THE STUDY OF A THREE SPECIES ECOSYSTEM WITH ONE ONE-PREY AND TWO-PREDATORS

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CERTIFICATE

The research work embodied in this dissertation entitled " THE STUDY OF THREE SPECIES ECOSYSTEM WITH ONE PREY AND TWO PREDATORS " has been carried out in the School of Environmental Sciences, Jawaharlal Nehru University, New Delhi. This work is original and has not been submitted in part or full for any other degree or diploma for any University.

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Dillip Kumar Panda

CONTENTS

CHAPTER-1

INTRODUCTION

A study of the dynamics of interacting species is of much interest in theoretical ecology. Mathematical models suggested to describe the interaction of two or more species populations consist of sets of coupled differential equations. The equations specify the growth rate of each species as a function of the sizes of the various interacting populations. In analyzing them, the first objective is tojudge their stability. This stability condition depends on the nature of the differential equations describing the model, i.e. they are linear or non-linear. It also depends on whether the equations are assumed to apply over all conceivable combination of population sizes (global stability) or only in the neighbourhood of an equilibrium point at which all growth rates are simultaneously zero (local stability).

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

We are basically interested in the 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 the phase space of the dynamical variables of the system and are independent of the 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 dynamical stable system may not display numerical constancy is that the system is continuously perturbed from within.

Many scientists have tried to find out periodic type of solutions in two species systems. Kolmogorov (1936) has given a theorem which tells about the existence of either a stable equilibrium point or a stable limit cycle. As a system become more complex, it becomes more difficult to study its stability behaviour. For three species systems, asymptotic stability and global asymptotic stability are two of the criteria most widely used. But neither of these criteria explain the concept of persistence in a satisfactory manner as they exclude any discussion of an initial-condition independent periodic behaviour in the long run, ie, any discussion of a limit cycle solution. Koch (1974) has studied the three species model containing one-prey and two predator species taking into account the predation of both the predators on a single prey. He has incorporated self-interactions for predators though competition between them is not included. Surprisingly he found that even though his system does not exhibit stable equilibrium condition, the computer calculations give limit cycle solutions for a certain range of interaction parameters. Thus the possibility of permanent co-existence of three species system can not be ruled out.

In our work, we begin with the study of some well known models for two species system which exhibit limit cycle behaviuor. It is a well known fact that there is no such theorem like that of kolmogorov for three species which can tell us about the limit cycle solutions. To study the limit cycle behaviour of three species system, we have made generalization of the parameters from certain two species to three species system in such a way that our model exhibits limit cycle solutions, independent of the initial conditions. Basically we consider a one prey-two predator system with the effect of prey on both the predators, and study the limit cycle behaviour of the system. Further, incorporating the mutual interaction between the predators we again study the limit cycle behaviour of the modified model. Fortunately both the cases exhibit limit cycle behaviour. The usefulness and relevance of our model stem from the fact that it exhibits limit cycle solution for a considerably wide range of the parameters.

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

CHAPTER-2

REVIEW OF SOME TWO-SPECIES ECOSYSTEM MODELS :

In this chapter, we will discuss the mathematical models of population growth and the prey-predator interactions.

In reality, the ecosystems are very complex. A fruitful way to proceed, is to consider simple and ideal ecosystems and build a quantitative basis for them. The realistic case can then be easily tackled. The most idealised system is one with a single species in an **unlimited** environment.

The population of organisms fluctuate in size. Only thing that can be said with certainty is, their sizes will never remain constant.

1. **Malthusian Model:**

For the development of a simple mathematical model following assumptions are made:

(i) The organisms are immortal and reproduce at a rate which is the same for every individual, that does not change with time.

(ii) The individuals have no effect on one another.

Consider a simple kind of ecosystem containing only one species. Let $N(t)$ be the size of the population at time t and r be the rate of increase of each individual (i.e, the per capita growth rate). The simplest differential equation describing growth can in that case be written as,

$$dN(t)/dt = rN(t) \tag{2.1}$$

which on solving gives,

$$\mathbf{N(t) = N(0)\exp(rt)} \tag{2.2}$$

where, $N(0)$ is the population size at time $t=0$

This is well known malthusian model for population growth. This model holds-good for a population size so small that there is no interference among its members.

2. **Pearl-verhulst logistic model** :

The 'environment, in reality, is not an unlimited one. Beacause of the growth of population the resources available to it become limited with the passage of time. Thus a stage is reached when the demands of the existing population on limited resources restrict further growth and the population is then at its "saturation level". The actual growth rate in the above expression must therefore also depend on the proporation of the maximum attainable population size that is still unrealized. If the maximum attainable size is K, then the unrealized proporation can be written as (K-N)/K, and the growth rate will became,

$$dN/dt = rN(1-N/K)$$

$$\text{or, } \mathbf{dN/dt = N(r-sN)} \tag{2.3}$$

where, $s = r/k$ and $r, s > 0$,

The expression (2.3) is well known pearl- verhulst logistic equation.

Solving equation (2.3) we get,

$$N(t) = \frac{r/s}{1 + \exp\{-r\ (t - t0)\}} \tag{2.4}$$

here, $r/s = K$, is the carrying capacity, which decides the saturation level of the population growth.

The constant exp(rt0) is related to the initial population size by,

$$\exp(rt0) = \frac{(r/s) - N\ (0)}{N\ (0)}$$

From the above expression one can infer that the population rises initially as in the previous case, but then the growth rate begins to slow down and then turns towards its asymptotic value which is (r/s). The equality K = (r/s) is the maximum limit that the population can reach and is therefore called the "carrying capacity" of the given environment.

3. **The Lotka-volterra Model** :

Consider a situation when there are two interacting populations in the given environment say, a prey and a predator. Two general assumptions taken in such a prey-predtator model are: (i) The two populations inhabit the same area, so densities are directly propertional to numbers.

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

The mathematical model for the interaction between a pair of species- a prey and a predator, was given independently by Lotka and Volterra.

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

$$dH/dt = a_1 H, \quad a_1 > 0.$$

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

$$dP/dt = - a_2 P, \quad a_2 > 0.$$

If the prey and the predator interact with each other then the interaction term is in general, a complicated function of H and P. But, here we consider the following equations for a prey-predator system in the deterministic approach to the problem:

$$dH/dt = H\,(a_1 - b_1\,P)$$

$$dP/dt = P\,(-a_2 + b_2\,H) \tag{2.5}$$

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

Here, a_1 and a_2 are the average rate of growth and decay per individual in the absence of other species and b_1 and b_2 are the interaction parameters.

Unfortunately, equation (2.5) can not be solved analytically. We have to take suitable approximation schemes and follow numerical methods. In view of their non-linear nature, it is unlikely that the full information content of these equations will be uncovered by such methods. It may be noted here that equation (2.3) is also non-linear, but its simple form enables us to solve it exactly by direct integration. That is no more possible when we come to equation (2.5). However, an exact result which is of crucial interest in the present context, can be established (pielou, 1977 ; Simmons 1981).

We can rewrite equation (2.5) as:

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

or, $a_2 \frac{dH}{H} - b_2 \, dH + a_1 \frac{dP}{P} - b_1 \, dP = 0$

Integrating, we get.

$$a_2 \log H - b_2 H + a_1 \log P - b_1 P = \log K \text{ -----} \quad (2.6)$$

$$a_1 \log P - b_1 P = - a_2 \log H + b_2 H + \log K$$

or, $$P^{a_1} e^{-b_1 P} = K H^{-a_2} e^{b_2 H} \text{ ------} \quad (2.7)$$

where, **K** is a constant given by,

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

in terms of H_0 and P_0, the initial values of H and p. Thus the system (2.5) possesses a conserved quality given by the left hand side of equation (2.6). The equation represents a family of closed curves in which each member of the family is characterised by a particular value of the constant K. One can not solve equation (2.7) for either H or P individually but we can determine the curves on which H and P will move. To do this, we equate the left hand sides of equation (2.3)

to new variables Z and W, and then plot the graphs C_1 and C_2 of the functions.

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

as shown in figure - 2.1

For Z = W, we are confined in the third quadrant to the line L. To the maximum value of Z given by the point A and C_1, there corresponds one point M on L and the corresponding point A′ and A" on C_2 leading to two values of H which determine the bounds between which it may vary. Similarly the minimum value of W given by B on C_2 leads to N on L and hence to B′ and B" as 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 curves C_3. Additional points are easily found by starting on L at a point R anywhere between M and N and projecting on the one hand on to C_1 and over to C_3. It is clear that changing the value 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 values, we obtain a family of ovals about the point S, which is all there is of C_3 when the minimum value of W equals the maximum value of Z. Now, we will see how the corresponding point (H,P) on C_3 moves around the curve as t increases. We can find out the equilibrium point by putting the right hand sides of

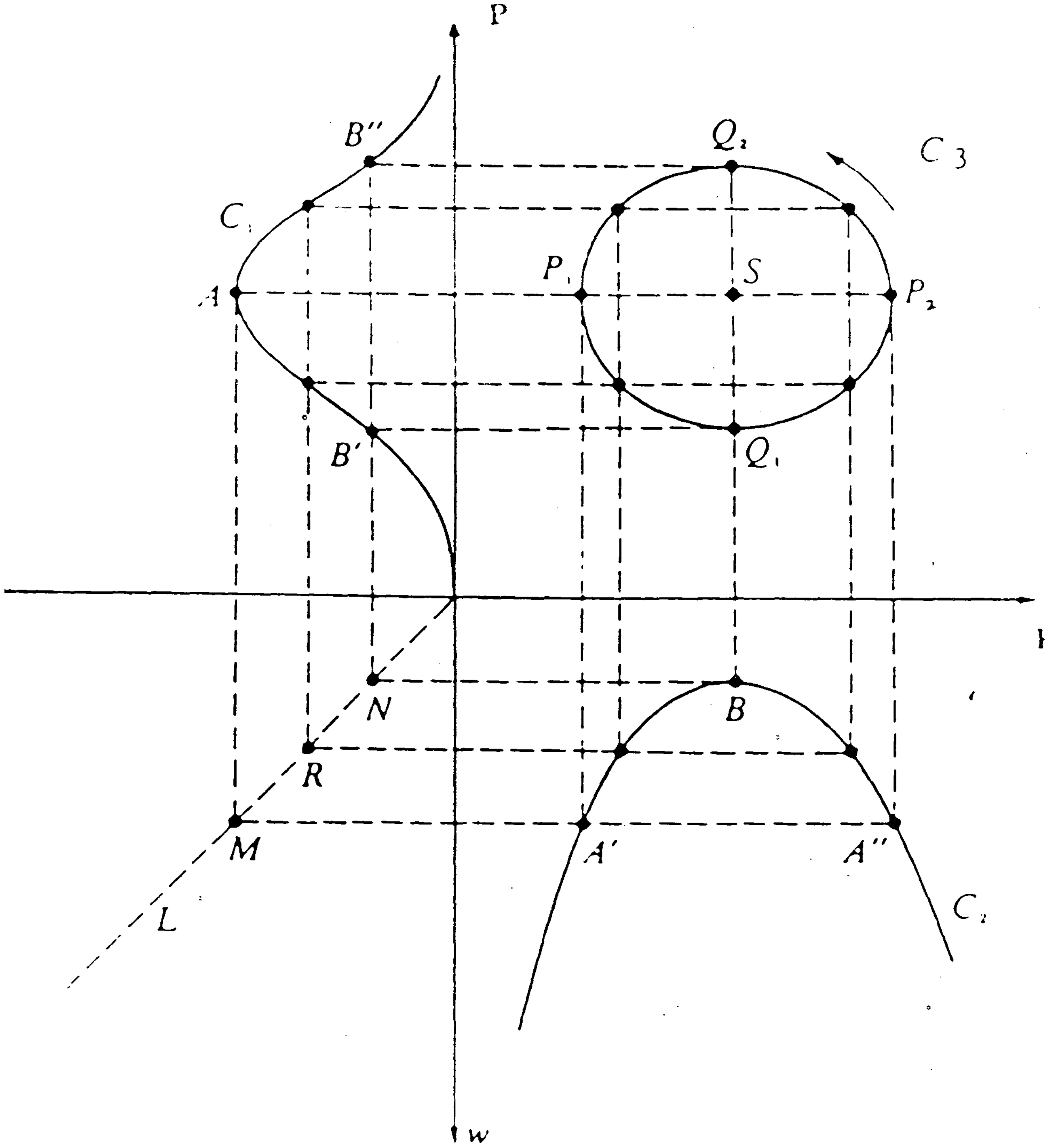


Fig. 1

equation (2.5) equals to zero i.e.,

$$a_1 H - b_1 PH = 0$$

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

Solving these equations, we get,

$$H^{*} = a_2 \backslash b_2 \qquad \text{----------} \quad (2.9)$$

$$P^{*} = a_1 \backslash b_1$$

Hence, the co-ordinates of S will be

$$H = a_2/b_2 \ , \ P=a_1/b_1 \qquad \text{----------} \quad (2.10)$$

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

This shows that both prey and predator populations under-go prolonged oscillations with constant amplitudes and these 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.

4. **The Leslie-Gower Model:**

An alternative fomulation of the prey-predator equations was suggested by Leslie and Gower (1960) (May 1972; pielou 1977) as follows:

$$dH/dt = H(a_1 - c_1 P)$$

$$dP/dt = P(a_2 - c_2 P/H) \qquad \text{-------} \quad (2.11)$$

where $a_1, a_2, c_1, c_2 > 0$.

To study the behaviour of the system, we use the isocline method. The H-isocline and P-isocline are the curves in P-H phase space on which the time rate of change of prey and pedator respectively are zero. Thus on H-isocline $dH/dt = 0$ and an P- isocline $dP/dt = 0$. From equation (2.11), we can write,

H - isocline:

$$dH/dt = 0 = H\ (a_1 - c_1 P)$$

$$\text{or,} \quad p^* = a_1/c_1 \qquad \text{----------} \quad (2.12)$$

P - isocline:

$$dP/dt = 0 = p(a_2 - c_2 P/H)$$

$$\text{or,} \quad H^* = c_2 P^*/a_2$$

$$= a_1 c_2/a_2 c_1 \qquad \text{-----------} \quad (2.13)$$

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

At point (p^*, H^*) both $dH/dt = 0$ and $dP/dt = 0$. This means that at this point the populations of prey and predator do not vary with time, so this point is the equilibrium point.

From equation (2.11), if $P>a_1/c_1$,

$$dH/dt = H\ (a_1 - c_1 P)$$
$$< H\ (a_1 - c_1\ a_1/c_1)$$
$$< 0$$

and $P < a_1/c_1$

$$dH/dt > H(a_1 - c_1\ a_1/c_1)$$
$$> 0.$$

Again if $H > C_2\ P/a_2$,

$$dP/dt = (a_2\ H - C_2\ P/H)$$
$$> (a_2\ c_2 P/a_2 - c_2\ P)\ P/H$$
$$> 0$$

and $H < c_2\ P/a_2$,

$$dP/dt = (a_2\ H - c_2\ P)\ P/H$$
$$< (a_2\ c_2\ P/a_2 - c_2 P)\ P/H$$
$$< 0$$

In the firgure(2.2) H-isocline and P-isocline are plotted,which are straight lines $P=a_1/c_1$ and $H= a_1\ c_2/a_2\ c_1$ respectively. We have given above the inequality conditions for all the four regions into which the region of positive H and positive P can be divided.

Suppose initially our system is at a point in region I. In this region H > 0 & P > 0 .It follows that H and P increases with time.Arrows show the direction of the

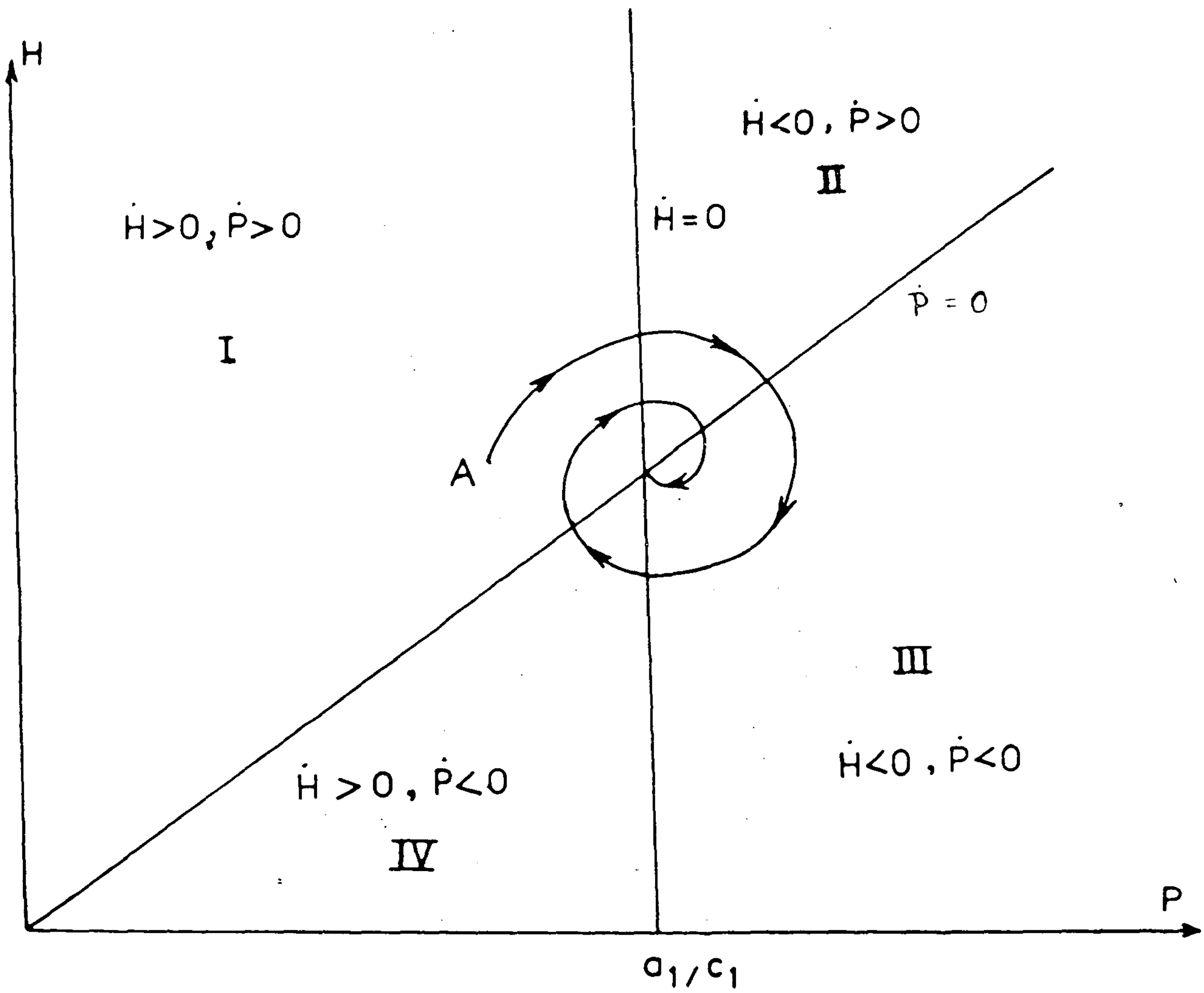


FIG. 2.2 PHASE SPACE DIAGRAM

movement along the trajectory. The trajectory will move towards the left from the point A and will meet the P-isocline. At this point dP/dt =o, and the tangent to the trajectory will be normal to the P-axis. In region-II both H and P increase with time. In this region, the trajectory will move to the right and will cross the H-isocline. At this point dH/dt =o, and the tangent to the trajectory will be normal to the H-axis. Similarly, we can draw the trajectory for regions III and IV. In the phase space the trajectory is a spiral which converges on the equilibrium point which is the intersection of H-isocline and P-isocline. Hence, each species population undergoes damped harmonic oscillations with time towards its equilibrium level.

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

Leslie's model is different from volterra's in the following ways:

(a) For volterra, whether predator increases or decreases in number depends only on the density of prey whereas for Leslie it depends on the number of prey per predator.

(b) Volterra's model relates the rate of increase of predators to the rate at which the prey are being eaten where as in Leslie's model there is no relationship between the rate at which predator eats and the rate at which it reproduces.

5. The Holling - Tanner Model:

Neither of the two preceeding models just discussed exhibit stable limit cycle. Kolmogorov has given the criteria for stable equilibrium point or stable limit cycle which are applicable to all two-species prey-predator models.

Here we will consider the Holling-Tanner model which is the representative of a great many non-linear models that produce stable limit cycles.

This model is basically slightly more elaborate than that of Leslie and Gower. The growth rate of the prey in the absence of predator is given by the logistic equation.

$$dH/dt = rH\,(1-H/K) \quad \text{-----------} \quad (2.13)$$

where, r-> intrinsic growth rate of prey and K -> 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 taken into account. 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 fig.(2.3). One of the equations which will produce a functional response like this (by C.S.Holling, 1969) is

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

Where, Y -> predation rate

W -> Maximum predation rate.

D -> a constant which determines how fast the functional response curve increases at low prey densities. Modified equation for prey can be written as :

$$dH/dt = H(1 - H/K) - WHP/(D + H) \quad --- (2.14)$$

In the above equation, it is assumed that in the absence of the predador, the prey population would grow logistically but in the presence of the prey, growth rate is reduced. The reduction in the growth rate of prey is due to the fact that the predator is now not merely a constant multiple of P. The factor W/(D+H) is taken by considering the probable effect on a predator attack rate of the density

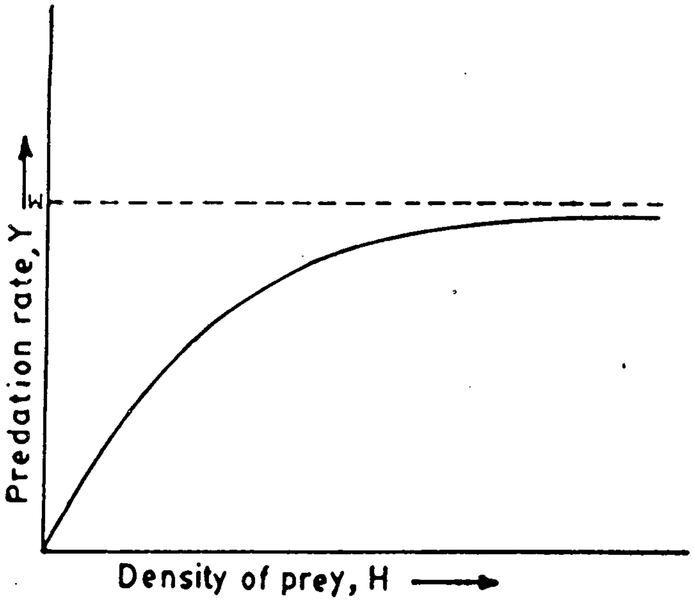


FIG. 2.3 Prey killed per predator per time, Y, as a function of prey density, H. The maximum predation rate is W

of the prey. Holling (1965) argued that the attack rate of the predador on prey as measured by the number of prey attacked per predator per unit of time, say Y, often takes the form Y = WH/(D+H). The relation shows that there must be a ceiling W to each predator's attack rate, which will not be exceeded whatever larger value the prey takes. Thus when H >>D, Y = W. The magnitude of the constant D varies directly with the prey's ability to evade attack, the more elusive the prey, the greater the value of D. The explanation for the functional response is that it takes the predator a certain amount of time to kill and eat each prey.

For the growth of the predator populations, an equation of the Leslie-Gower form may still be taken :

$$dP/dt = sP\,(1- P/\gamma H) \qquad (2.15)$$

Where, s -> intrinsic growth rate of predators.

γ -> number of prey required to support one predator at equilibrium.

Equations (2.14) and (2.15) give a complete formulation of the Holling-Tanner model. Applying Kolmogorov theorem to the system of equations in the present model, it is infered that latter exhibits either a limit cycle or stable equilibrium. The latter possibility can be checked by applying the neighbourhood stability analysis.

The equilibrium points H^* and P^* can be obtained by putting the right hand sides of the equations (2.14) and (2.15) equal to zero. From equation (2.15) we get,

$$P^* = \gamma H \qquad \text{---------} \qquad (2.16)$$

and from equation (2.14)

$$1-H^*/K \; - \; \frac{(W\gamma/r)\,H^*}{H^* + D} \; = \; 0 \qquad \text{---------} \qquad (2.17)$$

Defining m and n as,

$$m = (W\gamma)/r$$

and

$$n = D/K$$

equation (2.17) takes the form,

$$H^{*2} + H^* K \quad (m+n-1) - nK^2 = 0$$

The solution of this equation may be written as,

$$H^* = D \;(1-m-n \pm R\;)/2n \qquad \text{-------} \qquad (2.18)$$

hence, $P^* = D \;(1-m-n \pm R\;)/(2n/\gamma)$.

where, $R = [(1-m-n)^2 + 4\,n]^{1/2}$

The solution with negative sign before R corresponds to a negative value of H^* and is therefore to be discarded. In the subsequent discussions we shall consider the solution with only the positive sign before R. We can rewrite the equations (2.14) and (2.15) as:

$$dH/dt = F_1\;(H,P) = rH\;(1-H/K)-WHP/(D+H) \qquad \text{-------} \qquad (2.19)$$

and $dP/dt = F_2 (H,P) = sP (1-P/\gamma H)$ ------- (2.20)

To study the behaviour of the system in the neighbour - hood of the equilibrium point (H^*, P^*) we have linearized the system of equations (see appendix-II) and got the set of equations that describe the population dynamics in the neighbourhood of the equilibrium point as :

$$dX(t)/dt = A\,X(t) \qquad \text{------- (2.21)}$$

Here X is a (2x1) matrix and A is the (2x2) " community matrix" and a_{ij} -. the element of this matrix describe the effect of species j upon species i near equilibrium.
The community matrix can be written as,

$$A = \begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix}$$

The elements of the community matrix A are :

$$a_{11} = (\partial F_1/\partial H)^* = rH^* [-1/K+(W/r)\ P^*/\{H^* + D\}^2]$$

$$a_{12} = (\partial F_1/\partial P)^* = -WH^*/(H^*+D)$$

$$a_{21} = (\partial F_2/\partial H)^* = s(P^*)^2/\gamma(H^*)^2 = \gamma s$$

$$a_{22} = (\partial F_2/\partial P)^* = -s(P^*)/\gamma H^* = -s$$

Now, the determinantal equation for the linearized system can be written as :

$$| A - \lambda I | = 0$$

The eigenvalues follow the equation,

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

For neighbourhood stability, the real parts of eigen value must be negative.

So, (1) $-(a_{11} + a_{22}) > 0$

$$\Rightarrow - H^* [r/k + WP^* /(D+H)^2] + s > 0 \qquad \text{---------} \quad (2.22)$$

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

$$\Rightarrow - s H^* [- r/k + WP^*/(D+H^*)^2] + \gamma sWH^*/(D+H^*)^2 > 0 \qquad \text{---------} \quad (2.23)$$

After simplification, we get, the condition for stability as:

$$s/r > 2(m-r)/(1+m+n+R) \qquad \text{---------} \quad (2.24)$$

If this condition is satisfied then the system possesses a stable equilibrium point. If this conidition is violated, then in accordance with the Kolmogorov theorem, the system will exhibit a limit cycle.

6. **A Modified Form of Holling and Tanner 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. In the prey equation they have introducted an interaction term different from that suggested by Leslie and Gower. The model of Holling and Tanner was modified by

Rai, Kumar and Pande (1991) for a two species system. In this model the per capita growth rate of predator is not propertional 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 occuring for H --> . This establishes a desirable rationship between prey's loss and predator's gain which does not exist in the Holling-Tanner model. The prdators functional response of Holling- Tanner type is retained in the new model. The behaviour of the rate equation, for predator near H=0 in this model improved over the Lislie-Gower and Holling-Tanner models.

The set of equations for two species system in this model can be written as:

$$dH/dt = a_1 H - b_1 H^2 - c_1 PH/(d_1 + H)$$
$$= F_1 (H,P) \qquad \text{-------} \quad (2.25)$$
$$dP/dt = - a_2 P + c_2 PH/(d_2 + H)$$
$$= F_2 (H,P) \qquad \text{-------} \quad (2.26)$$

Where, a_1, b_1, c_1, d_1, a_2, c_2 & d_2 are positive constants.

Applying Kolomogorov theorem (Appendix-1) to this system, we see that the theorem is satisfied for the system under the conditions,

$$c_2 > a_2 \qquad \text{------ (2.27)}$$

and $$a_1/b_1 > d_2a_2/(c_2-a_2)$$

If the above conditions are satisfied, then the system always leads to solutions exhibiting either stable equilibrium or limit cycles. The neighbourhood stability analysis around the equilibrium point will decide the behaviour of the system.

The equilibrium populations of the system are :

$$H^* = a_2\, d_2 \;/\; (c_2-a_2)$$

and $$P^* = a_1\, d_1/c_1+a_2d_2/c_1(c_2-a_2)^2\,[a_1(c_2-a_2) -b_1(d_1c_2-a_2d_1+a_2d_2)] \qquad \text{------- (2.28)}$$

To study the behaviour of the system in the neighbour - hood of the equilibrium point (H^*, P^*) we have linearized the system of equations (see appendix-II) and got the set of equations that describe the population dynamics in the neighbourhood of the equilibrium point as :

$$dX\,(t)/dt = A\,X(t) \qquad \text{------- (2.21)}$$

Here X is a (2x1) matrix and A is the (2x2) " community matrix" and a_{ij} - the element of this matrix describe the effect of species j upon species i near equilibrium.

The community matrix can be written as,

$$A = \begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix}$$

The elements of the community matrix "A" are:

$$a_{11} = (\partial F_1/\partial H)^* = a_1 - 2b_1H^* - c_1d_1P^*/(d_1+H^*)^2$$

$$a_{12} = (\partial F_1/\partial P)^* = -d_1\ H^*/(d_1+H^*)$$

$$a_{21} = (\partial F_2/\partial H)^* = c_2d_2P^*/(d_2+H^*)^2$$

$$a_{22} = (\partial F_2/\partial P)^* = -a_2+c_2H^*/(d_2+H^*) = 0$$

The determinantal equation for it can be written as,

$$|A - \lambda I| = 0$$

The eigenvalues follow the equation:

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

According to Routh-Horwitz criteria, (appendix-II) stable equilibrium point for the system exists if the eigenvalues have negative real parts. This is true only if,

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

$$\Rightarrow a_{11} < 0 \qquad , \text{ as } a_{22} = 0$$

$$\Rightarrow 2b_1\ [a_2d_2/(c_2-a_2)] + b_1\ d_1-a_1 > 0 \qquad \text{----------- (2.29)}$$

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

$\Rightarrow\ a_{12}\ a_{21} < 0$, as $a_{22} = 0$

$\Rightarrow d_2 > 0$ ....(2.30)

Since, inequality (2.30) satisfied for all cases, the choice of parameters which satisfy the inequality (2.29) will lead to stable equilibrium and the coice violating it will lead to stabel limit cycles (figures 2.4 & 2.6).

One prey-one predator system:

Table 2.1

Numerical input for different parameters:

CASE-I

$a_1 = 3.0$	$x = 85$
$b_1 = 0.01$	$y = 25$
$c_1 = 30$	figs. 2.4 & 2.5
$d_1 = 100$	
$a_2 = 1.0$	
$c_2 = 3.0$	

CASE-II

Remaining parameters	
the same as above	
except $a_1 = 18$	$x = 120$
	$y = 40$
	figs. 2.6 & 2.7

CASE-III

Same as case-I	$x = 120$
	$y = 40$
	figs. 2.8 & 2.9

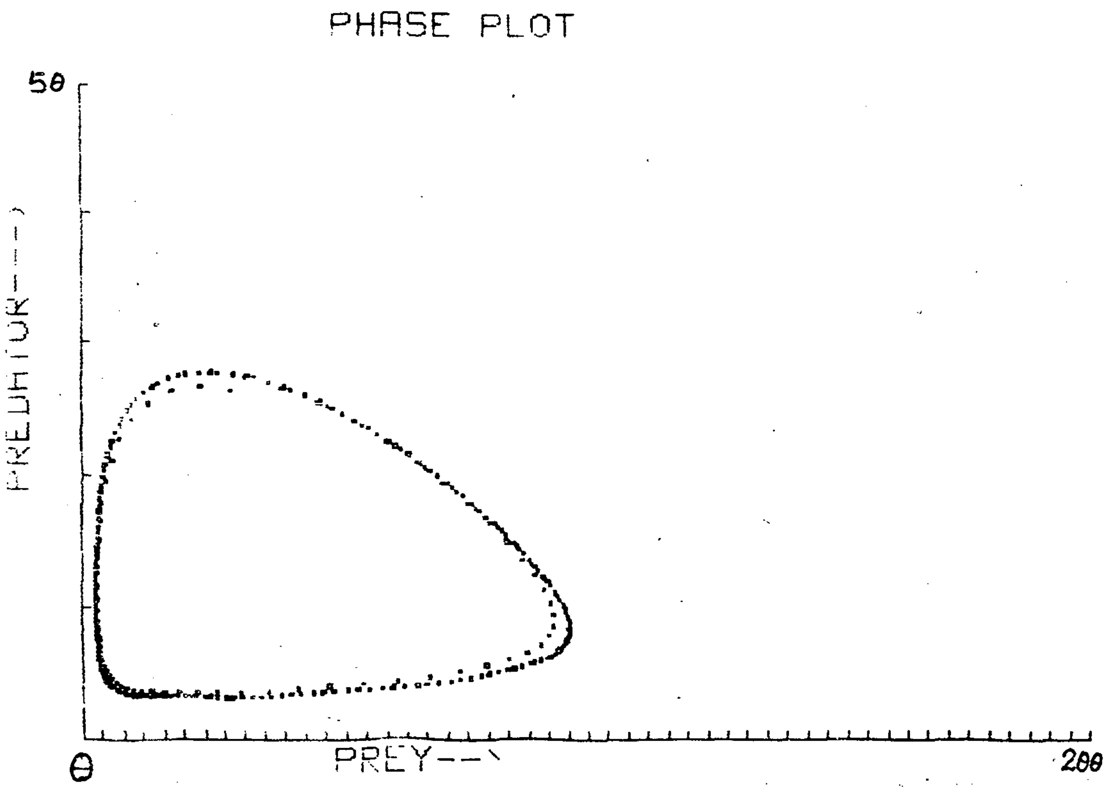


fig.2.4

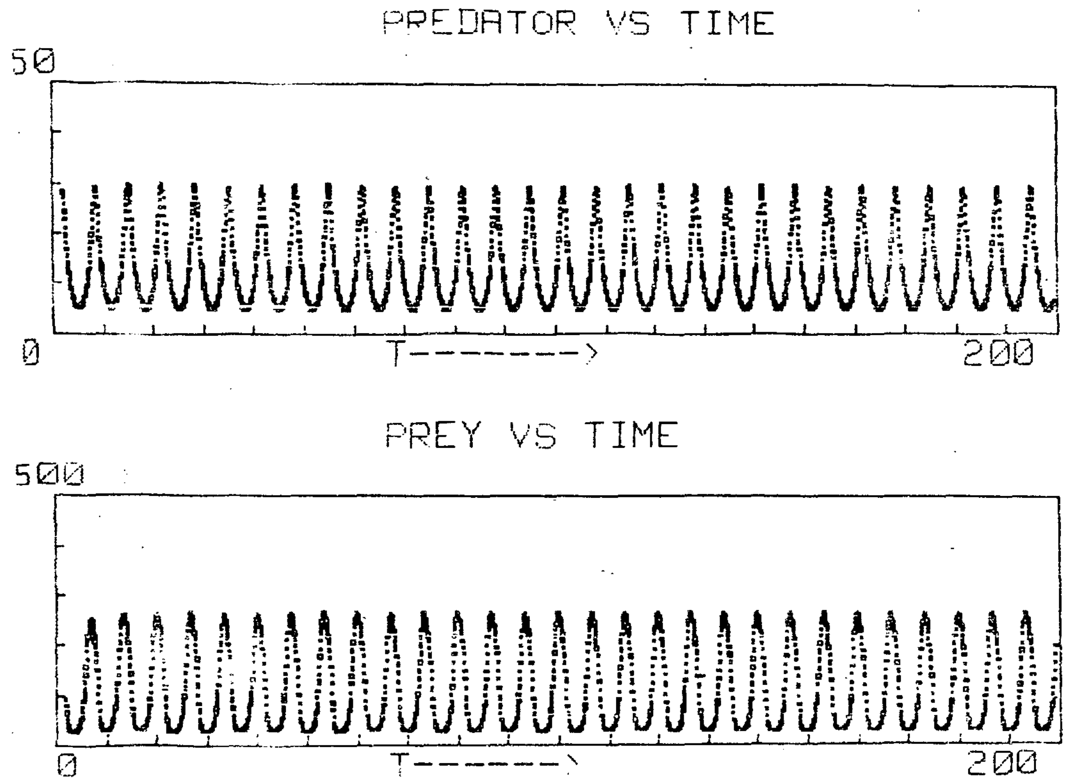


fig.2.5

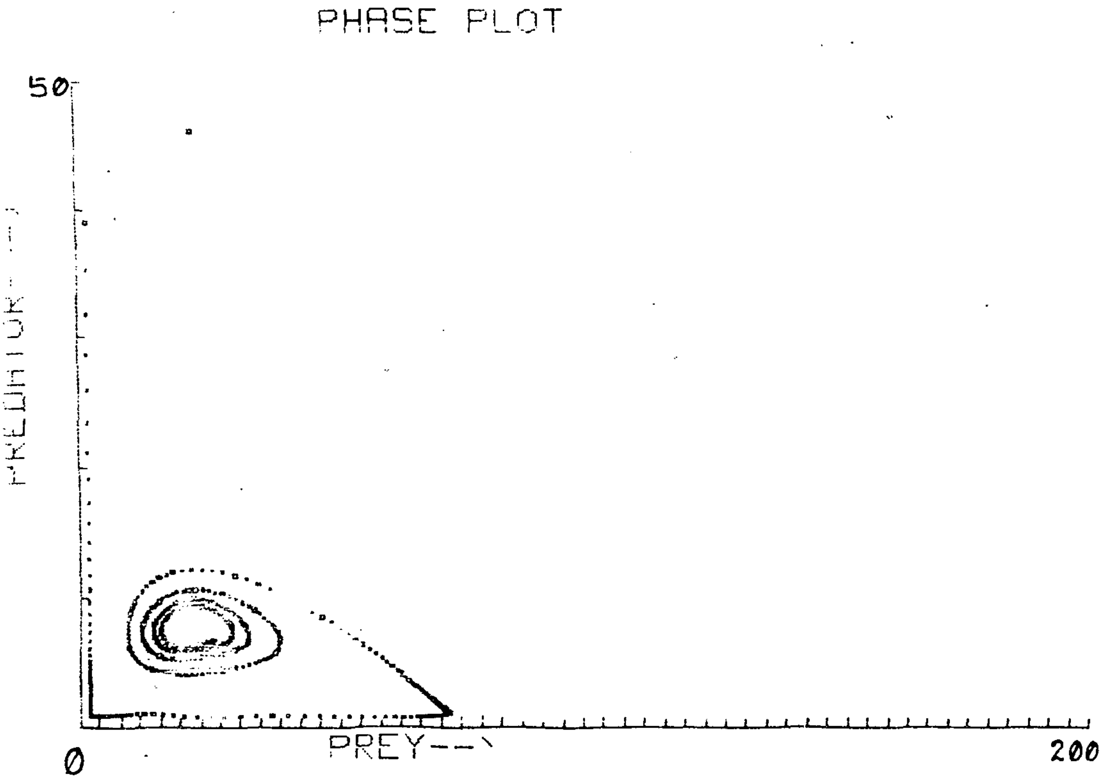


fig.2.6

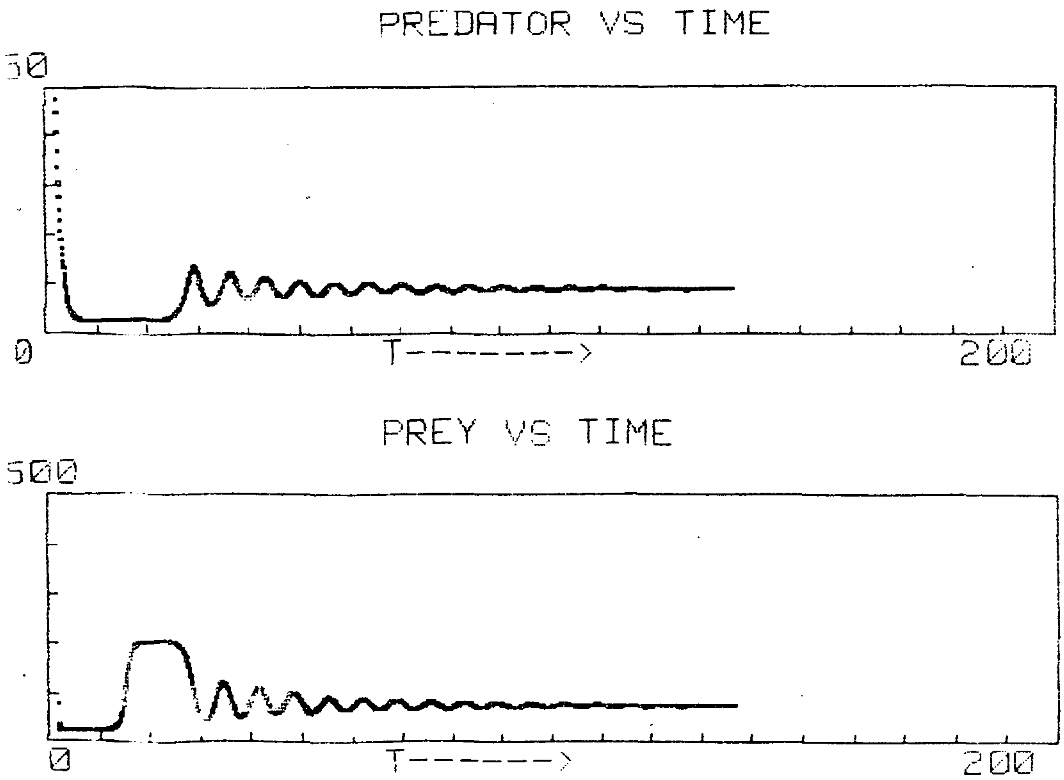


fig.2.7

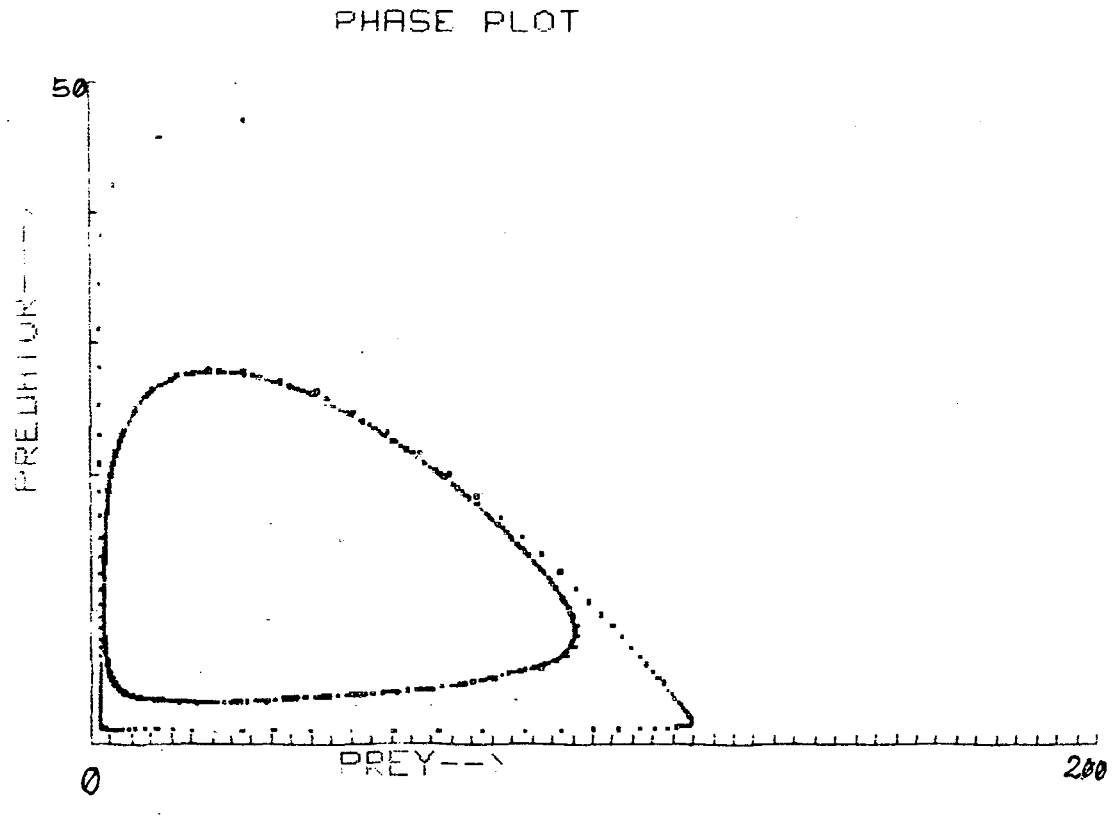


fig.2.8

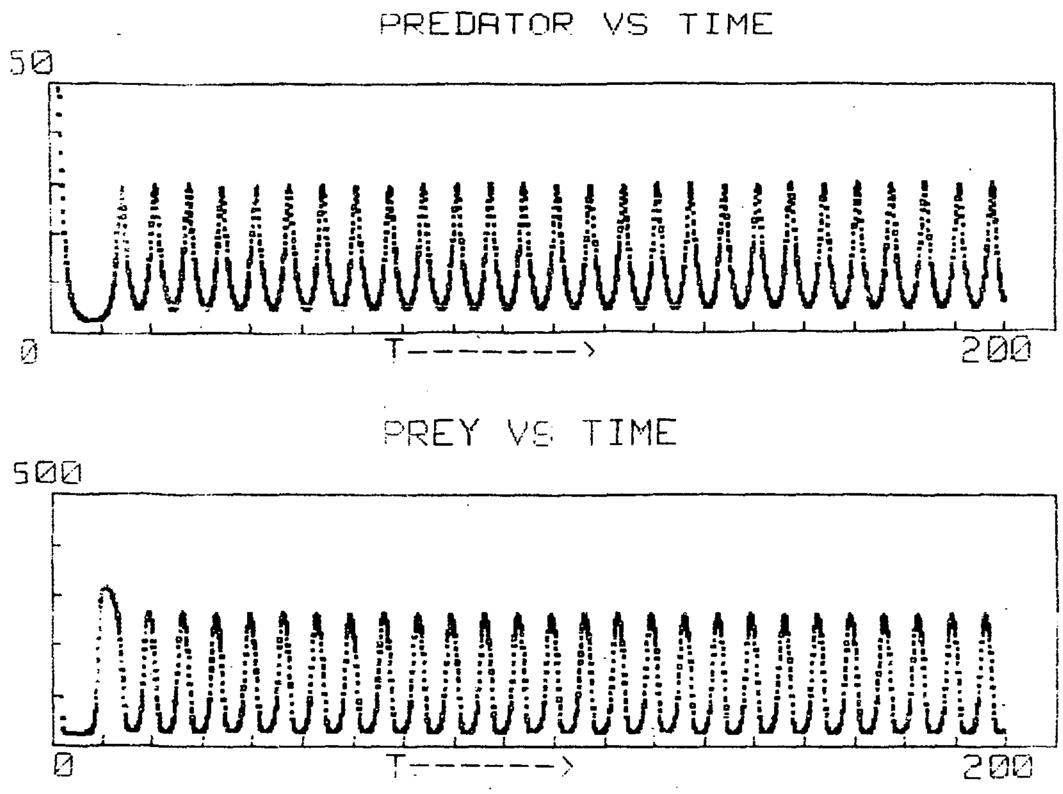


fig.2.9

CHAPTER - 3

GENERALISATION TO THREE SPECIES: AN APPROACH TO FIND THE LIMIT CYCLE SOLUTION TO ONE PREY-TWO PREDATOR ECOSYSTEM

In the previous chapter we have discussed about the limit cycle behaviour of a two species system. We shall now construct a new three species system with one prey and two predators. As will be seen, this model is a generalisation to three species of several two species systems described earlier.

Consider a prey of population size x and two predators of population sizes y and z respectively. Here we have treated two predators y and z similar in some respects and both of them prey on x. We have taken the interaction of the prey and predators and studied their behaviour in phase space. Then, in addition to the prey-predator interactions, we have included the competition between the predators.

The growth rate of the prey in the absence of predator is given by,

$$dx/dt = a_1 x - b_1 x^2$$

where, $b_1 = a_1/K$

K --> Carrying capacity or the maximum prey population allowed by the limited resources provided by the environment.

In the presence of the predators, mortality from predation must be substracted from the right side of equation (3.1). It is the product ofthe predation rate (the number killed per predator per unit time) and the number of predators. A detail study of different models [especially Holling (1965)] have shown that the predation rate increases with prey density. This type of functional response was shown by Holling to be characteristics of invertebrate predators, while that of vertebrate predators differs because they can learn to search for a particular prey that has become more abundant. Here we are taking the former case as the predator is assumed to have no alternative prey and therefore should be continuously searching for the prey. The functional response equation can be written as,

$$q_1 = c_1 x/(d_1 + x)$$

where, q_1 --> the predation rate.

In the above expression c_1 is the maximum value that q_1 can reach when the predator can not kill more prey even if latter is available to the former,and d_1 is a constant determining how fast the functional response increases at low densities of the prey.

Treating the second predator z in a similar way, the mortality from the second predator can be written as

$$q_2 = c\,x / (d_2 + x)$$

where, c, d_2 are positive constants having similar meaning as that of c_1 and d_1 respectively.

Thus, in the presence of two predators, the complete equation for the prey becomes,

$$dx/dt = a_1x - b_1x^2 - c_1xy/(d_1 + x) - cxz/(d_2 + x) \quad \text{-- (3.2)}$$

The growth ofthe predators, without taking the interaction between them, as in the Lotka-Volterra case can be written as,

$$dy/dt = - a_2y + c_2xy/(d_1 + x) \quad \text{--- (3.3)}$$

$$dz/dt = - a_3z + c_3xz/(d_2 + x) \quad \text{--- (3.4)}$$

Where, a_2 and a_3 are the net growth (decay) rates for the predators y and z respectively. The predators dwindle to nothing in the absence of prey, since the reproduction is then impossible. This is why negative sign is taken in the first term in equation (3.3) & (3.4).

Now taking the competition between two predators, the equations (3.3) & (3.4) have to be modified.

Thus, the complete dynamics of this one prey-two predator system is given by the following sets of equations,

$$dx/dt = a_1x - b_1x^2 - c_1xy/(d_1 + x) - cxz/(d_2 + x) \quad \text{--- (3.5)}$$

$$dy/dt = - a_2y + c_2xy/(d_1 + x) - k_1yz \quad \text{--- (3.6)}$$

$$dz/dt = -a_3z + c_3xz/(d_2 + x) - k_2yz \quad \text{--- (3.7)}$$

Here, k_1 and k_2 are the competition coefficients arise because of the competition between two predators,

and, a_1, b_1, c_1, d_1, d_2, c, a_2, c_2, k_1, a_3, c_3, $k_2 > 0$

To study, the behaviour of one prey-two predator system in phase space and hence to study their variation with time:

In a two species system given by,

$$\begin{aligned} dx/dt &= a_1 x - b_1x^2 - c_1xy/(d_1 + x) \\ dy/dt &= -a_2 y + c_2xy/(d_2 + x) \end{aligned} \quad \text{--- (3.8)}$$

the condition for the existence of stable equilibrium point, with the application of Kolmogorov theorem (appendix - I) and Routh-Hurwitz criteria (appendix - II) becomes,

$$2b_1[a_2 d_2 / (c_2 - a_2)] + b_1 d_1 - a_1 > 0 \quad \text{--- (3.9)}$$

and $$d_2 > 0 \quad \text{--- (3.10)}$$

Since condition (3.10) is satisfied always, the choice of parameters which violate the inequality of equation (3.9) lead to solutions with stable limit cycles. As there is no such theorem like Kolmogorov theorem to check the stability of the system we have taken the parameters for the three species same as that of two species and the remaining perameters are chosen by trial and error method which satisfy the limit cycle condition.

As is well known, it is not possible to write down the exact analytical solution for the type of three species system discussed above. But we can study the behaviour of the system-whether or not these systems are capable of possessing stable equilibrium or stable limit cycle. We are interested in limit cycle solutions. For this, we have taken recourse to approximation schemes and numerical methods. For numerical analysis, we have used Runge-Kutta approximation method.

The main results of our model are systematised in Table-3.1 The specimen results of it are plotted in figures 3.1 to 3.42. In drawing phase-space figures, we have reduced the three dimensional phase space into 2 two - dimensional ones - by taking projections of the trajectory of the system on XY-plane and XZ-plane. We see from the figures that with respect to time, the sizes of all the three populations oscillate perpetually with amplitude and periods that soon tend to a limit that is independent of their intial sizes and depends only on the constants of the system - thus our system of three species exhibit limit cycle in phase space.

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 (2.1). With the introduction of a second predator, it becomes a three species system. 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. Keeping the constants for 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 exhibit limit cycle solutions. Then we found out the range of the parameters of the three species system within which the system still exhibits limit cycle solutions. This is achieved by changing one parameter at a time. Furthermore, we have taken different initial population sizes of the species and ensured that they lead to the same final result for the chosen set of parameters for the system.This shows that we have the proper limit cycle solutions .

One prey-Two predator system :

Table 3.1

Numerical inputs for different parameters -

$a_1 = 3.0$	$a_2 = 1.0$
$b_1 = 0.1$	$c_2 = 3.0$
$c_1 = 30$	$a_3 = 1.0$
$c = 25$	$c_3 = 3.0$
$d_1 = 100$	$k_1 = 0.012$
$d_2 = 100$	$k_2 = 0.01$

For finding the range of parametric values, we have varied the numerical value of some of the parameters one at a time.

Table 3.2 gives in detail (i) the minimum and maximum value of different parameters,(ii) the initial conditions, (iii) number of corresponding figures and (iv) the behaviour of the three species system in phase-space.

TABLE - 3.2

Value of Parameters	Initial Condition	No. of Corresponding figures	Behaviour in Phase space
CASE - A : WITHOUT CONSIDERING THE INTERACTION BETWEEN PREDATORS			
case 1 :			
$a_1 = 3, a_2 = 1$			
$c_1 = 30,\ c = 25$	$x = 40$		
$d_1 = 100, c_2 = 3$	$y = 25$	3.1 & 3.2	Limit Cycle
$d_2 = 100, c_3 = 3$	$z = 25$		
$a_2 = 1 = a_3$			
case 2 :			
Remaining parameters			
the same as	$x = 40$		
case 1 except	$y = 25$	3.3 & 3.4	Limit Cycle
$a_1 = 4$	$z = 25$		
case 3 :			
Remaining parameters			
the same as	$x = 40$		
case 1 except	$y = 25$	3.5 & 3.6	Limit Cycle
$a_1 = 2.9$	$z = 25$		

case 4 :			
Remaining Parameters			
the same as	$x = 70$		
case 1 except	$y = 40$	3.7 & 3.8	Limit Cycle
$a_1 = 4$	$z = 40$		
case 5 :			
Remaining Parameters			
the same as	$x = 40$		
case 1 except	$y = 30$	3.9 & 3.10	Limit Cycle
$a_1 = 3$	$z = 30$		
case 6 :			
Remaining parameters			
the same as	$x = 40$		
case 1 except	$y = 20$	3.11 & 3.12	Stable
$b_1 = 0.013$	$z = 20$		Equilibrium
case 7 :			
Remaining parameters			
the same as	$x = 40$		
case 1 except	$y = 25$	3.13 & 3.14	Limit Cycle
$b_1 = 0.008$	$z = 25$		
case 8 :			
Remaining Parameters			
the same as	$x = 40$		
case 1 except	$y = 25$	3.15 & 3.16	Limit Cycle
$c_1 = 50$	$z = 25$		

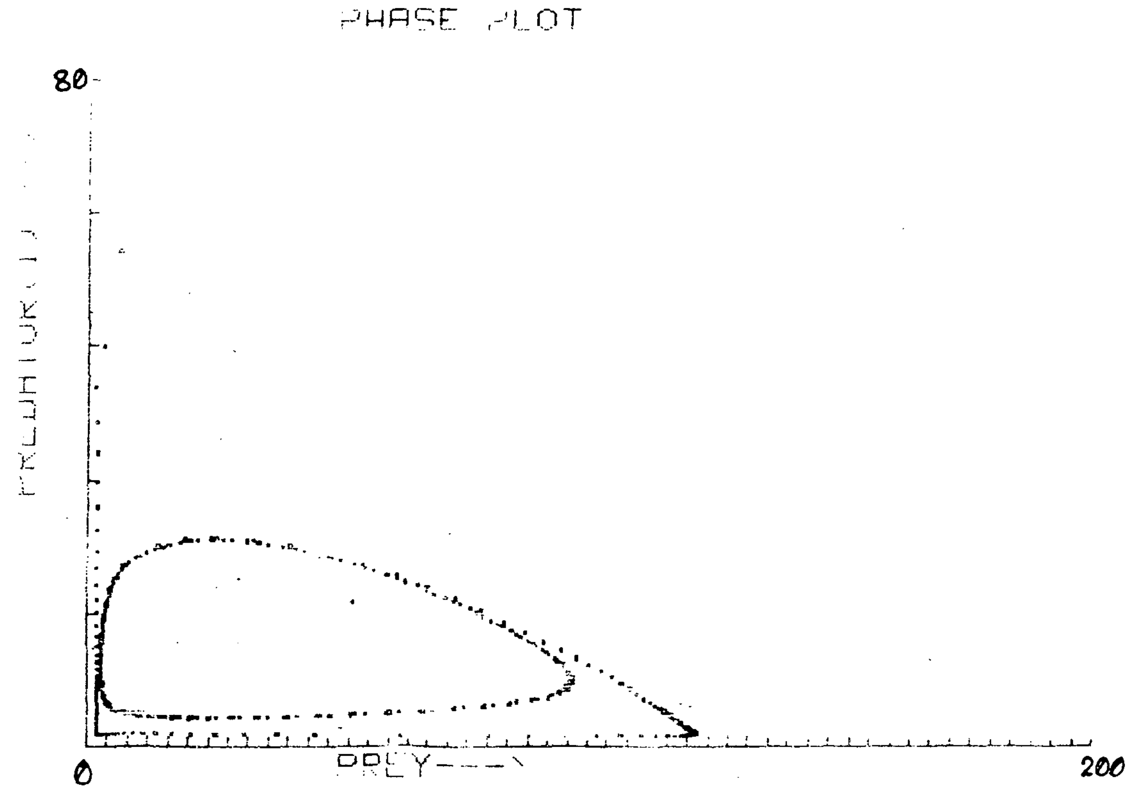
case 9 :			
Remaining Parameters			
the same as	$x = 80$		
case 1 except	$y = 30$	3.17 & 3.18	Limit Cycle
$c_1 = 18$	$z = 30$		
case 10 :			
Remaining Parameters			
the same as	$x = 40$		
case 1 except	$y = 25$	3.19 & 3.20	Limit Cycle
$b_1 = 0.01$	$z = 25$		
case 11 :			
Remaining Parameters			
the same as	$x = 70$		
case 1 except	$y = 50$	3.21 & 3.22	Limit Cycle
$c_1 =20$	$z = 50$		
case 12 :			
Remaining Parameters			
the same as	$x = 30$		
case 1 except	$y = 20$	3.23 & 3.24	Limit Cycle
$b_1 = 0.012$	$z = 20$		
case 13 :			
Remaining Parameters			
the same as	$x = 45$		
case 12 except	$y = 20$	3.25 & 3.26	Limit Cycle
$c = 18$	$z = 20$		

case 14			
Remaining Parameters			
the same as	x = 45		
case 1 except	y = 20	3.27 & 3.28	Limit Cycle
c = 18 & b_i =0.01	z = 20		
case 15			
Remaining Parameters			
the same as	x = 80		
case 1 except	y = 30	3.29 & 3.30	Limit Cycle
c = 37	z = 30		
case 16			
Remaining Parameters			
the same as	x = 80		
case 1 except	y = 30	3.31 & 3.32	Stable
c = 18	z = 30		Equilibrium

CASE B : WITH THE INCLUSION OF COMPETITION BETWEEN THE PREDATORS

case 17			
Remaining Parameters			
the same as	x = 40		
case 16 except	y = 20		
k_1 = 0.01,	z = 20	3.33 & 3.34	Stable
k_2 = 0.016			Equilibrium

case 18 :			
Remaining Parameters			
the same as	$x = 45$		
case 1 except	$y = 20$	3.35 & 3.36	Stable
$c=18$, $c_2 = 3$	$z = 20$		Equilibrium
$c_3 = 3.1, k_1 = .01$			
$k_2 = 0.016$			
case 19 :			
Remaining parameters			
the same as	$x = 80$		
case 1 except	$y = 30$	3.37 & 3.38	Limit Cycle
$c = 18$, $k_1 = .012$	$z = 30$		
$k_2 = 0.009$			
case 20 :			
Remaining Parameters			
the same as	$x = 45$		
case 1 except	$y = 20$	3.39 & 3.40	Limit Cycle
$k_1 = 0.01$,	$z = 20$		
$k_2 = 0.016$			
case 21 :			
Remaining Parameters			
same as case	$x = 80$		
case 20 except	$y = 30$	3.41 & 3.42	Stable
$k_2 = 0.014$,	$z = 30$		Equilibrium
$d_1 = 105$			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80
PREDATOR(1)
PREY--->
0
200

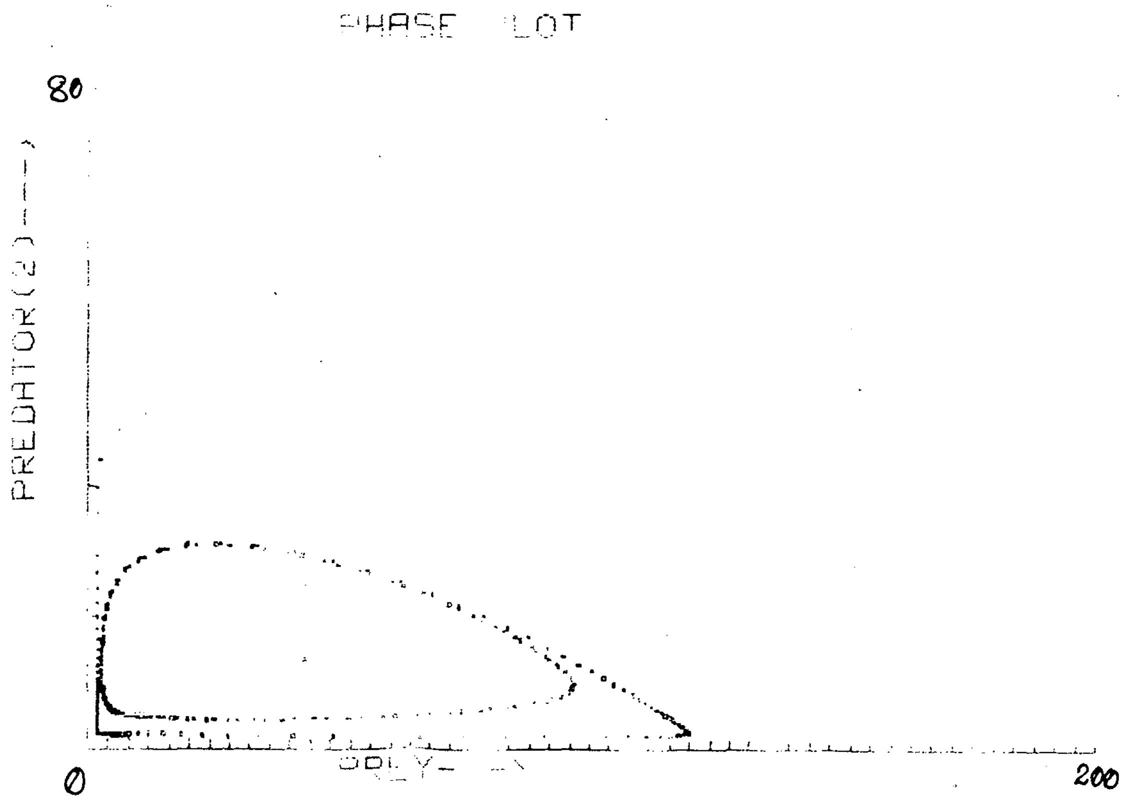

PHASE PLOT
80
PREDATOR(2)--->
PREY--->
0
200

fig.3.1

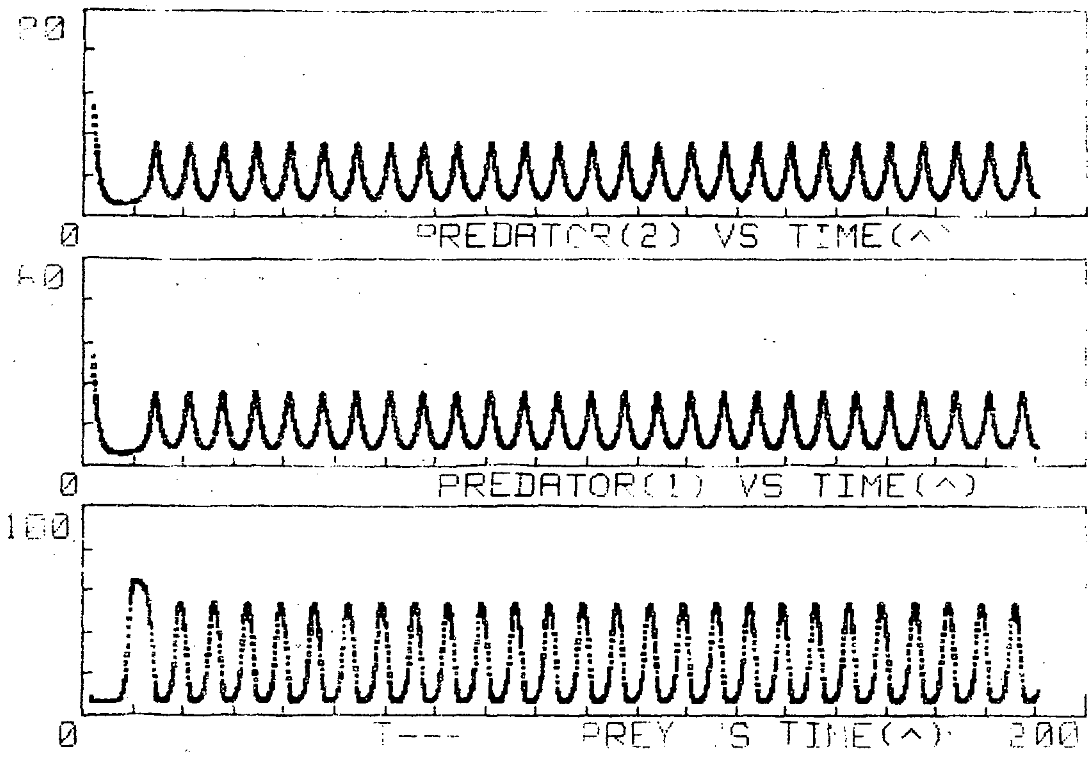
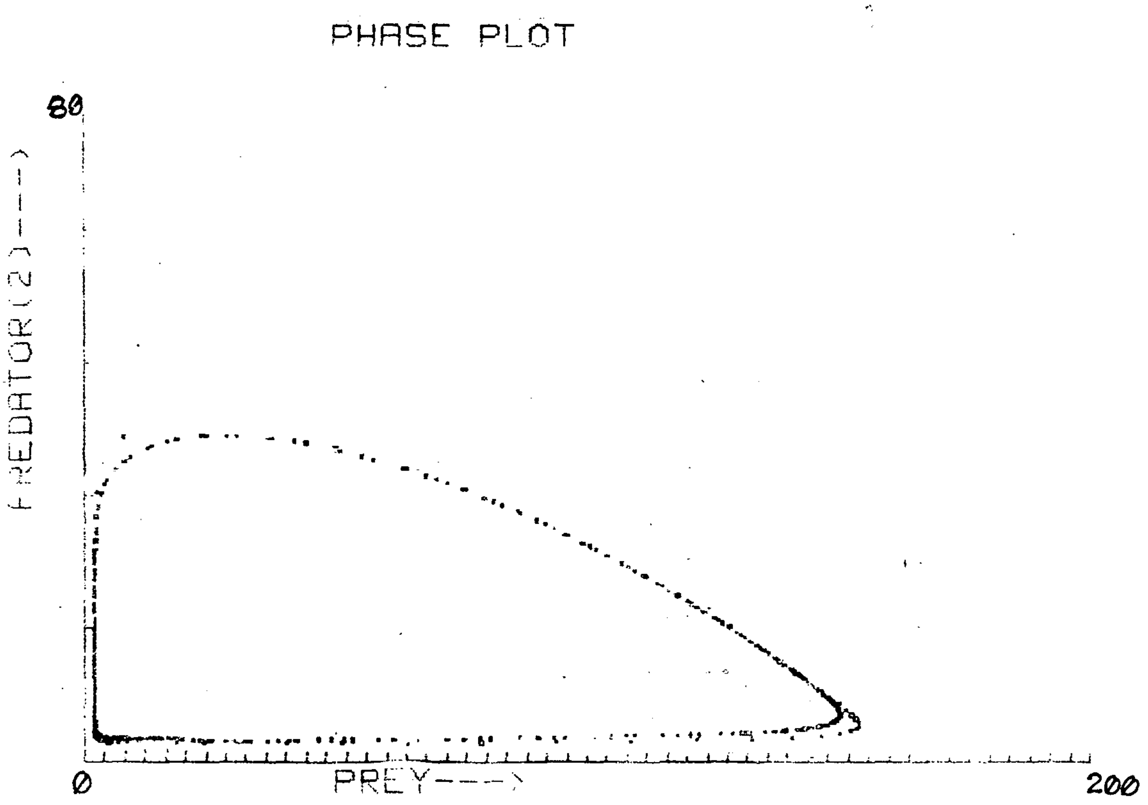

80
0
PREDATOR(2) VS TIME(^)
60
0
PREDATOR(1) VS TIME(^)
100
0
T---
PREY VS TIME(^)
200

fig.3.2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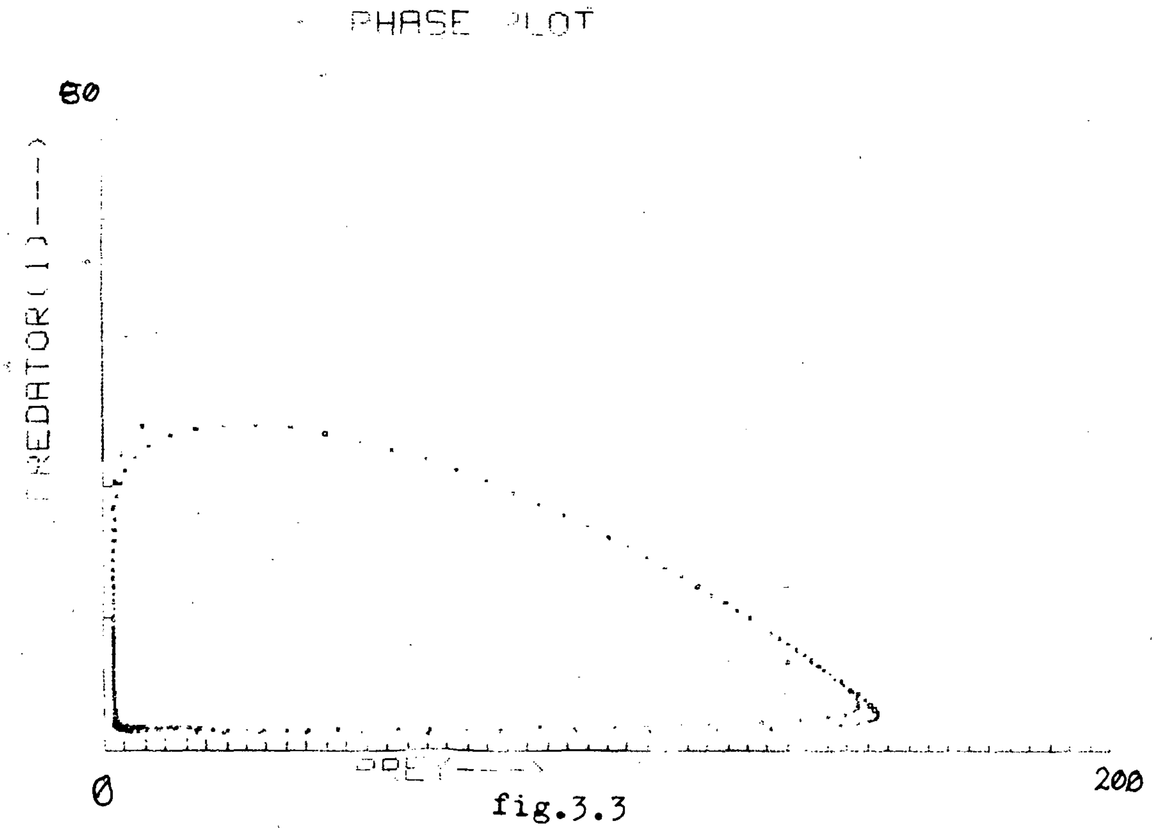
PREDATOR(2)--->
0
PREY--->
200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50
PREDATOR(1)--->
0
200

fig.3.3

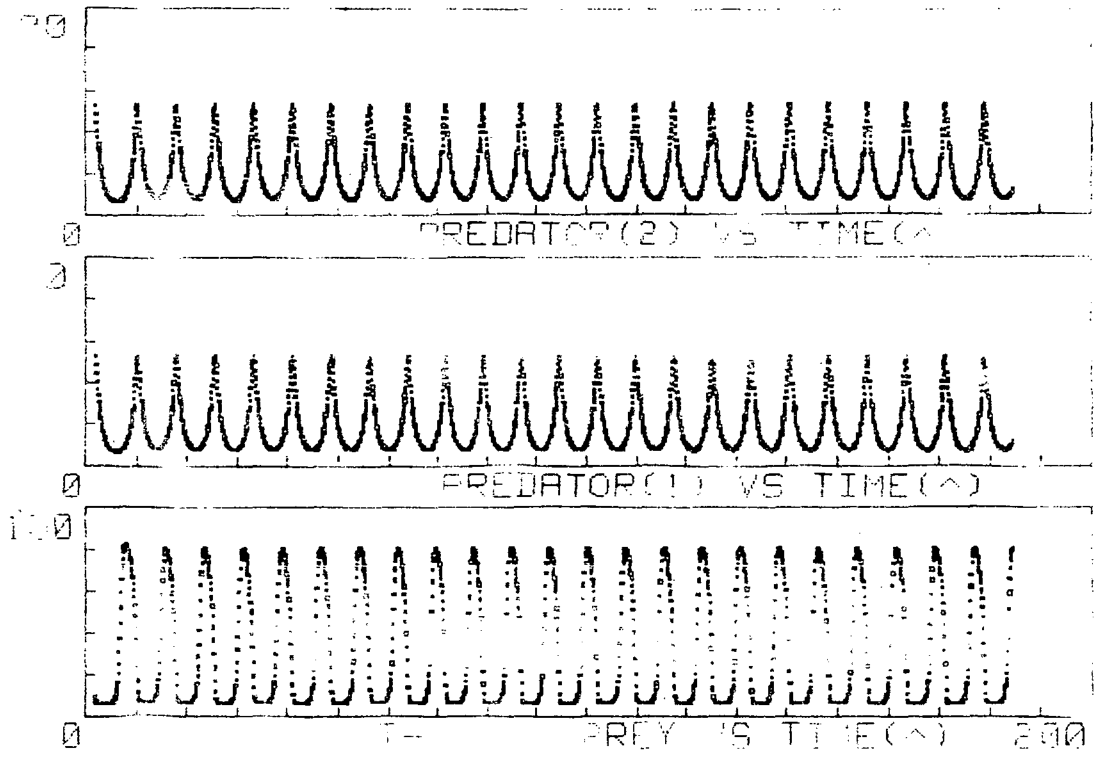
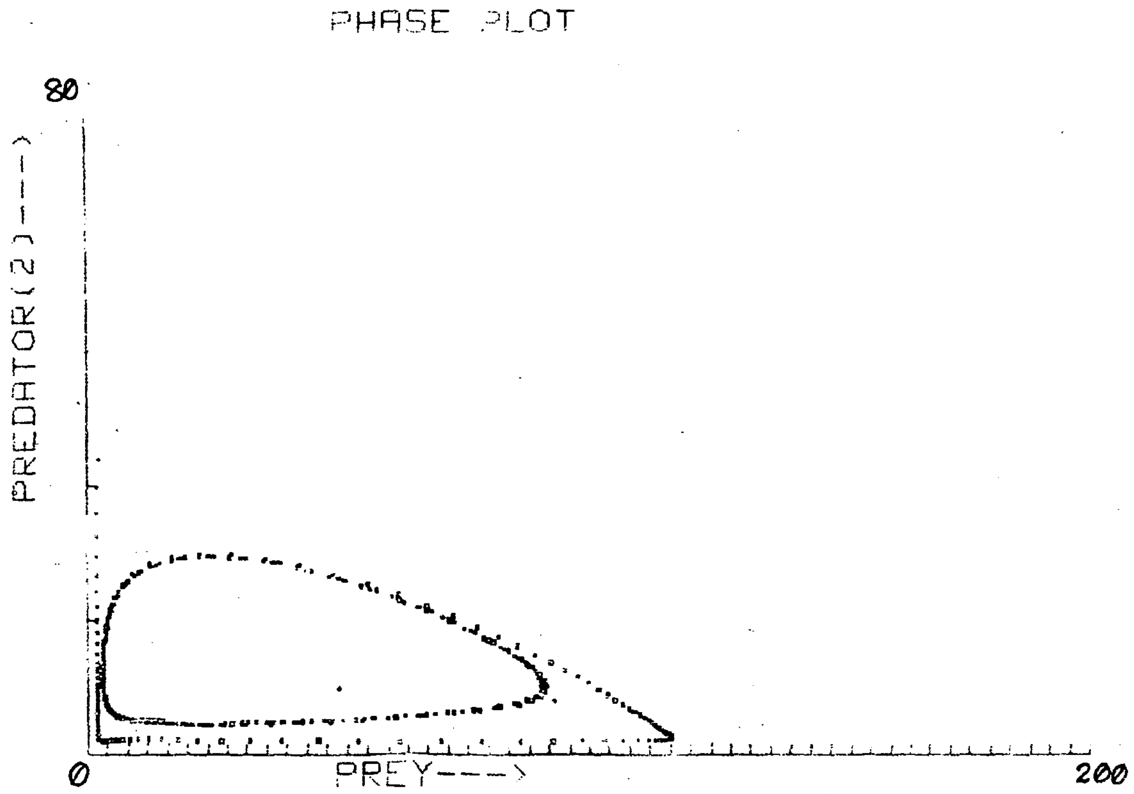
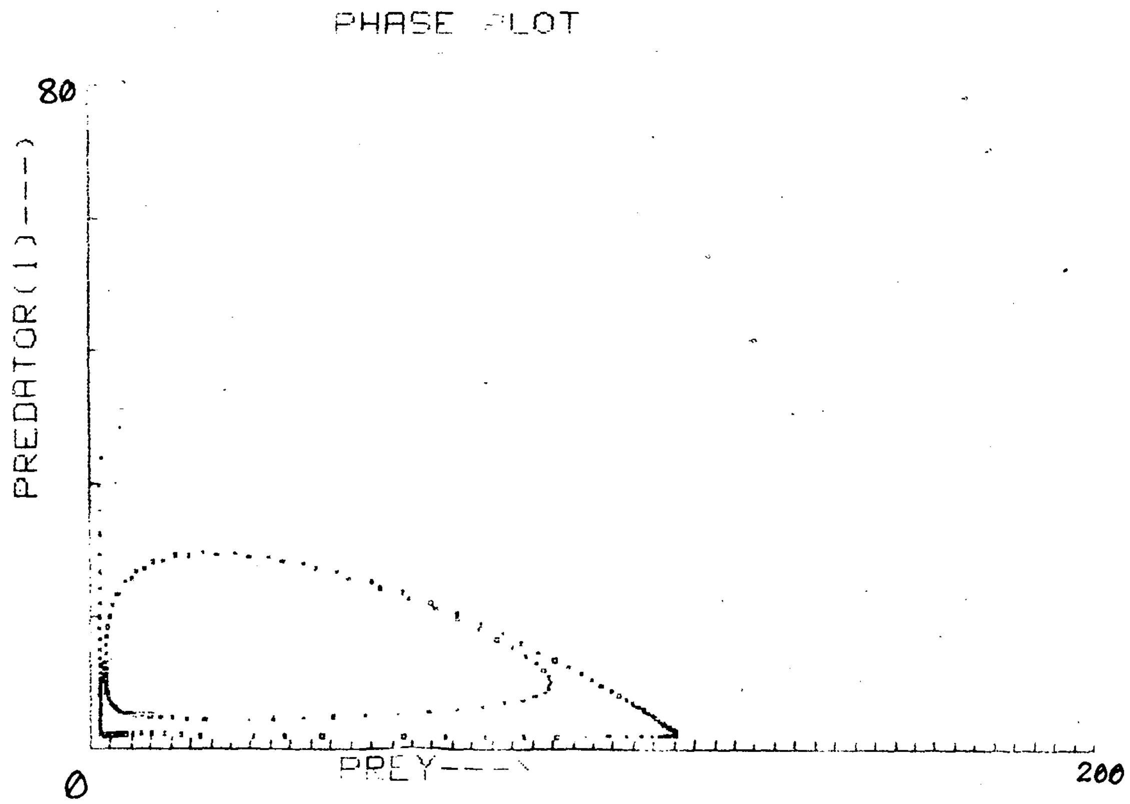


fig.3.4


PHASE PLOT
80
PREDATOR(2)--->
0
PREY--->
200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PREDATOR(1)--->
0
PREY--->
200

fig.3.5

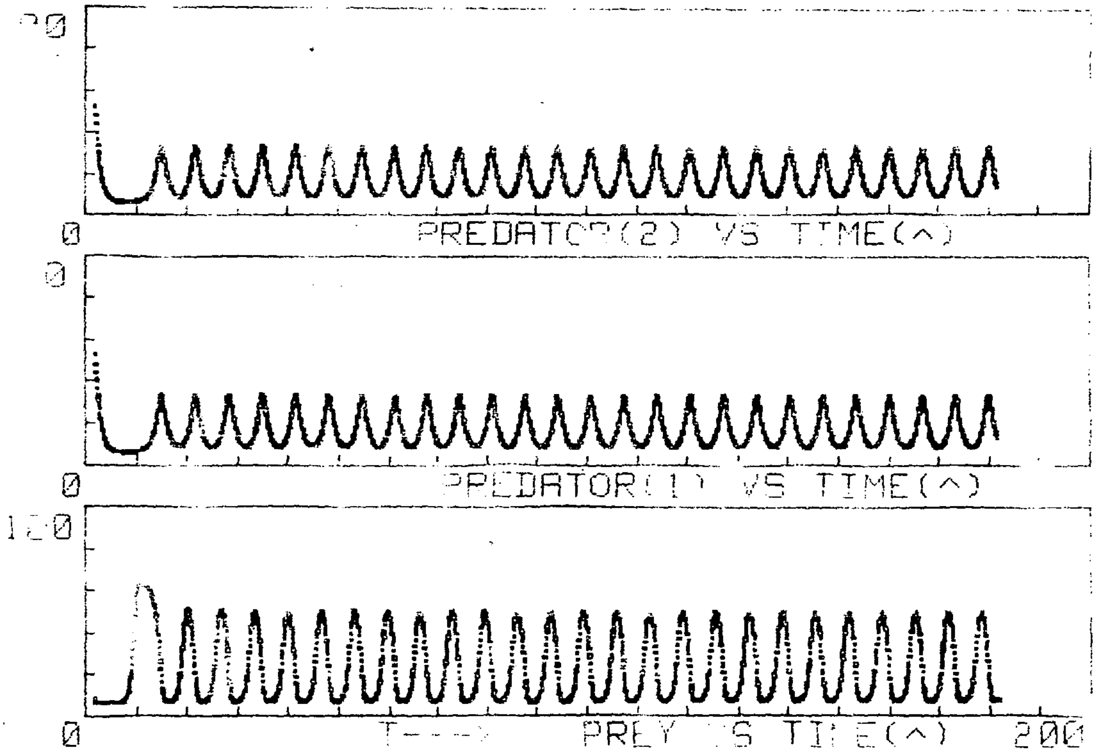
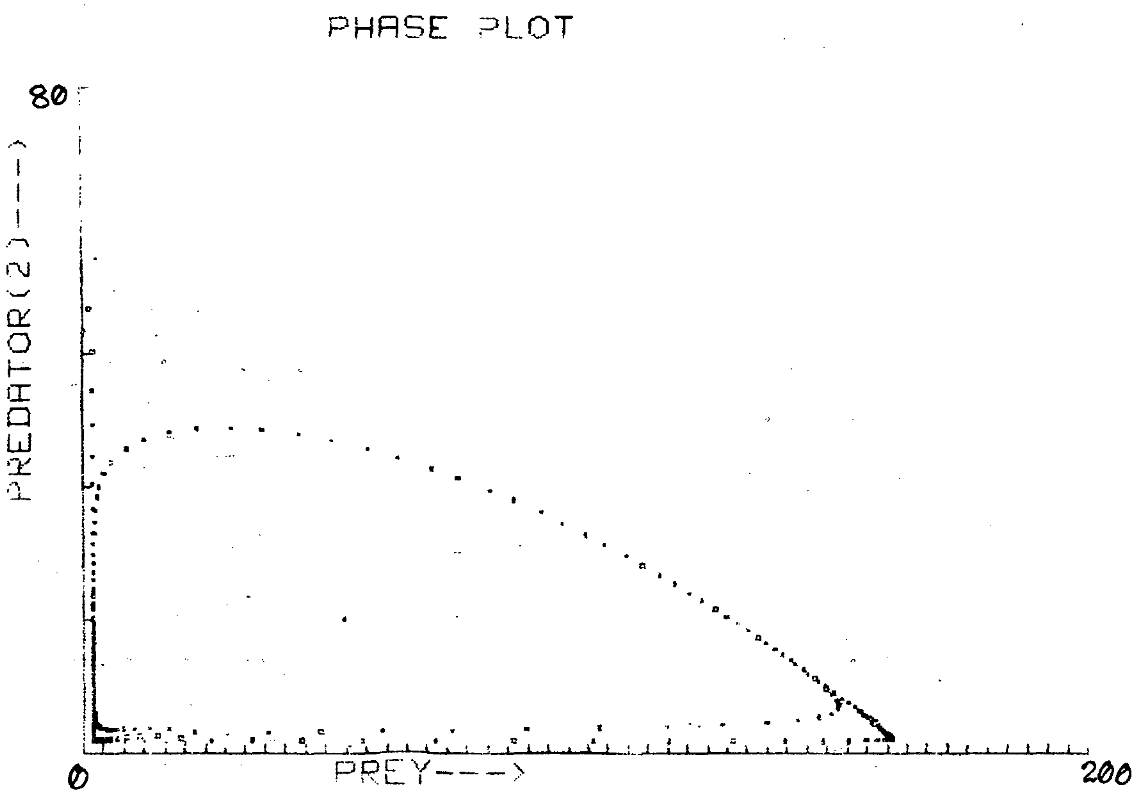


fig.3.6


PHASE PLOT
80
PREDATOR(2)--->
0
PREY--->
200

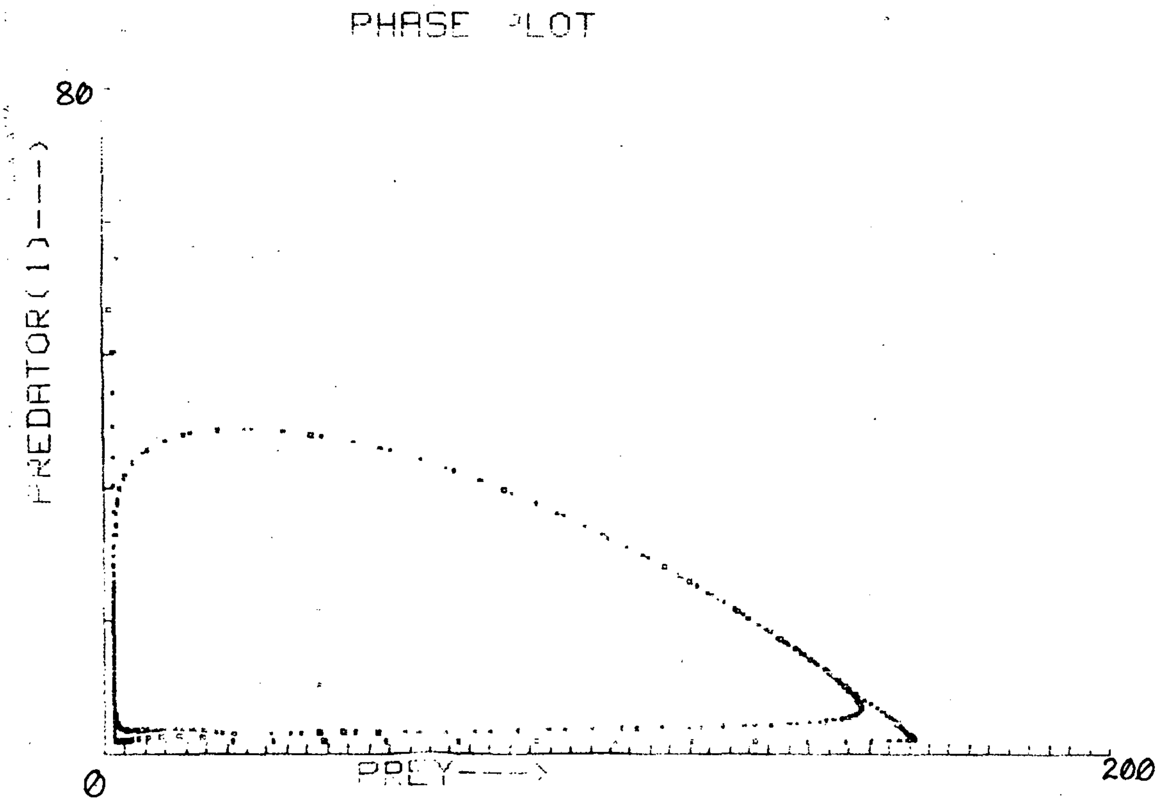

PHASE PLOT
80
PREDATOR(1)--->
0
PREY--->
200

fig.3.7

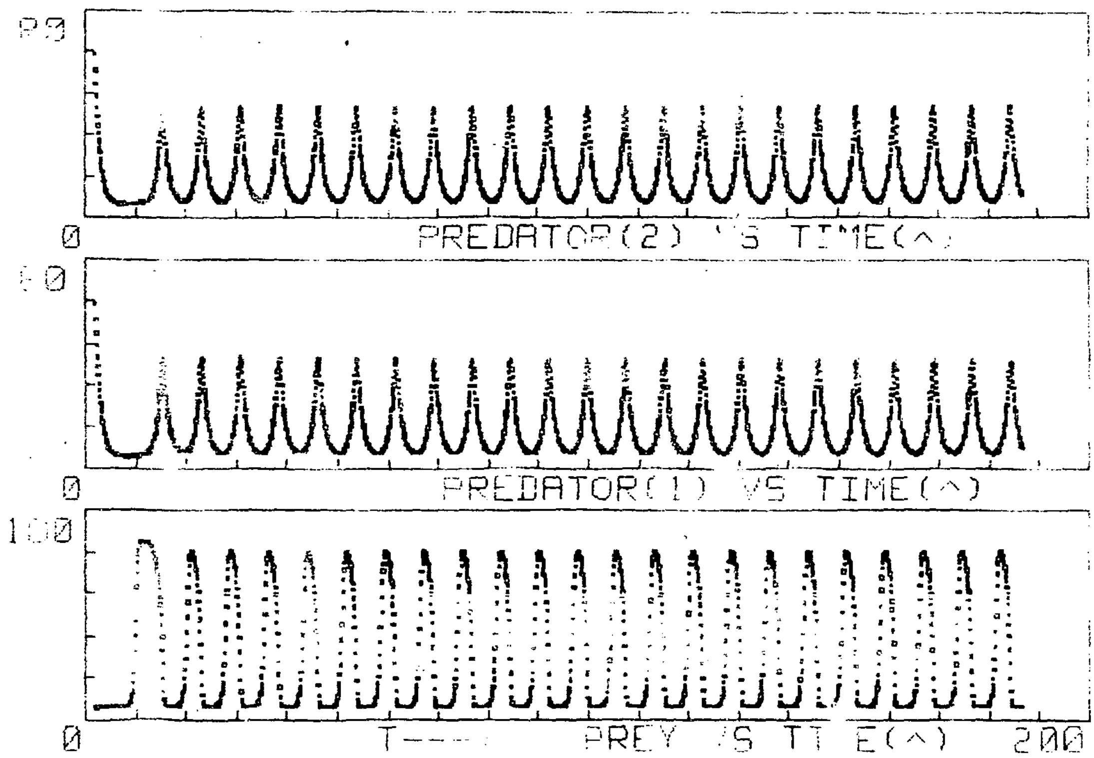
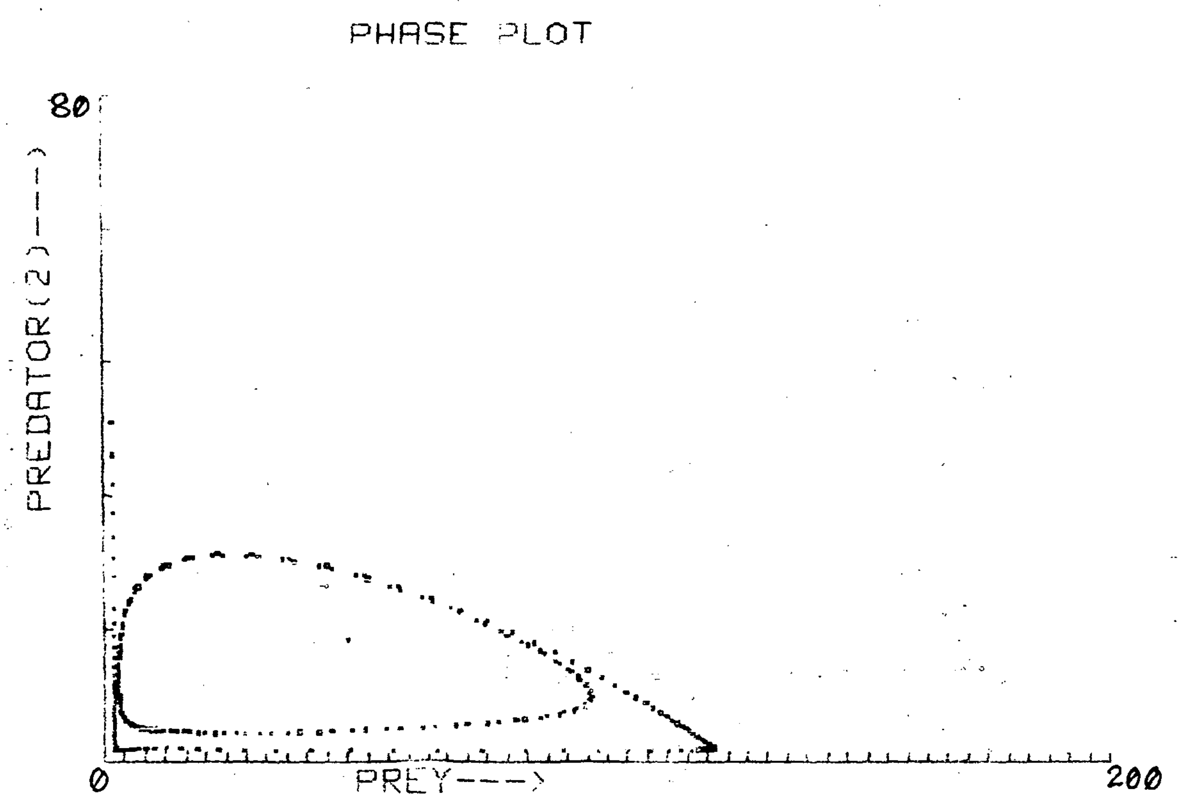
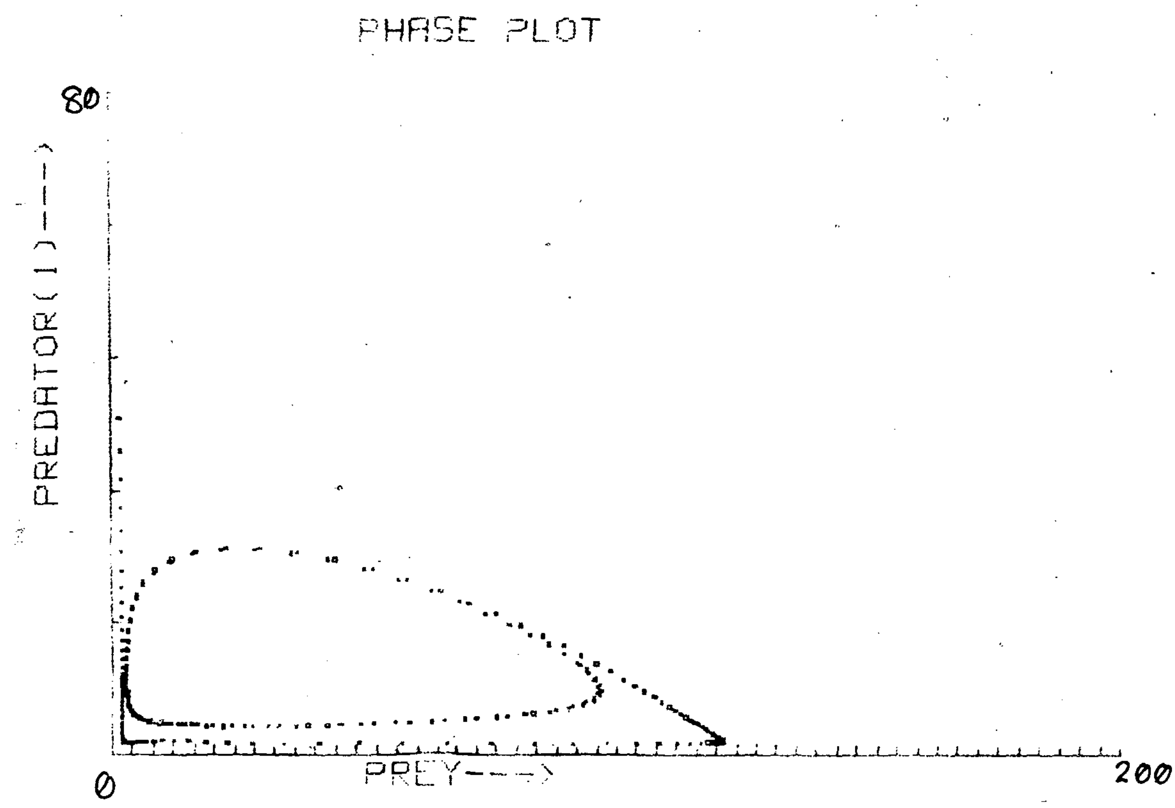


fig.3.8


PHASE PLOT
80
PREDATOR(2)--->
0
PREY--->
200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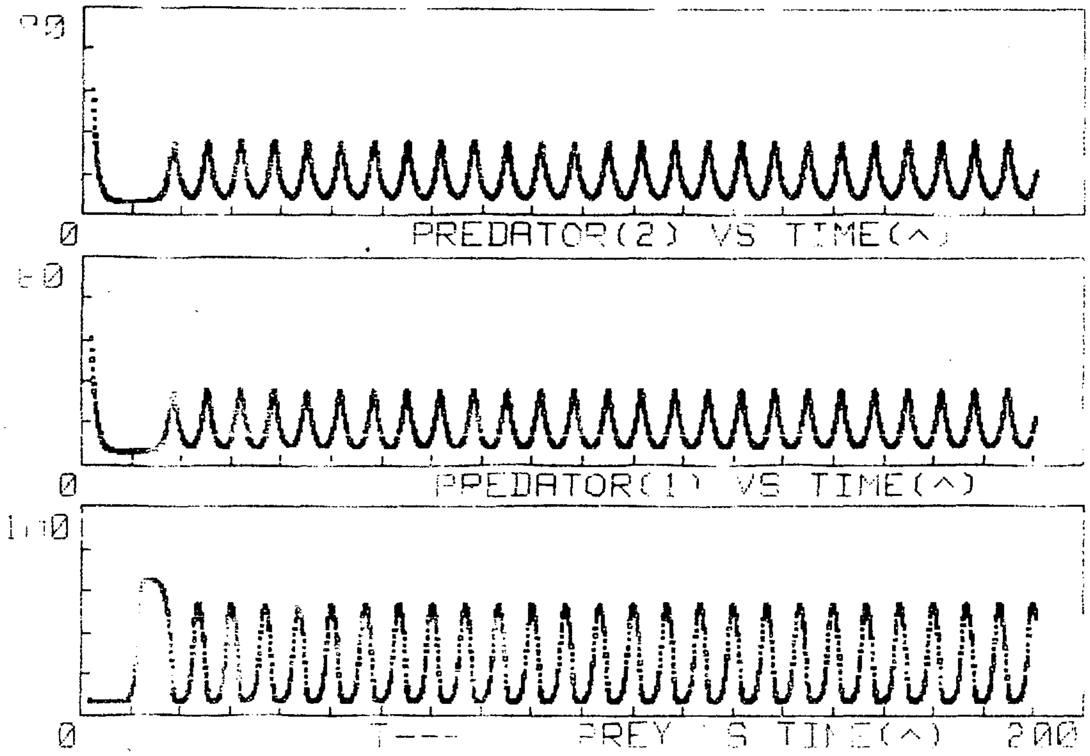
80
PREDATOR(1)--->
0
PREY--->
200

fig.3.9



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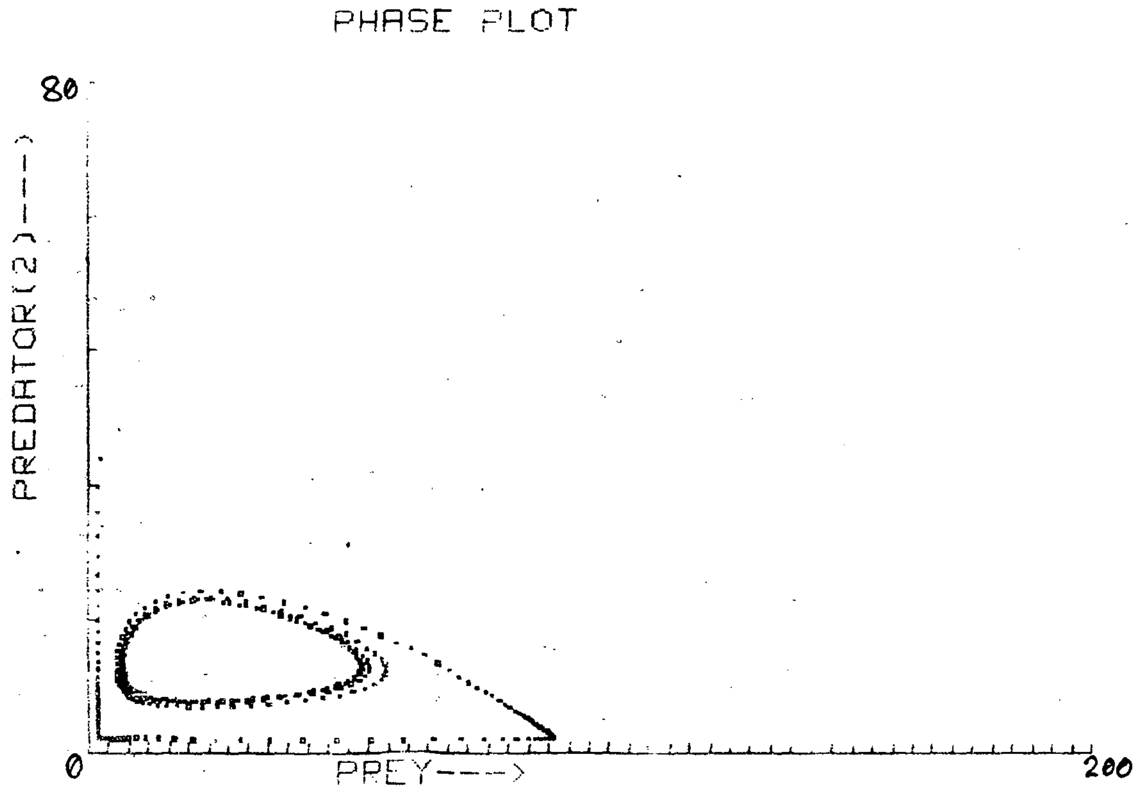
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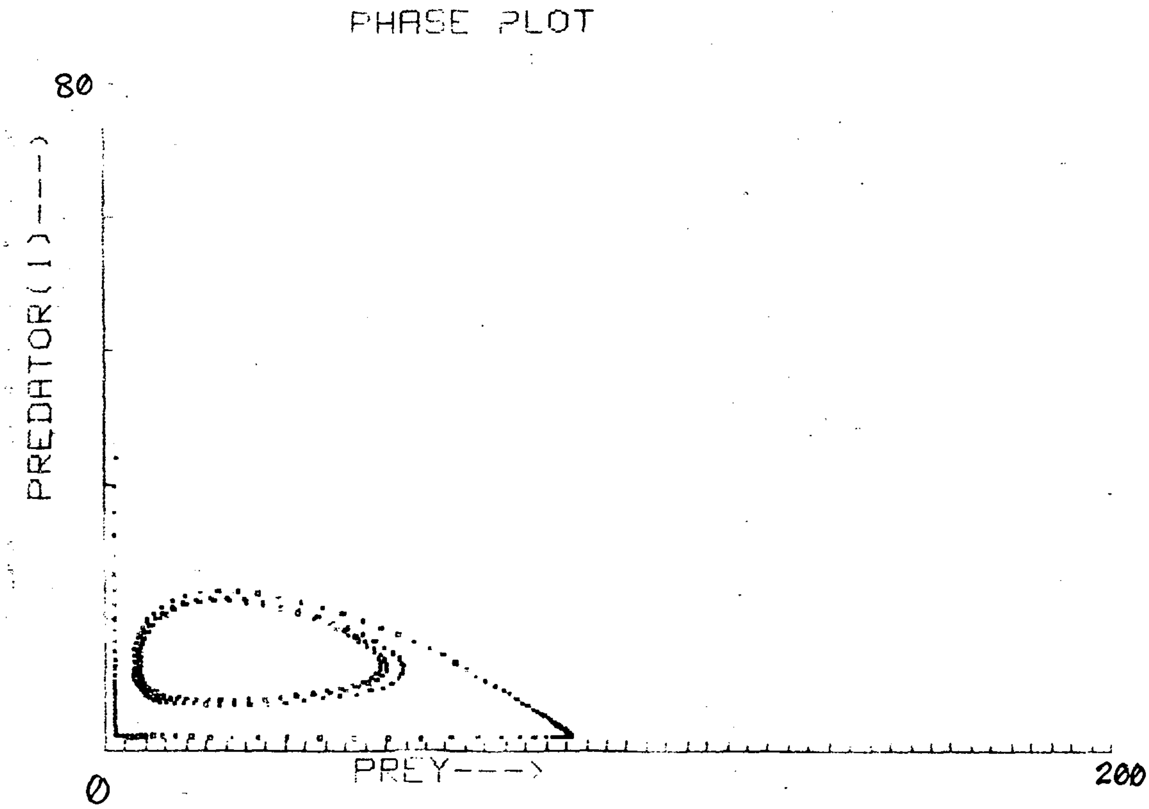
80
PREDATOR(2)---->
0
PREY--->
200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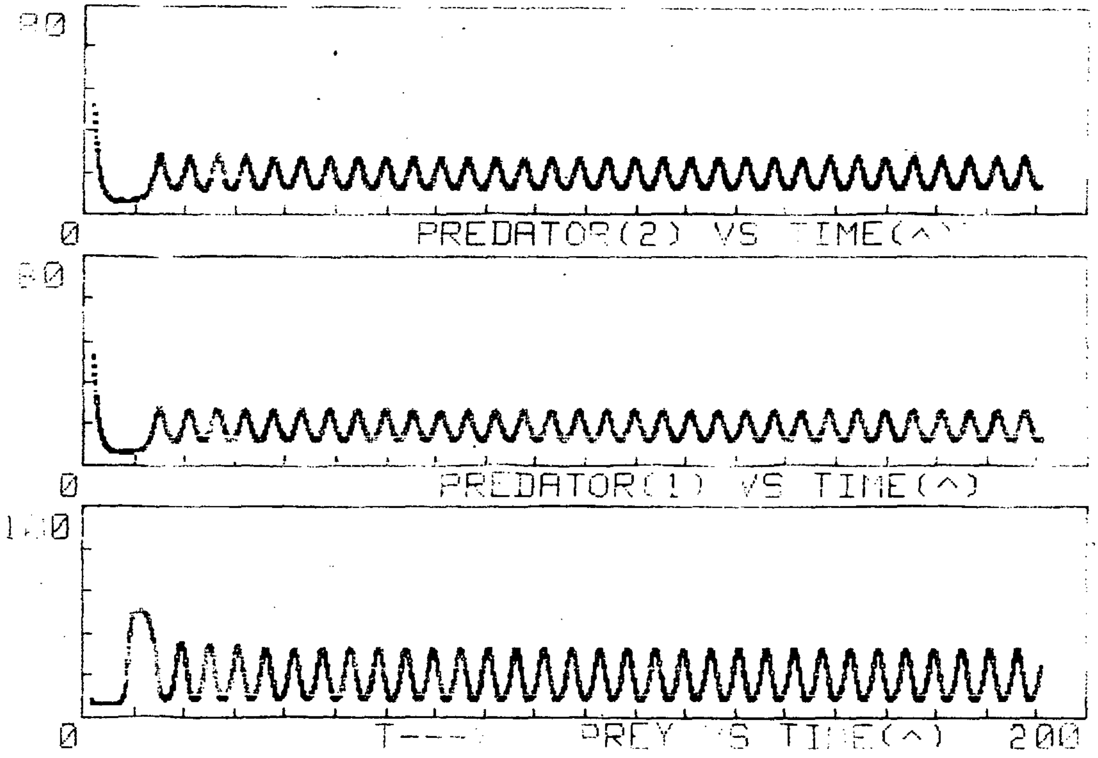
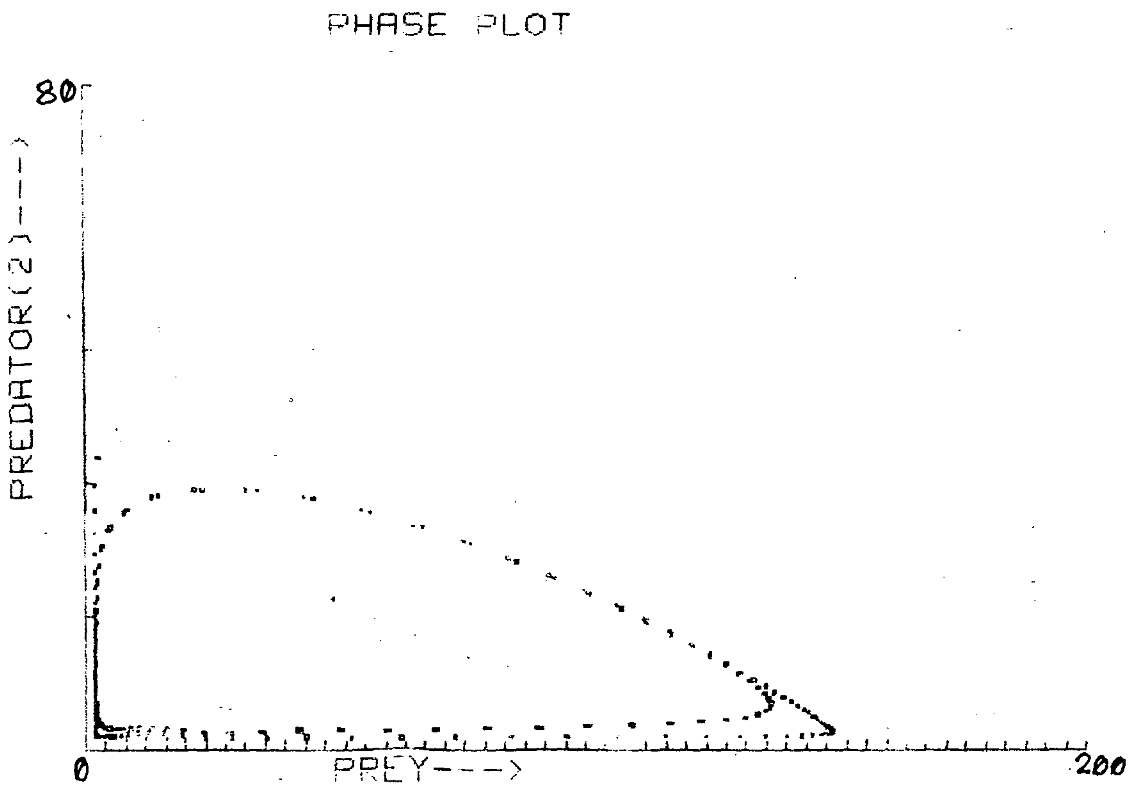
80
PREDATOR(1)---->
0
PREY--->
200

fig.3.11



80
0
PREDATOR(2) VS TIME(^)
80
0
PREDATOR(1) VS TIME(^)
100
0
T---
PREY VS TIME(^)
200

fig.3.12


PHASE PLOT
80
PREDATOR(2)--->
0
PREY--->
200

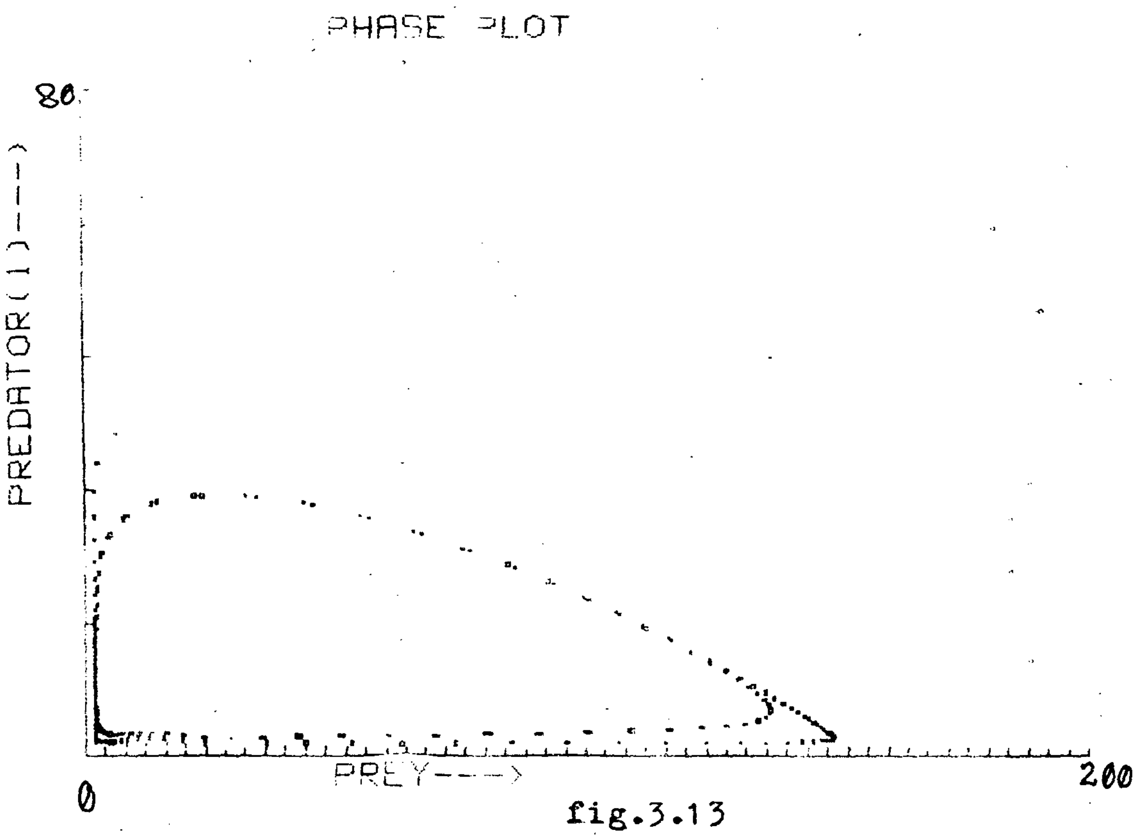

PHASE PLOT
80
PREDATOR(1)--->
0
PREY--->
200

fig.3.13

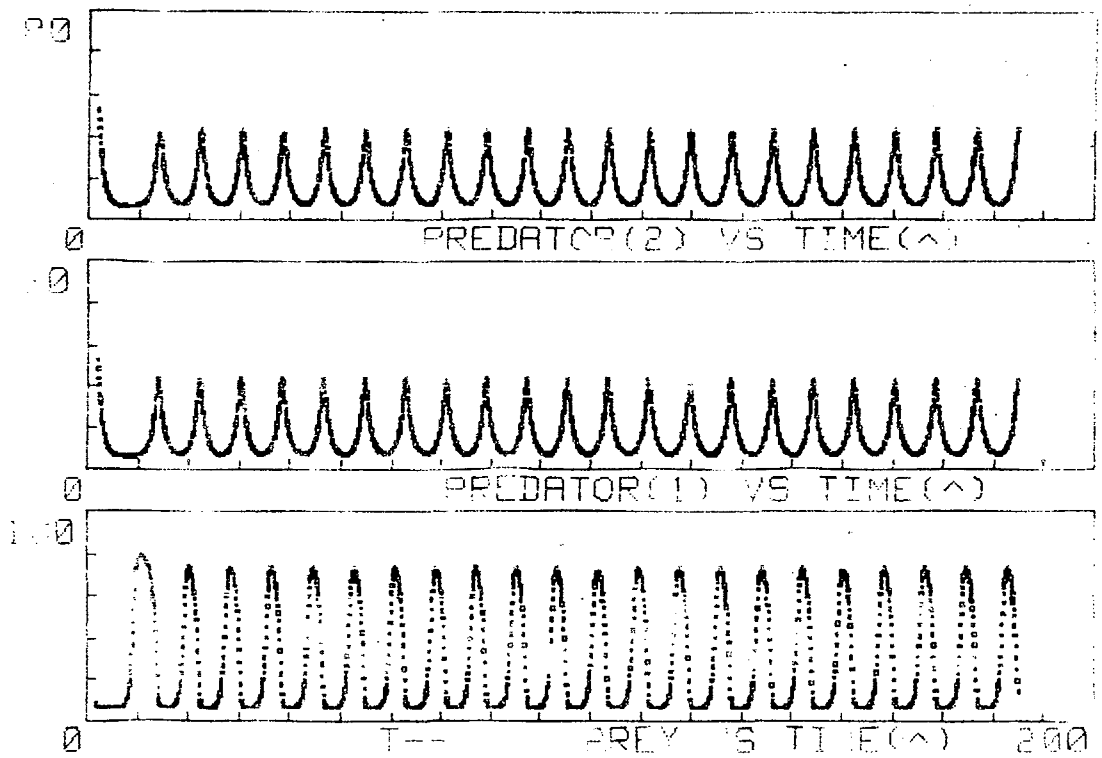
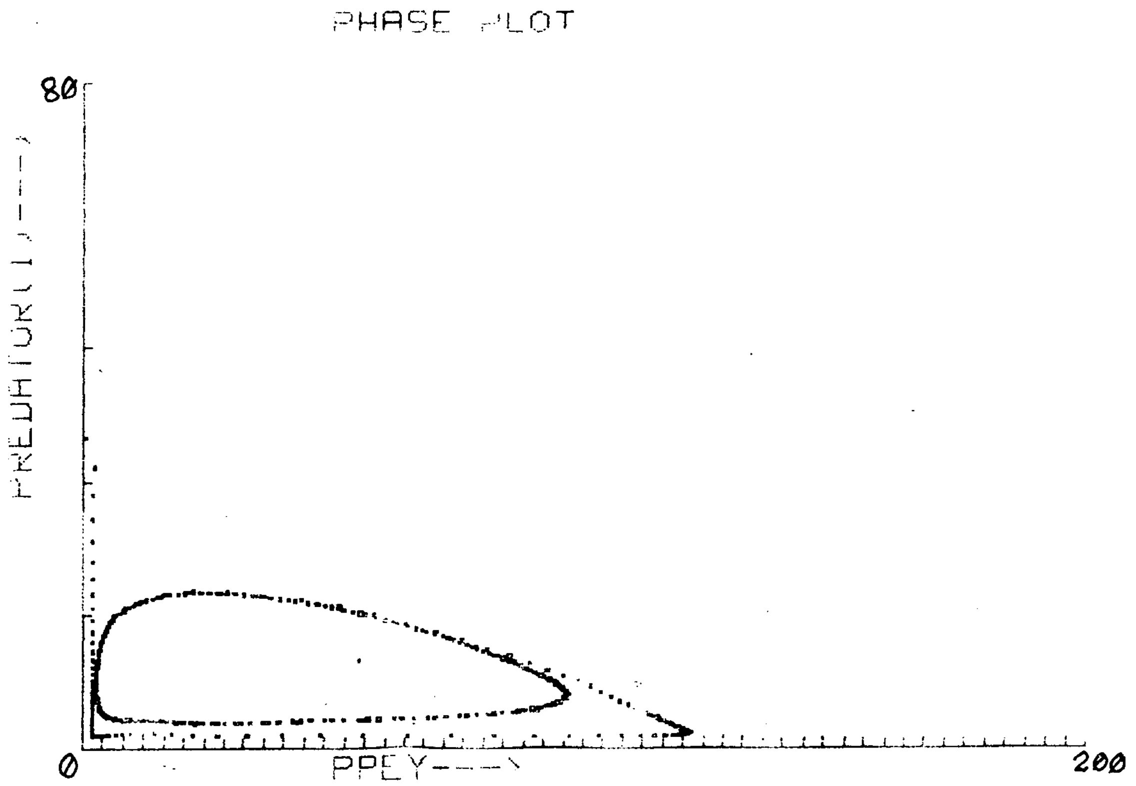
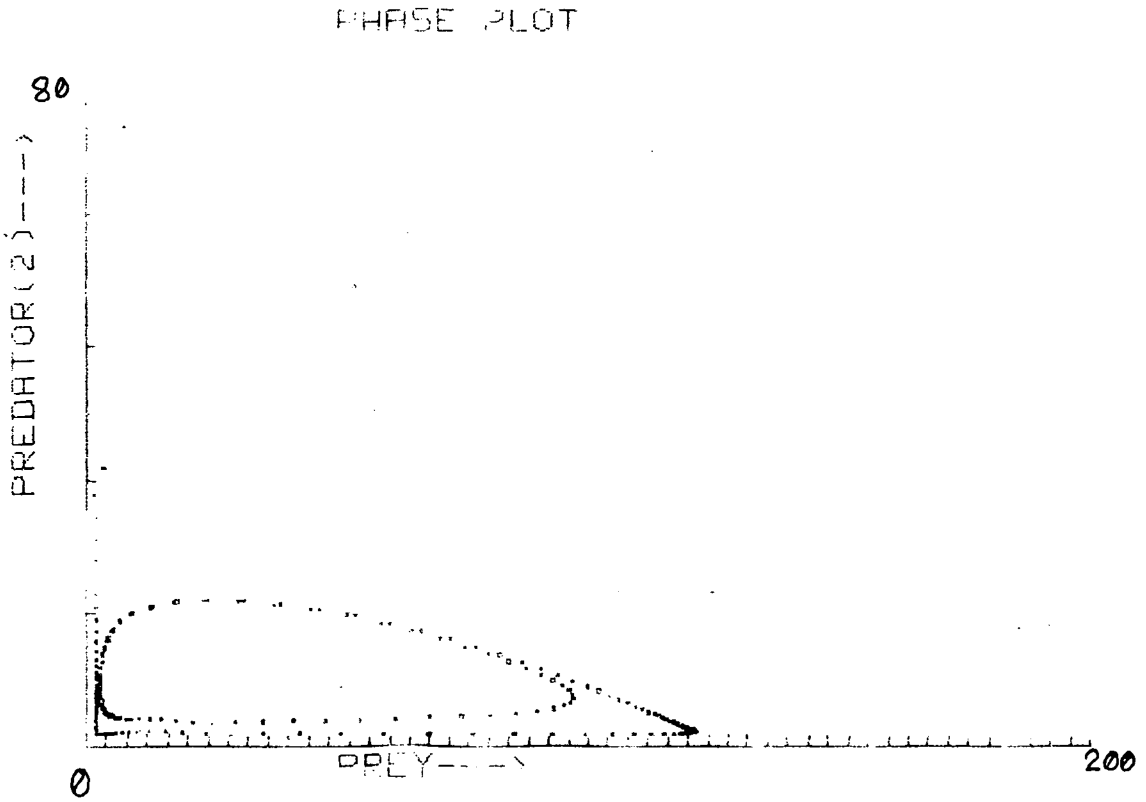


fig.3.14


PHASE PLOT
80
PREDATOR(1)--->
0
PREY--->
200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80
PREDATOR(2)--->
0
PREY--->
200

fig.3.15

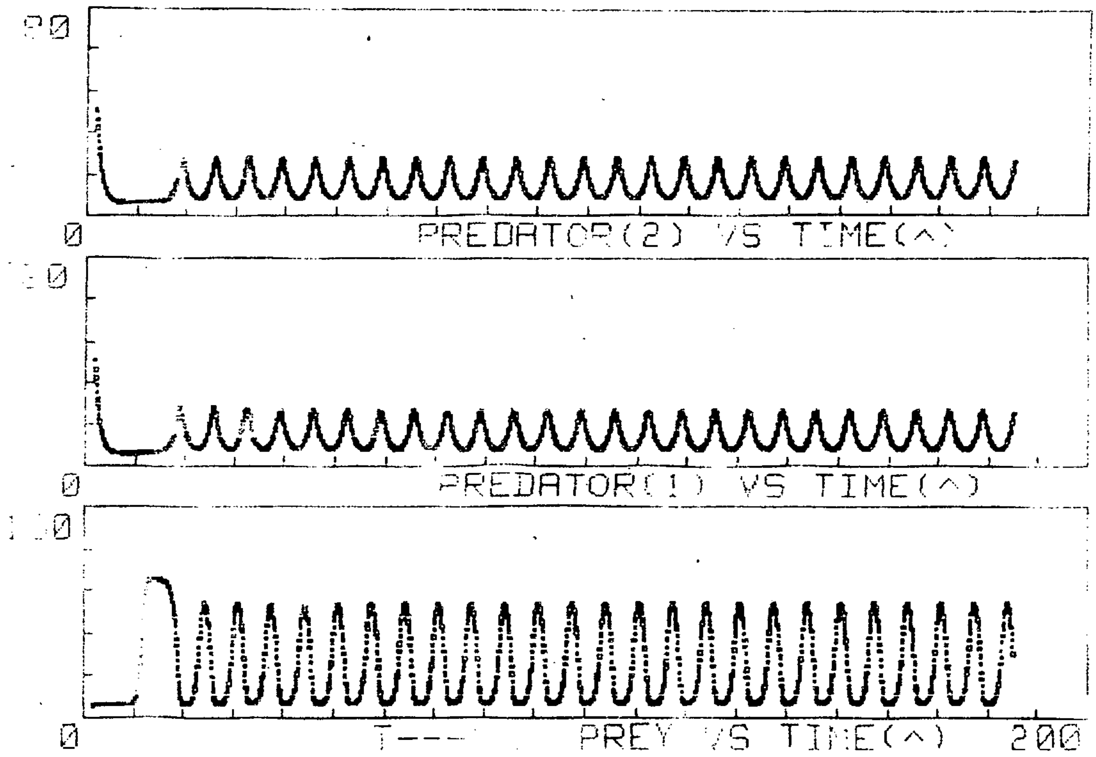
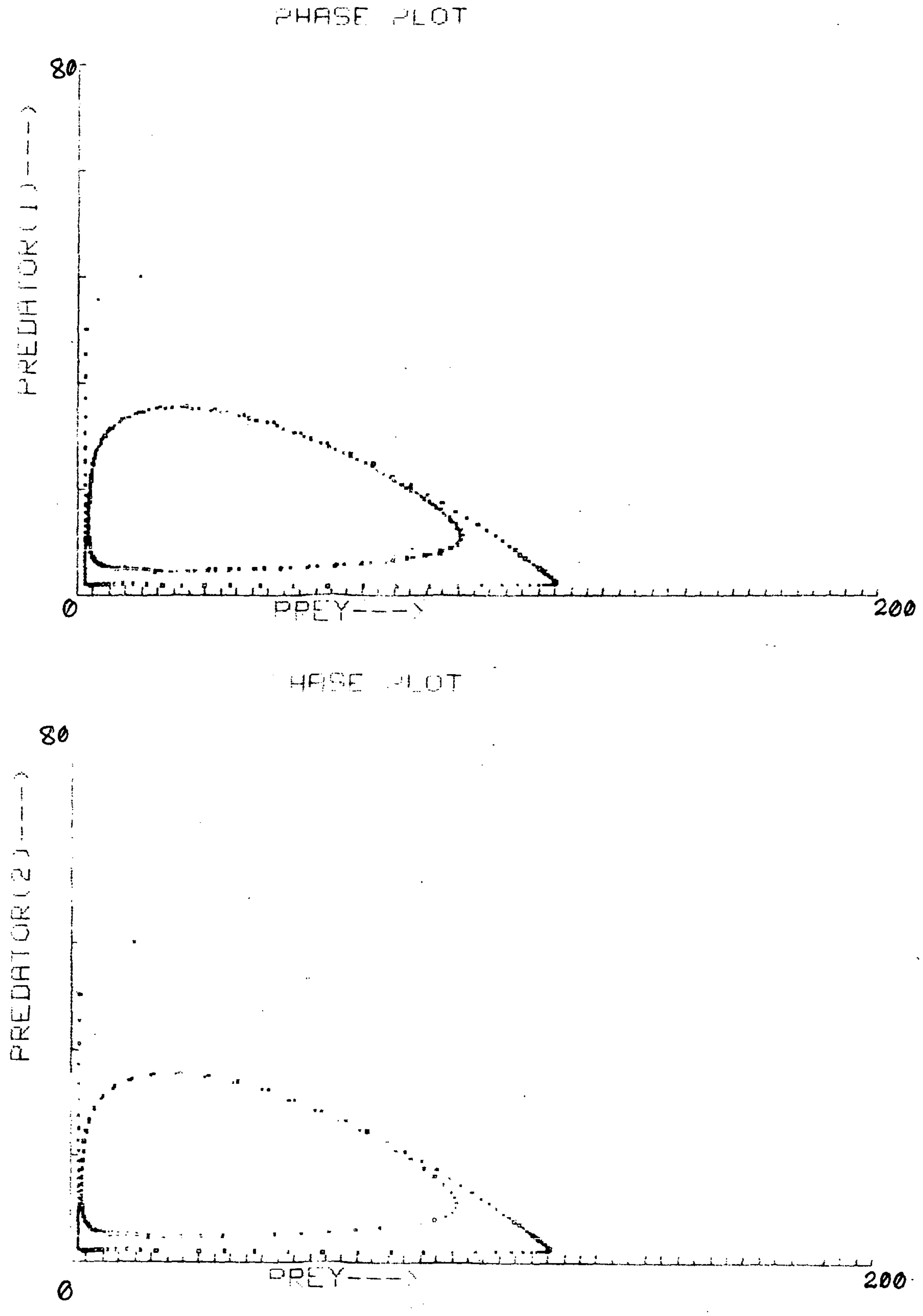


fig.3.16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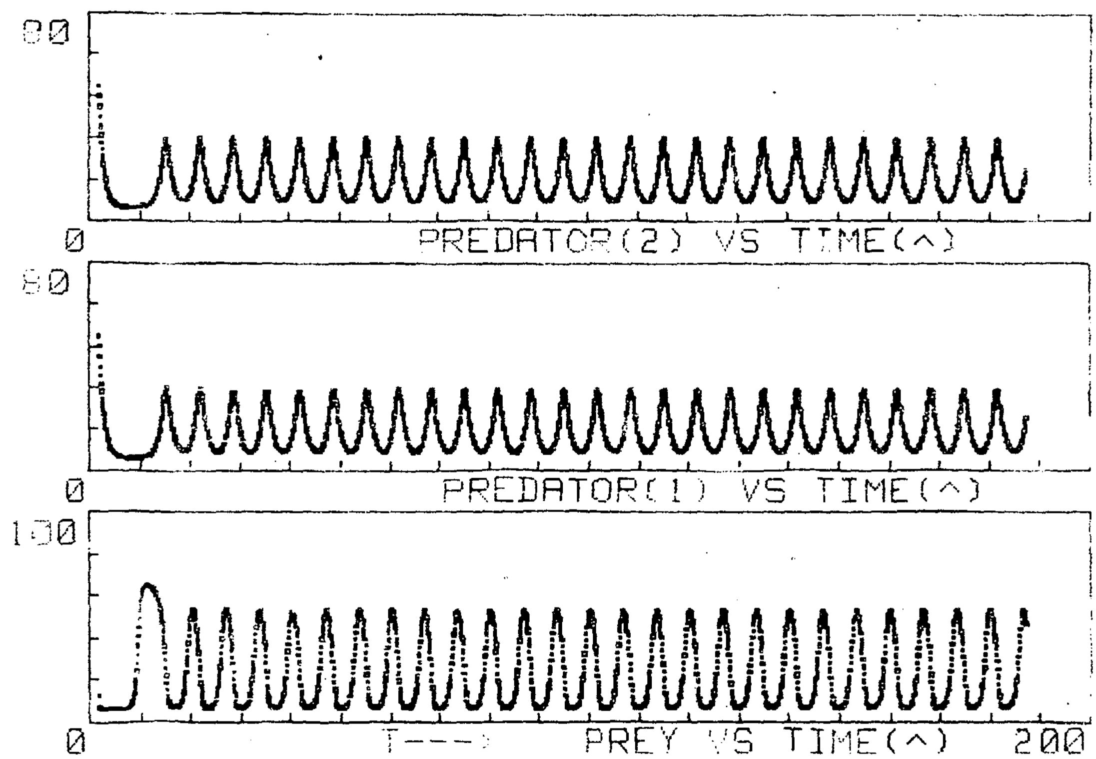
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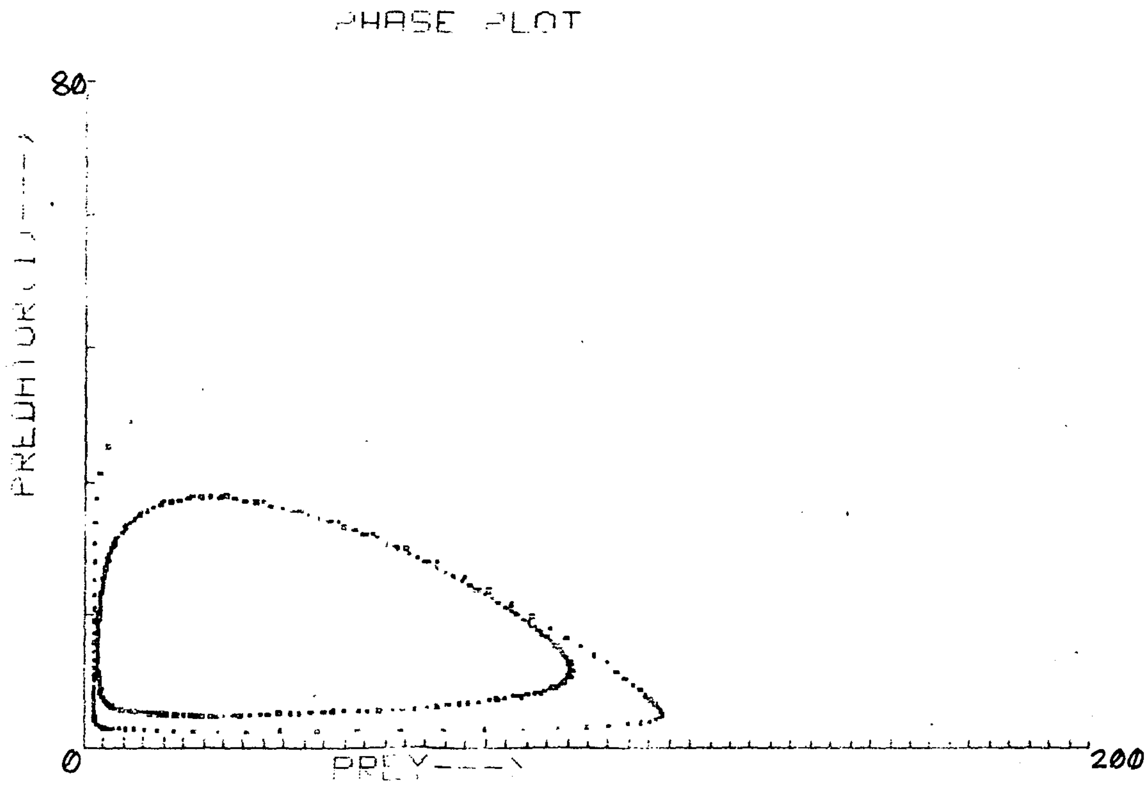
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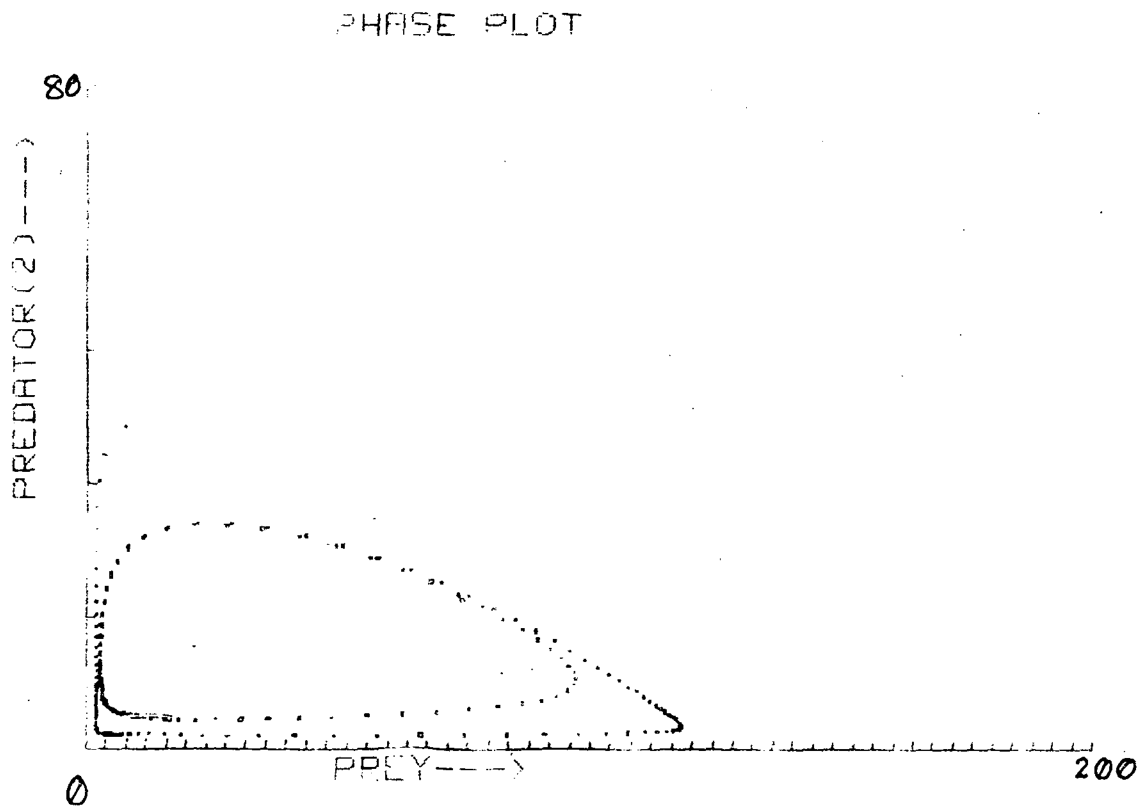
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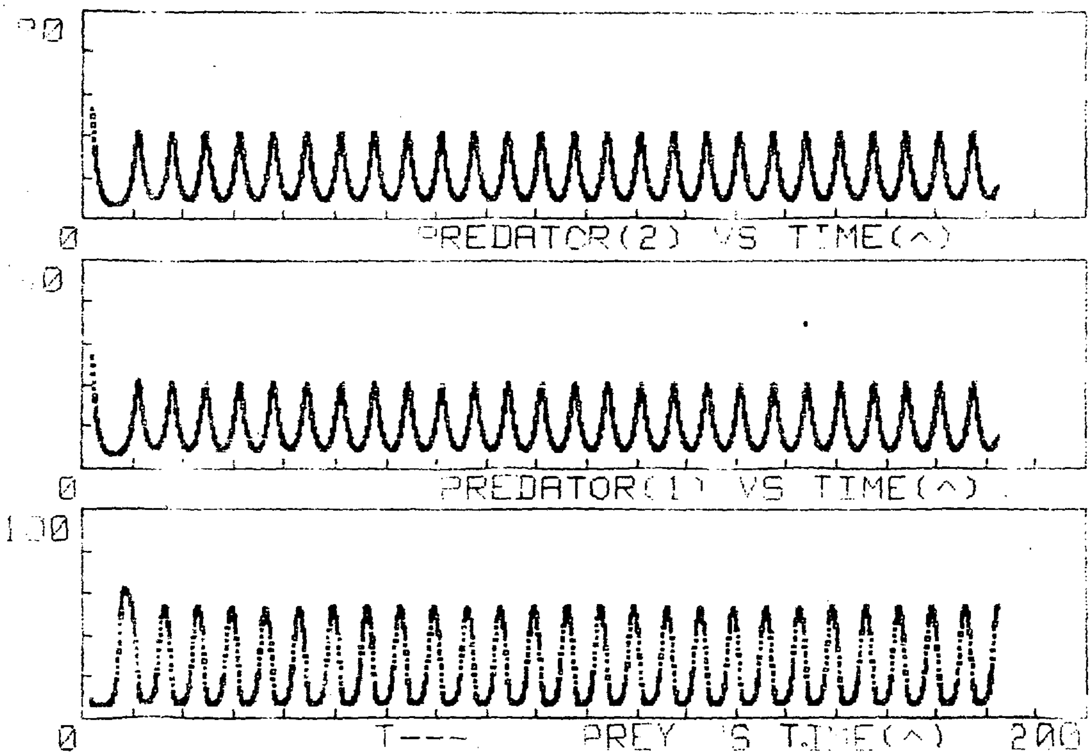

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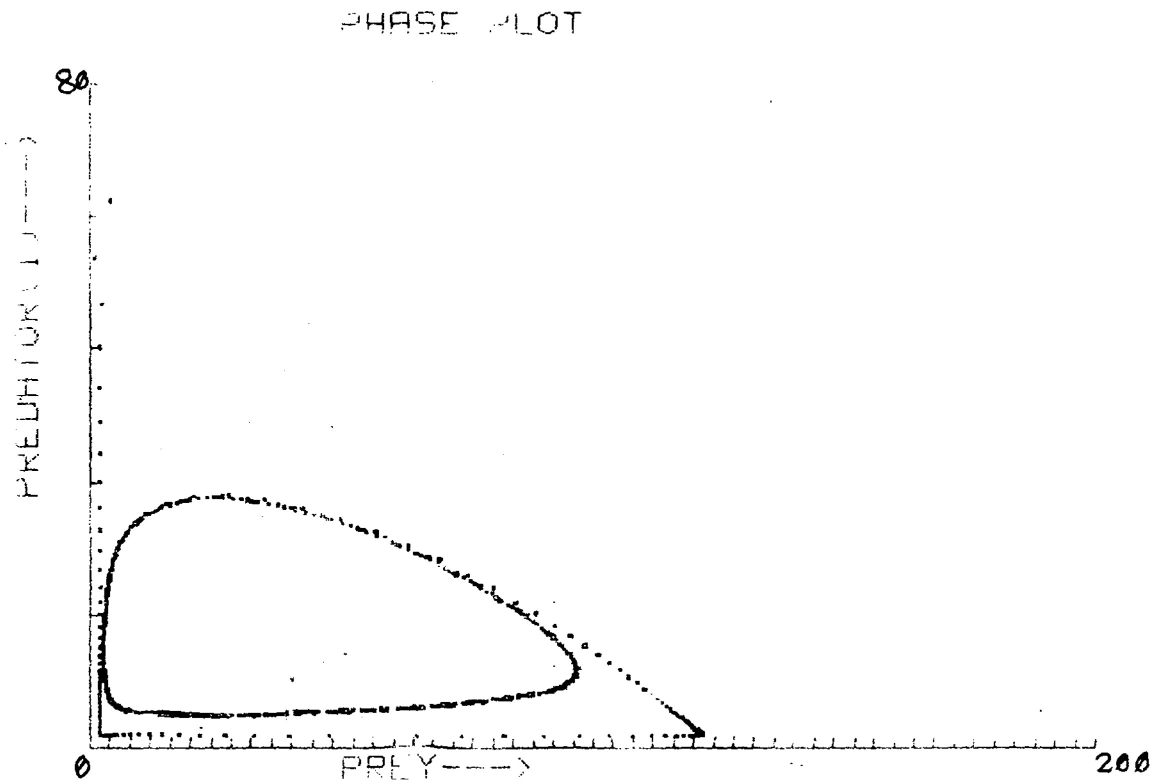
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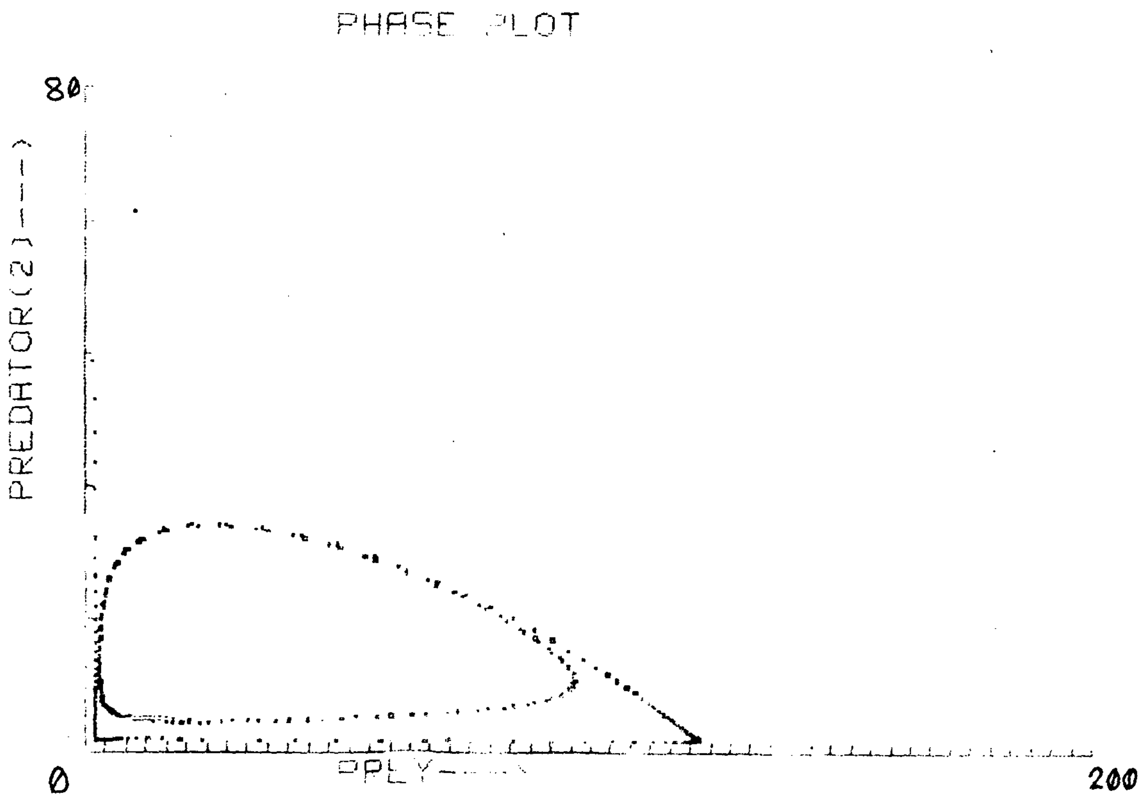
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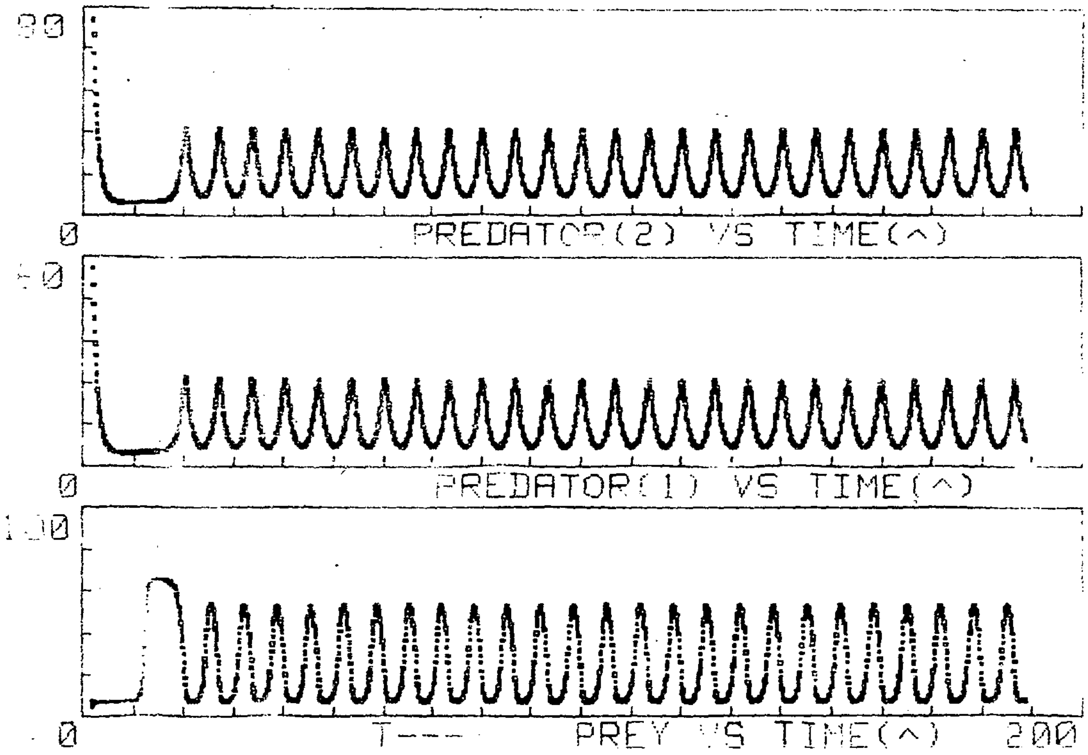
fig.3.21



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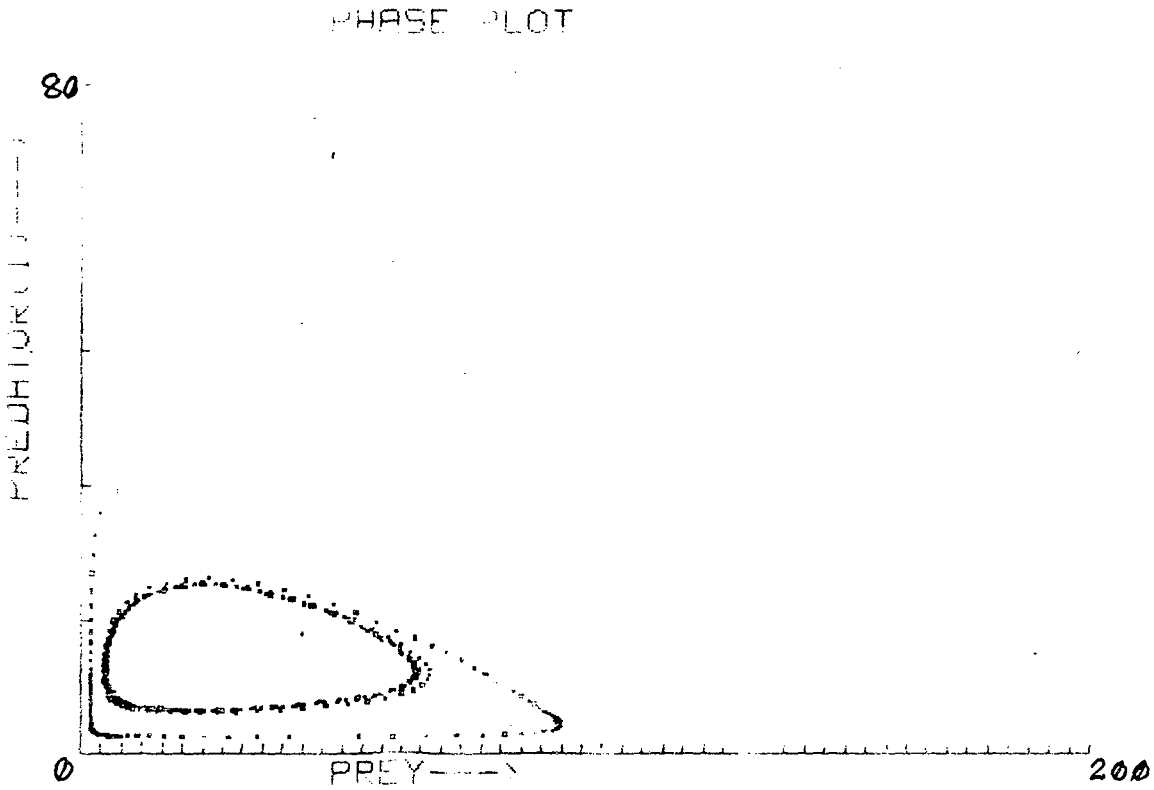

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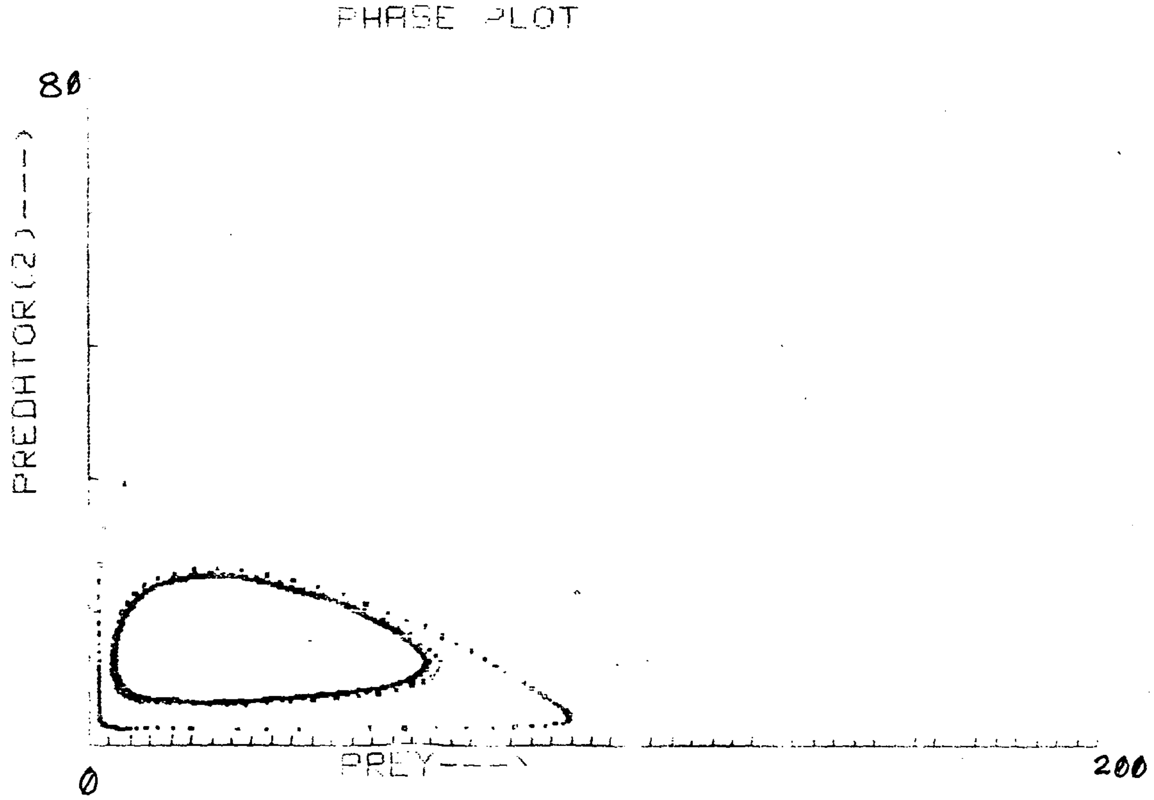

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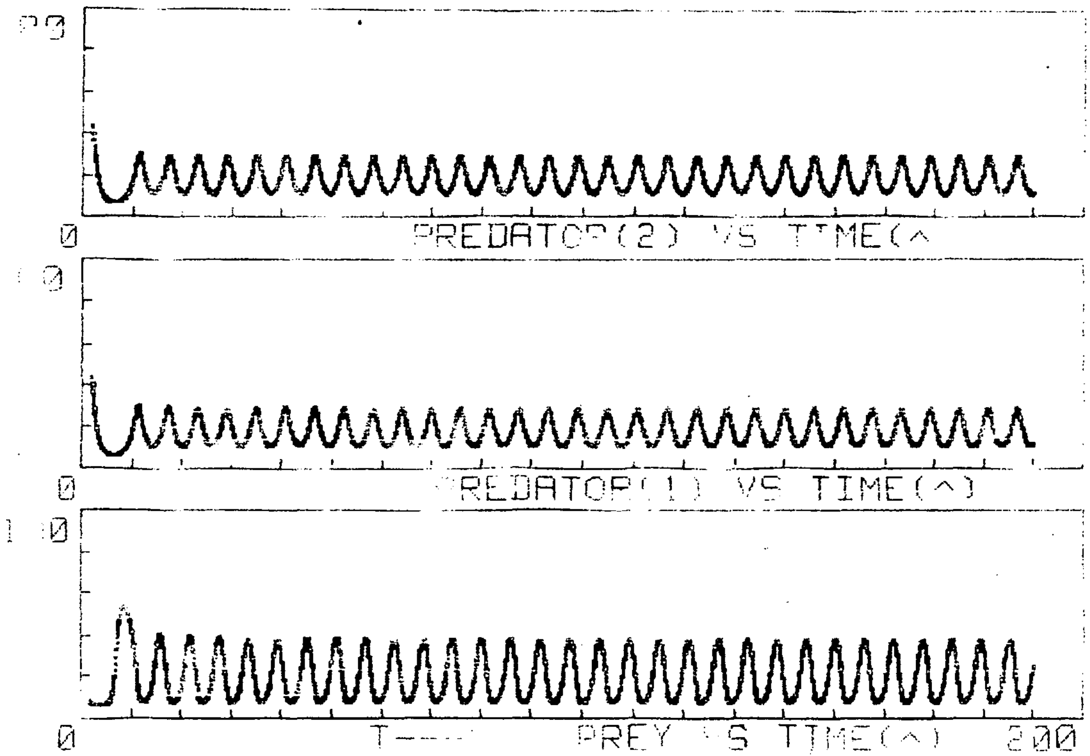

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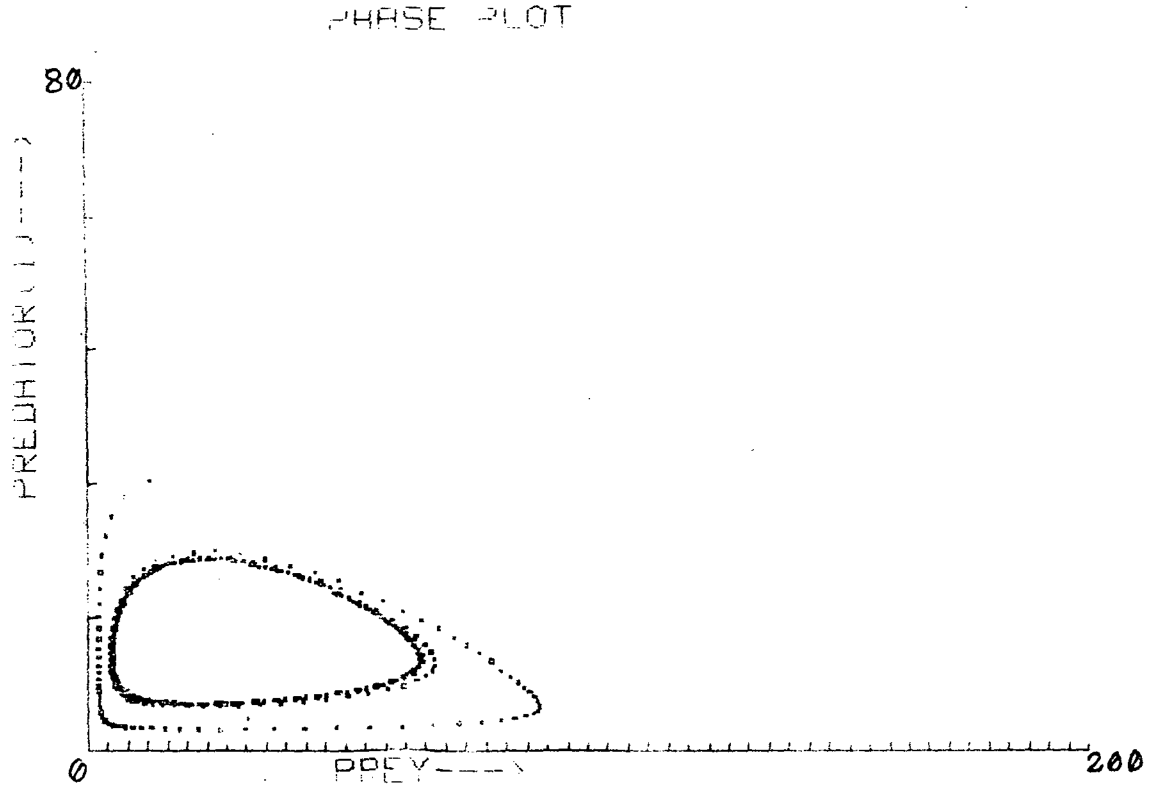
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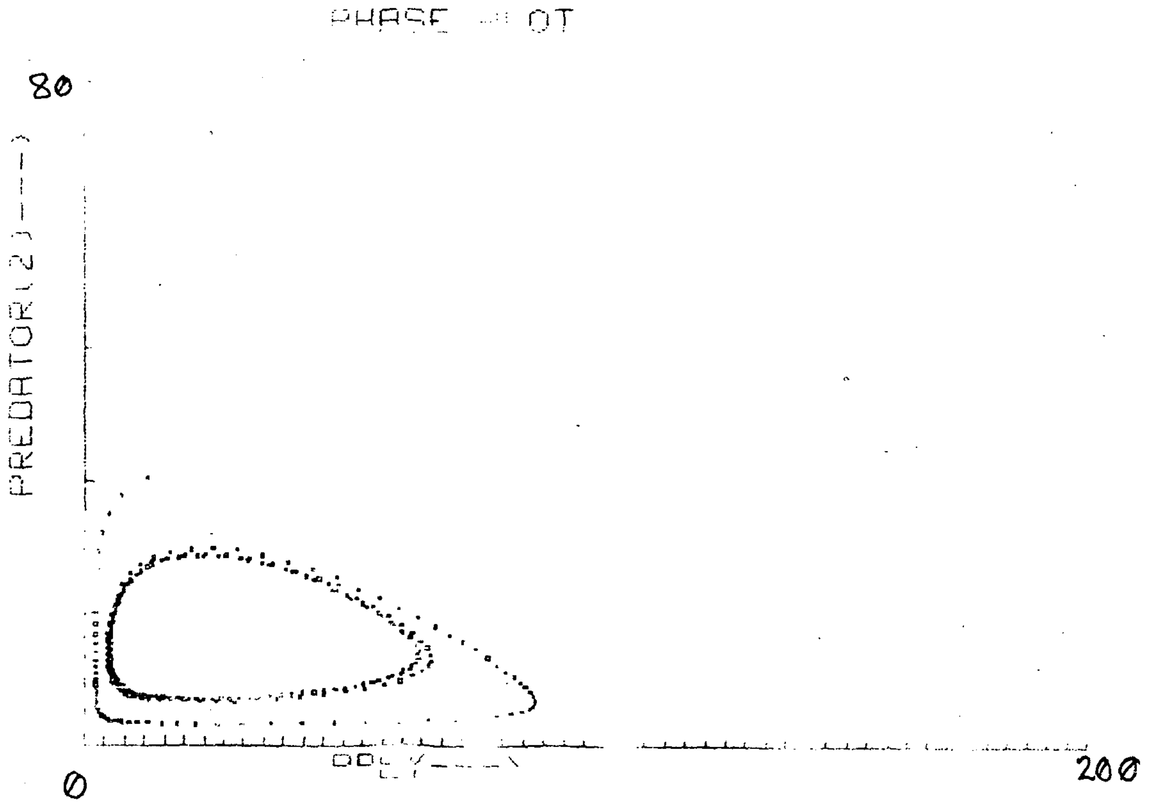
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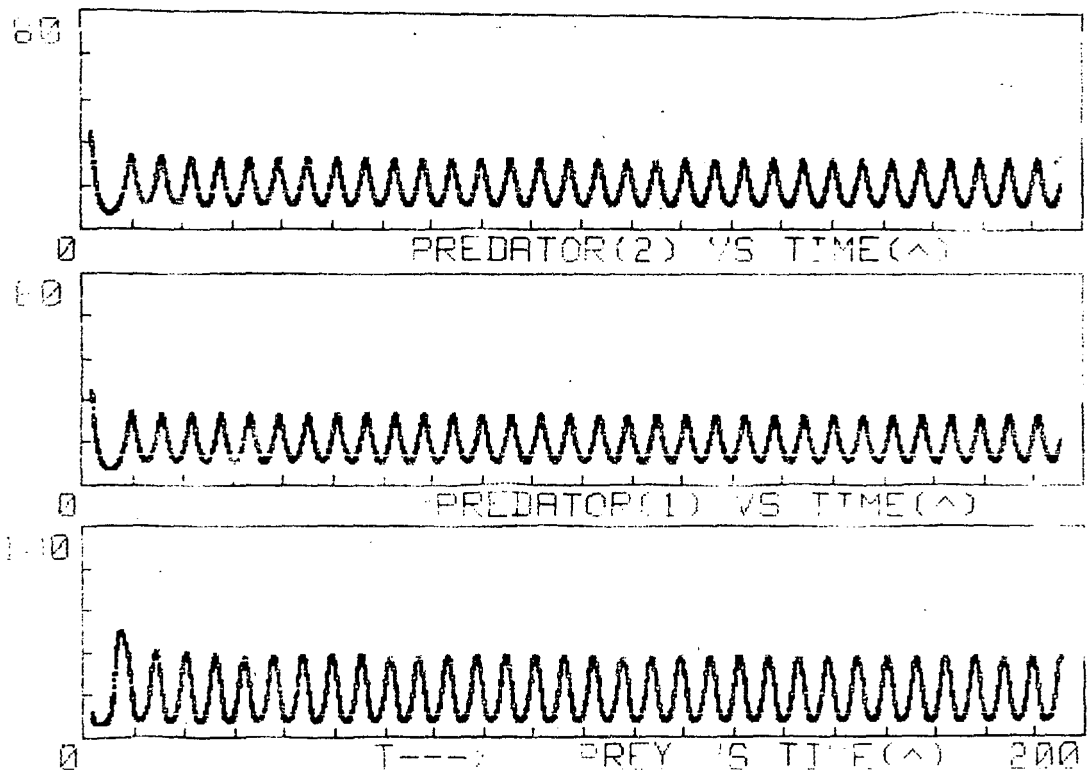
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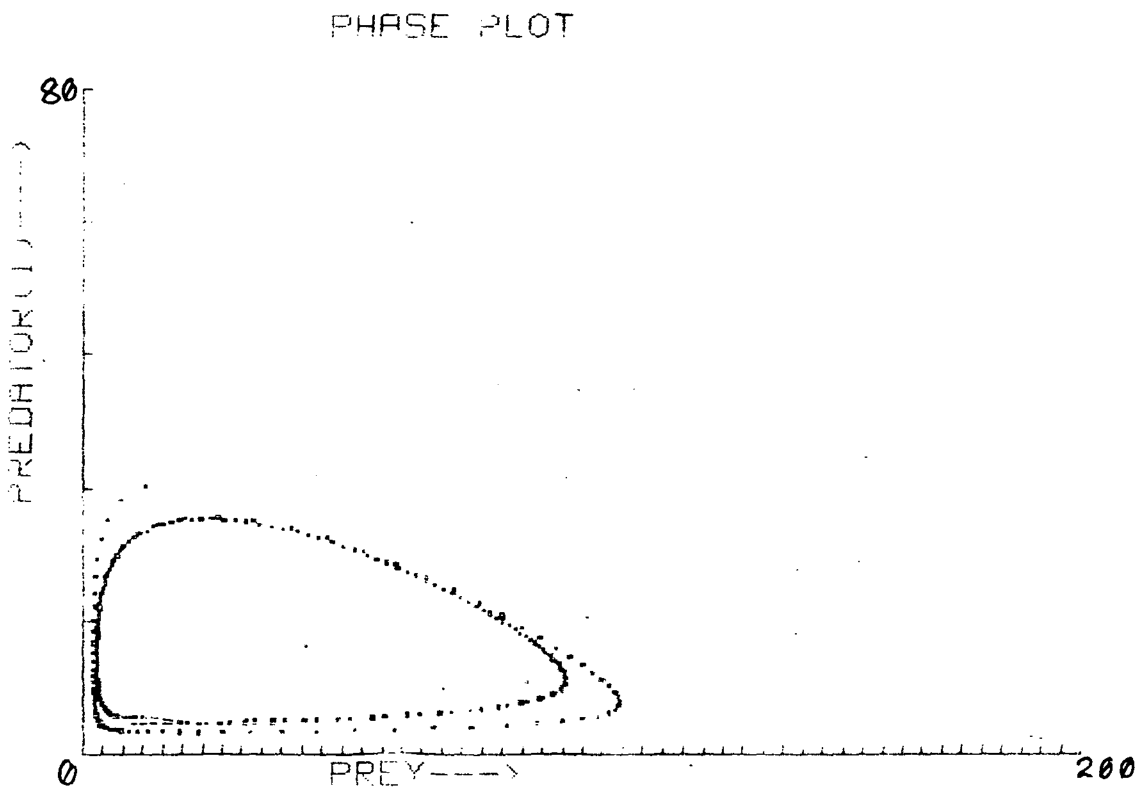
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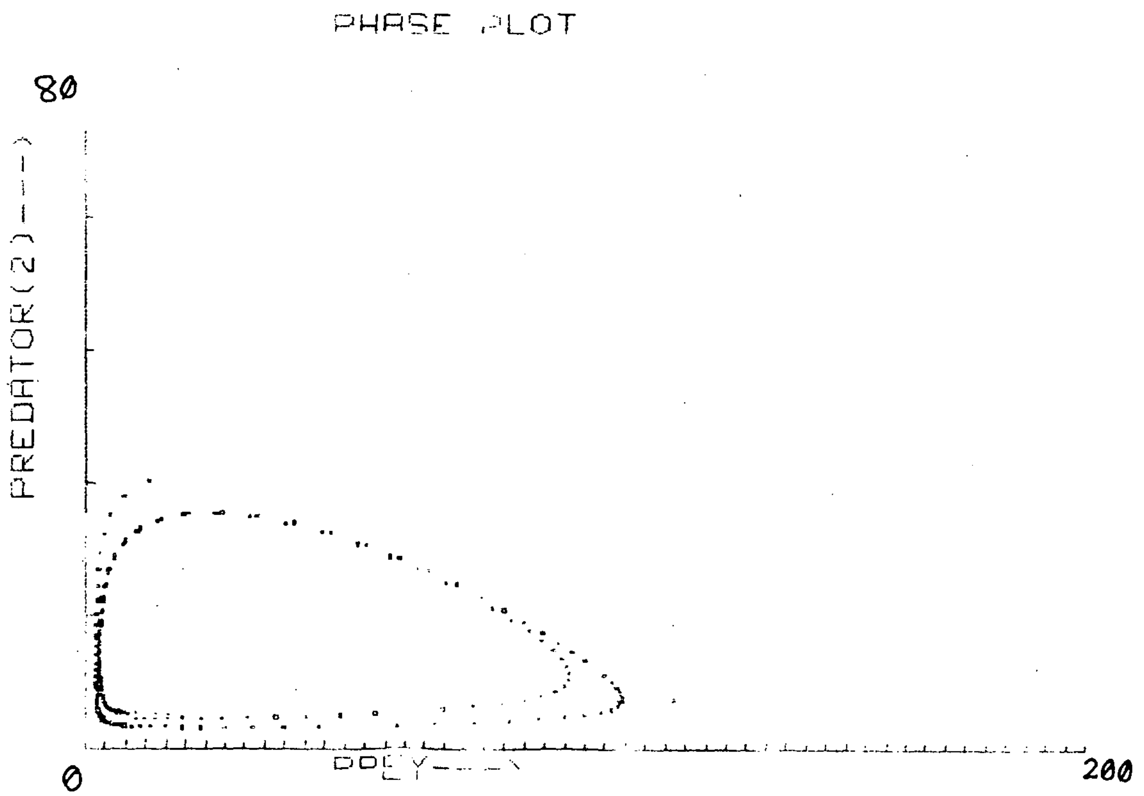
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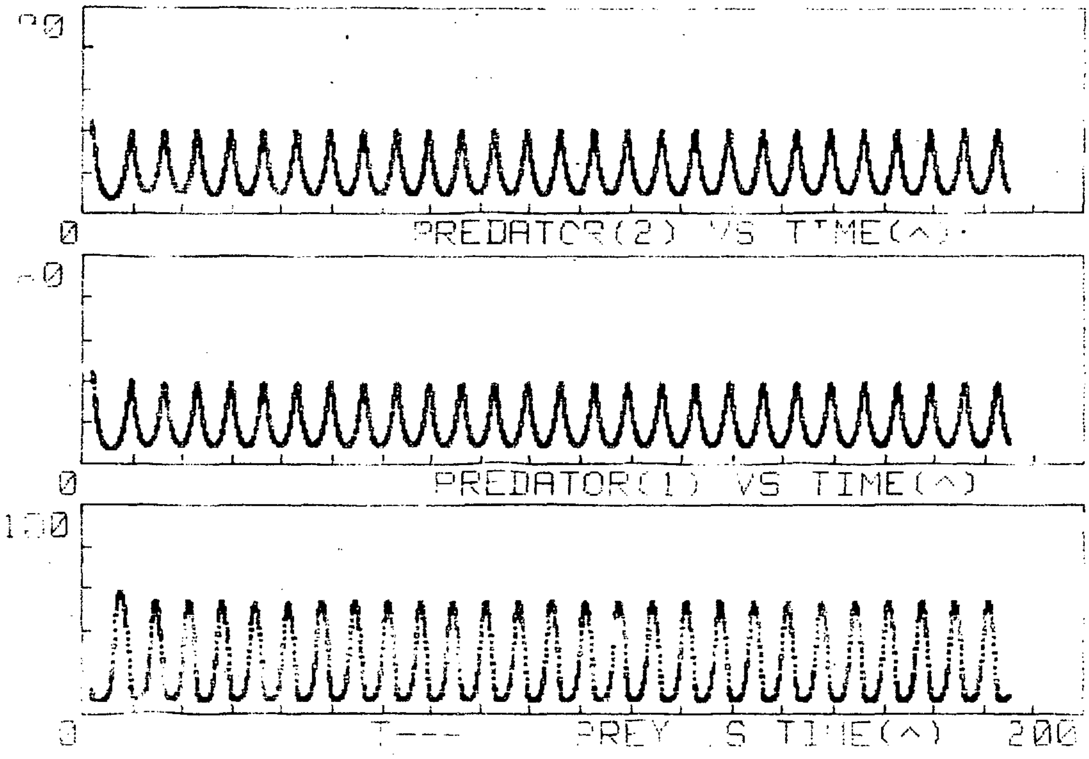
fig.3.27



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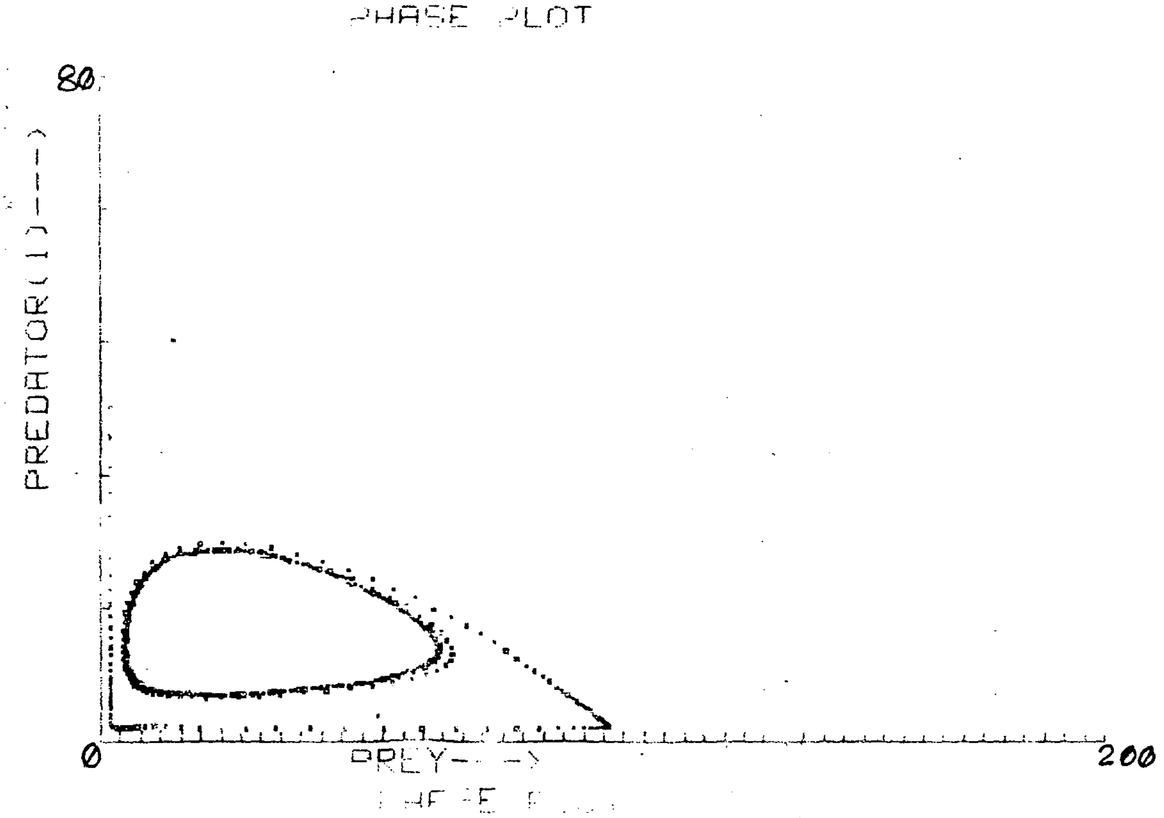

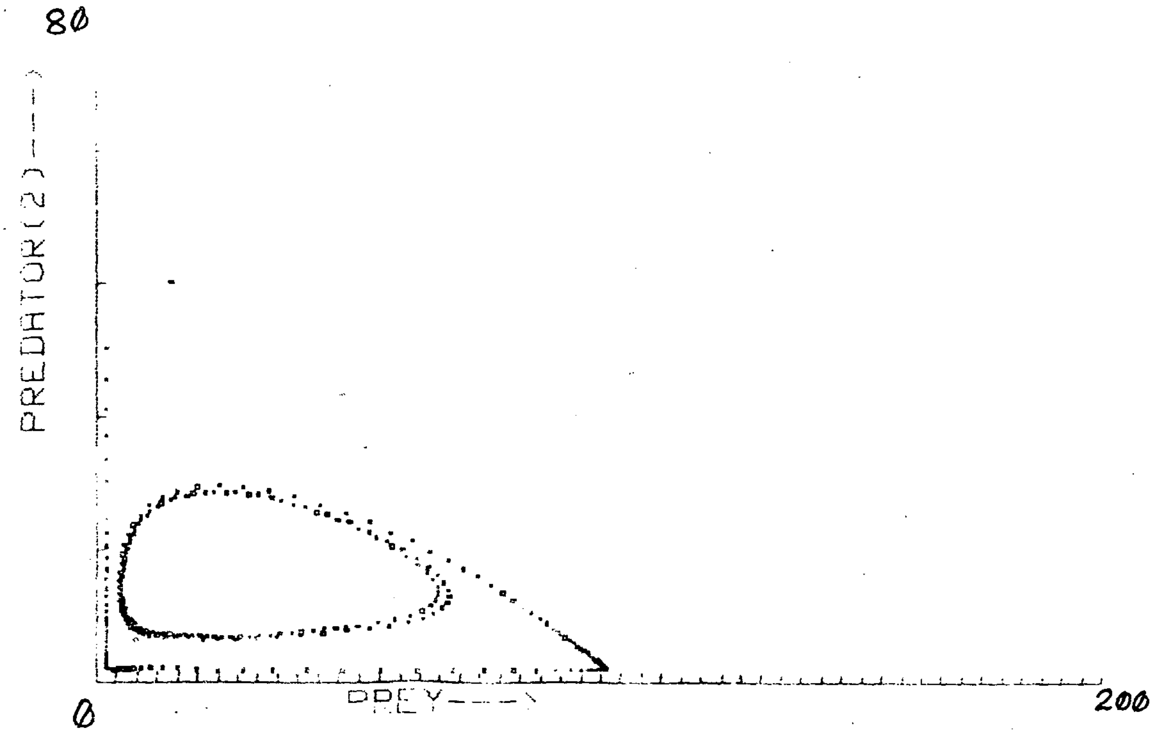

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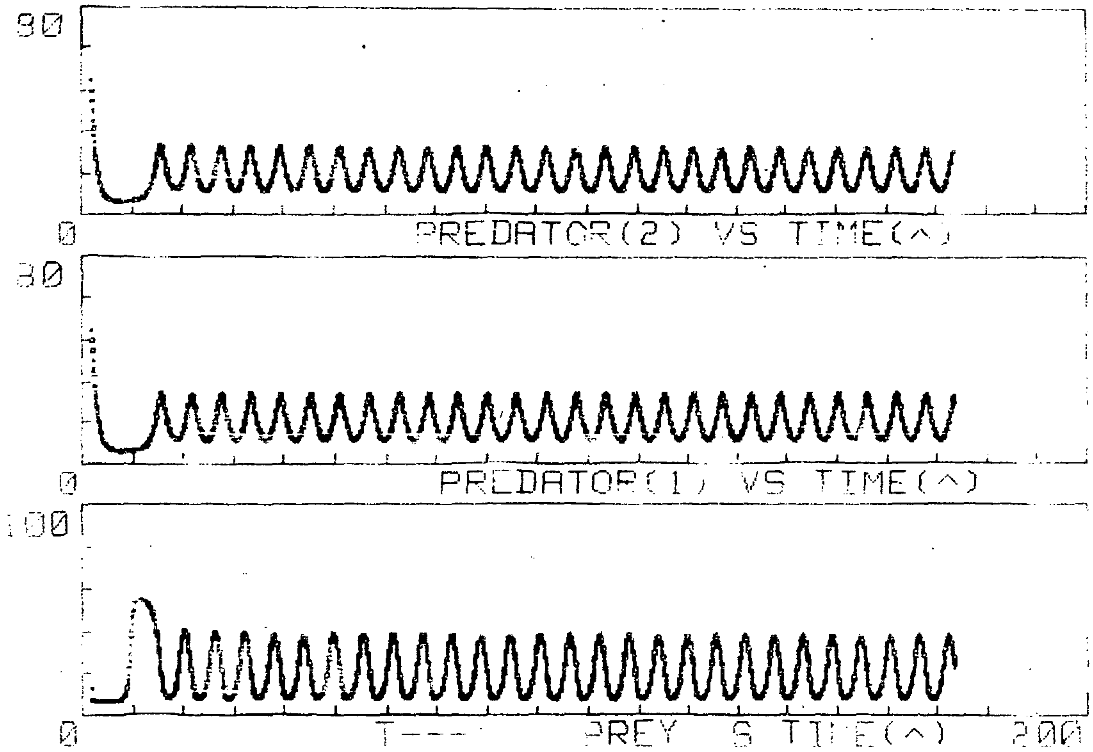

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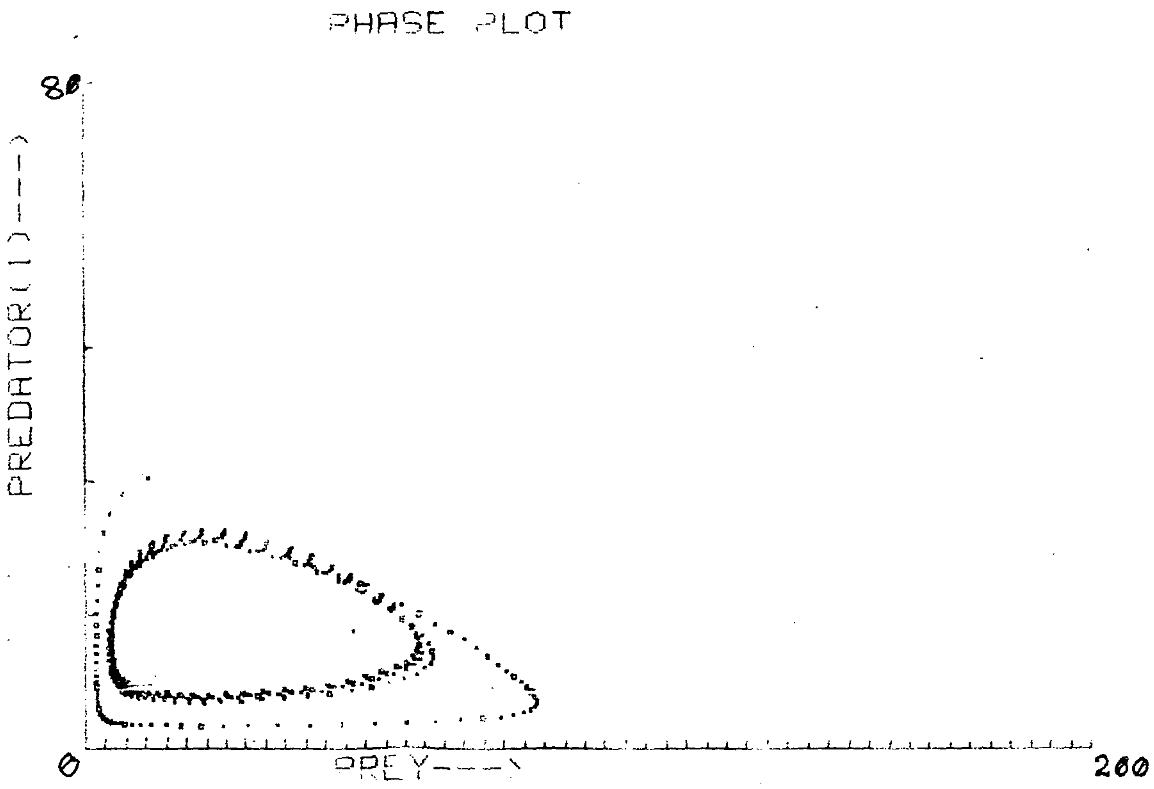
fig.3.30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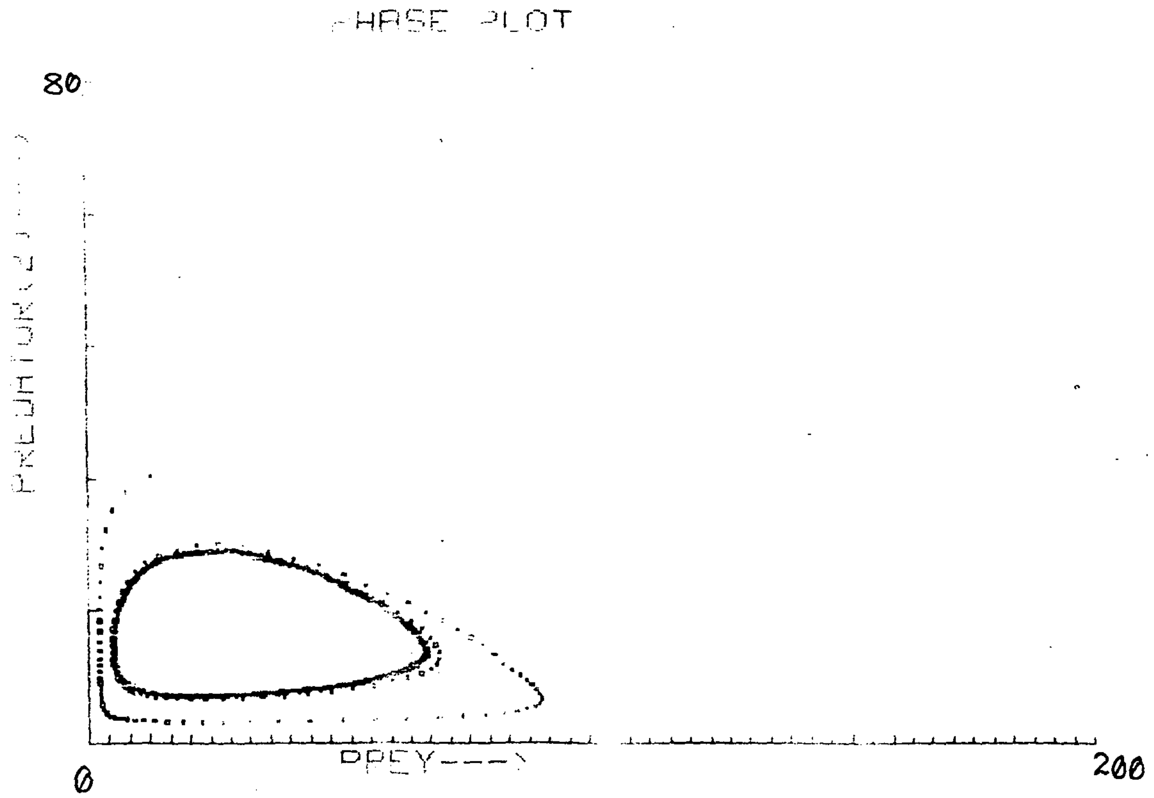
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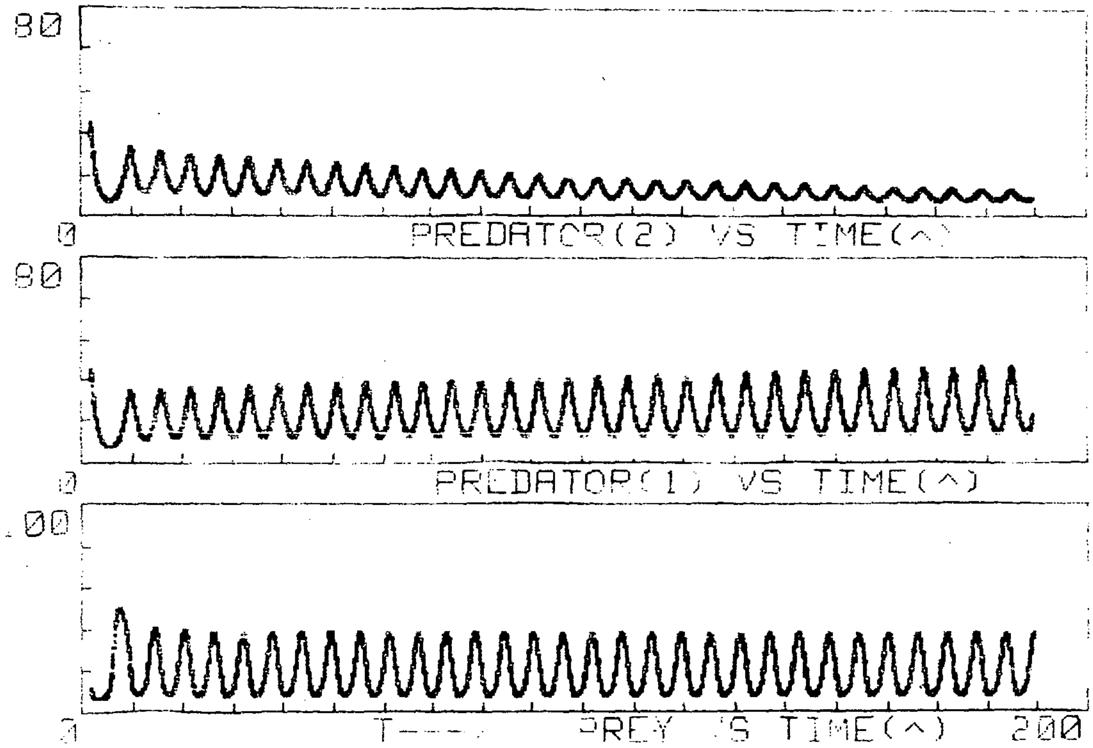
fig.3.31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PREY VS TIME(^)
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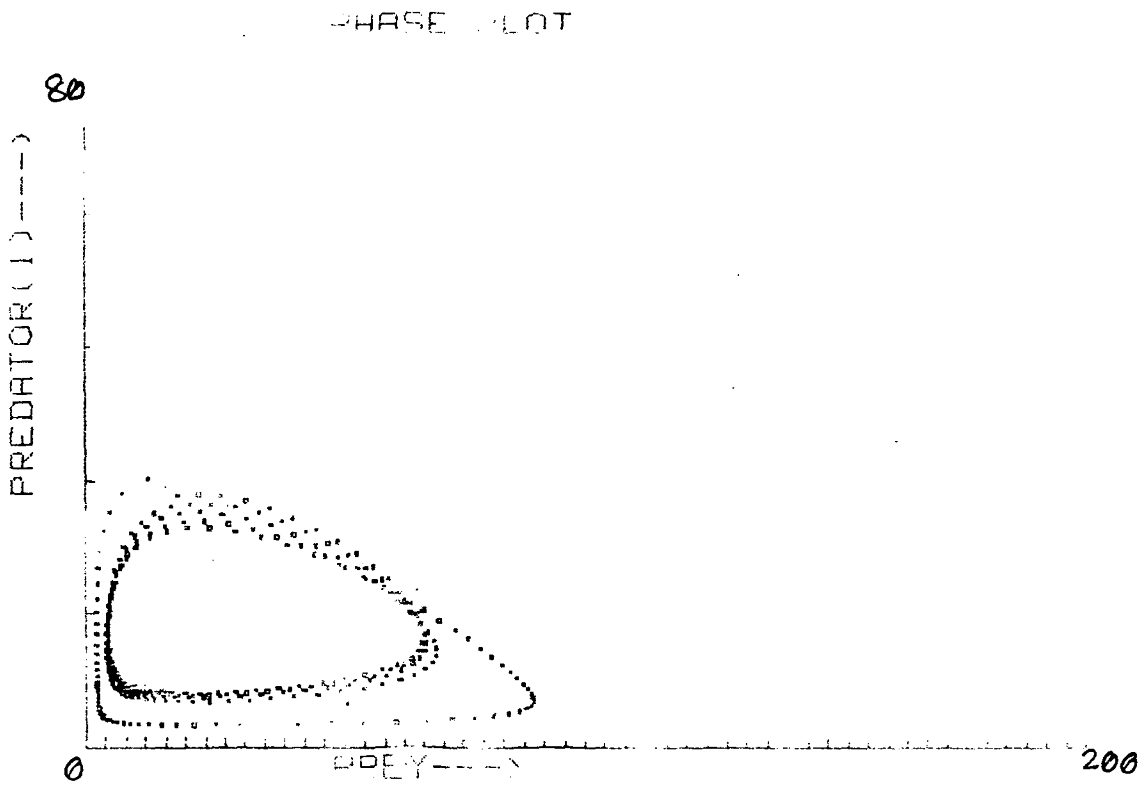
fig.3.32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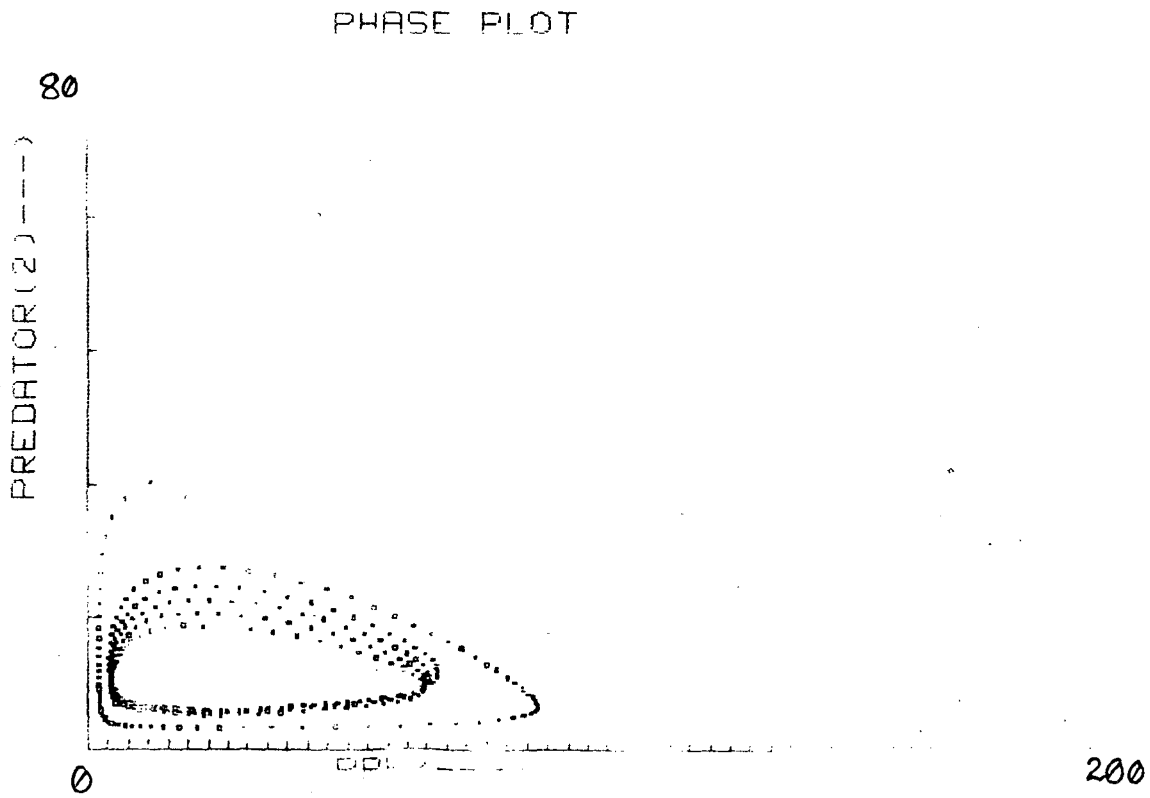
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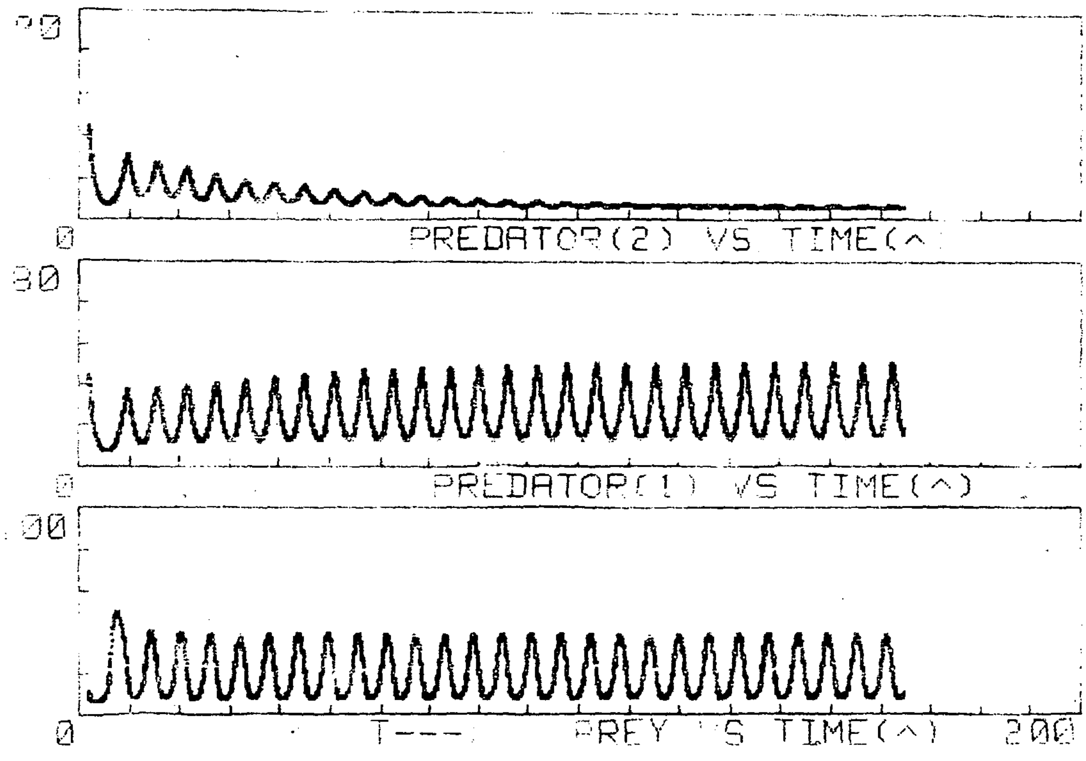

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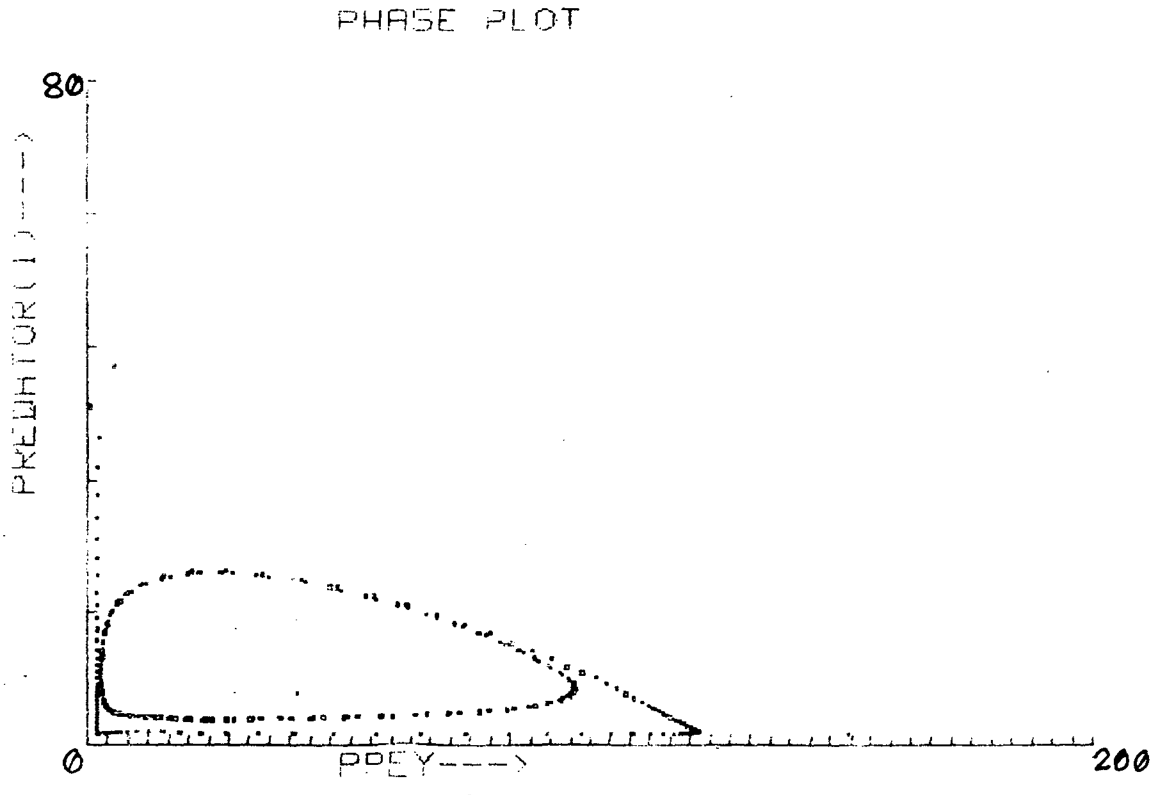
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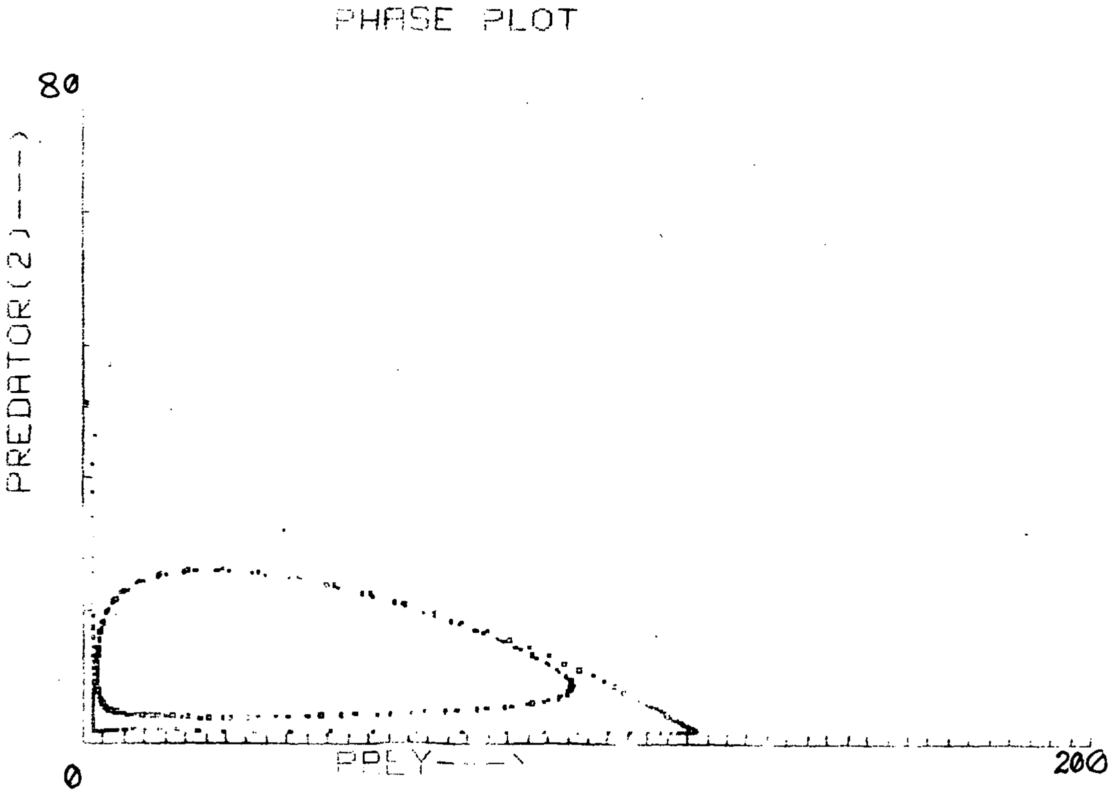
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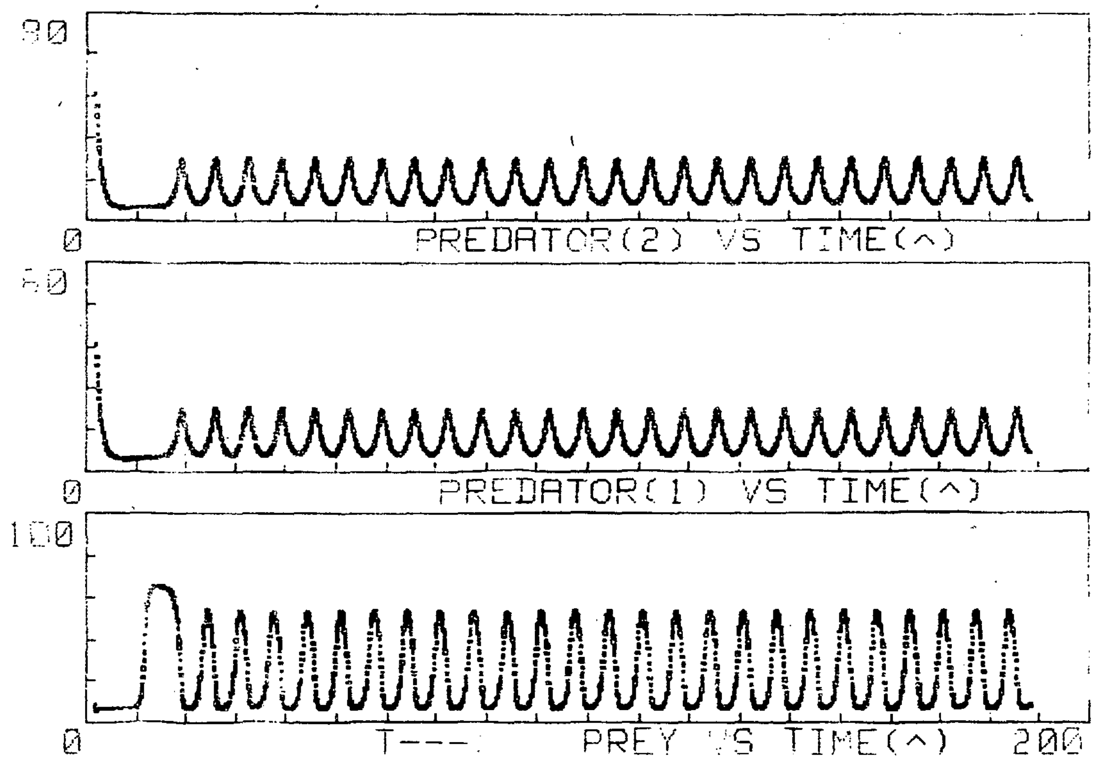
fig.3.35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PREY VS TIME(^)
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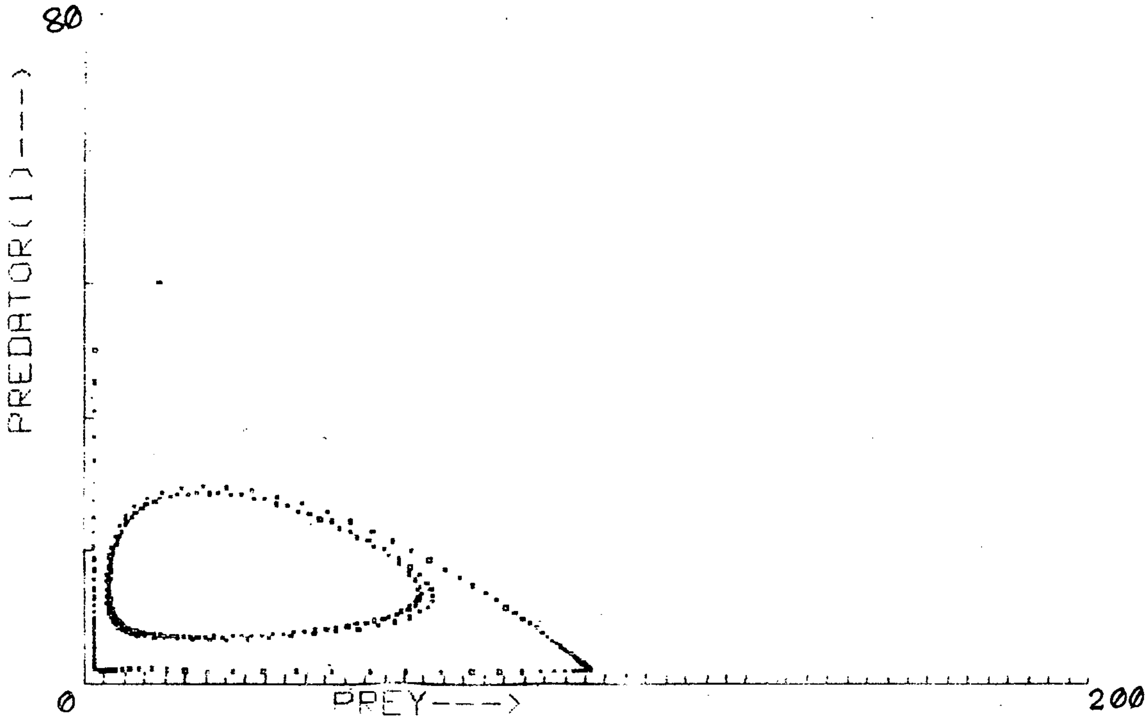

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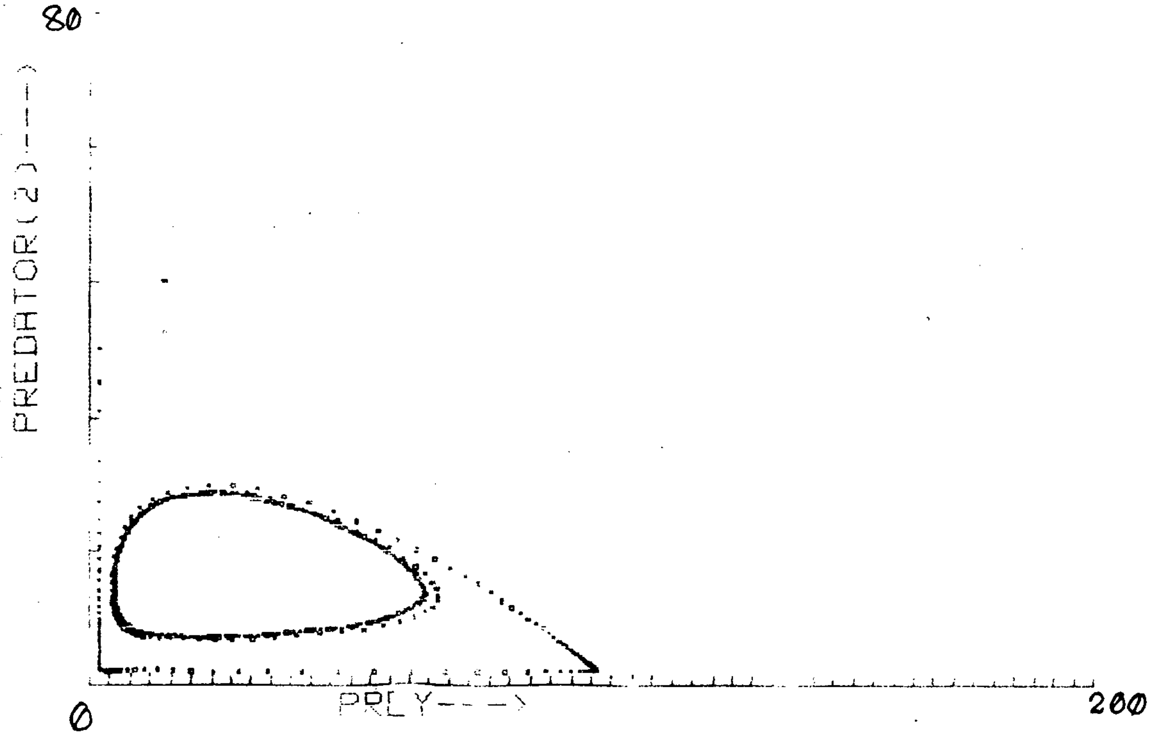

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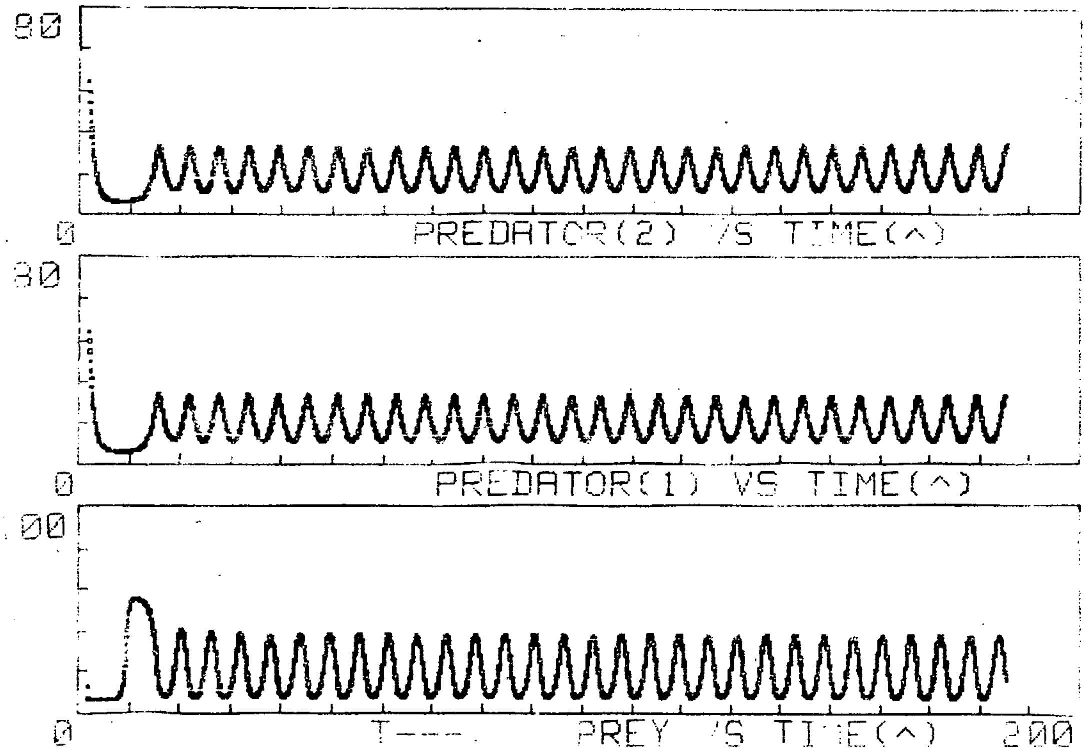
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PREDATOR(1) VS TIME(^)
100
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PREY VS TIME(^)
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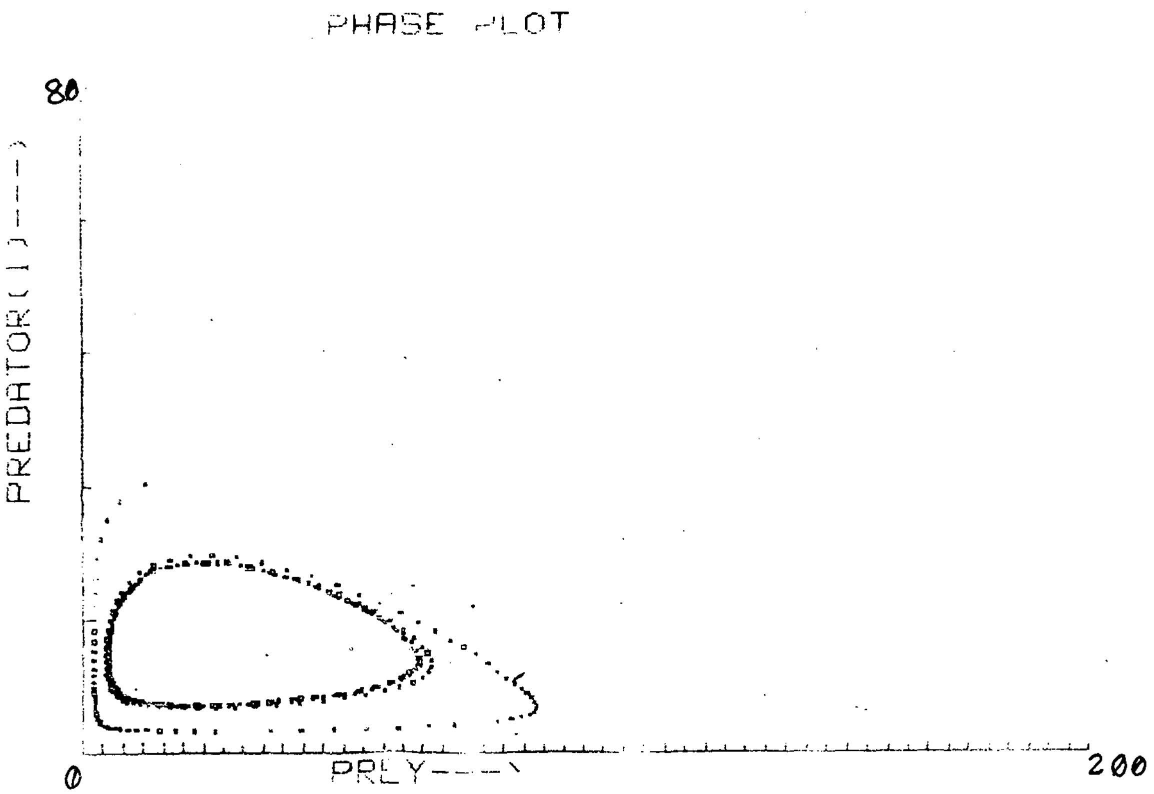
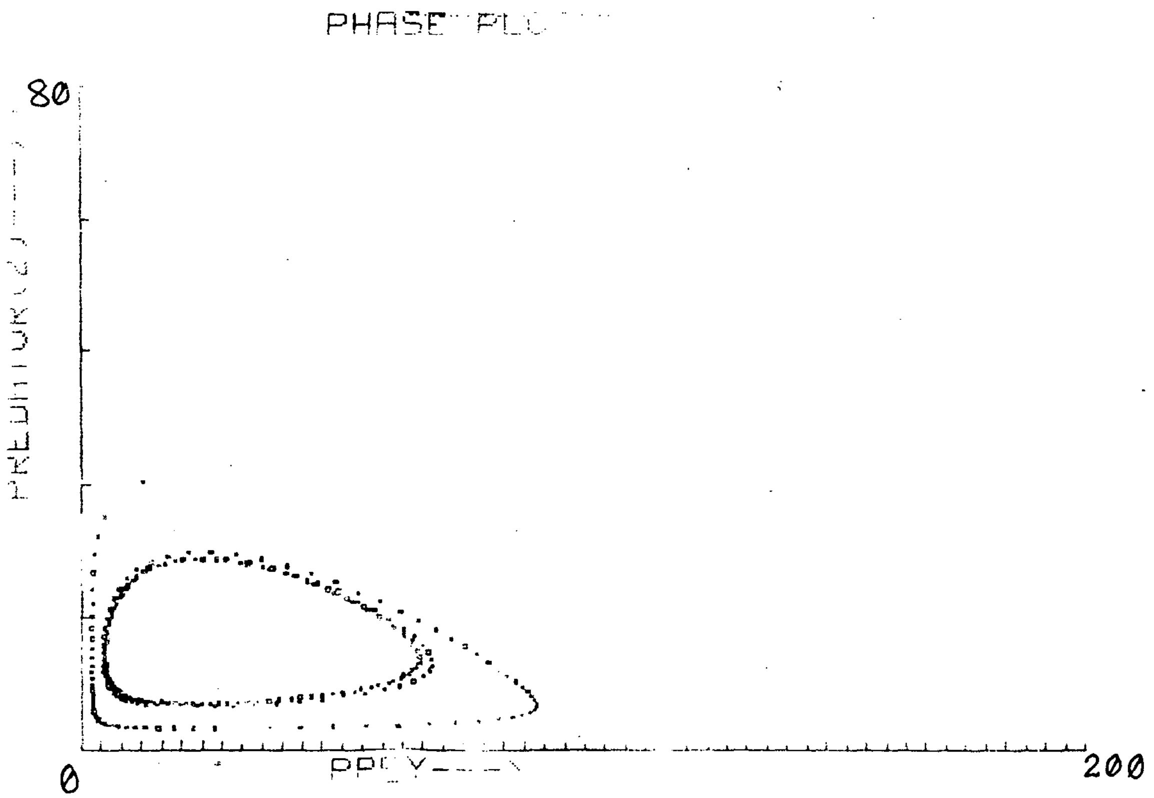
fig.3.38





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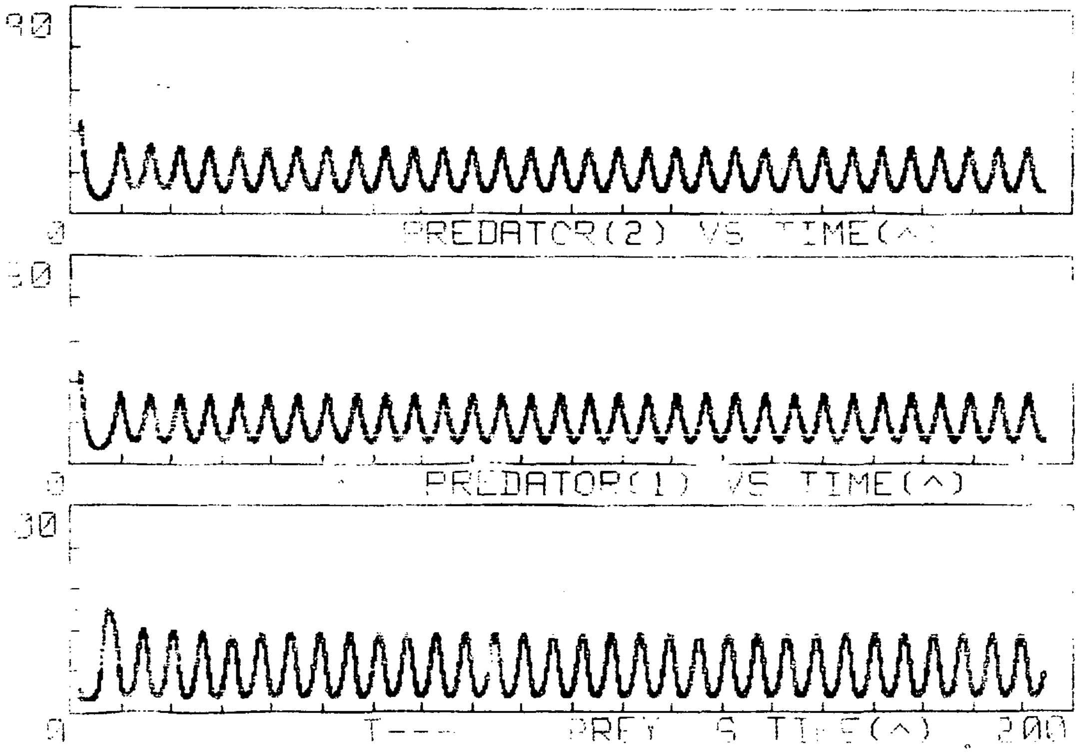

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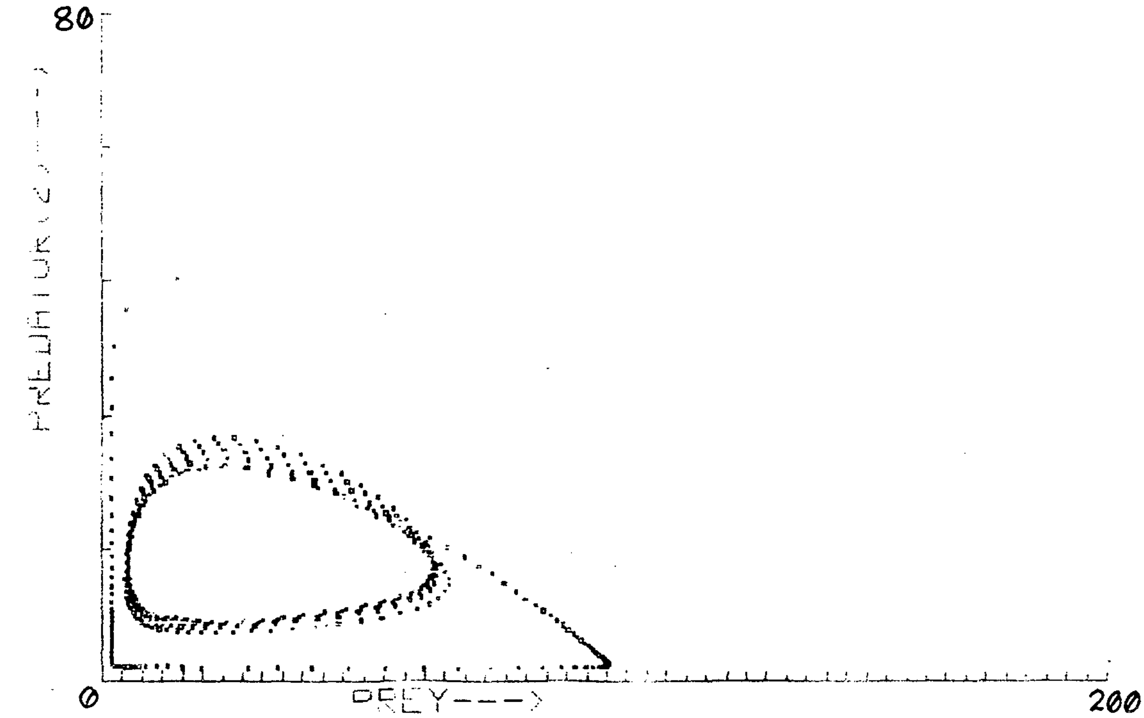

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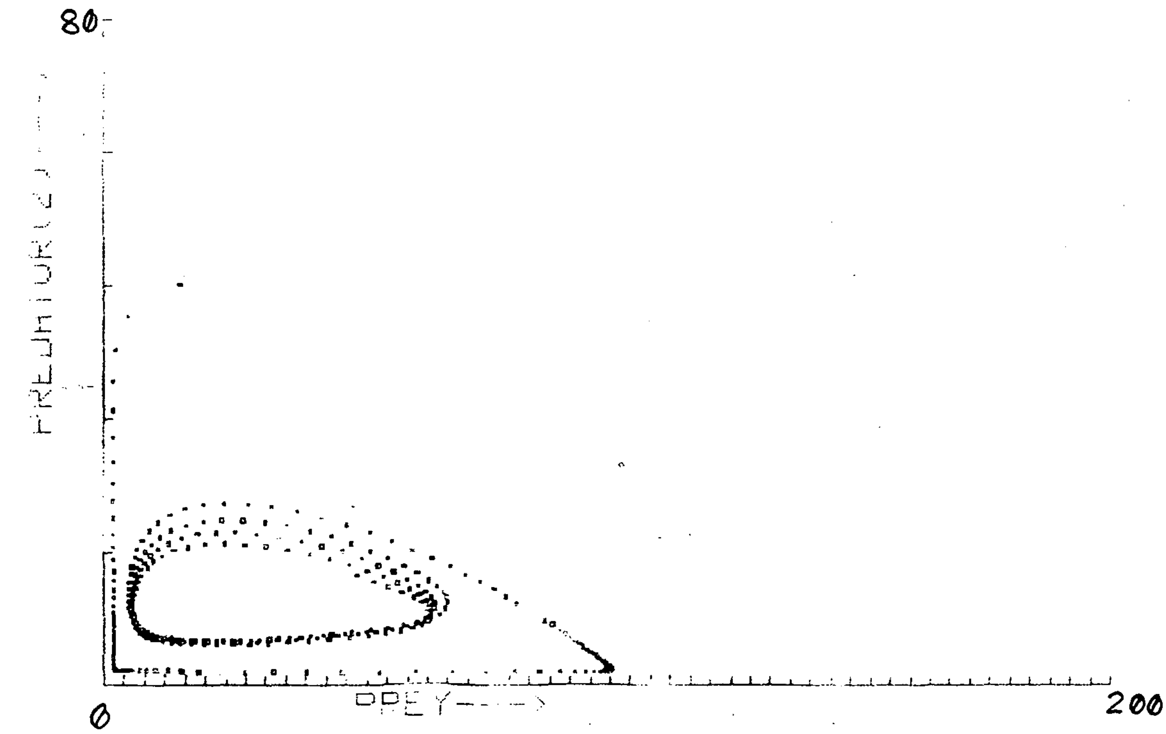

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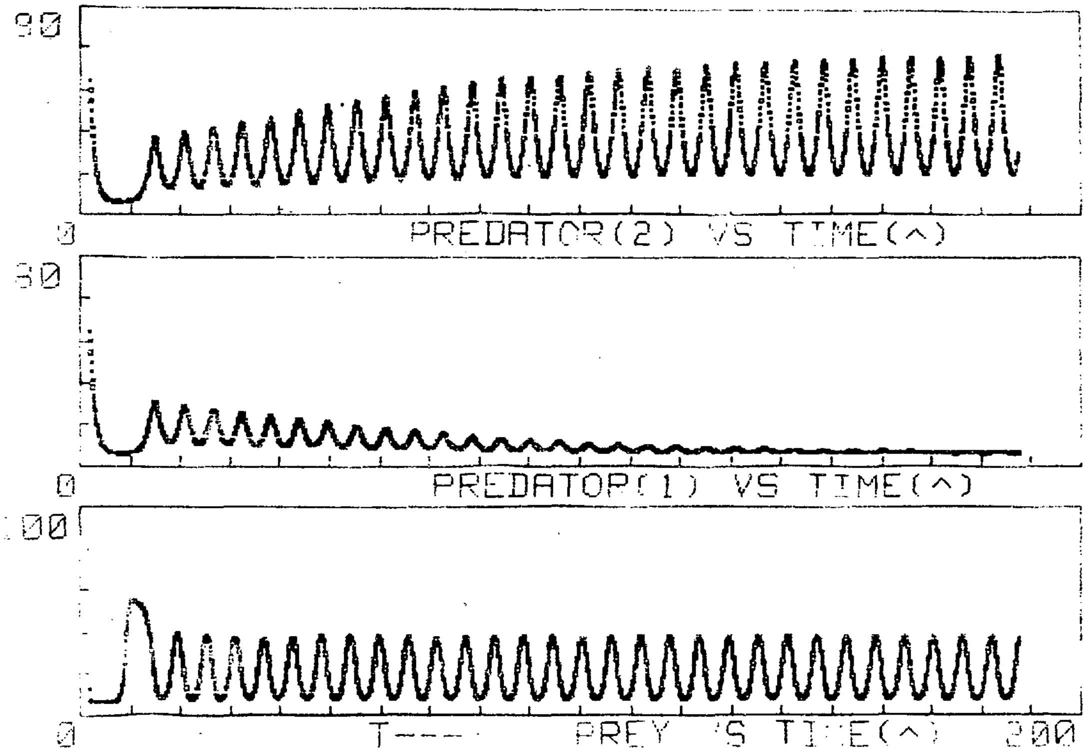
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fig.3.42

CHAPTER - 4

CONCLUSION :

We have studied a three species system with one prey & two predactors. This is done by extending a two species system to a three species system with limit cycle solution in mind. We first started with a one prey-one predator system. Then by applying Kolmogorov's theorem and linearized stability analysis around the equilibrium point, the conditions for the system to exhibit limit cycle solutions were found.

A second predator species was introduced into the system, which then led to a set of three coupled non-linear differential equations describing the new situation. The equations so obtained can not be solved analytically. For numerical work, we first chose the parametric values of the two species system which leads to limit cycle solutions.The rest of the parameters of the three species system were then chosen by trial and errorin a way that we finally had thelimit cycle solutions once more .We also studied our solution under variation of parameters one at a time.

The calculations were of course repeated with different initial value for the populations and it was seen that the results remain unchanged asymptotically.The same pattern was also seen in the individual amplitude versus time plots of different populations.The limit cycle nature of the solutions was therefore established.

Though our calculations were primarily aimed at studing the system without mutual competition between the two predators,some positive results were also obtained and reported here for a few cases when small but somewhat similar interaction terms representing the above competition were included.

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APPENDIX-I

THE KOLMOGOROV THEOREM:

Kolmogorov has given the criteria for stable equilibrium point or a limit cycle behaviour which are applicable essentially to all two species prey-predator models. This is due to the fact that, the form in which kolmogorov wrote the equations for the one prey-one predator system is quite general. The general equation for two species prey -predator can be written as:

$$dH/dt = H\ F\ (H,P)$$

$$dp/dt = P\ G\ (H,P)$$

This theorem says that predator-prey system of the above form have either a stable equilibrium point or a stable limit cycle, provided that F and G_i are continuous functions of H and P, with continuous first derivatives throughout the domain H>o, P>o and following conditions are satisfied:-

(i) $F/\ P < 0$

(ii) $H\ (\ F/\ H) + P(\ F/\ P) < 0$

(iii) $G/\ P < 0$

(iv) $H\ (\ G/\ H) + P\ (\ G/\ P) > 0$

(v) $F\ (0,0) > 0$

It is also required that there exist quantities A,B,C such that,

(vi) $F(0,A) = 0$ with $A > 0$

(vii) $F(B,0) = 0$ with $B > 0$

(ix) $H(C,0) = 0$ with $C > 0$

(ix) $B > C$.

The proof of the theorem comes from the poincare Bendixson theorem (Minorsky, 1962). In biological terms, Kolmogorov's conditions are:

(i) for any given population size, the per capita rate of increase of the prey species is a decreasing function of the number of predators.

(ii) the rate of increase of the prey is a decreasing function of population size.

(iii) the rate of increase of predators decreases with their population size.

(iv) the rate of increase of predator is an increasing function of population size.

(v) when both populations are small the prey have a positive rate of increase.

(vi) there can be a predator population size sufficiently large to stop further increase of prey species, even when the prey are rare.

(vii) there is a critical prey population size B beyond which they can not increase even in the absence of predators (a resource or other self limitation).

(viii) there is a critical prey size c that stops further increase in predators, even if they be rare.

(ix) B>c, otherwise the system will collapse.

This theorem may be applied to a system to show that it possesses either a stable limit cycle or a stable equilibrium point. A conventional neighbourhood analysis reveals whether the equilibrium point is stable or not, here we consider the linearized version of the model in the neighbourhood of the equilibrium point and use the so called Routh-Hurwitz criteria.

APPENDIX-II

THE LINEARIZED STABILITY ANALYSIS:

The multispecies population dynamics can be written by a set of m equations as:

$$dN_i(t)/dt = F_i\,[N_1\,(t),\ N_2\,(t), \ldots\ldots Nm(t)] \text{ ------ } (1)$$

$$i = 1 \to m$$

here the growth rate of i^{th} species at time t is given by some non-linear function Fi of all relevent interacting population. The population size at equilibrium point, N_i, are obtained from m algebric equations obtained by putting all growth rates zero.

$$F_i\ (N_1{}^*,\ N_2{}^* \ldots\ldots\ldots\ N_m{}^*) = 0 \text{ ------- } (2)$$

expanding about this equilibrium, for each population we write,

$$N_i\ (t) = N_i{}^* + x_i\ (t) \text{ -------- } (3)$$

Where, X_i the measures the initially small perturbation to the i^{th} population. Expanding equation (1) by Taylor series expansion around this equilibrium point and neglecting all terms which are of second or higher order in x, a linearized approximation is obtained .

$$dx_i(t)/dt = \sum_{j=1}^{m} a_{ij}\ x_j\ (t) \text{ ------- } (4)$$

The set of equations (4), describe the population dynamics in the neighbourhood of the equilibrium point. In matrix notation, we can rewrite equation (4) as:

$$dX(t)/dt = AX(t) \qquad \text{----------} \quad (5)$$

Here X (t) is (mx1) coloumn matrix x_i and A is (m x m) column matrix x_i and A is (m x m) "community Matrix" whose elements a_{ij} describe the effect of species j on species i near equilibrium.

The elements a_{ij} depend upon the details of the original equations (1) and on value of equilibrium population according to recipe

$$a_{ij} = (\partial F_i/\partial N_j)^* \qquad \text{-----------} \quad (6)$$

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

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

$$x_i\ (t) = \sum_{j=1}^{m} C_{ij} \exp\ (\lambda_j\ t) \qquad \text{---------} \quad (7)$$

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 (j = 1,2,...m) which characterize the temporal behaviour of the system are eigen values of matrix A.

Substituting (7) into (5) we get,

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

or, $\quad (A - \lambda \; I) \quad X \; (t) \quad = \quad 0 \qquad$ -------- (9)

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

$$\det \; (A - \lambda \; I) \quad = o \qquad \text{---------------} \qquad (10)$$

This is a m^{th} order polynamial equation in of matrix A. They may in general be complex numbers, $\lambda = \zeta + i\xi$; in any of terms of equation the real part ζ produces exponential growth or decay, and imaginary part ξ produces sinusoidal oscillatons. It is clear that perturbation to the equilibrium populations will die away in time if any only if, all eigen values λ have negative real parts, If any of eigen values has a positive real part, that exponential factor will grow ever larger as time goes on and constantly 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 for polynomial of is ,

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

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

The conditions for m = 2,3,4 are

m = 2	$a_1 > 0$, $a_2 > 0$
m = 3	$a_1 > 0$, $a_3 > 0$, $a_1a_2 > 0$
m = 4	$a_1 > 0$, $a_3 > 0$, $a_4 > > 0$
	$a_1 a_2 a_3 > a_3^2 + a_1^2 a_4$