

**ON SUSTAINING LIMIT CYCLE BEHAVIOUR  
WHEN EXTENDING ONE PREY-ONE PREDATOR  
TO A TWO PREY-ONE PREDATOR SYSTEM**

*Dissertation submitted to the Jawaharlal Nehru University  
in partial fulfilment of the requirements  
for the award of the degree of*  
**MASTER OF PHILOSOPHY**

**MUKUT BHANDARI**

**SCHOOL OF ENVIRONMENTAL SCIENCES  
JAWAHARLAL NEHRU UNIVERSITY  
NEW DELHI - 110067  
INDIA**

**1994**

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NEW DELHI - 110067

*School of Environmental Sciences*

*July, 1994.*

## **CERTIFICATE**

Certified that this dissertation entitled "**ON SUSTAINING LIMIT CYCLE BEHAVIOUR WHEN EXTENDING ONE PREY-ONE PREDATOR TO A TWO PREY-ONE PREDATOR SYSTEM**" submitted by **MUKUT BHANDARI** in partial fulfilment of the requirements for the award of the degree of **Master of Philosophy** of Jawaharlal Nehru University is his own work and has not been previously submitted for any other degree of this or any other university.

*Mukut Bhandari*

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# CHAPTER I

## INTRODUCTION

A detailed study of dynamics of interacting species is of much interest in theoretical ecology. Mathematical models used to describe the interaction of two or more species of populations generally consist of a set of differential equations. The equations give the growth rate of each species as function of the various interacting populations. In analysing the models the first objective is to know the stability of the system. This stability depends upon whether the differential equations describing the system are linear or nonlinear. It also depends on whether the equations are assumed to apply over all possible combinations of populations (case of Global Stability) or only in the neighbourhood of an equilibrium point (case of local stability).

Stability can be of equilibrium type or of periodic solution type. If the equations describing the system are linear, then we get only linear type stability. In this case, we test the stability by means of Routh-Horwitz criteria. If the differential equations are non-linear, then both types of stability are possible. Since the equations of population ecology are non-linear we have to explore both possibilities. The analysis for stable equilibrium can in most cases still be done by treating these equations as approximately linear in sufficiently small neighbourhood of the equilibrium point and then using Routh-Horwitz criteria to judge their local stability in that neighbourhood. A nonlinear model that is unstable in the neighbourhood of the equilibrium point may be stable in the wider sense that it exhibits a stable limit cycle.

In this work, we are basically interested in limit cycle solutions. The existence of a limit cycle is an important property of a large number of non-linear systems. Limit cycles correspond to closed curves in phase space of dynamical variables of the system and are independent of initial conditions. They imply that the system has a stable pattern of behaviour and yet it does not display numerical constancy of any of the state variables. The reason why a dynamically stable system may not display numerical constancy is that the system is continuously perturbed from within.

A lot of work has been done to find out the periodic type solutions in the two species system. Kolmogorov (1936) has given a theorem which tells about the existence of stable equilibrium (or limit cycle) in two species systems. No such type of theorem exists for system of three or more species. As the system becomes more complex (more species, more interactions) it becomes more difficult to analyse the stability question.

The main objective of the present work is to see whether it is possible to introduce, into a one prey-one predator system which exhibits limit cycle solution, a second prey species and still get limit cycle solutions. And we also wish to investigate within what range of parameters of initial two species system do we still get limit cycles for the three species system. Since for a three species system there is no theorem (like Kolmogorov's theorem for two species system) which can tell us whether a system may possess a stable equilibrium point or stable limit cycle, we have used only numerical methods to see whether the system possesses stable limit cycles or not.

The plan of the present work is as follows : In chapter II first certain two species models are described. Kolmogorov's theorem and certain conditions for which the two

species systems may possess limit cycle solutions are used. Next a one prey-one predator mixed model of Rai, Kumar and Pande (1991) is discussed and then it is extended for a two prey-one predator system. In Chapter-III we have analysed the above two prey-one predator model. The range of various parameters, within which the three species system still exhibits limit cycle solutions, is determined. The range of various parameters of the three species system is compared with the range of the same parameters of the two species system. Relevant conclusions emerging from this comparison are then discussed. As illustration of our solutions, phase space trajectories of the two species system as well as the three species system are shown. The variations of the population densities of prey and predator with time are also shown.

The numerical analysis of the model has been performed on HP-9836 computer using Runge-Kutta fourth order approximations method.



## CHAPTER II

# REVIEW OF SOME TWO SPECIES ECOSYSTEM MODELS

Ecosystems in general are very complex. It is useful to consider first the simple idealised ecosystems and build a quantitative basis for them before trying to tackle successfully the realistic ones. The most idealised system is one with a single species in an environment in which the resources are unlimited. It may be assumed that in such a system the growth rate per individual is same for all individuals and is furthermore a constant in time. If we level this growth rate by  $r$  and the population at time  $t$  by  $N(t)$  then the time rate of change of the population is given by the equation.

$$\frac{dN(t)}{dt} = rN(t) \quad (2.1)$$

Which on solving gives

$$N = N_0 e^{rt} \quad (2.2)$$

where  $N_0$  is the population at time  $t = 0$

This is the well known Malthusian picture of populations growth where population rises exponentially with time.

The environment is in reality not an unlimited one. The food available to the population is sooner or later going to become limited because of rising population. Hence the growth rate  $r$  has to be such that it shows a decrease as the population rises.

The simplest possibility that we could consider is if  $r$  is replaced by  $r-sN$ , where  $s$  is a positive constant. The equation describing the population growth is then

$$\frac{dN}{dt} = (r-sN)N \quad (2.3)$$

This equation is the well known Pearl-Verhulst logistic equation of population growth, which leads to the result

$$N(t) = \frac{r/s}{1 + e^{-r(t-t_0)}} \quad (2.4)$$

Where the constant  $e^{rt_0}$  is related to the initial population by

$$e^{rt_0} = \frac{(r/s) - N(0)}{N(0)} \quad (2.5)$$

According to this picture, the population rises initially as in the Malthusian model, but as the population rises the growth rate begins to slow down and the population turns towards its asymptotic value which is  $(r/s)$ . The value  $N = r/s$  is the maximum that the population can reach and is therefore called the 'carrying capacity' of the given environment.

### The Lotka-Volterra Model

We now consider a situation where we have two interacting populations in a given environment, say a prey and a predator. Two very general assumptions used in such prey-predator model are :

- 1) The two populations inhabit the same area, so the densities are directly proportional to the numbers.

- 2) There is no time lag in the responses of either population to changes due to the other.

An interesting and mathematically elegant model for the interaction between a pair of species - a prey and a predator, was given independent by Lotka (1925) and Volterra (1926)

If H is the population of prey at any time t, in the absence of predator, its growth equation in simplest form is given by

$$\frac{dH}{dt} = a_1 H, \quad a_1 > 0$$

If P is the population of predator at any time t, its growth (decay) equation in absence of prey can be written as

$$\frac{dP}{dt} = -a_2 P, \quad a_2 > 0$$

If the prey and predator are in the same niche and if they interact, then the interaction term is, in general, a complicated function of H and P. But here we consider the simple quadratic form which is a product of the two populations. Consider the following equations for a prey-predator system.

$$\begin{aligned} \frac{dH}{dt} &= (a_1 - b_1 P) H \\ \frac{dP}{dt} &= (-a_2 + b_2 H) P \end{aligned} \tag{2.6}$$

where  $a_1, a_2, b_1, b_2 > 0$

Here  $a_1$  and  $a_2$  are average rate of growth and decay per individual in the absence of the other species and  $b_1, b_2$  are interaction parameters. If the niche is not overlapping the interaction is reduced and the values of  $b_1$  &  $b_2$  are very small. The sign in the interaction terms in the above equations are based on the expectation that the interactions will generate predators at the cost of the prey.

Unfortunately equations (2.6) & (2.7) can not be solved analytically. We have to take recourse to approximate schemes and numerical methods. In view of their non-linear nature it is unlikely that full information content of these equations is uncovered by such methods. However an exact result which is of crucial importance in the present context can be established.

We can write

$$\frac{dH}{dP} = \frac{(a_1 - b_1 P)H}{(-a_2 + b_2 H)P}$$

of

$$\frac{(-a_2 + b_2 H)}{H} dH = \frac{(a_1 - b_1 P)}{P} dP$$

Integrating we get

$$a_2 \ln H - b_2 H + a_1 \ln P - b_1 \ln P = \ln K \quad (2.7)$$

$$\therefore KH^{-a_2} e^{b_2 H} = P^{a_1} e^{-b_1 P} \quad (2.7a)$$

Where K is a constant given by

$$K = H_0^{a_2} P_0^{a_1} e^{-b_2 H_0} e^{-b_1 P_0} \quad (2.8)$$

in terms of initial values of H and P denoted by  $H_0$  and  $P_0$  respectively.

We thus, see that system (2.6) possesses a conserved quantity given by the right hand side of equation (2.7). The equation represents a family of closed curves in which each member of the family is characterised by a particular value of K. We can not solve equation (2.7a) for H or P individually but we can determine the curves on which H and P will move. To do this we equate the right and left hand sides of equation (2.7a) to new variables Z and W respectively and then plot the graphs  $C_1$  and  $C_2$  of the function.

$$Z = P^{a_1} e^{-b_1 P} \quad \text{and} \quad W = KH^{-a_2} e^{b_2 H}$$

as shown in figure (1).

For  $Z = W$ , we are confined in the third quadrant to the line (figure 2.1). C. To the maximum value of Z given by point A on  $C_1$ , there corresponds one point M on L and the corresponding points A' and A'' on  $C_2$  leading to two values of H which determine the bounds between which H may vary. Similarly minimum value of W given by B on  $C_2$  leads to N on L and hence to B' and B'' on  $C_1$  and these points determine the bounds on P. In this way we find the points  $P_1, P_2$  and  $Q_1, Q_2$  on the desired curve  $C_3$ . Additional points are easily found by starting on L at a point R anywhere between M and N and projecting on one hand onto  $C_1$  and over to  $C_3$  and on the other, onto  $C_2$  and again over to  $C_3$ . It is clear that the changing values of K raises or lowers the points A and B, and this expands or contracts the curve  $C_3$ . Accordingly, when K is given various

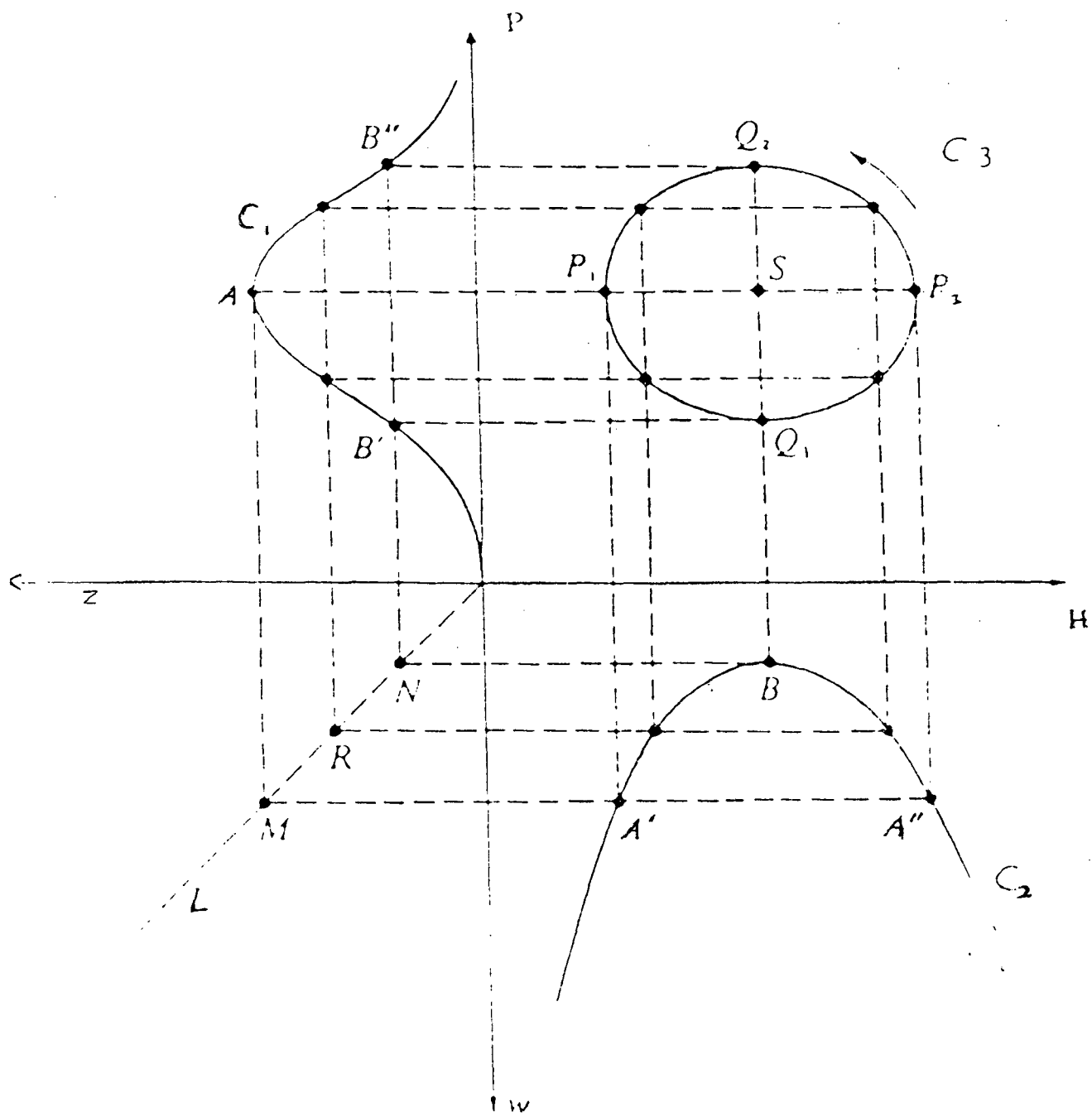


FIG. 2-1

values, we obtain a family of ovals about the point S.

Now, we will see how the point (H,P) on  $C_3$  moves around the curve as time  $t$  increases. We can find out the equilibrium point by putting the right hand side of equation (2.6) equal to zero i.e.

$$a_1 H - b_1 PH = 0$$

$$-a_2 P + b_2 PH = 0$$

Solving these equations, we get the equilibrium values •

$$H^* = a_2/b_2$$

$$P^* = a_1/b_1$$

Hence coordinates of point S will be

$$H = a_2/b_2, P = a_1/b_1$$

When  $H < a_2/b_2$ ,  $dP/dt$  is negative, so the point on  $C_3$  moves down as it traverses the arc  $Q_2 P_1 Q_1$ . Similarly, it will move up along the  $Q_1 P_2 Q_2$ . Hence as time  $t$  increases, the points on  $C_3$  move in anticlockwise direction.

This shows that both prey and predator populations undergo oscillations with constant amplitudes. The amplitudes would be determined by the initial population sizes,  $H_0$  and  $P_0$ . This behaviour is generally referred to as one of neutral stability.

### The Leslie Gower model

An alternative formulation of prey-predator equations was suggested by Leslie and Gower (1960). The rate equations for Prey  $H$  and predator  $P$  are given by

$$\frac{dH}{dt} = (a_1 - c_1 P)H \quad (2.9)$$

$$\frac{dP}{dt} = (a_2 - c_2 \frac{P}{H})P \quad (2.10)$$

Where  $a_1, a_2, c_1, c_2 > 0$

We use isocline method to study the system. The H-isocline and P-isocline are the curves in P-H phase space on which the time rate of change of prey and predator respectively are zero. Thus on H-isocline  $dH/dt = 0$  and on P-isocline  $dP/dt = 0$ .

From equations (2.9) and (2.10) we can see that

$$\text{H isocline : } P = a_1 / c_1$$

$$\text{P isocline : } H = (c_2/a_2)P$$

Thus both isoclines are straight lines which intersect at point  $(P^*, H^*)$  where

$$P^* = \frac{a_1}{c_1} \quad \text{and} \quad H^* = \frac{a_1 c_2}{a_2 c_1} \quad (2.11)$$

At point  $(P^*, H^*)$  both  $dH/dt = 0$  and  $dP/dt = 0$ . This means that at this point the populations of prey and predators remain constant with time, hence this point is the equilibrium point. We do not know yet whether this point is stable or unstable. From equations 2.9 and 2.10 we see if

$$P > \frac{a_1}{c_1} \quad \text{then} \quad \frac{dH}{dt} < 0$$

and vice-versa

similarly if

$$H > \frac{c_2 P}{a_2} \quad \text{then} \quad \frac{dP}{dt} > 0$$



and vice-versa

In the figure 2.2 we have plotted the H-isocline and P isocline. We have given the inequality conditions for all the four regions into which the positive H and positive P quadrant can be divided.

Suppose initially our system is at a point in region I. In this region  $dH/dt > 0$ ,  $dP/dt > 0$ . It follows that both H and P increases with time. Arrows show the direction in which trajectory moves. The trajectory will move towards the right and meet the H isocline. At H-isocline  $dH/dt = 0$  and tangent to trajectory will move normal to H isocline. In region II  $dH/dt < 0$ ,  $dP/dt > 0$  hence trajectory will move towards right side so that H decreases and P increases (slope at any point of trajectory is negative). The trajectory then meets P isocline, in which  $dP/dt = 0$  and tangent to the trajectory will be normal to P isocline. Similarly we can draw the trajectory for regions III and IV. The path of the trajectory in P-H phase space is spiral which converges at equilibrium point. Hence, each species population undergoes damped oscillations with time towards the equilibrium level.

This model takes into account the likely effect on predator's per capita growth rate of the relative sizes of interacting populations. Thus larger the ratio P/H the smaller the number of prey per predator and consequently, the less rapid the growth of predator population.

Leslie's formulations is different from Volterra's in the following ways :

1. For Volterra, whether predator increases or decreases in number depends only

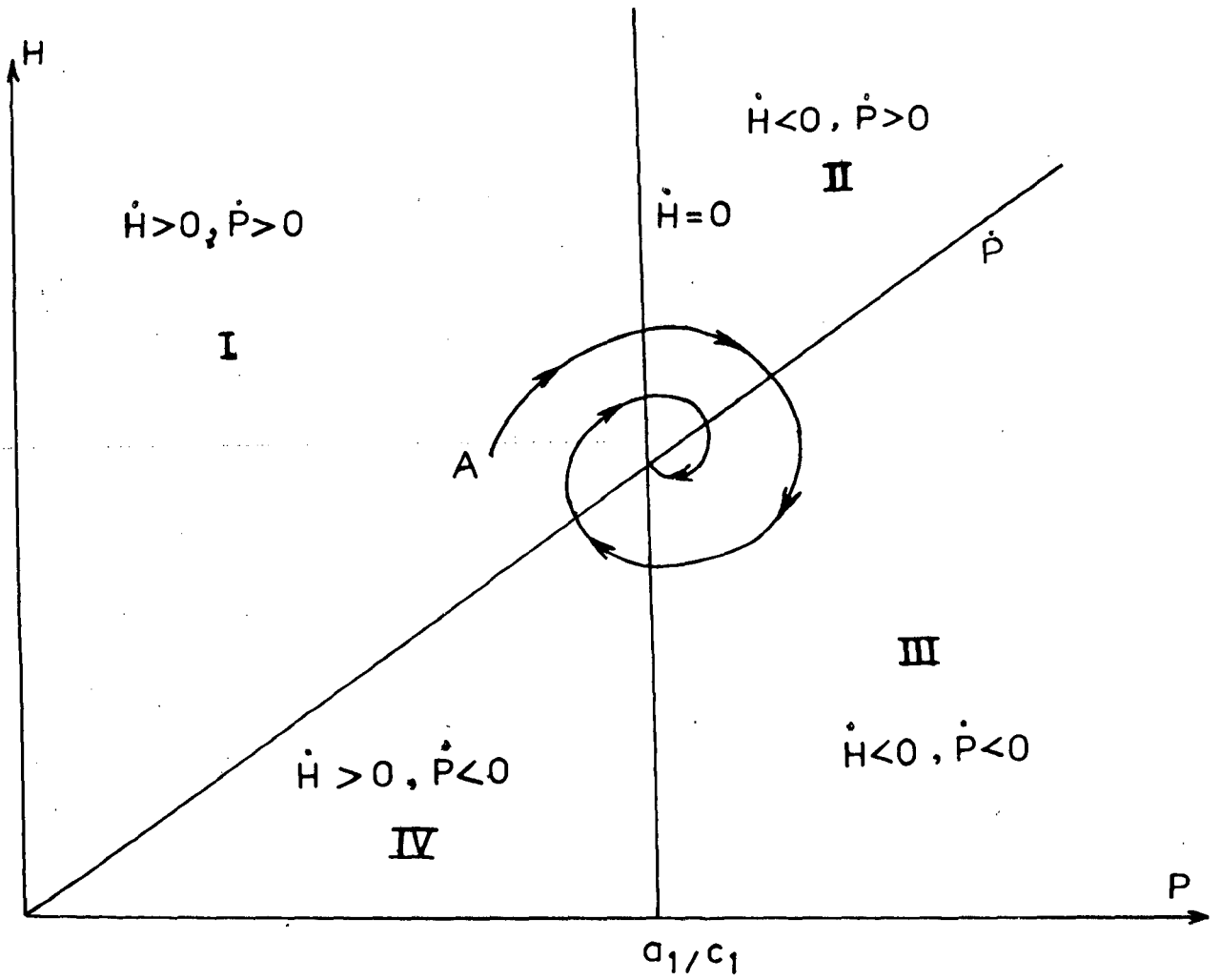


FIG. 2.2 PHASE SPACE DIAGRAM

on the density of prey whereas for Leslie it depends on the number of prey per predator.

2. Volterra's model relates the rate of increase of predators to the rate at which the prey are being eaten whereas in Leslie's formulations there is no relationship between the rate at which predator eats and the rate at which it reproduces.

### The Holling-Tanner model

The Holling Tanner model is slightly more elaborate than that of Leslie and Gower. The growth rate of prey H in the absence of predators P is given by the logistic equation

$$\frac{dH}{dt} = rH \left(1 - \frac{H}{K}\right) \quad (2.12)$$

Where  $r$  is intrinsic growth rate of prey and

$K$  is maximum number of prey allowed by the resources of the system.

When the predators are present in the system, the mortality from predators must be subtracted from the right side of equation (2.12). This mortality is the product of predation rate (number of prey killed per predator per unit time) and the predator number. Many studies have shown that the predation rate increases with prey density in the manner shown in figure 2.3. One of the equations which will produce a functional response like this (by C.S. Holling 1969) is

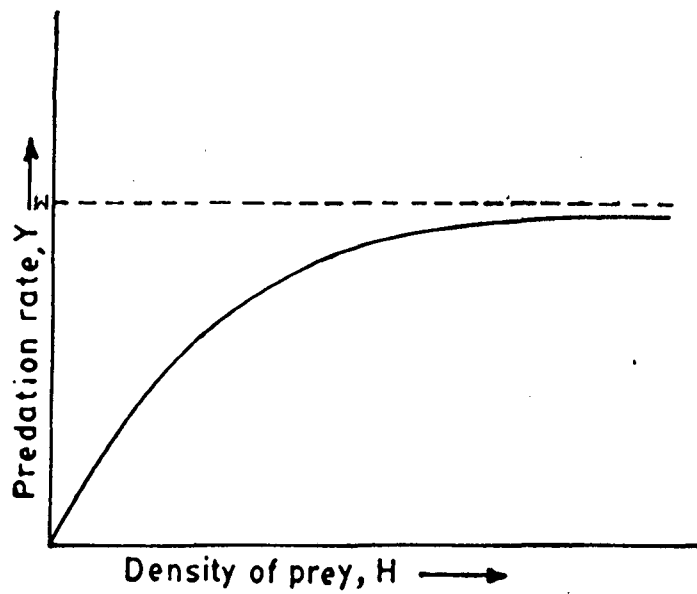


FIG. 2.3 Prey killed per predator per time,  $Y$ , as a function of prey density,  $H$ . The maximum predation rate is  $W$

$$Y = \frac{WH}{D+H}$$

where Y is predation rate

W is maximum predation rate

D is a constant determining how fast the functional response curve increases at low prey densities.

Thus we see that at very low prey densities predation rate is directly proportional to prey density and at very high prey density, it is constant. Each predator has a maximum predation rate at certain prey density. If prey density increases further then predator will not kill (or will not be able to kill) at higher rate. The predation rate is thus saturated. For a given prey density the constant D is directly proportional to the time required for predator to search for and find a prey and is therefore determined by the protection afforded to the prey by the habit.

The complete equation for prey now becomes

$$\frac{dH}{dt} = rH \left( 1 - \frac{H}{K} \right) - \frac{WHP}{D+H} \quad (2.13)$$

For growth rate of predator population, an equation of Leslie-Gower form is taken  
be taken

$$\frac{dP}{dt} = sP \left( 1 - \frac{JP}{H} \right) \quad (2.14)$$

Where  $r$  is the growth rate of predators

$J$  is the number of prey required to support one predator at equilibrium.

when  $P$  equals  $H/J$ .

The equations (2.13), (2.14) give the complete formulation of the Holling-Tanner model. We now do the stability analysis of this model.

The equilibrium point of the system is obtained by putting  $dH/dt = 0$  and  $dP/dt = 0$ . Thus putting R.H.S. of equations 2.13 and 2.14 equal to zero we get

$$P^* = H^*/J \quad (2.15)$$

$$1 - \frac{H^*}{K} - \frac{WH^*/rJ}{D+H^*} = 0 \quad (2.16)$$

Now Let  $\alpha = W/rJ$

$$\beta = D/K$$

Then solution of equation 2.16 for  $H^*$  is given by

$$H^* = D (1 - \alpha - \beta + R) / (2\beta) \quad (2.17)$$

where  $R = [(1 - \alpha - \beta)^2 + 4\beta]^{1/2}$

$$\text{Hence } P^* = D (1 - \alpha - \beta + R) / (2\beta J) \quad (2.18)$$

To study the behaviour of the system we proceed to a neighbourhood stability analysis (See Appendix - I). Let us rewrite the equations :

$$\frac{dH}{dt} = F_1(H,P) = rH \left(1 - \frac{H}{K}\right) - \frac{WHP}{D+H} \quad (2.13)$$

$$\frac{dP}{dt} - F_2(H,P) = sP\left(1 - \frac{JP}{H}\right) \quad (2.14)$$

To construct the community matrix, we evaluate all partial derivatives of  $F_1, F_2$  at  $(H^*, P^*)$  this gives

$$a_{11} = \left(\frac{\partial F_1}{\partial H_1}\right)^* = H^* \left[ -\frac{r}{K} + \frac{WP^*}{(D+H^*)^2} \right]$$

$$a_{12} = \left(\frac{\partial F_1}{\partial P}\right)^* = \frac{WH^*}{(D+H^*)}$$

$$a_{21} = \left(\frac{\partial F_2}{\partial H}\right)^* = s \frac{JP^{*2}}{H^{*2}} - \frac{s}{J}$$

$$a_{22} = \left(\frac{\partial F_2}{\partial P}\right)^* = -s \frac{JP^*}{H^*} - s$$

The determinantal equation for eigenvalue  $\lambda$  reduces to

$$\lambda^2 - (a_{11} + a_{22})\lambda + a_{11}a_{22} - a_{12}a_{21} = 0$$

For neighbourhood stability, the real parts of eigenvalues  $\lambda$  must be negative.

This holds only if

$$(1) \quad -(a_{11} + a_{22}) > 0$$

$$\rightarrow -H^* \left[ -\frac{r}{K} + \frac{WP^*}{(D+H^*)^2} \right] + s > 0 \quad (2.19)$$

$$(2) \quad a_{11} a_{22} - a_{12} a_{21} > 0$$

$$\rightarrow -sH^* \left[ -\frac{r}{K} + \frac{WP^*}{(D+H^*)^2} \right] + \frac{sWH^*}{J(D+H^*)} > 0 \quad (2.20)$$

By doing some mathematical manipulations and substituting values of  $H^*$  and  $P^*$  we get the condition for stability

$$\frac{s}{r} > \frac{2(\alpha - R)}{1 + \alpha + \beta + R} \quad (2.21)$$

If this condition is satisfied then the model possesses a stable equilibrium point. If this condition is violated, then in view of the Kolmogorov theorem, we can conclude that the system will possess a limit cycle. A brief discussion of the Kolmogorov theorem and the conditions under which it is applicable is given in Appendix (II). The general formulation of the stability analysis in the local limit is given in Appendix (I).

#### A Mixed Model

In the Holling-Tanner model, the equation for time rate of change for predator  $P$  was identical to the one used by Leslie and Gower. It was in prey equation in which they introduced an interaction term different from Leslie and Gower. Improvising on the idea of Holling and Tanner a two species model was constructed by Rai, Kumar and Pande (1991). In this model the per capita growth rate of predator is not proportional to simply the population rate ( $P/H$ ) but rather to a factor which is similar in form as predator's attack rate with a ceiling occurring for  $H \rightarrow \infty$ . This establishes a desirable relationship between prey's loss and predator's gain which does not exist in the Holling-Tanner model. The predators functional response of Holling-Tanner type is retained. In this process the behaviour of the rate equation for predator near  $H = 0$  is now improved over the Leslie-Gower and Holling Tanner models.

The model is thus given by equations



$$\frac{dH}{dt} = a_1 H - b_1 H^2 - \frac{W_1}{D_1 + H} PH \quad (2.22)$$

$$\frac{dP}{dt} = -aP + \frac{W}{D+H} HP \quad (2.23)$$

where  $a_1, b_1, W_1, D_1, a, W, D$  are constants, all are positive

Application of Kolmogorov theorem to this model shows that the theorem is satisfied by it under the conditions.

$$W > a \quad (2.24)$$

$$\frac{a_1}{b_1} > \frac{Da}{W-a} \quad (2.25)$$

If the above constraints are satisfied, then the model will always lead to solutions possessing either stable equilibrium or limit cycles. A local stability analysis around the equilibrium point will decide as to which possibility will arise and when.

The equilibrium populations of the system are

$$H^* = \frac{aD}{W-a}$$

$$P^* = \frac{a_1 D_1}{W_1} + \frac{aD}{W_1(W-a)^2} [a_1(W-a) - b_1(D_1 W - aD_1 + aD)]$$

The element  $a_{11}, a_{12}, a_{21}$  and  $a_{22}$  of the community matrix  $A$  are given by

The determinantal equations for eigenvalues reduces to the quadratic

$$\lambda^2 - a_{11}\lambda - a_{12}a_{21} = 0$$

$$a_{11} = a_1 - 2b_1H^* - \frac{W_1D_1P^*}{(D_1+H^*)^2}$$

$$a_{12} = -\frac{W_1H^*}{(D_1+H^*)}$$

$$a_{21} = \frac{WD}{(D+H^*)^2}P^*$$

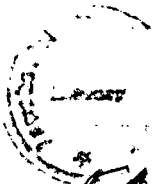
$$a_{22} = -a + \frac{WH^*}{D+H^*} = 0$$

Stable equilibrium point for the system exists if the eigenvalues have negative real parts. This happens if the following conditions are satisfied (Routh-Horwitz Criteria).

$$a_{12} a_{21} < 0 \quad \rightarrow \quad D > 0 \quad (2.26)$$

$$a_{11} < 0 \quad \rightarrow \quad 2b_1 \left( \frac{aD}{W-a} \right) + b_1D_1 - a > 0 \quad (2.27)$$

Since inequality 2.26 always holds true, because D is a positive constant, the choice of parameters which respects inequality (2.27) will lead to stable equilibrium and a choice violating it will lead to stable limit cycles (Figures 2.4 and 2.5).

  
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PHASE SPACE DIAGRAM

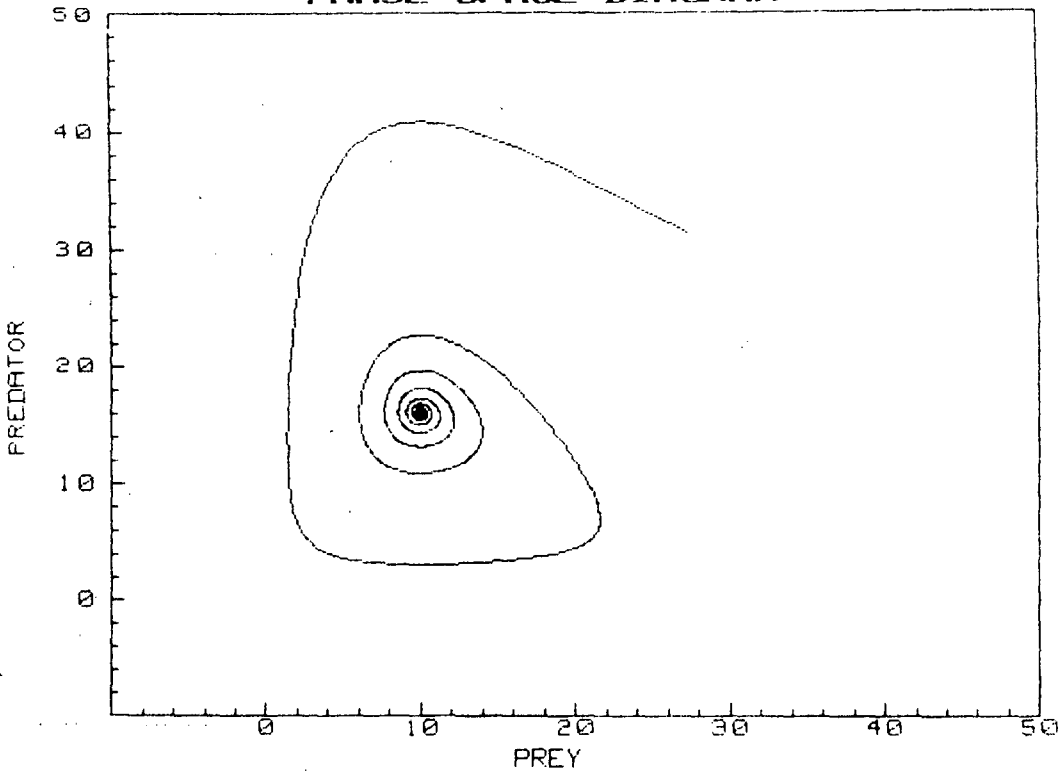


Fig. 2.4  $a_1=1.3, b_1=.05, a_2=1, w=1, w_1=1, D_1=10, D_2=10$

PHASE SPACE DIAGRAM

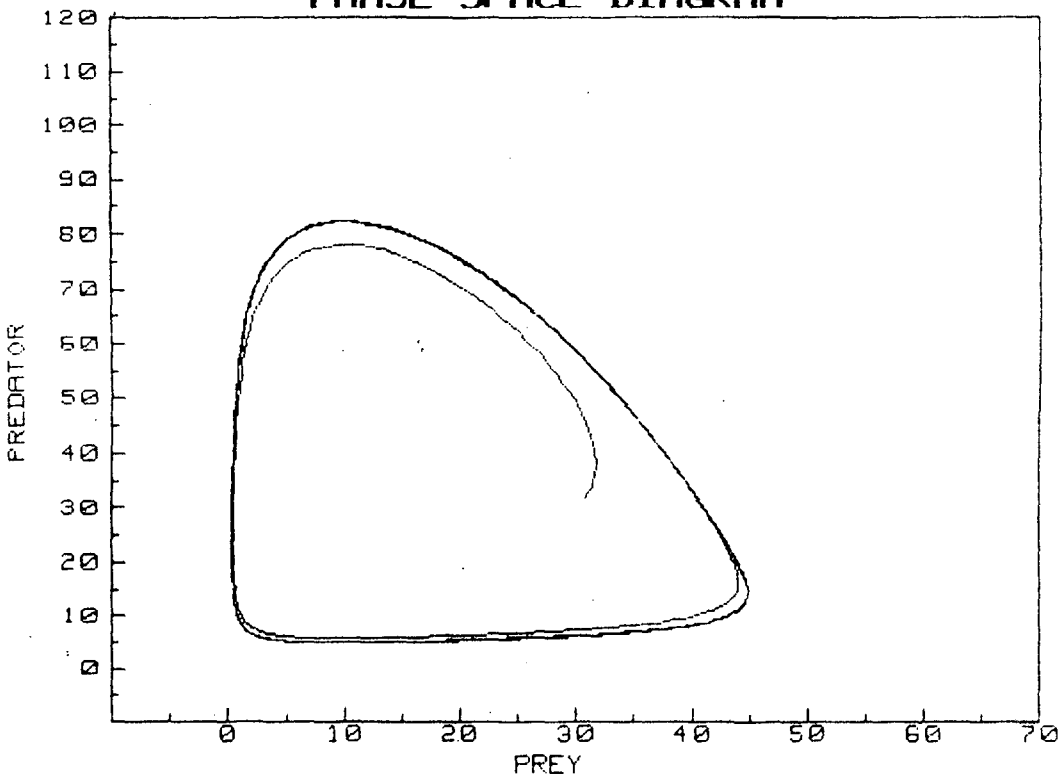


Fig. 2.5  $a_1=2.5, b_1=.05, a_2=1, w=1, w_1=1, D_1=10, D_2=10$

## A Two prey-one predator model

We now extend the model, given Rai, Kumar and Pande, from one prey-one predator to two prey-one predator system. We have slightly modified the parameters used in their model. The prey-predator interactions terms in the rate equations for the two species are taken simply proportional to each other, as in the Lotka-Volterra case. Thus the equations are :

$$\frac{dH}{dt} = a_1H - b_1H^2 - \frac{c_1PH}{d_1+H} \quad (2.28)$$

$$\frac{dP}{dt} = -a_3P + \frac{\alpha_1c_1PH}{d_1+H} \quad (2.29)$$

The constants  $a_1$ ,  $b_1$ ,  $c_1$ ,  $d_1$  and  $a_3$  have the usual meaning and are all positive. Here the notation (used in equations 2.22 and 2.23) are different. The term  $\alpha_1$  here is the efficiency of conversions of prey consumed to predator population growth. Thus the contribution of predation to the growth rate of predator is now proportional to the predation rate. The number of parameters in this model are reduced, hence this model is simpler. The condition for the existence of stable equilibrium point now reduces to

$$2b_1 \left( \frac{a_3d_1}{\alpha_1c_1 - a_3} \right) + b_1d_1 - a_3 > 0 \quad (2.30)$$

The choice of parameters which violate the above inequality lead to solutions with stable limit cycles.

A second prey species is now introduced into the system. We assume that the second prey species do not compete with existing prey species in the system for

resources. Due to the introduction of second prey species into the system the predator will now start eating second prey species also. The effect of this will be that the predation rate of first prey species will be reduced. Thus the predators per capita predation rate of first prey is not only function of density of first prey species but also of density of second prey species. The per capita predation rate of first prey species can now be written as (Noi Meir 1981).

$$Y = \frac{c_1 V_1}{d_1 + V_1 + V_2} \quad (2.31)$$

where  $V_1$  and  $V_2$  now denote the two prey species

$C_1$  is maximum predation rate of first prey species

$d_1$  is constant which determines how fast the functional response curve increases at low prey densities. For a given prey it is proportional to the time required for a predator to search for and find a prey and is determined by the protection afforded to the prey by the habitat.

If we compare the predators per capita predation rate of first prey species in two species system (where only first prey exists) and three species system (where second prey also exists), we will see that presence of the second prey  $V_2$  in system has the effect of increasing the constant  $d_1$  (which is proportional to the time required for predator to search for and find the prey) from  $d_1$  (in two species system) to  $d_1 + V_2$ . This effectively decreases the predators per capita predation rate of first prey species. The predator's per capita predation rate of first prey species is shown in Fig (2.6).

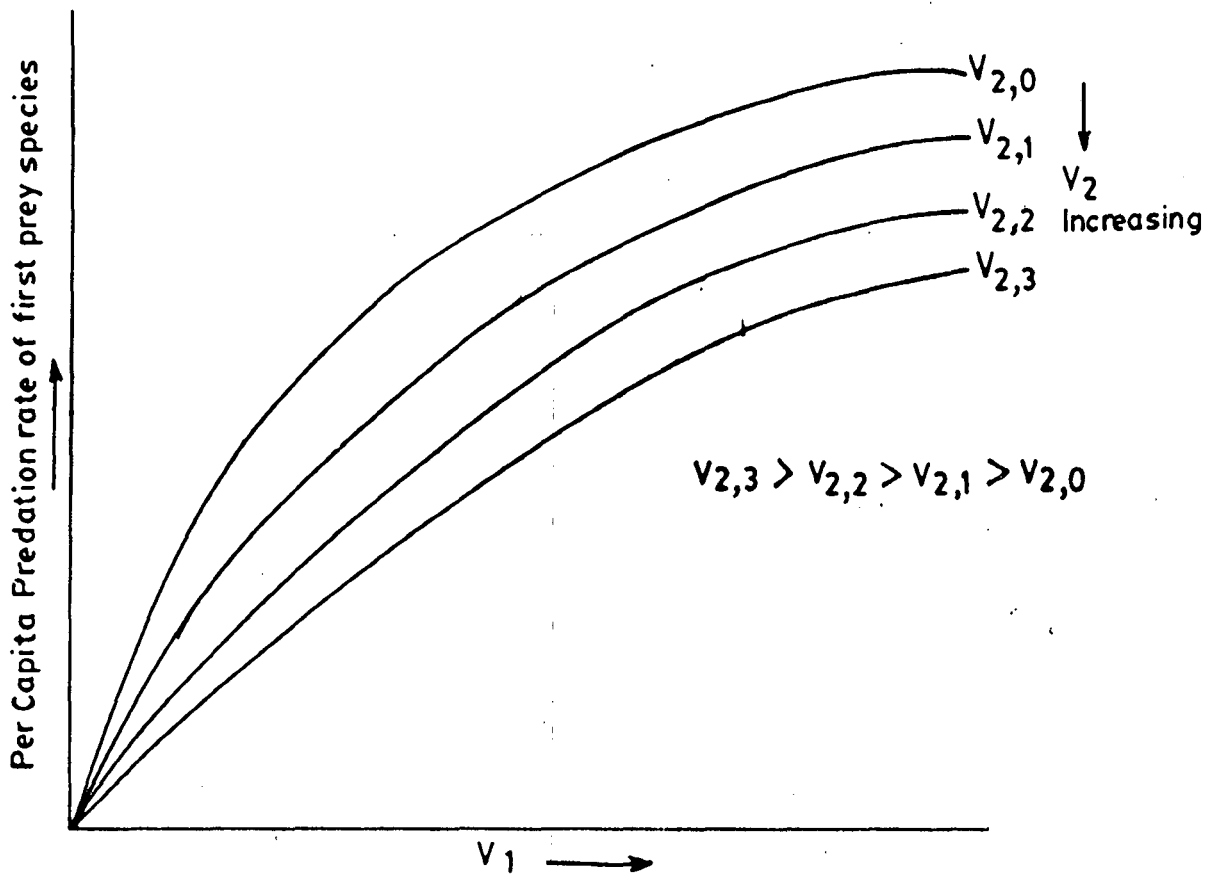


FIG. 2.6 Predator's per capita predation rate

The predation rate of second prey species can be written using similar arguments.

Thus after the introduction of second prey species the rate equations for system will be

$$\frac{dV_1}{dt} = a_1V_1 - b_1V_1^2 - \frac{c_1PV_1}{d_1+V_1+V_2} \quad (2.32)$$

$$\frac{dV_2}{dt} = a_2V_2 - b_2V_2^2 - \frac{c_2PV_2}{d_2+V_1+V_2} \quad (2.33)$$

$$\frac{dP}{dt} = -a_3P + \alpha_1 \frac{c_1PV_1}{d_1+V_1+V_2} + \alpha_2 \frac{c_2PV_2}{d_2+V_1+V_2} \quad (2.34)$$

where  $a_2, b_2, c_2, d_2, \alpha_2$  are parameters related to second prey species, all of which are positive. The introduction of second prey species into the system does not alter the parameters of first prey species. For a three species system there does not exist any theorem, corresponding to Kolmogorov's theorem in two species system, which can tell the conditions under which a system will exhibit stable limit cycles or stable equilibrium point. Hence we resort to the numerical methods to study the behaviour of above system.

# CHAPTER III

## ANALYSIS OF THE TWO PREY ONE PREDATOR MODEL

Recently John Loman (1988) has studied a system consisting of the two non-competing prey species and a predator using a graphical method. He initially starts with a two species system of one prey and one predator which is at stable equilibrium. The graphical method is used to predict the circumstances under which a second prey species can be introduced into the system such that stable equilibrium is still maintained. He has shown that depending upon the circumstances, the introduction of an alternative prey may either reduce the equilibrium density of the first prey or it may lead to increased density of first prey population. The former phenomena is termed as 'apparent competition' and the later one the 'apparent mutualism' (Holt 1977). The scope of the study was limited to systems with populations at stable equilibrium point.

We have considered a similar extension of a one pre-one predator system to a two prey one predator system with more general limit cycle solutions in mind. We start with a two species system discussed in the last chapter (the mixed model of Rai, Kumar and Pande 1991).

The dynamics of prey and predator are described by

$$\frac{dV_1}{dt} = a_1V_1 - b_1V_1^2 - \frac{c_1PV_1}{d_1+V_1} \quad (3.1)$$



$$\frac{dP}{dt} = -a_3P + \alpha_1 \left( \frac{c_1PV_1}{d_1 + V_1} \right) \quad (3.2)$$

where  $a_1, b_1, c_1, d_1, a_3, \alpha_1$  are constants all of which are positive.

As we have already discussed in the last chapter, the application of Kolmogorov's theorem give the following conditions for the system to possess either stable limit cycle solutions or stable equilibrium point.

$$\alpha_1 c_1 > a_3 \quad (3.3)$$

$$\frac{a_1}{b_1} > \frac{d_1 a_3}{\alpha_1 c_1 - a_3} \quad (3.4)$$

The linear stability analysis around equilibrium point give the following condition for the equilibrium point to be stable.

$$2b_1 \left( \frac{a_3 d_1}{\alpha_1 c_1 - a_3} \right) + b_1 d_1 - a_3 > 0 \quad (3.5)$$

If this condition for the existence of stable point is violated then the system will exhibit limit cycles.

When a second prey species is introduced into the system, the system becomes a three species systems of two prey and one predator. Now not only has the rate equation of second prey to be introduced but the rate equation of the predator and first prey have also to be modified. As we have discussed in the previous chapter, the rate equations for two prey species and one predator are described by the following equations.

$$\frac{dV_1}{dt} = a_1V_1 - b_1V_1^2 - \frac{c_1PV_1}{d_1+V_1+V_2} \quad (3.6)$$

$$\frac{dV_2}{dt} = a_2V_2 - b_2V_2^2 - \frac{c_2PV_2}{d_2+V_1+V_2} \quad (3.7)$$

$$\frac{dP}{dt} = -a_3P + \frac{\alpha_1c_1PV_1}{d_1+V_1+V_2} + \frac{\alpha_2c_2PV_2}{d_2+V_1+V_2} \quad (3.8)$$

As it is well known, it is not possible to write down the exact analytical solution for the type of three species system discussed above. The bulk of information obtainable from these models consists in knowing whether or not these systems are capable of possessing stable equilibrium or stable limit cycles.

We are basically interested in the case in which in a prey-predator system, which exhibits limit cycle solutions, an alternative prey species is introduced. We want to see whether the system, which is now a two prey-one predator system, still exhibits limit cycle solutions. We also want to investigate how in such a situation the range of parameters of initial one prey one predator system, within which limit cycle solutions were possible, changes with the introduction of second prey species.

In our study we use the Runge-Kutta fourth order approximation method to study the population densities of preys and predator at various times. We have then taken the projections of the trajectory of the system on  $V_1$  P plane and  $V_2$  P plane. If the system exhibits limit cycle in phase space of  $V_1$ ,  $V_2$  and P then the projections of the system trajectory on the coordinate planes  $V_1$  P and  $V_2$  P will also be trajectories which asymptotically reach definite closed curves. The same closed curves will be reached for

varying initial conditions so long as the model parameters are not changed.

We start with one prey one predator system and choose a set of parameters for which the system exhibits limit cycles. The values of parameters are given in table 1. Next we find the range of each parameter of the above two species system within which the systems still exhibits the limit cycle solutions. To determine the range, each parameter is varied, one at a time, keeping other parameters to the initial chosen value. For example the range of parameters  $c_1$  (The maximum predation rate) is from 19 to 40. The other parameters are the same as given in table - I. Similarly the range of other parameters is determined.

When the second species is introduced into the system it becomes a three species problem. The number of parameters required to define the system is increased. The new parameters are the ones which are associated with the second prey species (see equation 3.7). Keeping the initially found parameters of the two species system the same, we find a set of parameters associated with the second prey species for which the three species system also exhibits limit cycle solutions. We have chosen three sets of parameters associated with the second prey species. Their values are given in table - II.

Now we determine the range of the parameters of the three species system within which the system still exhibits limit cycle solutions. Here we take only those parameters which were also the parameters of the initial two species system. For the two species system we have already determined their range for limit cycle solutions. The same parameters are now varied in the three species system. Thus to determine the range of  $a_1$  (the growth rate of first prey species) in the three species system, we keep all other

parameters to their chosen values and vary  $a_1$ . The minimum and the maximum values of  $a_1$  within which the three species system exhibits limit cycles constitutes the range of  $a_1$ . For example, for the first set of parameters of the three species systems (table - II) the system exhibits limit cycles between 2.5 to 5.3 hence it is the range of  $a_1$  for the three species systems. Similarly the range of  $b_1$  (self interaction term for first prey species) is determined by keeping the values of all other parameters of the three species system fixed and varying  $b_1$  till the limit cycle solutions exist. The range of  $b_1$  is between .007 to .020. In a similar way the range of  $c_1$  is found to be between 16 and 33, range of  $d_1$  is between 75 and 205, range of  $a_3$  is between 0.8 and 1.3 and range of  $\alpha_1$  is between 1.3 and 2.9.

The whole procedure is repeated for the second and the third set of parameters of the three species system. The range of parameters of the initial two species system as well as the full three species system (three sets) are shown in table-III.

**TABLE - I**

**Initial Two Species System**

$$a_1 = 3.3 \quad , \quad a_3 = 1.0$$

$$b_1 = .01 \quad , \quad \alpha_1 = 0.1$$

$$c_1 = 20 \quad , \quad d_1 = 100$$

**Rate equations of the one prey one predator system**

$$\frac{dV_1}{dt} = a_1 V_1 - b_1 V_1^2 - \frac{c_1 P V_1}{d_1 + V_1}$$

$$\frac{dP}{dt} = -a_3 P + \frac{\alpha_1 c_1 P V_1}{d_1 + V_1 + V_2}$$

**TABLE II**  
**Three Species System**

**Set I**

$a_1 = 3.3$	$a_2 = 3.5$	$a_3 = 1$
$b_1 = 0.01$	$b_2 = 0.02$	$\alpha_1 = 0.1$
$c_1 = 20$	$c_2 = 20$	$\alpha_2 = 0.1$
$d_1 = 100$	$d_2 = 100$	

---

**Set II**

$a_1 = 3.3$	$a_2 = 3.1$	$a_3 = 1$
$b_1 = 0.01$	$b_2 = 0.01$	$\alpha_1 = 0.1$
$c_1 = 20$	$c_2 = 15$	$\alpha_2 = 0.1$
$d_1 = 100$	$d_2 = 80$	

---

**Set III**

$a_1 = 3.3$	$a_2 = 3.1$	$a_3 = 1.0$
$b_1 = 0.01$	$b_2 = 0.01$	$\alpha_1 = 0.1$
$c_1 = 20$	$c_2 = 20$	$\alpha_2 = 0.1$
$d_1 = 100$	$d_2 = 100$	

---

**Rate equations of the two prey one predator system**

$$dV_1/dt = a_1 V_1 - b_1 V_1^2 - c_1 PV_1/(d_1 + V_1 + V_2)$$

$$dV_2/dt = a_2 V_2 - b_2 V_2^2 - c_2 PV_2/(d_2 + V_1 + V_2)$$

$$dP/dt = -a_3 P + \alpha_1 c_1 PV_1/(d_1 + V_1 + V_2) + \alpha_2 c_2 PV_2/(d_2 + V_1 + V_2)$$

**TABLE III**

**Ranges of various parameters for limit cycle solutions**

Parameter		Initial two species system	Set-I three species system	Set-II three species system	Set-III three species system
$a_1$	min.	3.1	2.5	2.3	2.2
	max.	6.3	5.3	4.2	3.5
$b_1$	min.	.005	.007	.008	.009
	max.	.010	.020	.045	.1
$c_1$	min.	19	16	13	11
	max.	40	33	22	20
$d_1$	min.	50	75	90	95
	max.	110	205	280	350
$a_3$	min.	0.5	0.8	1.0	1.0
	max.	1.0	1.3	1.3	1.4
$\alpha_1$	min.	0.10	0.7	0.06	0.04
	max.	0.20	.15	0.11	0.11

In table-III we have compared the range of various parameters associated with the first prey before the introduction of second prey species into the system as well as after its introduction into the system.

The study of various parameters viz.  $a_1$  (growth rate)  $b_1$  (self interaction terms),  $c_1$  (maximum predation rate),  $d_1$  (term proportional to time required for search and kill of prey),  $a_3$  (decay rate of predator) and  $\alpha_1$  (efficiency of conversion of prey consumed to growth rate of predator) show that a range still exist within which the new three species system exhibits limit cycle solutions. The range of parameters does not remain the same. In some cases the range is shifted to the lower side (e.g.  $a_1$ ,  $c_1$  etc) and in same cases the range is shifted to the upper side (e.g.  $b_1$ ,  $d_1$ ,  $a_3$  etc).

If we compare the range of  $c_1$  (the maximum predation rate) we find that the minimum and the maximum value of predations rate in the two species system are 19 and 40. Corresponding values for the three species system (set-I) are 13 and 33. The introduction of second species into the ecosystem reduces the value of maximum predation rate of the first species. Similarly comparing the values of constant  $d_1$  (term proportional to search time for prey), we see that minimum and maximum values in two species system are 50 and 110. For three species system (set-I) corresponding values are 75 and 205. We observe that time required for search and capture of first prey is increased after second species is introduced into the ecosystem. Set - II and set- III also corroborate above facts. Both effects are due to the reason that the predation pressure on first prey is reduced when second species is introduced into ecosystem. Also since predator spends some time for search and capture of second prey species hence effective search time for finding first prey is increased.

The figures 3.1 to 3.35 show some specimen results of the computer calculations. The numerical inputs for each figure are mentioned in figure caption table-I. figure 3.1 to 3.6 are phase space diagrams for the initial two species system. For three species system we have drawn the projection of the system trajectory on  $V_1$ -P and  $V_2$ -P planes. As can be seen from figures, these are also the closed curves. We have verified that for each case the same curve is reached even when initial conditions are changed. Thus the trajectories in the phase space of  $V_1, V_2, P$  end up in the limit cycles. Corresponding to each phase space diagram, the time development of each species of the system is also shown.



In figure 3.31 to 3.35 we have compared the time development of the population densities of initial two species system with final three species systems. Here, for the three species systems only the parameters related to the second species are changed. The other parameters for the three species systems are same as that of the two species system. The numerical inputs for each figure are mentioned in figure caption table II. It can be seen that the range of the population of the first prey is increased when the second prey species is introduced into the system. This is analogous to the phenomena of "apparent mutualism", observed by Loman (1988).

### FIGURE CAPTION TABLE - I

- 1) Fig. 3.1 Initial Conditions :  $V(0) = 130$   $P(0) = 15$   
 Numerical inputs for different parameters  
 $a_1 = 3.3$      $b_1 = .01$      $c_1 = 30$   
 $a_3 = 1.0$      $\alpha_1 = 0.1$      $d_1 = 100$
  
- 2) Fig. 3.2 Initial Conditions :  $V(0) = 40$      $P(0) = 22$   
 Numerical inputs same as above.
  
- 3) Fig. 3.3 Initial Conditions :  $V(0) = 130$      $P(0) = 15$   
 Numerical inputs for different parameters  
 $a_1 = 3.3$      $b_1 = .01$      $c_1 = 30$   
 $a_3 = 1.0$      $\alpha_1 = 0.1$      $d_1 = 105$
  
- 4) Fig. 3.4 Initial Conditions :  $V(0) = 50$      $P(0) = 20$   
 Numerical inputs same as above
  
- 5) Fig. 3.5 Initial conditions :  $V(0) = 130$      $P(0) = 15$   
 Numerical inputs for different parameters  
 $a_1 = 3.3$      $b_1 = .01$      $c_1 = 30$   
 $a_3 = 0.8$      $\alpha_1 = 0.1$      $d_1 = 100$
  
- 6) Fig. 3.6 Initial conditions :  $V(0) = 40$      $P(0) = 40$   
 Numerical inputs same as above
  
- 7) Fig. 3.7 Initial Conditions :  $V_1(0) = 75$      $V_2(0) = 80$      $P(0) = 30$   
 Numerical inputs for different parameters  
 $a_1 = 4.3$      $b_1 = 0.01$      $c_1 = 20$      $d_1 = 100$   
 $a_2 = 3.5$      $b_2 = 0.2$      $c_2 = 20$      $d_2 = 100$   
 $a_3 = 1.0$      $\alpha_1 = 0.1$      $\alpha_2 = 0.1$

- 8) Fig. 3.8 Initial Conditions :  $V_1(0) = 110$   $V_2(0) = 60$   $P(0) = 65$   
 Numerical inputs same as above
- 9) Fig. 3.9 Initial conditions :  $V_1(0) = 105$   $V_2(0) = 90$   $P(0) = 15$   
 Numerical inputs for different parameters  
 $a_1 = 3.3$   $b_1 = 0.01$   $c_1 = 20$   $d_1 = 100$   
 $a_2 = 3.5$   $b_2 = 0.02$   $c_2 = 20$   $d_2 = 100$   
 $a_3 = 1.0$   $\alpha_1 = 0.1$   $\alpha_2 = 0.1$
- 10) Fig. 3.10 Initial conditions :  $V_1(0) = 110$   $V_2(0) = 80$   $P(0) = 75$   
 Numerical inputs same as above
- 11) Fig. 3.11 Initial conditions :  $V_1(0) = 240$   $V_2(0) = 190$   $P(0) = 22$   
 Numerical inputs for different parameters  
 $a_1 = 3.3$   $b_1 = 0.01$   $c_1 = 16$   $d_1 = 100$   
 $a_2 = 3.5$   $b_2 = 0.02$   $c_2 = 20$   $d_2 = 100$   
 $a_3 = 1.0$   $\alpha_1 = 0.1$   $\alpha_2 = 0.1$
- 12) Fig. 3.12 Initial conditions :  $V_1(0) = 90$   $V_2(0) = 60$   $P(0) = 65$   
 Numerical inputs same as above
- 13) Fig. 3.13 Initial conditions :  $V_1(0) = 120$   $V_2(0) = 90$   $P(0) = 15$   
 Numerical inputs for different parameters  
 $a_1 = 3.3$   $b_1 = 0.01$   $c_1 = 16$   $d_1 = 150$   
 $a_2 = 3.5$   $b_2 = 0.02$   $c_2 = 20$   $d_2 = 100$   
 $a_3 = 1.0$   $\alpha_1 = 0.1$   $\alpha_2 = 0.1$
- 14) Fig. 3.14 Initial conditions :  $V_1(0) = 100$   $V_2(0) = 60$   $P(0) = 65$   
 Numerical inputs same as above

- 15) Fig. 3.15 Initial conditions :  $V_1(0) = 75$   $V_2(0) = 80$   $P(0) = 30$   
 Numerical inputs for different parameters  
 $a_1 = 3.3$   $b_1 = 0.01$   $c_1 = 20$   $d_1 = 100$   
 $a_2 = 3.5$   $b_2 = 0.02$   $c_2 = 20$   $d_2 = 100$   
 $a_3 = 1.0$   $\alpha_1 = 0.08$   $\alpha_2 = 0.1$
- 16) Fig. 3.16 Initial conditions :  $V_1(0) = 30$   $V_2(0) = 20$   $P(0) = 80$   
 Numerical inputs same as above
- 17) Fig. 3.17 Initial conditions :  $V_1(0) = 160$   $V_2(0) = 145$   $P(0) = 22$   
 Numerical inputs for different parameters  
 $a_1 = 3.3$   $b_1 = 0.02$   $c_1 = 20$   $d_1 = 100$   
 $a_2 = 3.1$   $b_2 = 0.01$   $c_2 = 15$   $d_2 = 80$   
 $a_3 = 1.0$   $\alpha_1 = 0.1$   $\alpha_2 = 0.1$
- 18) Fig. 3.18 Initial conditions :  $V_1(0) = 40$   $V_2(0) = 50$   $P(0) = 70$   
 Numerical inputs same as above
- 19) Fig. 3.19 Initial conditions :  $V_1(0) = 240$   $V_2(0) = 220$   $P(0) = 20$   
 Numerical inputs for different parameters  
 $a_1 = 3.3$   $b_1 = 0.01$   $c_1 = 15$   $d_1 = 100$   
 $a_2 = 3.1$   $b_2 = 0.01$   $c_2 = 15$   $d_2 = 80$   
 $a_3 = 1.0$   $\alpha_1 = 0.1$   $\alpha_2 = 0.1$
- 20) Fig. 3.20 Initial conditions :  $V_1(0) = 130$   $V_2(0) = 90$   $P(0) = 75$   
 Numerical inputs same as above

- 21) Fig. 3.21 Initial conditions :  $V_1(0) = 110$   $V_2(0) = 140$   $P(0) = 225$   
 Numerical inputs for different parameters  
 $a_1 = 3.3$   $b_1 = 0.01$   $c_1 = 20$   $d_1 = 200$   
 $a_2 = 3.1$   $b_2 = 0.01$   $c_2 = 15$   $d_2 = 80$   
 $a_3 = 1.0$   $\alpha_1 = 0.1$   $\alpha_2 = 0.1$
- 22) Fig. 3.22 Initial conditions :  $V_1(0) = 80$   $V_2(0) = 50$   $P(0) = 40$   
 Numerical inputs same as above
- 23) Fig. 3.23 Initial conditions :  $V_1(0) = 155$   $V_2(0) = 150$   $P(0) = 22$   
 Numerical inputs for different parameters  
 $a_1 = 2.3$   $b_1 = 0.01$   $c_1 = 20$   $d_1 = 100$   
 $a_2 = 3.3$   $b_2 = 0.01$   $c_2 = 20$   $d_2 = 100$   
 $a_3 = 1.0$   $\alpha_1 = 0.1$   $\alpha_2 = 0.1$
- 24) Fig. 3.24 Initial conditions :  $V_1(0) = 70$   $V_2(0) = 40$   $P(0) = 40$   
 Numerical inputs same as above
- 25) Fig. 3.25 Initial conditions :  $V_1(0) = 170$   $V_2(0) = 150$   $P(0) = 32$   
 Numerical inputs for different parameters  
 $a_1 = 3.3$   $b_1 = 0.03$   $c_1 = 20$   $d_1 = 100$   
 $a_2 = 3.3$   $b_2 = 0.01$   $c_2 = 20$   $d_2 = 100$   
 $a_3 = 1.0$   $\alpha_1 = 0.1$   $\alpha_2 = 0.1$
- 26) Fig. 3.26 Initial conditions:  $V_1(0) = 30$   $V_2(0) = 100$   $P(0) = 85$   
 Numerical inputs same as above

- 27) Fig. 3.27 Initial conditions:  $V_1(0) = 38$   $V_2(0) = 8$   $P(0) = 18$   
 Numerical inputs for different parameters  
 $a_1 = 3.3$   $b_1 = 0.01$   $c_1 = 20$   $d_1 = 200$   
 $a_2 = 3.3$   $b_2 = 0.01$   $c_2 = 20$   $d_2 = 100$   
 $a_3 = 1.0$   $\alpha_1 = 0.1$   $\alpha_2 = 0.1$
- 28) Fig. 3.28 Initial conditions:  $V_1(0) = 40$   $V_2(0) = 90$   $P(0) = 85$   
 Numerical inputs same as above
- 29) Fig. 3.29 Initial conditions:  $V_1(0) = 80$   $V_2(0) = 30$   $P(0) = 30$   
 Numerical inputs for different parameters  
 $a_1 = 3.3$   $b_1 = 0.01$   $c_1 = 20$   $d_1 = 100$   
 $a_2 = 3.3$   $b_2 = 0.01$   $c_2 = 20$   $d_2 = 100$   
 $a_3 = 1.0$   $\alpha_1 = 0.06$   $\alpha_2 = 0.1$
- 30) Fig. 3.30 Initial conditions:  $V_1(0) = 70$   $V_2(0) = 50$   $P(0) = 40$   
 Numerical inputs same as above

## FIGURE CAPTION TABLE - II

- 1) Fig. 3.31 Initial populations :
- $$V(0) = 50 \quad P(0) = 60$$
- Numerical inputs for different parameters
- $$a_1 = 3.3 \quad b_1 = 0.01 \quad c_1 = 20 \quad d_1 = 100$$
- $$a_3 = 1.0 \quad \alpha_1 = 0.1$$
- 2) Fig. 3.32 Initial conditions :
- $$V_1(0) = 70 \quad V_2(0) = 50 \quad P(0) = 42$$
- Numerical inputs for different parameters:
- $$a_1 = 3.3 \quad b_1 = 0.01 \quad c_1 = 20 \quad d_1 = 100$$
- $$a_2 = 4.3 \quad b_2 = 0.01 \quad c_2 = 20 \quad d_2 = 100$$
- $$a_3 = 1.0 \quad \alpha_1 = 0.1 \quad \alpha_2 = 0.1$$
- 3) Fig. 3.33 Initial conditions :
- $$V_1(0) = 70 \quad V_2(0) = 50 \quad P(0) = 42$$
- Numerical inputs for different parameters:
- $$a_1 = 3.3 \quad b_1 = 0.01 \quad c_1 = 20 \quad d_1 = 100$$
- $$a_2 = 3.3 \quad b_2 = 0.005 \quad c_2 = 20 \quad d_2 = 100$$
- $$a_3 = 1.0 \quad \alpha_1 = 0.1 \quad \alpha_2 = 0.1$$

4) Fig. 3.34 Initial conditions :

$$V_1(0) = 80 \quad V_2(0) = 50 \quad P(0) = 40$$

Numerical inputs for different parameters.

$$a_1 = 3.3 \quad b_1 = 0.01 \quad c_1 = 20 \quad d_1 = 100$$

$$a_2 = 4.3 \quad b_2 = 0.01 \quad c_2 = 15 \quad d_2 = 100$$

$$a_3 = 1.0 \quad \alpha_1 = 0.1 \quad \alpha_2 = 0.1$$

5) Fig. 3.35 Initial conditions :

$$V_1(0) = 80 \quad V_2(0) = 50 \quad P(0) = 40$$

Numerical inputs for different parameters:

$$a_1 = 3.3 \quad b_1 = 0.01 \quad c_1 = 20 \quad d_1 = 100$$

$$a_2 = 3.0 \quad b_2 = 0.01 \quad c_2 = 15 \quad d_2 = 80$$

$$a_3 = 1.0 \quad \alpha_1 = 0.1 \quad \alpha_2 = 0.1$$



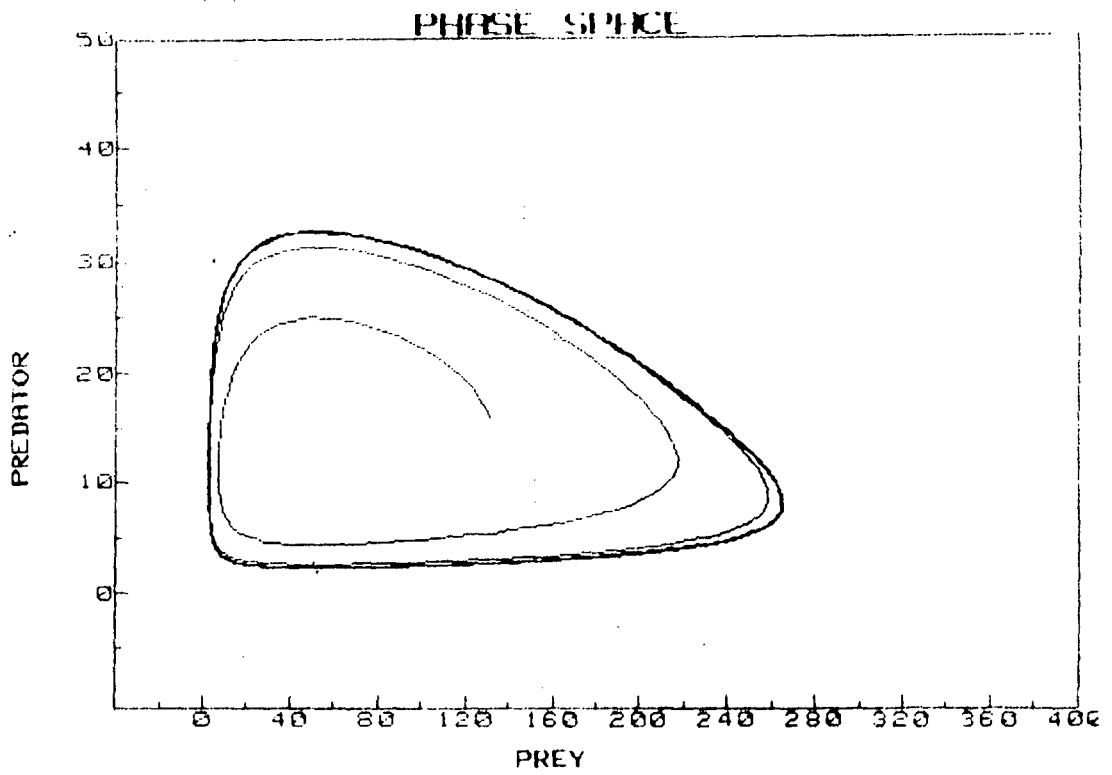


Fig.

Fig. 3.1 Phase space diagram of the one prey one predator system

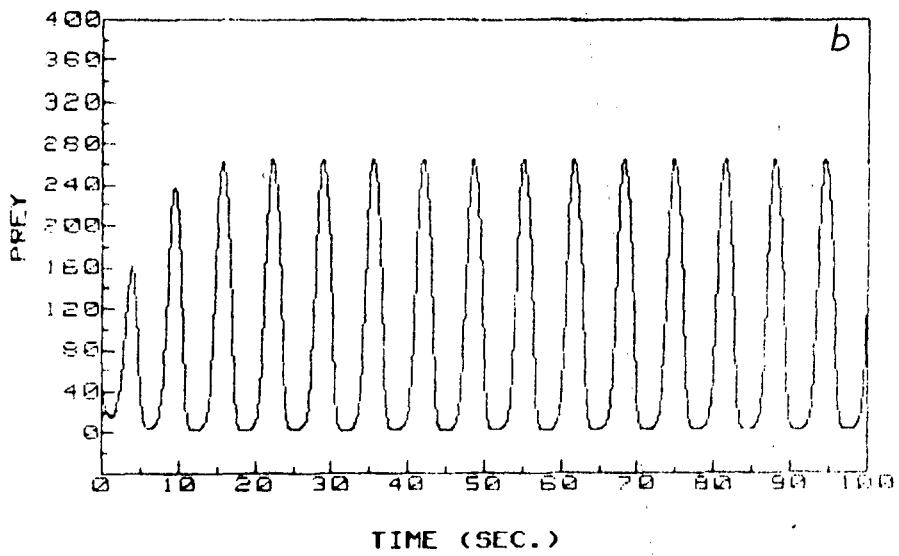
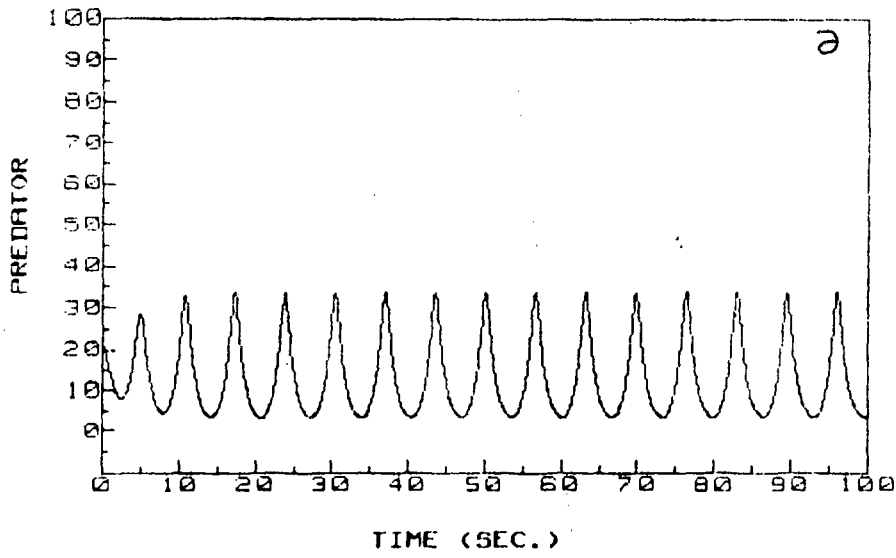


Fig.3.2 Variation of population densities with time in the one prey-one predator system

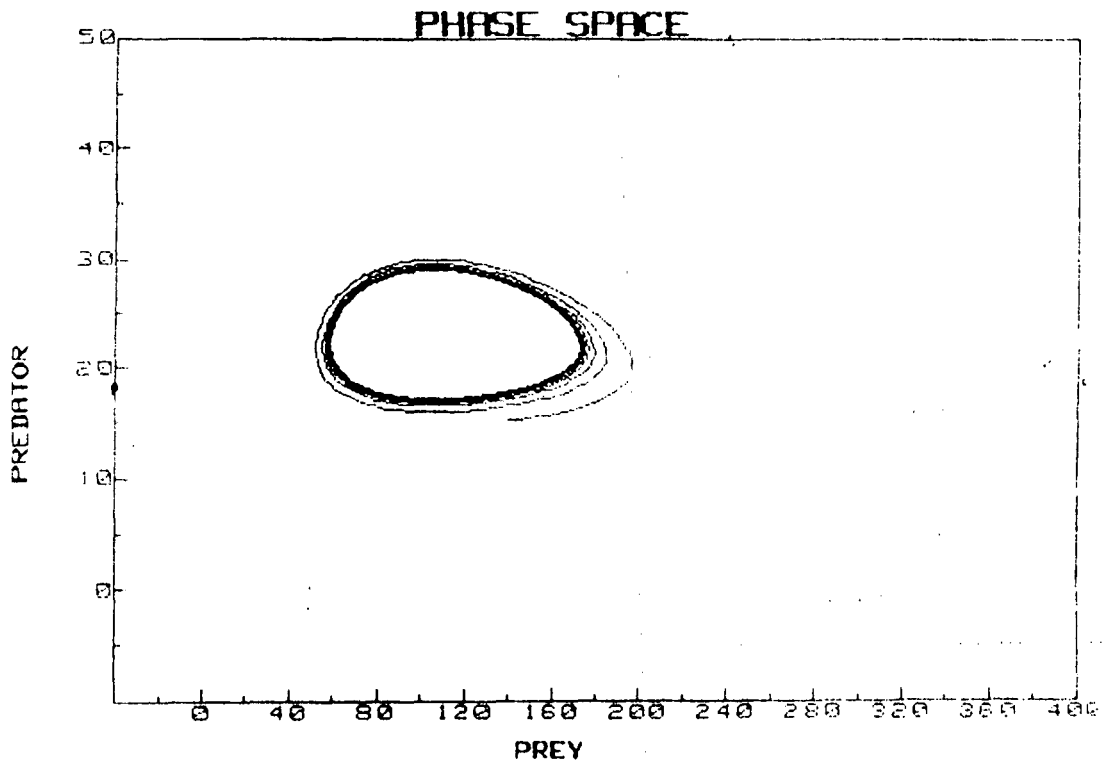


Fig.3.3 Phase space diagram of the one prey one predator system

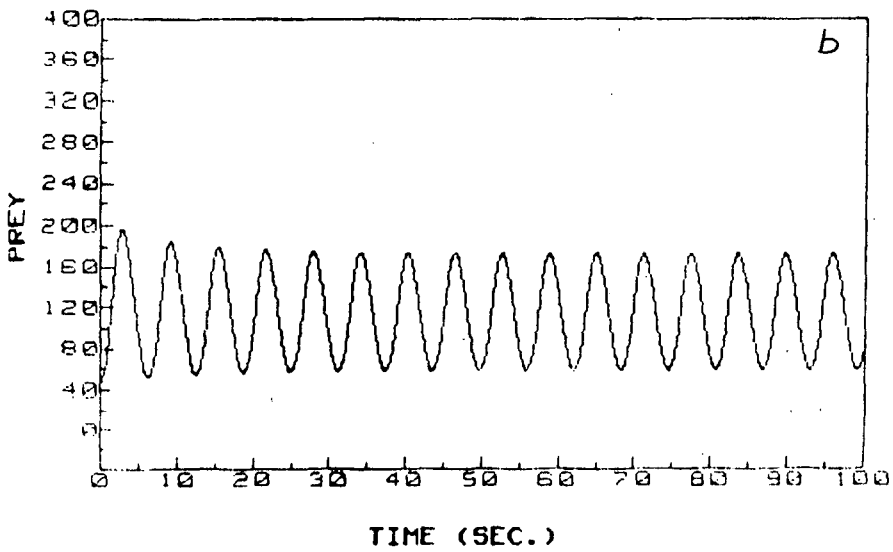
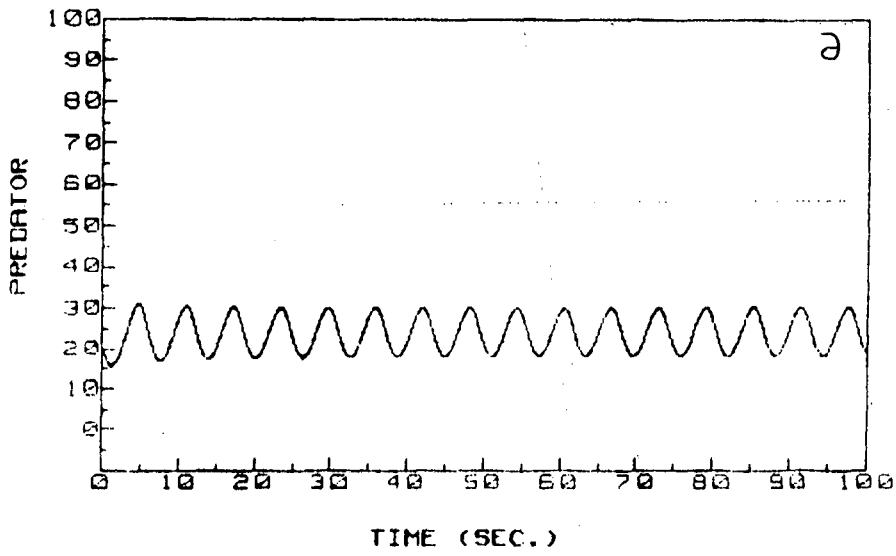


Fig. 3.4 Variation of population densities with time in the one prey-one predator system

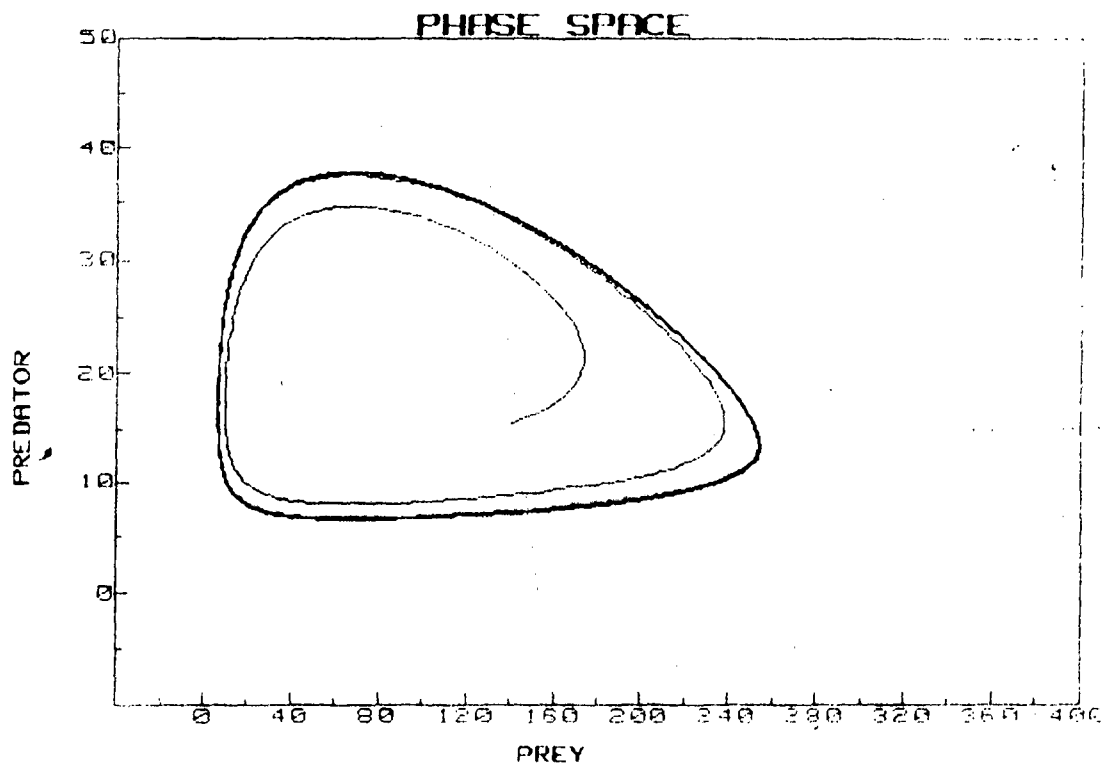


Fig.3.5 Phase space diagram of the one prey one predator system

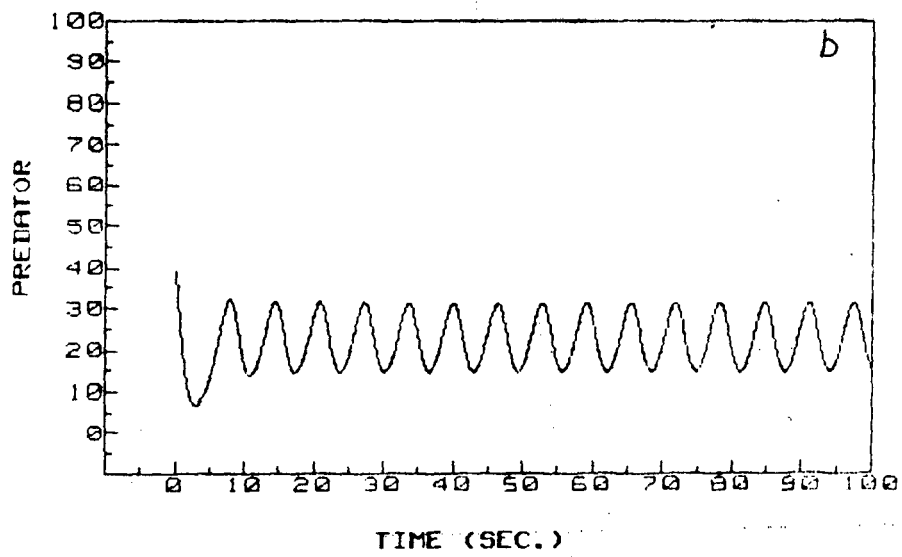
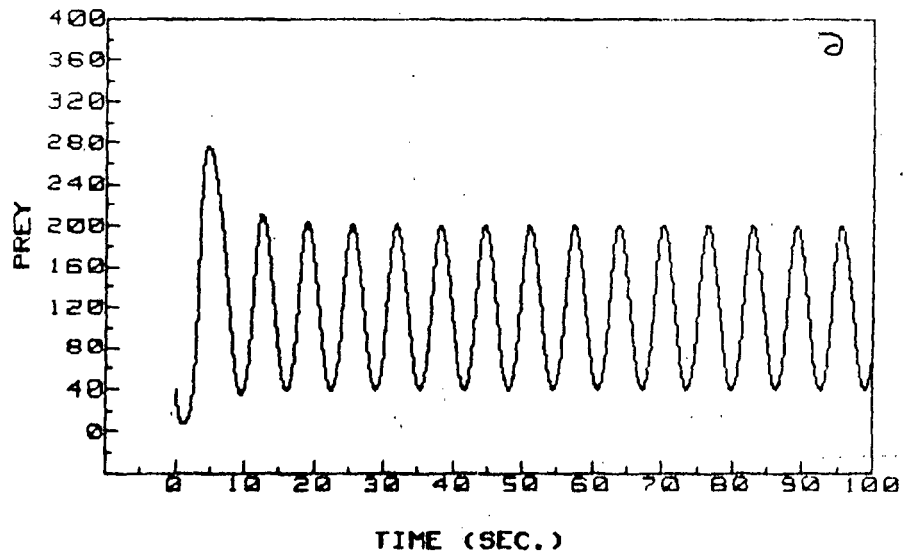


Fig.3.6 Variation of population densities time in the one prey-one predator system

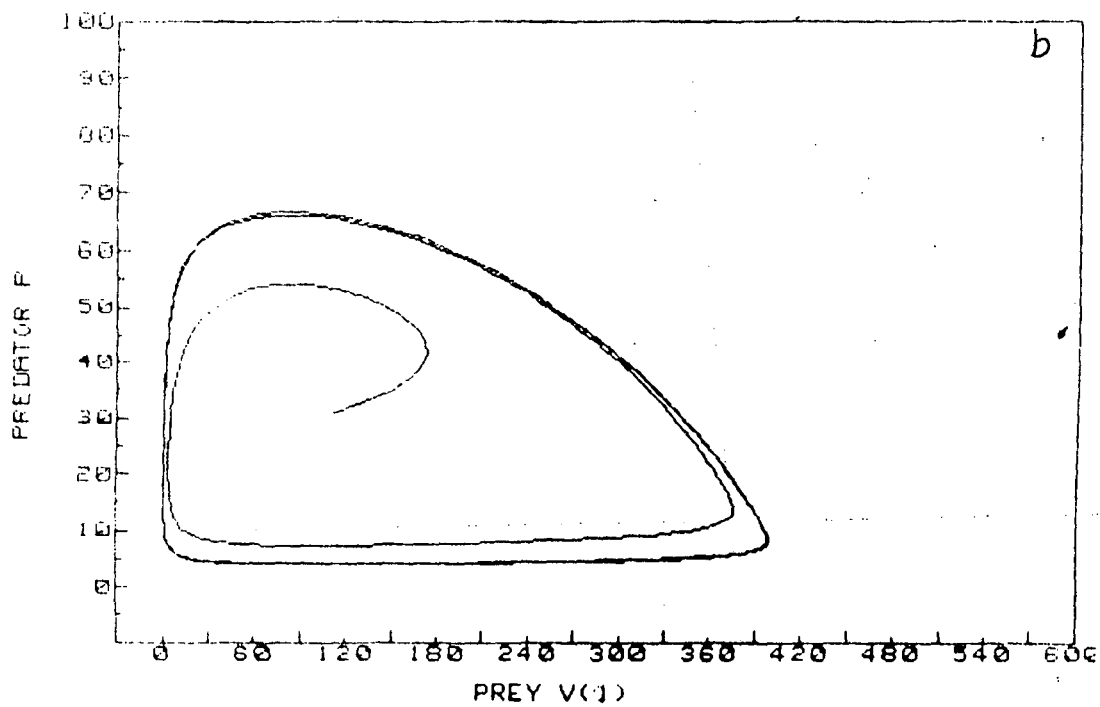
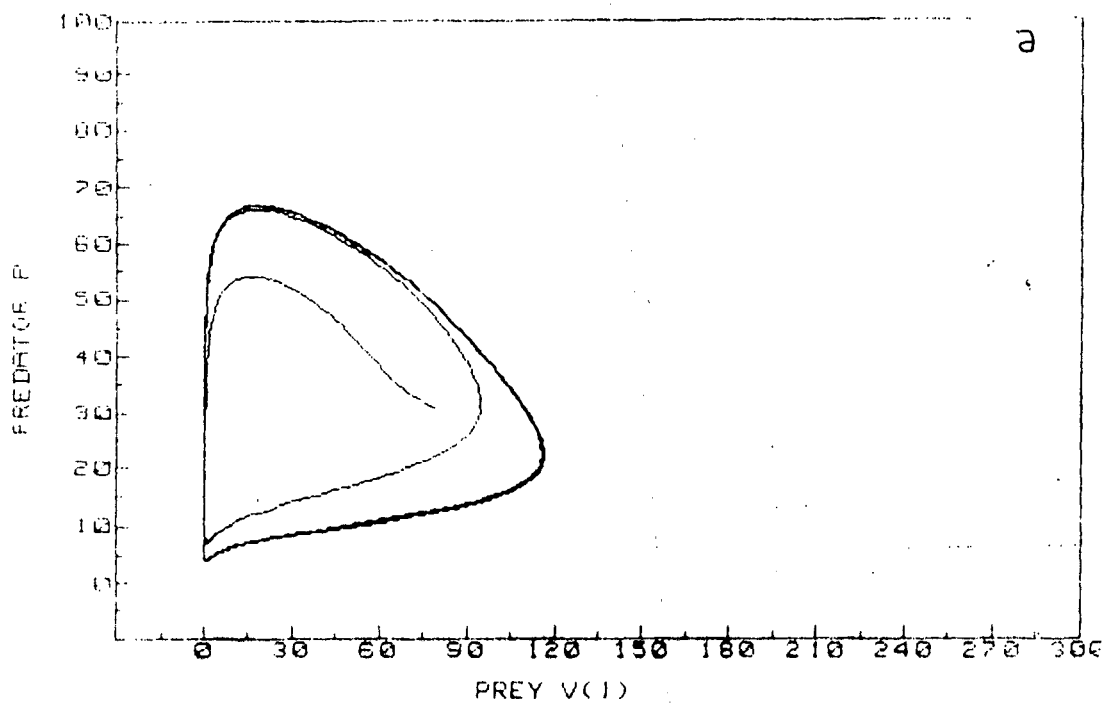


Fig.3.7 Projection of population trajectory on a)  $U(1)$ - $P$  plane, b)  $U(2)$ - $P$  plane for the three species system

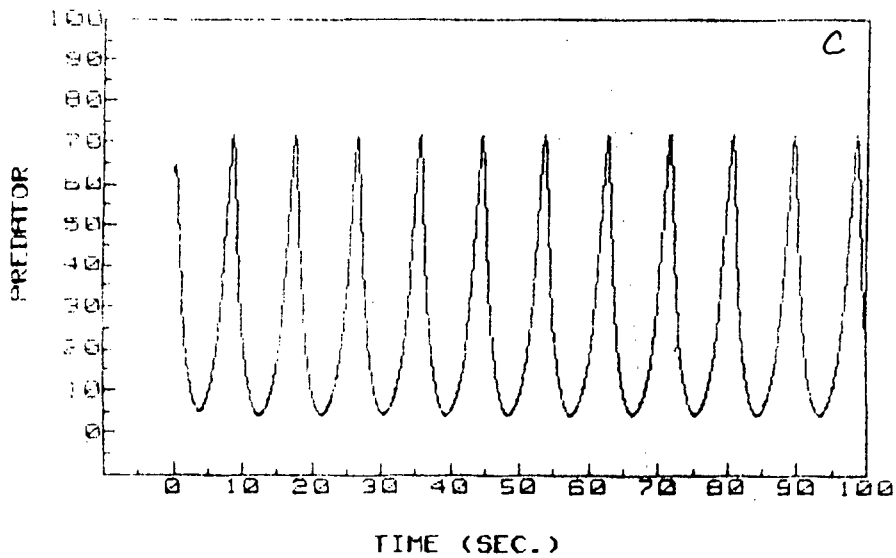
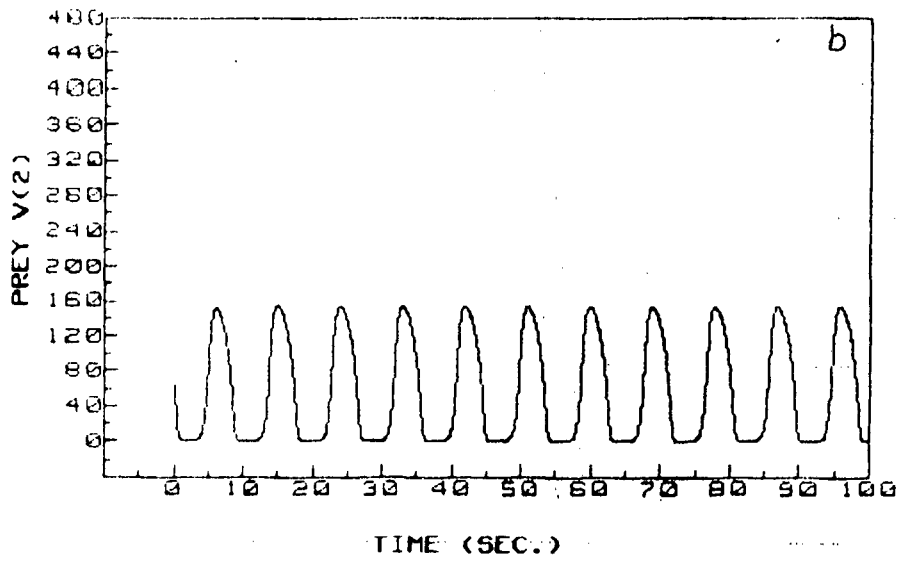
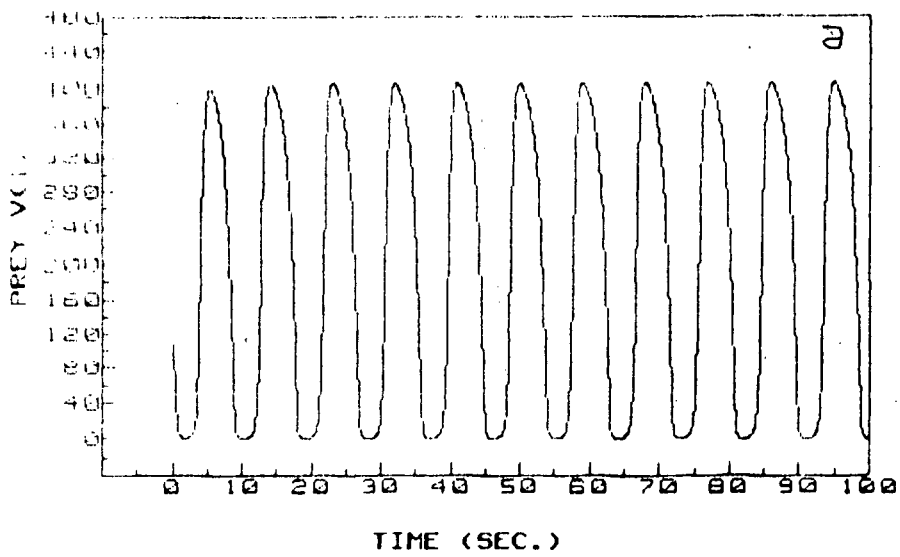


Fig. 3.8 Variation of population densities with time in the two prey-one predator system  
 a) first prey b) second prey c) predator



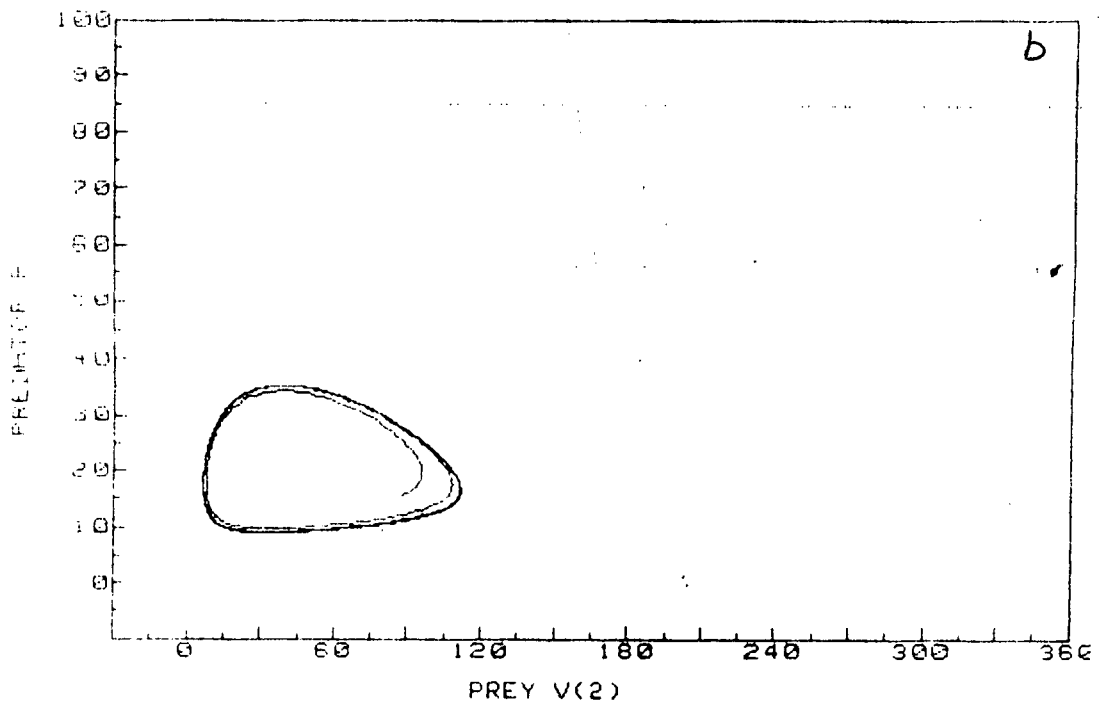
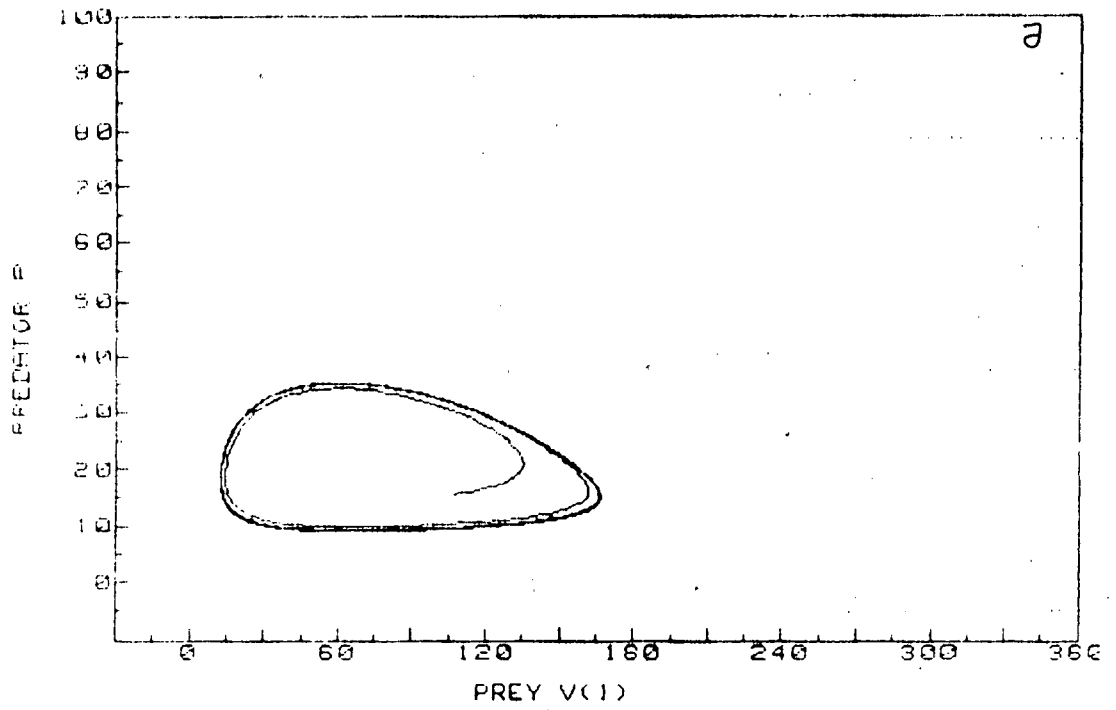


Fig.3.9 Projection of population trajectory on a)  $V(1)$ - $P$  plane, b)  $V(2)$ - $P$  plane for the three species system

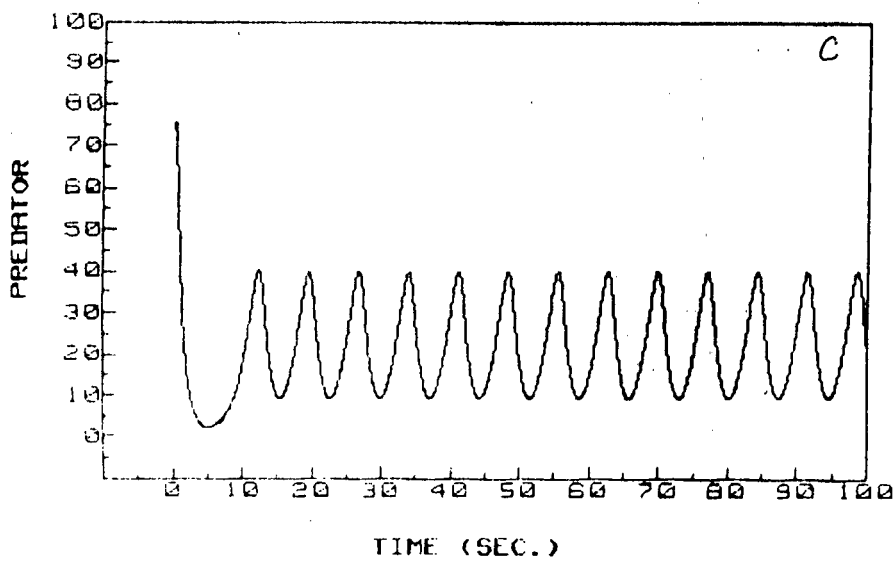
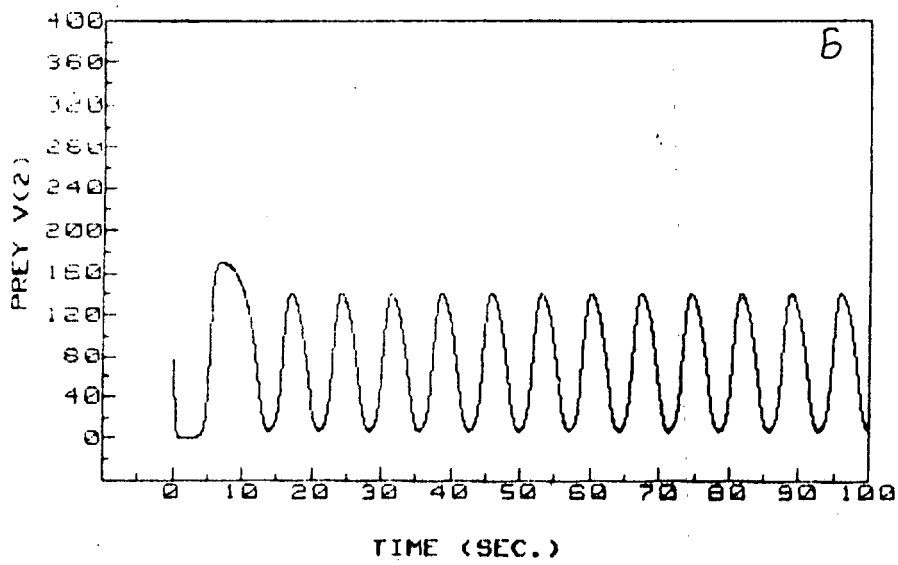
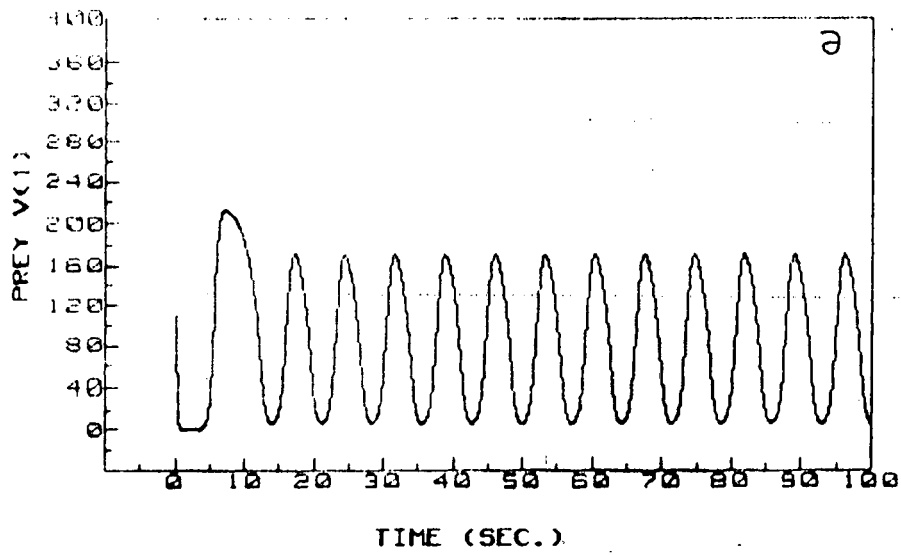


Fig. 3.10 Variation of population densities with time in the two prey-one predator system  
 a) first prey b) second prey c) predator

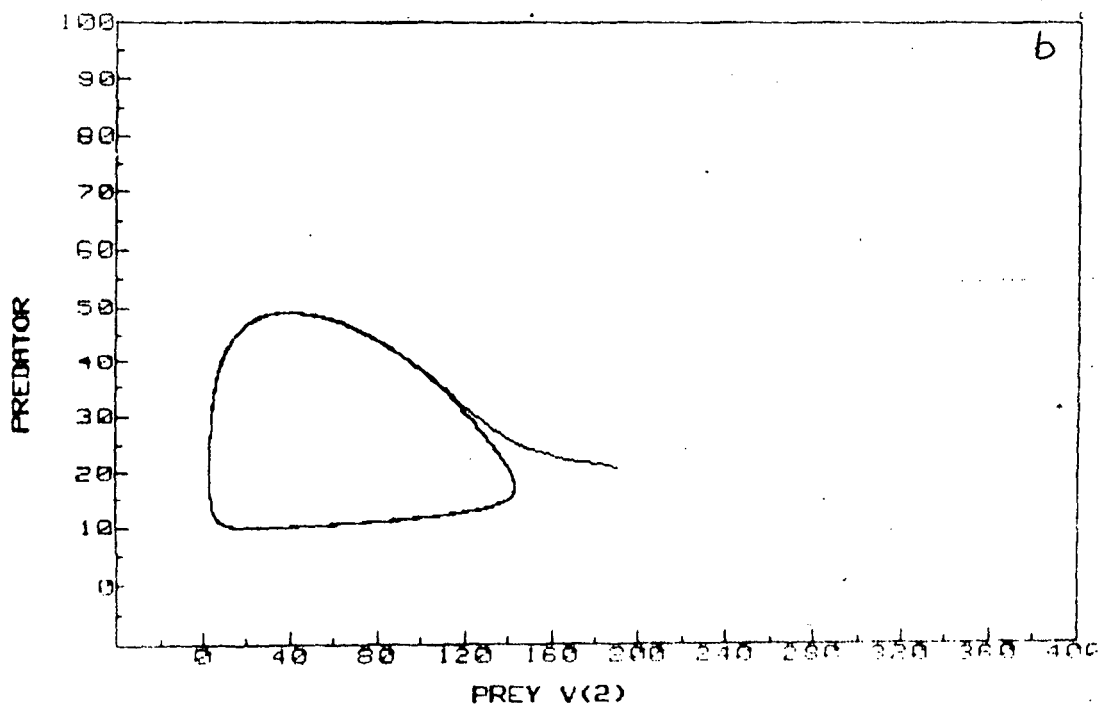
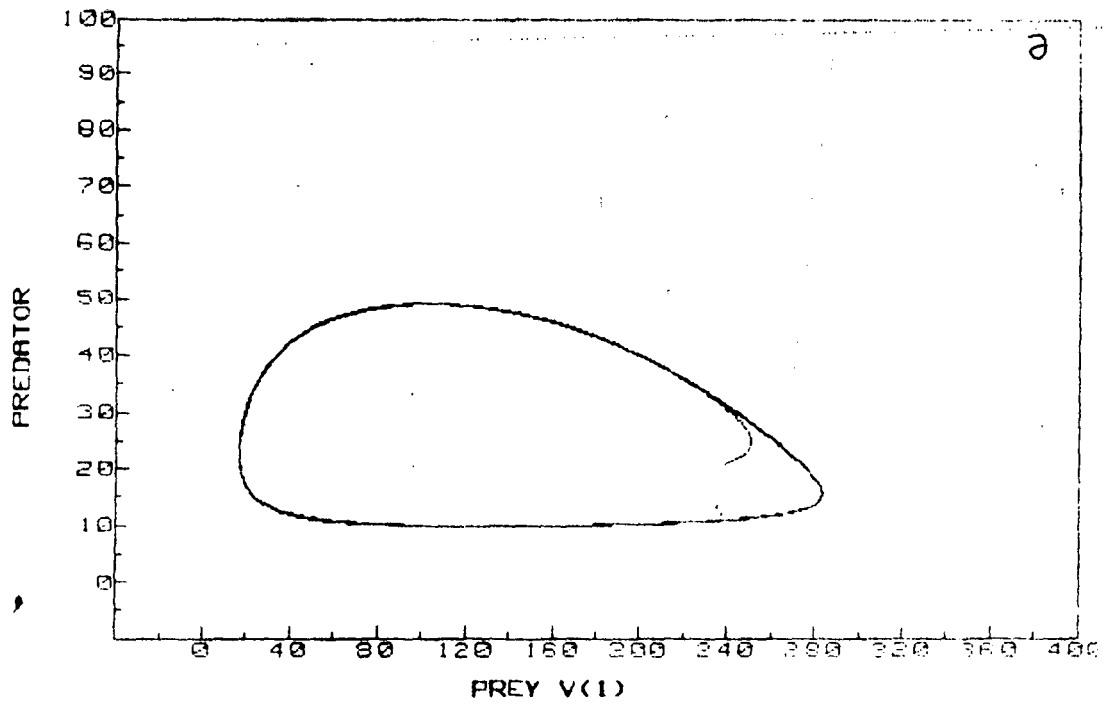


Fig. 3.11 Projection of population trajectory on a)  $V(1)$ - $P$  plane, b)  $V(2)$ - $P$  plane for the three species system

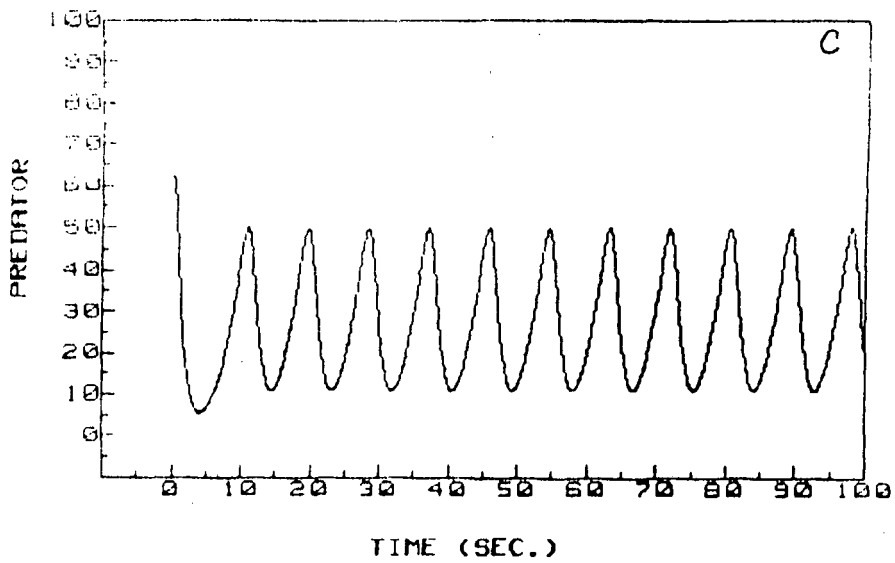
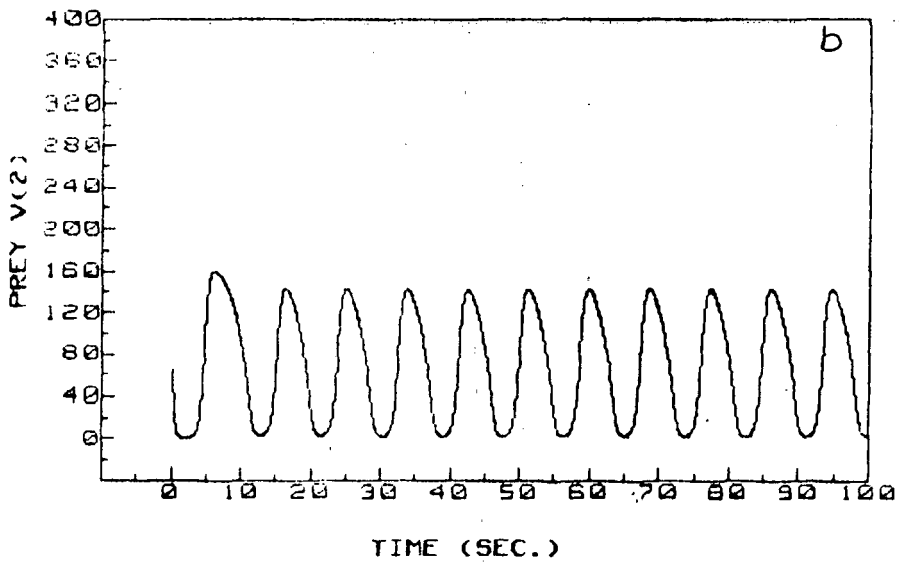
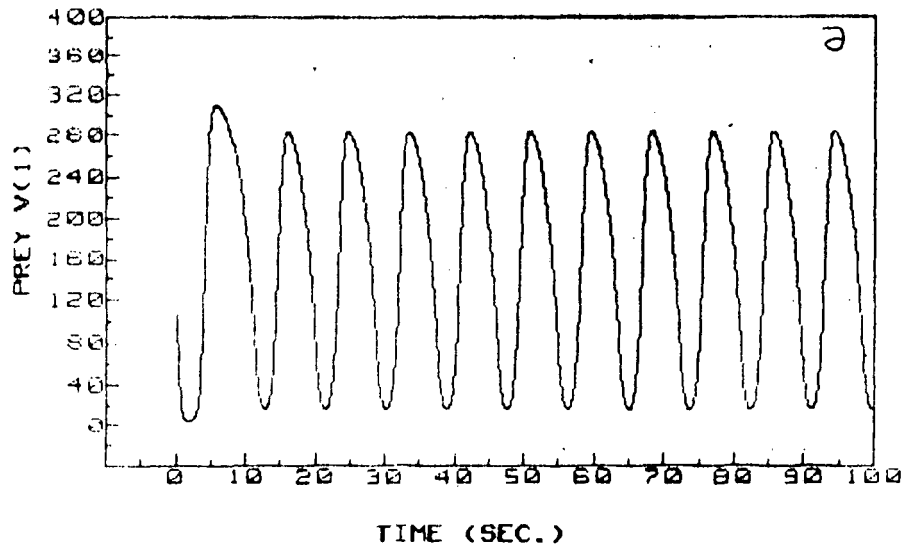


Fig. 3.12 Variation of population densities with time in the two prey-one predator system  
 a) first prey b) second prey c) predator

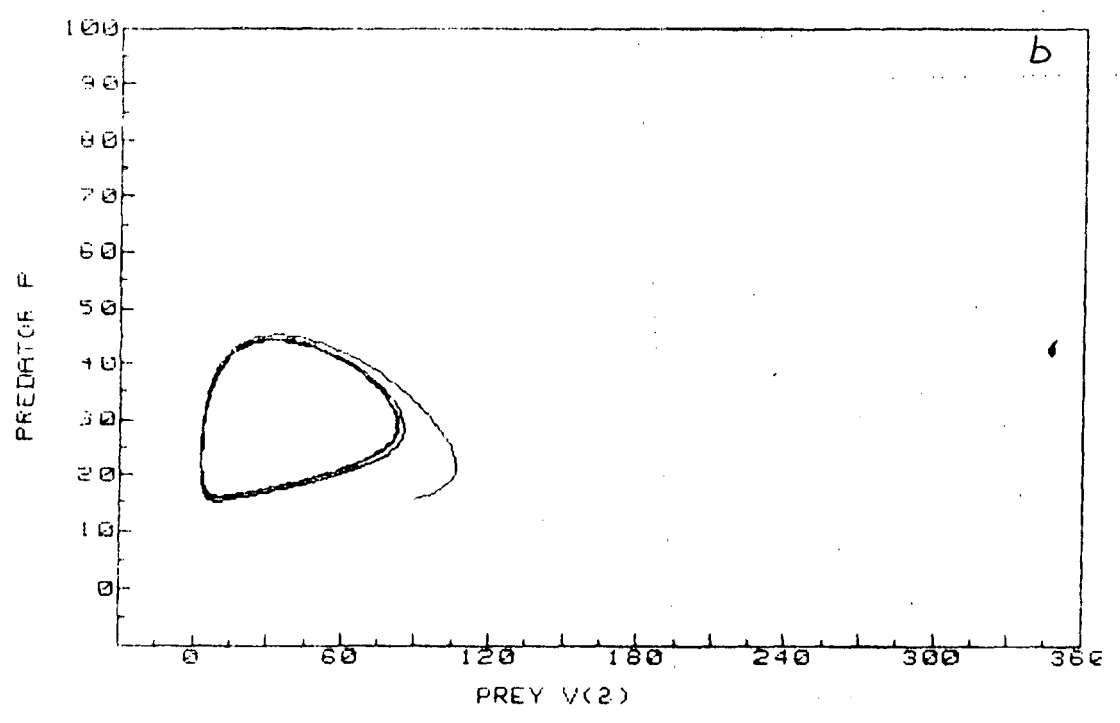
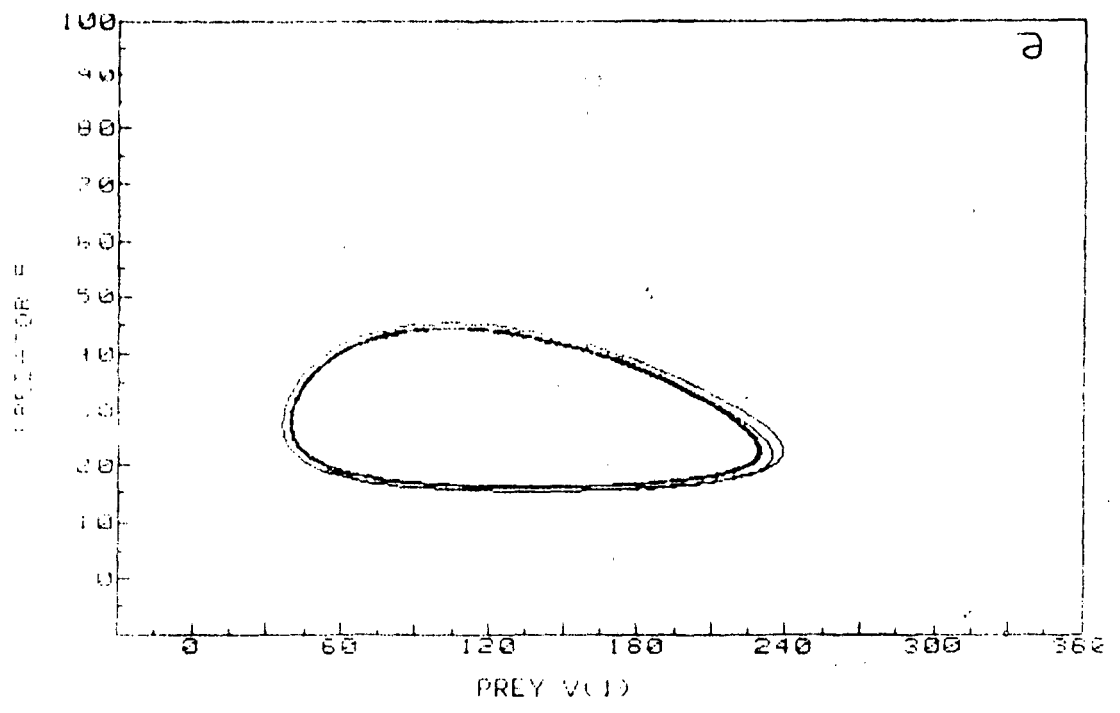


Fig.3.13 Projection of population trajectory on a)  $V(1)$ - $P$  plane, b)  $V(2)$ - $P$  plane for the three species system

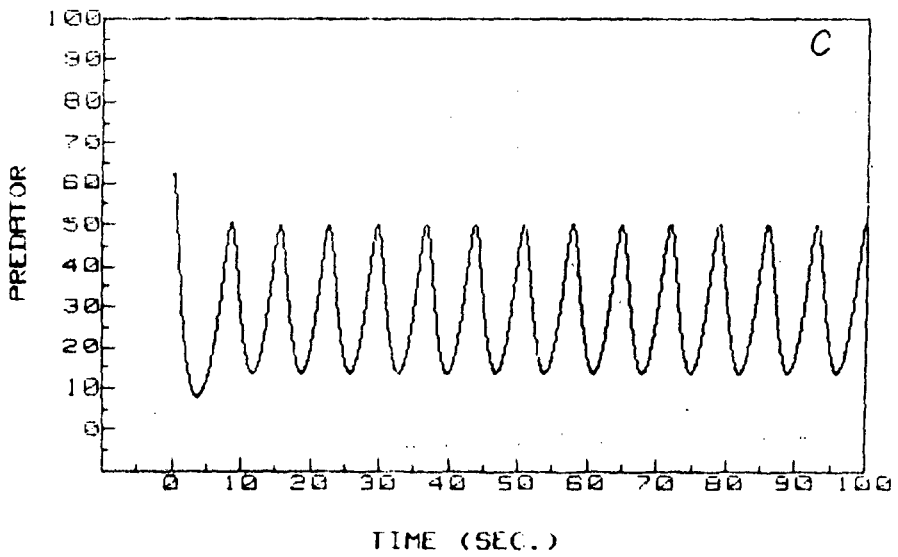
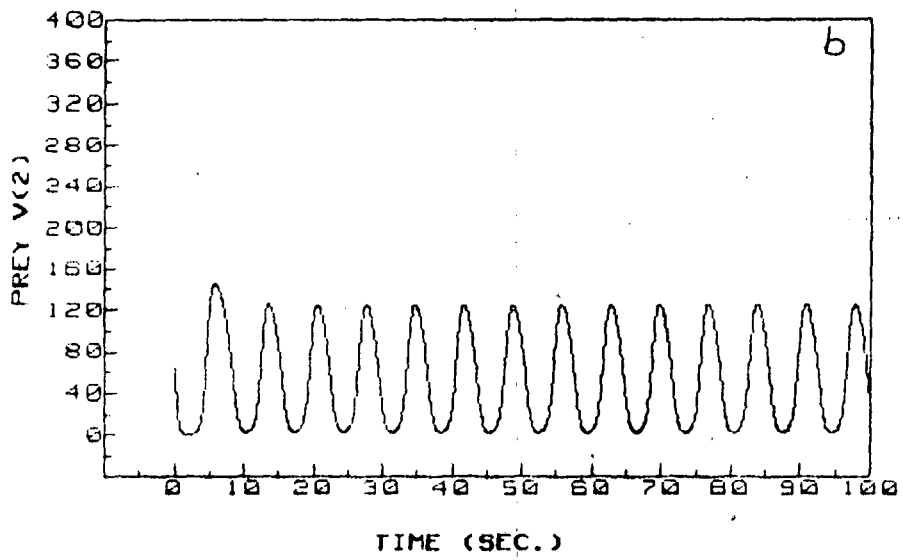
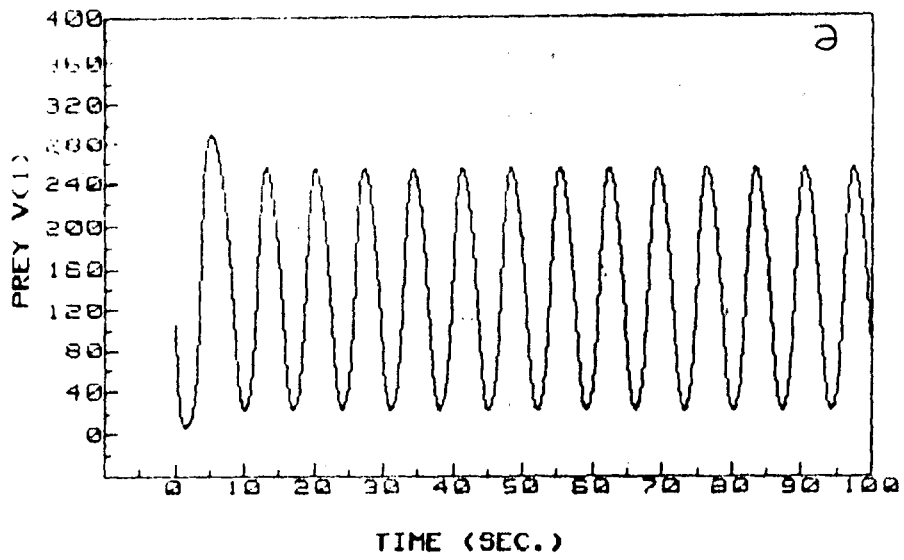


Fig. 3.14 Variation of population densities with time in the two prey-one predator system  
 a) first prey b) second prey c) predator

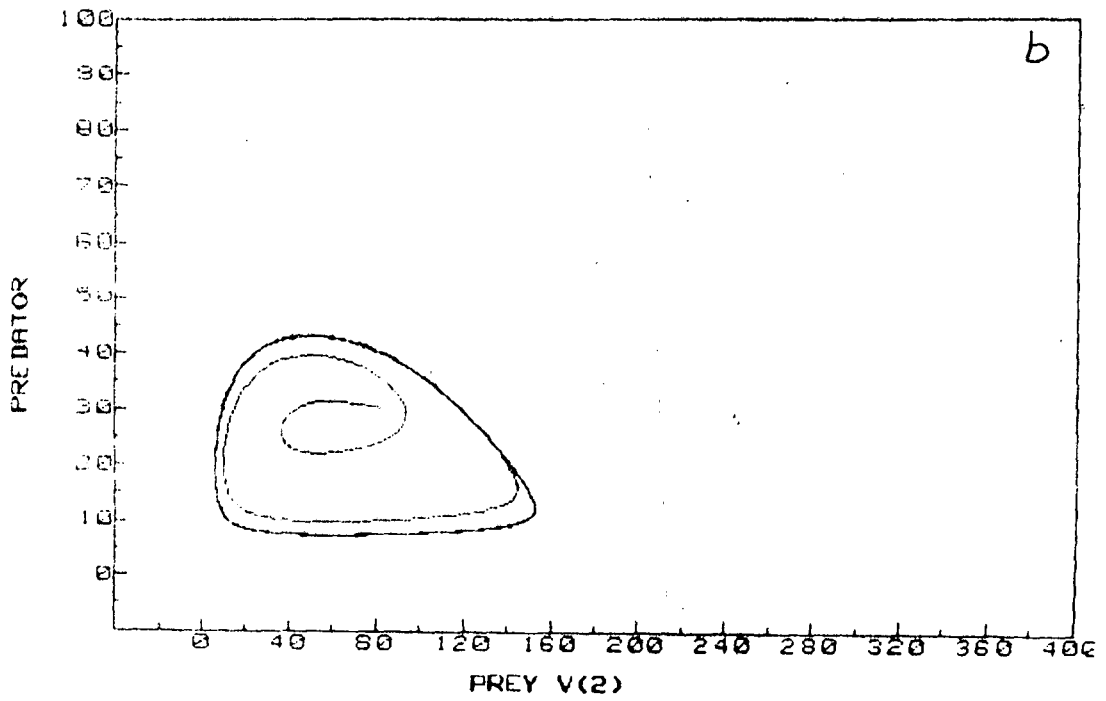
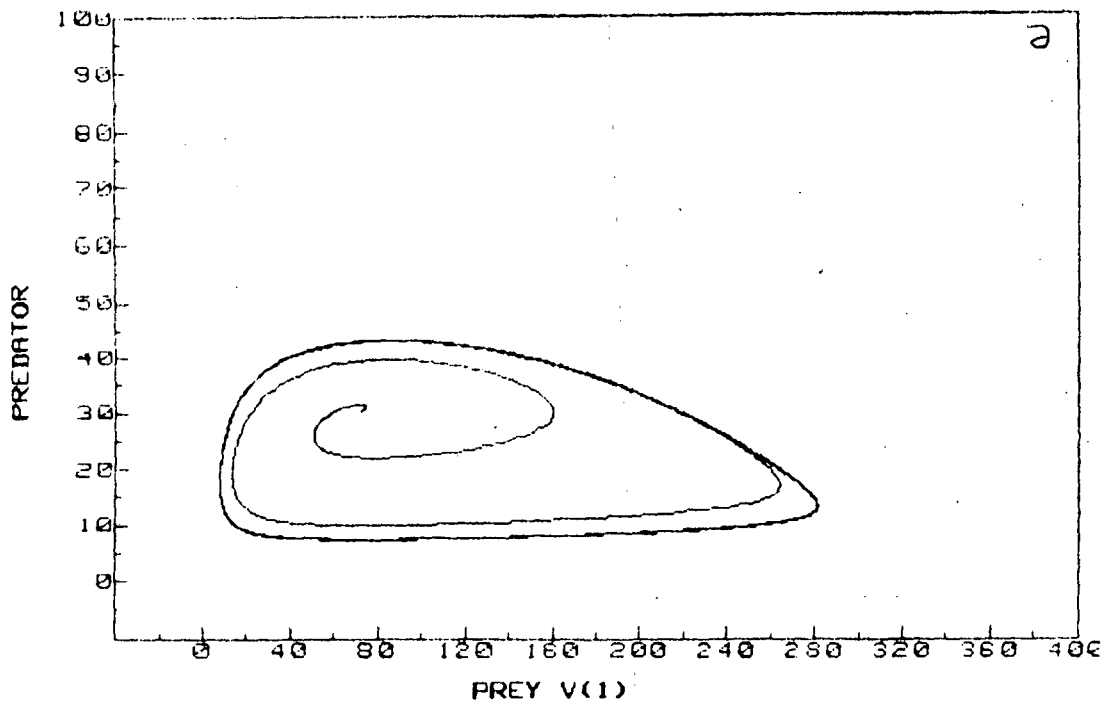


Fig. 3.15 Projection of population trajectory on a)  $V(1)$ - $P$  plane, b)  $V(2)$ - $P$  plane for the three species system

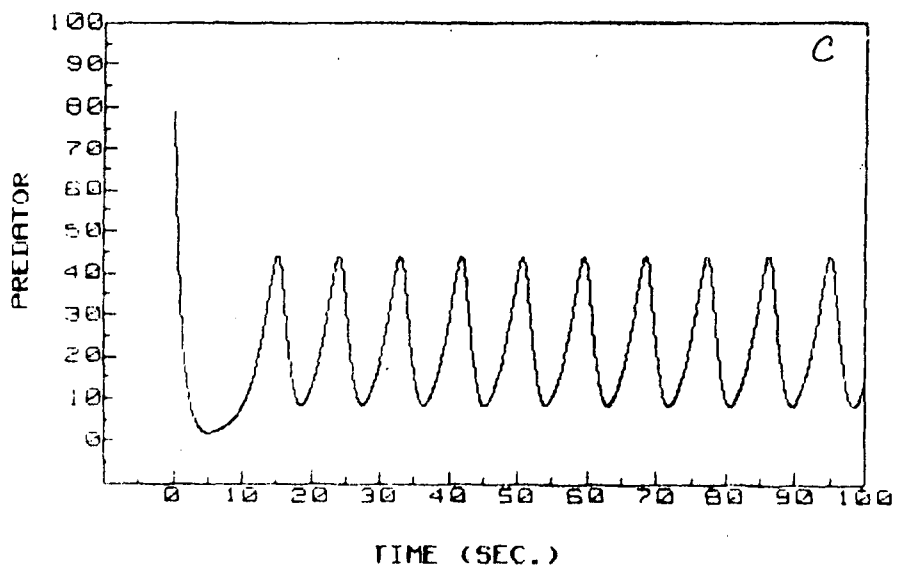
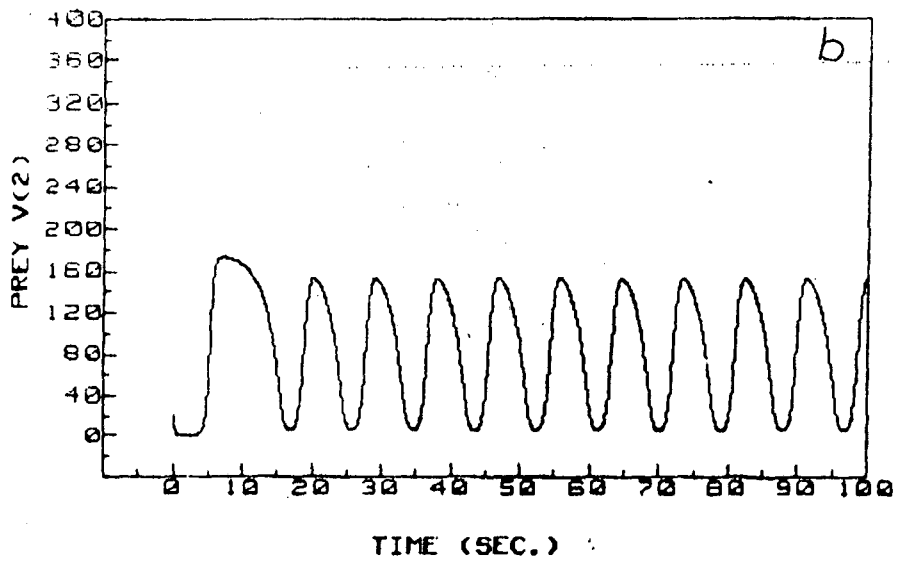
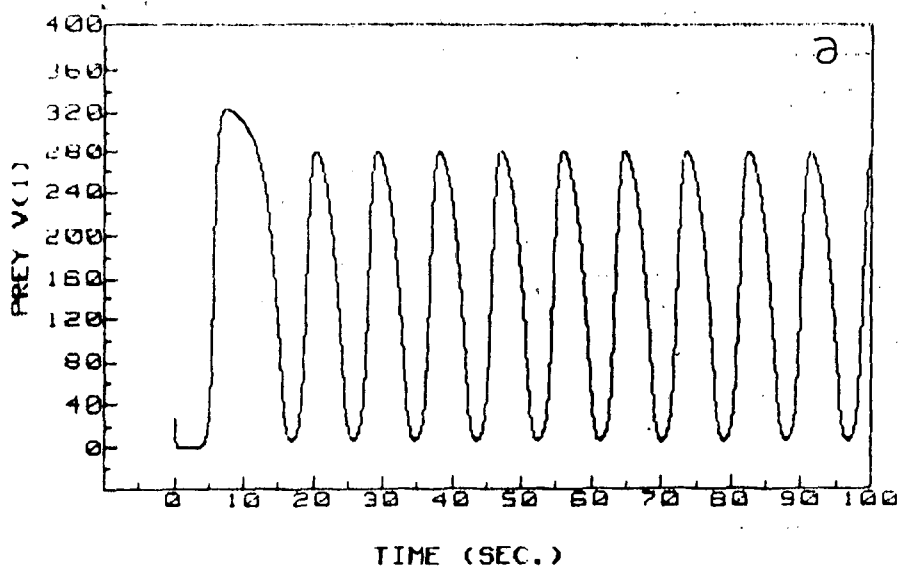


Fig. 3.16 Variation of population densities with time in the two prey-one predator system  
 a) first prey b) second prey c) predator



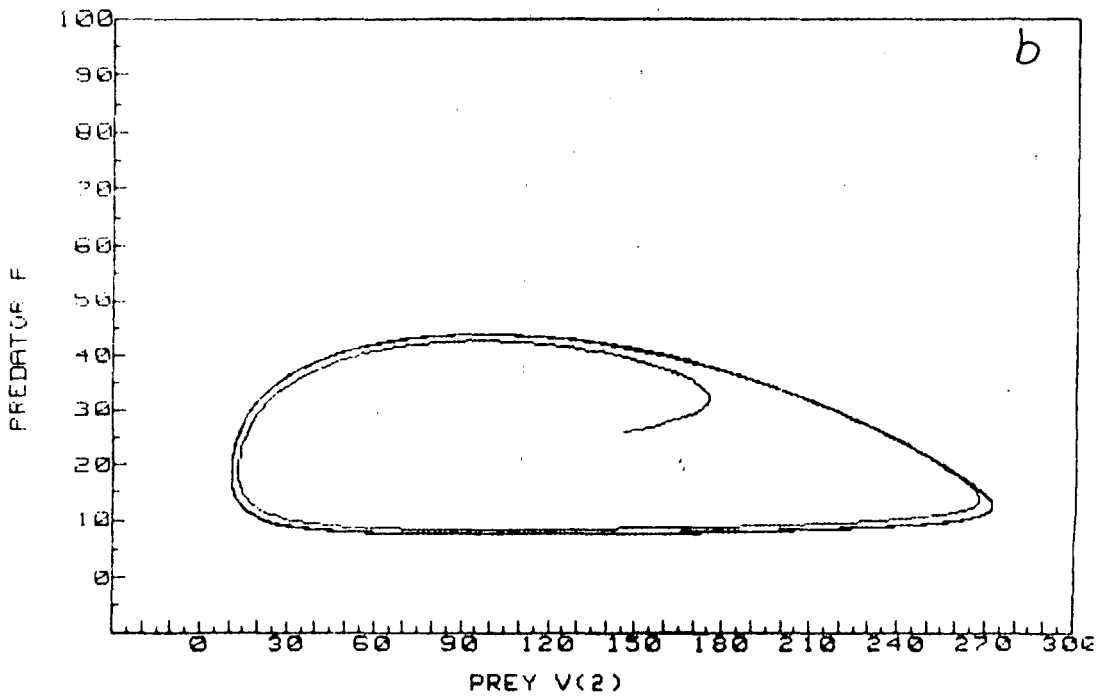
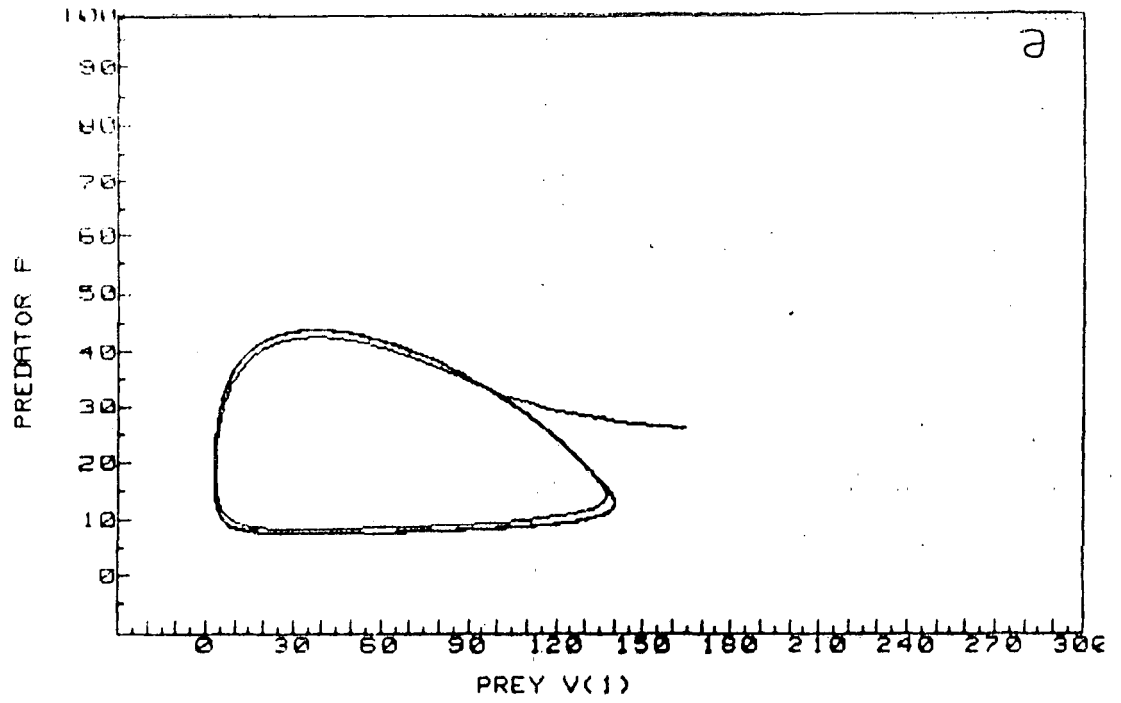


Fig. 3.17 Projection of population trajectory on a)  $U(1)$ - $P$  plane, b)  $U(2)$ - $P$  plane for the three species system

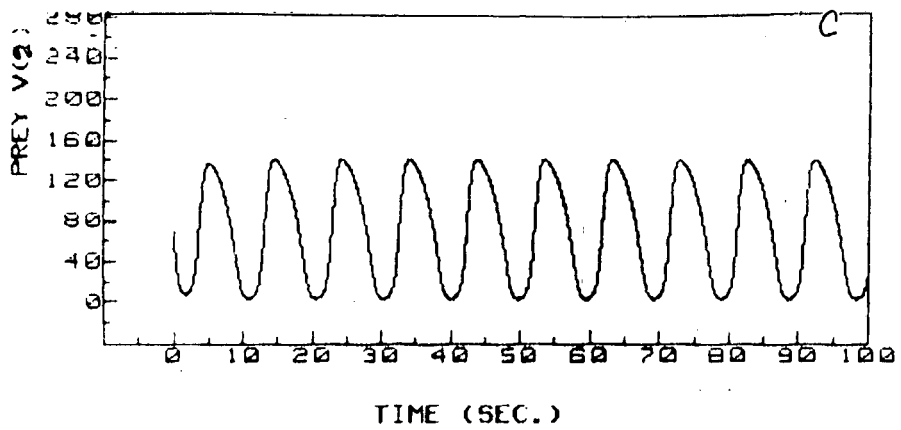
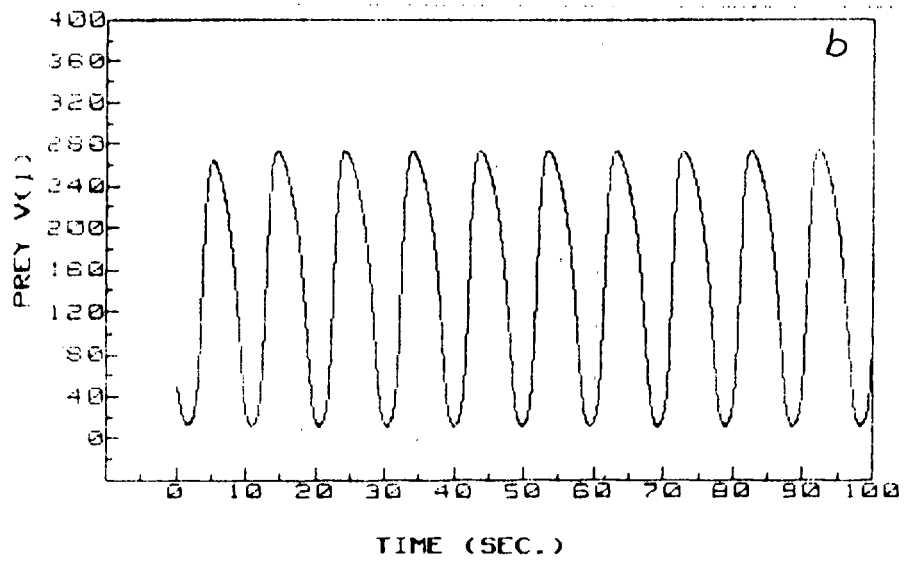
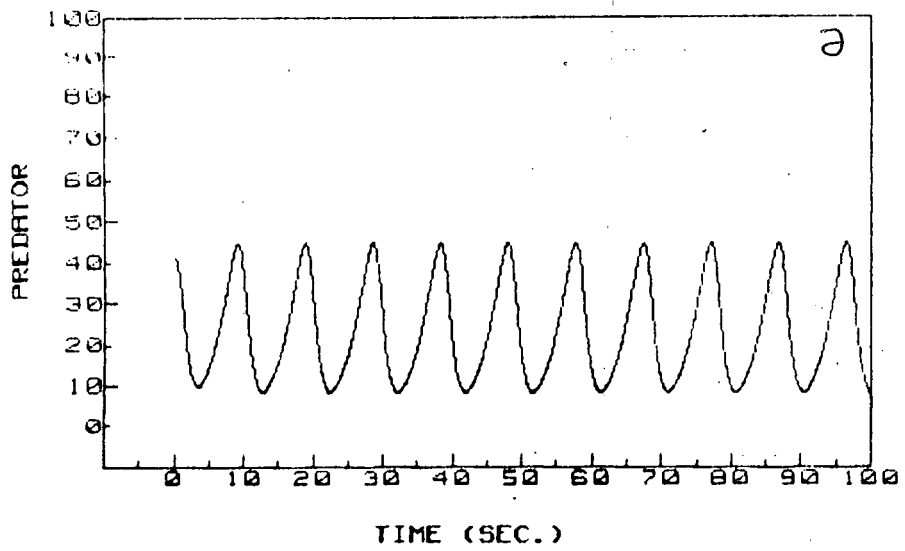


Fig. 3.18 Variation of population densities with time in the two prey-one predator system. a) first prey b) second prey c) predator

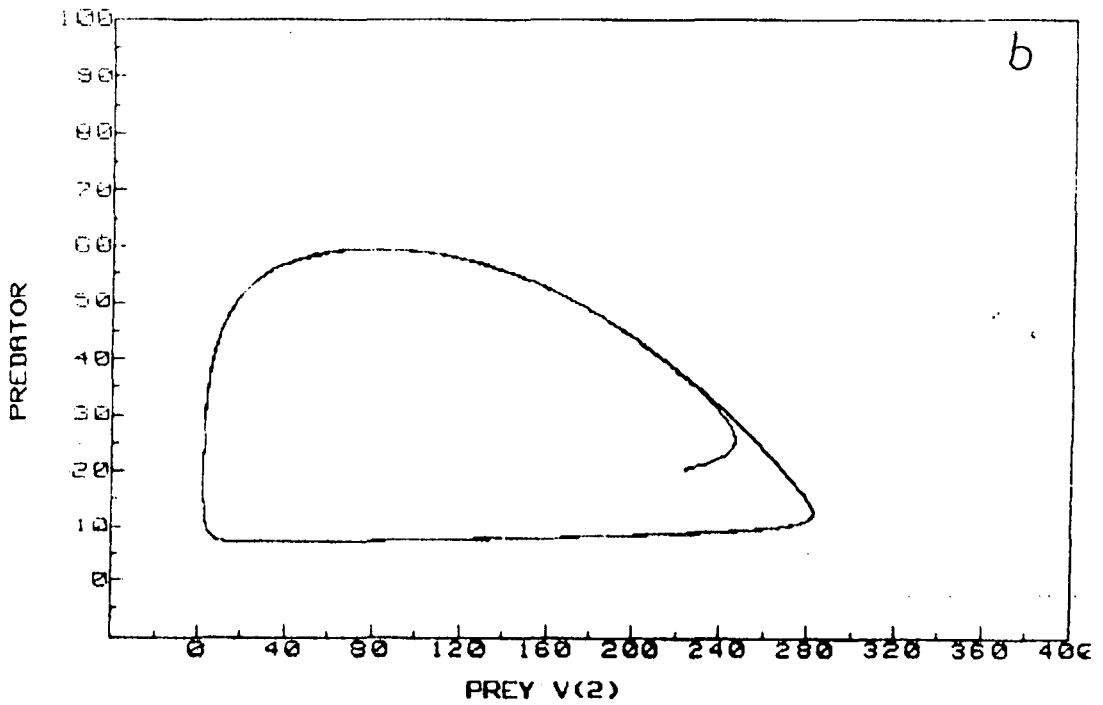
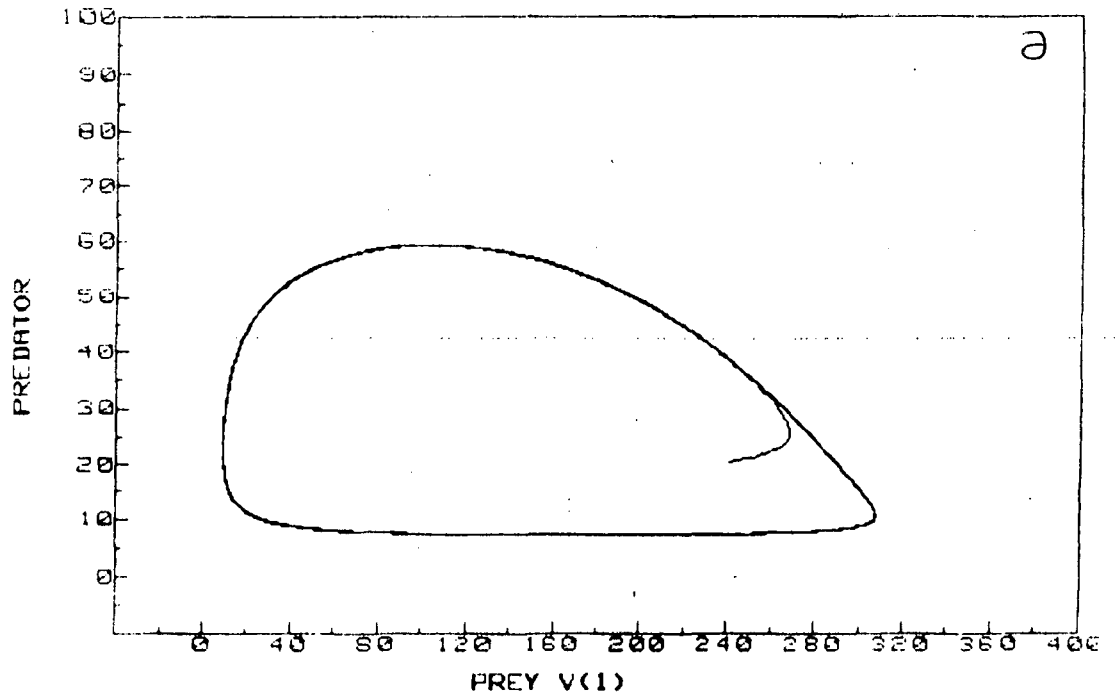


Fig. 3.19 Projection of population trajectory on a)  $U(1)$ - $P$  plane, b)  $U(2)$ - $P$  plane for the three species system

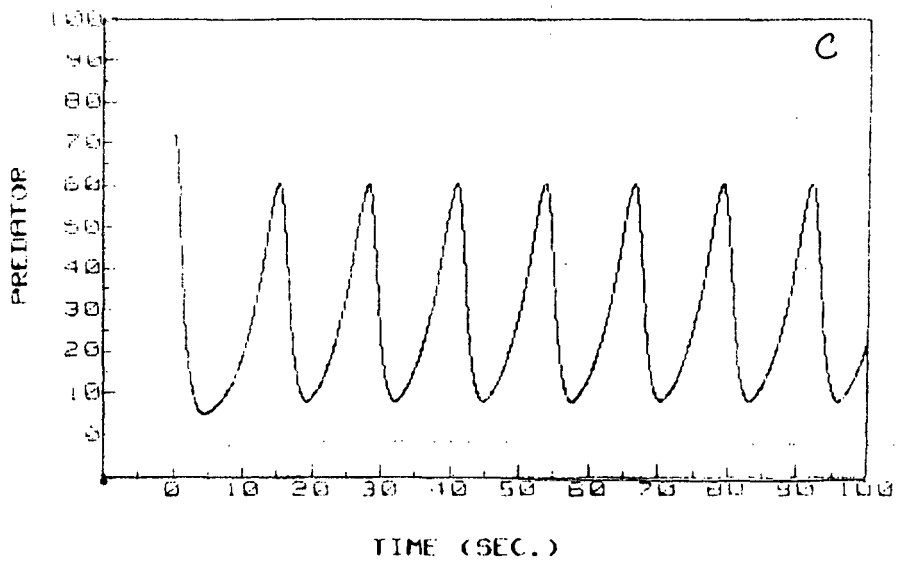
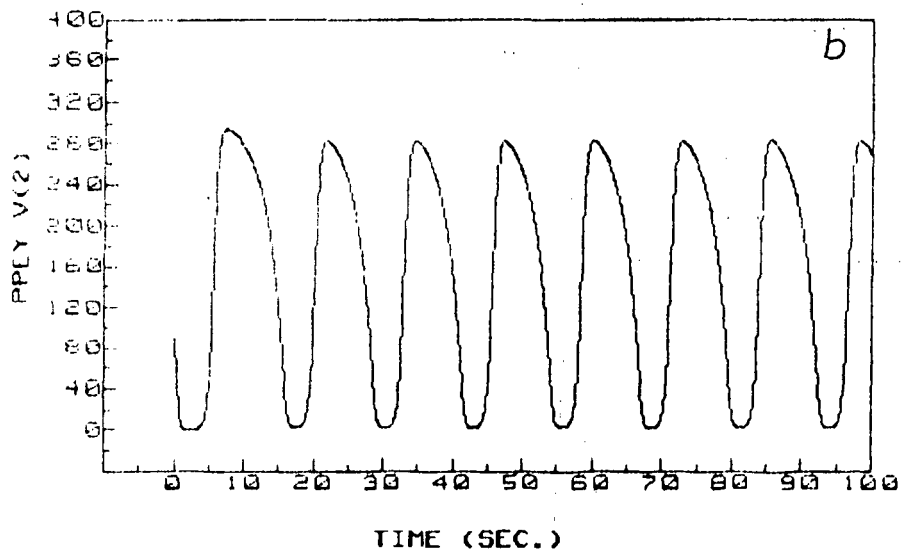
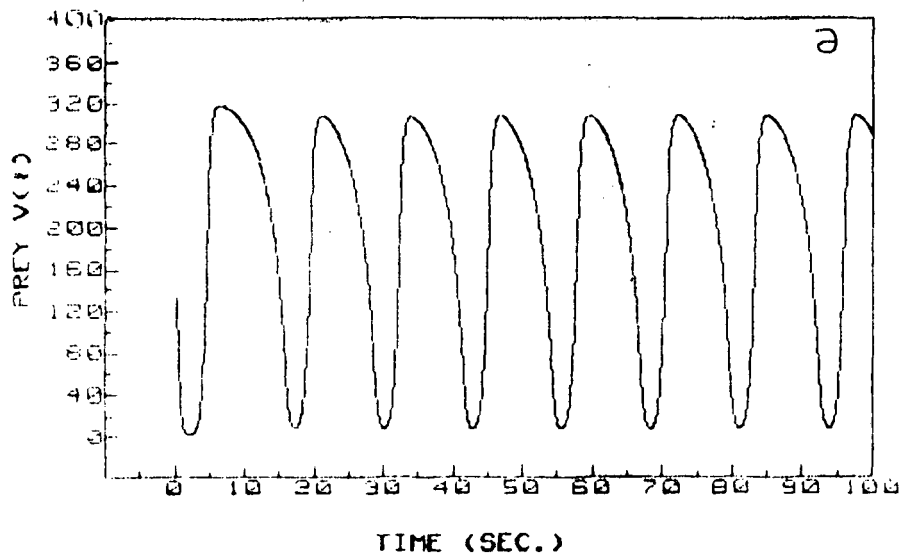


Fig.3.20 Variation of population densities with time in the two prey-one predator system  
 a) first prey b) second prey c) predator

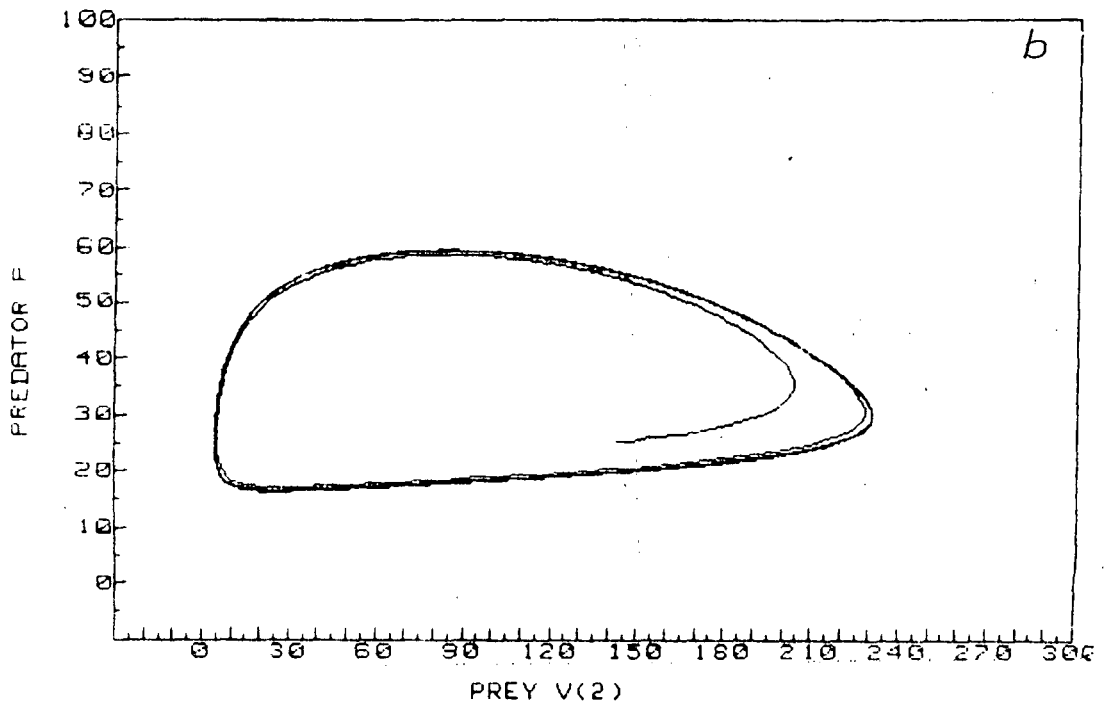
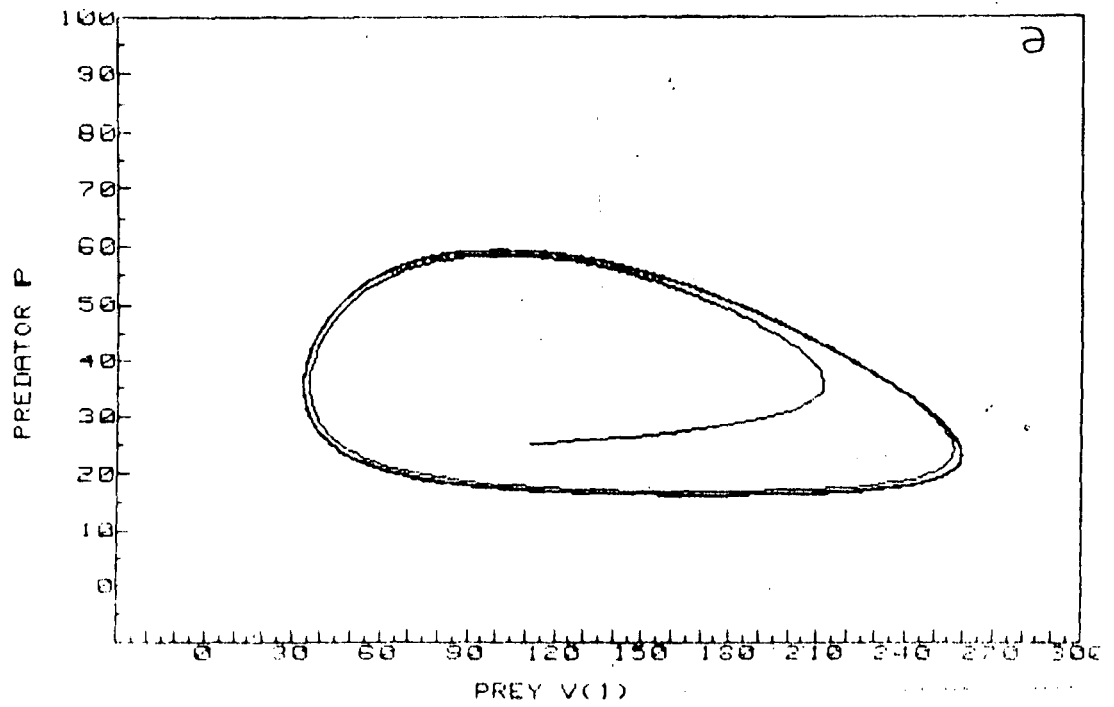


Fig. 3.21 Projection of population trajectory on a)  $V(1)$ - $P$  plane, b)  $V(2)$ - $P$  plane for the three species system

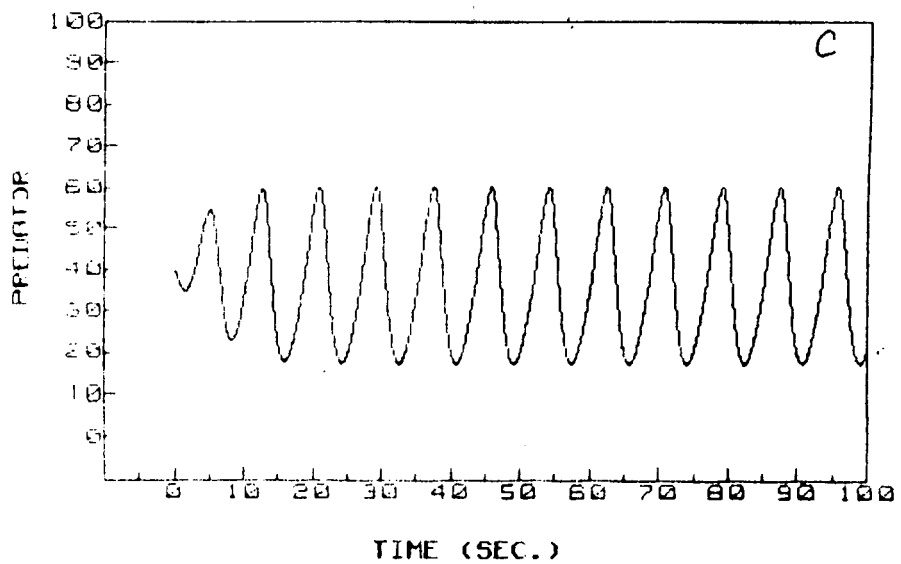
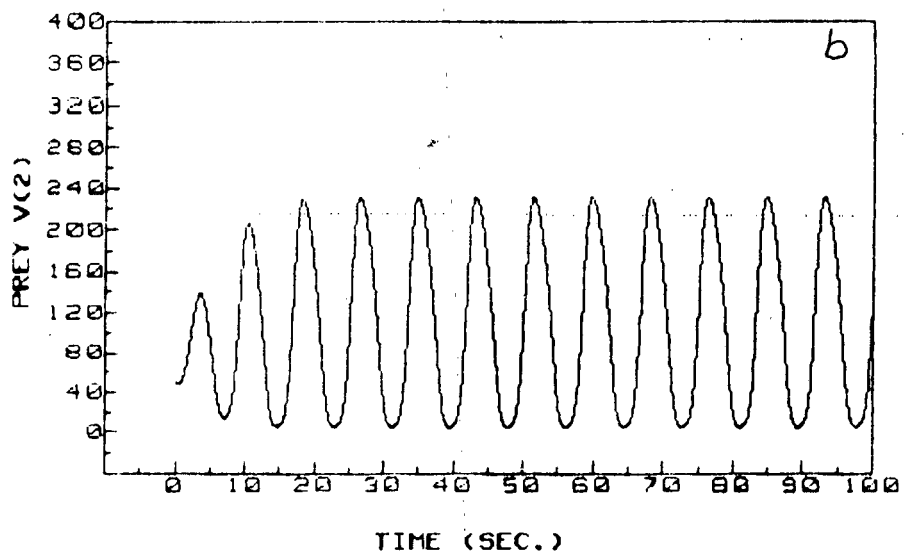
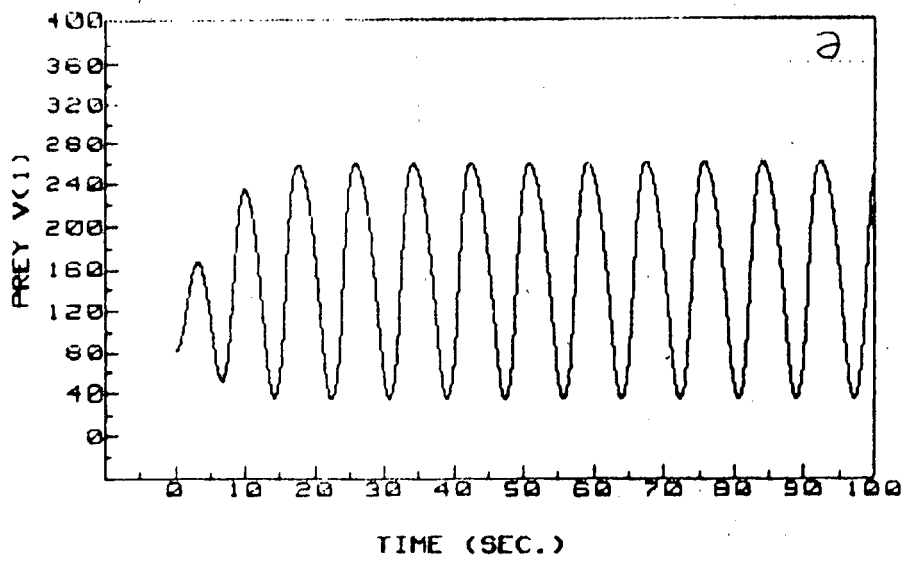


Fig. 3.22 Variation of population densities with time in the two prey-one predator system  
 a) first prey b) second prey c) predator

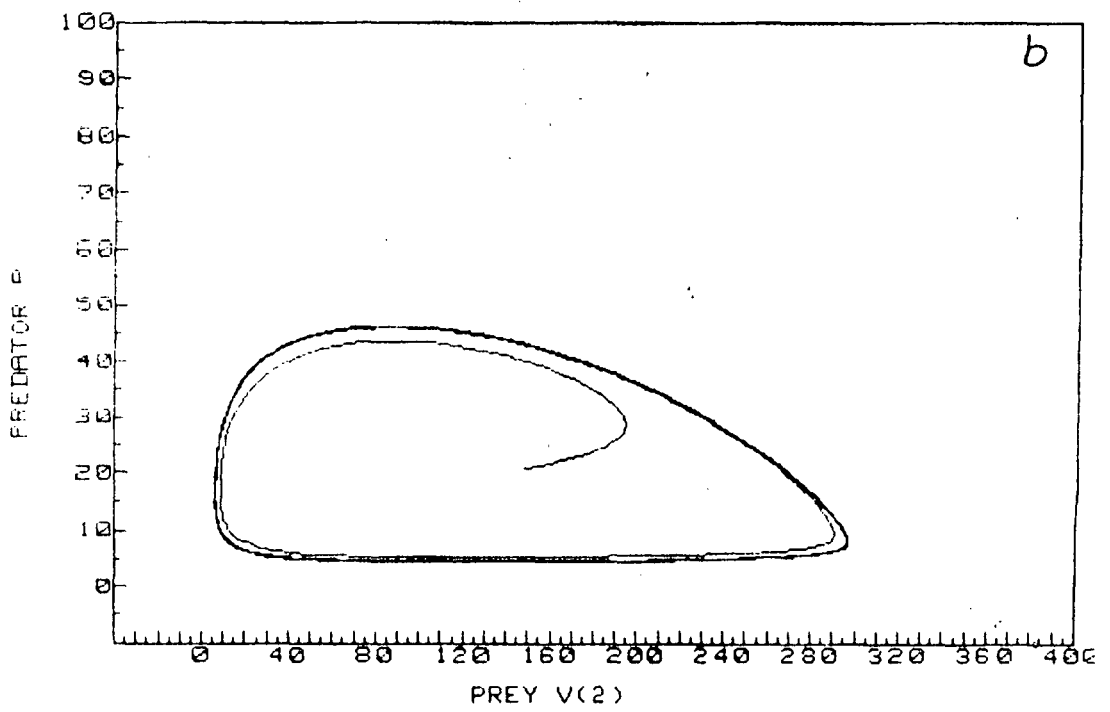
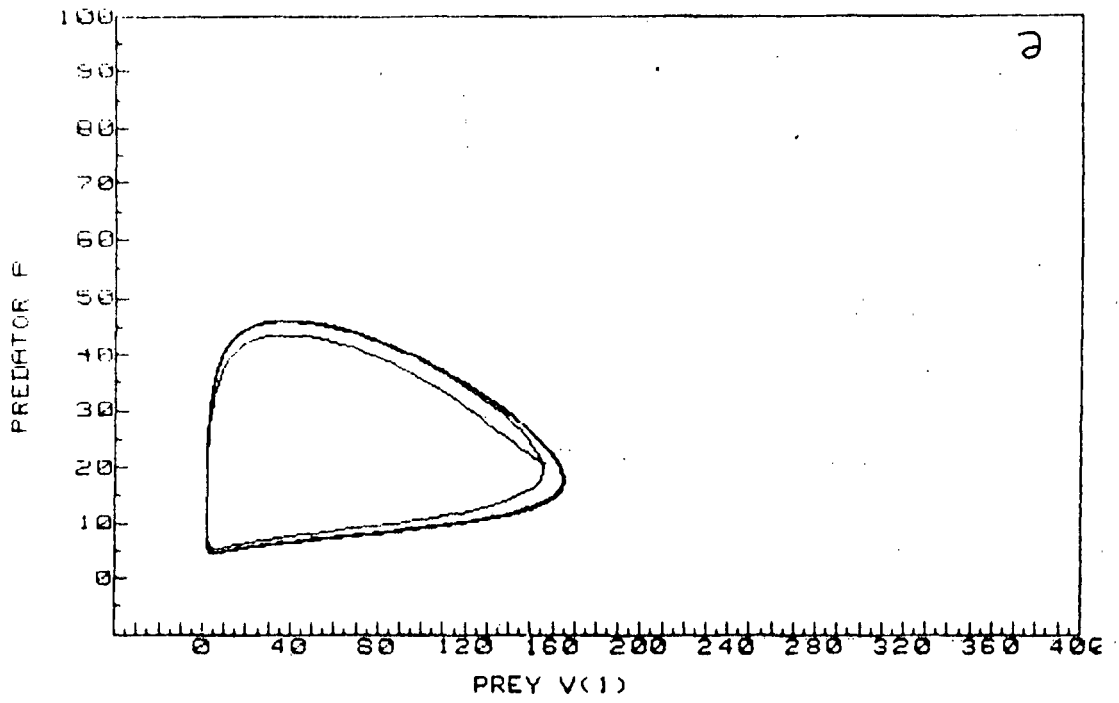


Fig. 3.23 Projection of population trajectory on a)  $V(1)$ - $P$  plane, b)  $V(2)$ - $P$  plane for the three species system

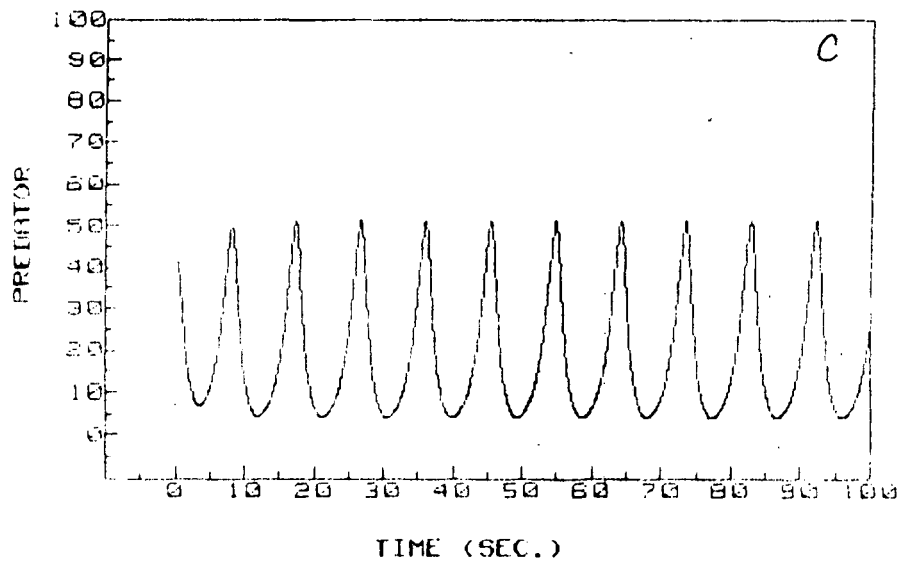
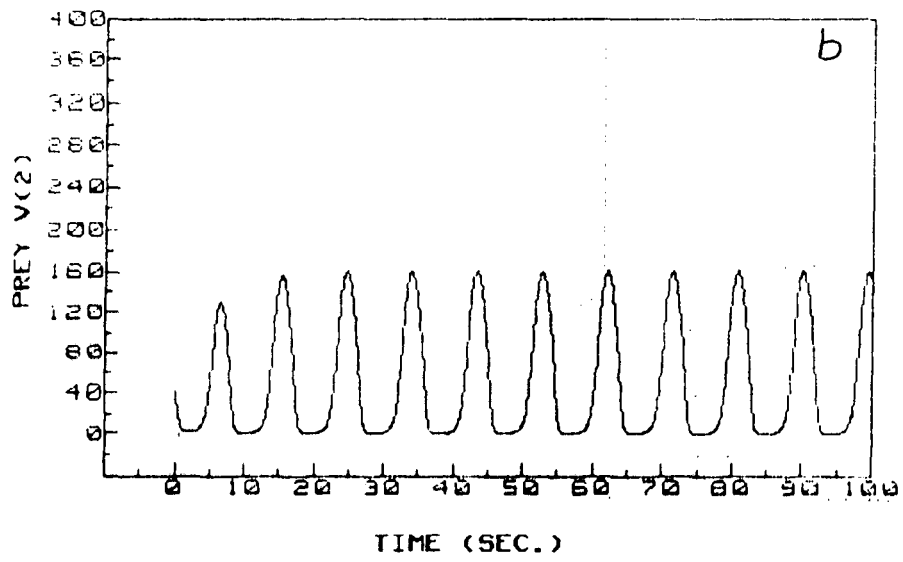
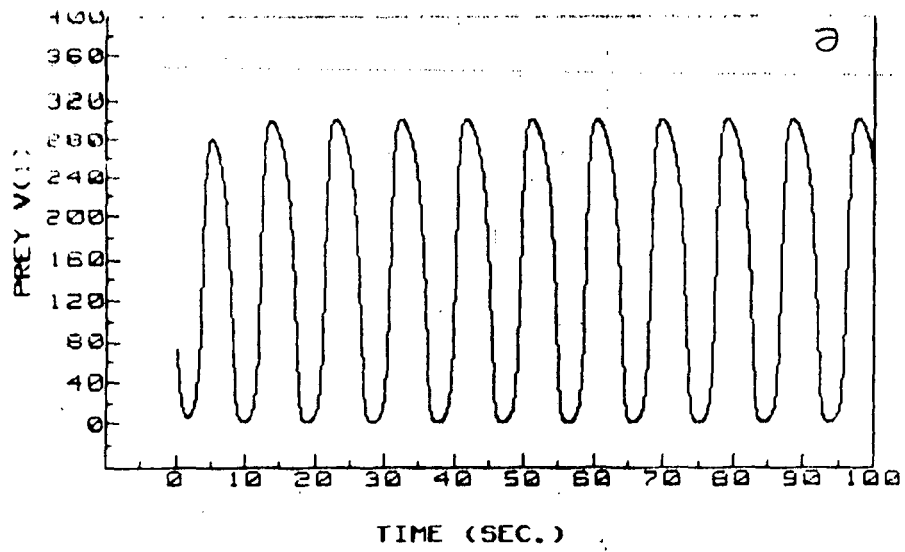


Fig. 3.24 Variation of population densities with time in the two prey-one predator system  
 a) first prey b) second prey c) predator



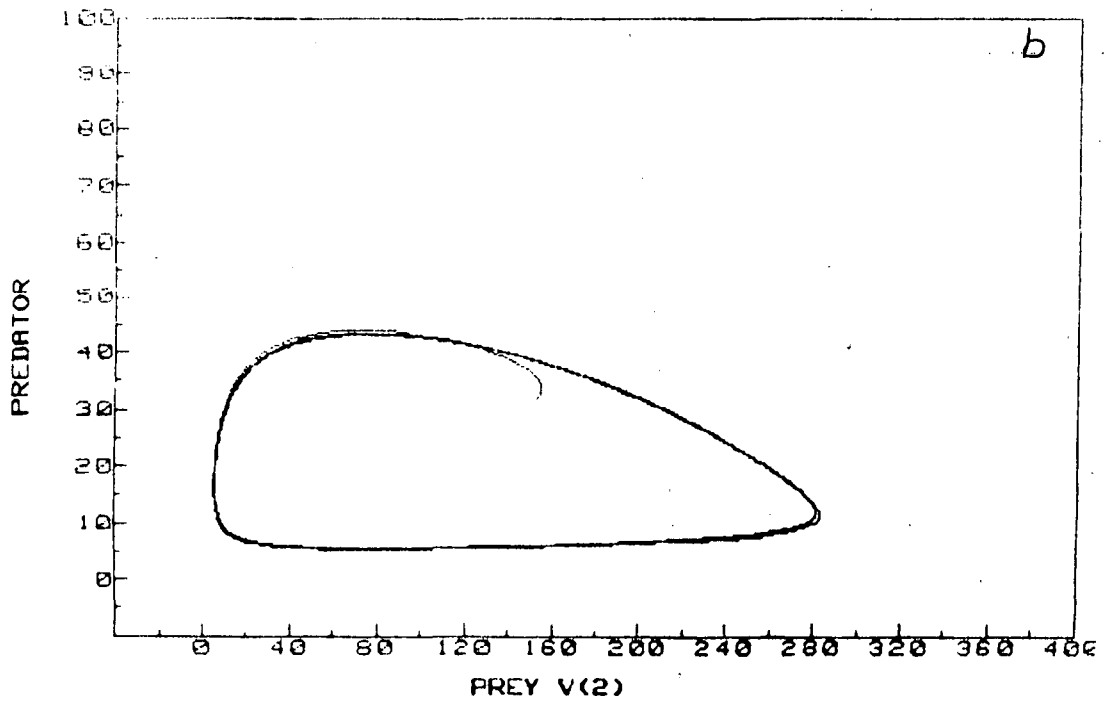
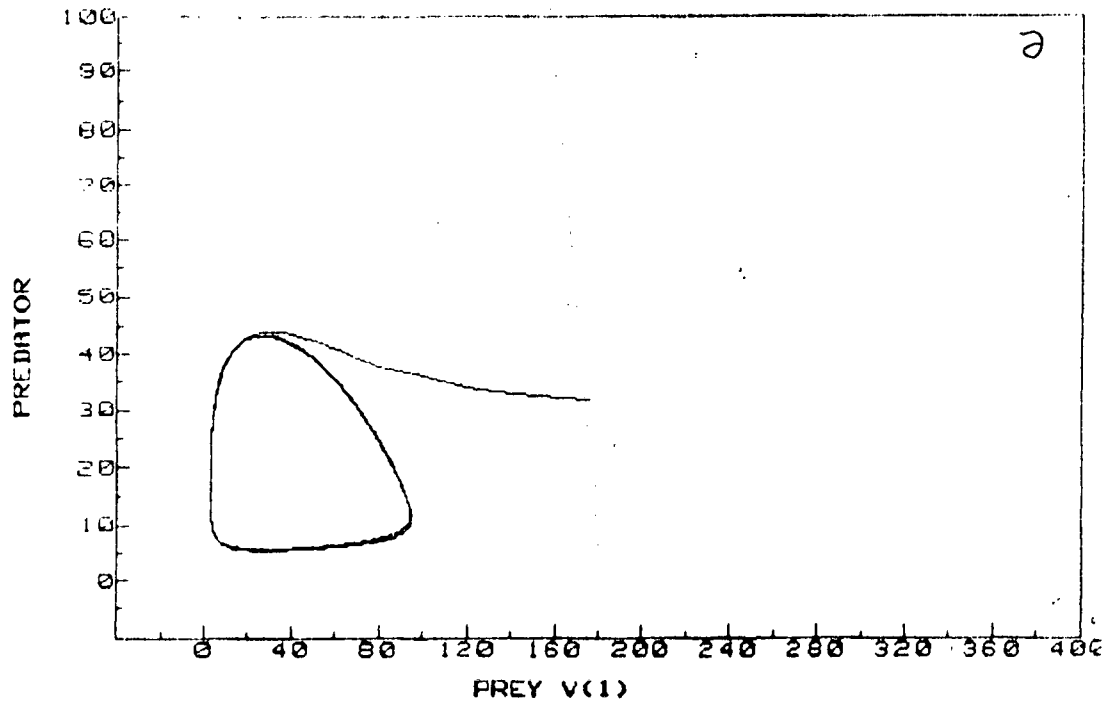


Fig. 3.25 Projection of population trajectory on a)  $V(1)$ - $P$  plane, b)  $V(2)$ - $P$  plane for the three species system

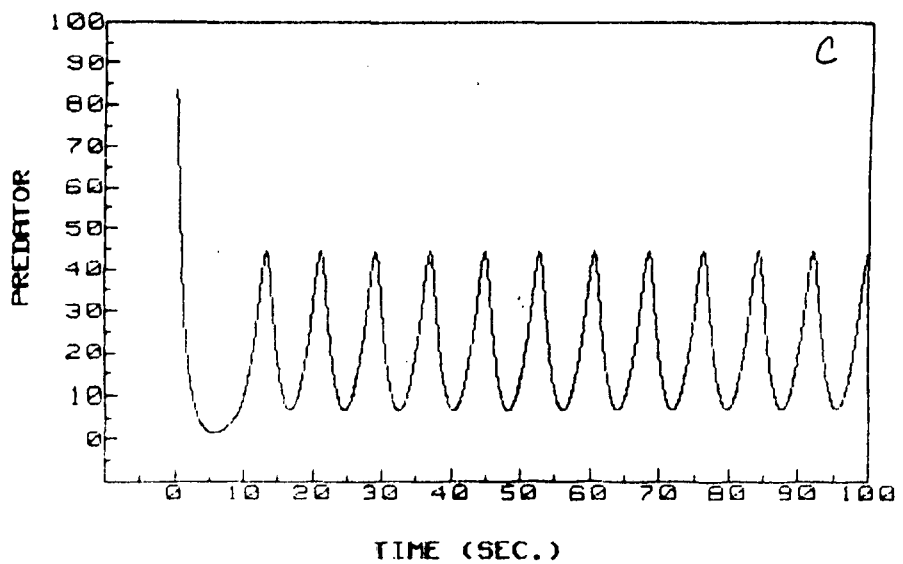
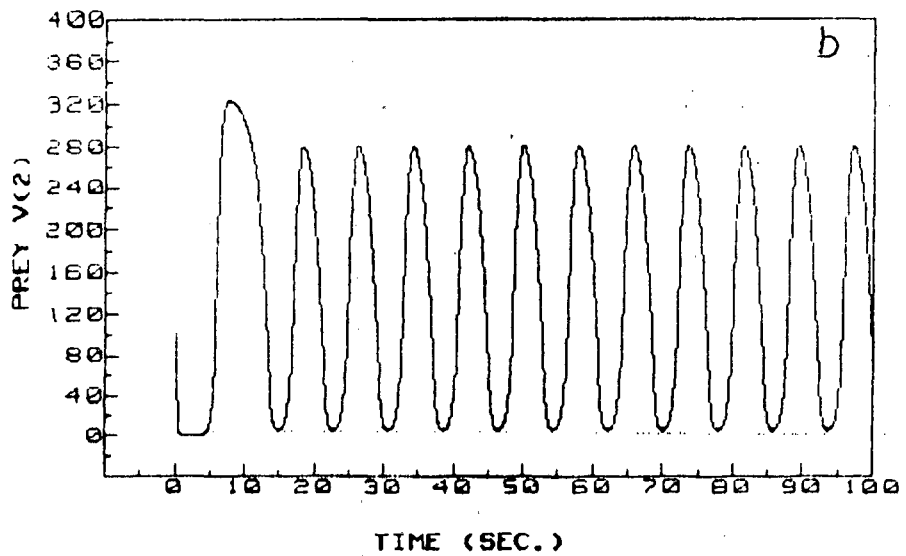
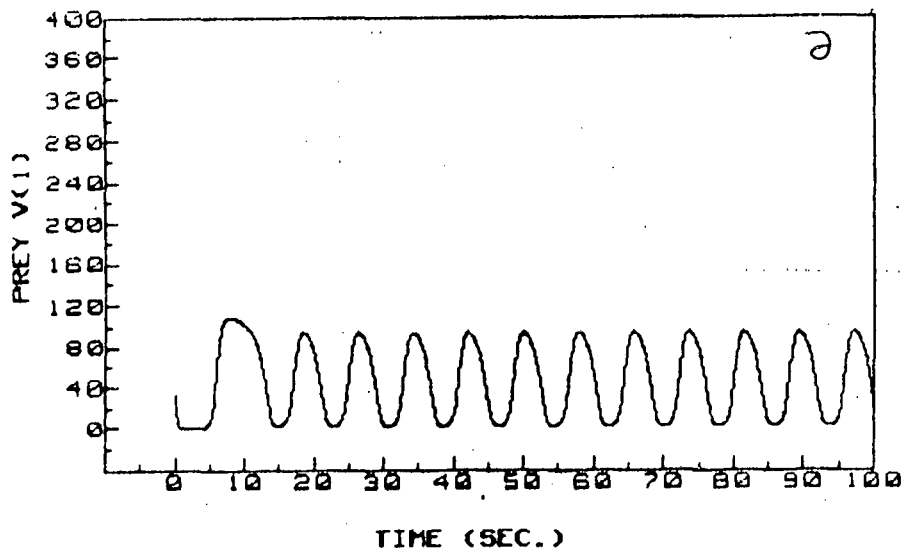


Fig. 3.26 Variation of population densities with time in the two prey-one predator system  
 a) first prey b) second prey c) predator

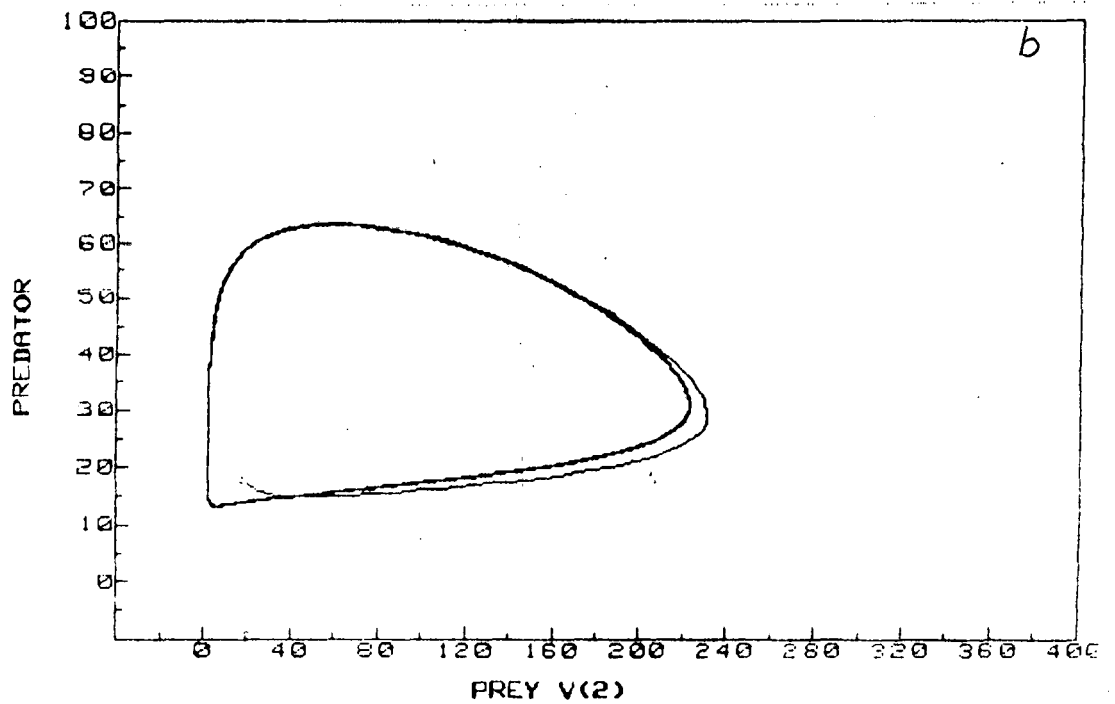
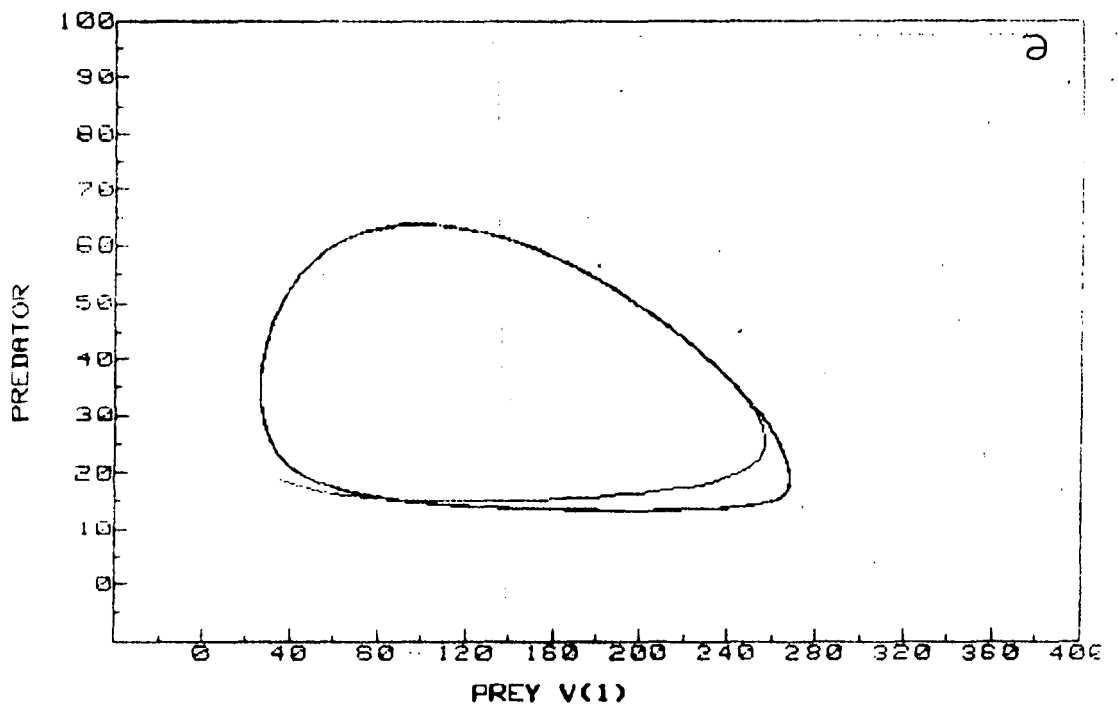


Fig. 3.27 Projection of population trajectory on a)  $U(1)$ - $P$  plane, b)  $U(2)$ - $P$  plane for the three species system

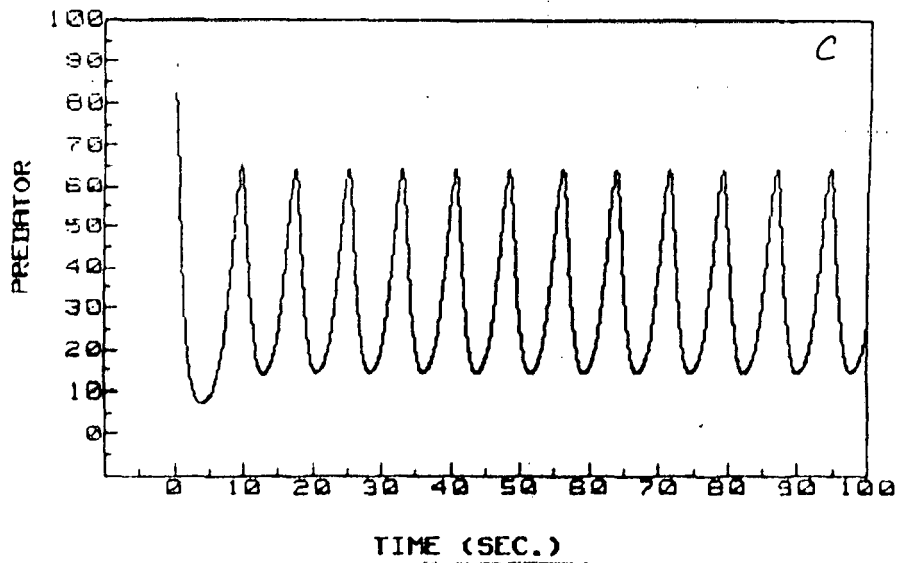
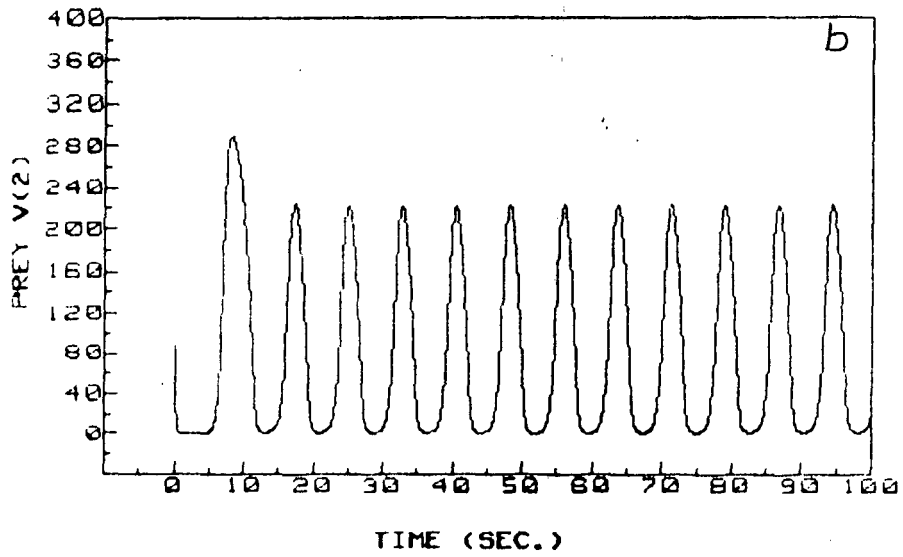
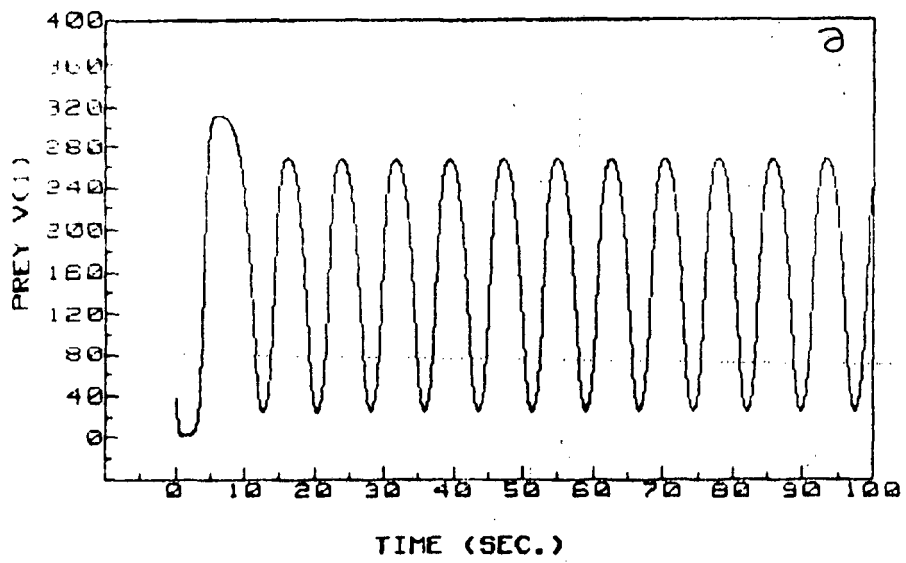


Fig. 3.20 Variation of population densities with time in the two prey-one predator system  
 a) first prey b) second prey c) predator

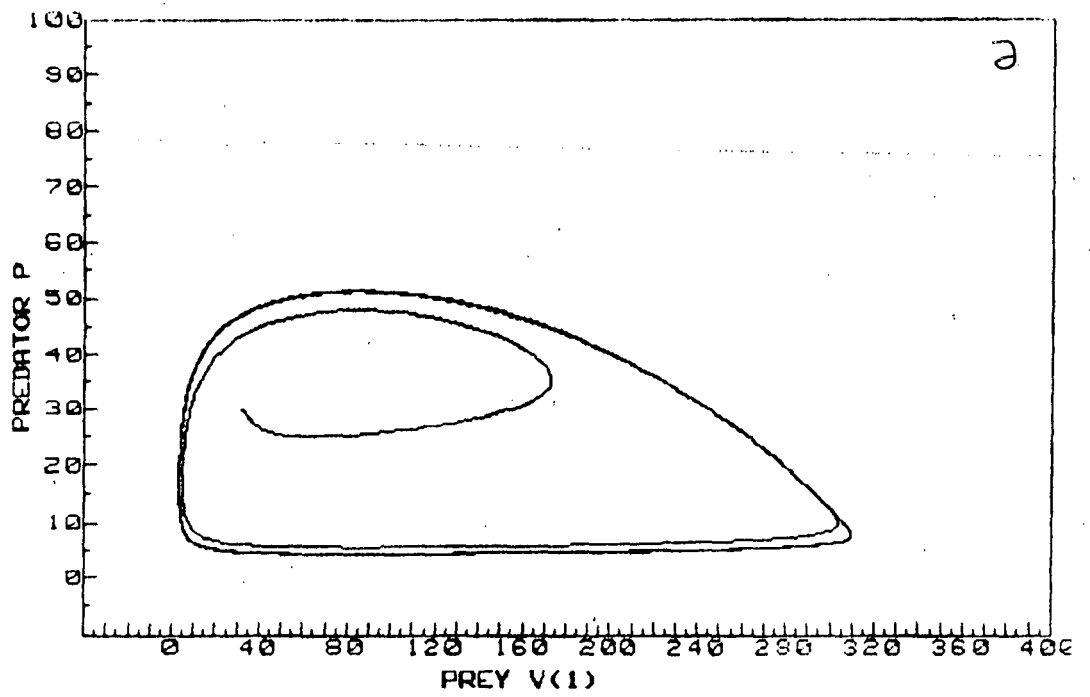


FIG.

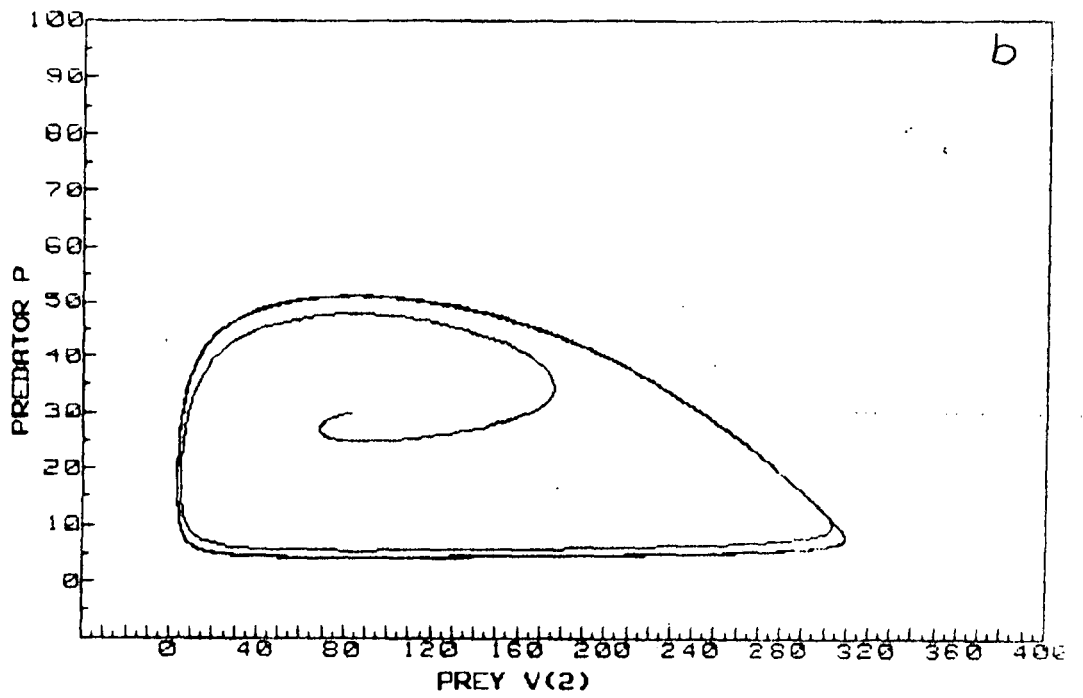


FIG.

Fig. 3-29 Projection of population trajectory on a)  $U(1)$ - $P$  plane, b)  $U(2)$ - $P$  plane for the three species system

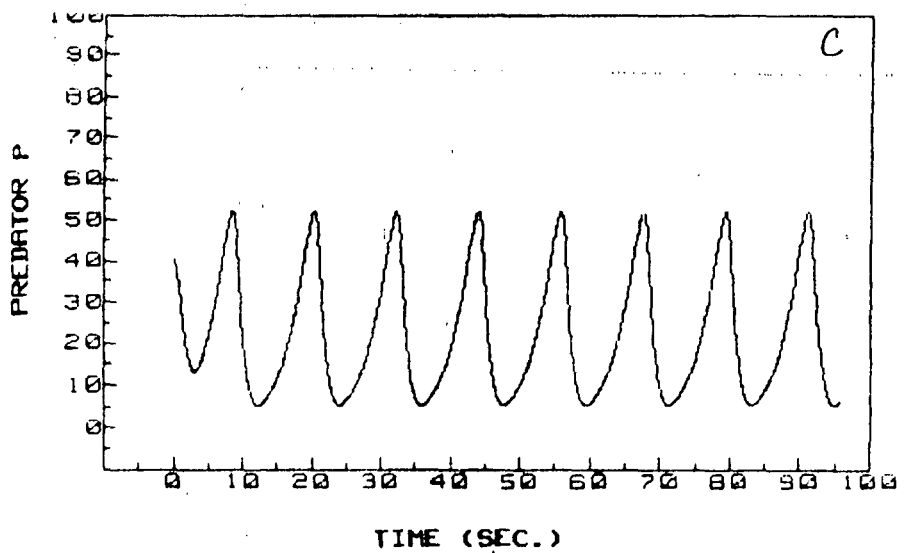
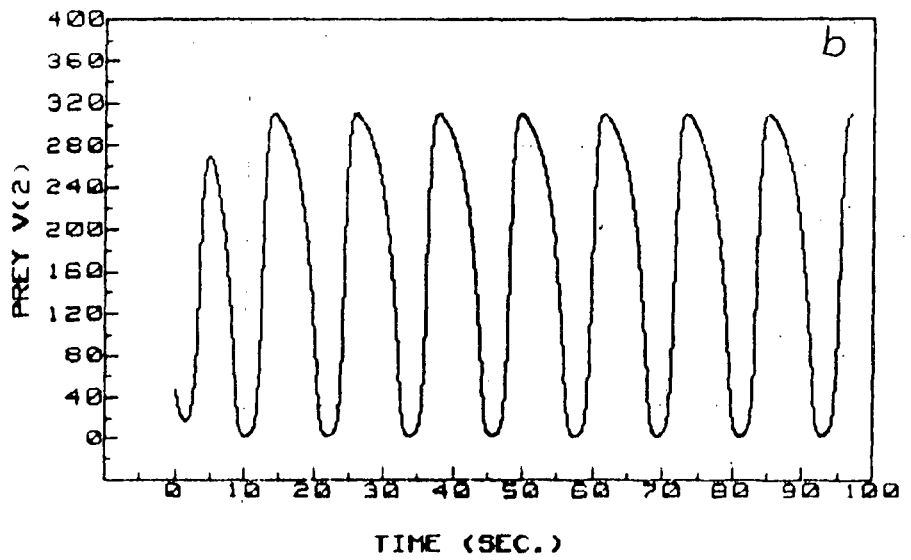
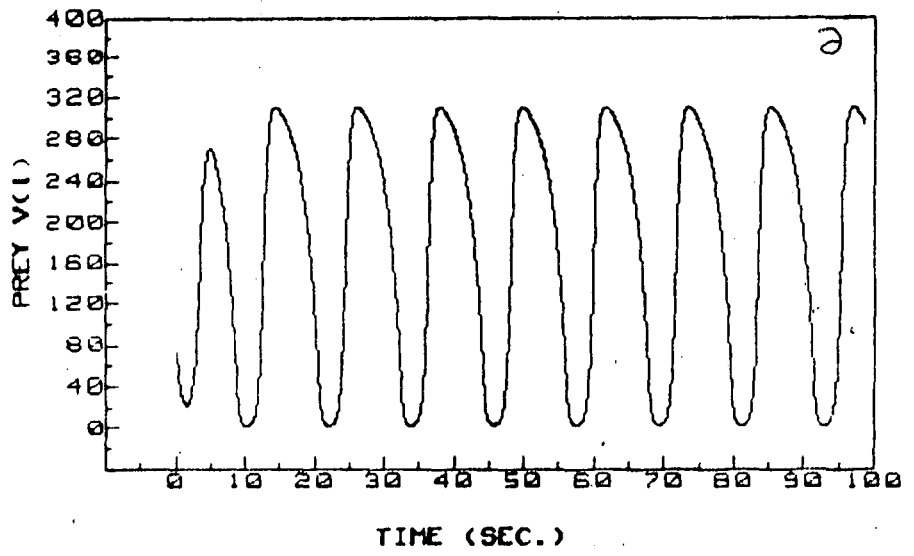


Fig.3.30 Variation of population densities with time in the two prey-one predator system  
 a) first prey b) second prey c) predator

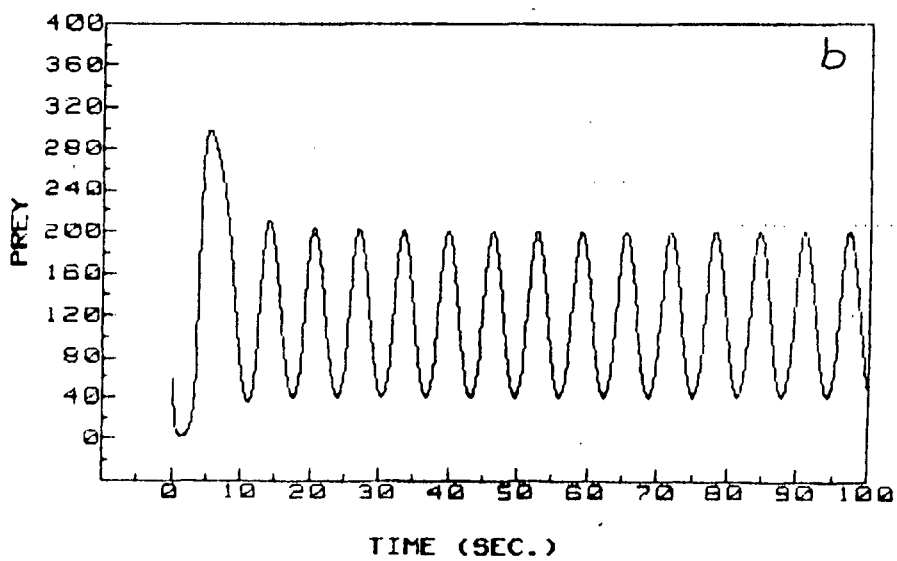
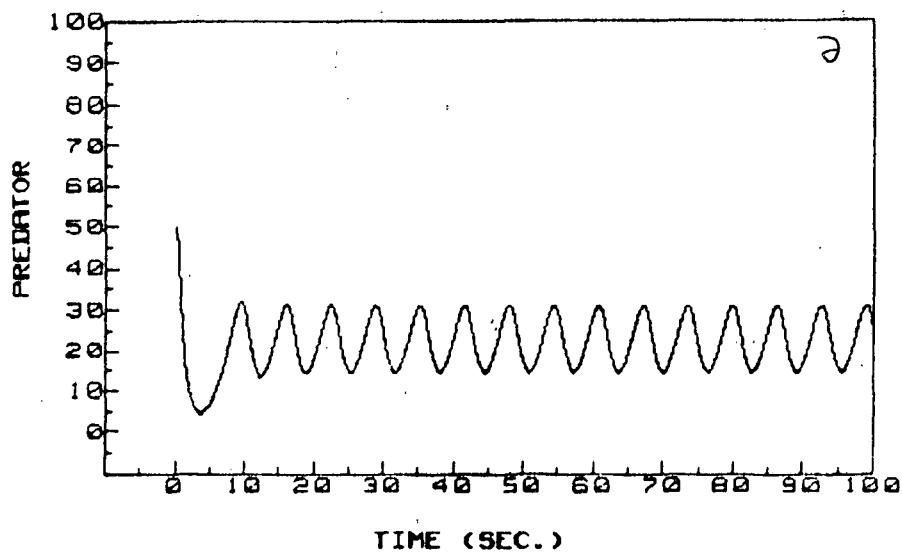


Fig.331 Variation of population densities with time in the one prey-one predator system

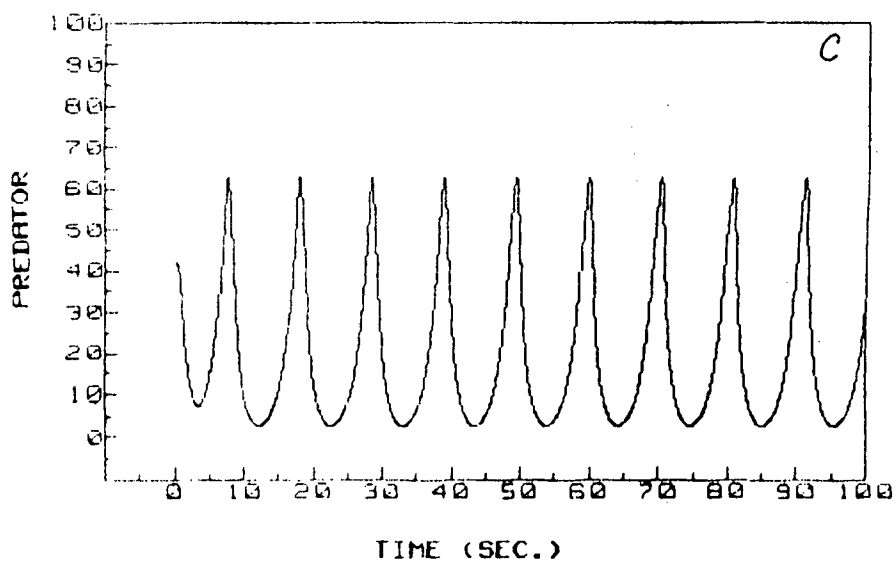
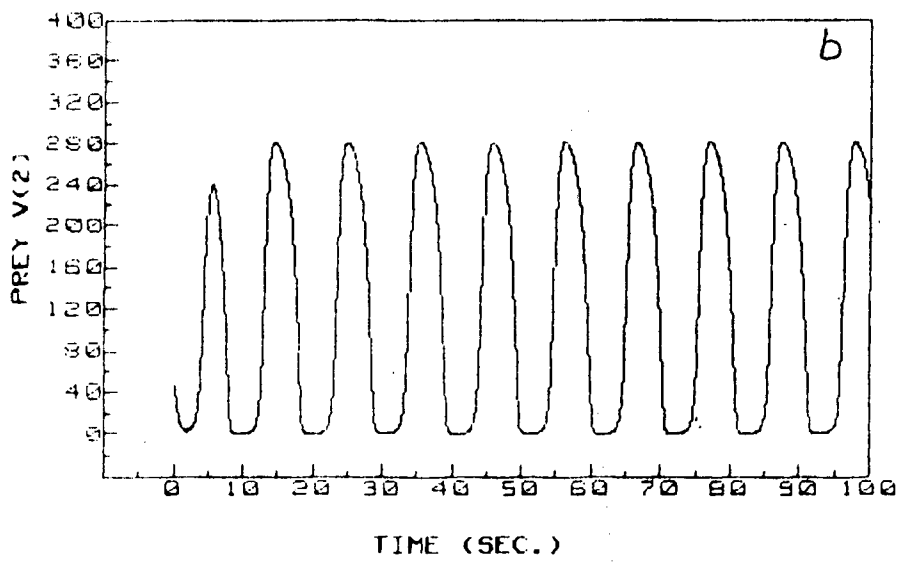
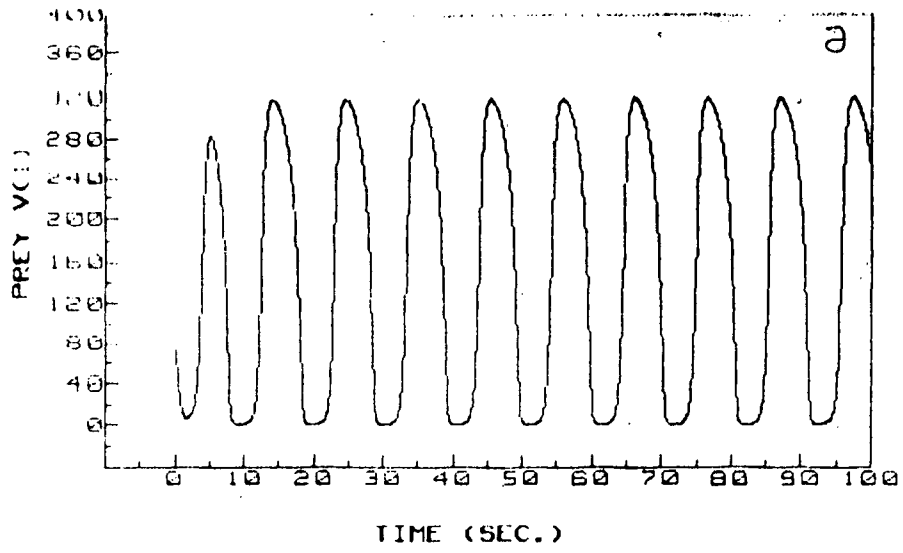


Fig. 3.32 Variation of population densities with time in the two prey-one predator system  
 a) first prey b) second prey c) predator



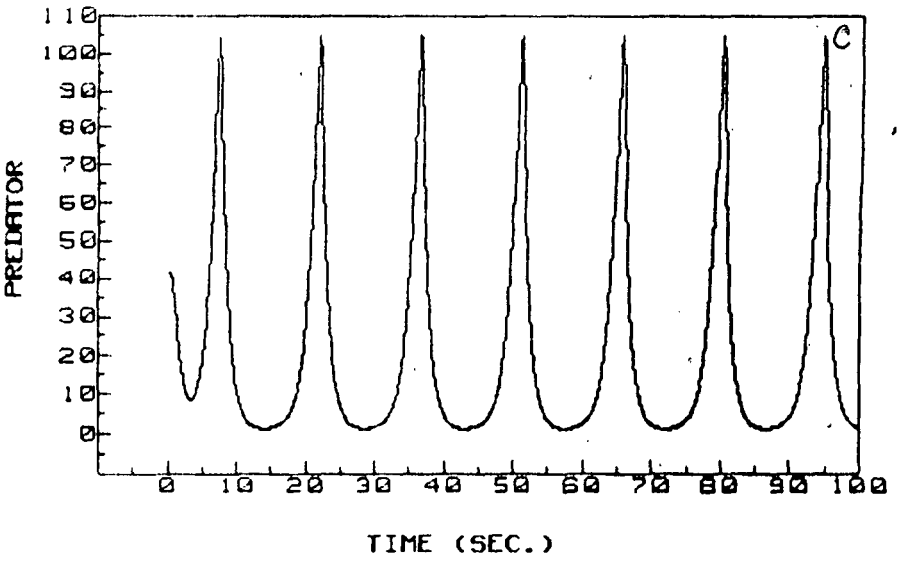
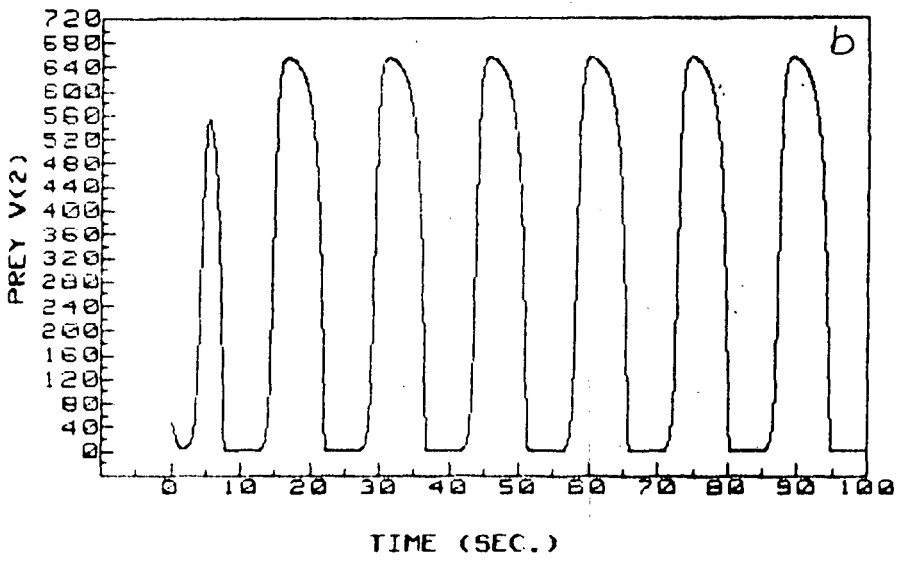
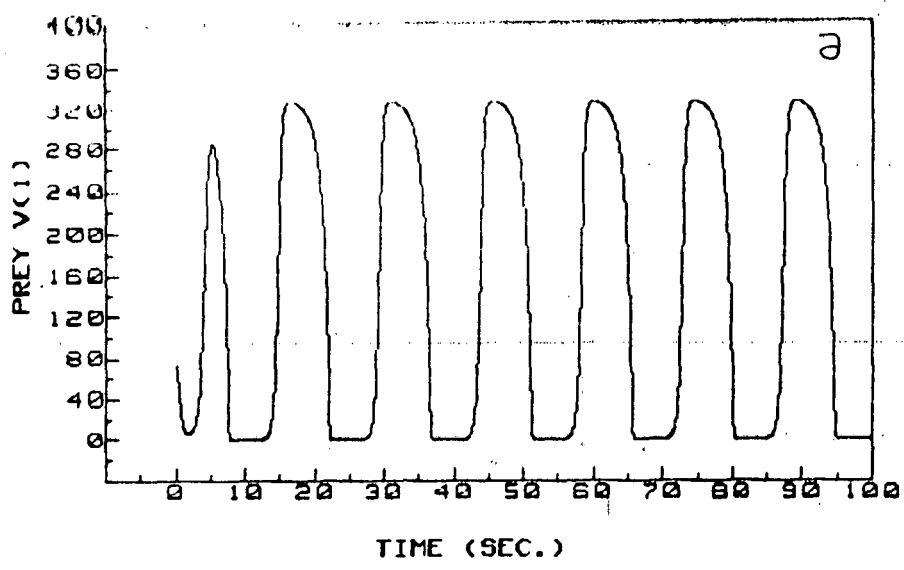


Fig. 3.33 Variation of population densities with time in the two prey-one predator system  
a) first prey b) second prey c) predator

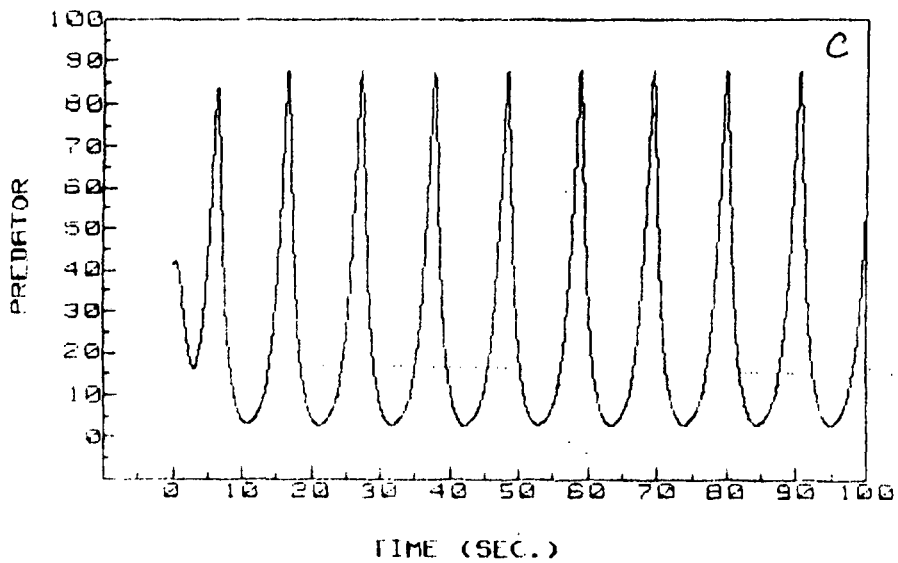
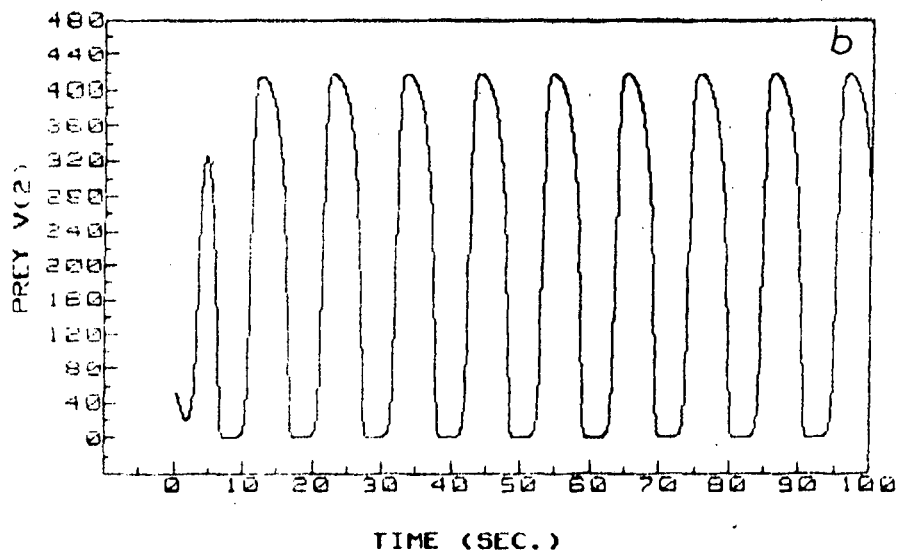
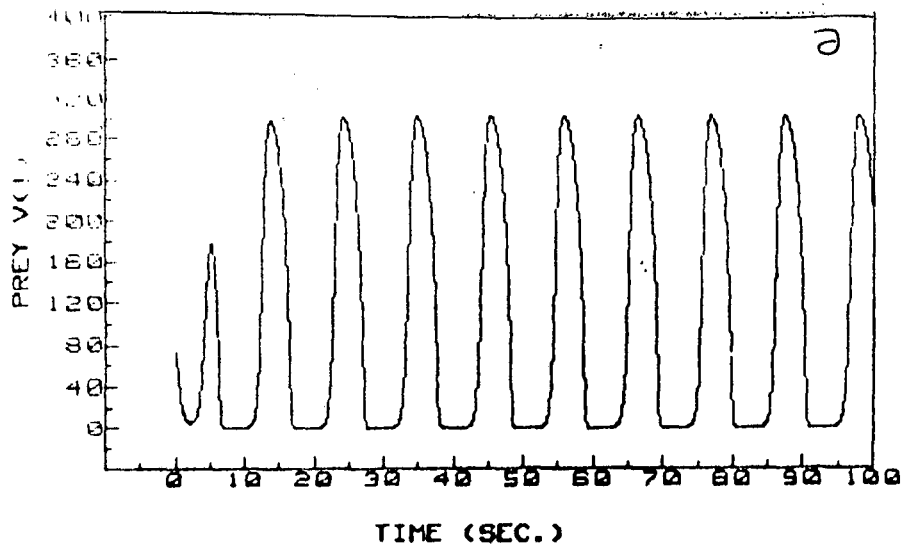


Fig. 334 Variation of population densities with time in the two prey-one predator system  
 a) first prey b) second prey c) predator

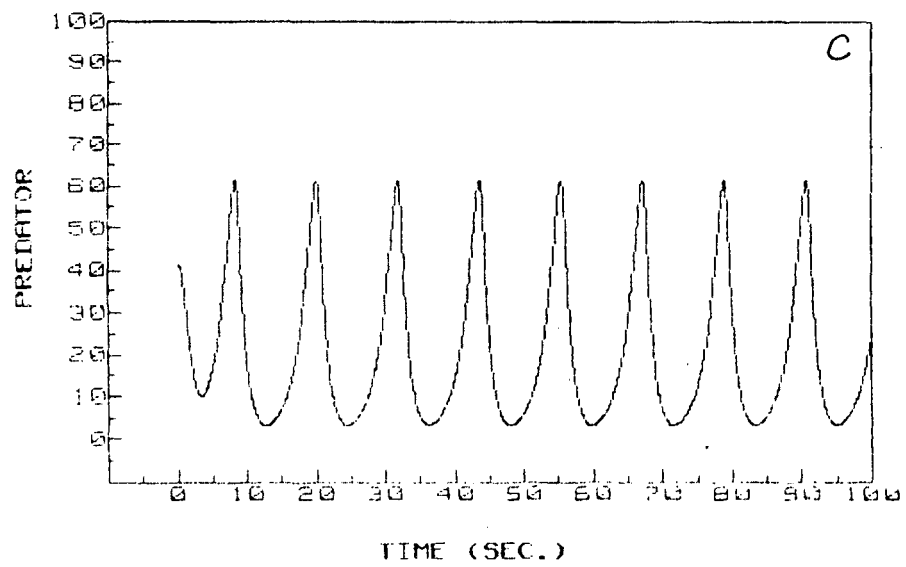
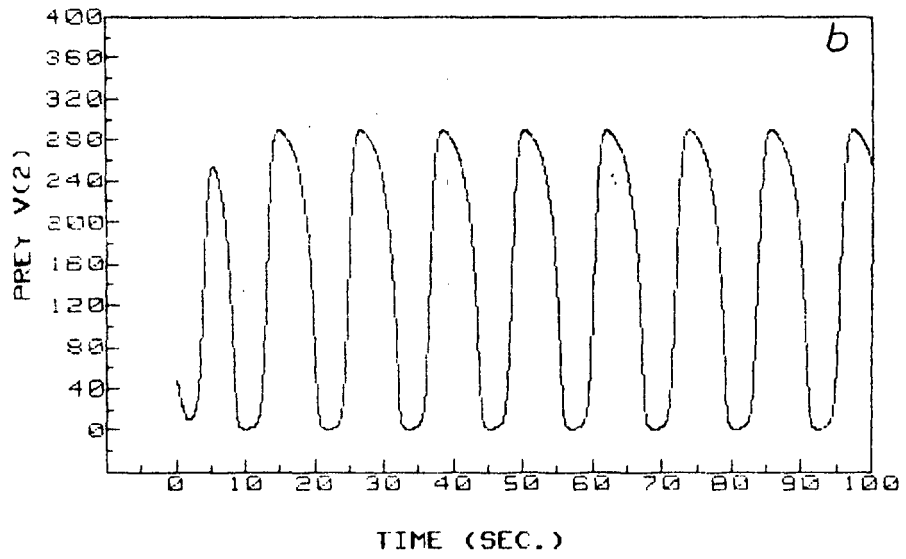
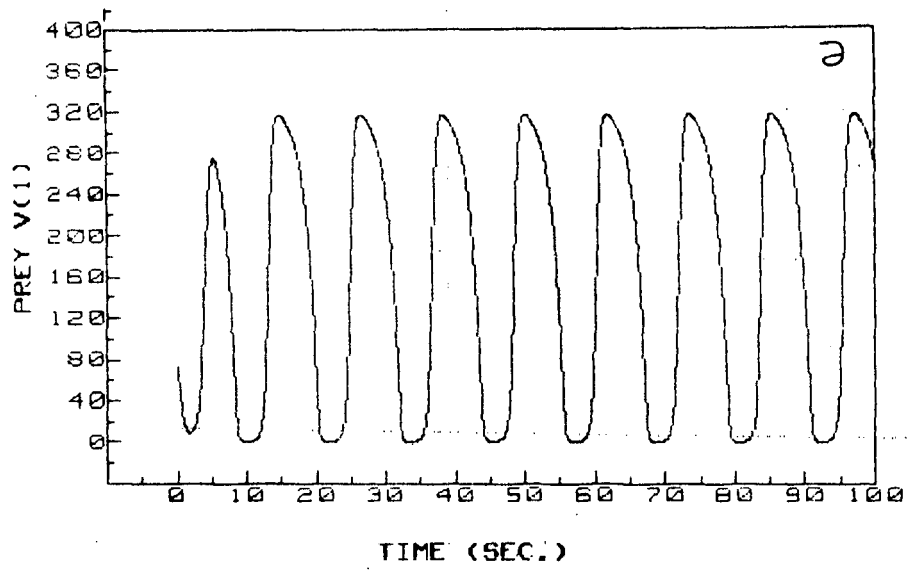


FIG. 3.35

## CHAPTER IV

# CONCLUSION

We have studied a three species system consisting of two prey species and one predator.

We were motivated by the paper of John Loman (1988) in which he has studied the extension of one prey one predator system to a two prey one predator system by introducing a second prey species into the two species system. He employed a graphical method, using consumption curve, production curve and auxiliary equation curve, to study the system. He confined his study to systems exhibiting stable equilibrium solutions only. A study of the two prey-one predator system was also done by Noy-Mier (1981) using isocline method.

We have studied here the extension of a two species system to a three species system with limit cycle solutions in mind. We first started with a one prey-one predator system. Then using Kolmogorov's theorems and Linear stability analysis around the equilibrium point, the conditions for the systems to exhibit limit cycle solutions were found. A set of parameters which obeyed the said conditions were chosen. We also found the range of each parameter within which the system still exhibited the limit cycle solutions. For this one parameter was varied at one time.

A second prey species was then introduced into the system. Thus one more rate equation (for second prey species) was incorporated into the system and also the rate equations for predator and first prey species were modified. We were able to find values

for the new parameters introduced into the system for which the three species system still exhibited limit cycle solutions. Three such sets of values were found. We also found for each set of parameters the range of old parameters within which the system exhibited limit cycle solutions. We found that a range still existed for which the three species system exhibited limit cycle oscillations, though the range of parameters was not the same as was for initial two species system. Thus we were able to show that it is possible to introduce into a two species system (one prey-one predator) a <sup>second</sup> ~~third~~ prey species so that the three species coexist in the dynamic equilibrium.

It was also observed that when second prey species is introduced into a one prey-one predator system then the range of population of first prey species is increased. This in an average sense at least, suggests "apparent mutualism" which was also found under certain conditions by Loman in his study.

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## APPENDIX - I

### THE LINEARIZED STABILITY ANALYSIS

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

$$\frac{dN_i(t)}{dt} = F_i(N_1(t), N_2(t), \dots, N_m(t)) \quad (1)$$

$$i = 1 \text{ to } m$$

here the growth rate of  $i^{\text{th}}$  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  $m$  algebraic equations obtained by putting all growth rates zero.

$$F_i(N_1^*, N_2^*, \dots, N_m^*) = 0 \quad (2)$$

expanding about this equilibrium, for each population we write

$$N_i(t) = N_i^* + x_i(t) \quad (3)$$

Where  $x_i$  measures the initially small perturbation to the  $i^{\text{th}}$  population. Taylor expanding each of the basic equations (1) around this equilibrium and discarding all terms which are of second or higher order in  $x$ , a linearized approximation is obtained

$$\frac{dx_i(t)}{dt} = \sum_{j=1}^m a_{ij} x_j(t) \quad (4)$$

This set of  $m$  equations describe the population dynamics in the neighbourhood of the equilibrium point. Equivalently, we may write, in matrix notation,

Here  $\mathbf{X}(t)$  is  $m \times 1$  column matrix of  $x_i$  and  $\mathbf{A}$  is  $m \times m$  "community matrix" whose

$$\frac{dX(t)}{dt} = A X(t) \quad (5)$$

elements  $a_{ij}$  describe the effect of species  $j$  in species  $i$  near equilibrium. The elements  $a_{ij}$  depend upon the details of the original equations (1) and on value of equilibrium populations, according to recipe

$$a_{ij} = \left( \frac{\partial F_i}{\partial N_j} \right)^* \quad (6)$$

The partial derivatives are evaluated at equilibrium values of all populations.

For the set of linear equations (5) the solution may be written

$$x_i(t) = \sum_{j=1}^m c_{ij} \exp(\lambda_j t) \quad (7)$$

$c_{ij}$  are constant which depend upon initial values of perturbations to the populations and the time dependence is contained solely in  $m$  exponential factors. The  $m$  constants  $\lambda_j$  ( $j=1,2,\dots,m$ ) which characterize the temporal behaviour of the system are so called eigen values of matrix  $A$ . They are found substituting (7) into (5) to get

$$\lambda x_{ij}(z) = \sum_{j=1}^m a_{ij} x_j(t) \quad (8)$$

or in more compact form

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

Here  $I$  is  $m \times m$  unit matrix. This set of equations possesses a non-trivial solution if and only if the determinant vanishes :

$$\det(A - \lambda I) = 0 \quad (10)$$

This is in effect  $m^{\text{th}}$  order polynomial equation in  $\lambda$  of matrix  $A$ . They may in general be complex numbers,  $\lambda = \zeta + i \xi$ ; in any of terms of equation the real part  $\zeta$  produces exponential growth or decay, and imaginary part  $\xi$  produces sinusoidal oscillations. It is clear that perturbation to the equilibrium populations will die away in time if and only if, all eigenvalues  $\lambda$  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-Horwitz Stability Criteria,

The equation of polynomial of  $\lambda$  is

$$\lambda^m + a_1 \lambda^{m-1} + a_2 \lambda^{m-2} + \dots + a_m = 0$$

The necessary and sufficient condition for all roots of above polynomial to be negative is that the coefficients  $a_1, a_2, \dots, a_m$  must fulfill Routh-Horwitz stability conditions.

The conditions for  $m = 2, 3, 4$  are

$$m = 2 \quad a_1 > 0, a_2 > 0$$

$$m = 3 \quad a_1 > 0, a_3 > 0, a_1 a_2 > 0$$

$$m = 4 \quad a_1 > 0, a_3 > 0, a_4 > 0, a_1 a_2 a_3 > a_3^2 + a_1^2 a_4$$

## APPENDIX - II

### KOLMOGOROV'S THEOREM

Consider a prey - predator system

$$\frac{dH}{dt} = H F(H,P)$$

$$\frac{dP}{dt} = P G(H,P)$$

Kolmogorov's theorem says that such a system will possess either a stable equilibrium point or stable limit cycle, provided that  $F$  and  $G$  are continuous functions of  $H$  and  $P$ , with continuous first derivatives, throughout the domain  $H \geq 0$ ,  $P \geq 0$  and that

1.  $\partial F/\partial P < 0$
2.  $H (\partial F/\partial H) + P (\partial F/\partial P) < 0$
3.  $\partial G/\partial P < 0$
4.  $H (\partial G/\partial H) + P (\partial G/\partial P) > 0$
5.  $F(0,0) > 0$

It also required that there exist quantities such that

6.  $F(0, A) = 0$  with  $A > 0$
7.  $F(B, 0) = 0$  with  $B > 0$
8.  $G(C, 0) = 0$  with  $C > 0$
9.  $B > C$

The proof of above theorem follows from Poincare-Bendixon theorem. The theorem also usually holds when certain above conditions are equalities (=) rather than in-equalities (< or >).

In more biological terms, Kolmogorov's conditions are roughly that

1. For any given population size (As measured by numbers) per capita rate of increase of prey species is decreasing function of number of predators,
2. The rate of increase of prey is a decreasing function of population size
3. Rate of increase of predators decreases with their population size.
4. The rate of increase of predators is an increasing function of population size.
5. When both populations are small the prey have a positive rate of increase
6. There can be a predator population size sufficiently large to stop further prey increase, even when prey are rare.
7. There is a critical prey population size B, beyond with they cannot increase even in absence of predators (a resource of other self limitations).
8. There is a critical prey size C that stops further increase in predators, even if they be rare
9. B must always be greater than C (otherwise system will collapse)