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VIKAS RAI
M. Phil (Area-I)

Under the supervision of
PROF. L. K. PANDE

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

1987

DEDICATED

TO

ONE

WHO INSPIRES ME

TO

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CERTIFICATE

Certified that the research work embodied in this dissertation entitled "A NEW PREY-PREDATOR MODEL" has been carried out at the School of Environmental Sciences, Jawaharlal Nehru University, New Delhi. The work is original and has not been submitted so far in part or full for any other degree or diploma of any University.

Vikas Rai
(VIKAS RAI)
CANDIDATE

L.K. Pande
(PROF. L.K. PANDE)
SUPERVISOR

V. Asthana
(PROF. V. ASTHANA)
DEAN

JULY 1987

School of Environmental Sciences,
Jawaharlal Nehru University,
New Delhi - 110 067

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Vikas Rai
VIKAS RAI

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Introduction

Models in theoretical population biology play a key role in making the understanding of complex ecosystems a possibility. There are two distinct types of models in theoretical ecology:

(i) "explanatory" or systems models whose behaviour is thought to duplicate, at least approximately, the true behaviour of the populations in existing phase of biological evolution.

(ii) models designed to predict the behavioural patterns of the different populations of an ecosystem in future, over long periods.

Models discussed in the present dissertation work belong to the first category. They are systems models designed to explain the behaviour of the populations having prey-predation interaction.

The Lotka-Volterra model discussed in the first chapter, possesses neutral stability. In other words, in a system governed by this model, both host(pre) and parasite

(predator) would undergo constant oscillations whose amplitudes would bear no relation to biology of the two species but only to the initial sizes of their populations. This kind of behaviour seems to be very unlikely for real ecosystems. So, in the next chapter, we discuss a more elegant model given by Leslie and Gower. It leads to solutions which have an asymptotic behaviour leading to stable equilibrium, which is independent of the initial conditions and depends on the intrinsic factors governing the biology of the system. So, although it marks a significant improvement over the one given by Lotka and Volterra, it is very much limited in its explanatory capability. This is the reason why we discuss a more elaborate model - Holling - Tanner model. This model is capable of generating solutions possessing stable equilibrium as well as stable limit cycles. In other words, the system modelled by Holling and Tanner behaves in such a way that the dynamics of two interacting populations depends upon the intrinsic attributes or the genetic features of the system concerned. But, this model too, has certain weaknesses.

The object of the present work is to devise a model which is free from the weaknesses inherent in the

Holling-Tanner model to certain extent and has the following features :

The per capita growth rate of the parasite is not proportional to the population ratio $\frac{P}{H}$ but rather to a factor which is similar in form as the parasite's attack rate with a ceiling W_1 occurring for $H \rightarrow \infty$. This establishes a desirable relationship between the host's loss and parasite's gain which does not exist in the Holling - Tanner model. The new interaction terms appearing in the rate equations thus also restore to some extent the symmetry which characterises the Lotka - Volterra model. In the process, we also find that the behaviour of the rate equation for the parasite near $H=0$ is now improved over that of the Leslie - Gower and Holling - Tanner models. The behaviour for $H \rightarrow \infty$, leading asymptotically to exponential growth for the parasite is common to all the models, but this possibility is always excluded due to the presence of the self interaction term in the rate equation for the host.

The value of the present model, which is discussed in detail in the 3rd Chapter, lies in the fact that it is

theoretically more sound in comparison to previous ones in view of what has been noted in the above; and at the same time it is capable of generating, besides stable equilibrium solutions, limit cycles, which signify oscillations for both the populations, which become independent of initial conditions asymptotically. The latter possibility is a more realistic one for living systems, which all the ecosystems indeed are.

CHAPTER 1

LOTKA-VOLTERRA MODEL

One of the earliest of host-parasite models is that devised by Lotka (1925) and independently by Volterra (1971). This so called model can be mathematically given by the following pair of coupled non-linear differential equations :

$$\frac{dH}{dt} = (a_1 - b_1 P) H \quad (1a)$$

$$\frac{dP}{dt} = (-a_2 + b_2 H) P \quad (1b)$$

where a_1 , b_1 , a_2 , b_2 are all positive constants.

In the above equations, H is the density of the host (prey) population, P is the density of the parasite (predator) population, a_1 is the intrinsic rate of increase of the host (prey) population, a_2 is the intrinsic death rate of the parasite (predator) population, and b_1 and b_2 are constants expressing the effect of the density of one species on the rate of growth of the other. The first equation tells us that the rate of change in the density of

host (prey) population with time is a function of the intrinsic rate of increase of the host (prey) minus losses due to the density of the parasite (predator) population. Similarly, the 2nd eqn. states that the rate of change in the density of the parasites (predators) is equal to a gain due to the density of the host (prey) minus the intrinsic rate of death.

The assumptions implicit in the model are :

- 1] Neither the host (prey) nor the parasite (predator) population inhibits its own rate of growth.
- 2] The environment is completely closed and homogeneous.
- 3] Every host or prey has an equal probability of being attacked.

Now, the question comes how will a system described by equations 1(a), 1(b) behave? Unfortunately the system described by equations 1(a) and 1(b) cannot be solved as such. On the other hand, if we think of its unknown

solution

$$H = H(t)$$

$$P = P(t)$$

as constituting the parametric equations of a curve in the H-P plane, then we can find the equation of this curve. On eliminating t in (a) and (b) by division, and separating the variables we obtain

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

Integrating gives us

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

or

$$P^{a_1} e^{-b_1 P} = K e^{b_2 H} H^{-a_2} \quad (2)$$

where the constant K is given by

$$K = H_0^{a_2} P_0^{a_1} e^{-b_2 H_0 - b_1 P_0}$$

in terms of the initial values of H and P .

Although we cannot solve (2) for either H or P, we can determine points on the curve by an ingenious method due to Volterra. To do this, we equate the left and right sides of (2) to new variables Z and W, and then plot the graphs C_1 and C_2 of the functions.

$$Z = P^{a_1} e^{-b_1 P} \quad \text{and} \quad W = K H^{-a_2} e^{b_2 H} \quad (3)$$

as shown in fig.(1). Since $Z = W$, we are confined in the third quadrant to the dotted line L. To the maximum value of Z, given by the point A on C_1 , there corresponds one P and via M on L and the corresponding points A' and A'' on C_2 - two H's, and these determine the bounds between which H 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'' on C_1 and these points determine the bounds for P. In this way, we can find the points P_1 , P_2 and a_1 , a_2 on the desired curve C_3 . Additional points were easily found by starting on L - projecting upto C_1 and over to C_3 , and then over to C_2 and upto C_2 , as indicated in Fig. (1). It is clear that changing the value of K raises or lowers the point 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 these is of C_3 when minimum value of W equals the maximum value of Z.

We next show that as t increases, the corresponding point (H, P) on C_3 moves around the curve in an anticlockwise direction. To see this, we begin by noting that eqns. 1(a) and 1(b) give the horizontal and vertical components of the velocity of this point. A simple calculation based on formulae (3) shows that the point S has coordinates $H = a_2/b_2$, and $P = a_1/b_1$. When $H < a_2/b_2$, it follows from the eqn. 1(b) that dP/dt is negative, so our point on C_3 moves down as it traverses the arc $Q_2P_1Q_1$. Similarly, it moves up along the arc $Q_1P_2Q_2$.

Thus, we find that system described by eqns. 1(a) and 1(b) is characterised by endlessly prolonged oscillations of constant amplitude and this amplitude will be determined by the chosen initial population sizes, H_0 and P_0 . In other words, the system has neutral stability, which means that the two populations undergo constant oscillations with amplitudes depending on the initial population sizes rather than on any intrinsic attributes of the two interacting species.

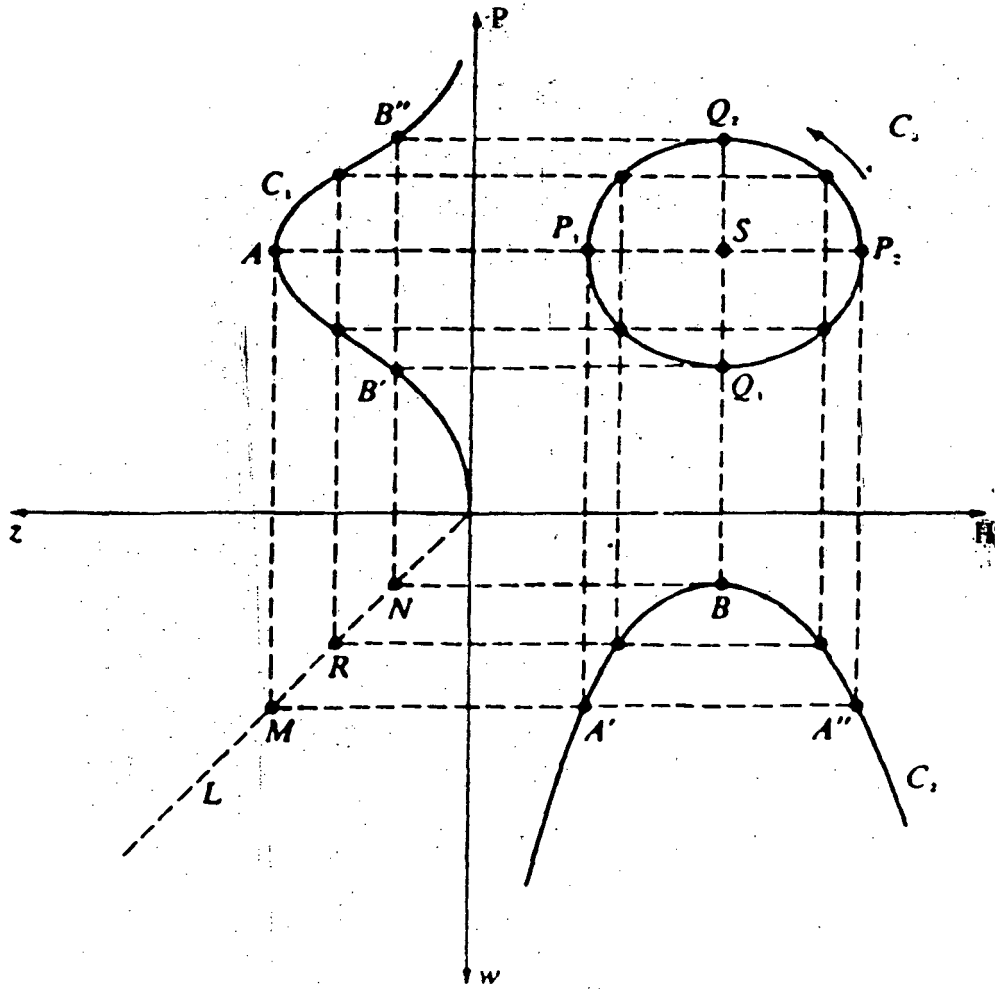


FIGURE 1

Another way of reaching the same conclusion, i.e. that the model possesses neutral stability, is by considering the behaviour of linear version of the model in the neighbourhood of its equilibrium points.

So, we consider the behaviour of the system in the neighbourhood of the equilibrium point (H^*, P^*) . The equilibrium populations H^* and P^* are the non-zero solutions obtained by putting $dH/dt = 0$ and $dP/dt = 0$ in equations 1(a) and 1(b). It gives us :

$$H^* = a_2/b_2$$

$$P^* = a_1/b_1$$

Defining

$$H - H^* = X_1$$

$$P - P^* = X_2$$

We obtain, near the equilibrium points, the following equations.

$$\frac{dX_i}{dt} = \sum_j a_{ij} x_j ; \quad i, j = 1, 2$$

$$\text{Where } a_{ij} = \left. \frac{\partial F_i}{\partial X_j} \right|$$

$$\begin{aligned} H &= H^* \\ P &= P^* \end{aligned}$$

and F_i are defined below in (4a) and (4b).

The elements a_{ij} of what is commonly known as the community matrix can now be calculated as follows :

Let us represent the right hand sides of eqns. 1(a) and 1(b) in the following manner :

$$F_1(H, P) \equiv H[a_1 - b_1 P] \quad (4a)$$

$$F_2(H, P) \equiv P[-a_2 + b_2 H] \quad (4b)$$

So, $a_{11} = \partial f_1 / \partial H = a_1 - b_1 P$

$$a_{12} = \partial f_1 / \partial P = -b_1 H$$

$$a_{21} = \partial f_2 / \partial H = b_2 P$$

$$a_{22} = \partial f_2 / \partial P = -a_2 + b_2 H$$

Evaluated at the equilibrium point (H^*, P^*) , these partial derivatives give

$$\begin{aligned} a_{11} &= 0, & a_{12} &= -b_1 a_2 / b_2 \\ a_{21} &= b_2 a_1 / b_1, & a_{22} &= 0. \end{aligned} \tag{5}$$

Now, the community matrix A can be written as

$$A = \begin{bmatrix} 0 & -b_1 a_2 / b_2 \\ b_2 a_1 / b_1 & 0 \end{bmatrix}$$

The eigenvalues of the matrix follow from the determinantal eqn. $\det. |A - \lambda I| = 0$, which here takes the form

$$\det \begin{vmatrix} -\lambda & -b_1 a_2 / b_2 \\ b_2 a_1 / b_1 & -\lambda \end{vmatrix} = 0$$

$$\lambda^2 + a_1 a_2 = 0 \tag{6}$$

Thus, the eigenvalues are the pair of purely imaginary numbers $\pm iw$, where for notational convenience we introduce $w = \sqrt{a_1 a_2}$.

The perturbations to host (prey) and parasite (predator) populations are linear combinations of the factors $\exp(\lambda_1 t)$ and $\exp(\lambda_2 t)$, with coefficients depending upon the initial disturbance. Here this means we have linear combinations of the purely oscillatory factors $e^{i\omega t}$ and $e^{-i\omega t}$, which is to say linear combinations of $\cos(\omega t)$ and $\sin(\omega t)$. That is, the stability is neutral, with perturbations leading to undamped pure oscillations, of frequency ω or period $(2\pi/\omega)$, but amplitudes depending on the initial conditions.

This "unnatural" behaviour of the model, leading to constant oscillations whose amplitudes would depend on the initial conditions rather than the intrinsic biological attributes of the interacting systems, probably makes further study of it unprofitable. We, therefore, turn to consideration of more realistic models.

Later authors have given more realistic models, yielding solutions that would asymptotically be independent of the initial conditions and depend only on the intrinsic attributes of the interacting system, e.g. the parameters a_1, a_2, b_1 , etc. in eqn. 1(a) and 1(b).

Leslie and Gower and later Holling and Tanner consider such models which mark significant improvement over the one by Lotka and Volterra. We will discuss these two models in detail in the next chapter.

CHAPTER - 2

LESLIE AND GOWER MODEL

This model is represented by the equations given below :

$$\frac{dH}{dt} = (a_1 - C_1 P) H \quad (2a)$$

$$\frac{dP}{dt} = \left(a_2 - C_2 \frac{P}{H} \right) P \quad (2b)$$

where all the constants $a_1, C_1, a_2, C_2 > 0$.

In the model following assumptions are inherent:

- (i) The rate of increase of a parasite (predator) population has an upper limit, and
- (ii) intraspecific competition has negligible effect on host's population growth.

In the above equations the parameter a_1 is intrinsic growth rate of host (or prey) and C_1 is the effect

of the density of the predator (or parasite) population on the population growth of the host (or prey). a_2 is the intrinsic growth rate of the parasite and the factor $C_2(P/H)$ tells us that the rate of the growth of the predator (or parasite) population is limited and causes a decrease in the rate of increase of the predator population as P increases.

Local stability analysis applying Ruth-Hurwit criteria leads to damped oscillations towards a stable equilibrium level in both populations. The details of the above analysis for the present model can be given as hereunder:

$$F_1(H,P) = (a_1 - C_1P) H$$

$$F_2(H,P) = (a_2 - C_2(P/H))P$$

Setting $F_1(H,P)$ and $F_2(H,P)$ equal to zero leads to

$$P^* = a_1/C_1 \text{ and } H^* = (a_1C_2/a_2C_1)$$

as the host and parasite populations are not zero. Now let us calculate various elements of the community matrix as follows :

$$\frac{\partial F_1}{\partial H} = a_1 - C_1 P$$

$$\frac{\partial F_1}{\partial P} = -C_1 H$$

$$\frac{\partial F_2}{\partial H} = C_2 \left(-\frac{P^2}{H^2} \right)$$

$$\frac{\partial F_2}{\partial P} = a_2 - C_2/H \quad (2P)$$

If we calculate these at equilibrium point $[P^*=(a_1/C_1), H^*=(a_1 C_2/a_2 C_1)]$, we get $a_{11} = 0$, $a_{12} = - (a_1 C_2/a_2)$, $a_{21} = (a_2^2/C_2)$, and $a_{22} = - a_2$.

The community matrix can be written as

$$A = \begin{bmatrix} 0 & -\frac{(a_1 C_2)}{a_2} \\ \frac{a_2^2}{C_2} & -a_2 \end{bmatrix}$$

The determinantal equation $(A - \lambda I) = 0$ will be

$$\begin{pmatrix} 0 - \lambda & -\frac{a_1 c_2}{a_2} \\ \frac{(a_2)^2}{(c_2)^2} & -a_2 - \lambda \end{pmatrix} = 0$$

$$\Rightarrow \begin{pmatrix} -\lambda & -\frac{a_1 c_2}{a_2} \\ \frac{(a_2)^2}{(c_2)^2} & -a_2 - \lambda \end{pmatrix} = 0$$

$$\Rightarrow \lambda^2 + a_2 \lambda + \left(-\frac{a_1 a_2}{c_2}\right) = 0 \quad (3)$$

As $a_2 > 0$ and $(a_1 a_2 / c_2) > 0$, eqn.(3) shows that the Leslie-Gower model possesses neighbourhood stability.

The basic characteristic of the Leslie-Gower model is that it leads to such a solution which is asymptotically independent of the initial conditions and depend only on the intrinsic attributes of the interacting system, e.g., the parameters a_1, C_1 , etc.

A typical trajectory governed by the model given by equations (2a) and (2b) has been shown in figure (2.1). In figure (2.2) the corresponding time development of the two populations has been shown.

We can also incorporate in the above model a self-interaction term like $-b_1 H^2$ in the equation for the time rate of change for the host. The equations of the model are then :

$$\frac{dH}{dt} = (a_1 - b_1 H - C_1 P) H \quad (4a)$$

$$\frac{dP}{dt} = (a_2 - C_2 P/H) P \quad (4b)$$

where all the constants a_1 , b_1 , C_1 , a_2 and C_2 are positive.

The local stability criteria can now be worked out as follows :

First of all let us find out the various elements of the community matrix A.

$$\frac{\partial F_1}{\partial H} = a_1 - C_1 P$$

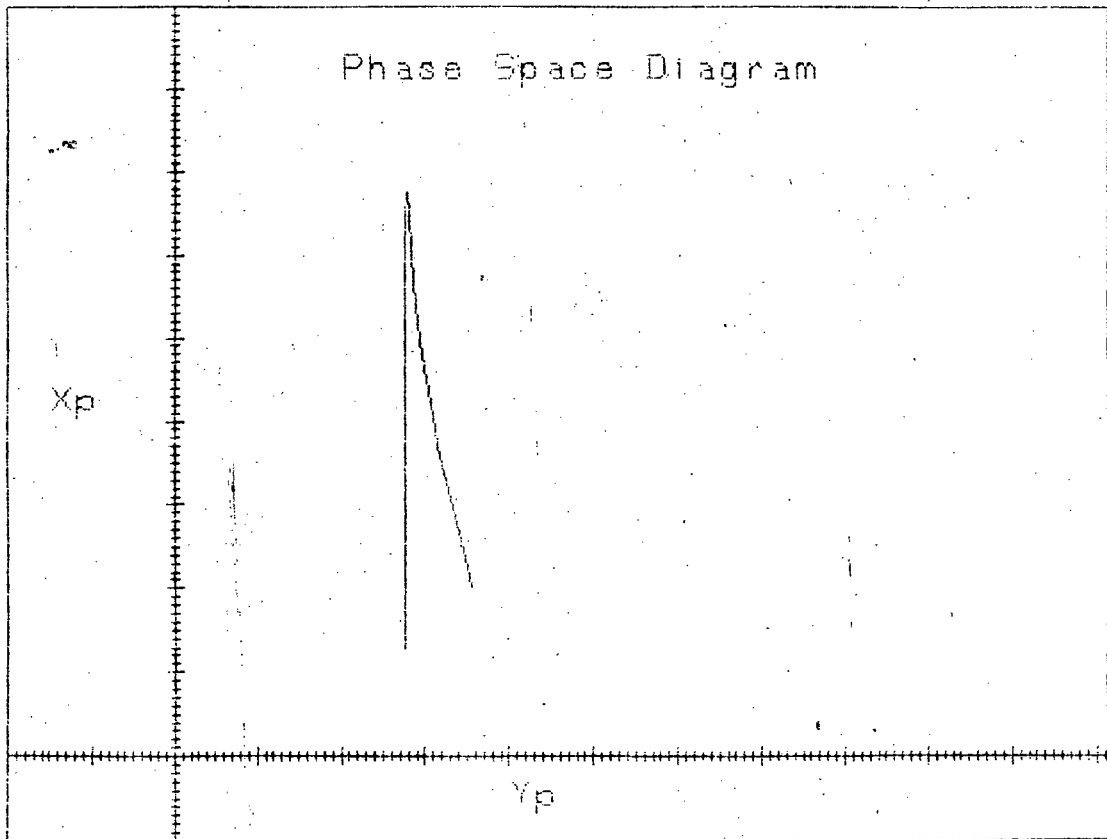


Fig. 2.1 X_p denotes the prey population and Y_p denotes Predator population. $a_1 = 1.2$, $C_1 = 0.05$, $a_2 = 1.5$, $C_2 = 0.01$, $X_p = 25$, $Y_p = 130$

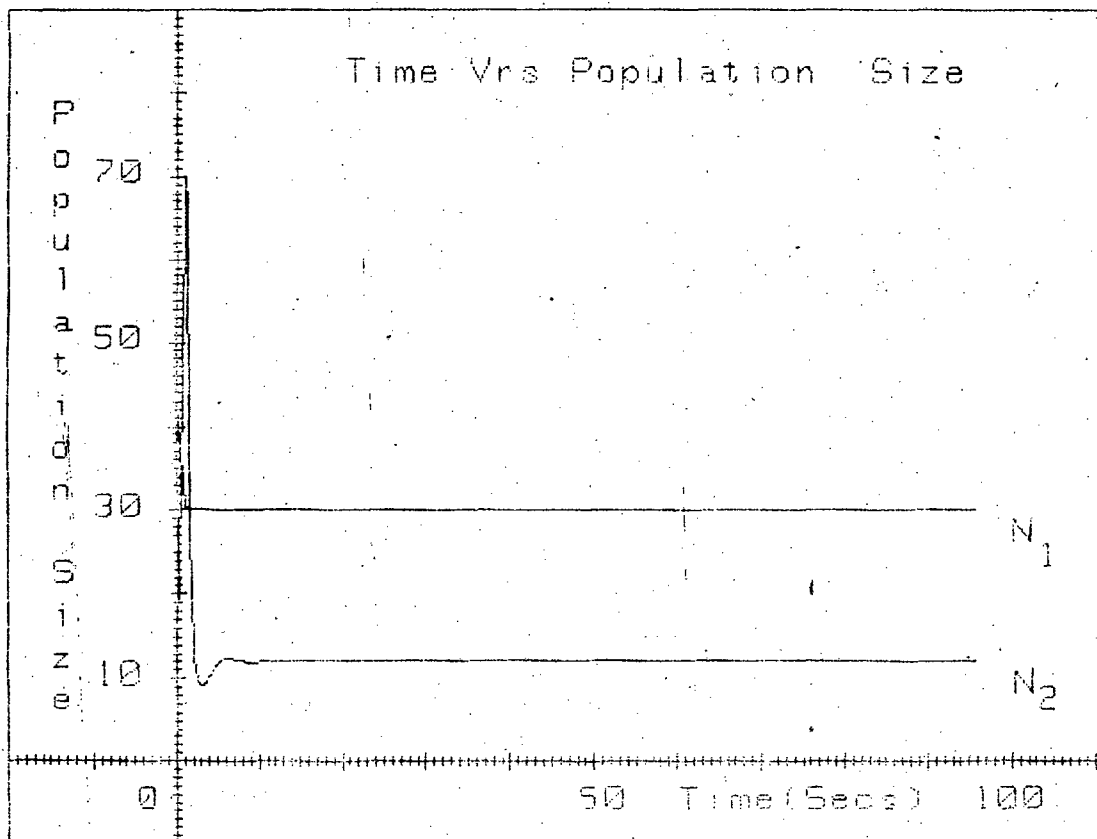


Figure 2.2. N_1 denotes the prey population and N_2 denotes the predator population.
 $a_1 = 1.2$, $C_1 = 0.05$, $a_2 = 1.5$, $C_2 = 0.01$, $N_1 = 25$,
 $N_2 = 30$.

$$\frac{\partial F_1}{\partial P} = -C_1 H$$

$$\frac{\partial F_2}{\partial H} = C_2 (P^2/H^2)$$

$$\frac{\partial F_2}{\partial P} = a_2 - C_2/H \quad (2P)$$

Now, let us evaluate each of these at the equilibrium point ($H^* = a_1 C_2 / a_2 C_1 + b_1 C_2$; $P^* = a_1 a_2 / a_2 C_1 + b_1 C_2$).

Various elements of the community matrix turn out to be as follows :

$$a_{11} = \left(\frac{\partial F_1}{\partial H} \right)^* = - \frac{a_1 b_1 c_2}{a_2 c_1 + b_1 c_2}$$

$$a_{12} = \left(\frac{\partial F_1}{\partial P} \right)^* = - \frac{a_1 c_1 c_2}{a_2 c_1 + b_1 c_2}$$

$$a_{21} = \left(\frac{\partial F_2}{\partial H} \right)^* = - \frac{a_2^2}{c_2},$$

and the last one is is

$$a_{22} = \left(-\frac{\partial F_2}{\partial p} \right)^* = -a_2$$

Community matrix A can now be written as



$$A = \begin{bmatrix} \frac{a_1 b_1 c_2}{a_2 c_1 + b_1 c_2} & \frac{a_1 c_1 c_2}{a_2 c_1 + b_1 c_2} \\ \frac{a_2^2}{c_2} & -a_2 \end{bmatrix}$$

The determinantal equation $(A - \lambda I) = 0$ gives us

$$\begin{pmatrix} \frac{a_1 b_1 c_2}{a_2 c_1 + b_1 c_2} - \lambda & \frac{a_1 c_1 c_2}{a_2 c_1 + b_1 c_2} \\ \frac{a_2^2}{c_2} & -a_2 - \lambda \end{pmatrix} = 0$$

$$\implies \lambda^2 + \left(a_2 + \frac{a_1 b_1 c_2}{a_2 c_1 + b_1 c_2} \right) \lambda$$

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$$+ \left(\frac{a_1 c_1 a_2^2 + a_1 a_2 b_1 c_2}{a_2^2 c_1 + b_1 c_2} \right) = 0 \quad (5)$$

Diss? $a_2^2 c_1 + b_1 c_2$

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$$\text{As } \left(a_2 + \frac{a_1 b_1 c_2}{a_2 b_1 + b_1 c_2} \right) > 0 \quad \text{and}$$

$$\left(\frac{a_1 c_1 a_2^2 + a_1 a_2 b_1 c_2}{a_2 c_1 + b_1 c_2} \right) > 0$$

because of all the constants are positive. Equation 5) shows that the system given by equations (4a) and (4b) also possesses neighbourhood stability.

Like Leslie-Gower model without self-interaction term in the rate eqn. for the host, this Leslie-Gower model (given by equations (4a) and (4b)) also leads to solutions which are asymptotically independent of initial conditions and depend only on the intrinsic attributes of the interacting system (e.g., constants a_1 , b_1 , C_1 , etc).

A typical trajectory governed by the model is shown in Fig. 2.3. and the corresponding time development of the two populations is given in Fig. 2.4.

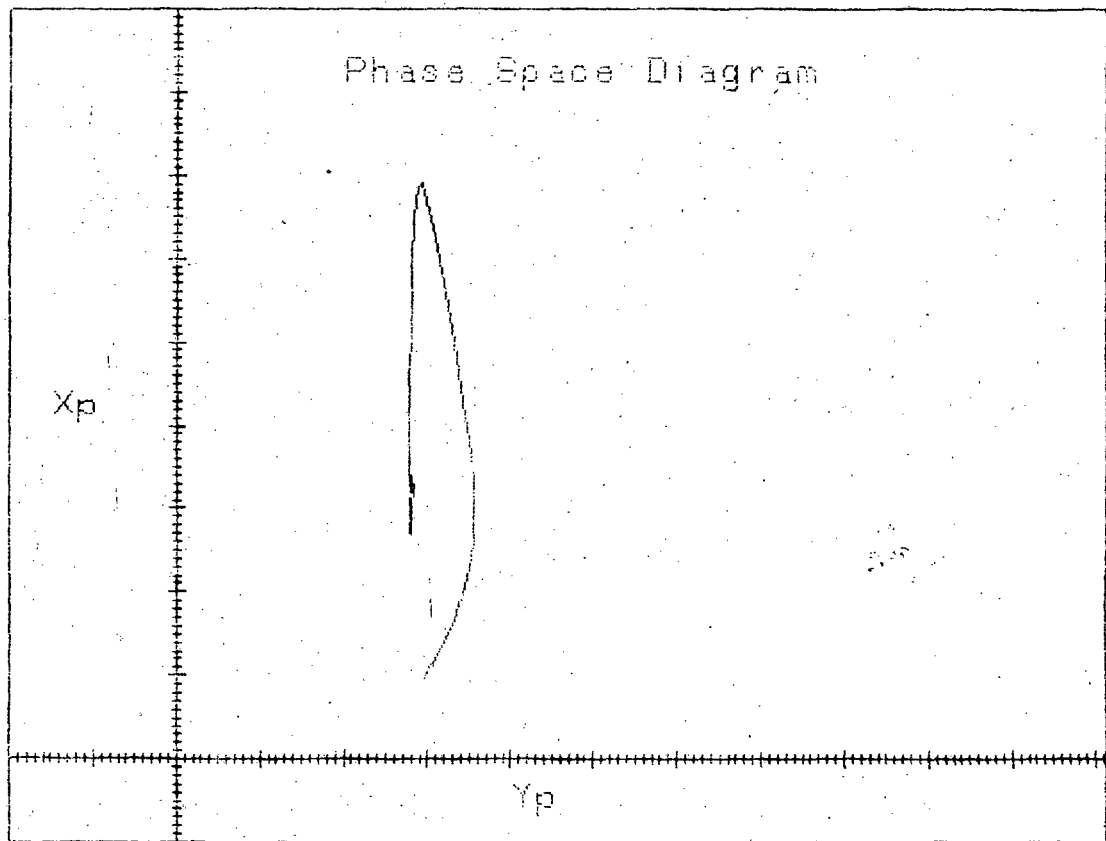


Figure 2.3 $a_1 = 2.5$, $b_1 = 0.005$, $c_1 = 0.02$, $a_2 = 1.5$,
 $c_2 = 0.05$, $X_p^1 = 50$, $Y_p = 40$.

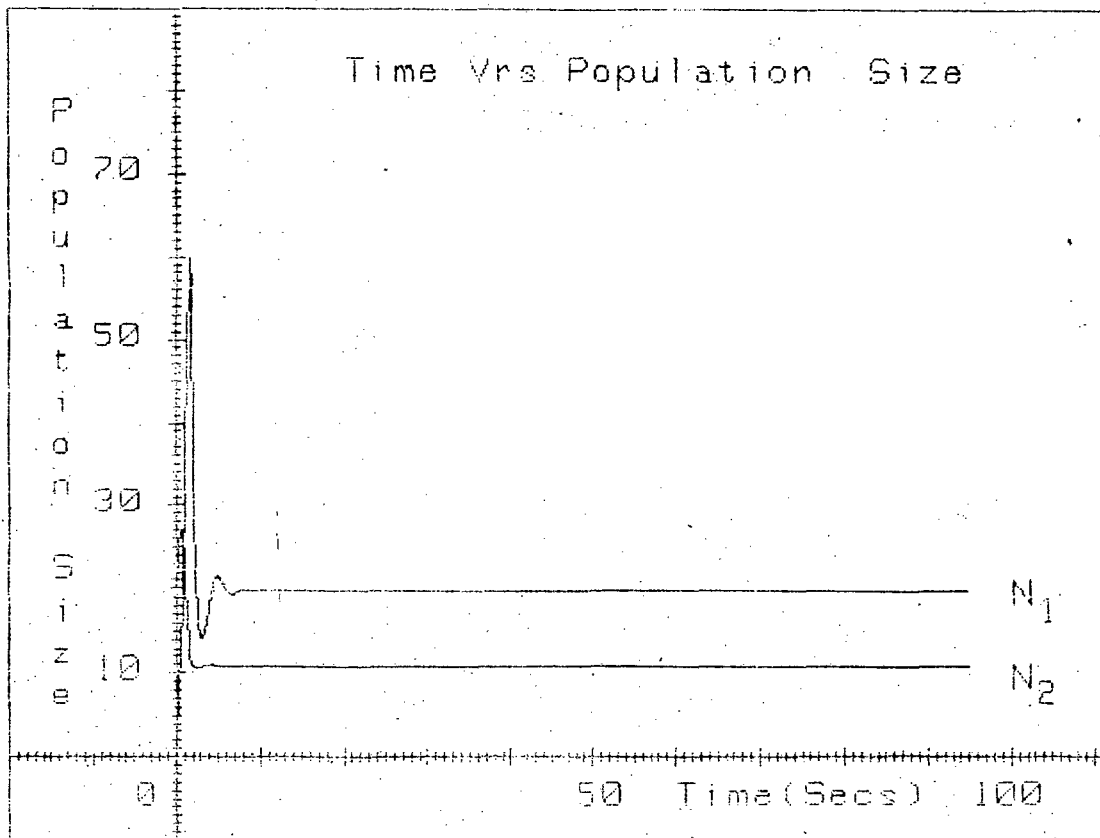


Figure 2.4 N_1 denotes the prey population and N_2 denotes the predator population. $a_1 = 2.5$, $b_1 = 0.005$, $c_1 = 0.02$, $a_2 = 1.5$, $c_2 = 0.05$, $N_1 = 50$, $N_2 = 40$.

Holling-Tanner Model

This model is given by the following equations :

$$\frac{dH}{dt} = \left(a_1 - b_1 H - \frac{W P}{D + H} \right) H \quad (6a)$$

$$\frac{dP}{dt} = \left(a_2 - c_2 \frac{P}{H} \right) P \quad (6b)$$

This model preserves the equation (2b) of Laslie-Gower model but the rate equation for the host (or prey) is completely different. Since the rate equation for the parasite is the same as that of the parasite in Leslie-Gower model, we need not explain the various terms in (6b) again. In eqn. (6a), a_1 is the intrinsic growth rate of host and b_1 measures the effect of intraspecific competition.

The assumption underlying eqn.(6a) is that in the absence of the parasite, the host population would grow logistically but if the former is present, the host's growth rate is reduced. The coefficient $(W/D+H)$ is achieved by considering the probable effect of the density of the host's

population on parasites attack rate. If this coefficient is multiplied by H (the host population at any instant of time), it gives the attack rate on the hosts per parasite. We denote it by y ,

$$y = \frac{W H}{D + H}$$

It is reasonable to assume that this rate would be a function of the parasite's ability to attack on the hosts. So, therefore, there should be a ceiling W to y no matter how large the host's population becomes. The quantity y does, indeed, have this property. It is obvious from the fact that when $H \rightarrow \infty$, $y \rightarrow W$, which is the maximum that it can reach. The constant D in equation (6a) measures the host's ability to evade attack. The larger the value of D , more elusive is the host in evading attack by parasites.

Let us analyse the model given by equations (6a) and (6b) both locally and globally. At first, we present the local stability analysis of the model.

Writing N_1 for the host (or prey) population and N_2 for the parasite (or predator) population in eqns. (6a) and (6b), we get

$$F_1(N_1, N_2) = a_1 N_1 \left[1 - \frac{b_1}{a_1} N_1 - \frac{W}{a_1} \frac{N_2}{N_1 + D} \right]$$

$$F_2(N_1, N_2) = a_2 N_2 \left[1 - \frac{N_2}{\left(\frac{a_2}{c_2}\right) N_1} \right]$$

$$F_1 = 0 \Rightarrow 1 - N_1^* \frac{b_1}{a_1} - \frac{W}{a_1} \frac{N_2^*}{(N_1^* + D)} = 0 \quad (7)$$

$$F_2 = 0 \Rightarrow N_2^* = \frac{a_2}{c_2} N_1^* \quad (8)$$

Let us define two quantities and

$$\alpha = \frac{W a_2}{c_2 a_1} \quad (9)$$

$$\beta = \frac{D b_1}{a_1} \quad (10)$$

The solution of the quadratic equation (7) for the host equilibrium population is given by :

$$N_1^* = \frac{D(1 - \alpha - \beta + R)}{2\beta}$$

where $R = [(1 - \alpha - \beta)^2 + 4\beta]^{1/2}$ (11)

and α and β are already defined.

To construct the community matrix we proceed as follows :

$$a_{11} = \left(\frac{\partial F_1}{\partial N_1} \right)^* = a_1 N_1^* \left[-\frac{b_1}{a_1} + \frac{(W/a_1) N_2^*}{(N_1^* + D)^2} \right]$$

$$a_{12} = \left(\frac{\partial F_1}{\partial N_2} \right)^* = -\frac{W N_1^*}{N_1^* + D}$$

$$a_{21} = \left(\frac{\partial F_2}{\partial N_1} \right)^* = \frac{a_2 (N_2^*)^2}{(a_2/c_2) (N_1^*)^2} = \frac{a_2^2}{c_2}$$

$$a_{22} = \left(\frac{\partial F_2}{\partial N_2} \right)^* = -\frac{a_2 N_2^*}{a_2/c_2 N_1^*} = -a_2$$

After calculating all the matrix elements it is very easy to write the community matrix. It looks like as :

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

where the matrix elements have already been evaluated.

Now, the determinantal eqn. $(A - \lambda I) = 0$ gives us

$$\lambda^2 + a\lambda + b = 0 \quad (12)$$

with $a = -(a_{11} + a_{22})$

$$b = a_{11}a_{22} - a_{12}a_{21}$$

Eqn. (12) is a quadratic eqn. It gives us

$$\lambda = \frac{-a \pm \sqrt{a^2 - 4b}}{2} \quad (13)$$

According to Ruth-Hurwitz criteria, the necessary and sufficient condition for the system to possess neighbourhood stability is that both eigen values λ should have -ve real parts. From eqn.(13) it is quite clear that both values of λ will have negative real parts in all the

cases. So, they obviously satisfy the Ruth-Hurwitz criteria provided $a > 0$, $b > 0$.

The condition $b > 0$ implies

$$-a_1 N_1^* a_2 \left[-\frac{b_1}{a_1} + \frac{(W/a_1) N_2^*}{(N_1^* + D)^2} \right] + \frac{W N_1^*}{(N_1^* + D)} - \frac{a_2^2}{C_2} > 0$$

$$\Rightarrow \frac{b_1}{a_1} - \frac{\alpha N_1^*}{(N_1^* + D)^2} + \frac{\alpha}{N_1^* + D} > 0$$

$$\Rightarrow \frac{\alpha N_1^*}{(N_1^* + D)^2} - \frac{\alpha}{N_1^* + D} < \frac{b_1}{a_1}$$

$$\Rightarrow -\frac{\alpha D}{(N_1^* + D)^2} < \frac{b_1}{a_1}$$

\Rightarrow a negative quantity is less than a positive quantity, which is always true.

The second condition, $a > 0$, clearly needs

$$a_2 - a_1 N_1^* \left[-\frac{b_1}{a_1} + \frac{\alpha N_1^*}{(N_1^* + D)^2} \right] > 0$$

After some algebraic manipulation using eqn.(11) for N_1^* along with the definitions (9), (10) and (12), we get the stability criterion as

$$\left(\frac{a_2}{a_1}\right) > \frac{2(\alpha - R)}{1 + \alpha + \beta + R} \quad (14)$$

In particular, for given α the largest value the R.H.S. can attain is $\frac{1}{\alpha}$ if $\alpha > 1$ or $(2\alpha - 1)$ if $\alpha < 1$ (this limit is being attained when $\beta \rightarrow 0$). Values of a_2/a_1 in excess of these limits consequently always imply stability.

The answer to the question whether the local stability condition (14) will or will not be satisfied will depend on the chosen values of various parameters involved in the inequality (14).

When we do the Kolmogorov analysis (which is discussed in detail, for convenience in the next Chapter), we find that it satisfies all the conditions imposed by Kolmogorov for a system to possess either a stable equilibrium point or a stable limit cycle.

The criterion (14), therefore, divides the region where the host - parasite (or predator-prey) equations (6a) and (6b) have a stable equilibrium point from the region where they exhibit stable limit cycle.

In figure 2.5, we take α to be unity, and show that what the stability criterion (14) implies about the parameters a_1/a_2 and a_1/b_1 . Similar stability boundaries can be shown for other values of α .

It is clear from the figure 2.5 that the system given by equations (6a) and (6b) possesses stable equilibrium point provided either one of $(a_1/b_1 > D)$ or (a_1/a_2) is not too large.

If both are largish (i.e. to say host population is characterised by relatively weak self-regulation and by host intrinsic growth rate which is significantly in excess of that of the parasite), the equilibrium point is not stable. In such cases, one gets the stable limit cycle behaviour. In figures 2.6 and 2.7 numerical calculations leading to both kinds of solutions have been given. Corresponding time development of the two

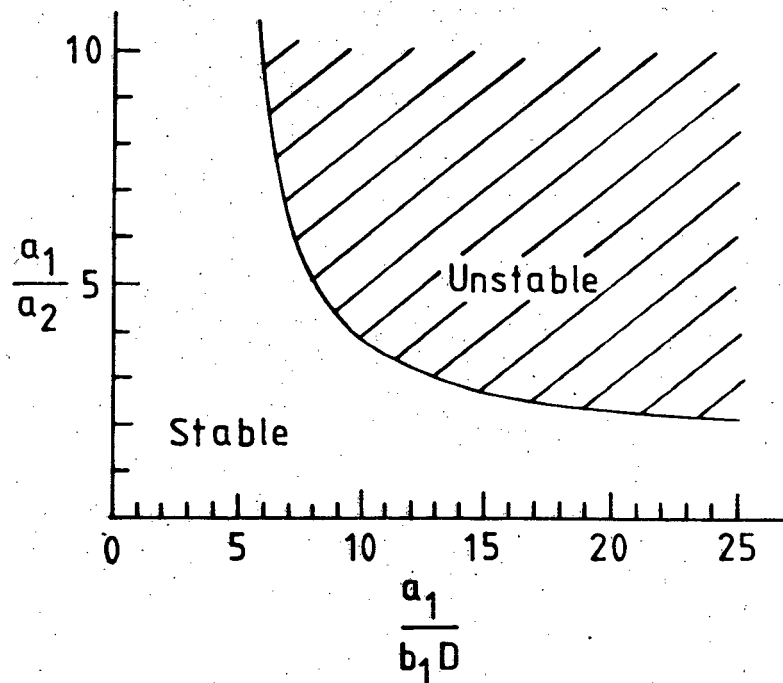


Fig 2:5. This figure shows the stability criterion (14), in terms of the parameter ratios $\frac{a_1}{a_2}$ and $\frac{a_1}{b_1 D}$, for predator - prey system characterised by equations (6a) and (6b). In the unhatched region of the parameter space, the equilibrium point is stable ; in the hatched region it is unstable. (Although the figure is for $\frac{W a_2}{C_2 a_1} = 1$, but qualitatively similar stability boundaries pertain to other values of this ratio).

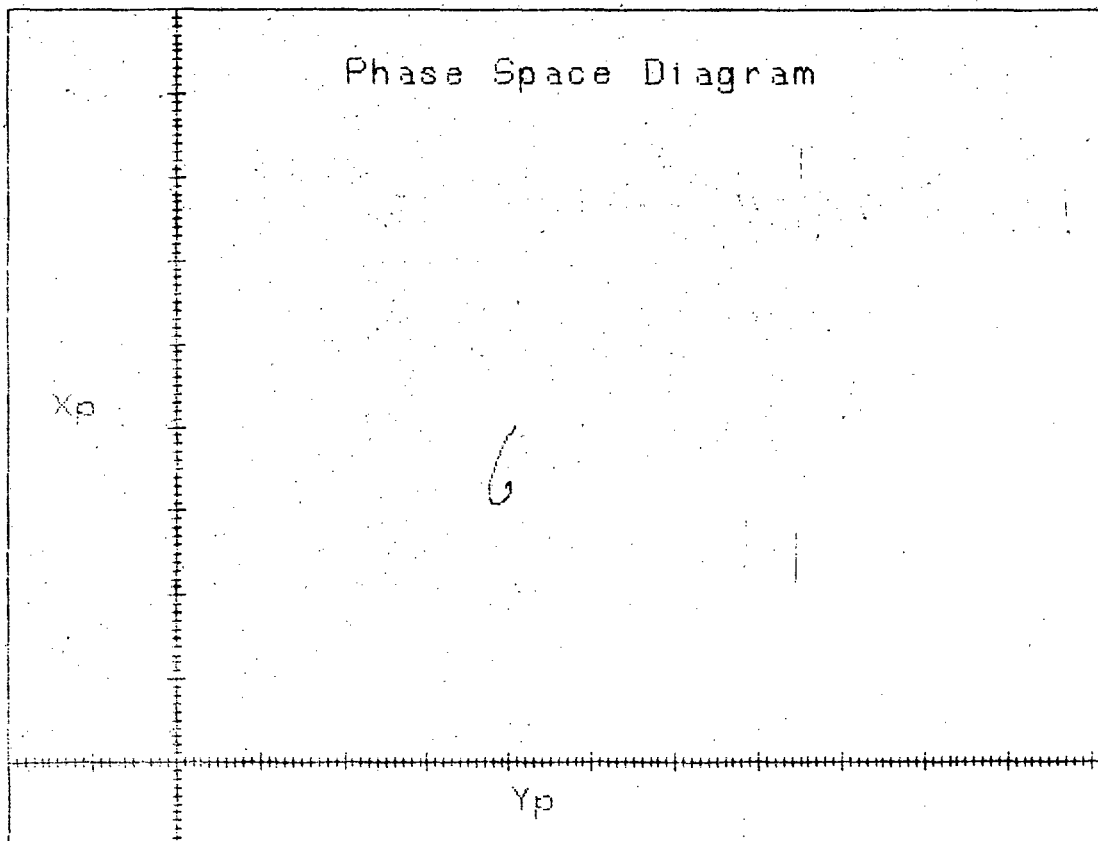


Figure 2.6 X_p denotes the prey population Y_p denotes the predator population.

$a_1 = 1.2$, $b_1 = 0.024$, $W = 1$, $D = 10$, $a_2 = 0.6$, $C_2 = .5$,
 $X_p = 20$, $Y_p = 30$.

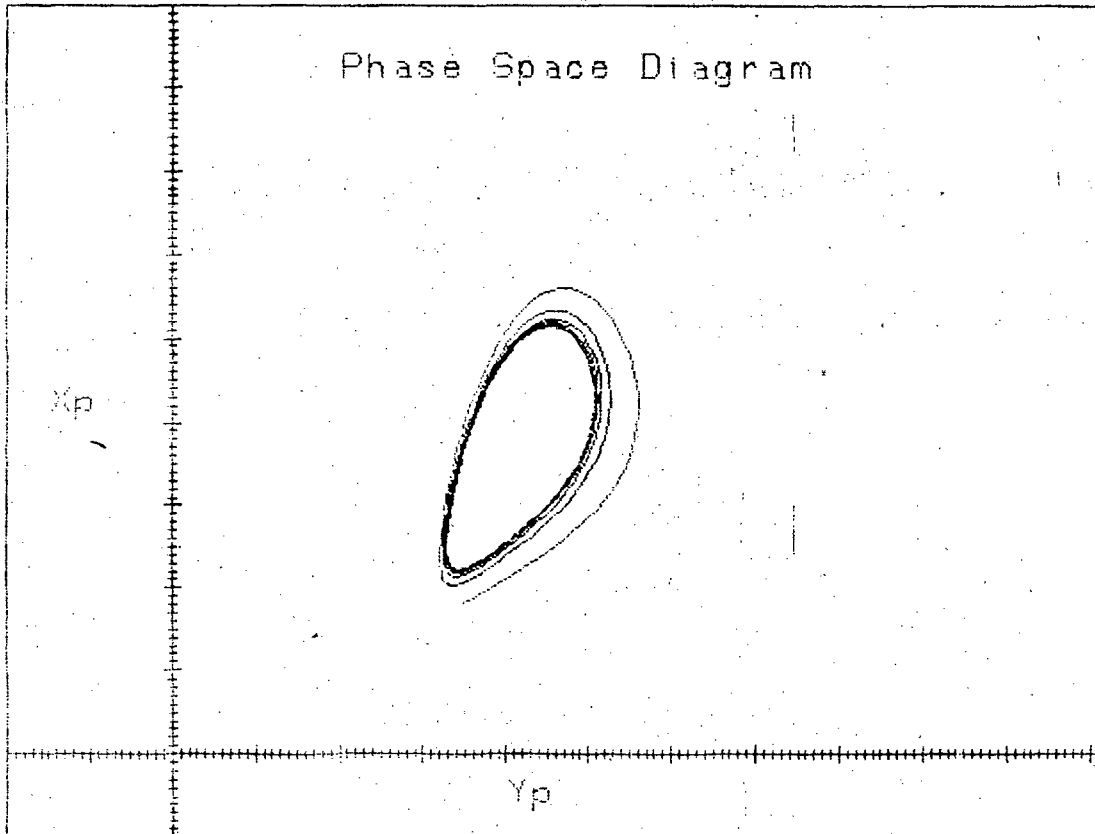


Figure 2.7 X_p denotes the prey population, Y_p denotes the predator population.

$$a_1 = 2, a_2 = .66, b_1 = .0133, D = 10, W = 1, C_2 = .33, \\ X_p = 20, Y_p = 30.$$

populations are given in Figures 2.8 and 2.9, respectively.

In the next chapter we will discuss our own model which is theoretically not any worse than above model, and it is even an improvement over the former in some respects.

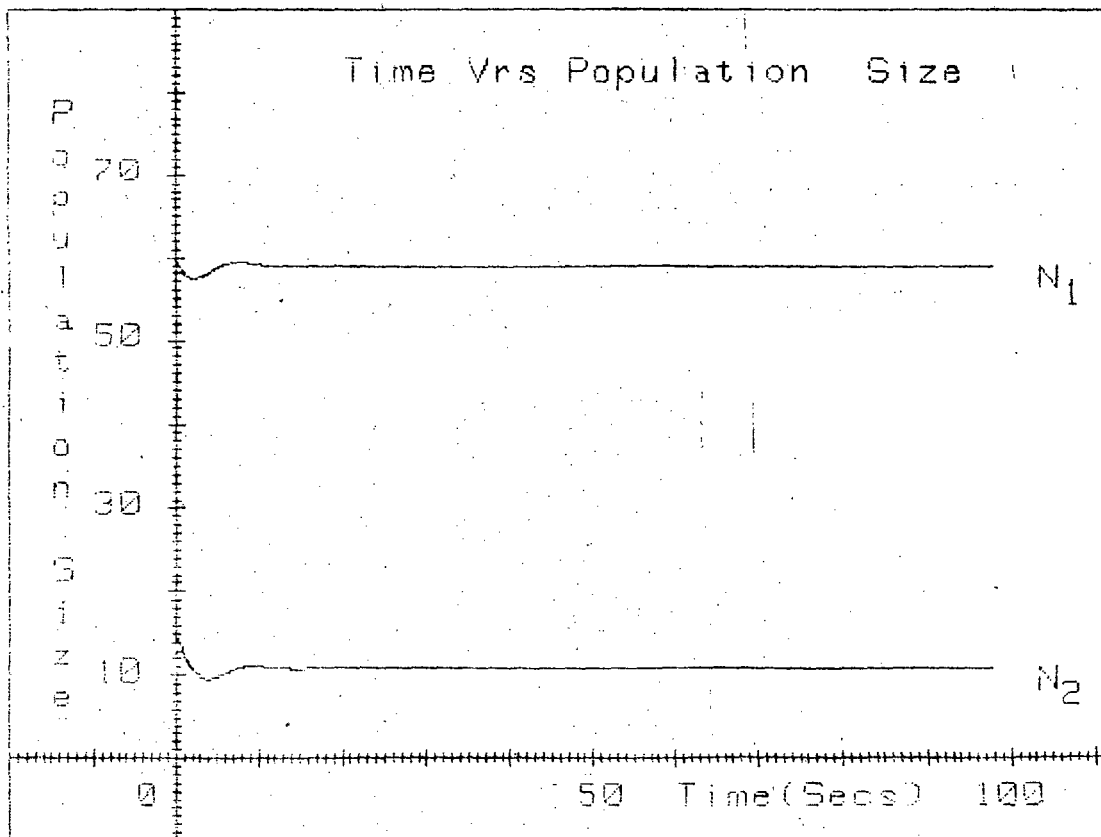


Figure 2.8 N_1 denotes the prey population and N_2 denotes the predator population.

$a_1 = 1.2$, $b_1 = 0.024$, $W = 1$, $D = 10$, $a_2 = 0.6$, $C_2 = .5$,
 $N_1 = 20$, $N_2 = 30$.

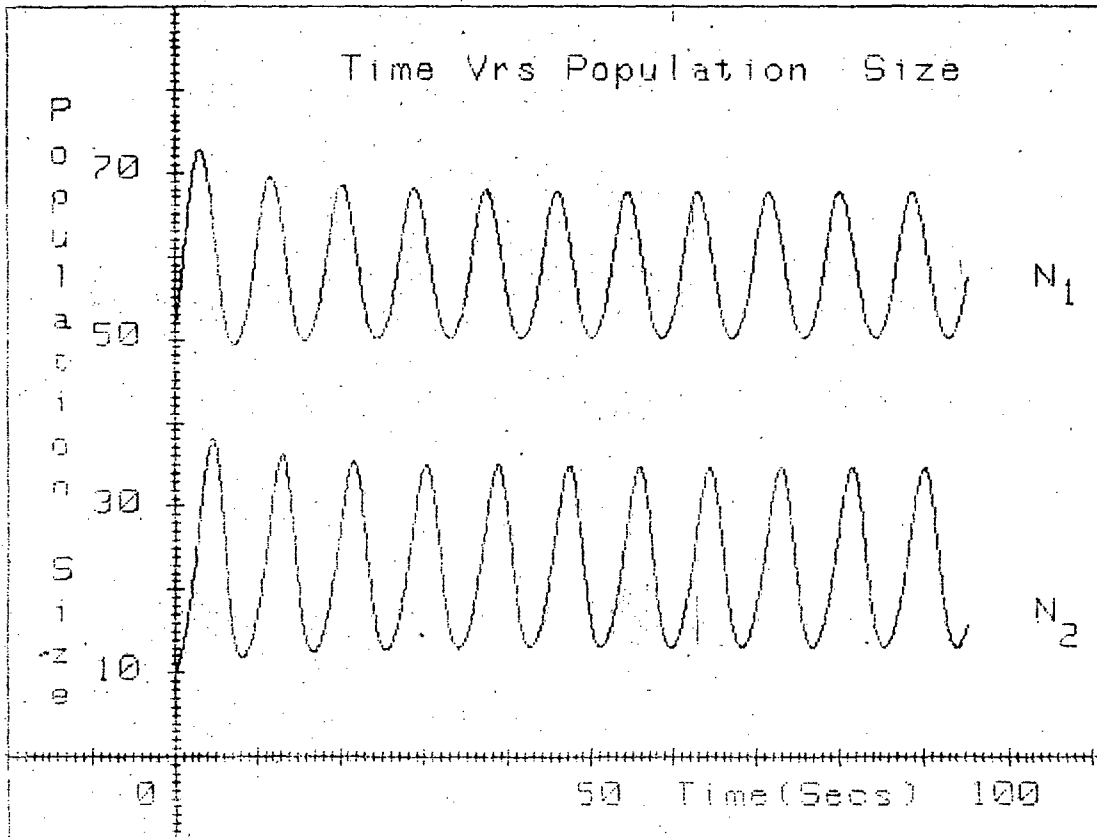


Figure 2.9 N_1 denotes the prey population and N_2 denotes the predator population.

$$a_1 = 2, a_2 = .66, b_1 = .0133, D = 10, W = 1, C_2 = .33,$$

$$N_1 = 20, N_2 = 30.$$

CHAPTER - 3

A NEW PREY-PREDATOR MODEL

In this Chapter, we improvise on the ideas contained in the Leslie-Gower and Holling - Tanner models to construct a new model which has the following features:

The per capita growth rate of the parasite is not proportional to the population ratio (P/H) but rather to a factor which is similar in form as the parasite's attack rate with a ceiling W_1 , occurring for $H \rightarrow \infty$. This establishes a desirable relationship between the host's loss and the parasite's gain which does not exist in the Holling-Tanner model.

The interaction terms in the new model appearing in the rate equations restore to some extent the symmetry which characterises the Lotka-Volterra model. Moreover, we also find that the behaviour of the rate equation for the parasite (or predator) near $H = 0$ is now improved over the Leslie-Gower and Holling-Tanner models. The behaviour for $H \rightarrow \infty$ leading to exponential growth for the parasite, is of course common to all the models, but this possibility is

always excluded due to the presence of the self-interaction term in the rate eqn. for the host.

The present model is given by the equations

$$\frac{dH}{dt} = a_1 H - b_1 H^2 - \frac{W}{D + H} P H \quad (3a)$$

$$\frac{dP}{dt} = -a_2 P + \frac{W_1}{D_1 + H} H P \quad (3b)$$

where $a_1, b_1, W, D, a_2, W_1, D_1 > 0$.

Now, let us see how this model behaves globally and locally. To see this we first do the Kolmogorov analysis of the model. Before the actual analysis is done, we would like to mention what is Kolmogorov theorem and what do the various Kolmogorov constraints mean in biological terms.

Kolmogorov theorem is often put in the following form :

If a system given by equations

$$\begin{aligned} \frac{dH}{dt} &= H F (H, P) \\ \frac{dP}{dt} &= p G(H, P) \end{aligned} \tag{4}$$

where H is the host (or prey) population at any instant of time and P is the parasite (or predator) population at the same instant of time; satisfies the following conditions :

- i) $\frac{\partial F}{\partial P} < 0$
- ii) $H \left(\frac{\partial F}{\partial H} \right) + P \left(\frac{\partial F}{\partial P} \right) < 0$
- iii) $\frac{\partial G}{\partial P} < 0$
- iv) $H \left(\frac{\partial G}{\partial H} \right) + P \left(\frac{\partial G}{\partial P} \right) > 0$
- v) $F(0,0) > 0$ and fulfils the requirements :
- vi) $F(0,A) = 0$, with $A > 0$
- vii) $F(B,0) = 0$, with $B > 0$
- viii) $G(C,0) = 0$, with $C > 0$

ix) $B > C$,

then it possesses either a stable equilibrium point or a stable limit cycle, provided that F and G are continuous functions of H and P , with continuous first derivatives, throughout the domain $H \geq 0$, $P \geq 0$.

In biological terms, Kolmogorov conditions can be put as follows :

i] for any given population size (as measured by numbers, biomass, etc.), the per capita rate of increase of the prey species is a decreasing function of the number of predators, and similarly (iii) the rate of increase of predators decreases with their population size. For any given ratio between the two species, (ii) the rate of increase of prey is a decreasing function of the population size while conversely (iv) that of the predators is an increasing function. It is also required that (v) when both populations are small the prey have a positive rate of increase, and that (vi) there can be a predator population size sufficiently large to stop further prey increase, even when the prey are rare. Condition (vii) requires a critical prey population size B , beyond which they cannot increase

even in the absence of predators (a resource or other self limitation), and (viii) requires a critical prey size C that stops further increase in predators, even if they be rare; unless (ix) $B > C$, the system will collapse. These biological constraints are spelled out more elaborately in Scudo (1971) or Rescigno and Richardson (1967).

KOLMOGOROV ANALYSIS OF THE PRESENT MODEL

In our case, functions $F(H,P)$ and $G(H,P)$ are :

$$F(H,P) \equiv a_1 - b_1 H - \frac{WP}{D+H}$$

$$G(H,P) \equiv -a_2 + \frac{W_1 H}{D_1 + H D_1}$$

$$(i) \quad \frac{\partial F}{\partial P} < 0 \implies W, D > 0$$

This condition is satisfied because W and D are both position constants.

$$(ii) \quad H \left(\frac{\partial F}{\partial H} \right) + P \left(\frac{\partial F}{\partial P} \right) < 0$$

$$\implies -b_1 D^2 H - b_1 H^3 - 2b_1 DH^2 < WDP$$

It is quite clear that 2nd condition is satisfied in the domain $H, P > 0$, as b_1, D, W are all positive constants.

$$(iii) \quad \frac{\partial G}{\partial P} = 0$$

$$(iv) \quad H \left(\frac{\partial G}{\partial H} \right) + P \left(\frac{\partial G}{\partial P} \right) > 0 \implies D_1 > 0$$

Positivity of D_1 clearly guarantees the satisfaction of this condition.

(v) The requirement $F(0,0) > 0$ needs $a_1 > 0$. As $a_1 > 0$, in our model this requirement is fulfilled.

$$vi) \quad F(0,A) = 0 \text{ gives } A = \frac{a_1 D}{W}, \text{ which is clearly}$$

positive as a_1 , D , W all are positive constants.

So, this requirement is also fulfilled.

$$\text{vii) } F(B, 0) = 0 \Rightarrow B = \frac{a_1}{b_1},$$

which is also clearly positive as a_1 and b_1 are both positive.

$$\text{viii) } G(C, 0) = 0 \Rightarrow C = \frac{a_2 D_1}{W_1 - a_2}. \text{ Since } C \text{ must be}$$

greater than zero, we get a constraint

$$W_1 > a_2 \tag{5}$$

(ix) The condition $B > C$ gives us another constraint

$$\frac{a_1}{b_1} > \frac{a_2 D_1}{W_1 - a_2} \tag{6}$$

Thus we see that an application of the Kolmogorov theorem to the model shows that the theorem is satisfied by it under the conditions :

 F.N: It can be noted here that the original Kolmogorov constraints can be sometimes relaxed in that an inequality can be replaced by an equality (see May

(1974), pp. 88).

$$W_1 > a_2 \quad (7a)$$

and

$$\frac{a_1}{b_1} > \frac{D_1 a_2}{W_1 - a_2} \quad (7b)$$

This means that under these constraints 7(a) and 7(b), the model will always lead to solutions possessing either stable equilibrium ^{point or} limit cycles.

LOCAL OR NEIGHBOURHOOD STABILITY ANALYSIS

$$\text{For H-isocline, } \frac{dH}{dt} = 0 \implies a_1 - b_1 H - \frac{WP}{D_1 + H} = 0$$

$$\text{For P-isocline, } \frac{dP}{dt} = 0 \implies a_2 = \frac{W_1 H}{D_1 + H}$$

The intersection of the two isoclines is the equilibrium point (H^*, P^*) , where

$$H^* = \frac{a_2 D_1}{W_1 - a_2}$$

$$P^* = \frac{a_1 D}{W} + \frac{a_2 D_1}{W (W_1 - a_2)^2} \times$$

$$[a_1 (W_1 - a_2) - b_1 (D W_1 - a_2 D + a_2 D_1)]$$

Writing N_1 for the host and N_2 for the parasite in the new model given by eqns. (3a) and (3b), we get

$$F_1 (N_1, N_2) = a_1 N_1 - b_1 N_1^2 - \frac{W}{D + N_1} N_1 N_2$$

$$F_2 (N_1, N_2) = -a_2 N_2 + \frac{W_1}{D_1 + N_1} N_1 N_2$$

Now, various elements of the communities matrix can be calculated to get the result :

$$a_{11} = \left(\frac{\partial F_1}{\partial N_1} \right)^* = a_1 - 2b_1 N_1^* - \frac{W D N_2^*}{(D + N_1^*)^2}$$

$$a_{12} = \left(-\frac{\partial F_1}{\partial N_2} \right)^* = -\frac{W N_1^*}{D + N_1^*}$$

$$a_{21} = \left(-\frac{\partial F_2}{\partial N_1} \right)^* = -\frac{W_1 D_1}{(D_1 + N_1^*)^2} N_2^*$$

$$a_{22} = \left(-\frac{\partial F_2}{\partial N_2} \right)^* = -a_2 + \frac{W_1 N_1^*}{D_1 N_1^*} = 0$$

The community matrix can be written as

$$A = \begin{bmatrix} a_1 - 2b_1 N_1^* - \frac{W D N_2^*}{(D + N_1^*)^2} & -\frac{W N_1^*}{D + N_1^*} \\ \frac{W_1 D_1 N_2^*}{(D_1 + N_1^*)^2} & 0 \end{bmatrix}$$

The determinantal equation $\det |A - \lambda I| = 0$ for the eigen values λ reduces to the quadratic eqn.

$$\lambda^2 + a\lambda + b = 0 \quad (8)$$

$$\text{with } a = -(a_{11} + a_{22}) \quad (9)$$

$$\text{and } b = a_{11} a_{22} - a_{12} a_{21} \quad (10)$$

For the system given by equations (3a) and (3b) to possess local stability two values of λ (λ_1 and λ_2) of the quadratic eqn.(8) must have negative real parts. For that it is essential that $a > 0$ and $b > 0$, where quantities a and b are defined by eqns. (9) and (10) respectively.

$$a > 0 \Rightarrow 2b_1 \left[\frac{a_2 D_1}{W_1 - a_2} \right] + b_1 D - a_1 > 0 \quad (11a)$$

$$b > 0 \Rightarrow D_1 > 0 \quad (11b)$$

These two are the conditions to be fulfilled if the model is to possess a stable equilibrium point type of stability. But positivity of the constant D_1 automatically guarantees (11b). Now, one is in a position to say that a choice of the various parameters which respect the constraint (11a) will thus lead to a solution with stable equilibrium point and a choice violating this will lead to limit cycles.

Numerical calculations leading to solutions which show equilibrium point behaviour are given in figures 3.1 to

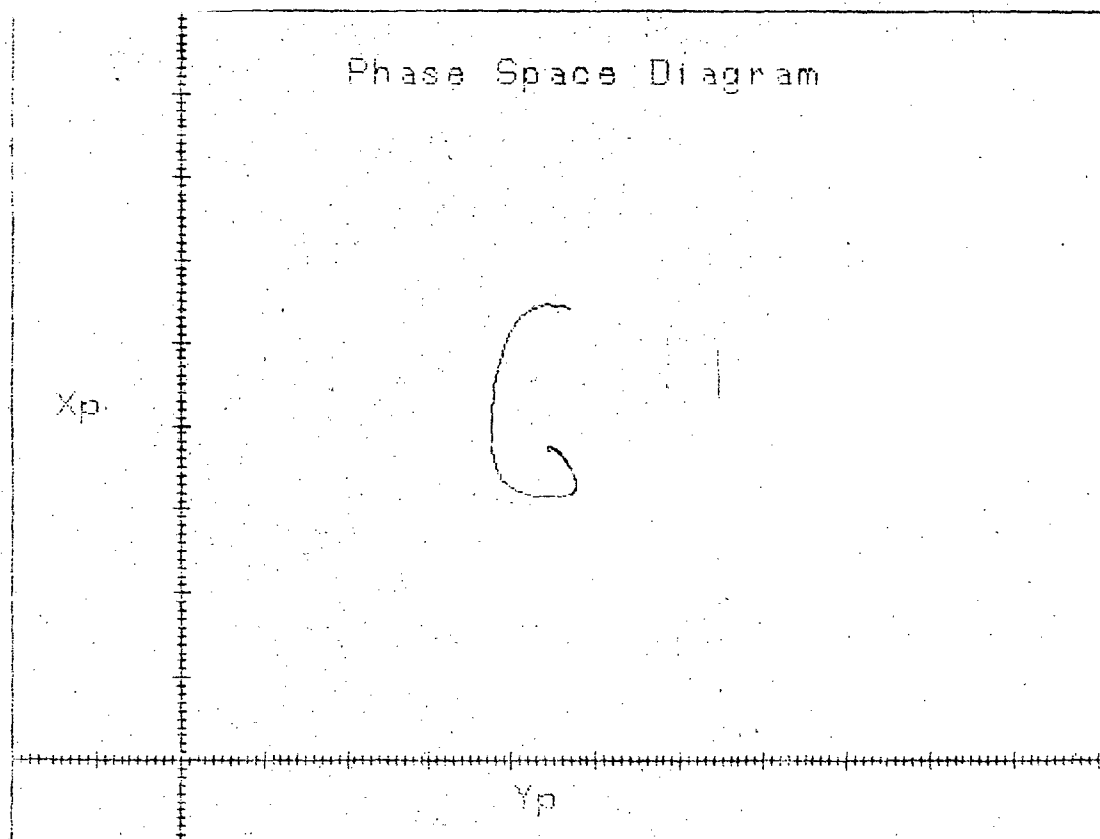


Figure 3.1 X_p denotes the prey population and Y_p denotes the predator population.

$$a_1 = 1.1, X_p = 20, Y_p = 30, b_1 = 0.05, a_2 = 1, W_1 = 2, D_1 = 10, D = 10, W = 1.$$

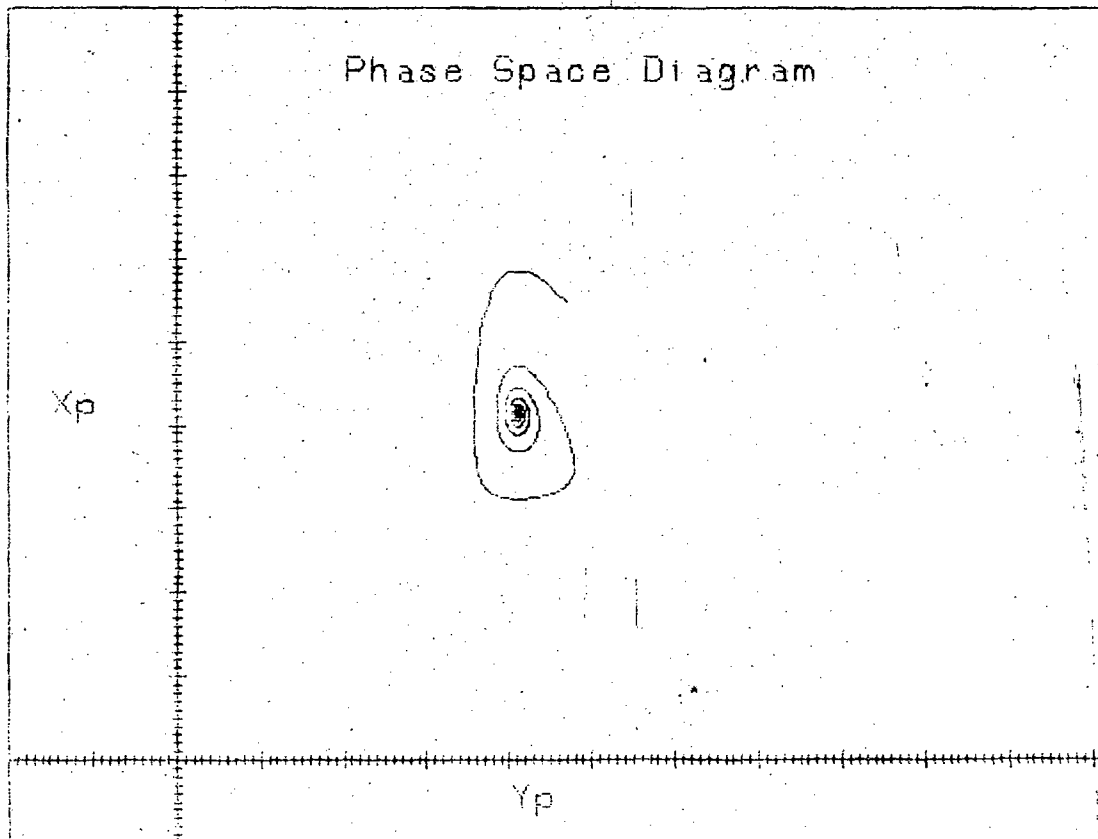


Figure 3.2 X_p denotes the prey population and Y_p denotes the predator population.

$$a_1 = 1.2, a_2 = 1, b_1 = 0.05, D = 10, D_1 = 10, W_1 = 2, \\ W = 1, X_p = 20, Y_p = 30.$$

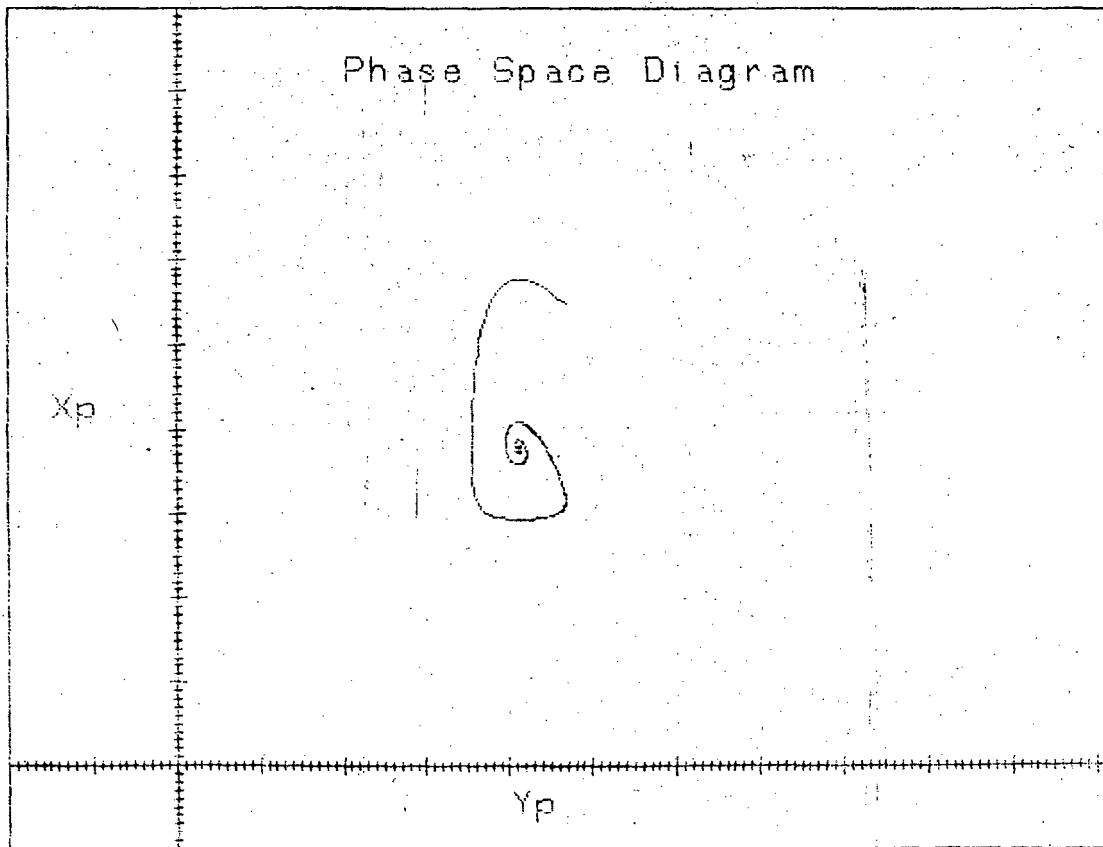


Figure 3.3 X_p denotes the prey population and Y_p denotes the predator population.

$a_2 = 1.2$, $X_p = 20$, $Y_p = 30$, $b_1 = 0.05$, $W = 1$, $W_1 = 2$,
 $D_1 = 10$, $D_2 = 10$, $a_1 = 1.2$.

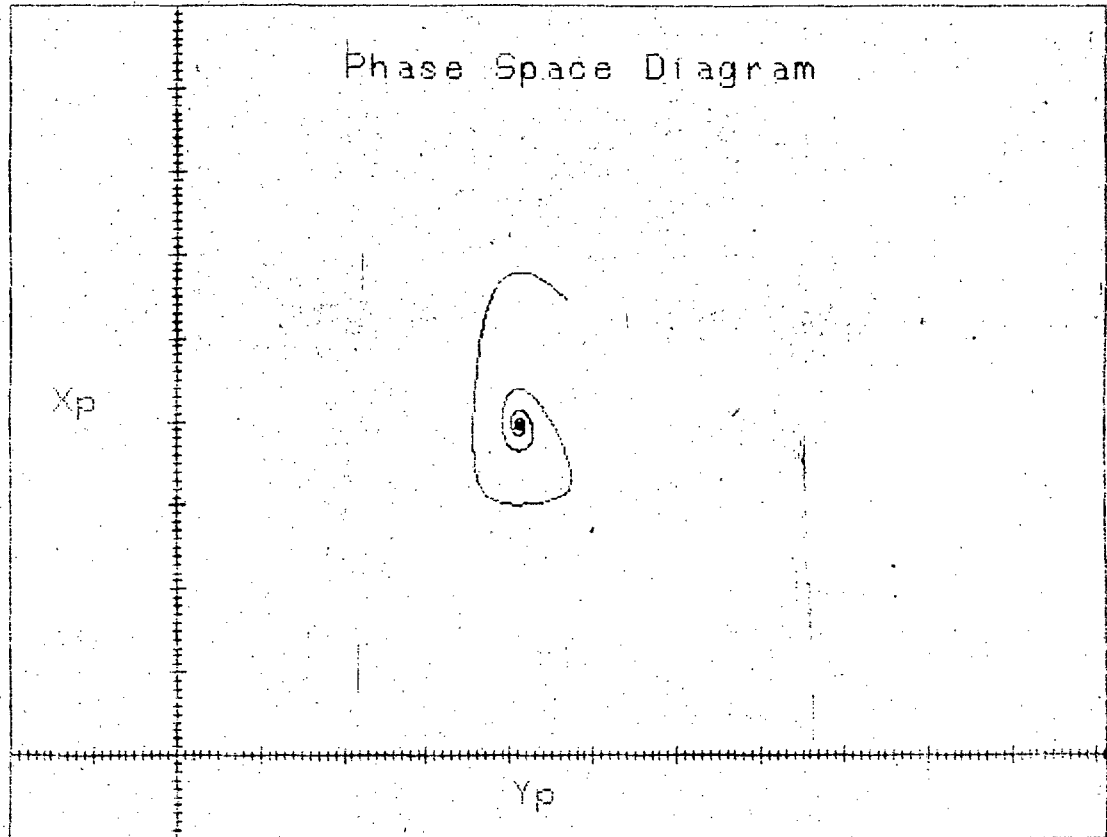


Figure 3.4 X_p denotes the prey population and Y_p denotes the predator population.

$a_1 = 1.3$, $X_p = 20$, $Y_p = 30$, $b_1 = 0.05$, $a_2 = 1$, $W_1 = 2$,
 $D = 10$, $D_1 = 10$, $W = 1$.

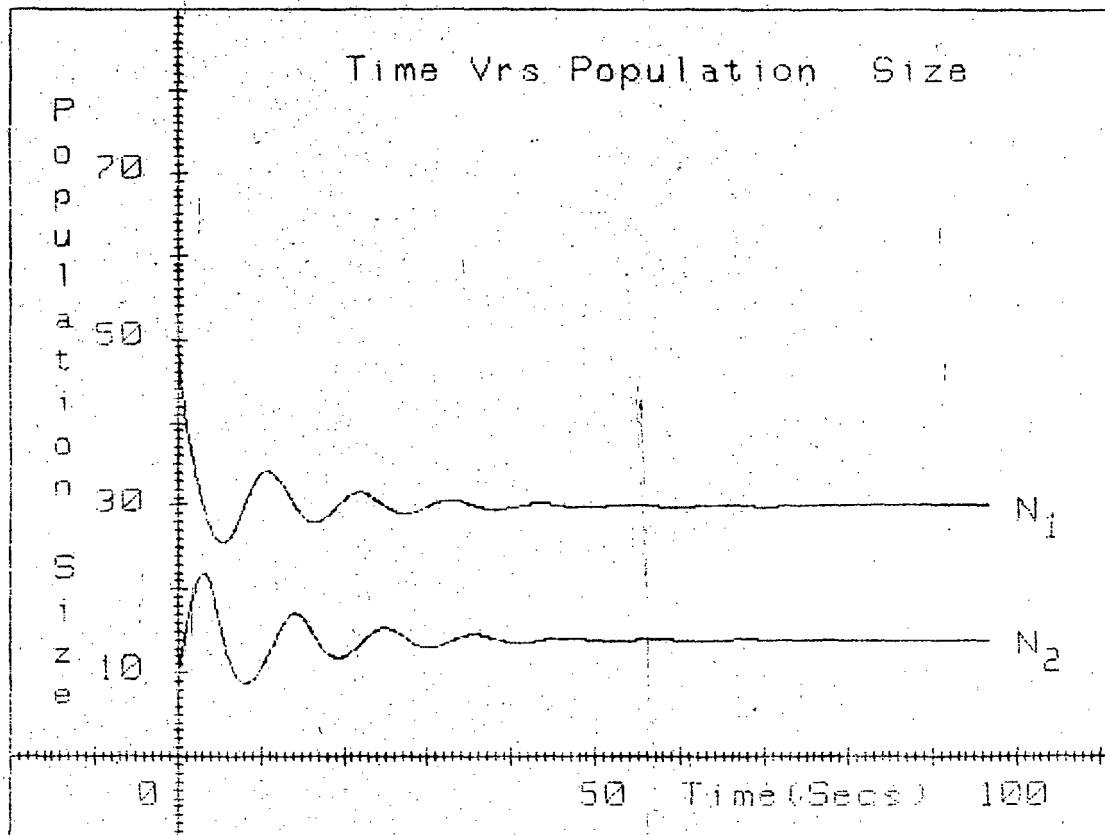


Figure 3.5 N_1 denotes the prey population and N_2 denotes the predator population.

$$a_1 = 1.2, a_2 = 1, b_1 = 0.05, D = 10, D_1 = 10, W_1 = 2, \\ W = 1, N_1 = 20, N_2 = 30.$$

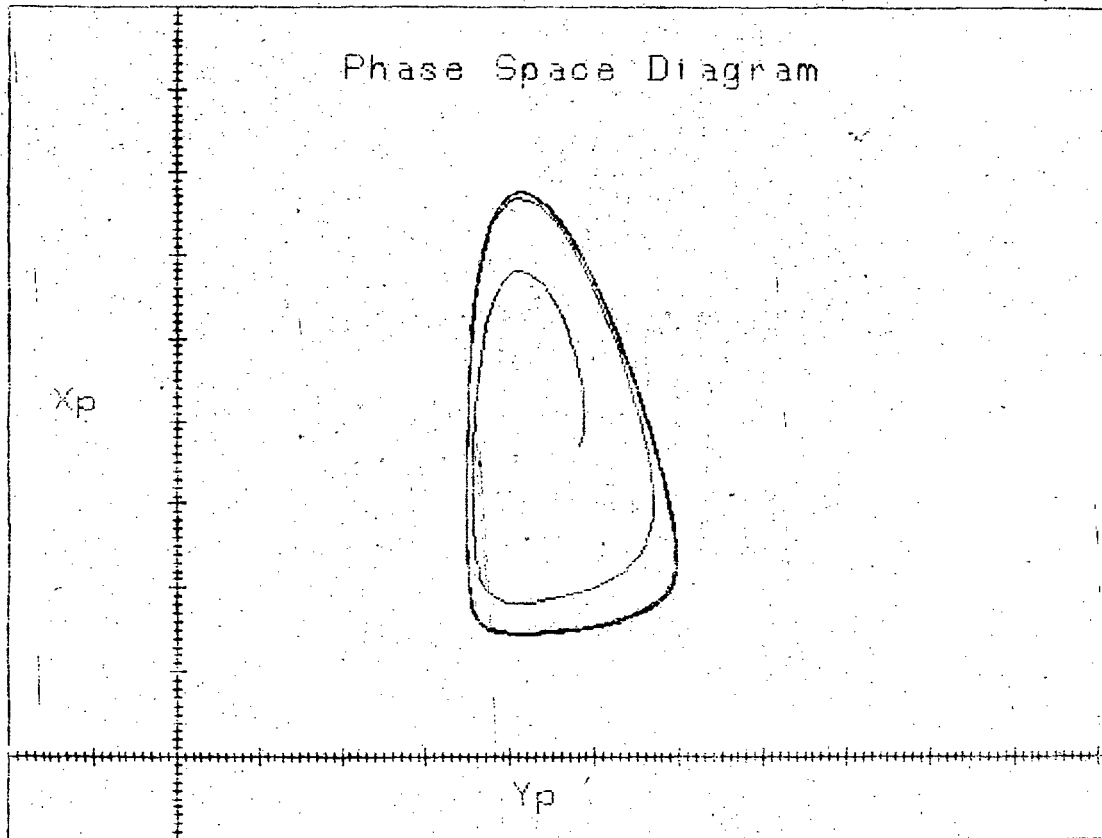


Figure 3.6 X_p denotes the prey population and Y_p denotes the predator population.

$$a_1 = 2.2, X_p = 20, Y_p = 30, b_1 = 0.05, a_2 = 1, W = 1, \\ W_1 = 2, D = 10, D_1 = 10.$$

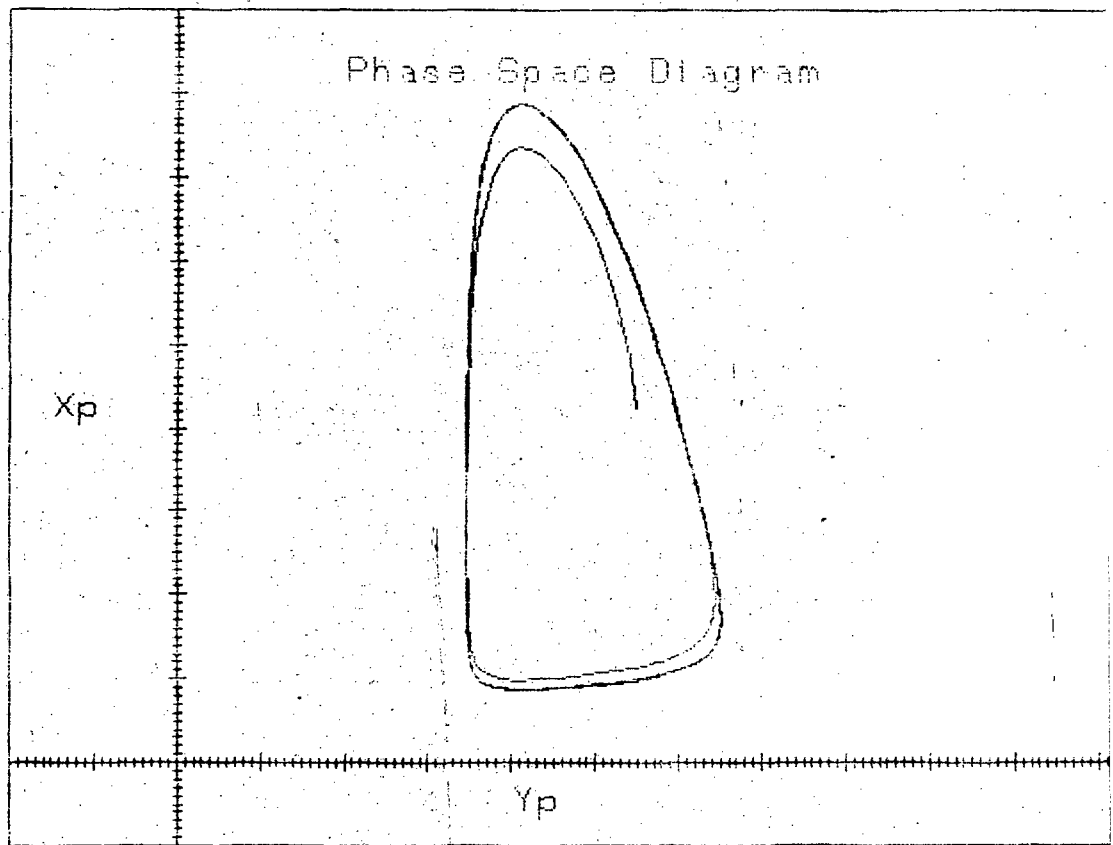


Figure 3.7 X_p denotes the prey population and Y_p denotes the predator population.

$$a_1 = 2.5, X_p = 30, Y_p = 40, b_1 = 0.05, D = 10, D_1 = 10$$

$$v = 1, W_1 = 2, a_2 = 1.$$

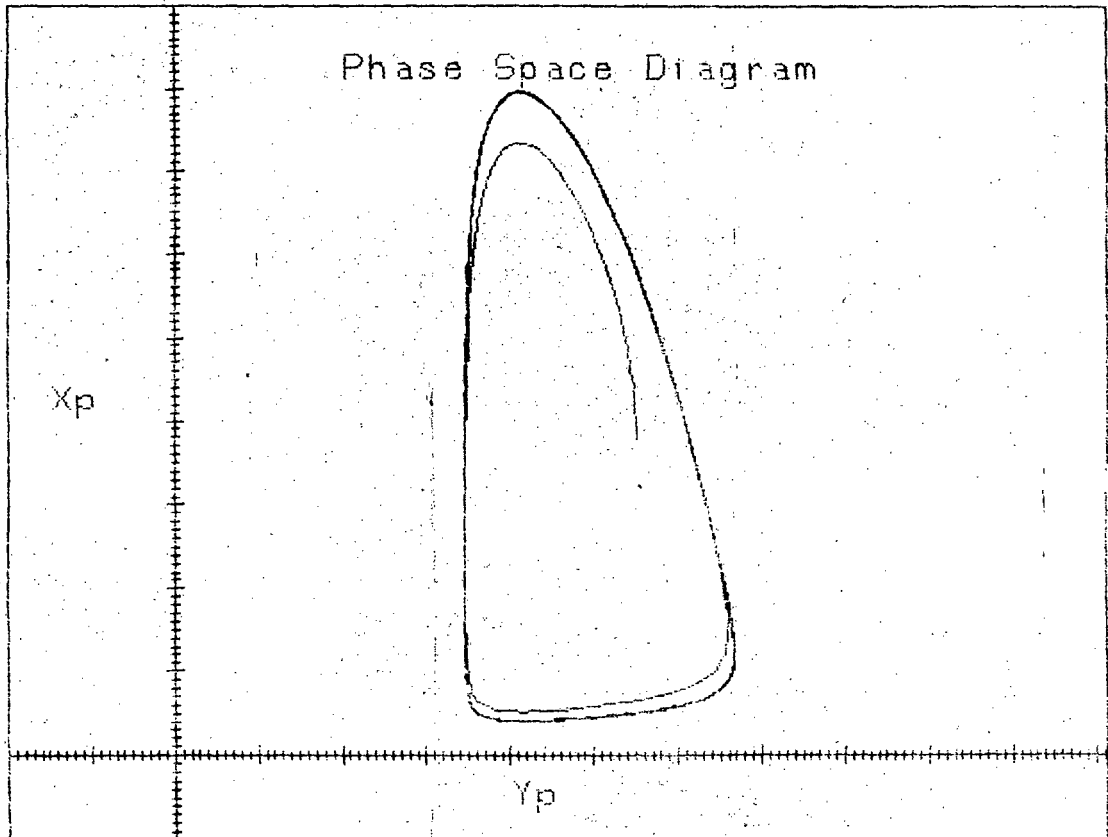


Figure 3.8 X_p denotes the prey population and Y_p denotes the predator population.

$$a_1 = 2.6, X_p = 30, Y_p = 40, b_1 = 0.05, D = 10,$$

$$D_1 = 10, W = 1, W = 2, a_2 = 1.$$

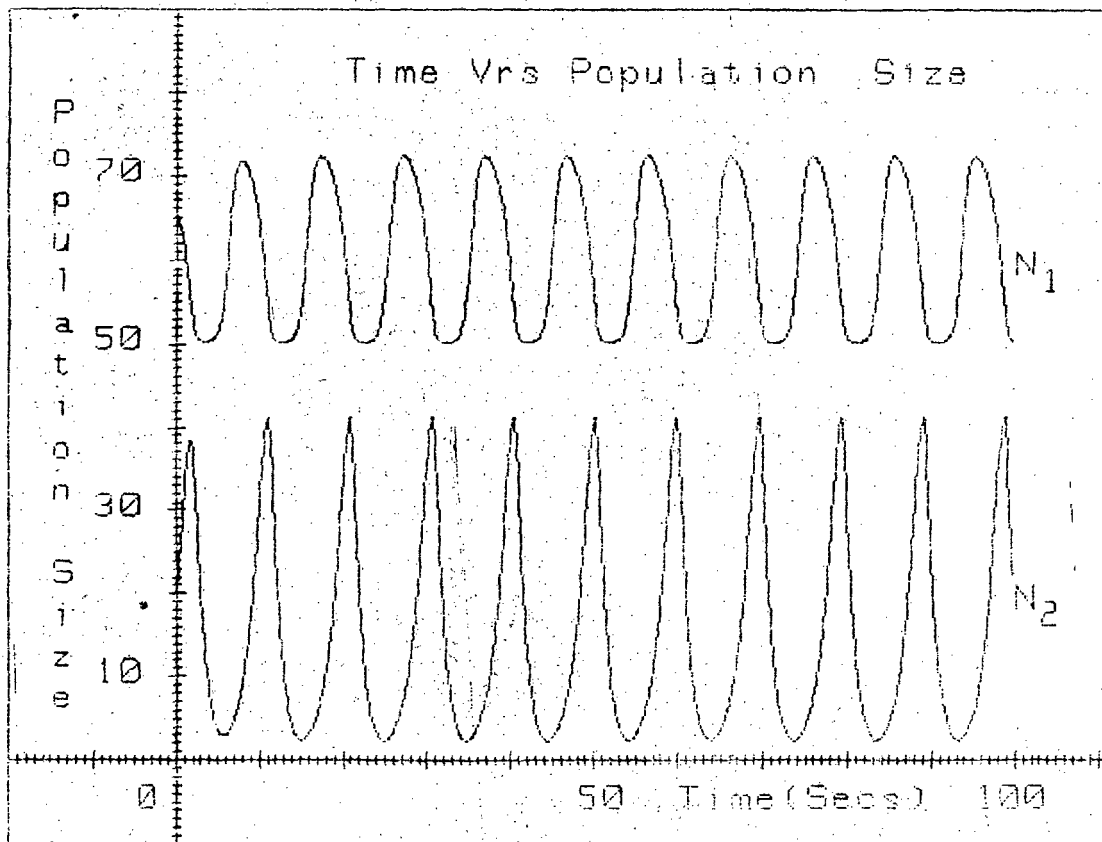


Figure 3.9 N_1 denotes the prey population and N_2 denotes the predator population.
 $a_1 = 2.5$, $N_1 = 30$, $N_2 = 40$, $b_1 = 0.05$, $D = 10$,
 $D_1 = 10$, $W = 1$, $W_1 = 2$, $a_2 = 1$.

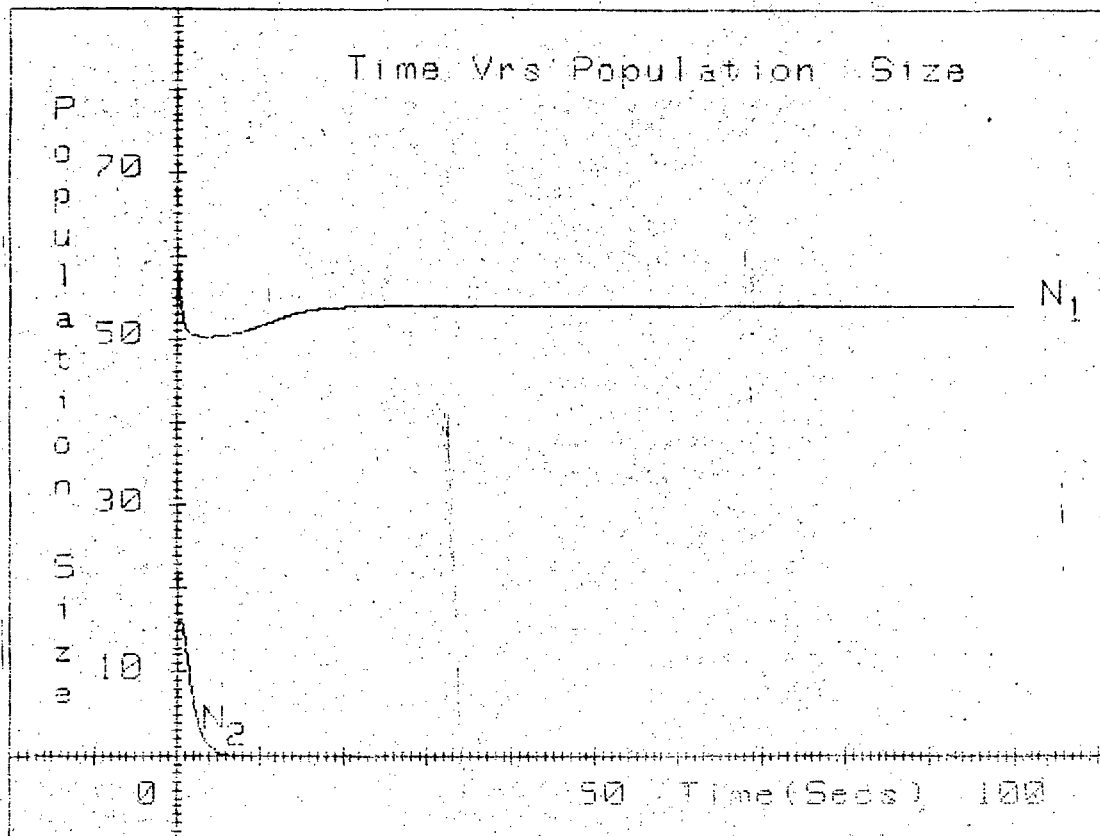


Figure 3.10 N_1 denotes the prey population and N_2 denotes the predator population.

$a_1 = 0.4$, $N_1 = 20$, $N_2 = 30$, $b_1 = 0.05$, $D = 10$,
 $D_1 = 10$, $W = 1$, $W_1 = 2$, $a_2 = 1$.

3.4. In figure 3.5, time development of two populations corresponding to phase portrait (Fig. 3.2) have been given.

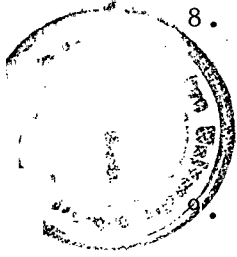
In figures 3.6 to 3.8 numerical calculations leading to stable limit cycle behaviour are given. In figure 3.9 time development of two populations corresponding to phase portrait (Fig. 3.7) are given.

Extinction of parasites (predators) are also possible in our model. It has been shown in Fig. 3.10.

Values of the constants and initial populations can be read from the legend.

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