1. Models of Malthus, Pearl and Verhulst:

In this chapter we will discuss mathematical models of population growth and of prey-predator interactions which are based on a number of simplifying assumptions.

Ecosystems are in general very complex. It is worthwhile to consider simple idealised ecosystems and build a quantitative basis for them, before hoping to tackle successfully the realistic ones. The most idealised system is one with a single species in an 'unlimited' environment.

All populations of organisms fluctuate in size. The only thing which can be said with certainty is that their sizes will not remain constant. For building a simple mathematical model, we assume that organisms are immortal and reproduce at a rate that is the same for every individual and does not change with time. It is also assumed that the individuals have no effect on one another.

If \( N_t \) be the size of the population at time \( t \) and \( r \) be the rate of increase per unit individual, the simplest differential equation describing population growth can be written as

\[
\frac{1}{N_t} \frac{dN_t}{dt} = r, \quad \text{or} \quad \frac{dN_t}{dt} = rN_t. 
\]
The solution of this equation is given by

\[ N_t = N_0 e^{rt} \]

Where \( N_0 \) is the population at time \( t = 0 \).

This Malthusian equation shows that population growth is exponential in a situation where the per capita rate of growth is constant and is independent of the size of the population. This can be true only for a population so small that there is no interference among its members. The growth of any population in a restricted environment must eventually be limited by a shortage of resources. Thus a stage is reached when the demands made by the existing population on these resources preclude further growth and the population is then at its "Saturation Level", a value determined by the "carrying capacity" of the environment.

Another way of putting it would be that the environment is in reality not an unlimited one. The food available to the population is sooner or latter going to become limited because of the rising population. Hence, the actual growth rate in the above equation should also depend on the proportion of the maximum attainable population size that is still unrealized. Let this maximum size be \( K \). The unrealized proportion when the population is of size \( N \) is thus \( (K - N)/K \). Hence, the growth rate is given by
\[ \frac{dN}{dt} = rN \left( 1 - \frac{N}{k} \right) \]

\[ = N \left( r - sN \right) \]  \hspace{1cm} (1)

where \( s = \frac{r}{k} \) and \( r, s > 0 \)

This is the well known Pearl - Verhulst logistic equation. Following standard nomenclature, \( r \) here is referred to as the intrinsic growth rate and \( K \) as the carrying capacity.

Solving the above equation, we get

\[ N(t) = \frac{\frac{r}{s}}{1 + e^{-r(t-t_0)}} \]

where the constant \( e^{rt_0} \) is related to the initial population by

\[ e^{rt_0} = \frac{\frac{r}{s} - N(0)}{N(0)} \]

According to this picture, the population rises initially as in the previous case, but then the growth rate begins to slow down and the population turns towards its asymptotic value which is \( \frac{r}{s} \). The value \( N = \frac{r}{s} \) is the maximum that the population can reach and is therefore appropriately named, as mentioned earlier, the carrying capacity of the given environment (Pielou 1977; Freedman 1980; May 1972; Smith 1974).
2. The Lotka - Volterra model:

We now consider a situation when we have two interacting populations in the given environment; say, a prey and a predator. Two very general assumptions used in such prey-predator models are

1. the two populations inhabit the same area, so densities are directly proportional to numbers.
2. there is no time lag in the responses of either population to changes due to the other.

An interesting and mathematically elegant model for the interaction between a pair of species - a prey and a predator, was given independently by Lotka (1924) and Volterra (1931). Volterra arrived at the model, after a statistical study of the variation in the fish catch obtained in the Adriatic sea, with the help of his friend D' Anconna. It was noted that the populations of two species of fish varied with the same time period but a little out of phase (Goel et. al. 1971; Volterra 1927).

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

\[
\frac{dH}{dt} = a_1 H, \quad a_1 > 0
\]
If \( P \) is the population of predator at any time \( t \), its growth (decay) equation in the absence of prey can be written as

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

If the prey and the predator are in the same niche and if they interact, then the interaction term is, in general, a complicated function of \( H \) and \( P \). But, we here consider the following equations for a prey - predator system in the deterministic approach to the problem:

\[
\frac{dH}{dt} = (a_1 - b_1 P) H
\]

\[
\frac{dP}{dt} = (-a_2 + b_2 H) P
\]

where \( a_1, a_2, b_1, b_2 > 0 \)

Here \( a_1 \) and \( a_2 \) are the average rate of growth and decay per individual in the absence of other species and \( b_1 \) and \( b_2 \) are the interaction parameters. If the niche is not overlapping the interaction is reduced and the value of \( b_1 \) and \( b_2 \) are very small. In the above equations, all the parameters are positive definite.
Unfortunately, equation (2) can not be solved analytically. We have to take recourse to approximation schemes and numerical methods. In view of their non-linear nature, it is unlikely that the full information content of these equations will be uncovered by such methods. It may be noted here that equation (1) is also non-linear, but its simple form enables us to solve it exactly by direct integration. That is no more possible when we come to equation (2). However, an exact result which is of crucial interest in the present context, can be established (Pielou 1977; Simmons 1981).

This is done as follows. From (2), we can write

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

or,

\[ a_2 \frac{dH}{H} - b_2 \frac{dH}{P} + a_1 \frac{dP}{P} - b_1 dP = 0 \]

Integrating, we get

\[ a_2 \log H - b_2 H + a_1 \log P - b_1 P = \log K \quad (2a) \]

or,

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

\[ \therefore \quad \frac{P^{a_1}}{e^{-b_1 P}} = K H - a_2 e^{b_2 H} \quad (3) \]

where K is a constant given by
\[ K = H_0 P_0 e^{a_2 a_1 -b_2 H_0 - b_1 P_0} \]

in terms of the initial values of \( H \) & \( P \) denoted, respectively by \( H_0 \) and \( P_0 \).

We, thus, see that system (2) possesses a conserved quantity given by the left hand side of equation (2a). The equation represents a family of closed curves in which each member of the family is characterised by a particular value of the constant \( K \). We cannot solve equation (3) for either \( H \) or \( P \) individually but we can determine the curves on which \( H \) and \( P \) will move. To do this, we equate the left and right hand sides of equation (3) to new variables \( Z \) and \( W \), and then plot the graphs \( C_1 \) and \( C_2 \) of the functions

\[
Z = P_1 e^{a_1 -b_1 P} \quad \text{and} \quad W = KH e^{b_2 H}
\]

as shown in Fig.1.

For \( Z = W \), we are confined in the third quadrant to the line \( L \). To the maximum value of \( Z \) given by the point \( A \) on \( C_1 \), there corresponds one point \( M \) on \( L \) and the corresponding point \( A' \) and \( A'' \) on \( C_2 \) leading to two values of \( H \) which determine the bounds between which \( H \) 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 on \( P \). In this way we find the points \( P_1, P_2 \) and \( Q_1, Q_2 \) on the desired curve \( C_3 \). Additional
Fig. 1
points are easily found by starting on $L$ at a point $R$ anywhere between $M$ and $N$ and projecting on the one hand onto $C_1$ and over to $C_3$, and on the other onto $C_2$ and over to $C_3$. It is clear that changing the value of $K$ raises or lowers the points $A$ and $B$, and this expands or contracts the curve $C_3$. Accordingly, when $K$ is given various values, we obtain a family of ovals about the point $S$, which is all there is of $C_3$ when the minimum value of $W$ equals the maximum value of $Z$.

Now, we will see how the corresponding point $(H, P)$ on $C_3$ moves around the curve as $t$ increases. We can find out the equilibrium point by putting the right hand sides of equation (2) equal to zero i.e.

$$a_1 H - b_1 PH = 0,$$
$$-a_2 P + b_2 PH = 0.$$

Solving these equations, we get

$$H^* = \frac{a_2}{b_2},$$
$$P^* = \frac{a_1}{b_1}.$$

Hence, the co-ordinates of $S$ will be

$$H = \frac{a_2}{b_2}, \quad P = \frac{a_1}{b_1}.$$

When $H < \frac{a_2}{b_2}$, $dP/dt$ is negative, so the point on $C_3$ moves down as it traverses the arc $Q_2P_1Q_1$. Similarly, it moves up along the
arc \( Q_1P_2Q_2 \). Hence, as \( t \) increases, points on \( C_3 \) move in an anti-clockwise direction.

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

3. **THE LESLIE - GOWER MODEL:**

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

\[
\frac{dH}{dt} = (a_1 - c_1P) \, H \\
\frac{dP}{dt} = (a_2 - c_2P/H) \, P
\]

where \( a_1, a_2, c_1, c_2 > 0 \).

The equilibrium point can be calculated by putting the right hand sides of the above equations equal to zero, i.e.,

\[
a_1 - c_1P = 0 \\
\Rightarrow P^* = a_1/c_1 \\
a_2 - c_2P/H = 0
\]
At the equilibrium point given by

\[ H^* = \frac{C_2 P^*}{a_2} = \frac{a_1 C_2}{a_2 C_2} \]

the prey-predator ecosystem reaches a dynamic balance. We will now show that such an equilibrium point is a stable one. Consider the points for which \( \frac{dH}{dt} = 0 \). They are given by the line

\[ (a_1 - C_1 P)H = 0 \]

\[ P = \frac{a_1}{C_1} \]

This line is the so-called H-isocline. If now

\[ P > \frac{a_1}{C_1}, \quad \frac{dH}{dt} = (a_1 - C_1 P) < (a_1 - C_1 \frac{a_1}{C_1}) < 0 \]

For

\[ P < \frac{a_1}{C_1}, \quad \frac{dH}{dt} > (a_1 - C_1 \frac{a_1}{C_1}) > 0 \]

Analogous arguments show that the line

\[ (a_2 - \frac{C_2 P}{H}) = 0 \]
or, \[ H = \frac{C_2P}{a_2} \]
represents the P-isocline, for which \( \frac{dP}{dt} = 0 \).

We note that if

\[
H > \frac{C_2P}{a_2}, \quad \frac{dP}{dt} = (a_2H - C_2P) \frac{P}{H} \]

\[
> (a_2 \times \frac{C_2P}{a_2} - C_2P) \frac{P}{H}
\]

\[
> 0
\]

Furthermore, for

\[
H < \frac{C_2P}{a_2}, \quad \frac{dP}{dt} = (a_2H - C_2P) \frac{P}{H}
\]

\[
= (a_2 \times \frac{C_2P}{a_2} - C_2P) \frac{P}{H}
\]

\[
< 0
\]

In the diagram drawn (Fig. 2) we have plotted the H-isocline and the P-isocline which are the straight lines \( P = \frac{a_1}{C_1} \) and \( H = \frac{(C_2P)}{a_1} \), respectively. We have given above the inequality conditions for all the four regions into which the region of positive \( H \) and positive \( P \) can be divided. Suppose, we start drawing the trajectory which the system will follow at some point A in the region I. In this region \( H > 0 \) and \( P < 0 \). It follows that \( H \) increases and \( P \) decreases as time increases. Arrows are added to the phase space diagram to
Fig. 2  PHASE-SPACE DIAGRAM
indicate the direction the trajectory will follow. So the trajectory will move towards left from the point A and will meet the \( P \)-isocline. At this point \( \frac{dP}{dt} = 0 \), and the tangent to the trajectory will be normal to the \( P \)-axis. In region II, \( \dot{H} > 0 \) and \( \dot{P} > 0 \) i.e. \( H \) & \( P \) both increase as time increases. In this region, the trajectory will move to the right and will cross the \( H \)-isocline. At this point \( \frac{dH}{dt} = 0 \), and the tangent to the trajectory will be normal to the \( H \)-axis. Similarly, we can draw the trajectory for regions III & IV. The phase space trajectory we get this way is a spiral which converges on the equilibrium point which is the intersection of \( H \)-isocline and \( P \)-isocline. Hence, each species population undergoes dwindling oscillations with time towards its equilibrium level.

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

Leslie's formulation is different from Volterra's in the following ways

1. For Volterra, whether the predator increases or decreases in number depends only on the density of prey, whereas for Leslie it depends on the number of prey per predator.
2. Volterra's model relates the rate of increase of the predators to the rate at which prey are being eaten whereas in Leslie's formulation there is no relationship between the rate at which a predator eats and the rate at which it reproduces.

4. THE KOLMOGOROV THEOREM:

Neither of the two models we have discussed in the above possess stable limit cycle. Kolmogorov has given the criteria for stable equilibrium point or a stable limit cycle which are applicable to essentially all two - species prey predator models. This is because the form in which Kolmogorov wrote the equations for the one prey-one predator system is quite general. The equations are:

\[
\begin{align*}
\frac{dH}{dt} & = H \cdot F(H,P) \\
\frac{dP}{dt} & = P \cdot G(H,P)
\end{align*}
\]

The Kolmogorov theorem says that predator - prey systems of the above form have either a stable equilibrium point or a stable limit cycle, provided that F and G are continuous functions of H & P, with continuous first derivatives, throughout the domain \( H > 0 \), \( P > 0 \) and that
It is also required that there exist quantities $A, B, C$ such that

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

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

(viii) $G(C, 0) = 0$ with $C > 0$

(ix) $B > C$

The proof of this theorem comes from the Poincare-Bendixson theorem (Minorsky, 1962). In biological terms, Kolmogrov's conditions are: (i) for any given population size, the per capita rate of increase of the prey species is a decreasing function of the number of predators (ii) the rate of increase of the prey is a decreasing function of population size (iii) the rate of increase of predator's decreases with their population size (iv) the rate of increase of predator is an increasing
function of population size \((v)\) when both populations are small
the prey have a positive rate of increase \((vi)\) there can be a
 predator population size sufficiently large to stop further prey
increase, even when the prey are rare. Condition \((vii)\) requires
a critical prey population size \(B\), beyond which they can not
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.

This theorem may be applied to a system to show that it
possesses either a stable limit cycle or a stable equilibrium
point. A conventional neighbourhood analysis reveals whether the
equilibrium point is stable. In neighbourhood stability analysis,
we consider the linearised version of the model in the
neighbourhood of the equilibrium point and use the so-called
Routh-Hurwitz criteria.

5. THE HOLLING - TANNER MODEL:

Now we will take the Holling - Tanner model which is
the representative of a great many non-linear models that produce
stable limit cycles. An application of the Kolmogorov theorem
to this model will show that, since the equilibrium point which
the model for certain ranges of parameters possesses is not a
stable one, the model necessarily has a limit cycle solution.
The Holling - Tanner model is only slightly more elaborate than that of Leslie and Gower. Let $H$ and $P$ be the prey and predator populations and $r$ and $s$ be the intrinsic growth rates of the prey and the predator respectively. Then the growth of the prey population is given by the logistic equation

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

(3)

where $K =$ maximum no. of prey allowed by some limited resource.

When predators are present, mortality from predation must be subtracted from equation (3). This mortality is the product of a predation rate, number killed per unit time, and the number of predators. This was incorporated by Holling (1965) in equation (3) by modifying the latter as follows:

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

(4)

where $W =$ maximum of the predation rate when the predator will not or can not kill more prey even when the prey are available.

$D =$ Constant determining how fast the functional response increases at low densities of prey.

In the above equation, it is assumed that in the absence of the predator, the prey population would grow
logistically but in its presence the prey growth rate is reduced. The reduction in the prey per capita growth rate caused by the predator is now not merely a constant multiple of $P$. The coefficient $W/(D+H)$ is arrived at by considering the probable effect on a predator attack rate of the density of the population of prey. Holling (1965) argued that the attack rate of predator on prey as measured by the number of prey attacked per predator per unit of time, say $Y$, often takes the form $Y = WH/(D+H)$. This relation allows for the fact that there must be a ceiling $W$, to each predator's attack rate, that will not be exceeded however great the prey density becomes. Thus when $H \gg D$, $Y \approx W$. The magnitude of the constant $D$ varies directly with the prey's ability to evade attack: the more elusive the prey, the greater the value of $D$. The obvious explanation for the functional response is that it takes the predator a certain amount of time to kill and eat each prey.

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

$$\frac{dP}{dt} = SP \left(1 - \frac{P}{\gamma H}\right)$$

Equations (4) and (5) give a complete formulation of the Holling - Tanner model.
Now, let us see how this model behaves globally and locally. To see this we first do the Kolmogorov analysis of the model.

In our case, functions $F(H,P)$ and $G(H,P)$ can be written as

$$F(H,P) = r - \frac{b_1 H}{H+D}$$
$$G(H,P) = S - \frac{b_2 P}{H}$$

where $b_1 = \frac{r}{k}$ and $b_2 = \frac{S}{\gamma}$

We note that:

$$\delta F \frac{< 0}{\delta P} \Rightarrow W, D > 0$$

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

$$H(\delta F/\delta H) + P(\delta F/\delta P) < 0 \Rightarrow -b_1 H^3 - 2b_1 H^2 D - b_1 HD^2 < WP$$

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

$$\delta G \frac{< 0}{\delta P} \Rightarrow b_2 > 0 \text{ i.e. } S/\gamma > 0$$
This condition is also satisfied because \( S \) and \( \gamma \) are positive constants.

(iv) \( H \left( \frac{\delta G}{\delta H} \right) + P \left( \frac{\delta G}{\delta P} \right) = 0 \)

(v) The requirement \( F(0, 0) > 0 \) needs \( r > 0 \). As \( r > 0 \), in the model this requirement is fulfilled.

(vi) \( F(0, A) = 0 \) gives \( A = rD/W \) which is clearly positive as \( r, D, W \) all are positive constants.

(vii) \( F(B, 0) = 0 \implies B = b/r_1 \) which is also clearly positive as \( r \) and \( b_1 \) are both positive.

(viii) \( G(C, 0) = s \) with \( C > 0 \).

The conditions (IV), (VIII) as well as the one yet to be discussed, namely the ninth one, are not quite satisfied in the present case. Yet the constraints that are satisfied impose enough conditions on the model so that it does possess either a limit cycle or stable equilibrium. This is in keeping with the known result that the Kolmogorov theorem is valid often even when not all its conditions are satisfied.

The present model thus possesses either a limit cycle or stable equilibrium. The latter possibly can be checked by going through a local or neighbourhood stability analysis. For this, we have to linearize this model around the equilibrium point using Taylor expansion and discarding all terms which are
of second or higher order in the population perturbations. After that, we have to construct the community matrix and calculate the eigenvalues of the matrix which follow from the determinantal equation.

If all the eigenvalues of the matrix have negative real parts, then the equilibrium point is a stable one and the model thus possesses a point of stable equilibrium. If all the eigenvalues do not satisfy this property, then the model does not possess a point of stable equilibrium. The relevant property of the eigenvalues can be tested by using the Routh-Hurwitz criteria. According to these criteria, if the equation for the eigenvalues \( \lambda \), for an m-dimensional matrix, is of the form

\[
\lambda^m + a_1 \lambda^{m-1} + a_2 \lambda^{m-2} + \ldots + a_m = 0
\]

then, for all the \( \lambda \)'s to have negative real parts, the \( a_i \)'s and certain combinations thereof must obey certain inequality constraints. For the case \( m=2 \), we only have \( a_1 \) and \( a_2 \) and the constraints on them are:

\[
a_1 > 0, \quad a_2 > 0
\]

For \( m=3 \), we have \( a_1, a_2 \) and \( a_3 \) and the constraints are:

\[
a_1 > 0, \quad a_3 > 0, \quad a_1 a_2 > a_3
\]
The equilibrium points \( H^* \) and \( P^* \) can be obtained by putting the right hand sides of the equations (4) and (5) equal to zero. From equation (5) we get:

\[
P^* = H^*
\]

(6)

and from equation (4)

\[
\frac{H^*}{1 - \frac{1}{K}} = \frac{(WY/r)H^*}{H^* + D} = 0
\]

(7)

It is convenient to define the two quantities \( \alpha \) and \( \beta \) by

\[
\alpha = \frac{(WY/r)}{r}
\]

\[
\beta = \frac{D}{K}
\]

Equation (7) then takes the form

\[
H^{*2} + H^*K(\alpha + \beta - 1) - \beta K^2 = 0
\]

The solution of this equation may then be written as

\[
H^* = D\left(1 - \beta - \frac{R}{2\beta}\right)/(2\beta)
\]

(8)

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

The solution with negative sign before \( R \) corresponds to a negative value of \( H^* \) and is therefore to be discarded. In the following, we shall consider the solution with only the positive sign before \( R \).
To consider the behaviour of the system in the neighbourhood of the equilibrium point \((H^*, P^*)\), we have to approximate equations (4) and (5) by using Taylor series expansions around \((H^*, P^*)\).

Re-writing equations (4) & (5) as

\[
\begin{align*}
\frac{dH}{dt} &= F_1(H, P) = rH \left[ 1 - \frac{H}{K} - \frac{(W/r)P}{H+D} \right] \\
\frac{dP}{dt} &= F_2(H, P) = SP \left[ 1 - \frac{P}{\gamma H} \right]
\end{align*}
\]

and expanding about the equilibrium point, for each population, we write

\[
\begin{align*}
H &= H^* + X_1(t) \\
P &= P^* + X_2(t)
\end{align*}
\]

where \(X_1(t)\) and \(X_2(t)\) measure the initially small perturbations to the prey and predator populations.

The Taylor series expansion around \(H^*\) and \(P^*\) can be written as

\[
\begin{align*}
\dot{H}^* &= F_1(H^*) + (H-H^*) \frac{\delta H^*}{\delta H} \dot{P}^* + (P-P^*) \frac{\delta P^*}{\delta P} + \text{higher terms}
\end{align*}
\]
Similarly for,

\[ \dot{P} = F_2(P^*) + (P-P^*) \frac{\delta P^*}{\delta P} (H-H^*) \]

\[ \frac{\delta P^*}{\delta H} P^* + \text{higher terms} \]

Putting

\[ H - H^* = X_1(t) \]

\[ P - P^* = X_2(t) \]

in the above equations and neglecting terms of second or higher order in the population perturbations, a linearized approximation is obtained as

\[ \frac{d}{dt} [H^* + X_1(t)] = F_1(H^*) + X_1(t) \frac{\delta H^*}{\delta H} + X_2(t) \frac{\delta H^*}{\delta P} \]

or

\[ \frac{dX_1(t)}{dt} = X_1(t) + \frac{\delta H^*}{\delta H} + X_2(t) \frac{\delta H^*}{\delta P} \]

Since \( F_1(H^*) = F_2(H^*) = 0 \), because at equilibrium point all species exhibit zero growth rate.

Similarly,

\[ \frac{dX_2(t)}{dt} = X_2(t) + \frac{\delta P^*}{\delta P} + X_1(t) \frac{\delta P^*}{\delta H} \]

\[ \frac{\delta P^*}{\delta H} P^* + \text{higher terms} \]
Now, putting

\[
\begin{align*}
\frac{\delta H}{\delta H} | \frac{\delta F_1}{\delta H} &= a_{11}, & \frac{\delta H}{\delta P} | \frac{\delta F_1}{\delta P} &= a_{12} \\
\frac{\delta P}{\delta H} | \frac{\delta F_2}{\delta H} &= a_{21}, & \frac{\delta P}{\delta P} | \frac{\delta F_2}{\delta P} &= a_{22}
\end{align*}
\]

The above equations can be written as

\[
\frac{dX_1(t)}{dt} = \sum_{j=1}^{2} X_j(t) a_{1j}
\]

and

\[
\frac{dX_2(t)}{dt} = \sum_{j=1}^{2} X_j(t) a_{2j}
\]

If we combine these equations, the general equation can be written as

\[
\frac{dX_1(t)}{dt} = \sum_{j=1}^{2} X_j(t) a_{1j}
\]  \hspace{1cm} (9)

This set of equations describe the population dynamics in the neighbourhood of the equilibrium point. Equivalently, we may write in matrix notation.
\[ \frac{dX(t)}{dt} = AX(t) \]

Here \( X \) is a column matrix with just two elements and \( A \) is the 2x2 "Community matrix" whose elements \( a_{ij} \) describe the effect of species \( j \) upon species \( i \) near equilibrium. The elements \( a_{ij} \) depend both on the details of the original equations (4) & (5), and on the values of the equilibrium populations.

The community matrix can be written as

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

Now, we have to evaluate all the partial derivatives at the point \((H^*, P^*)\). So we get

\[
a_{11} = \left( \frac{\delta F_1}{\delta H} \right)^* = rH^* \left[ - \frac{1}{K} + \frac{(W/r)P^*}{(H+D)^*} \right]
\]

\[
a_{12} = \left( \frac{\delta F_1}{\delta P} \right)^* = \frac{-WH^*}{H+D}
\]

\[
a_{21} = \left( \frac{\delta F_2}{\delta H} \right)^* = \frac{S(P^*)^2}{Y(H^*)^2} = \gamma S
\]

\[
a_{22} = \left( \frac{\delta F_2}{\delta P} \right)^* = \frac{-SP^*}{\gamma H^*} = -S
\]

Now, we will consider the equation

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\[
\frac{dX(t)}{dt} = AX(t)
\]

or

\[ \dot{X} = AX \]  \hspace{1cm} (9)

If \( \Omega \) be a matrix that diagonalises \( A \), we have

\[
\Omega^{-1}A\Omega = D
\]

where \( D \) is a diagonal matrix with element \( \lambda_i \) \( (i=1,2) \), being the eigenvalues of \( A \).

Equation (9) then leads to

\[
\Omega^{-1} \dot{X} = \Omega^{-1}A\Omega\Omega^{-1}X
\]

\[ \cdot \cdot \cdot \]

\[ Y = DY \]

where

\[
\Omega^{-1} \dot{X} = Y
\]

\[ \Omega^{-1}X = Y \]

This equation can be solved easily and the solutions are

\[ Y_i = C_i e^{\lambda_i t} \]

where \( C_i \) are constants which depend on the initial conditions.

The elements \( X_1, X_2 \) of the matrix \( X \) can be evaluated by the result.
\[ X = \Omega Y \]

So that we finally get

\[ X_j = \sum_{i} \Omega_{ji} C_i e^{\lambda_i t} \]

or,

\[ X_j = \sum_{i=1}^{2} S_{ji} C_i e^{\lambda_i t} \]

These equations now completely determine the populations \( H \) and \( P \). It is clear from these equations that under the condition

\[ \text{Re} (\lambda_i) < 0, \quad i=1, 2 \]

\[ X_j \longrightarrow 0 \quad \text{as} \quad t \longrightarrow \infty \]

This implies that

\[ H \longrightarrow H^* \quad \text{for} \quad t \longrightarrow \infty \]

\[ P \longrightarrow P^* \]

Thus asymptotically the system reaches the equilibrium point. This shows that the system possesses stable equilibrium.

Note that \( \lambda_i \) are nothing but the eigenvalues of the matrix \( A \) which follow from the characteristic equation

\[ \det | A - \lambda I | = 0 \quad , \quad I = 2 \times 2 \text{ unit matrix} \]

or

\[ \begin{vmatrix} a_{11} - \lambda & a_{12} \\ a_{21} & a_{22} - \lambda \end{vmatrix} = 0 \]
\[ \lambda^2 + a\lambda + b = 0 \]

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

\[ b = a_{11}a_{22} - a_{12}a_{21} \]

The necessary and sufficient condition for the system to possess neighbourhood stability is that both the eigenvalues \( \lambda \) have negative real parts. Following the Routh-Hurwitz criteria, this requires that both the coefficients \( a \) and \( b \) be positive.

The condition \( b > 0 \) requires

\[ b = rSH^* \left[ \frac{1}{K} - \frac{aH^*}{(H+D)^2} + \frac{a}{(H+D)^2} \right] > 0 \]

where

\[ (Wy) \]

\[ \alpha = \frac{a}{r} \]

which is fulfilled automatically.

The other condition, \( a > 0 \), clearly requires

\[ S - rH^* \left[ - \frac{1}{K} + \frac{aH^*}{(H+D)^2} \right] > 0 \]

After some algebraic manipulation, we get

\[ \frac{S}{r} > \frac{2(a - R)}{1 + a + \beta + R} \quad (10) \]
Hence, for stability the value of $S/r$ is always greater than the above limit.

The stability condition (10) may or may not be satisfied, depending on the values of the relevant parameters $a$, $b$, $S$, and $r/S$. Hence, the inequality (10) divides the region where the prey-predator equations have a stable equilibrium point from the region where they exhibit stable limit cycle.

If $a$ is unity and the value of $K/D$ or $r/S$ is not too large, we get stable equilibrium point. But if the values of $K/D$ and $r/S$ are largish, the equilibrium point is not stable and limit cycle results. This is confirmed by the computer calculations. The system trajectories in phase-space all converge on a single closed curve whose shape and position depend only on the coefficients of equations (4) and (5), the form of the trajectory is, ultimately, independent of its starting point i.e. we get a stable limit cycle (Fig. 3). The variation of populations with time is shown in Fig. 4.

In general, our models suggest that prey-predator systems are likely to exhibit stable limit cycle when there is relatively weak intraspecific prey population regulation (relatively large $K$), and the intrinsic growth rate of the prey population exceeds that of its predators. (Cook 1965; Case and Gilpin 1974; De Angelis 1975; Gilpin & Ayala 1973; Gilpin 1972; Gomatam 1974; Grenney et. al.1973; Kazarinoff & Driessche 1978;
Phase Space Diagram

Fig. 3
Fig. 4

Time Vrs Population Size

Population Size

0 30 100

Time (Secs)

N1

N2
May 1972; May 1973; May 1973b; Rescigno and Richardson 1967; Rosenzweig and MacArthur 1963; Stewart et. al. 1973; Williams 1980). This is in accordance with the facts reviewed by Tanner (1975) for eight pairs of prey species and their major predators.