A STUDY OF THE EFFECT OF HARVESTING AND/OR STOCKING IN INTERACTING TWO-SPECIES POPULATION MODELS

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CERTIFICATE

The research work presented in this dissertation has been carried out in the School of Environmental Sciences, Jawaharlal Nehru University, New Delhi - 110 067. The work is original and has not been submitted in part or full for any other degree or diploma of any university.

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C O N T E N T S

CHAPTER I

The problem of harvesting of one or more species
of populations from multi-species ecosystems is of much
practical relevance. It is important to know how harve-
sting could be done either for brief periods at different
times or in a continues manner, such that the basic
stability characteristics of the ecosystem, which is
being interfered with in this process, do not get dis-
turbed. It is obvious that harvesting in an arbitrary
way, as regards either the rate of harvesting or the
total amount to be harvested, will generally leave the
system destabilized and, as a result, many or all the
species which would otherwise coexist in the ecosystem may face
extinction. Given any harvesting procedure, it may be
expected, however, that within certain constraints, the
ecosystem being subjected to this process may be capa-
ble of sustaining itself without any of its component
species getting exterminated. The objective of the
present thesis is to investigate these constraints in
some given situations where the relevant ecosystems
are well defined and the harvesting procedures are
properly parameterized.

As our first example, we chose an ecosystem with
two competing species (the competition exists here
between the two species as well as between individuals
of the same species - represented by certain self-inter-
action terms). The method used is the graphical method
which employs "isoclines". The main results that we
obtain from here concern the derivation conditions
under which the ecosystem preserves stable equili-
brium under what is often called "proportional" (or
"constant effort") harvesting. It is seen that the
system is able to maintain stable equilibrium under
this harvesting only if it satisfied conditions of
stable equilibrium even in the absence of harvesting.
We then show that this basic result can be derived in
a more algebraic way without involving any graphical
techniques, by considering the conditions of stable
equilibrium for the system with and without harvest-
ing and by requiring that the equilibrium populations
be always positive. The advantage of looking at the
problem in this way is that generalization to harve-
sting in multi-species systems is then possible. We
illustrate this point by considering in detail a com-
peting three-species model. The conditions under which
the system can be subjected to harvesting without
losing its property of stable equilibrium are then

obtained. These conditions are, admittedly, not expressible in as simple and elegant a form as in the two species case, but their usefulness is nevertheless no less.

We next take up the two-species systems where the species are prey and predator. The first example is that of the original Lotka-Volterra model. We discuss harvesting in this model with simple but interesting and useful results. We then consider the prey-predator model which includes prey self-interaction, giving thereby a carrying capacity to the prey. It is convenient to discuss harvesting in this model using the isocline method once more.

Some recent developments in literature have led to an extention of this approach to a larger class of prey-predator models which possess not only solutions of the stable equilibrium type but solutions also including unstable equilibria and the associated limit cycles leading to sustained oscillations in the system. We conclude the present thesis with a general discussion of such models and the problem of harvesting therein. In this context, we discuss the harvesting problem in detail in Holling's model.

2.1   Our objective in this Chapter is to study
harvesting especially vis-a-vis the stability of a
dynamical system which models the competing species.
We shall confine ourselves to just two species and
investigate the harvesting policies which retain the
stable coexistence of these species. The approach is
to describe the full non-linear topology of the phase
plane in which the point representing the two popula-
tions move and thereby present a global stability
analysis.

In deriving the governing system of non-
linear differential equations, we first specify the
growth of each population in the absence of the other.
We assume that it is logistic. Thus,

$$\dot{N_1} = \frac{dN_1}{dt} = \lambda_1 N_1 - \alpha_{11} N_1^2 \ (\text{if } N_2 = 0)$$

$$\dot{N_2} = \frac{dN_2}{dt} = \lambda_2 N_2 - \alpha_{22} N_2^2 \ (\text{if } N_1 = 0)$$

where   and   denote the two species;
and   are positive constraints with the usual mean-
ings of Malthusian growth rates and self-regulatory
factors. To take into consideration their competi-
tion for the same resource, factors must be augmented

which retard the growth rate of each species in the presence of the other. We assume that they are proportional to the size of both populations. Therefore, the full governing system for two competing species is

$$\dot{N}_1 = \lambda_1 N_1 - \alpha_{11} N_1^2 - \alpha_{12} N_1 N_2$$

$$\dot{N}_2 = \lambda_2 N_2 - \alpha_{21} N_2 N_1 - \alpha_{22} N_2^2 \qquad (1)$$

Kapoor (1980) considers this system and studies harvesting at length using the isocline method. We present it here in order to provide the requisite base for subsequent investigation and then show that his results can be derived by using neighbourhood stability analysis which is readily amenable to n-species generalization.

To begin with, we draw the isoclines for the system. These are the straight lines corresponding to $N_1 = 0$ and $N_2 = 0$, and are therefore, given simply by

$$\lambda_1 - \alpha_{11} N_1 - \alpha_{12} N_2 = 0 \quad ; \quad \lambda_2 - \alpha_{21} N_1 - \alpha_{22} N_2 = 0 \qquad (2)$$

When we plot these lines, four non-degenerate situations arise (see Fig. 1). We now let

$$\frac{\lambda_2 \alpha_{12}}{\lambda_1 \alpha_{22}} = M_1 \quad ; \quad \frac{\lambda_2 \alpha_{11}}{\lambda_1 \alpha_{21}} = M_2 \qquad (3)$$

Therefore, for situation I: $M_1 < 1, M_2 < 1$; for II: $M_1 > 1, M_2 > 1$; for III: $M_1 < 1, M_2 > 1$; and for IV: $M_1 > 1, M_2 < 1$.

Using M_1 and M_2 as the axes, we are now in a position to depict these non-degenerate situations on the M_1-M_2 plane. Fig. 2 shows that the first quadrant is fragmented into four regions corresponding to these situations. In situation I, N_1 alone will survive; in II, N_2 alone will survive; in III, both N_1 and N_2 will coexist indefinitely and in IV, which describes an unstable saddle point, either of the species will survive, depending on the initial populations. This figure also shows the five degenerate situations:

V: $M_1 < 1$, $M_2 = 1$ (N_1 alone will survive)

VI: $M_1 > 1$, $M_2 = 1$ (N_2 alone will survive)

VII: $M_1 = 1$, $M_2 < 1$ (N_1 alone will survive)

VIII: $M_1 = 1$, $M_2 > 1$ (N_2 alone will survive)

IX: $M_1 = 1 = M_2$ (N_1 and N_2 will coexist but depending on the initial populations).

We are now ready to incorporate into the model the effect of harvesting. Let us consider the policy of harvesting in which it is done at rates proportional

to the population. Thus, the governing system now takes the form

$$\dot{N_1} = \lambda_1 N_1 - a_{11} N_1^2 - a_{12} N_1 N_2 - \lambda_1 k_1 N_1$$

$$\dot{N_2} = \lambda_2 N_2 - a_{21} N_2 N_1 - a_{22} N_2^2 - \lambda_2 k_2 N_2$$

Or, alternatively,

$$\dot{N_1} = \lambda_1 (1-k_1) N_1 - a_{11} N_1^2 - a_{12} N_1 N_2$$

$$\dot{N_2} = \lambda_2 (1-k_2) N_2 - a_{21} N_2 N_1 - a_{22} N_2^2 \qquad (4)$$

where $0 < k_1 < 1$ and $0 < k_2 < 1$; consequently, M_1 and M_2 are transformed to M_1' and M_2' respectively, where

$$M_1' = \frac{\lambda_2 (1-k_2) a_{12}}{\lambda_1 (1-k_1) a_{22}} = \frac{M_1}{M_3}$$

$$M_2' = \frac{\lambda_2 (1-k_2) a_{11}}{\lambda_1 (1-k_1) a_{21}} = \frac{M_2}{M_3} \qquad (5)$$

and

$$M_3 = \frac{1-k_1}{1-k_2}$$

Thus, we are in a position to transform the system from any one of the four non-degenerate situations to any other, through some degenerate situations, by changing M_3. So we discuss all the possibilities that arise.

A) SITUATION I PREVAILS BEFORE HARVESTING:

In this case where situation I prevails before harvesting, N_1 alone survives, and the condition for this is

$$M_1 < 1 \quad ; \quad M_2 < 1 \tag{6}$$

After havesting, four cases can arise:

(i) N_1 alone continues to survive. For this we need

$$M_1/M_3 < 1 \quad \text{and} \quad M_2/M_3 < 1$$

or $M_3 > M_1$ and $M_3 > M_2$

or $M_3 > \max(M_1, M_2)$ \hfill (7)

Since both M_1, $M_2 < 1$, this will be certainly true if

$$M_3 = (1-k_1)/(1-k_2) > 1 \quad \text{OR} \quad k_1 < k_2$$

But it will also be true if $k_1 > k_2$ and   .

$$0 < k_1 - k_2 < (1-M_2)(1-k_2) \; if \; M_2 > M_1$$

$$\text{OR} \quad 0 < k_1 - k_2 < (1-M_1)(1-k_2) \; if \; M_1 > M_2 \tag{8}$$

(ii)   The second species, N_2, alone will survive. That is, the condition

$$\frac{M_1}{M_3} > 1 \quad \text{and} \quad \frac{M_2}{M_3} > 1 \tag{9}$$

is to be satisfied. Or, alternatively,

$$M_3 < M_1 \quad \text{and} \quad M_3 < M_2$$

$$\Rightarrow \quad M_3 < \min(M_1, M_2) \tag{10}$$

This will be true if $M_3 = (1-k_1)/(1-k_2) < 1$

$\Rightarrow \quad k_1 > k_2.$ But it will also be true if

$$k_1 - k_2 > (1-k_2)(1-M_1) > 0 \quad \text{if} \quad M_1 < M_2$$
$$k_1 - k_2 > (1-k_2)(1-M_2) > 0 \quad \text{if} \quad M_2 < M_1$$

or $\quad k_1 - k_2 > (1-k_2) \max\{(1-M_1), (1-M_2)\} > 0 \tag{11}$

(iii) Both species can coexist in stable equilibrium, if

$$M_1/M_3 < 1 \quad \text{and} \quad M_2/M_3 > 1 \tag{12}$$

or $\quad M_3 > M_1 \quad \text{and} \quad M_3 < M_2$

This will be satisfied only when

$$M_1 < M_3 < M_2 \quad \Rightarrow \quad M_2 > M_1$$

$$\text{OR,} \quad a_{11} a_{22} > a_{12} a_{21} \tag{13}$$

which is the condition for stable equilibrium before harvesting. This implies that if unstable equilibrium prevails before harvesting, then situation I cannot be transformed to situation III.

(iv)   Both species coexist in unstable equilibrium
and ultimate survival of either species depends on
the initial populations. This requires

$$M_1/M_3 > 1 \quad \text{and} \quad M_2/M_3 < 1 \tag{14}$$

or $\quad M_3 < M_1 \quad$ and $\quad M_3 > M_2$

$$\Rightarrow \quad M_2 < M_1 \Rightarrow a_{11}a_{22} < a_{12}a_{21}$$

which implies that before harvesting the system is
in unstable equilibrium.

We now discuss the evolution of I into II,
III and IV possibly through some degenerate situa-
tions by continuously decreasing M_3 from ∞ to 0.

The situation wherein the first species, N_1,
alone survive can arise in three cases:

$$0 < M_1 < M_2 < 1 \tag{15a}$$

$$0 < M_2 < M_1 < 1 \tag{15b}$$

$$0 < M_1 = M_2 < 1 \tag{15c}$$

Case a) As long as $M_3 > M_2$, the first species alone
continues to survive; when $M_3 = M_2$, we have the
degenerate situation V; when $M_1 < M_3 < M_2$ both

species coexist in stable equilibrium. Should M_3
decrease still further and become equal to M_1, we
get the degenerate situation VIII and finally when
$M_3 < M_1$, we get the situation II where N_1 disappears.
Case b) In an analogous manner, the situation I can
be transformed to II through VII, IV and VI successively.
Case c) Here I transforms to II through IX.

It is clear from the foregoing that I transforms
to III if $M_2 > M_1$, or to IV if $M_2 < M_1$ and to neither
if $M_2 = M_1$.

B) SITUATION II PREVAILS BEFORE HARVESTING:

Here the second species, N_2, alone survives.
The condition is

$$M_1 > 1 \; ; \; M_2 > 1 \tag{16}$$

The discussion is quite similar to the above. The
results, simply put, are: II will be transformed to
(i) situation I if

$$M_3 > max \, (M_1, M_2) > 1 \tag{17}$$

(ii) situation II if

$$M_3 < min \, (M_1, M_2) \tag{18}$$

(iii)   situation III if

$$M_1 < M_3 < M_2 \tag{19}$$

(iv)   situation IV if

$$M_1 > M_3 > M_2 \tag{20}$$

Again, the evolution of II by harvesting, to I, III and IV is exactly opposite to that of I. As M_3 increases from 0 to ∞, situation II evolves into I

a)   through VIII, III and V if $M_1 < M_2$

b)   through VI, IV and VII if $M_2 > M_1$

c)   through IX if $M_1 = M_2$.

C)   SITUATION III PREVAILS BEFORE HARVESTING:

By far, this situation is most appealing to practical interest. Here both populations coexist in stable equilibrium. The requisite condition is

$$M_1 < 1 \; ; \; M_2 > 1 \tag{21}$$

It will be transformed by harvesting to

(i)   situation I if

$$M_1/M_3 < 1 \quad \text{and} \quad M_2/M_3 < 1$$

or $M_3 > M_1$ and $M_3 > M_2$ (22)

If $M_3 > M_2$, it is automatically greater than M_1 because $M_2 > 1 > M_1$.

(ii) situation II if

$$M_1/M_3 > 1 \quad \text{and} \quad M_2/M_3 > 1$$

$$\text{or} \quad M_1 > M_3 \quad \text{and} \quad M_2 > M_3 \tag{23}$$

Again, if $M_3 < M_1$, it is automatically less than M_2.

(iii) situation III itself, if

$$M_1/M_3 < 1 \quad \text{and} \quad M_2/M_3 > 1$$

$$\text{or} \quad M_3 > M_1 \quad \text{and} \quad M_3 < M_2$$

$$\Rightarrow \quad M_1 < M_3 < M_2 \tag{24}$$

(iv) situation IV if

$$M_1/M_3 > 1 \quad \text{and} \quad M_2/M_3 < 1$$

$$\text{or} \quad M_3 < M_1 \quad \text{and} \quad M_3 > M_2 \tag{25}$$

clearly this is impossible.

Thus, III can be transformed to II $(M_3 < M_1)$ through VIII $(M_3 = M_1)$, or to I $(M_3 > M_2)$ through V $(M_3 = M_2)$. No harvesting policy can transform III to IV.

D) SITUATION IV PREVAILS BEFORE HARVESTING:

The equilibrium coexistence is unstable and the requisite condition is

$$M_1 > 1 \; ; \quad M_2 < 1 \tag{26}$$

This situation, after harvesting, can be transformed to

(i) situation I if

$$M_1/M_3 < 1 \quad \textbf{and} \quad M_2/M_3 < 1$$

or $\quad M_3 > M_1 \quad$ **and** $\quad M_3 > M_2 \tag{27}$

Since $M_1 > 1$; $M_2 < 1$, M_3 is automatically greater than M_2 if $M_3 > M_1$.

(ii) situation II if

$$M_1/M_3 > 1 \quad \textbf{and} \quad M_2/M_3 > 1$$

or $\quad M_3 < M_1 \quad$ **and** $\quad M_3 < M_2 \tag{28}$

Again, since $M_1 > 1$, $M_2 < 1$, M_3 is automatically less than M_1 if $M_3 < M_2$.

(iii) situation III if

$$M_1/M_3 < 1 \quad \textbf{and} \quad M_2/M_3 > 1$$

or $\quad M_3 > M_1 \quad$ **and** $\quad M_3 < M_2 \tag{29}$

which is impossible.

(iv) situation IV itself if

$$M_1/M_3 > 1 \qquad \text{and} \qquad M_2/M_3 < 1$$

or, $\qquad M_3 < M_1 \qquad$ and $\qquad M_3 > M_2$ $\qquad\qquad$ (30)

which implies $M_1 > M_3 > M_2$.

Thus, IV can be transformed to II $(M_3 < M_2)$ through VI $(M_3 = M_2)$ or to I $(M_3 > M_1)$ through VII $(M_3 = M_1)$.

The foregoing graphical analysis of harvesting is rather laborious. However, it can be put in a much condensed and elegant form and this is what Kapoor does in a preprint. We summarise, in the following, the analysis contained in this preprint.

We notice that, by harvesting, the point (M_1, M_2) is mapped onto the point (M_1', M_2') where Eq. (5) is satisfied. The line joining these two points passes through the origin $(0, 0)$, since the mapping is necessarily a scaling. Hence, any state represented by (M_1, M_2) can now be transformed to (M_1', M_2') by harvesting, provided Eq. (5) is satisfied, or, in other words, the line joining the two points passes through the origin. This remarkable result is central to further analysis.

starting from a point in any state or situation on M_1 - M_2 plane, we can delineate the evolution of the system as k_1 and k_2 change.

$\hat{2}$.2   It may be noted that the analysis of the pre-ceeding section shows that in case of a competing two species system (where self-interactions are also included), harvesting in a way that the system conti-nues to possess stable equilibrium is only possible if the system possesses stable equilibrium even with-out harvesting. The precise conditions on the harve-sting are then deducible. From a physical point of view, it is only a situation like this which should be of practical interest. Harvesting for systems which are not stable to begin with, i.e., which do not sustain their different components, without being subjected to harvesting, and which are not able to sustain themselves similarly when subjected to harve-sting, is a problem only of academic interest and not one which would have relevance as far as applications are concerned.

We would now like to emphasize that the above result, though obtained in the previous section by the method of isoclines, can also be worked out with-out recourse to such a graphical method, by looking

at the conditions of stable equilibrium for the system
with and without harvesting and the conditions for
the positivity of the equilibrium populations. What
is being suggested here is actually equivalent to the
same thing as done in the previous section, but the
advantage now is that one need not take recourse to
graphical methods, but has only algebraic manipula-
tions to perform. That this is an advantage is not
so obvious when one is dealing with only a two-species
system where isoclines are to be drawn on two-dimen-
sional planes only, but becomes quite obvious when
one goes to multispecies systems. As an illustration
we will use this approach to discuss harvesting in a
competing three-species system. The results obtained
will be quite explicit though not in as simple and
elegant a form as in the two-species case.

To proceed further now, we work out the stable
equilibrium conditions for the system of interest.
Since we will be using this result for both the two
species case discussed earlier as well as the promised
three-species case, and since it is no more difficult
to write down the main result for an arbitrary multi-
species system, we shall work with the multi-species
case. The dynamics of the system is here given by the
following k coupled equations, where k is the number

of species involved:

$$\frac{dN_i}{dt} = N_i \left\{ r_i - \sum_{j=1}^{k} a_{ij} N_j \right\};$$

$$1, j = 1, 2, \ldots, k \qquad (31)$$

The equilibrium populations N_i* are given by

$$N_i^* \left\{ r_i - \sum_{j=1}^{k} a_{ij} N_j^* \right\} = 0$$

which, under the assumption $N_i^* \neq 0$, reduces to

$$r_i - \sum_{j=1}^{k} a_{ij} N_j^* = 0 \qquad (32)$$

We now do a Taylor expansion around the point $N_i = N_i*$ and keep only the lowest order terms, thus getting,

$$\dot{N}_i = F_i(N^*) + \sum_{j=1}^{k} (N_j - N_j^*) \left(\frac{\partial N_i}{\partial N_j} \right)_{N = N^*}$$

where, we have put

$$\dot{N}_i = F_i(N)$$

and $F_i (N*)$ is then the value of this quantity evalua-
ted at the equilibrium point $N = N*$, i.e., $N_1 = N_1*$,
$N_2 = N_2*$, ..., etc. It is easy to check that

$$\left(\frac{\partial \dot{N_i}}{\partial N_j} \right)_{N = N^*} = - a_{ij} N_i^* \; ;$$

$$j = 1, 2, \ldots, k$$

and $\quad F_i(N^*) = 0.$

So we get

$$\dot{N_i} = - N_i^* \sum_{j=1}^{k} a_{ij} (N_j - N_j^*) \tag{33}$$

Putting

$$u_i = N_i - N_i^* \tag{34}$$

We can write the above equation as

$$\dot{u_i} = - N_i^* \sum_{j=1}^{k} a_{ij} u_j \tag{35}$$

Or, simply as

$$\dot{u_i} = \sum_{j=1}^{k} b_{ij} u_j \tag{36}$$

where, $\quad b_{ij} = - N_i^* a_{ij} \tag{37}$

The last quantity is often referred to as the community matrix (Pielou, 1977; May, 1974). It is clear now that if all the eigen values of this matrix have negative real parts, then

$$N_i \ (t \rightarrow \infty) \rightarrow 0$$

that is, all the N_i asymptotically reach their respective equilibrium values N_i^*, leading to the situation of stable equilibrium. The conditions for our system to possess stable equilibrium are thus the conditions for the community matrix of the system to have negative real parts for all its eigen values. To ensure that these eigen-values have negative real values, we can involve the well-known Routh-Hurwitz criteria, which lead to a set of inequalities. We shall not write down here these inequalities for the general k-species case.

Let us now come back to the two-species case discussed in the previous section. The equations describing this system are:

$$\frac{dN_1}{dt} = r_1 N_1 - a_{11} N_1^2 - a_{12} N_1 N_2$$

$$\frac{dN_2}{dt} = r_2 N_2 - a_{21} N_1 N_2 - a_{22} N_2^2 \qquad (38)$$

The equilibrium populations N_1^* and N_2^* are given by the equations

$$r_1 - a_{11} N_1^* - a_{12} N_2^* = 0$$

$$r_2 - a_{21} N_1^* - a_{22} N_2^* = 0 \qquad (39)$$

So, we get

$$N_1^* = \frac{\lambda_1 a_{22} - \lambda_2 a_{12}}{a_{11} a_{22} - a_{12} a_{21}}$$

$$N_2^* = \frac{\lambda_2 a_{11} - \lambda_1 a_{21}}{a_{11} a_{22} - a_{12} a_{21}} \tag{40}$$

The community matrix b is now given by

$$b = \begin{bmatrix} -N_1^* a_{11} & -N_1^* a_{12} \\ & \\ -N_2^* a_{21} & -N_2^* a_{22} \end{bmatrix} \tag{41}$$

For the system to possess stable equilibrium, the eigen-values of this matrix should have negative real parts. The condition for this, following Routh and Hunwitz, are

$$(N_1^* a_{11} + N_2^* a_{22}) > 0 \tag{42}$$

and

$$(a_{11} a_{22} - a_{12} a_{21}) > 0 \tag{43}$$

It is clear that these conditions for stable equilibrium by themselves donot guarantee that the

stable equilibrium point will be in the first quadrant in the N_1 - N_2 plane. The complete set of conditions for the system to possess a physically acceptable stable equilibrium are, therefore, equations (42) and (43) supplemented with

$$N_1^* > 0$$

$$N_2^* > 0 \tag{44}$$

This positivity property of N_1^* can be ensured in two different ways, namely, by either taking

$$a_{11} a_{22} - a_{12} a_{21} > 0 \tag{45}$$

and

$$k_1 a_{22} - k_2 a_{12} > 0 \tag{46}$$

$$k_2 a_{11} - k_1 a_{21} > 0$$

or

$$a_{11} a_{22} - a_{12} a_{21} < 0 \tag{47}$$

and

$$k_1 a_{22} - k_2 a_{12} < 0 \tag{48}$$

$$k_2 a_{11} - k_1 a_{21} < 0$$

Clearly conditions (47) and (48) are not compatible with the conditions of stable equilibrium. So, we have to accept the set of conditions (45) and (46). Note that the condition (45) is the same as condition (43). Furthermore, the conditions (46) clearly imply this, as they can be combined into a product combination

$$\ell_1 \ell_2 \, a_{11} a_{22} \; > \; \ell_1 \ell_2 \, a_{21} a_{21}$$

or simply,

$$a_{11} a_{22} \; > \; a_{12} a_{21}$$

It may be further noted that in view of the positivity of all the a_{ij} as well as the positivity of N_1^* and N_2^*, condition (42) is automatically satisfied. The conditions that we need to consider therefore, are simply the conditions (46).

The foregoing discussion remains valid even in the presence of harvesting in the manner done in the previous section - the only change is that we have to make the following substitutions:

$$\ell_1 \longrightarrow \ell_1 (1 - k_1)$$
$$\ell_2 \longrightarrow \ell_2 (1 - k_2)$$

(49)

The condition (46) then takes the form:

$$\lambda_1 (1-k_1) a_{22} - \lambda_2 (1-k_2) a_{12} > 0$$

$$\lambda_2 (1-k_2) a_{11} - \lambda_1 (1-k_1) a_{21} > 0 \qquad (50)$$

Following the notation of the previous section, we may write for (46),

$$M_1 \equiv \frac{\lambda_2 a_{12}}{\lambda_1 a_{22}} < 1 \qquad (51)$$

and

$$M_2 \equiv \frac{\lambda_2 a_{11}}{\lambda_1 a_{21}} > 1 \qquad (52)$$

Likewise, we get from (50)

$$\frac{\lambda_2 (1-k_2) a_{12}}{\lambda_1 (1-k_1) a_{22}} < 1$$

or

$$\frac{\lambda_2 a_{12}}{\lambda_1 a_{22}} < \frac{1 - k_1}{1 - k_2} \qquad (53)$$

and

$$\frac{\lambda_2 (1-k_2) a_{11}}{\lambda_1 (1-k_1) a_{21}} > 1$$

or

$$\frac{k_2 \, a_{11}}{k_1 \, a_{21}} \;>\; \frac{1-k_1}{1-k_2} \tag{54}$$

From equations (51) and (52), we now get, for stable equilibrium for the situation without harvesting:

$$M_1 \;<\; M_2 \tag{55}$$

From equations (53) and (54) we get, using the relation,

$$M_3 \;=\; \frac{1-k_1}{1-k_2} \tag{56}$$

the condition

$$M_1 \;<\; M_3 \;<\; M_2 \tag{57}$$

This last result gives the constraint under which harvesting can be done on the system without the system losing its basic property of stable equilibrium. Clearly, this constraint implies the constraint given by equation (55) which implies stable equilibrium for the system without harvesting. We have discussed this point earlier.

Let us now generalize these results to the case of a three-species competing system (with all the self-interactions included as before). The system is given by the following set of equations:

$$\frac{dN_1}{dt} = z_1 N_1 - a_{11} N_1^2 - a_{12} N_1 N_2 - a_{13} N_1 N_3$$

$$\frac{dN_2}{dt} = z_2 N_2 - a_{21} N_2 N_1 - a_{22} N_2^2 - a_{23} N_2 N_3 \tag{58}$$

$$\frac{dN_3}{dt} = z_3 N_3 - a_{31} N_3 N_1 - a_{32} N_3 N_2 - a_{33} N_3^2$$

Following the method described earlier, we can now get the conditions for stable equilibrium for this system by looking at the associated community matrix. The equilibrium populations N_1^*, N_2^* and N_3^* are of course given by the equations:

$$z_1 - a_{11} N_1^* - a_{12} N_2^* - a_{13} N_3^* = 0$$

$$z_2 - a_{21} N_1^* - a_{22} N_2^* - a_{23} N_3^* = 0 \tag{59}$$

$$z_3 - a_{31} N_1^* - a_{32} N_2^* - a_{33} N_3^* = 0$$

The community matrix b is given by the element

$$b_{ij} = - N_i^* a_{ij} \quad ; \quad i, j = 1, 2, 3 \tag{60}$$

The conditions for stable equilibrium are now the conditions for the eigenvalues of the matrix b to have all negative real parts. Following the Routh-Hunwitz analysis, we find that these conditions are:

$$N_1^* a_{11} + N_2^* a_{22} + N_3^* a_{33} > 0 \qquad (61)$$

$$N_1^* a_{11} \left(N_1^* a_{11} N_2^* a_{22} + N_1^* a_{11} N_3^* a_{33} \right.$$

$$+ N_2^* a_{22} N_2^* a_{22} + N_2^* a_{22} N_3^* a_{33}$$

$$\left. + N_2^* a_{22} N_3^* a_{33} + N_3^* a_{33} N_3^* a_{33} \right)$$

$$+ N_2^* a_{22} N_2^* a_{22} N_3^* a_{33} + N_2^* a_{22} N_3^* a_{33} N_3^* a_{33}$$

$$>$$

$$N_1^* a_{11} \left(N_2^* a_{21} N_1^* a_{12} + N_3^* a_{31} N_1^* a_{13} \right)$$

$$+ N_1^* a_{12} N_2^* a_{22} N_2^* a_{21} + N_1^* a_{13} N_3^* a_{33} N_3^* a_{31}$$

$$+ N_1^* a_{12} N_2^* a_{23} N_3^* a_{31} + N_1^* a_{13} N_2^* a_{21} N_3^* a_{32}$$

$$+ N_2^* a_{22} N_2^* a_{32} N_3^* a_{23} + N_2^* a_{23} N_3^* a_{33} N_3^* a_{32} \qquad (62)$$

and

$$D \equiv (a_{11}a_{22}a_{33} + a_{13}a_{21}a_{32} + a_{12}a_{23}a_{31})$$

$$- (a_{11}a_{23}a_{32} + a_{12}a_{21}a_{33} + a_{13}a_{22}a_{31}) \quad (63)$$

From equations (59), the equilibrium population N_1^*, N_2^* and N_3^* can also be calculated easily and the result is:

$$N_1^* = \left[\begin{array}{l} \lambda_3(a_{12}a_{23} - a_{13}a_{22}) \\ + \lambda_2(a_{13}a_{32} - a_{12}a_{33}) \\ + \lambda_1(a_{22}a_{33} - a_{32}a_{23}) \end{array} \right] \Bigg/ D \quad (64)$$

$$N_2^* = \left[\begin{array}{l} \lambda_3(a_{13}a_{21} - a_{23}a_{11}) \\ + \lambda_2(a_{11}a_{33} - a_{13}a_{31}) \\ + \lambda_1(a_{23}a_{31} - a_{33}a_{21}) \end{array} \right] \Bigg/ D \quad (65)$$

$$N_3^* = \left[\begin{array}{l} \lambda_3(a_{11}a_{22} - a_{12}a_{21}) \\ + \lambda_2(a_{12}a_{31} - a_{11}a_{32}) \\ + \lambda_1(a_{21}a_{32} - a_{22}a_{31}) \end{array} \right] \Bigg/ D \quad (66)$$

Since we wish to have the stable equilibrium point in the first octant of the N_1-N_2-N_3 space, we must now impose the conditions:

$$N_1^* > 0 \;\; ; \;\; N_2^* > 0 \;\; \text{and} \;\; N_3^* > 0 \qquad (67)$$

Once more there are two sets of solutions, one corresponding to the denominator D being greater than zero and the other corresponding to D being less than zero From equation (63), it is clear that the choice is already made for us. We thus have, in view of the constraints (67):

$$D > 0$$

$$\left\{ \lambda_3 (a_{12} a_{23} - a_{13} a_{22}) + \lambda_2 (a_{13} a_{32} - a_{12} a_{33}) \right.$$
$$\left. + \lambda_1 (a_{22} a_{33} - a_{32} a_{23}) \right\} > 0 \qquad \cdot (68)$$

$$\left\{ \lambda_3 (a_{13} a_{21} - a_{23} a_{11}) + \lambda_2 (a_{11} a_{33} - a_{13} a_{31}) \right.$$
$$\left. + \lambda_1 (a_{23} a_{31} - a_{33} a_{21}) \right\} > 0 \qquad (69)$$

and
$$\left\{ \lambda_3 (a_{11} a_{22} - a_{12} a_{21}) + \lambda_2 (a_{12} a_{31} - a_{11} a_{32}) \right.$$
$$\left. + \lambda_1 (a_{21} a_{32} - a_{22} a_{31}) \right\} > 0 \qquad (70)$$

Let us, for convenience, use the notation:

$$A = (a_{12}a_{23} - a_{13}a_{22})$$

$$B = (a_{13}a_{32} - a_{12}a_{23})$$

$$C = (a_{22}a_{33} - a_{32}a_{23})$$

$$E = (a_{13}a_{21} - a_{23}a_{11}) \tag{71}$$

$$F = (a_{11}a_{33} - a_{13}a_{31})$$

$$G = (a_{23}a_{31} - a_{32}a_{21})$$

$$H = (a_{11}a_{22} - a_{12}a_{21})$$

$$I = (a_{12}a_{31} - a_{11}a_{32})$$

$$J = (a_{21}a_{32} - a_{22}a_{31})$$

The conditions (68) - (70) can now be written more compactly in the form

$$\lambda_3 A + \lambda_2 B + \lambda_1 C > 0$$

$$\lambda_3 E + \lambda_2 F + \lambda_1 G > 0 \tag{72}$$

$$\lambda_3 H + \lambda_2 I + \lambda_1 J > 0$$

As already mentioned, these conditions as well as the condition

$$D > 0 \tag{63}$$

correspond, along with conditions (61) and (62), to the system having stable equilibrium with the

equilibrium populations all positive. Clearly,
conditions (72) and (63), which already imply posi-
tivity of N_i*, render condition (61) superfluous,
as it is automatically satisfied once one remembers
that the aij are all positive. Condition (62) is,
of course, not automatically satisfied, but depends
on the values of various quantities occuring in it,
but there is a wide variety of choice for these
quantities for which the condition can be satisfied.

Let us now consider the three-species case
with harvesting. The equations of the system takes
the form:

$$dN_1/dt = \lambda_1 N_1 - a_{11} N_1^2 - a_{12} N_1 N_2 - a_{13} N_1 N_3 - \lambda_1 k_1 N_1$$

$$dN_2/dt = \lambda_2 N_2 - a_{21} N_2 N_1 - a_{22} N_2^2 - a_{23} N_2 N_3 - \lambda_2 k_2 N_2 \tag{73}$$

$$dN_3/dt = \lambda_3 N_3 - a_{31} N_3 N_1 - a_{32} N_3 N_2 - a_{33} N_3^2 - \lambda_3 k_3 N_3$$

where

$$0 < k_1 < 1 \; ; \; 0 < k_2 < 1 \; ; \; 0 < k_3 < 1 \tag{74}$$

Clearly, the above equations differ from the
original ones, namely equations (58), by the addition
of k_1, k_2, k_3 terms. These additional terms can be
taken care of by the following substitutions:

$$\lambda_1 \longrightarrow \lambda_1 (1-k_1)$$

$$\lambda_2 \longrightarrow \lambda_2 (1-k_2) \tag{75}$$

$$\lambda_3 \rightarrow \lambda_3 (1-k_3)$$

The constraints for the system to possess
stable equilibrium in the positive domain of N_1, N_2
and N_3 can thus be obtained from the constraints
given earlier for the case without harvesting. The
constraints are thus:

$$\ell_3 A + \ell_2 B + \ell_1 C > k_3 A + k_2 B + k_1 C$$
$$\ell_3 E + \ell_2 F + \ell_1 G > k_3 E + k_2 F + k_1 G \qquad (72')$$
$$\ell_3 H + \ell_2 I + \ell_1 J > k_3 H + k_2 I + k_1 J$$

and the inequalities (61), (62) and (63). Of these
last three, one inequality (63) remains unchanged,
and the inequalities (61) and (62) have the same form
as before except that N_1^*, N_2^* and N_3^* are now given
by equations (64), (65) and (66) respectively only
after the substitutions (75) have been incorporated
into them. With (72') and (63) valid, the N_1^* are
all positive and the constraint (61) is, as before,
automatically satisfied. Constraint (62) is not
automatically satisfied, but given the aij as fixed
from the no-harvesting case, it can be satisfied by
suitable restraining of the N_1^*, which amounts to
putting constraints on k_1, k_2 and k_3. So the conditions

for stable equilibrium in the presence of harvesting
we have to worry about are thus the conditions (72')
and (62). Once these constraints are respected, we can
subject our system to harvesting without disturbing its
basic stability property, i.e., the persistence of the
three species N_1, N_2 and N_3. Unfortunately, it is not
possible to put the above constraints in a more elegant
form, as was possible in case of the two-species system,
but given specific situation with corresponding
numerical values for the various a_{ij}, the estimate of
the allowed range for the harvesting parameters k_1,
k_2 and k_3 can be done without any difficulty by an
elementary numerical exercise.

CHAPTER III

3.1   In this chapter, we wish to consider harvesting
in prey-predator models. In this context, one of the
simplest models of interacting populations is the
original one of Lotka and Volterra, taken usually as
a paradigm of mathematical modeling. It has been
reviewed extensively (e.g., May, 1974; Maynard
Smith, 1974; Goel, Maitra and Montroll, 1971), neverthe-
less, we briefly describe it here and then go on to
the theme of harvesting in this frame-work.

In order to explain why the percentage of
sharks and other predatory fish caught in the Medite-
rranean Sea rose dramatically during the World War I
when there was a reduction in fishing, Volterra
suggested a model whose equations are isomorphic to
those given by Lotka for the hypothetical chemical
reaction mechanism:

$$A + X \xrightarrow{k_1} 2X$$
$$X + Y \xrightarrow{k_2} 2Y \qquad\qquad (1)$$
$$Y \xrightarrow{k_3} B$$
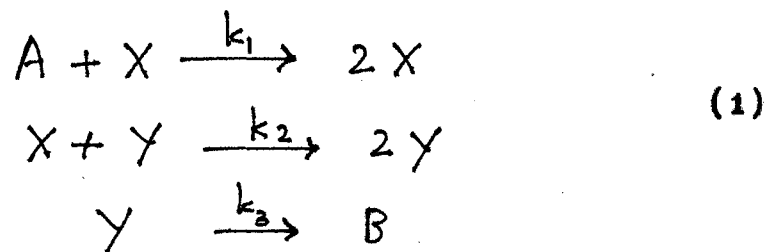
where X and Y are intermediaries, k_1, k_2 and k_3 are
the reaction rate constants. A and B are the reactant

0

and the product respectively, whose concentrations
are kept constant. This implies that the system is
open and so there has to be an exchange of matter
with the surroundings.

Denoting the concentrations of A, X, Y, β
by a, x, y, b respectively, the law of mass action,
gives the following kinetic equations:

$$\dot{x} = \frac{dx}{dt} = \alpha x - \beta xy$$

$$\dot{y} = \frac{dy}{dt} = \beta xy - \gamma y \tag{2}$$

where $\alpha = k_1 a$, $\beta = k_2$ and $\gamma = k_3 b$
In terms of ecology, x and y denote the prey and
the predator populations respectively; α is the
Malthusian rate of growth of the prey; β is the anti-
symmetric equivalence factor which represents the
effect of binary collisions on the interacting
populations and γ is the rate of natural decrease of
the predator. (Volterra, of course, chose a system
in which   in the second equation in the above is
replaced by another constant $\delta \neq \beta$. The
following analysis is valid also for this general case).

The trajectories of (2) for $x \neq 0$; $y \neq 0$
are the solution curves of the first order differential

equation:

$$\frac{dy}{dx} = \frac{y(-\gamma + \beta x)}{x(\alpha - \beta y)}$$ (3)

This equation is separable since we can write it in the form:

$$(\alpha/y - \beta)\, dy = dx\,(-\gamma/x + \beta)$$

Thus, the transcendental equation

$$\alpha \ln y - \beta y + \gamma \ln x - \beta x = c$$ (4)

where $c = $ constant

is the set of solution trajectories of the system (2)

Literature regarding closure and periodicity of this set of trajectories, and the ergodicity of the system is copious, therefore, without further discussion, we summarize the results:

1)   Equation (4) defines a family of closed curves for $x, y > 0$

2)   Let $x(t)$ and $y(t)$ be solutions of (2) with $x(0), y(0) > 0$. Then $x(t+T) \equiv x(t)$ and $y(t+T) \equiv y(t)$ for some positive T.

3)   Let $x(t), y(t)$ be a periodic solution of (2), with period T. Then

$$\langle x \rangle = \frac{1}{T} \int_0^T x(t)\,dt = \hat{x}$$

$$\langle y \rangle = \frac{1}{T} \int_0^T y(t)\,dt = \hat{y}$$

<div align="right">(5)</div>

where $\hat{x}$, $\hat{y}$ are the equilibrium values of x, y, i.e., γ/β and α/β respectively. As is well known, by using the linear perturbation methods, one determines the stability characteristics of the equilibrium points of the dynamical system represented by (2). Of the two equilibrium points {viz. (0,0) and (γ/β, α/β)}, only one (i.e., the latter) is meaningful biologically. Introduction of a small perturbation in this equilibrium point and Taylor expansion of each of equations (3) around this perturbed equilibrium point will result in a community matrix (May, 1974), with eigenvalues, λ_i ; $i = 1, 2$ which are a pair of purely imaginary numbers, $\pm i\omega$ where $\omega = \sqrt{\alpha\gamma}$. That is, the stability is neutral, with perturbation leading to undamped homogenous temporal oscillations of frequency ω or period $2\pi/\omega$

We are now ready to include the effects of fishing (i.e., harvesting of fish population) and explain the conundrum posed at the out-set of this section. We assume that fishing is done at a rate proportional to the size or concentration of the fish.

Consequently, fishing decreases the population of prey fish at a rate $\mathcal{E}x(t)$ and decreases the population of predator fish at a rate of $\mathcal{E}y(t)$. The constant of proportionality, $\mathcal{E}$, reflects the intensity of fishing. Thus, the situation is described by the modified system of differential equations

$$dx/dt = \alpha x - \beta xy - \mathcal{E}x$$
$$dy/dt = -\gamma y + \beta xy - \mathcal{E}y \qquad (6)$$

Or, alternatively,

$$dx/dt = \alpha' x - \beta xy$$
$$dy/dt = -\gamma' y + \beta xy \qquad (7)$$

where $\alpha' = (\alpha - \mathcal{E})$ and $\gamma' = (\gamma + \mathcal{E})$

This system is similar to that decribed by equations (2), provided $\alpha > \mathcal{E}$. Hence, the time averages of $x(t)$ and $y(t)$ are now

$$\langle x(t) \rangle = \frac{\gamma'}{\beta} = \frac{\gamma + \mathcal{E}}{\beta} \qquad (8)$$

and

$$\langle y(t) \rangle = \frac{\alpha'}{\beta} = \frac{\alpha - \mathcal{E}}{\beta}$$

Consequently, for sufficiently small ε, i.e., moderate fishing, the prey population, on the average would increase, whereas, the predator population would decrease. Conversely, if there is a reduction in fishing as happened during the World War I, then the predator population would actually increase and the prey population would decrease. This remarkable result, then, completely explains the 'fishy' phenomenon that Volterra encountered.

Thus far, we have confined ourselves to a prey-predator system without any self-interaction. In the following, we present a slightly different but more realistic situation, which is then analyzed by using the isocline method.

Hence, we include the effect of self-interaction for the prey. The resultant model is

$$\dot{x} = ax - bx^2 - cxy$$
$$\dot{y} = -ey + c'xy \qquad (9)$$

The assumptions under-lying are:

a)   In the absence of predation, the prey would follow the logistic growth, with intrinsic rate of increase a and carrying capacity, $K = a/b$.

b)   The rate at which prey are consumed is proportional to the product of the numbers of predator and prey.

c)   Conversion of prey to predator is 'real time', i.e., there is no time delay in prey consumption and the resultant predator increment.

In order to understand how this system behaves, we employ once more the techniques of the isocline method. At time t, the state of the system is fully described by the values of x and y. To each state, therefore, there corresponds a point in the x-y plane or the phase plane. If we find out the directional arrow.of the movement at each such point (x,y) then we can join-up these arrows to form trajectories which, then, will tell us how the system dynamics operates.

To begin with, we plot the isoclines in this phase plane. When $\dot{x} = 0$, the resultant equation will depict a line which is called the prey isocline, since x denotes prey in the model. Analogously, when $\dot{y} = 0$, the predator isocline will emerge (see Fig. 3).

From (9), it follows that

$$a - bx - cy = 0 \text{ when } \dot{x} = 0$$
$$-e + c'x = 0 \text{ when } \dot{y} = 0$$

(10)
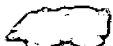
For equilibrium, x and y should simultaneously be zero. This is possible only when

$$\hat{x} = e/c' \quad \text{and} \quad \hat{y} = \frac{a}{c} - \frac{he}{cc'}, \qquad (11)$$

And since x and y should necessarily be positive, $a/h > e/c'$. This inequality states that for an equilibrium with both prey and predator present, the carrying capacity of prey, $K = \frac{a}{b}$ should be high enough to support the predator.

Now, we go to the dynamics of the system, by inserting the directed arrows. We note that for $x > e/c'$, $\dot{y} > 0$ and for $x < e/c'$, $\dot{y} < 0$. Similarly, for the points above the straight line a - bx - cy = 0, $\dot{x} < 0$ and below it $\dot{x} > 0$. This implies that if we start with any initial point in the phase plane, the resultant trajectory would be a spiral. The nature of the spiral depends on the slope of the prey isocline: if it is negative, then the spiral is convergent and the equilibrium point is called a focus. Otherwise, it is a divergent spiral. The physical interpretation of a convergent anti-clockwise spiral is that both prey and predator oscillate temporally with damping

amplitude and the trajectories of the system all converge on to the equilibrium point. Even when disturbed, the system reaches back this point. This point is, therefore, a point of stable equilibrium.

We are now in a position to include the effects of harvesting and/or stocking in the prey and/or the predator. ⌐⌐⌐

Case a) Harvesting of Prey only:

We assume that the rate of harvesting of prey is proportional to the size of the population being harvested and the effort is defined as the constant of proportionality. Thus, the model transforms to

$$\dot{x} = ax - bx^2 - cxy - \alpha x$$
$$\dot{y} = -ey + c'xy \tag{12}$$

where α = effort of harvesting of prey > 0.

From (12), a set of new isoclines are obtained whose equations are

$$(a - \alpha) - bx - cy = 0 \quad \text{when } \dot{x} = 0$$
$$-e + c'x = 0 \quad \text{when } \dot{y} = 0 \tag{13}$$

We immediately see that the new predator isocline is identical to the one that has been obtained before harvesting of prey. But, the new prey isocline _is_ different: it describes a straight line which is parallel to the one obtained previously. See Fig. 4 for graphical representation.

Hence, we say that the effect of constant effort harvesting of prey results in shifting of prey isocline downwards. In order to sustain the stable equilibrium, the following conditions on α immediately arise:

$$\alpha \ < \ \frac{\mu e}{c'} \ - \ a$$

(14)

Case b) Stocking of Prey only:

In a similar spirit (since stocking, mathematically speaking, is just the opposite of harvesting, we see that for constant effort stocking of prey, the prey isocline would shift upwards. A point to note here is that stability _per se_ imposes no theoretical limit on the effort of stocking, though the carrying capacity of the ecosystem may curtail infinite stocking.

<u>**Case c)**</u>   **Harvesting of Predator only:**

Once again, under the assumption of constant effort harvesting of predator, the model becomes

$$\dot{x} = ax - bx^2 - cxy$$

$$\dot{y} = -ey + c'xy - \beta y \tag{15}$$

with the resultant isoclines,

$$a - bx - cy = 0 \quad \text{when } \dot{x} = 0$$

$$-(e+\beta) + c'x = 0 \quad \text{when } \dot{y} = 0 \tag{16}$$

See Fig. 5 for graphical representation.

It is evident that constant effort harvesting of predator will result in the translation of the predator isocline to the right. Accordingly, the stable equilibrium point will move toward the x-axis. To ensure coexistence, we have the following condition

$$\frac{e+\beta}{c'} < \frac{a}{b}$$

or

$$\beta < \frac{c'a}{b} - e \tag{17}$$

<u>Case d)</u> Stocking of Predator only:

Analogously, when we stock the predator at a
proportional rate, the predator isocline will move to
the left and as a consequence, the equilibrium
point will move toward the y-axis. Again, the
condition of coexistence imposes the following
constraint:

$$\frac{e - \beta}{c'} > 0$$

$$\Rightarrow \quad \beta < e \tag{18}$$

In short, we, therefore, conclude that either
harvesting or stocking doesn't destabilize a system
which is inherently stable as is the case here;
though there are limits on the respective efforts in
order to ensure the coexistence of the species.
Incidentally, it should be clear from the above
discussion that the problem of simultaneous harves-
ting or stocking or harvesting in one case and stocking
in the other, is easily workable, as we only have to
superpose the results obtained separately for the
appropriate harvesting or stocking of either prey or
predator. We shall therefore not go any further into
this matter.

3.2   The major draw-back of the prey-predator
models we have studied so far is that their prey
isoclines possess a constant gradient throughout the
domain $x > 0$, $y > 0$. In the Lotka-Volterra model,
it is zero, thereby imparting neutral stability to
the system and generating prey-predator oscillations
with their amplitudes dependent on the initial condi-
tions. Should there be a perturbation, these patho-
logical oscillations (as May (1974) refers to them)
attain a different set of amplitudes, and, clearly,
this is a fragile result. On the other hand, we have
a system whose prey isocline has a constant negative
slope. This renders the system asymptotically stable
implying no oscillations in the long run of time.
But, the field evidence is contrary; we do observe
stable oscillations in the ecosystems. In order to
obviate this difficulty, we assume, on reasonable
theoretical grounds, that the prey isocline has a
unique maximum; and, further, imposing a set of con-
straints which are well defended on the basis of both
theory and a corpus of field data, we generate models
which exhibit precisely the same stable oscillatory
behaviour. These models possess an unstable equili-
brium point around which the trajectories asymptotically

converge, irrespective of the initial conditions, on to an orbit called the 'stable limit cycle'. In addition to this unique feature, they also have a stable equilibrium point.

The point which is central in the foregoing is the attainment of a unique maximum by the prey isocline; which implies that it is a 'humped' structure. This humpedness is the root-cause of instability, thereby, upon super-imposition of additional constraints, leads to the limit cycle behaviour. Therefore, the pertinent question now is: why the prey isocline has a hump, and, one finds a full answer in the analysis of Rosenzweig (1969). The hump, consequently, appears to be an indispensible feature for most of more meaningful models. However, it should be reiterated that the presence of hump alone will not ensure stable oscillatory behaviour. That is, the hump is a necessary criterion but not sufficient, and, in order to elicit the required limit cycle dynamics, one imposes further constraints, as has been said, just before, Kolmogoroff (1936) is the first to embody these constraints into a rather robust theorem, by application of which one is able to show (May, 1972) for these models that they possess either a stable point equilibrium or a stable limit cycle.

We shall now substantiate these bare essentials.

For an ecosystem comprising a prey, x(t) and a predator, y(t), the dynamics may be written, in the following general form:

$$\dot{x} = \frac{dx}{dt} = x\, f(x,y)$$
$$\dot{y} = \frac{dy}{dt} = y\, G(x,y) \tag{19}$$

Let us suppose that it is possible for us to cast equations (19) into the form:

$$\dot{x} = f(x) - h(x,y)$$
$$\dot{y} = -ay + k\,h(x,y) \tag{20}$$

These equations are essentially the same as those which describe the Rosenzweig-MacAnthur model. Here, $f(x)$ is the intrinsic growth rate of x in the absence of predators, $h(x,y)$ is the rate of predation, k is usual equivalence factor and a is the mortality rate of the predator.

Assumption 1:

Predator has no intraspecific competition.

Assumption 2:

The functional response, or the rate at which an individual predator takes prey depends solely on the prey population.

This transforms (20) to

$$\dot{x} = \bigcirc f(x) - y\, h(x)$$
$$\dot{y} = -ay + k\, y\, h(x) \qquad (21)$$

when $y = 0$, $h(x) = \alpha/k \Rightarrow \dot{x} =$ constant will describe the predator isocline.

Assumption 3:

The prey productivity curve, $f(x)$ is a bell-shaped function. That is, the reproductive rate declines for small x as well as large x.

Assumption 4:

The functional response curve, $b(x)$ is such that it increases with x, but, tapers off, for large x. That is, $d\, h(x)/dx$ tends to zero as x increases.

With either of these assumptions, the prey isocline $x = 0$ will give rise to a hump (Rosenzweig, 1969; Maynard Smith, 1974).

Now, reverting to equations (19), we assume the applicativity of Kolmogoroff Theorem. This imposes further properties on $F(x,y)$ and $G(x,y)$ (May, 1974):

(i) $\quad \partial F/\partial y < 0$ $\hspace{4cm}$ (22a)

(ii) $\quad x\,\partial F/\partial x + y\,\partial F/\partial y < 0$ $\hspace{2cm}$ (22b)

(iii) $\quad \partial G/\partial y < 0$ $\hspace{4cm}$ (22c)

(iv) $\quad x\,\partial G/\partial x + y\,\partial G/\partial y > 0$ $\hspace{2cm}$ (22d)

(v) $\quad F(0,0) > 0$ $\hspace{4cm}$ (22e)

and there exists α, β and γ such that

(vi) $\quad F(0,\alpha) = 0$, $\alpha > 0$ $\hspace{2.5cm}$ (22f)

(vii) $\quad F(\beta,0) = 0$, $\beta > 0$ $\hspace{2.5cm}$ (22g)

(viii) $\quad G(\gamma,0) = 0$, $\gamma > 0$ $\hspace{2.5cm}$ (22h)

(ix) $\quad \beta > \gamma$ $\hspace{4.5cm}$ (22i)

A lucid interpretation of these conditions within the context of ecology, is given in May (1974).

Next, what we do is to look for a model which satisfies all the assumptions and conditions enumerated above and, then, study harvesting and stocking in detail. There are quite a few models which fill the bill (Rosenzweig, 1971) and we select, for tractability, the model which is attributed to Holling (see Brauer and Soudack, 1978).

3.3 Holling's model is given by the equations:

$$\dot{x} = x\, f(x,y)\,, \quad f(x,y) = \alpha\left(1 - \frac{x}{k}\right) - \frac{y}{x+D}$$

$$\dot{y} = y\, G(x,y)\,, \quad G(x,y) = \frac{\beta D\,(x-J)}{(J+D)(x+D)} \tag{23}$$

Rearranging the various terms, we can write these equations as

$$\dot{x} = \alpha x\left(1 - \frac{x}{k}\right) - \frac{xy}{x+D}$$

$$\dot{y} = -A(x)\,y + B y\,\frac{x}{x+D} \tag{24}$$

where $A(x) = \beta D J/(x+D)(J+D)$ and $B = \beta D/(J+D)$

We see, here that the mortality rate of predator is a function of the prey population. When $x = 0$, that is no prey, it is a constant $\beta J/(J+D)$. As x increases, the mortality rate of predator decreases; however, it can never become zero, solely for the fact

that x has a ceiling, K.

Comparing with eq. (21), we set

$$f(x) = \alpha \left(1 - \frac{x}{k}\right) x$$

$$h(x) = \frac{x}{x + D} \quad ; \quad k = \beta = \frac{\beta D}{J + D} \tag{25}$$

Though the assumption (3) is not satisfied here, we can check that the assumption (4) is. Hence, the prey isocline will have a hump. Running down the list of conditions of Kolmogoroff theorem, we can routinely verify that they are satisfied, though, actually, the inequality (22c) turns out to be equality Still, the robustness of the theorem makes applicability possible.

When $\quad \dot{x} = o \Rightarrow f(x, y) = o$

ie

$$y = (x + D)\left(1 - \frac{x}{k}\right)\alpha \tag{26}$$

is the prey isocline. It has a unique maximum at $x = \frac{k - D}{2}$, x-intercept at (K, 0) and y-intercept at (0, Dα).

Analogously, when $\dot{y} = 0$, we have $G(x, y) = 0$, i.e.,

<div align="right">(27)</div>

which is the predator isocline. Clearly, it is a
straight line, parallel to the y-axis.

At this point, we take note of the Kolmogoroff
theorem (see Albrecht et al. 1974 and Brauer, 1976).
According to this theorem, the system

$$dx/dt = x \, F(x,y)$$

$$dy/dt = y \, G(x,y)$$

once has initial values in the first quadrant of the
phase plane, has solutions, if (22a-22l) are satis-
fied, such that each solution remains in a bounded
subset of the first quadrant and tends for $t \to \infty$
either to the equilibrium point ($\bar{x}, \bar{y}$) if ($\bar{x}, \bar{y}$)
is a stable equilibrium point or to a limit cycle
around ($\bar{x}, \bar{y}$) if ($\bar{x}, \bar{y}$) is an unstable equilibrium
point. Furthermore, ($\bar{x}, \bar{y}$) is a stable equilibrium
point if

$$\bar{x} \, \frac{\partial f}{\partial x}(\bar{x}, \bar{y}) + \bar{y} \, \frac{\partial G}{\partial y}(\bar{x}, \bar{y}) < 0$$

and an unstable one if

$$\bar{x} \, \frac{\partial f}{\partial x}(\bar{x}, \bar{y}) + \bar{y} \, \frac{\partial G}{\partial y}(\bar{x}, \bar{y}) > 0$$

Now if $G(x,y)$ is independent of y, as it is in the present case, so that the predator isocline is the vertical line $x = J$, the above inequalities reduce simply to

$$\frac{\partial f}{\partial \hat{x}}(\hat{\lambda},\hat{y}) < 0 \tag{28}$$

or

$$\frac{\partial f}{\partial \eta}(\hat{\lambda},\hat{y}) > 0 \tag{29}$$

Clearly, the negativity constraint here is valid for

$$\hat{\lambda} = J > \frac{K-D}{2}$$

i.e.,

$$K < 2J + D \tag{30a}$$

and the positively constraint for

$$K > 2J + D \tag{30b}$$

We thus have the result that so long as $K < 2J + D$, our system possesses stable equilibrium and for $K > 2J + D$, limit cycle oscillations emerge. As K becomes increasingly larger and larger, the amplitudes of the oscillations also become very large

and the trajectories come very near to the axes.
Thus, practically speaking, due to this proximity,
any external perturbation might lead to extinction
of the population.

Having investigated the basic relevant proper-
ties of this model, we now turn to harvesting and
stocking (Brauer and Soudack, 1982).

The model with constant effort harvesting and/or
stocking becomes

$$\dot{x} = x \left\{ \alpha \left(1 - \frac{x}{k}\right) - y/(x+D) \right\} - E_1 x$$

$$\dot{y} = y \left\{ \frac{\beta D(x-J)}{(J+D)(x+D)} \right\} - E_2 y \qquad (31)$$

where, E_1 and E_2 are the respective harvesting (if
positive) or stocking (if negative) efforts. Eq.(31)
can be written in the form

$$\dot{x} = x \left\{ \alpha \left(1 - \frac{x}{k}\right) - y/(x+D) - E_1 \right\}$$

$$\dot{y} = y \left\{ \frac{\beta D(x-J)}{(J+D)(x+D)} - E_2 \right\} \qquad (32)$$

which are similar to those that describe the model
without harvesting, but for the fact that the new iso-
clines are given by

$$\alpha \left(1 - \frac{\lambda}{k}\right) - \gamma/(\eta + D) = E_1$$

$$\frac{\beta D (\lambda - J)}{(J + D)(\eta + D)} = E_2 \qquad (33)$$

intersection of which gives a new equilibrium point.

In order to see how these new isoclines are positioned with respect to the old ones, without actual plotting, we need only to observe that $F_y < 0$ and $G_x > 0$. The former implies that increasing E_1 moves the prey isocline down while decreasing E_1 moves it up (Fig. 6). Analogously, the latter implies that increase in E_2 moves the predator isocline to the right while decrease in E_2 moves it to the left (Fig. 7).

Because of the hump of the prey isocline, which demarkates domains of stability and instability (of course with limit cycles), the following situations arise:

A.   When the System is Initially Stable $(J < (K-d)/2)$:

Here the equilibrium point is on the right slope of the hump.

case 1: Harvesting of Prey only:

As we have noted earlier increase in or incorporation of E_1 (i.e., harvesting of prey), moves the prey

isocline down, and consequently, the equilibrium
point slides down along the predator isocline, x = J.
Since in this process the hump moves left, the equilibrium
point still remains in the domain of stability. It
will, however, come very close to X-axis for a large
E_1, and for further increment, the x intercept of the
prey isocline will fall short of the x intercept of
predator isocline, thereby leading to extinction of
the predator. This infact, puts a ceiling on E_1,
which clearly is

$$E_1^+ = F(J,0)$$

$$= \alpha\left(1-\frac{J}{K}\right) \tag{34}$$

<u>Case ii</u>: Stocking of Prey only:

Stocking of prey (i.e., negative E_1) moves the
prey isocline up and correspondingly, the hump moves
to the right. Thus, for some particular value, equili-
brium point may ride over the hump, thereby engendering
limit cycles. If we decrease E_1 still further, the
resultant large amplitudes of the limit cycle, will
render the system prone to environmental 'noise'.

<u>Case iii</u>: Harvesting of Predator only:

Utilizing the fact that increase in E_2 will
translate the predator isocline to the right, we can

easily observe that the system which is initially stable, will remain so even after harvesting of predator. But, as a result, the equilibrium point will slide down the right slope of the hump, coming dangerously close to x-axis. In order to ensure the co-existence of both populations, we have the following upper limit on E_2:

$$E_2^+ = G(K, o)$$

$$= \frac{\beta D (k - J)}{(J + D)(K - D)} \tag{35}$$

case iv: Stocking of Predator only:

Since stocking (i.e., negative E_2) will move the predator isocline to the left, we observe that for a particular value of E_2, the equilibrium point may ride over the hump, thus eliciting limit cycles. Any further increase will result in larger amplitudes. The upper limit on the predator stocking effort (or lower limit on E_2), thus, is when the predator isocline merges with Y-axis, and clearly, it is:

$$E_2^- = G(O, D\alpha)$$

$$= \frac{-\alpha \beta D^2 J}{J + D} \tag{36}$$

Treatment of the next situation (i.e., when the system is initially unstable) is quite similar. We state the results:

(i)   Harvesting of Prey or Predator will render the system stable.

(ii)   Stocking of prey or predator will only increase the amplitude of the limit cycle, thereby imparting vulnerability to the system.

For situations wherein various combination of these practices occur simultaneously, it is not difficult to see that appropriate superpositions of the results obtained here would suffice.

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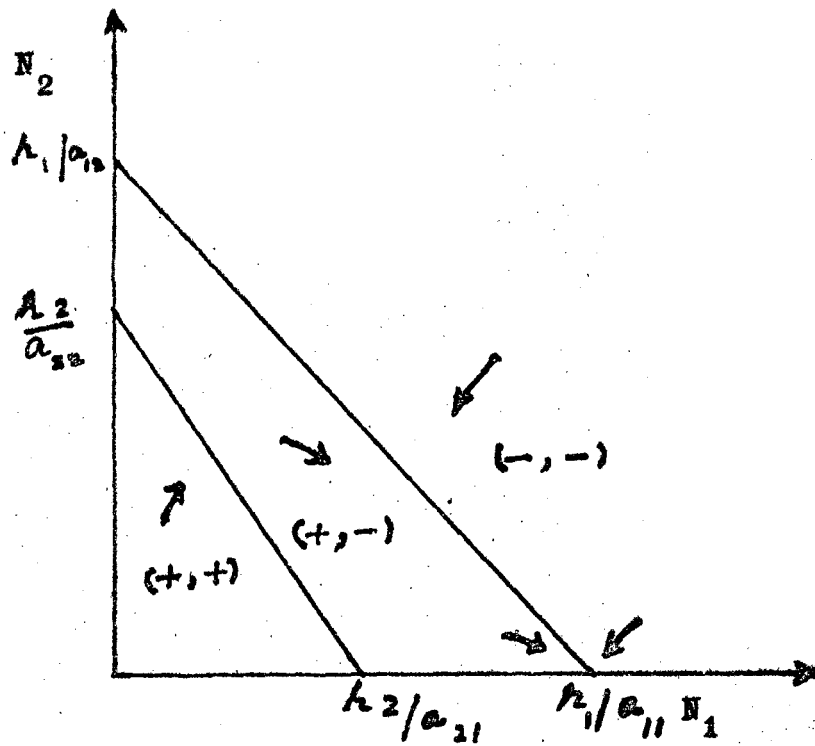
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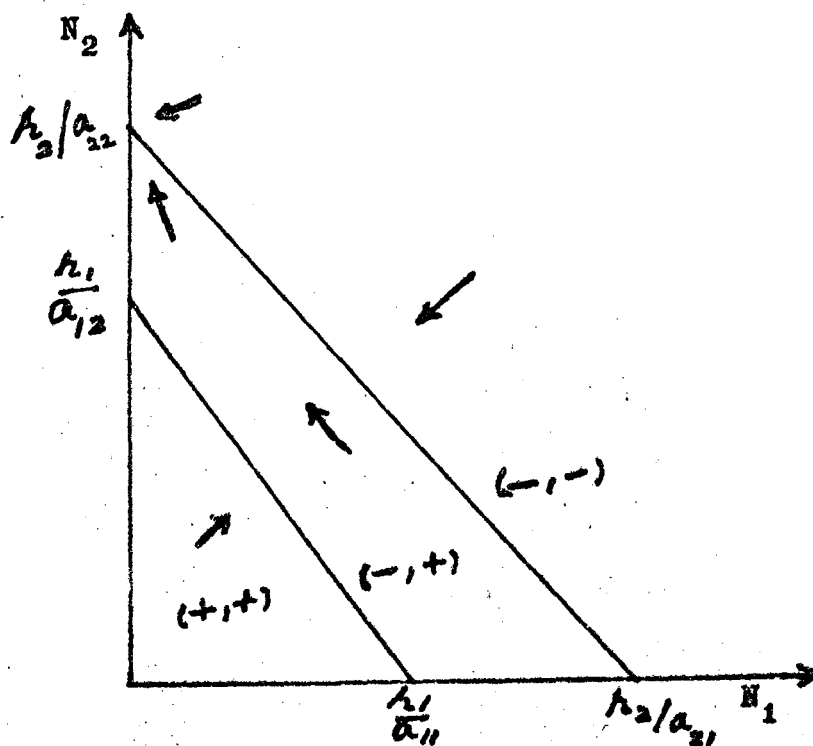
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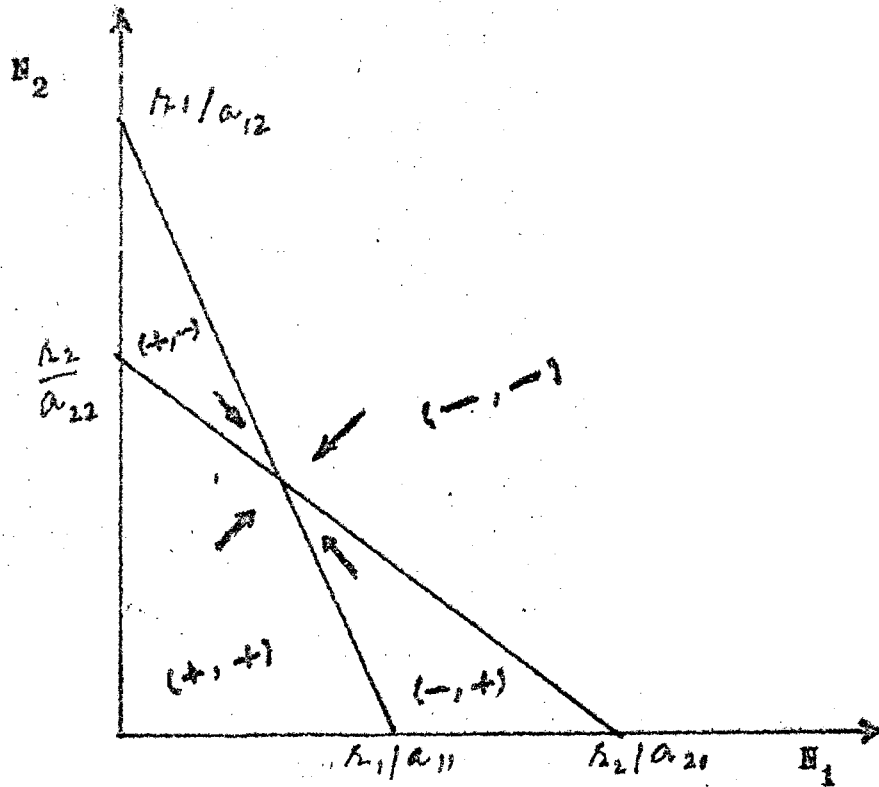
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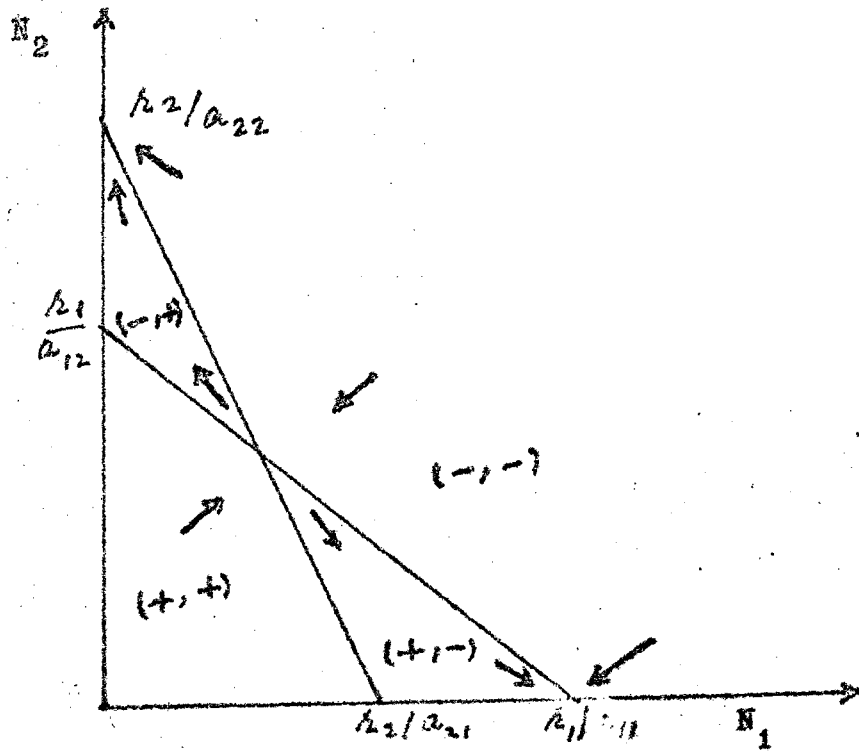
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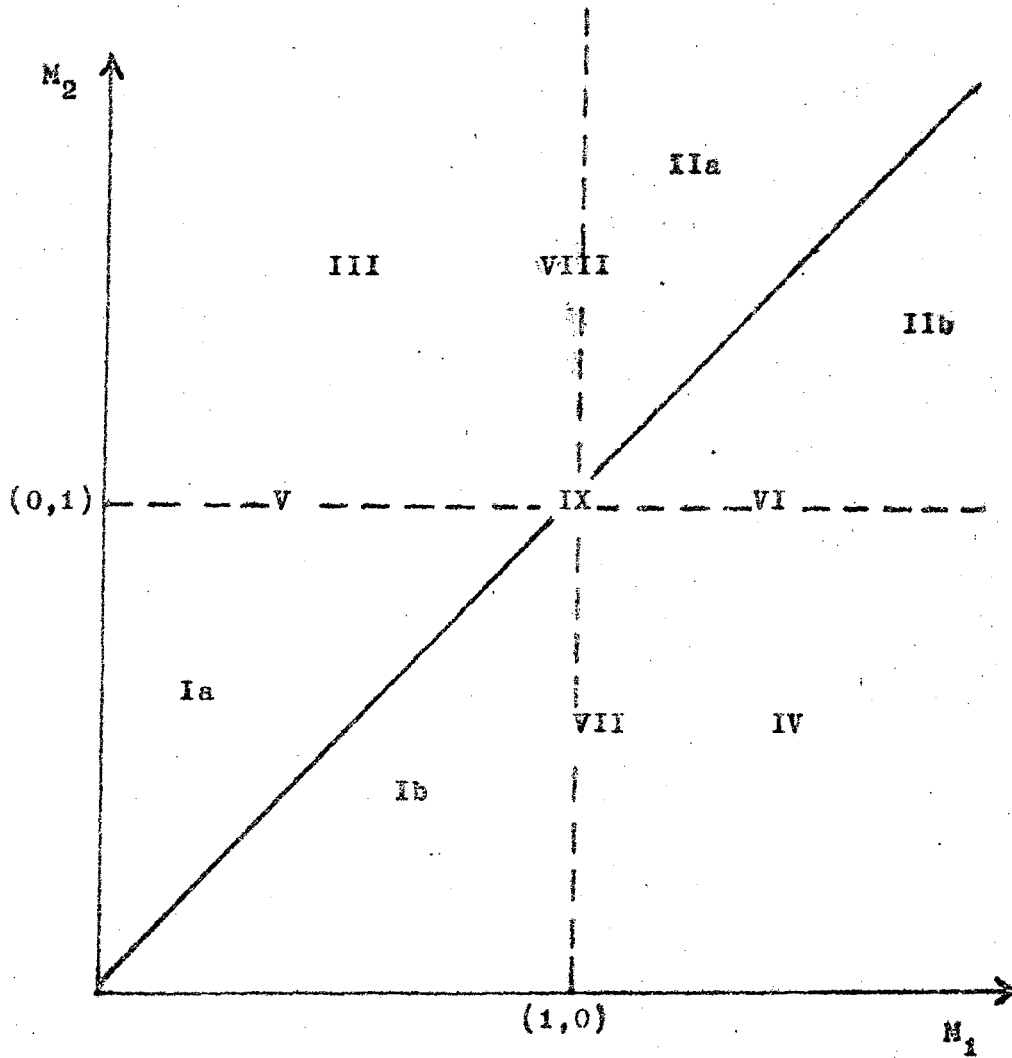
FIG 2

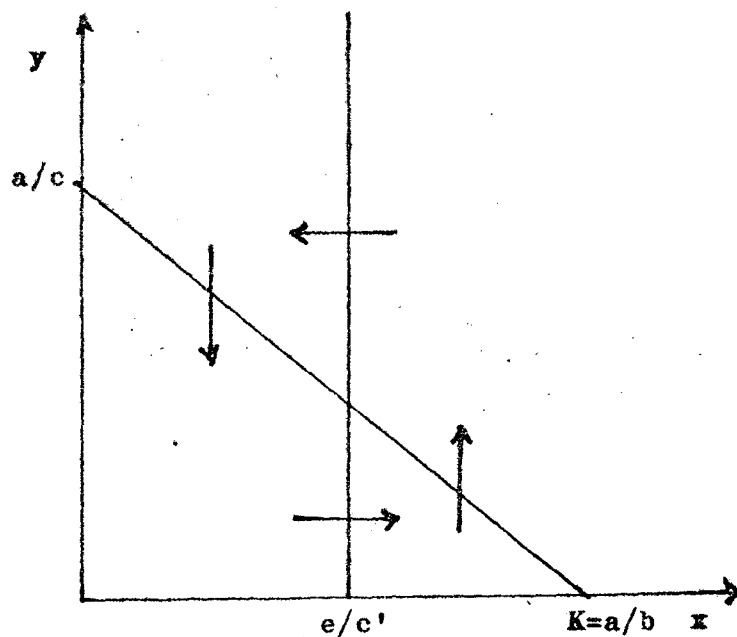FOUR NONDEGENERATE AND FIVE DEGENERATE SITUATIONS
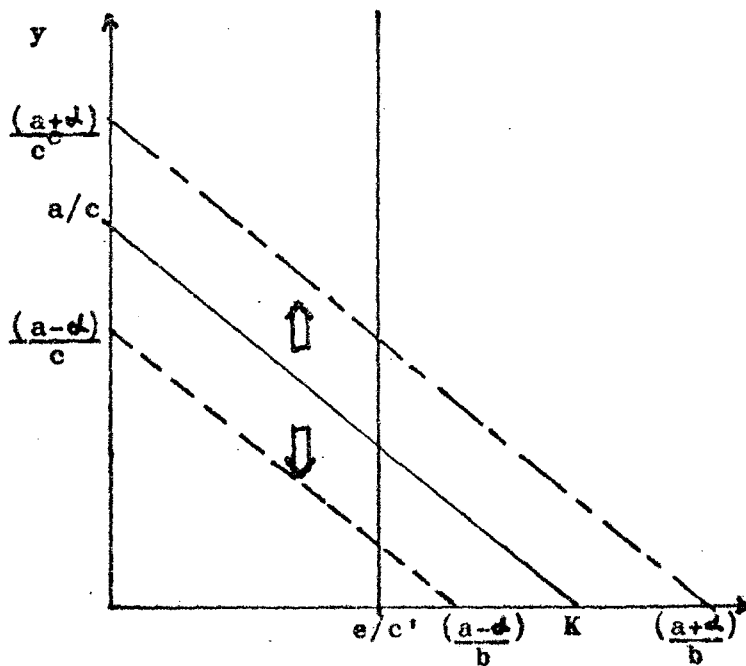
FIG 3 SEE TEXT FOR EXPLANATION

FIG 4

——————— ORIGINAL PREY ISOCLINE
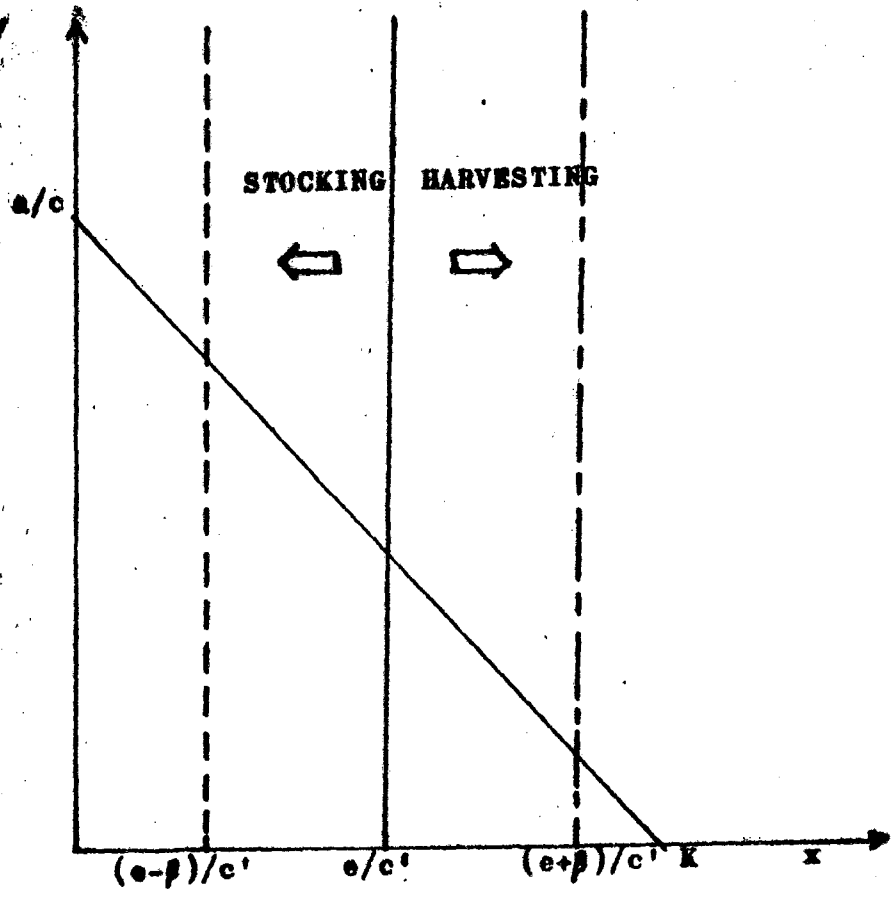
— · —— · — WITH PREY STOCKING ONLY

— — — — WITH PREY HARVESTING ONLY

FIG 5

ORIGINAL PREDATOR ISOCLINE
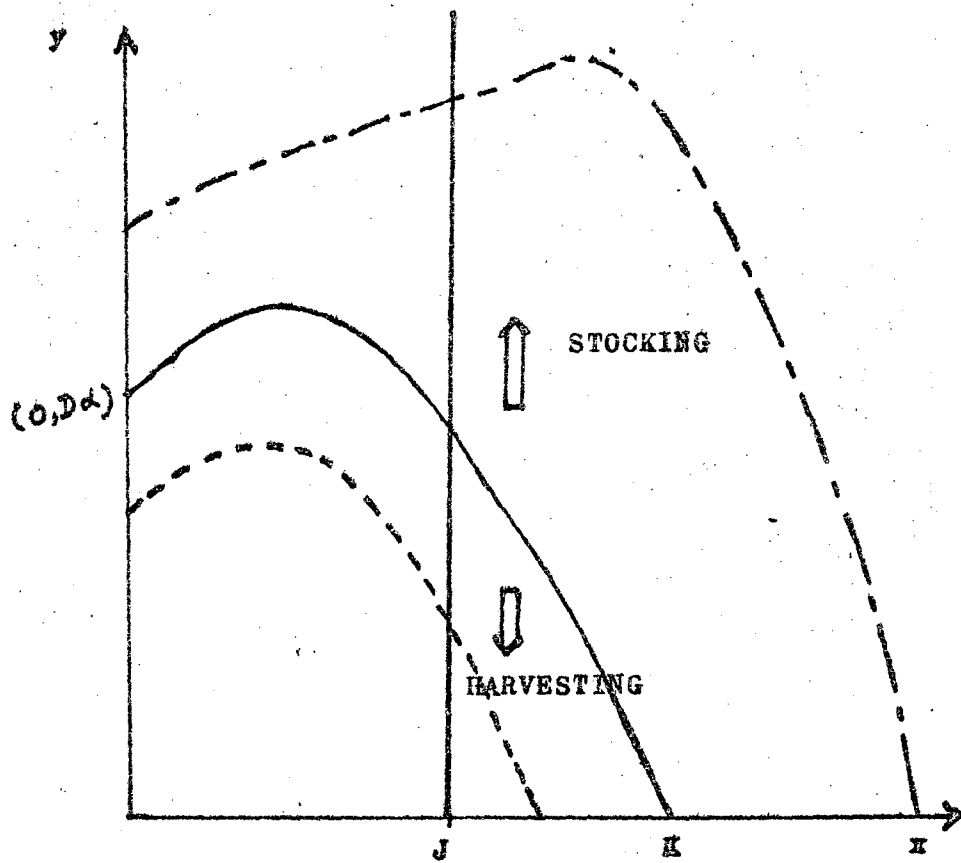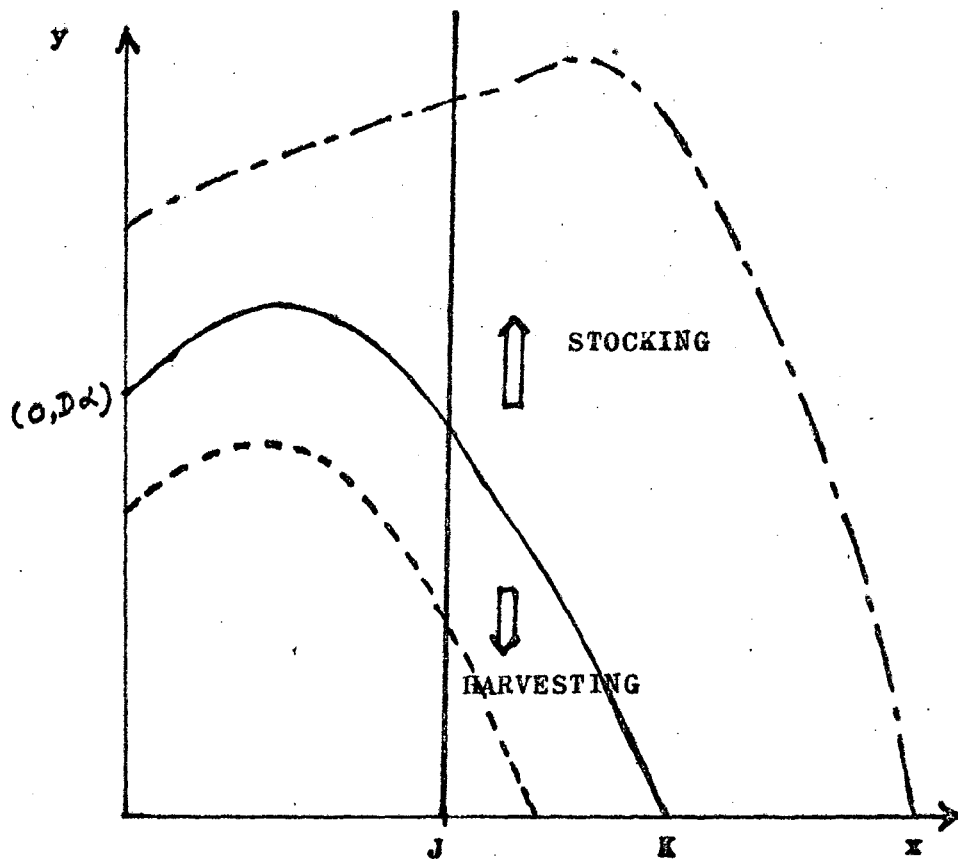WITH PREDATOR STOCKING ONLY
WITH PREDATOR HARVESTING ONLY

FIG 6: ISOCLINES FOR PREY HARVESTING AND STOCKING

FIG 6: ISOCLINES FOR PREY HARVESTING AND STOCKING