3 b a \right) / \left\{ \epsilon_1^2 b c + c a \epsilon_2^2 + a b \epsilon_3^2 \right\} \dots 11$$

Therefore, from equation (9), we get,

$$N_1 = (\epsilon_1 \epsilon_4 / a) (\epsilon_1 b c + ac\epsilon_2 + \epsilon_3 ba) / (\epsilon_1^2 bc + ca\epsilon_2^2 + ab\epsilon_3^2)$$
12,

by substituing the value of N_2 from equation (11).

Similarly the value of N₃ is calculated to be

$$N_3 = (\epsilon_4 \epsilon_3 / c) (\epsilon_1 b c + ac\epsilon_2 + \epsilon_3 ba) / (\epsilon_1^2 bc + ca\epsilon_2^2 + ab\epsilon_3^2) \dots 13$$

Now from equation(4),

$$N_4 = \epsilon_2 \{ N_1 + N_2 + N_3 \} / bN_2$$

or,
$$N_4 = (bc \in \{1, +ac \in \{2, +ab \in \{3\}\}\}) / abcor$$
,

or,
$$N_4 = \epsilon_1 / a + \epsilon_2 / b + \epsilon_3 / c$$
(14)

case (ii): n > 0

Now setting equation(4) to zero, we have,

$$dN_1/dt = 0$$



Now again dividing equation (16) by equation (17), we have,

$$\epsilon_2 / \epsilon_3 = b N_2^n / c N_3^n$$

$$\Rightarrow N_3 = (\epsilon_3 b / c\epsilon_2)^{1/n} N_2 \qquad ... \qquad ...$$

Now substituing the values of N_1 and N_3 from equations (19) and (20) in equation (18), we have.

$$\epsilon_4 = a[\{(\epsilon_1 b/a\epsilon_2)^{1/n} N_2\}^{n+1} + bN_2^{n+1} + c\{(\epsilon_3 b/c\epsilon_3)^{1/n} N_2\}^{n+1}] / [\{(\epsilon_1 b/a\epsilon_2)^{1/n} N_2\}^n + N_2^n + \{(\epsilon_3 b/c\epsilon_2)^{1/n} N_2\}^n]$$

$$\Rightarrow \epsilon_4 \left(\epsilon_1 \text{ bc } + \text{ac} \epsilon_2 + \epsilon_3 \text{ ab} \right) / \text{ac} \epsilon_2 = b N_2 \left\{ c^{1/n} \epsilon_1^{(n+1)/n} b^{1/n} + a^{1/n} c^{1/n} \epsilon_2^{(n+1)/n} + b^{1/n} a^{1/n} \epsilon_3^{(n+1)/n} \right\} / \left\{ (ac)^{1/n} \epsilon_2^{(n+1)/n} \right\}$$

$$\begin{split} N_2 &= \epsilon_4 \left(\epsilon_1 \text{ bc } + ac\epsilon_2 + \epsilon_3 \text{ ab} \right) \left\{ (ac)^{1/n} \epsilon_2^{-(n+1)/n} \right\} / \left(abc\epsilon_2 \right) \left\{ c^{1/n} \epsilon_1^{-(n+1)/n} b^{1/n} + a^{1/n} c^{1/n} \epsilon_2^{-(n+1)/n} \right\} \\ &+ b^{1/n} a^{1/n} \epsilon_3^{-(n+1)/n} \right\} \end{split}$$

$$N_1 = (\epsilon_1 \ b / \ a \epsilon_2)^{1/n} \in {}_{4} (\epsilon_1 \ bc \ + \ ac \epsilon_2 \ + \epsilon_3 \ ab) \{ (ac)^{(1-n)/n} \epsilon_2^{-1/n} \} \ / \ b \{ (cb)^{1/n} \epsilon_1^{-(n+1)/n} \}$$

$$+(a c)^{1/n} \epsilon_2^{(n+1)/n} +(b a)^{1/n} \epsilon_3^{(n+1)/n}$$

$$N_1 = \epsilon_1^{1/n} \in {}_{4} (\epsilon_1 bc + ac\epsilon_2 + \epsilon_3 ab) \{ (bc)^{(1-n)/n} \epsilon_2^{-1/n} \} / a \{ (cb)^{1/n} \epsilon_1^{-(n+1)/n} \epsilon_2^{-(n+1)/n} \} / a \{ (cb)^{1/n} \epsilon_1^{-(n+1)/n} \} / a \{ (cb)^{1/n} \epsilon_1^{-(n+1)/n} \epsilon_2^{-(n+1)/n} \} / a \{ (cb)^{1/n} \epsilon_1^{-(n+1)/n} \} / a \{ (cb)^{1/n}$$

$$+(a c)^{1/n} \epsilon_2^{(n+1)/n} + (b a)^{1/n} \epsilon_3^{(n+1)/n}$$
22

$$N_3 = (\epsilon_3 \, b / c \epsilon_2)^{1/n} \epsilon_4 (\epsilon_1 \, bc + ac \epsilon_2 + \epsilon_3 \, ab) \{ (ac)^{(1-n)/n} \epsilon_2^{-1/n} \}$$

$$/ b \{ (cb)^{1/n} \epsilon_1^{(n+1)/n} + (ac)^{1/n} \epsilon_2^{(n+1)/n} + (ba)^{1/n} \epsilon_3^{(n+1)/n} \}$$

or,
$$N_3 = \epsilon_1 \epsilon_3^{1/n} (b \ a)^{(1-n)/n} (\epsilon_1 \ bc + ac\epsilon_2 + \epsilon_3 \ ab) / c \{ (cb)^{1/n} \epsilon_1^{(n+1)/n} + (a \ c)^{1/n} \epsilon_2^{(n+1)/n}$$

$$+(b a)^{1/n} \epsilon_3^{(n+1)/n}$$
23

Again
$$N_4 = \epsilon_2 \{ N_1^n + N_2^n + N_3^n \} / bN_2^n$$

The equlibrium points of the system are given by equations (12), (11), (13), (14) when n=1 and by equations (22), (21), (23), (24) when n > 0

case - B

Now taking the other set of equations for predatory rates k_1 , k_2 , k_3 given by equation (3) the prey predator interaction in equation (1) gets transformed to

$$dN_{1}/dt = \{ \epsilon_{1} - a N_{4} / \{1 + (N_{2} * N_{3} / N_{1})^{n} \} N_{1}$$

$$dN_{2}/dt = \{ \epsilon_{2} - bN_{4} / \{1 + (N_{1} * N_{3} / N_{2})^{n} \} \} N_{2}$$

$$dN_{3}/dt = \{ \epsilon_{3} - cN_{4} / \{1 + (N_{1} * N_{2} / N_{3})^{n} \} \} N_{3}$$

$$dN_{4}/dt = \{ -\epsilon_{4} + a N_{1} / \{1 + (N_{2} * N_{3} / N_{1})^{n} \} + bN_{2} / \{1 + (N_{1} * N_{3} / N_{2})^{n} \}$$

$$+ cN_{3} / \{1 + (N_{1} * N_{2} / N_{3})^{n} \} N_{4}$$

The equilibrium points of equation (25) can be worked out by setting the above equation to zero. But instead of solving the equation analytically, we have solved it by using BASICS programing. In the discussion part we have compared the results of equation (25) with that of equation (4). The above equations are solved by computer simulations using the Rungei-Kutta fourth method.

Analysis of the equilibrium points

The equilibrium points of the above system are given by equations (12), (11), (13), (14) for N_1, N_2, N_3, N_4 respectively for $n = (1, and by equations (22), (21), (23), (24) for <math>N_1, N_2, N_3, N_4$ respectively for n > 0 for case-A

CASE:A.

The same kinds of equilibrium points are found here which were found in the review of two prey one predator model as this the extended switching functions of Tansky. The trivial point is (0, 0, 0, 0); and other points can be found out by putting any of the prey or predator species to zero. The local stability analysis of Q* can be done by using the Routh-Hurwitz Criteria. This

can be done by expanding the equilibrium point around its neighbourhood by Taylor series expansion and then neglecting the higher order terms. We know the characteristic equations for the matrix $(A - \lambda I) = 0$ in k- species is,

$$f(\lambda) = \lambda^{k} + c_{1} \lambda^{k-1} + c_{2} \lambda^{k-2} + \dots + c_{k} = 0$$

where k is the number of species in the system, and for our system it is 4. So the eigenvalue equation for k = 4 is,

$$f(\lambda) = \lambda^4 + c_1 \dot{\lambda}^3 + c_2 \lambda^2 + c_3 \lambda + c_4 = 0$$

The Hurwitz matrix for four species is given below:

$$H_1 = (C_1), H_2 = \begin{bmatrix} C_1 & 1 \\ C_3 & C_2 \end{bmatrix}$$
 $H_3 = \begin{bmatrix} C_1 & 1 & 0 \\ C_3 & C_2 & C_1 \\ 0 & 0 & C_3 \end{bmatrix}$

$$H_{4} = \begin{bmatrix} C_{1} & 1 & 0 & 0 \\ C_{3} & C_{2} & C_{1} & 1 \\ C_{5} & C_{4} & C_{3} & C_{2} \\ C_{7} & C_{6} & C_{5} & C_{4} \end{bmatrix}$$

The Routh-Hurwitz conditions of stability are:

$$C_1 > 0$$
, $C_3 > 0$, $C_4 >> 0$, $C_3 C_1 C_2 > C_3 + C_1^2 C_4$

It is found that the system is locally stable i.e. if we disturb the system, then the system rebounds back to its original state. The coexisting poin satisfy the above conditions. So it is a stable equlibrium point.

Chapter-IV

RESULTS AND DISCUSSION

Results of the Four Species System

(I) For case: A (Graph No. 4 - 12.1)

From the above model we observed the following points:

- 1. The system always attains a equilibrium state for a particular set of parameters.
- 2. When n = 1 or $n \ge 0$, switching phenomena is observed.
- 3 When n=2, or n>2, then some sort of switching property is observed but with the lapse of time this system leads to a stable equilibrium point. In all cases the stable equilibrium point is obtained. Again it is observed that the predator populations goes steadily to the coexisting point whereas, the prey populations after some fluctuations attains a stedy state.

TNTERPRETATION OF THE GRAPH (No 4.)

In the beginning of the graph it is observed that the predator takes N_2 , N_3 species frequently and neglects the N_1 species. After some time, when N_2 , N_3 become less the predator takes the N_1 species. From the graphs it is found that the predator population falls first which may be due to the insufficient number of prey species. At t = 1(sec), the predator population becomes maximum. So it starts eating the prey species. After sometime it is found that the stable equilibrium is reached among the four species. So it is concluded that the steady state point is attained for the four species system.

Case-B (Ggraph No. 13.0 - 19.2)

The second case switching functions are only introduced in the model. We have only studied it's behaviour by numerical analysis in computer by using the Runge-Kutta fourth order method. Here we have observed two types of graphs. In one type of graphs, we found that the system leads to the stable equilibrium point as found in the case-A. In other types of graphs it is observed that

there is oscillatory type of behaviour. So it is concluded from this graphs that the oscillatory type of curves says about the existence of switcing of predator in the system. So this case includes both the stable equilibrium and oscillatory types of solutions.

INTERPRETATION OF THE GRAPH (Graph No. 13 & 17)

There are two types of graphs observed in this case. Some graphs show that there is a stable equilibrium point like the previous one (case :A). Some graphs show the oscillatory type of behaviours persists in the system. The graphs 10, 11, 12 give one kind of observation. Here the curves are that of case I where after certain time of predation, the prey-predator steady state is arrived. So the system behaves like the stable one. The graphs 13, 14, 15, 16 give another kind of results. Here the oscillatory type of behaviour of prey predator populations with time is observed. Again after some fluctuations, the system leads to a oscillatory type of solutions. So these graphs give the information about the oscillatory behaviour of the system. In this case we have always taken 0 < n < 1 for our convenience.

The equations of Case-A are as follows:

$$\begin{split} dN_1/\,dt &= \left[\, \epsilon_1 \, -a \, N_4 \, / \, \left\{ 1 + (N_2/\,N_1)^n + (N_3/\,N_1)^n \right\} \, \right] \, N_1 \\ dN_2/\,dt &= \left[\, \epsilon_2 \, -b \, N_4 \, / \, \left\{ 1 + (N_1/\,N_2)^n + (N_3/\,N_2)^n \right\} \, \right] \, N_2 \\ dN_3/\,dt &= \left[\, \epsilon_3 \, -c \, N_4 \, / \, \left\{ 1 + (N_1/\,N_3)^n + (N_2/\,N_3)^n \right\} \, \right] \, N_3 \\ dN_4/\,dt &= \left[\, -\epsilon_4 \, +a \, N_1 \, / \, \left\{ 1 + (N_2/\,N_1)^n + (N_3/\,N_1)^n \right\} \, +b \, N_2 \, / \, \left\{ 1 + (N_1/\,N_2)^n + (N_3/\,N_2)^n \right\} \right] \, N_4 \end{split}$$

The equilibrium points are:

$$\begin{split} \mathbf{N_1} &= \epsilon_1^{1/n} \epsilon_4 \ (\epsilon_1 \ bc \ + \ ac\epsilon_2 \ + \epsilon_3 \ ab) \{ (bc)^{(1-n)/n} \epsilon_2^{-1/n} \} \ / \ a \{ (cb)^{1/n} \epsilon_1^{-(n+1)/n} \\ &+ (a \ c \)^{1/n} \epsilon_2^{-(n+1)/n} \ + (b \ a \)^{1/n} \epsilon_3^{-(n+1)/n} \ \} \\ \mathbf{N_2} &= \epsilon_4 \ (\epsilon_1 \ bc \ + \ ac\epsilon_2 \ + \epsilon_3 \ ab) \{ (ac)^{(1-n)/n} \epsilon_2^{-1/n} \} \ / \ b \{ (cb)^{1/n} \epsilon_1^{-(n+1)/n} \\ &+ (a \ c \)^{1/n} \epsilon_2^{-(n+1)/n} \ + (b \ a \)^{1/n} \epsilon_3^{-(n+1)/n} \} \end{split}$$

$$N_3 = \epsilon_1 \epsilon_3^{1/n} (b \ a)^{(1-n)/n} \ (\epsilon_1 \ bc + ac\epsilon_2 + \epsilon_3 \ ab) / c \ \{ (cb)^{1/n} \ \epsilon_1^{(n+1)/n} + (a \ c)^{1/n} \epsilon_2^{(n+1)/n} + (b \ a)^{1/n} \epsilon_3^{(n+1)/n} \}$$

$$N_4 = \{ (cb)^{(1-n)/n} \epsilon_1^{1/n}/a + (ac)^{(1-n)/n} \epsilon_2^{1/n}/b + (ba)^{(1-n)/n} \epsilon_3^{1/n}/c \} / (abc)^{(1-n)/n}$$

Table-1 Different sets of parameter for the prey and predator equations (Case A)

												_	
Set	N ₁ (o)	N ₂ (0)	N ₃ (0)	N ₄ (0)	ϵ_1	ϵ_2	€3	€4	8	Ь	С	n	Fig. No.
1st	14	15	27	35	6	3	5	25	1.4	2	1.2	1 _	4 & 4.1
2nd	10	15	27	35	6	7	8	39	1.9	1.6	1	3	5 & 5.1
3rd	10	15	27	35	2	3	4	40	1.9	1.6	1.1	2	6 & 6.1
4th	14	15	17	35	4	1.6	1.7	15	1.4	1	1.2	2	7 & 7 .1
5th	14	15	17	35	4	1.6	1.7	15	1.4	1	1.2	1	8 & 8.1
6th	11	10	11	32	3.5	2	1.8	15	1.1	1.2	1.1	3	9 & 9.1
7th	13	12	14	38	5.9	3,9	2.9	5	J1.2	1.2	1.2	2	10 & 10.1
8th	13	12	14	38	7.92	3.9	5.9	7.5	1.2	1.2	1.2	2	11 & 11.1
9th	12	10	11	32	4.1	4.9	5.1	7.5	1	1.2	1.1	1	12 & 12.1

The equations of Case-B are as follows:

$$\begin{split} dN_1/\,dt &= \left[\epsilon_1 - a \ N_4/\!/\left\{1 + \left(N_2 * N_3/\!/N_1\right)^n\right\} N_1 \\ dN_2/\,dt &= \left[\epsilon_2 - bN_4/\!/\left\{3 + \left(N_1 * N_2/\!/N_3\right)^n\right\}\right] N_2 \\ dN_3/\,dt &= \left[\epsilon_3 - cN_4/\!/\left\{3 + \left(N_1 * N_2/\!/N_3\right)^n\right\}\right] N_3 \\ dN_4/\,dt &= \left[-\epsilon_4 + a \ N_1/\!/\left\{3\right\} + \left(N_2 * N_3/\!/N_1\right)^n\right\} + bN_2/\!/\left\{1 + \left(N_1 * N_3/\!/N_2\right)^n\right\} \\ &+ cN_3/\!/\left\{1 + \left(N_1 * N_2/\!/N_3\right)^n\right\}\right] N_4 \end{split}$$

Table-2: Different sets of parameter for the prey and predator equations (Case B)

Set	N ₁ (0)	N ₂ (0)	N ₃ (0)	N ₄ (0)	ϵ_{l}	ϵ_2	ϵ_3	€4	a	ь	c	n	Fig. No.
1 st	7 0	80	60	100	0.15	0.12	0.3	1.2	0.02	0.01	0.03	0.5	13 & 13.1
2nd	50	60	40	70	0.14	0.09	0.28	0.3	0.019	0.008	0.02	0.7	14, 14.1 & 14.2
3rd	50	60	40	80	0.14	0.09	0.28	1.1	0.019	0.008	0.02	0.4	15 & 15.1
4th	90	80	100	130	0.19	0.16	0.35	1.7	0.03	0.02	0.04	0.5	16, 16.1, 16.2, 16.3 & 16.4
5th	540	544	535	580	0.19	0.07	0.25	0.5	0.012	0.004	0.019	0.7	17, 17.1 & 17.2
6th	600	610	590	650	0.19	0.09	0.28	1.2	0.019	0.005	0.02	0.5	18, 18.1 & 18.2
7th	35	34	36	84	0.1	0.04	0.13	0.3	0.013	0.002	0.011	0.6	19, 19.1 & 19.2

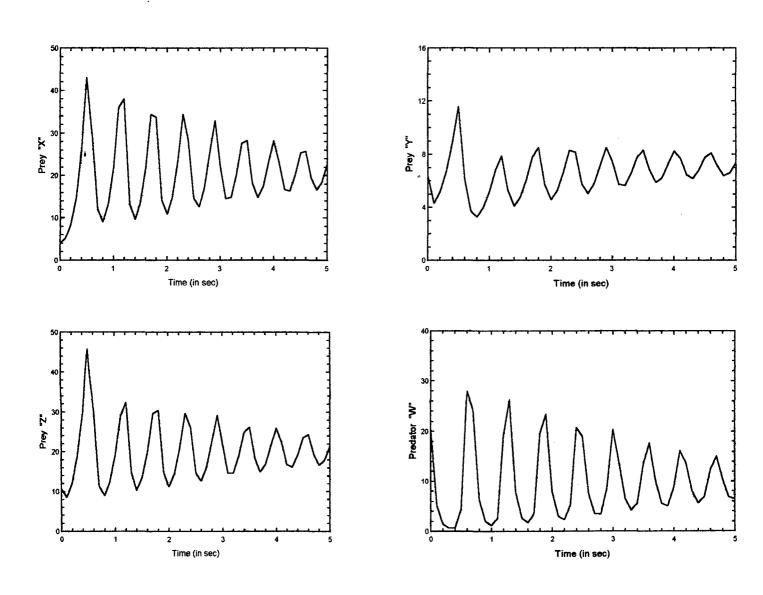


Figure 4: Variation of prey-predator population with time.

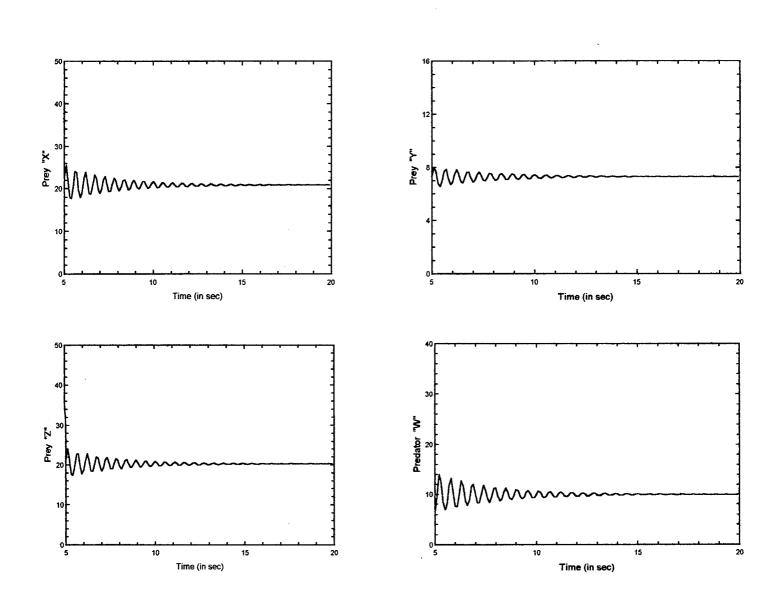


Figure 4.1: Variation of prey-predator population with time.

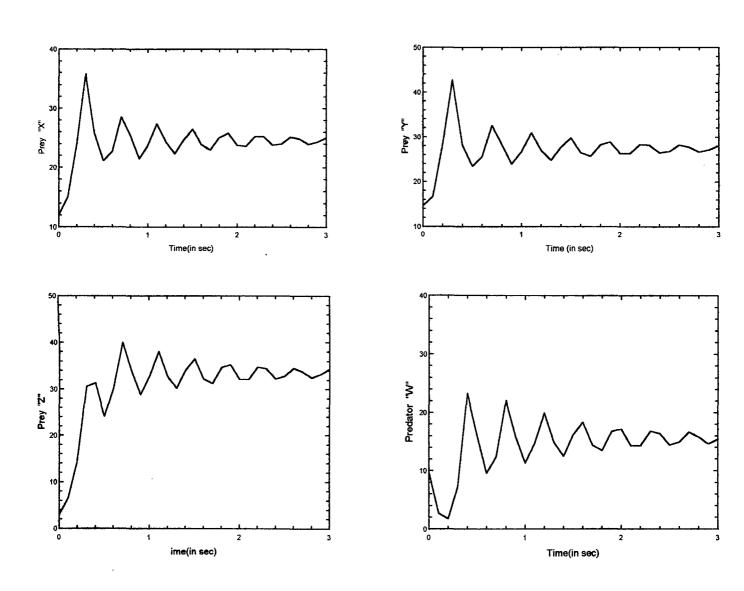


Figure 5: Variation of prey-predator population with time.

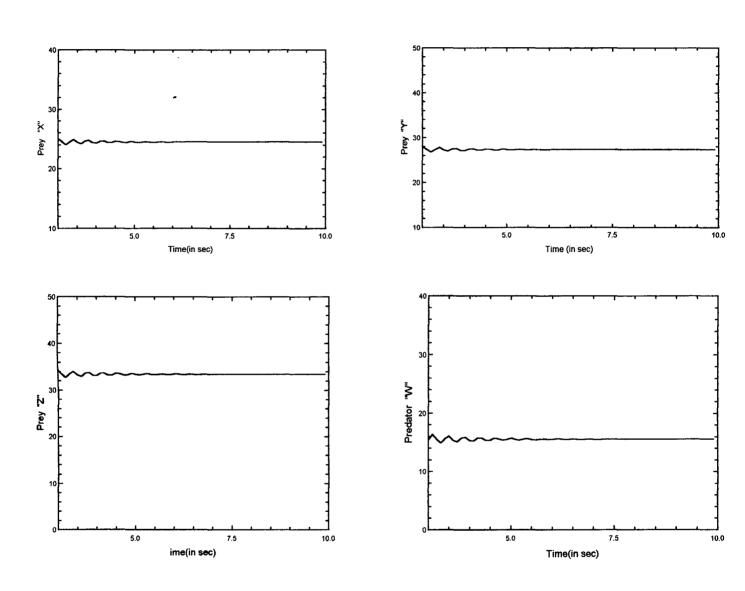


Figure 5.1: Variation of prey-predator population with time.

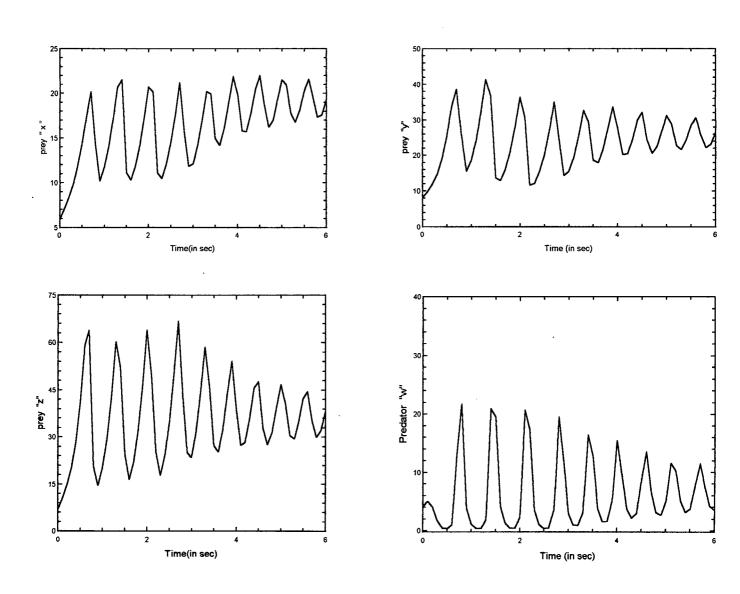


Figure 6: Variation of prey-predator population with time.

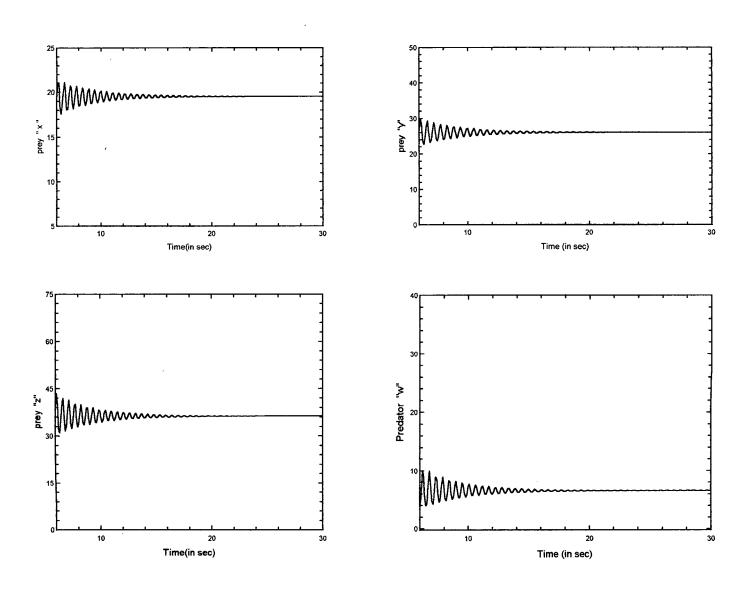


Figure 6.1: Variation of prey-predator population with time.

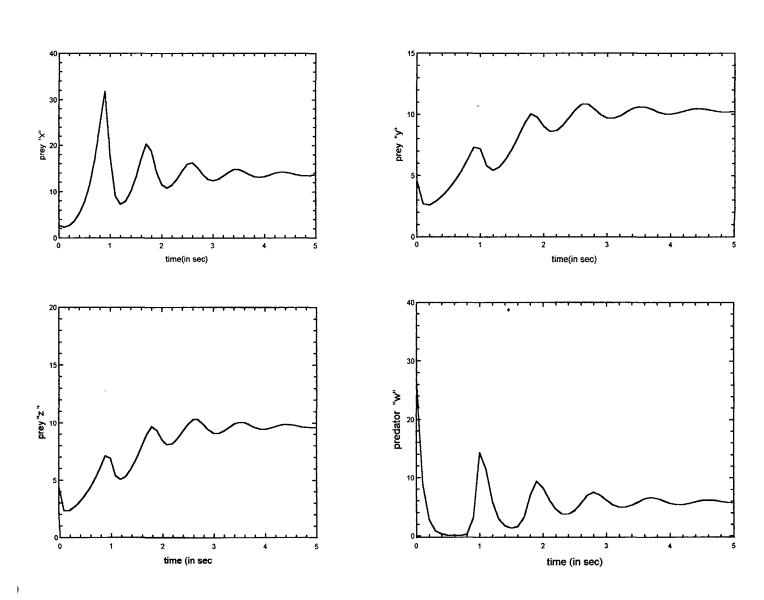


Figure 7: Variation of prey-predator population with time.

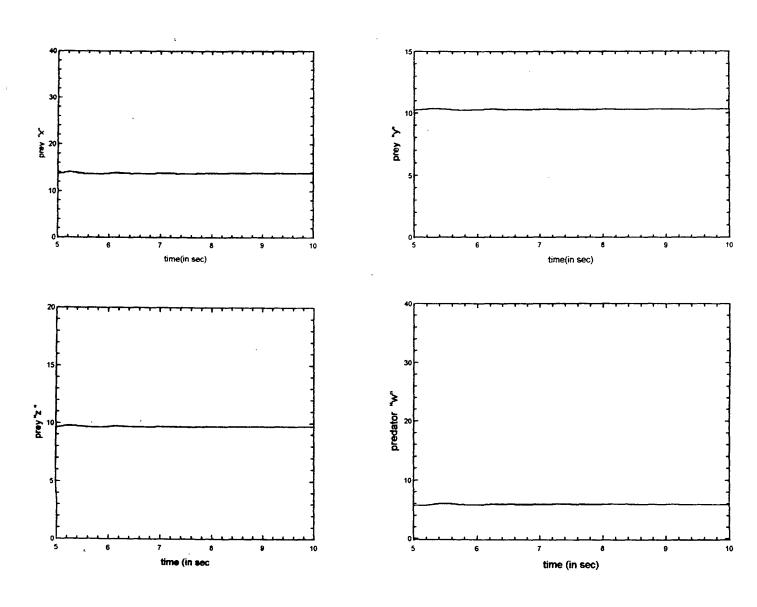


Figure 7.1: Variation of prey-predator population with time.

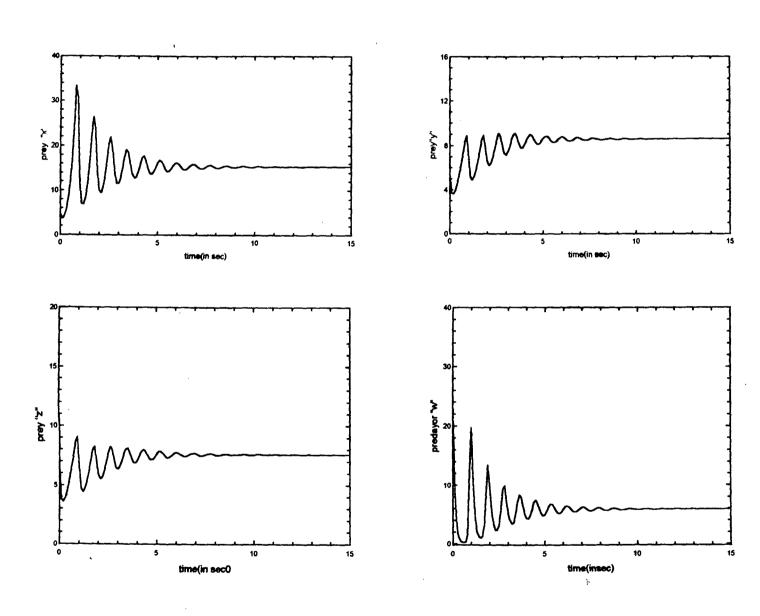


Figure 8: Variation of prey-predator population with time.

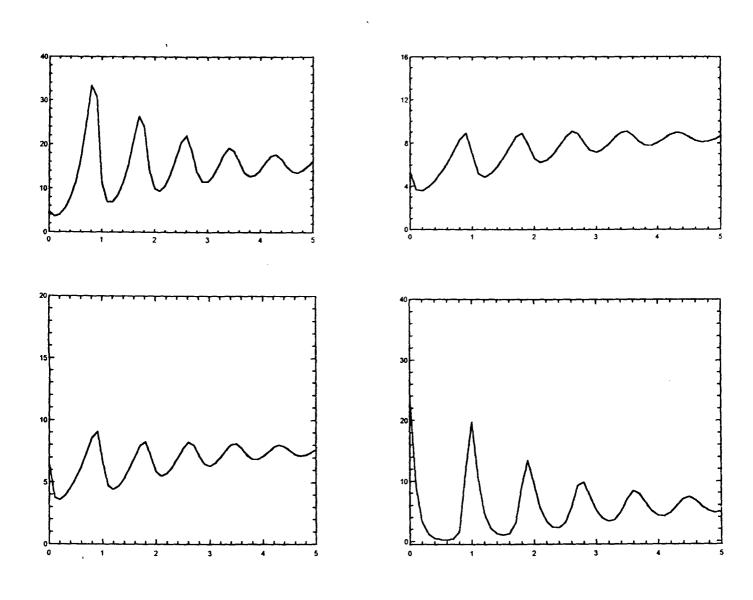


Figure 8.1: Variation of prey-predator population with time.

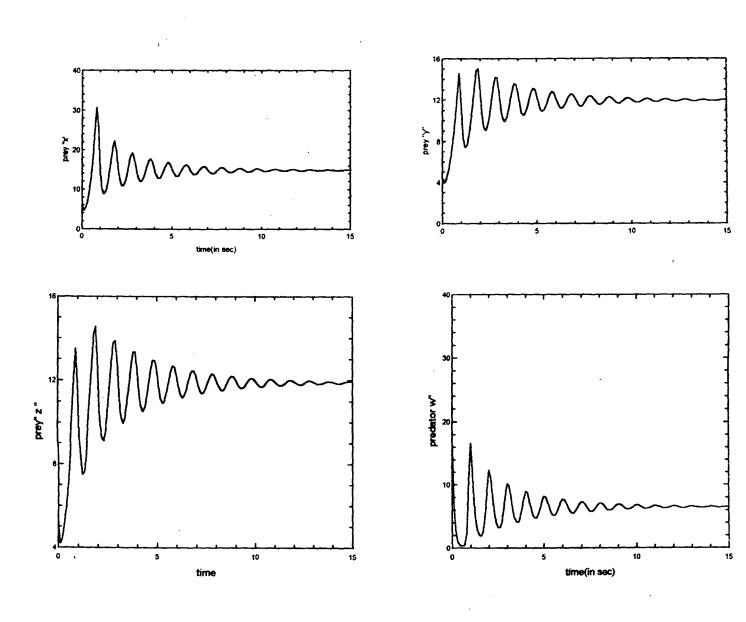


Figure 9: Variation of prey-predator population with time.

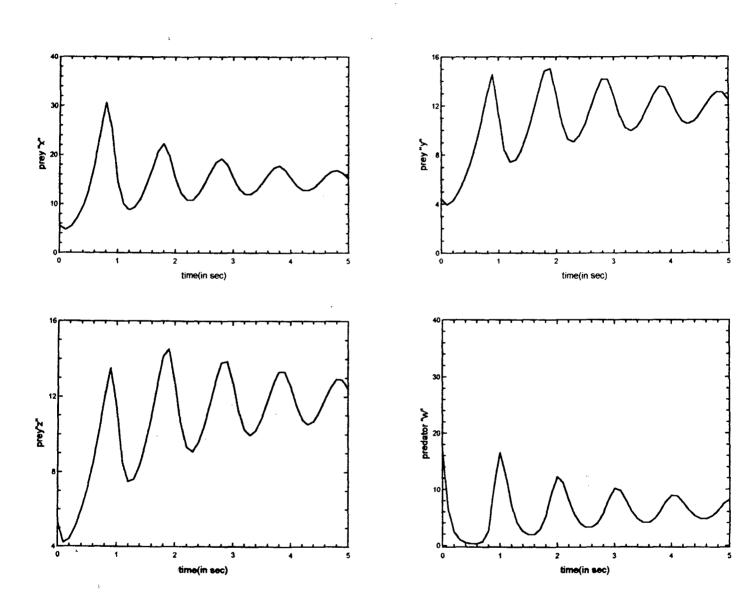


Figure 9.1: Variation of prey-predator population with time.

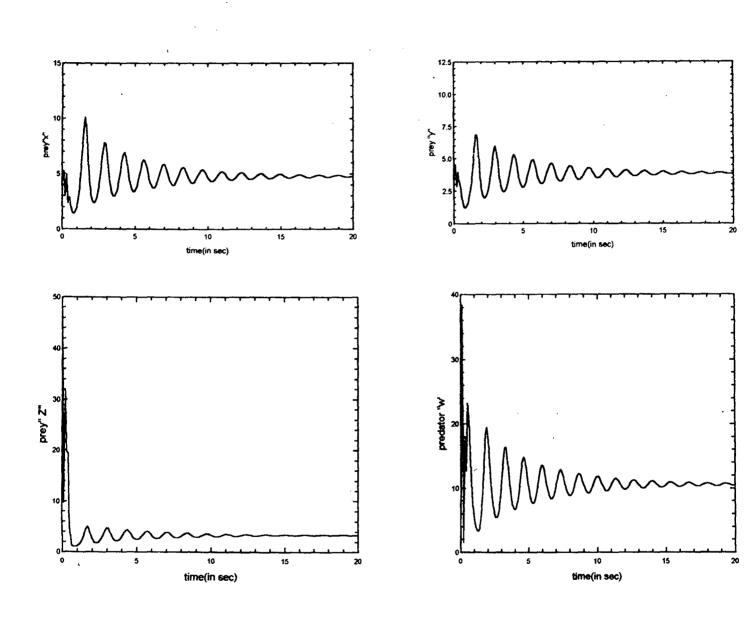


Figure 10: Variation of prey-predator population with time.

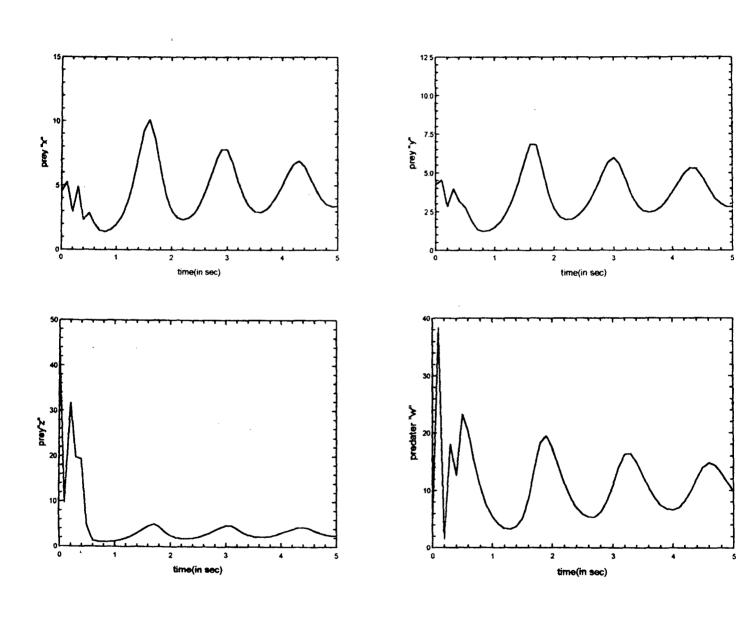


Figure 10.1: Variation of prey-predator population with time.

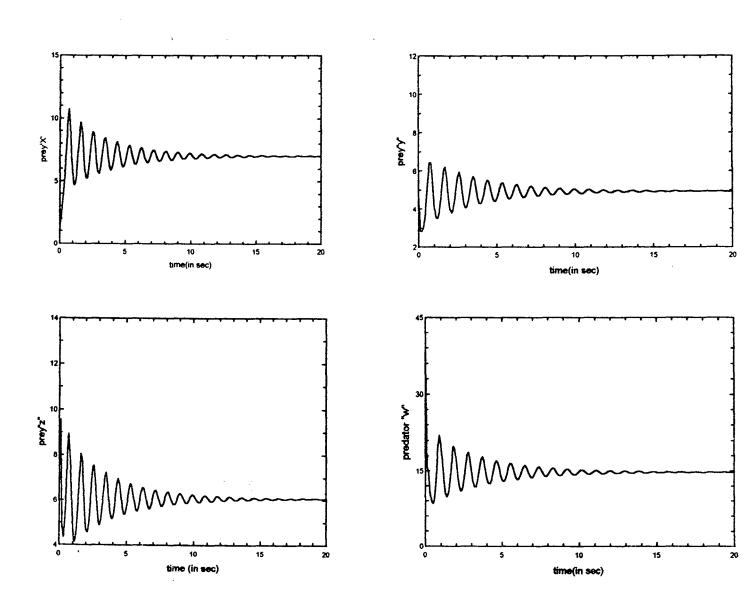


Figure 11: Variation of prey-predator population with time.

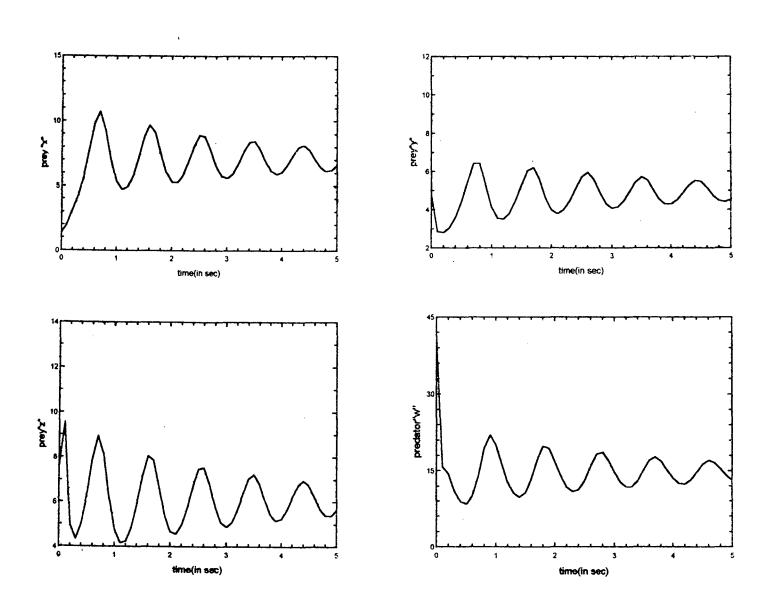


Figure 11.1: Variation of prey-predator population with time.

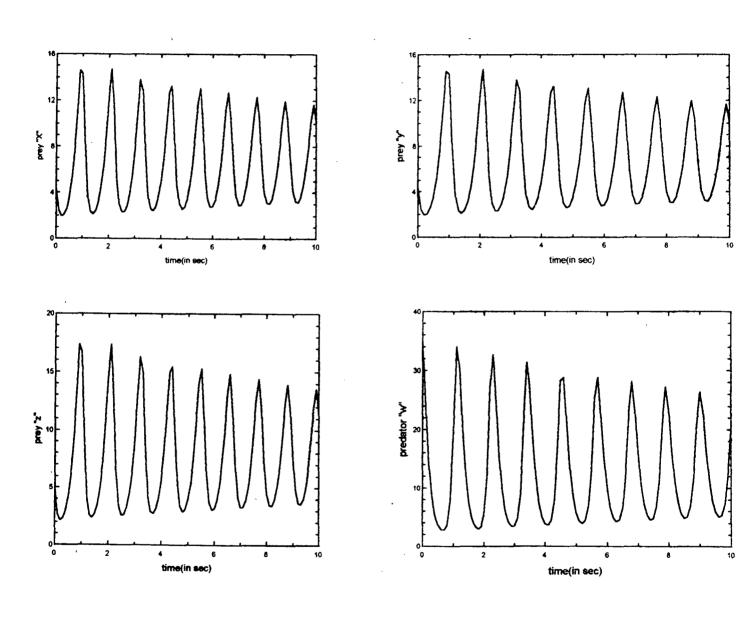


Figure 12: Variation of prey-predator population with time.

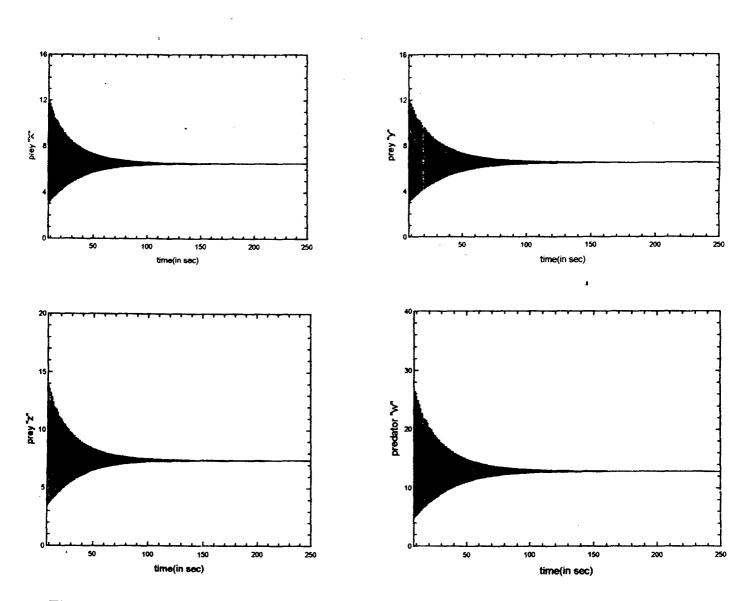


Figure 12.1: Variation of prey-predator population with time.

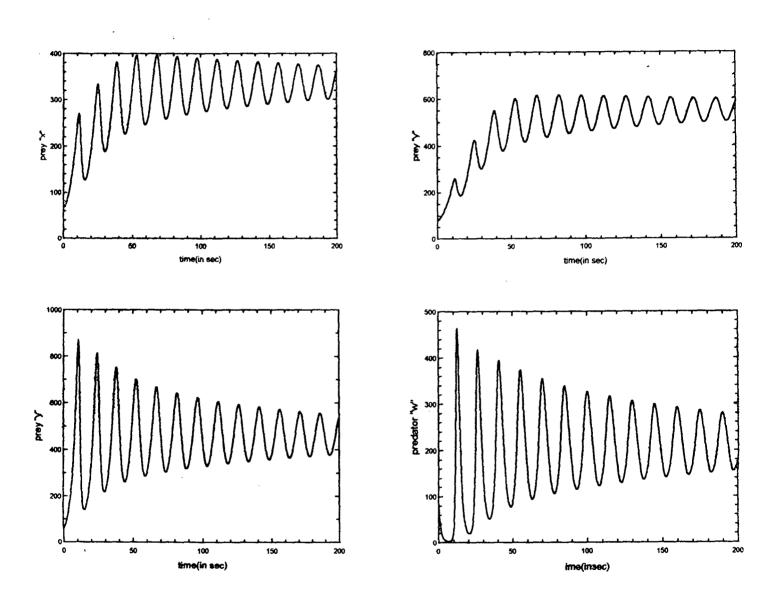


Figure 13: Variation of prey-predator population with time.

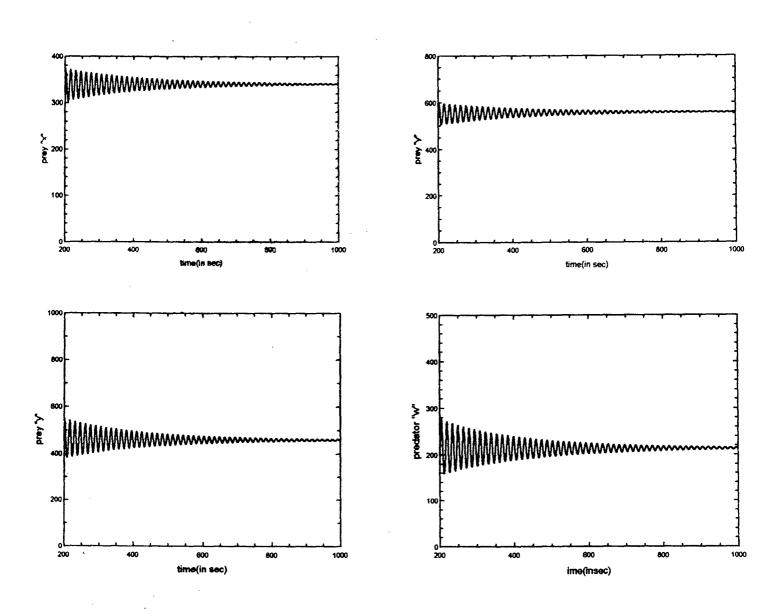


Figure 13.1: Variation of prey-predator population with time.

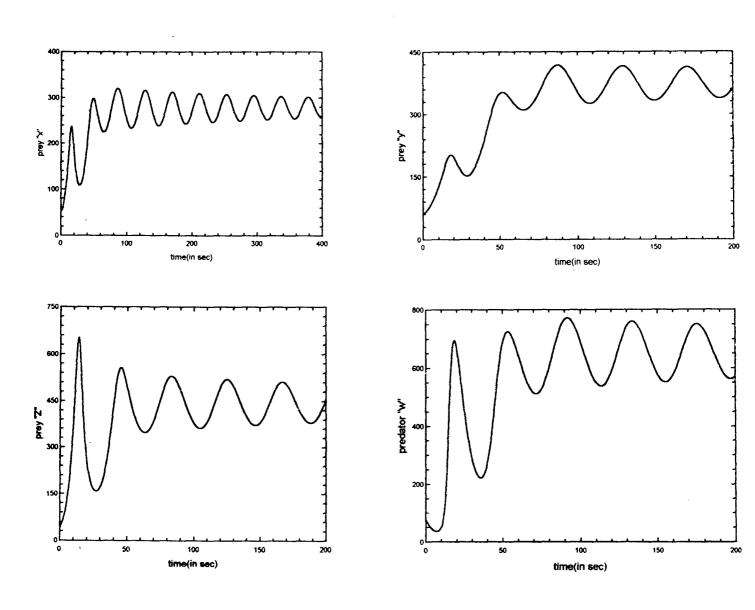


Figure 14: Variation of prey-predator population with time.

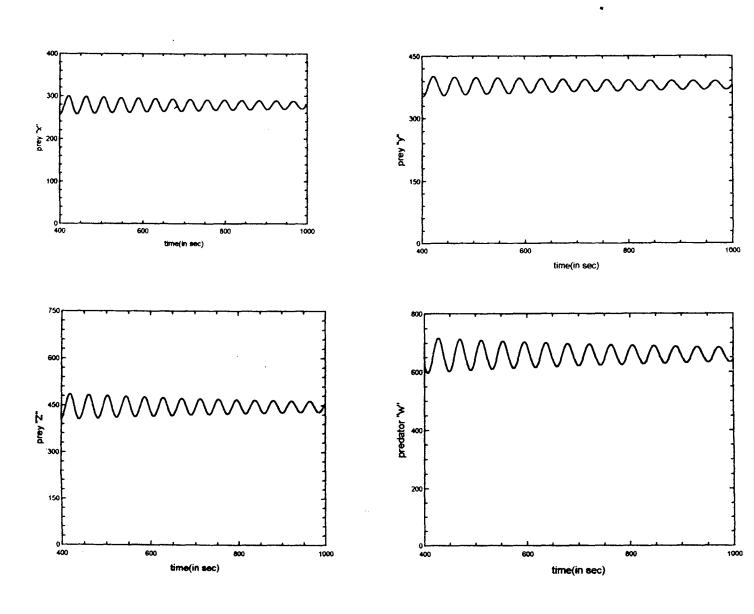


Figure 14.1: Variation of prey-predator population with time.

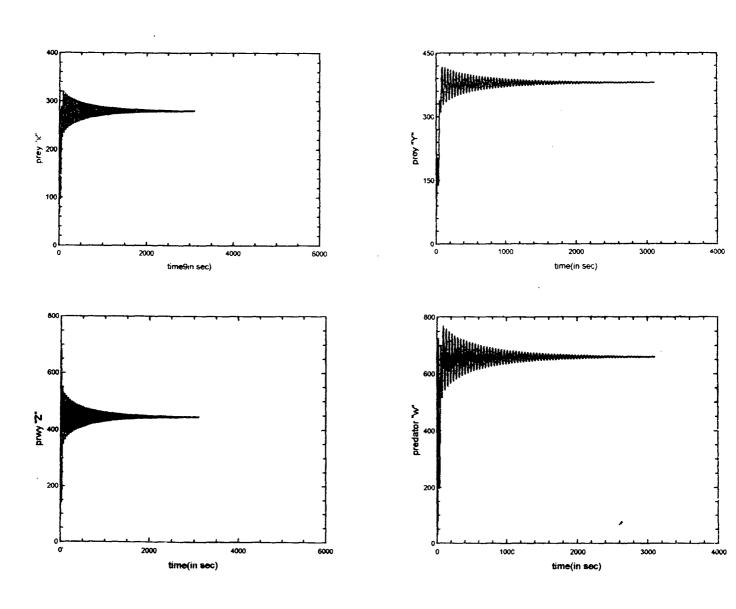


Figure 14.2: Variation of prey-predator population with time.

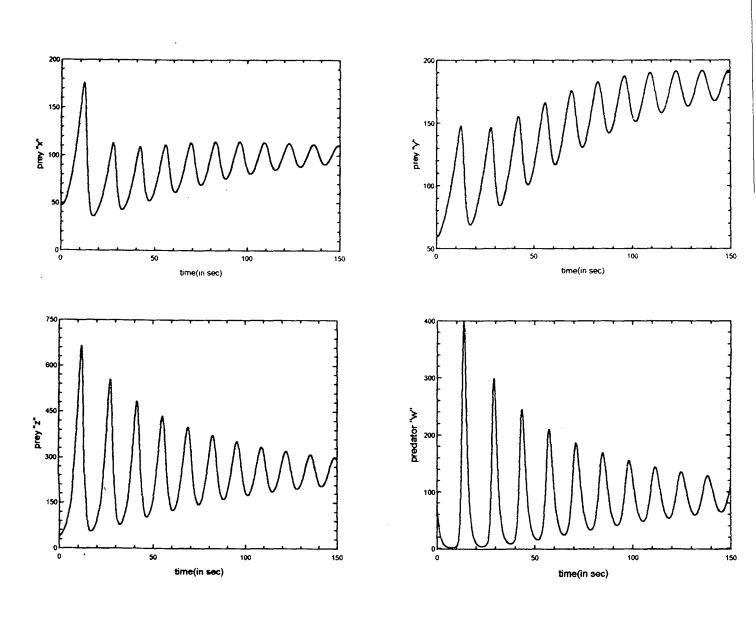


Figure 15: Variation of prey-predator population with time.

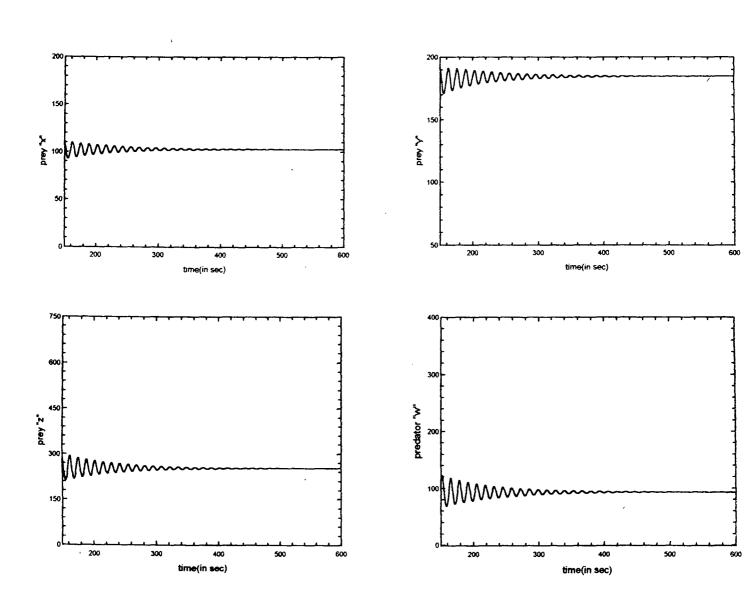


Figure 15.1: Variation of prey-predator population with time.

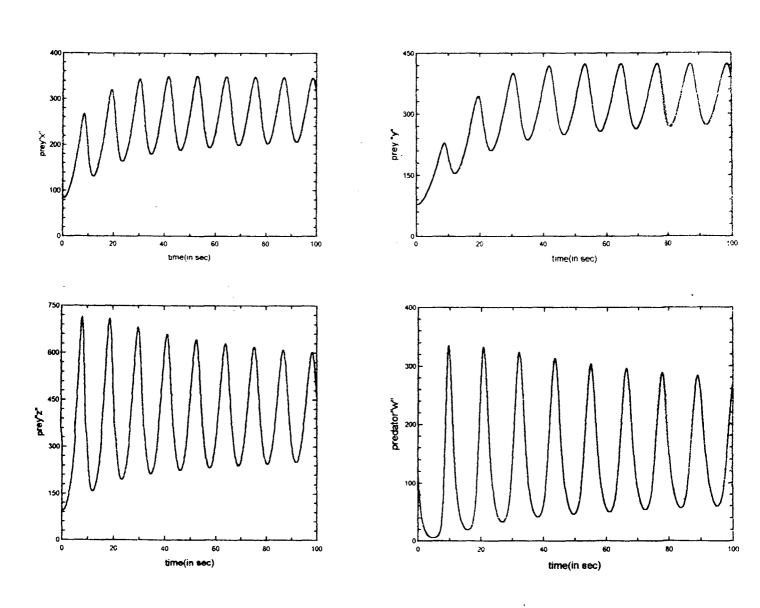


Figure 16: Variation of prey-predator population with time.

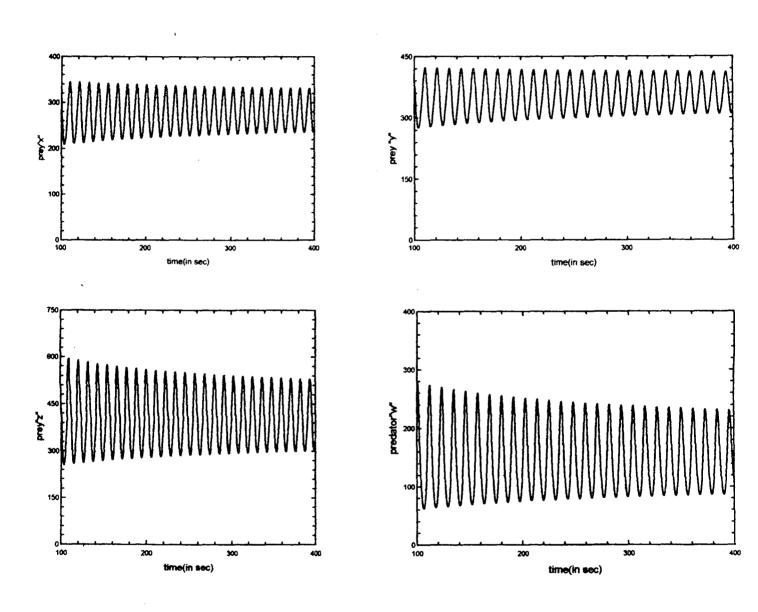


Figure 16.1: Variation of prey-predator population with time.

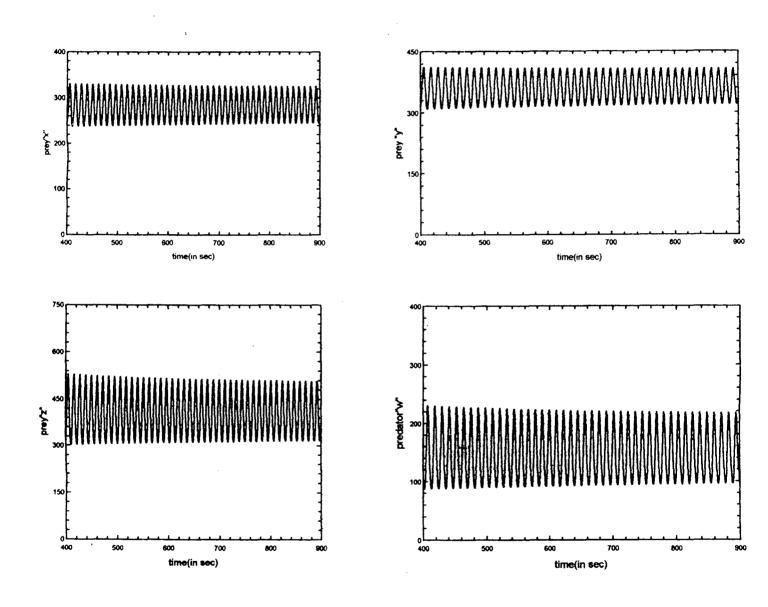


Figure 16.2: Variation of prey-predator population with time.

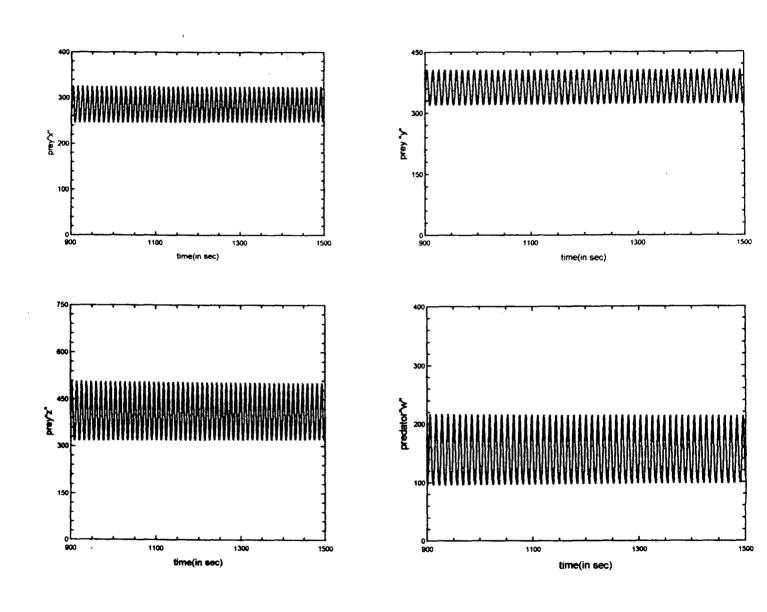


Figure 16.3: Variation of prey-predator population with time.

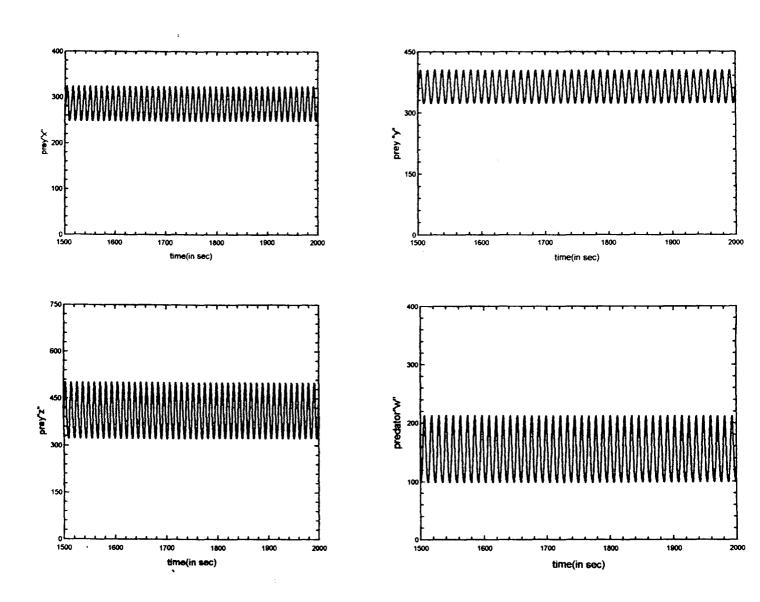


Figure 16.4: Variation of prey-predator population with time.

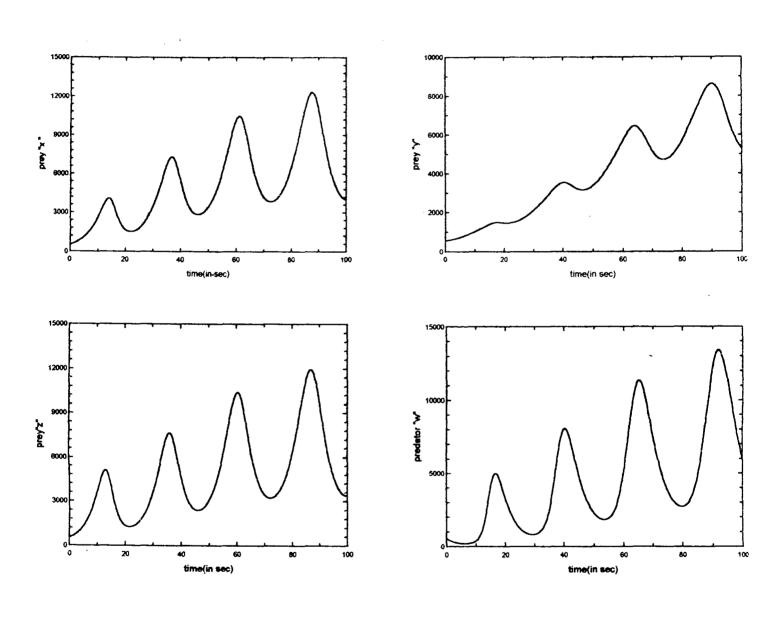


Figure 17: Variation of prey-predator population with time.

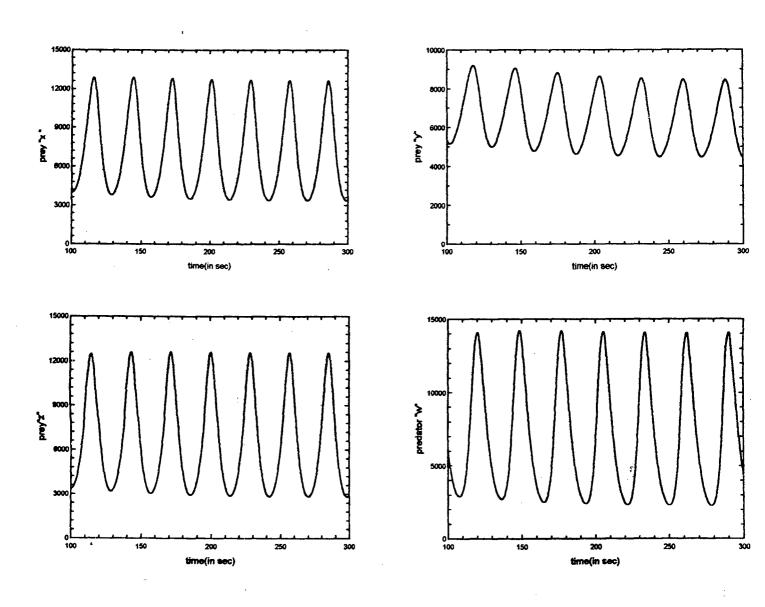


Figure 17.1: Variation of prey-predator population with time.

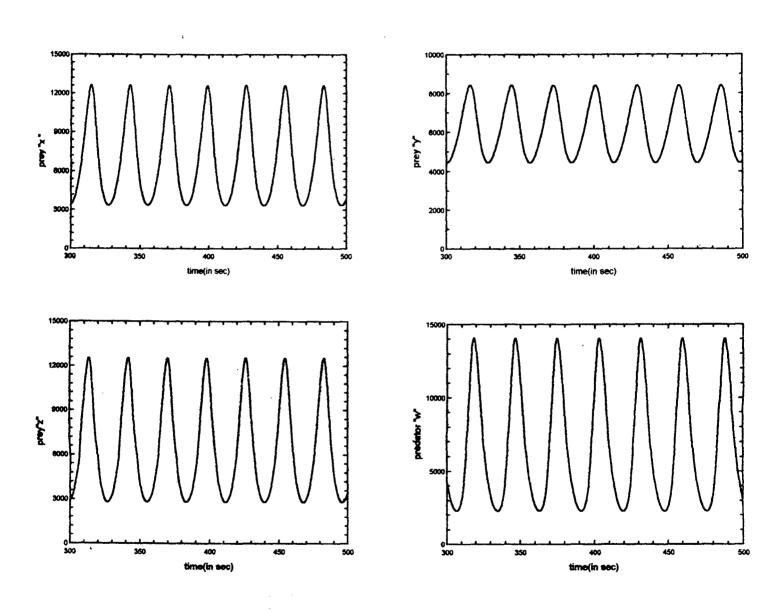


Figure 17.2: Variation of prey-predator population with time.

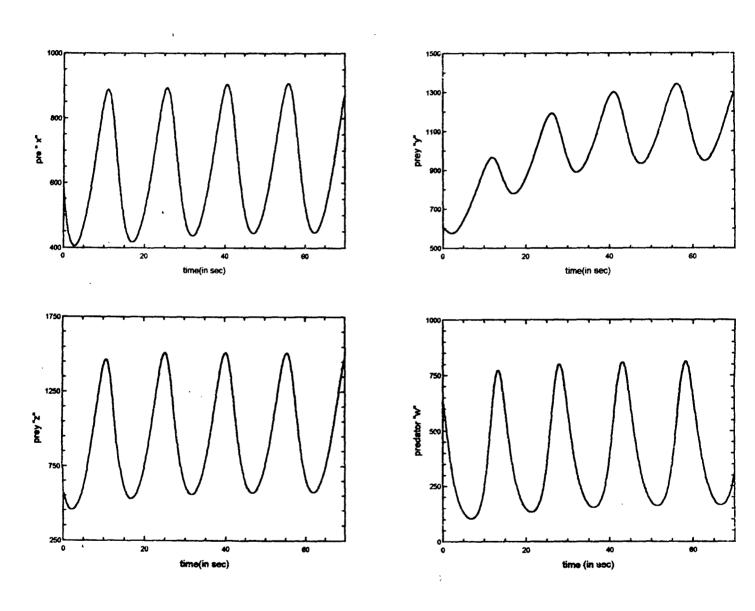


Figure 18: Variation of prey-predator population with time.

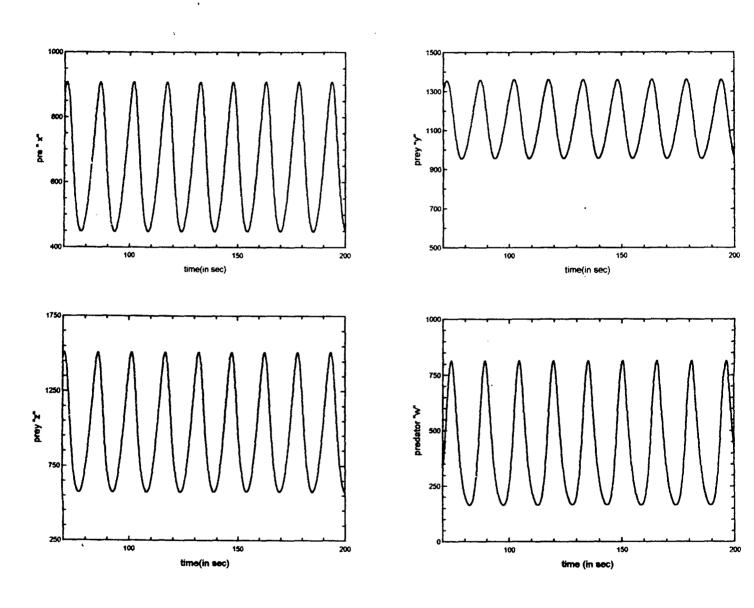


Figure 18.1: Variation of prey-predator population with time.

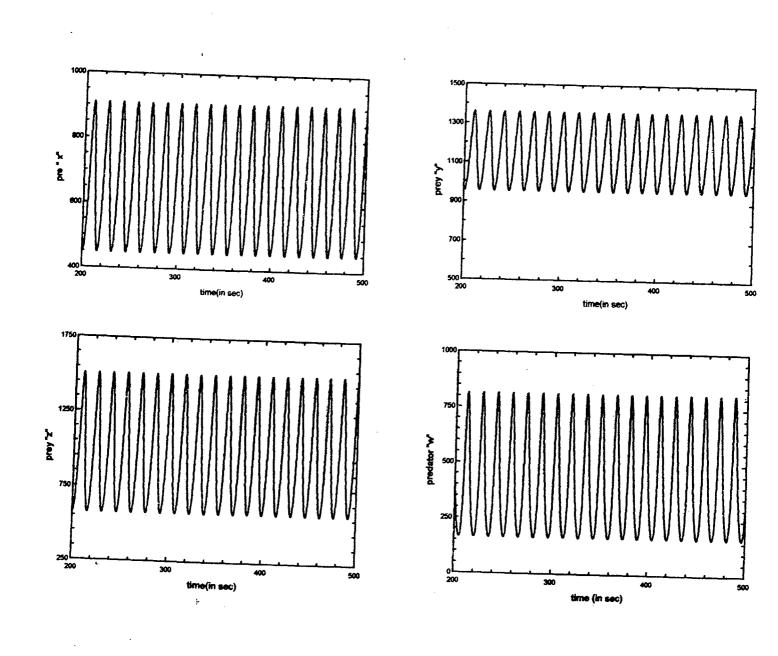


Figure 18.2: Variation of prey-predator population with time.

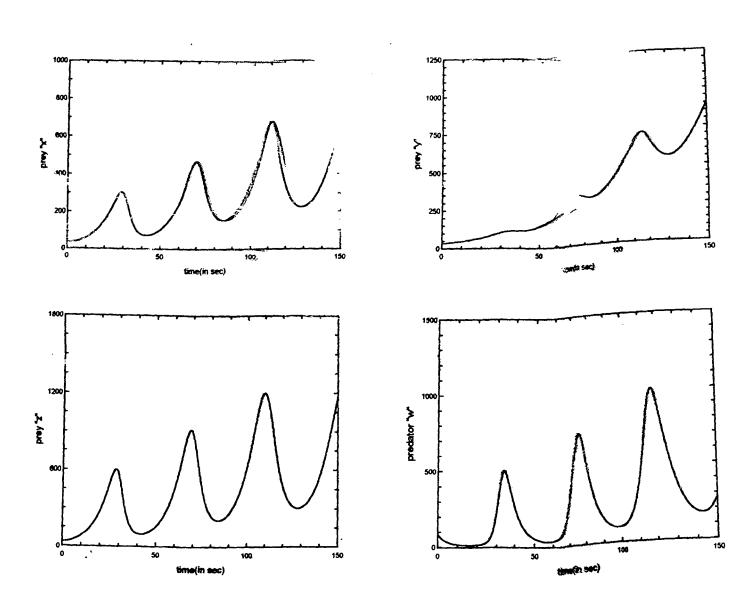


Figure 19: Variation of prey-predator population with time.

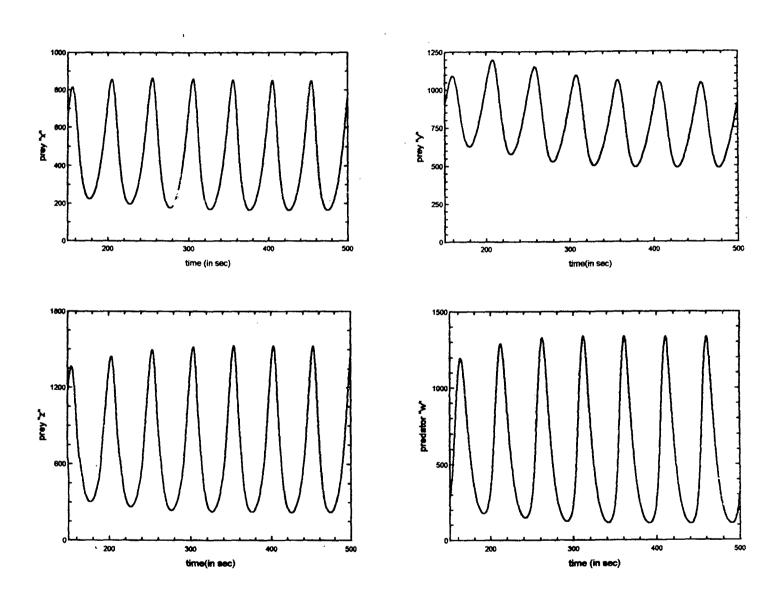


Figure 19.1: Variation of prey-predator population with time.

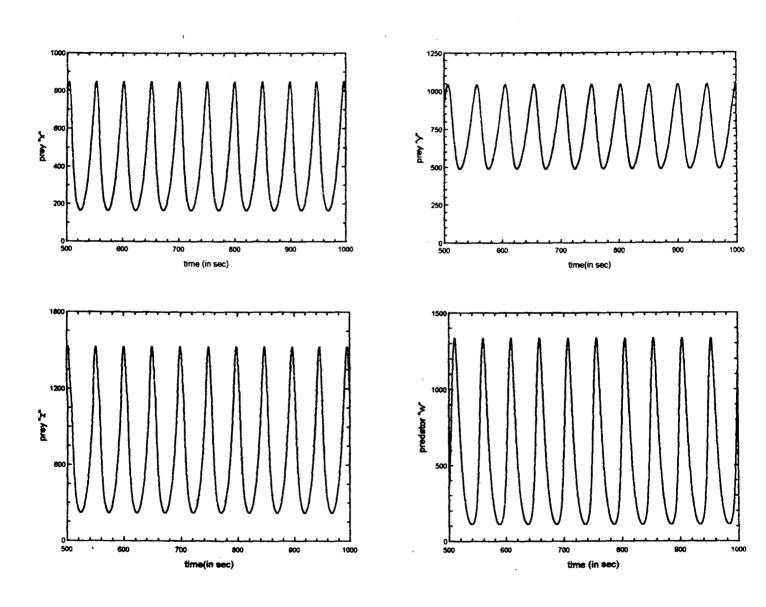


Figure 19.2: Variation of prey-predator population with time.

SUMMARY AND CONCLUSION

Switching is a mechanism by which the predator diverts it's attention to the most abundant prey species. We have studied the switching behaviour of the predator in the four species system. First we observed the behaviour of the prey predator population with time in three species system and found that the system always attains a stable coexisting state. Then we extended this switching mechanisms to the four species by adding another prey into the system. In the four species system, two cases of switching functions were found to be possible. In case-A the switching functions were the extended switching functions of Tansky(1978). So the same type of stable equilibrium state was observed. In the case-B, we introduced another possible switching terms to study the prey predator model. These switching terms give the idea of existence of both stable and oscillatory type of solutions. The case-B is studied only by computer simulations. Here we have taken different values of n and according to theory, the switching becomes sharper with increasing the value of n. It is also shown in some graphs. We have only taken n from 0.1 to 3 for our convenience. It can take any value from 1 to infinity, but not zero. Some further works may be done on this in near future to study its behaviour for larger values of n.

Switching is a mechanism by which the proper balance is maintained in the ecosystem. For any ecosystem, predation is necessary. In the absence of predators, the prey species may grow like the Malthusian one. The switching phenomena is observed easily in the case-B of four species model which is discussed. This model can be extended to inter- and intra- specific competitions. So some other behaviours may be studied in near future.

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APPENDIX-I

Suppose multispecies population dynamics are given by a set of m equations.

$$dN_i/dt = F_i (N_1(t), N_2(t), ..., N_m(t))$$
(1)

where i = 1 to m

Here the growth rate of i^{th} species at time t is given by some non-linear function F_i of all relevant interacting populations. The equilibrium populations N_i , are obtained from m algebric equations obtained by putting all growth rates zero.

$$F_i(N_1, N_2,, N_m) = 0$$
 (2)

Expanding about this equilibrium, for each population we write

$$N_i(t) = N_i + x_i(t)$$
 (3)

Where x_i measures the small perturbation to the ith population. Taylor's expansion of each of the basic equations (1) around this equilibrium and discarding all second or higher order terms, a linearised approximation is obtained

$$dx_{i}(t) / dt = \sum a_{ij} x_{j}(t)$$

$$i = 1$$
(4)

$$\mathbf{a}_{ij} = (\partial \mathbf{F}_i / \partial \mathbf{N}_i) \qquad (6)$$

The partial derivatives are evaluated at equilibrium values of all populations. For the set of linear equations (5) the solutation may be written

$$m$$

$$x_{i}(t) = \sum_{j=1}^{\infty} c_{ij} \exp(\lambda_{j} t)(7)$$

where c_{ij} are constant which depend upon initial values of perturbations to the populations and the time dependance is contained soley in m exponential factors. The m constants λ_j (j = 1,2,...,m) which characterise the temporal behaviour of the system are so called eigrn values of matrix A. They are found substituing (7) into (5) to get

$$\lambda \mathbf{x}_{ij}(\mathbf{z}) = \sum_{j=1}^{m} \mathbf{a}_{ij} \mathbf{x}_{j}(t)$$
 (8)

or in more compact form

$$(A - \lambda I) x (t) = 0 \qquad (9)$$

Here I is m x m unit matrix of equations possesses a non-trivial solutation if and only if the deter minant vanishes:

$$\det \cdot (\mathbf{A} - \lambda \mathbf{I}) = 0$$

This is in effect mth order polynomial equation in λ of matrx A. They may in general be comolex numbers, $\lambda = \zeta + i\xi$; in any of the terms of equation, the real part ζ produces sinusoidal oscillations. It is clear that perturbation to the equilibrium populations will die away in time if and only if, all eigenvalues λ have negative real parts. If any one of eigenvalues has a positive real part, that exponential factor will grow ever larger as time goes on, and consequently the equilibrium is unstable. The special case of neutral equilibrium is obtained if one or more eigenvalues are purely imaginary numbers and rest have negative real parts.

Routh-Hurwitz stability criteria

The equation of polynomial of λ is

$$\lambda^{m} + c_{1}\lambda^{m-1} + c_{2}\lambda^{m-2} + \dots + c_{m} = 0$$

The necessary and sufficient condition for all roots of above polynomial to be negative is that the coefficients c_1 , c_2 ,, c_m must fulfill the Routh-Hurwitz stability conditions. The conditions for m = 2, 3, 4 are

m = 2
$$c_1 > 0$$
, $c_2 > 0$
m = 3 $c_1 > 0$, $c_3 > 0$, $c_1c_2 > 0$
m = 4 $c_1 > 0$, $c_3 > 0$, $c_4 > > 0$, $c_1c_2c_3 > c_3^2 + c_1^2c_4$

APPENDIX-II: DISCUSSION ON SWITCHING IN MATHEMATICAL MODELS

Here we shall give brief discussion on the swiching property of predation. Let us consider the average numbers of individuals of two prey species captured by a predator per unit time and denote them as

$$X(x,y) = k_1(x,y)x,$$
 $Y(x,y) = k_2(x,y)y,$

The predation rates are given by $k_1(x,y) = k_1$, $k_2(x,y) = k_2$, $k_2(x,y) = k_2$ in the classical Volterra equation and $k_1(x,y) = k_1 x / (x + y)$, $k_2(x,y) = k_2 y / (x + y)$ in the present model. Here, as a definition of switching, we assume the conditions

$$\begin{split} \partial/\partial x * k_1(x,y) &> 0, & \partial/\partial y * k_1(x,y) &< 0 \\ \partial/\partial x * k_2(x,y) &< 0, & \partial/\partial y * k_2(x,y) &> 0 \end{split}$$

For x greater than equal to 0 and y greater than equal to 0.

The funtions adopted in our model really satisfy these conditions.

```
DECLARE SUB gunc2 (x!(), nn!, f!())
        SCREEN 9
        CLS
        nn = 4
        DIM x0(nn)
        DIM z(nn), x(nn), k1(nn), k2(nn), k3(nn), k4(nn), f(nn)
        OPEN "pb1" FOR OUTPUT AS #1
        OPEN "pb2" FOR OUTPUT AS #2
        OPEN "pb3" FOR OUTPUT AS #3
        OPEN "pb4" FOR OUTPUT AS #4
        READ h, tin, tend, hprint
        DATA .1,0,250,.1
        FOR I = 1 TO nn
        READ x0(I)
        NEXT
        DATA 12,10,11,32
        e1 = 4.1
        e2 = 4.9
        e3 = 5.1
        e4 = 7.5
        aa = 1
        bb = 1.2
        cc = 1.1
        n = 1
        j = 0
        'VIEW
        WINDOW (0,0,0)-(tend, 245)
        FOR I = 1 TO nn
        z(I) = x0(I)
        NEXT
        tout = tin
250
                    'output from subprogram comes here
10
       j = j + 1
         'plotting done here
        'print z(1), z(2), z(3), z(4)
        tp = tout
        xp = z(1)
        yp = z(2)
        zp = z(3)
        wp = z(4)
        PRINT #1, told, xp
        PRINT #2, told, yp
        PRINT #3, told, zp
        PRINT #4, told, wp
        IF j = 1 THEN 15
        LINE (told, xo)-(tp, xp)
        LINE (told, yo)-(tp, yp)
        LINE (told, zo)-(tp, zp)
        LINE (told, wo)-(tp, wp)
15
                 told = tp
        xo = xp
        yo = yp
        zo = zp
        wo = wp
        IF tout < tend THEN GOTO 20
        'circle()00000000
                 STOP
20
        t = tout
        tout = tout + hprint
25
        FOR I = 1 TO nn
        x0(I) = z(I)
        NEXT
        CALL gunc2(x0(), nn, f())
30
                FOR I = 1 TO nn
```

```
kl(I) = h * f(I)
NEXT
FOR I = 1 TO nn
x(I) = z(I) + kl(I) / 2
NEXT
CALL gunc2(x(), nn, f())
FOR I = 1 TO nn
k2(I) = h * f(I)
NEXT
FOR I = 1 TO nn
x(I) = z(I) + k2(I) / 2
NEXT
CALL qunc2(x(), nn, f())
FOR I = 1 TO nn
k3(I) = h * f(I)
NEXT
FOR I = 1 TO nn
x(I) = z(I) + k3(I)
NEXT
CALL gunc2(x(), nn, f())
FOR I = 1 TO nn
k4(I) = h * f(I)
NEXT
FOR I = 1 TO nn
x(I) = z(I) + (k1(I) + 2 * k2(I) + 2 * k3(I) + k4(I)) / 6
NEXT
FOR I = 1 TO nn
z(I) = x(I)
NEXT
GOTO 10
STOP
END
SUB gunc2 (x(), nn, f()) STATIC
SHARED h, s, e1, e2, e3, e4, aa, bb, cc, n
f(1) = x(1) * e1 - aa * x(1) * x(4) /
(1 + (x(2) / x(1)) ^n + (x(3) / x(1)) ^n)
f(2) = x(2) * e2 - bb * x(2) * x(4) /
(1 + (x(1) / x(2)) ^ n + (x(3) / x(2)) ^ n)
f(3) = x(3) * e3 - cc * x(3) * x(4) /
(1 + (x(1) / x(3)) ^ n + (x(2) / x(3)) ^ n)
f(4) = -x(4) * e4 + aa * x(1) * x(4) / (1 + (x(2) / x(1)) ^ n +
(x(3) / x(1)) ^ n) + bb * x(2) * x(4) / (1 + (x(1) / x(2)) ^ n +
(x(3) / x(2)) ^ n) + cc * x(3) * x(4) / (1 + (x(1) / x(3)) ^ n +
(x(2) / x(3)) ^ n)
'PRINT e1, e2, e3, aa, bb, n
'INPUT "", hjk
END SUB
```

