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**Mathematical models and theories
on Oscillations in Populations
The Early Phase**

by

BARUNDEB BANERJEE

**Issued by the Director
Zoological Survey of India, Calcutta**

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MATHEMATICAL MODELS AND THEORIES
ON OSCILLATIONS IN POPULATIONS
THE EARLY PHASE

BY

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CHAPTER I

POPULATION CONCEPT

It is a common observation that certain groups of organisms continue to increase under a set of favourable environmental conditions, but in the face of sudden or violent changes in the environment, or in the biological characteristics of the organisms, the population starts declining. The individuals comprising the population may of course die naturally without facing the vagaries of weather, but frequently such changes follow an orderly growth and decline, giving the impression of cyclic repetitions or oscillations. Long term studies indicate that population changes, inclusive of growth and decline, over a period of time follow some definite mathematical and biological patterns even during the phases of oscillations. The mathematical models, based on the biological parameters, tend to give meaningful expressions to the complicated biological processes involved in the oscillations of the populations and their regulation. It is more appropriate to describe them as sings rather than language (Watt 1962, 1968).

Apart from its numerical or statistical configuration, the population can be described to have the following five general characteristics (Allee *et al*, 1955) :

1. A definite composition is constant for a particular moment of time, but this may fluctuate with age.
2. It shows definite growth, differentiation and a division of labour.
3. The population has a genetic background.
4. Population is integrated by both genetic and ecological factors which operate independently or may be interdependent.
5. The population must meet the impact of the environment in order to survive.

Although these characteristics provide a biological background for developing logical concepts on populations, the latter can perhaps be best described as a group of similar organisms set in a frame that is limited in respect to both time and space (Pearl, 1937). The groups effect is, in fact, most fundamental to any concept on population growth and decline : quantitative expressions like birth and death rates virtually become meaningless

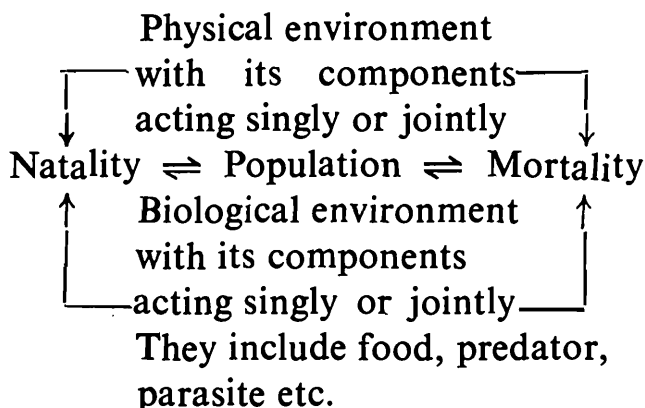
if they are considered outside the context of group effect. The term population therefore logically covers all those individuals of one species which are sufficiently integrated to have influence on one another (Richards 1961). Consequently, the population will have a fairly well defined spatial distribution, though it can hardly be continuous.

It is difficult to visualize a natural population outside the context of its numerical abundance, spatial distribution and natural decline, all of which are mutually dependent. Divergent opinions have been expressed about the mechanisms of population regulation, and the state in which population actually exists in nature. Nicholson (1957), for example, believes that insect populations stay in nature in a state of equilibrium, and depending on the climatic and physical conditions, do they oscillate around this level. Though essentially agreeing with this concept, Richards (1961) advocated a cautious approach, to avoid over simplification of the rather complex process of maintaining an equilibrium density. Solomon (1949), Andrewartha and Birch (1954) and Milne (1962) believe in varying degrees that population and environment must go hand in hand in developing any conceptual framework, though they hold divergent views on the scope, definition and limitation of various processes involved in the regulation of insect numbers. Clark *et al* (1968) have introduced the concept of life-system in population studies and have discussed at length its importance in the practical control of pests. The life-system is essentially an expression of the innate relationship between population and environment, both biotic and physical, in their totality. There is, however, little doubt that innumerable factors interact to influence the survival and growth of a population, albeit, disagreements about the factors that are of more consequence than others in influencing the dynamics of the population.

To evaluate the innate relationship between the population and its environment, it is most essential to fully appreciate the biological characteristics of the species. This requires a thorough knowledge of the behaviour, habitat, life-cycle of the species, and the interrelationships between the various systems that make the population a viable unit in time and space.

A population system is perhaps best perceived as a dynamic entity, in which the input is natality, and the mortality is the output. Both these opposite, yet interdependent forces, under the influence of environment at biotic and physical levels tend to keep the population in a steady state, but deviations cause oscillations. The components of the environment may act singly

or interact with each others to cause oscillations in the population. This input-output dynamics can be illustrated as follows :



Mathematical models in population ecology are used first to identify the various parameters involved in the system, and finally to give tangible expressions to sequences of their operations. The use of mathematics in population is fairly recent and a brief but interesting earlier history has been reviewed by Watt (1962). One of the earliest mathematical models on population growth was that of Lotka and Volterra (Chapman, 1931); though this model with its various extensions was based on concepts that are not always biologically true, yet Lotka-Volterra model was the starting point for many refine models of later years. The general approach in this model was however sound, as indeed was Nicholson and Baileys (1935) model on host-parasitic interactions. The latter with modification has also been used in situations other than host-parasitic associations (Klomp, *et al* 1964, for example). In contrast to the broad generalities implicit in the earlier models, the current trend is to consider and evaluate individual parameters operative in ecological interactions involved in population growth. These models therefore rely heavily, perhaps rightly, on observed ecological processes, rather than abject presumptions, however accurate they might be. Consequently, the trend is to collect precise field data over a long range of time before drawing conclusions and constructing models (Morris, 1963a). Also worth noting in this connection is Fujita's (1954) model on the effect of density on fecundity, in which a comparative approach is taken to find out the fundamental characteristics common to a great variety of situations. This approach is indeed the slated objective of the many current models, but admittedly, many have fallen short of this objective. Interesting applications of mathematics have also been made in the area bioenergetics (Slobodkin, 1959; Odum, 1960).

The most important characteristic of a mathematical model should be its realistic nature : though assumptions are perhaps

unavoidable, yet they must be sound and reasonable. Since principal objective of a mathematical model is to describe the complex ecological interactions and processes in some conceivable ways, this can only be achieved, if the concepts and approaches are sensible and not isolated from biological reality. Mathematical models in population ecology are after all means, and not ends by themselves.

The object for information on insect populations and their oscillations using mathematical model is manifold. An applied entomologist, for example, must have an extensive knowledge of the distribution and abundance of pests (Banerjee, 1981) before long-term control measures can be suggested. Medical entomologist must know the conditions that encourage the rapid growth of the population of disease carrying insects or vectors. Considering the wide importance of population studies, Moris (1960) suggests that analytical studies should be extensive when they concern only the distribution of the species over a large area, or prediction of damage and control measures. Intensive studies, on the other hand, should involve population studies within the same area over long time range : such studies have considerable fundamental importance in so far as the construction of life-tables, energy budgets and productivity studies are concerned (Banerjee 1979a). There are other ways in which the application of mathematical models and computers have helped determining the optimum points in population growth with which the applied entomologists are mostly concerned. Watt (1961, 1964a) demonstrated that mathematical models can be utilized, aided by computers, to optimize the management procedures and strategies in biological and insecticidal control of pest species.

CHAPTER II

POPULATION GROWTH

Increasing its population is a basic attribute of all living organisms : and it is also easy to visualize that their numerical abundance will increase or decrease with time depending on resources. However, even for a most simple form of population growth, the development and construction of a model to describe the population growth process is not an easy proposition. It is, for example, essential to determine the exact relationship between various functional units involved in population growth, and to analyze them as functions of time. It is equally important that in ultimate analysis population growth process represent a change in the functional qualities of these entities, which we will first seek to explain through a series of stochastic models and then by various deterministic models.

STOCHASTIC MODELS

The stochastic models are based on assumption that the system which regulates the growth process changes according to laws of probability. The various systems and theories of stochastic method have been discussed by Cox and Miller (1965) and Bartlett (1960). Stated briefly, stochastic models not only explain the general sequence of events but the inherent variability of the system as well.

1. Linear growth model

Although in its simplest form, population growth can be best defined as the balance between birth and death rates, in the animals with simplest form or organization, i.e. in unicellular organisms like bacteria and amoeba, the death process could even be unimportant in a relative sense. The concept is based on the fact that population growth in these organisms occurs by binary or multiple fissions; consequently the question of death, in its conventional sense, does not arise. One way of looking into the mathematics of the process is to invoke the principles of probability.

Let an individual at a point of time has the probability $\lambda\Delta t + O(\Delta t)$ of splitting into two at a latter time $(t, t + \Delta t)$ where λ is the birth i.e. the fission rate. This expression does

not consider the age factor which is difficult to assess in unicellular organisms : secondly, it implies, in the absence of any parameter for population reduction, that the population will go on increasing indefinitely as a linear process. In practice, the population does not and cannot grow indefinitely : even the contamination of the food media due to crowding is a source of external mortality. However, accepting for the time being, that a linear birth process does in fact operate, we can say if there are $n(t)$ individuals at a time t and $n(t)$ as a continuous function of t , then, $\lambda n(t) \Delta t$ individuals will be produced in $(t, t + \Delta t)$ so that

$$n(t) = n_0 e^{\lambda t}$$

where n_0 is the initial population and λ the linear birth rate. This equation is a deterministic solution to a stochastic process. Now in situations where the overall population $N(t)$ at a time t , is a random variable, instead of continuous one, the probability of a birth at a time $(t, t + \Delta t)$ will be $i \lambda \Delta t + O(\Delta t)$ provided

$$N(t) = i$$

However, population at any particular time is likely to have some variability due to physiological distress under crowded conditions and the coefficient of this variation for $N(t)$ under this condition is

$$\frac{(i - e^{-\lambda t})^{1/2}}{\sqrt{n_0}} \approx \frac{1}{n_0}$$

when $t \rightarrow \infty$

II. Non-linear birth rate

So far we have considered relatively simple situations in population growth in assuming $n(t)$ to be an ever increasing function. It is however possible to have a reduction in the birth rate due to operation of factors like crowding. This will automatically render the linear growth process inoperative, and a non-linear process will become functional. The effect of this reduction, or individual variation in reproduction on the probability of birth rate, then becomes

$$P_i(t) = -i(\lambda' + \lambda'') P_i(t) + (i - I)\lambda' P_{i-1}(t) + (i - Z)\lambda'' P_{i-Z}(t)$$

where λ' and λ'' are the differential birth rates of various individuals in the population, i instantaneous growth rate and P is the population level at a time t .

This equation can be sequentially extended by incorporating multiple fission by one single individual in the population.

III. Birth and Death rates as non-linear functions

The models discussed so far do not consider death processes though it is easier to visualize a population growth process in terms of changes in both birth and death rates. If we consider that an individual at a time interval, from t to $(t, t + \Delta t)$, has the chances $\lambda \Delta t + P(\Delta t)$ of producing a new individual and a chance of $\mu \Delta t + O(\Delta t)$ dying, with λ is the birth rate and μ the death rate, then

$$P_i(t) = -i(\lambda - \mu) P_i(t) + (i-1)\lambda P_{i-1}(t) + (i-1)\mu P_{i+1}(t)$$

The connotations in this equation are the same as before.

IV Varied birth and death rates for male and female

We have so far dealt with simple populations in which sex is undifferentiated. In higher organisms, the rates of birth and death in a population may vary according to the sex of the individuals. It is therefore essential to take this aspect into consideration while extending stochastic models to populations where individuals are classed according to their sex. It is reasonable to assume that

(1) if at a time t , a female has the probability of

$$\lambda_1 \Delta t + O(\Delta t) \text{ and } \lambda_2 \Delta t + O(\Delta t)$$

producing a male or female offspring respectively, then at a later time $(t + t + \Delta t)$

(2) the probability of death at $(t + t + \Delta t)$ for males and female is $\mu_1 \Delta t + O(\Delta t)$ and $\mu_2 \Delta t + O(\Delta t)$ respectively.

Implied here is the assumption that individuals produced in course of time to enrich the population are mutually independent and that probabilities at the time $(t, t + \Delta t)$ are dependent on the numbers of males and females at the beginning of the time scale, say, t . In this case extinction of the females, which is necessary for the whole population to become extinct, will occur with the probability

$$1(\mu_2 \geq \lambda_2)$$

$$(\mu_2/\lambda_2)^{n_1} \quad (\mu_2 < \lambda_2)$$

where n_1 is the initial number of females, and λ , and μ_2 are the birth and death rates respectively.

Deterministic Models

Having examined the simple stochastic models on population growth, we will now examine the growth processes with their extensions and roots using a series of deterministic models. Unlike stochastic models, deterministic models are based on the theory of maximum likelihood and are therefore somewhat easier to work with.

V The Logistic model

Population growth of animals under a limited supply of food, and without competition mostly follows the pattern implicit in the logistic equation. This implies that a population is capable of growing only upto a certain maximum depending upon available resources. In its simplest form, the population growth process can be derived from the assumption that the rate of increase drops as a linear function of density, expressed as:

$$\frac{dn}{dt} = r_m N \frac{(K-N)}{K}$$

where r_m = innate capacity of increase of species and is same as b , the potential rate of increase of an individual (Andrewartha and Birch, 1954). The value of r_m or b is species specific.

N = Population size.

K = Maximum growth possible, which could be the equilibrium number. This is the saturation level, or carrying capacity for a population.

$(K-N)/K$ = Unutilized opportunity for population growth. This is the fraction by which the population falls short of the maximum attainable size in a given set of conditions.

N/K = Utilized opportunity for population growth. With the decrease in the value of $(K-N)/K$, that is, as the population grows actively, N/K approaches unity with time.

This equation expresses the rate of change of the population (dN) with respect to the change in time. Considering the average rate of change for the individual (dN/N) against the change in time, the equation can also be expressed as

$$\frac{dN}{Ndt} = r_m - \frac{r_m}{K} (N)$$

so that the average growth rate becomes the linear function of the degree of saturation N/K . When the ratio is nearly zero, the growth rate is at its maximum and when the system is well saturated, the growth rate is zero.

The model described assumes an equilibrium level to which a population will ultimately reach, and that furtherest the population is away from this equilibrium level, the more rapidly does it grow. However, in practice, the situation may not be as simple because the roots of the growth equations can at certain stage lead to oscillations in populations. In a very general way, oscillations are produced when a tendency to geometric increase is balanced by density-dependent controlling factors (Macfadyen, 1963), including a negative fed-back loop.

It follows therefore that as the population increases, the controlling factors also become vigorously operative leading ultimately to a reduction in overall population. If these factors operate instantaneously on an expanding population, no oscillations would possibly occur. But if there is a time lag say, T , between population increase and the operation of the controlling force, and $N/K = Y$ then amplitude of oscillations may increase or die out depending on the degree of the value of T

Although it is an ideal axiom for population growth, logistic model cannot be fitted uncritically to every situation. However, in its classical form logistic equation has been fitted to *Paramecium caudatum* (Gause, 1934), *Drosophila melanogaster* (Pearl, 1930), the ant *Atta sexdens rubropilosa* (Bitancourt, 1941) and to the growth of bee populations in colonies (Bodenheimer, 1937). Allee *et al* (1955) have discussed in details several other classical applications of logistic model to various laboratory and field populations.

One principle disadvantage of the uncritical, often theoretical, application of logistic model is that it does not take cognizance of the oscillations and fluctuations in natural insect populations.

It is equally true that populations often cross the theoretical upper asymptote, that is, the attainable maximum size, when the conditions are conducive, rather than remaining steady. Moreover, an absolute limit to the upper asymptote is also difficult because rarely this limit remains 'fixed' and in some cases it may not be reached at all. It is also possible that under certain circumstances the population will oscillate above or below the theoretical upper asymptote. Assuming the upper asymptote is not a fixed entity, discernible trends in a population would be either (i) to move towards the equilibrium density or/and (ii) a change in the equilibrium level itself. The latter in its turn may vary according to the spatial limitations particularly in the laboratory cultures (Banerjee, 1966b).

The logistic model, in its classical sense, does not consider anything of the mortality in a growing population, neither does it consider the variability in birth rates. In a population having individuals with reduced birth rate and/or with reduced mortality, population growth cannot be expressed satisfactorily by saying that as $(K-N)/K$ decreases from 1 to 0 with rising density, dN/dt falls off correspondingly. Although it is fairly well-known that for most populations there is a maximum limit to exponential growth, the linear fall in dN/dt ratio with rising density is difficult to establish in classical logistic model. For example, in the usual equivalent to logistic equation

$$N = \frac{a}{1 + e^{b-ct}}$$

(where a , b and c are constants and t is the time) a set of nonlinear normal equation is clearly produced. A direct solution of the parameter values a , b and c for linearity is not possible, but can be achieved by application of Marquardt's (1963) combination of Taylor series and Gradient methods.

Marquardt's algorithm also gives the best least square fit and a numerical solution is given by Conway *et al* (1970). Although in solving the parameters for nonlinearity, the Taylor Series by itself cannot be used, because if the initial trial values used are proximal, the convergence will not occur at all, the series nevertheless gives a good approximation to the population growth as a function of time. The population growth, N , as a variable time t , can be best approximated by the equation

$$N = N_1 + [Nt]T + [N_t]T^2/L^2 + \dots + D_t^h N]T^h/L^h$$

where $T=t-t_1$, is small. The term $N_1+[N_t]T$ is the first approximation: this together with the one with T^2 is the second approximation and so on. Generally more the "terms" are, the better will be the approximation and by extending the model to infinite number of terms, a perfectly exact value is obtained. It is also important to note that the multiple species extension of the logistic model can be justified from many different standpoints. It might be regarded as simple collision model by different species or it might be regarded as representing the first term in Taylor's expansion of any much more complex model.

VI. Exponential Model

The exponential model of Lotka (1925) is in many respects more realistic than the logistic model. The population growth rate, r , in this model is expressed as,

$$\frac{dn}{dt} = rN$$

The equation can also be expressed as

$$N_t = N_0 e^{rt}$$

where N_0 = initial population at a time = 0.

N = population at time t .

e = base of natural logarithm.

r = intrinsic rate of population increase, a constant for each species. This is same as b or r_m of Birch (1948) and Andrewartha and Birch (1954) or capacity for increase (Laughlin, 1965; Leslic, 1966).

When expressed in logarithmic form, the equation becomes

$$\text{Log}_e N_t = \text{Log}_e N_0 + rt$$

A modification of Birch's method for determining the intrinsic rate of population increase is given by Howe (1953). Although r is supposed to be a fixed entity for a species under a set of biotic conditions, in many studies discrepancies were found between expected and observed values of r (Lefkovitch, 1963 : Messenger, 1964). The value of r may even vary from time to time depending on biotic and climatic conditions (Watson, 1964). French and Kaaz (1968), for example, noted that the value of r in *Paromyscus maniculatus sonoriensis* increases from $r=0.1897$ to $r=0.3547$, if they are irradiated at 1 roentgen/day : in this species, the value

of r has also been reported to vary according to elevation (Dumire, 1960). The calculated values of r for a few more species are shown in table 1. Although some criticisms on the utility r has been made, it still gives a good approximation of the intrinsic rate of population increase than any other parameter.

Table 1.1 : The intrinsic rate of increase of some animals under laboratory conditions (after Macfadyen, 1963; Banerjee, 1974b, 1978)

Species	Net reproductive rate	Intrinsic rate of increase/day	Finite rate of increase
<i>Tribolium castaneum</i>	275.0	0.101	6.86
<i>Calendra oryzae</i>	113.6	0.109	6.36
<i>Pediculus humanus</i>	30.6	0.111	6.24
<i>Microtus agrestis</i>	5.9	0.0125	55.44
<i>Rattus norvegicus</i>	25.7	0.0147	47.14
<i>Oligonychus coffeae</i>	11.53	0.72	5.24
<i>Odontotermes redemanni</i>	10.02	0.96	2.61

Exponential model also gives a meaningful expression to the time-lag involved between successive population growth. On theoretical ground, where r is a positive constant the population will continue to grow exponentially, but when negative the population will decline exponentially and the population will be stabilized when $r=0$. The parameter, r , is therefore basically a density-dependent factor because when it is the decreasing function of density i.e. declining as the population increases, the population will be ultimately stabilized. On the other hand, when it is an increasing function of density, the population will increase indefinitely or decline to extinction. It thus follows that when dN/dt is a positive function, N will be on increase, and it will reach the equilibrium density, N_E , when $dN/dt=0$.

The exponential model holds good only when death, immigration and emigration processes are ignored. When death rate is considered, the exponent, r , can be expressed simply as the difference between birth and death rates. In fact, the changes in the growth rates of populations do intrinsically reflect the variation in the natality (b) and mortality rates (d). By taking these parameters, the generalized model of population growth can also be expressed as :

$$N_t = N_0 (b-d)^t$$

where b is the birth rate and d death rate. Clearly when $b > d$ the population peaks, and declines when $b < d$: when $b = d$ the population will be stabilized.

The birth rate or natality in the exponential model is best defined as the amount by which the initial number of individuals will increase during a short time interval, in the absence of mortality or movements away from that area (Clerk *et al*, 1968). Depending upon the circumstances, the birth rate could be exponential, finite and crude.

Likewise the death rate or mortality, is defined as the amount by which the population will be reduced within a short span of time in the absence of birth rate. Death rate could be exponential (d), finite (e^{-d}) or crude (D) depending on overall demography.

It follows that since the exponential model describes the population growth between a time-lag, the potential population growth will have to be a positive factor. Any limit approached by N_{t+1}/N_t will naturally have to be a positive constant. However, any subtle change in environment could affect the intrinsic rate of increase of any species (Fenchel, 1974) though the roots of this growth equation may also lead to oscillations (Jansen, 1975).

The Taylor series, which was earlier invoked in connection with the logistic model, is also applicable to the exponential model, as long as the functions in the exponential equation can be differentiated. Thus

$$e^x = 1 + X + X^2/2 + X^3/6$$

If the functions are not differentiable, $X = X_1$, then Taylor series will fail.

VII. Population growth models under varied food supply and environment

The various extensions of logistic and exponential models discussed, so far, are applicable only to situations where population grows under a steady and uniform supply of food. It is therefore worth examining the effects of altering food supply on the population growth process. Although the ingestion of food itself involves a series of complex stages that are additive (Caperon,

1967); for a population density, n , with individuals taking an optimum amount of food to reproduce, the growth rate will be :

$$(1/N)(dn/dt) = [K_3 C_0 / q / n] b / (b + K_3 / K_1)$$

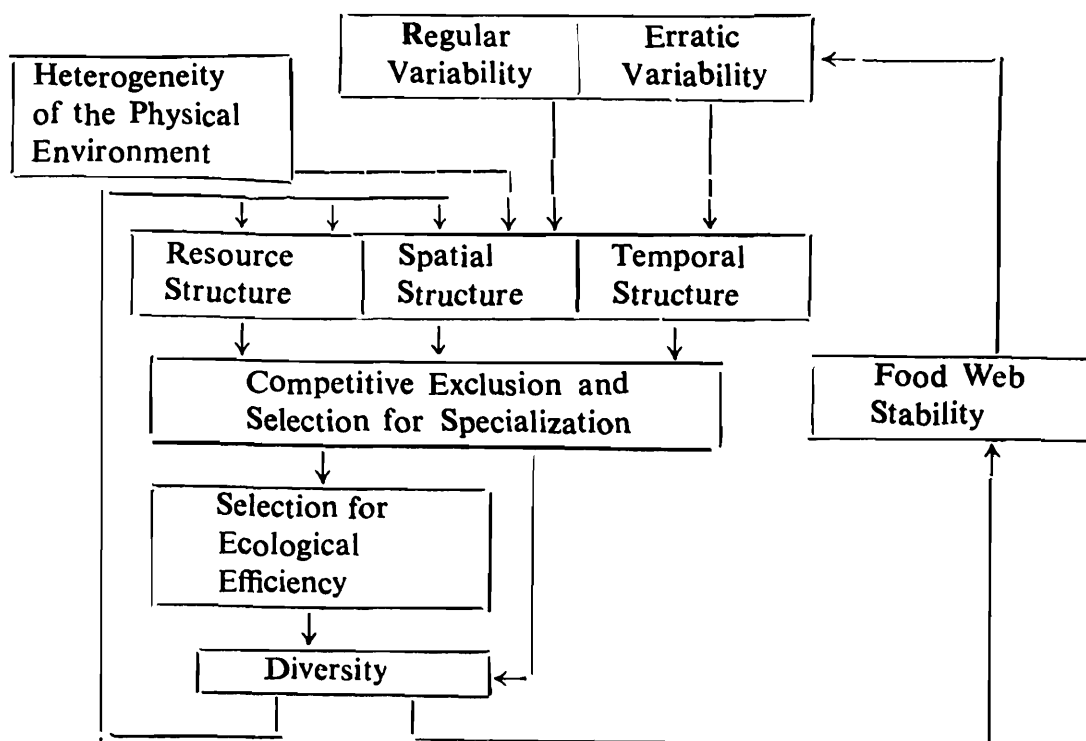
where K_1 , K_2 , K_3 , C_0 are the rate constants for different aspects of food ingestion, and the capacity for innate rate of increase. This equation also describes the rate of growth as a function of food concentration.

Apart from food, populations under laboratory and field conditions are liable to exposure to fluctuations in the environment. It is fairly well known that the components of environment and their interactions act singly or jointly to influence the course of population growth. The problems associated with the evaluation of climatic effects on population, particularly the confounding of the climatic effects with biological interactions have been discussed (Henson, 1966). The significance and the consequences of erratic and non-erratic environmental variability on population fluctuations are also known (Green, 1969), and a model on the operation and effects of environmental variability on population variability is shown below :

Solid arrow = "increases"

Dashed arrow = "decreases"

Variability on population variability is shown



It is generally believed that both environmental and population variabilities are positively correlated, although a direct cause and effect relationship is somewhat difficult to establish. A mathematical expression of the consequences of environmental of variabilities on population growth is given by (Tanner, 1966) :

$$E(N_{t+1}) = bN_t[E(f)] = bN_t[\overline{f(O, E_t)}]$$

in which the function $[f(OE_t)]$ determines the relationship between b and the population density when environmental variability is functional, and in its absence $[f(O, E_t)]$ becomes operative. Obviously random fluctuations of environment occur independent of the density. Therefore the interactions between population and environment may have some variability, and in extreme case such interactions could vary independent of the density. In such situations, the coefficient N_t in the function $f(N_t, E_t)$ could even become zero.

VIII. Composite model for birth, death and migratory progresses

It is rational to assume that for a growing population, under natural condition, there is a migratory process, in addition to birth and death processes. The migratory process covers both immigration and emigration, which neither the logistic nor the exponential models and their various extensions take into consideration. A composite population should in theory be made up of both migrant and non-migrant individuals having a constant birth and death rates. These composite parameters can be expressed meaningfully only in models based on the principles of matrix algebra (Usher and Williamson, 1970; Bailey, 1968; Smith, 1969; Leslie, 1948).

Consider a population with a distinct spatial distribution located at points i ($0 \leq i < n$), and V is the emigration rate from any location in all directions, so that the emigration from the location to either $(i+1)$ or $(i-1)$ is $\frac{1}{2} V_0$. Having λ_1 and M_1 as birth and death rates respectively for non-migrant part of the population, and λ_2 and M_2 as birth and death rates respectively for the migrant population, the changes in population size at different locations is given by a matrix leading to the equations :

$$\begin{aligned} R_1 &= 1 + \lambda_1 - M_1 \\ R_2 &= 1 + \lambda_2 - M_2 \end{aligned}$$

R_1 and R_2 are the coefficients for the net population increase for

migrant and non-migrant populations respectively. If, on the other hand, the size of an unit of colony at time t and location i , is $m_i(t)$, the population growth can be expressed in the column vector :

$$m(t) = \{m_0(t), m_1(t), \dots, m_n(t)\}$$

Possible extensions of this model for spatially distributed populations have been discussed by Bailey (1968).

IX. Models involving the age-structure of the population

Due to the overlapping of generations, and variation in the birth and death rates, populations at any point of time may be made up of individuals at various stages of development. Consequently, the age of the individuals in a population will vary, and because of this variability, the birth and death rates would also be influenced. The models described earlier are based on the assumption of a stable-age distribution of the individuals in the population. To be realistic, it is essential that the growth models express the dependence of the population on age as well as the size of the individuals. Sinko and Streifer (1967, 1969) have suggested models, that consider the size and age variation of the individuals in the population.

Consider the density function as, $n(t, a, m)$, which is dependent on time, t , age a , and a variable, m , representing physical attributes (like size) affecting the physiology of the animals; then the average growth rate of the population $g(t, a, m)$ at age a , mass m and at a time t , is obtained from

$$g(t, a, m) = \frac{dm}{dt} = \frac{dm}{da}$$

and the average death rate $D(t, a, m)$ from

$$\int_{m_0}^{m_1} \int_{a_0}^{a_1} D(t, a, m) (t, a, m) da dm$$

which shows the number of animals that will die between ages a_0 to a_1 , and size (mass) m_0 to m_1 .

Much in the same way the logistic model of population growth can also be derived from Von Foersters (1958) equation by integrating it to age from zero to infinity :

$$\frac{dn}{dt} = n(t,0) - \int_0^{\infty} D(t,a)n(t,a)da$$

where $n(t, 0)$ is the rate at which an animal enters into the population. In doing this transformation, it is assumed that birth and death rates are independent of age, which is hardly true. Therefore, even with this modification logistic equation fails to give meaningful expression to dependence on birth and death processes of population growth rate.

Obviously there are practical difficulties in sorting out individual age in a natural or even in artificial population. A way out of this situation is to classify the individuals according to their stages of development rather than age *per se*. The developmental stages are easily recognizable and by using matrices (Leslie, 1945), population growth of animals, grouped by stages, can be conveniently expressed (Lefkovich, 1965).

Consider that in a species there are, S , distinct stages with n_i , t individuals in growth stage i ($i=1, 2, \dots, S$) at a time t : then the total population at that time t , is $n_1t + n_2t + \dots + n_st = N_t$. Implied in this equation is the understanding that the number of individuals of each stage at a later time $t+1$, is a function of the population at time t . The relationship between the numbers in P stage at time $t+1$, and all other stages at time t , can also be described as :

$$n_{1,t+1} = m_{p,j,t} n_{j,t} + m_{p,2,t} n_{2,t} + \dots + m_{p,S,t} n_{S,t} = n_{P,t+1}$$

where $m_{p,j,t}$ ($j=1,2, \dots, s$) express the biological dependence of the P th stage at time $t+1$ upon J th stage at time t , n being the population level.

Besides differences in age-structure, the time lapse or period, taken by insects in passing from one stage or instar to the next is of importance. If this variation is too large, it positively affects the growth of population by introducing an element of heterogeneity. Let C be the probability of survival of an egg or any developmental stage to become an adult, and the time taken for the whole process be T : then the number of new individuals in the next stage of development in the interval t to $t+dt$ will be

$$c(a^{-bx} - T)X_{t-T} \delta t$$

where $(a^{-bx}) \delta t$ is the number of eggs or developmental stages

produced at interval δt and follows the logistic function (Maynard-Smith, 1968). The overall change in population can therefore be expressed as

$$\delta X = C(a - bX_{t-T})X_{t-T}\delta t - \mu X_t \delta t$$

where μ is the death rate.

Finally, age-structure of the population is of great biological significance, not because it affects the birth and death rates, but because of the way it influences the entire process of population regulation and oscillations. This is so because age-specific fecundity rises with age to a peak and then falls : the age specific mortality drops to a minimum prior to the reproductive phase of an animal, and then rises with age.

CHAPTER III

POPULATION REGULATION AND INTERACTION

Although in many laboratory populations, particularly those of protozoa and yeasts (Gause, 1934), steady-state densities were obtained, these cannot be ascribed as phenomenon common to all animals. It is more common for populations to fluctuate, albeit within a limit, even in a constant environment. There are many classical examples of population fluctuations under laboratory and field conditions. Park, Gregg and Lutherman (1941) maintained three species of granary beetles (*Tribolium confusum*, *Gnathoceros cornutus* and *Trogoderma versicolor*), in the same kind of food media, and under the identical conditions of temperature, light and humidity. In spite of this absolute manipulation of environment, the populations of the three species did fluctuate, with each species reflecting its inherent growth pattern. Other interesting examples of fluctuations in *Tribolium* populations under varied laboratory conditions have been reported by Park and Frank (1950), Park (1954), and Park, Leslie and Mertz (1964), and in the dermestid beetle *Anthrenus flavipes* (Banerjee, 1966b).

Apart from these and many other well documented laboratory studies, fluctuations in the natural populations of arthropods and other animals have been reviewed by Allee *et al* (1955) and Macfadyen (1963). Recurring pattern of population cycle under varied ecological conditions for tropical arthropods have been demonstrated by Banerjee (1966d, 1967a, 1967b, 1970a, 1970b, 1971d, 1974, 1975, 1979a, 1980), Banerjee and Kakoti (1968). Cyclic population dynamics and abundance over a long range period have been studied extensively in larch tortix (Baltensweiler 1966), and by far most interesting case histories are those of the pine loopers (Klomp, 1966a, 1966b).

Most studies on fluctuations and oscillations indicate that animal numbers are regulated basically as a result of interactions between various complex biological and physical factors. Because of the complexity of the situation, it is difficult to postulate mathematical models that will accurately describe all factors involved in regulations all at the same time. However, the role of some of the major biological factors, and the models that attempt to

describe them individually will be discussed under the following heads :

- (i) Variation in reproductive level.
- (ii) Variation at population level.
- (iii) Assessment of regulation.

I. Variation in reproductive level

A. Lag in utilization of reproductive potentiality :

Evidence from the earlier experimental work of Park (1934), Boyce (1946), Crombie (1946) and Rich (1956) suggests that interference with copulation and oviposition, particularly at high densities, prevents populations from rising significantly above the equilibrium level, and can even bring down the population below the equilibrium level as well. Under a constant environment, with a steady supply of food, the age-specific fecundity may go down in continuously running generations as the milieu becomes crowded (Banerjee, 1966b), but this may happen also due to physical interference with copulation in crowded conditions. A mathematical approach to the problem suggested Klomp *et al* (1964), is based on Nicholson—Bailey's model, and cannot possibly be extended to all situations (Banerjee, 1979b).

It is assumed in this model that all animals in the experimental arena make random movements and that the number of contacts between the sexes are proportional to the square of density. Therefore, when the total population is reduced to half, the expected number of contacts will be reduced to a quarter, that is, proportional to the square of the density. With different number of males (m) and females (f), the expected number of contacts will be:

$$C = k. m. f.$$

where K is the index of activity of the males and females. Now, because of the random movements, females which do not contact males, or which contact males more than once, will be distributed according to the Poisson series. The fraction of females F which does not contact the males at all is therefore :

$$F = e^{-P}$$

where P is the mean number of contacts per female.

It follows therefore that the fraction of the female population that will have contacts with males $(1-F)$ is

$$(1-F) = 1 - e^{-k \cdot m}$$

In deriving this equation it is assumed that males are ready to copulate at every contact : the fraction of female is therefore dependent on male density and independent of sex ratio. In situations, or in species, where males have limited capacity for copulation, the sex ratio is most likely to influence the fraction of female population that will be fertilized. Moreover, since the mean number of contacts by each male (c/m) is proportional to the female density, f , the fraction of female fertilized will remain constant only upto a value of f where (c/m) is at its maximum. Consequently, at higher female densities, the fraction fertilized will decrease proportionately.

By carrying the hypothesis further, the effects of high density levels on different phases or aspects of the reproductive processes can in certain cases be expressed through the following relationships (Watt, 1960) :

1. Egg production rate against time

$$\frac{dE}{dt} = K \{NP - (1-aE)\}$$

2. Mating rate against density

$$\frac{dP}{d} = bP(1-P)$$

3. Density to interference

$$\frac{dI}{dN} = -f(1 - 1 \text{ min})$$

The parameters in these equations are :

- E = a constant—the intrinsic rate of oviposition.
- N = population density.
- P = effect of probability of contact on fecundity.
- $(1-aE)$ = effect of competition for oviposition.
- a = area required for an egg.
- E = number of eggs laid in time t.

These models indicate the density—dependence nature of the reproduction, though they have been tested only under crowded conditions created artificially with spatial limitations. They may not however truly express what goes on under natural conditions, because crowding due to spatial limitations is uncommon in the field and it is possible mating speed movements are not always random but directed (Banerjee, 1979b).

B. Changes in reproductive value

Animals in higher taxa show definite periodicity in their reproduction. Success during the phase of multiplication causes the population to peak and it is equally true that the population may fail to reach the equilibrium density if reproduction fails : the latter happens when breeding process is interfered with due to the lack of available resources like food, breeding place and protection against predation. Provided the reproductive rate is constant, and reproductive functions are unhindered, the success in reproduction is two consecutive reproductive phases can be predicted from :

$$\Delta X_n = (R_0 - 1)X_n$$

where R_0 , the reproductive rate, depends on x_n in such a way that when x is too large, R_0 becomes less than one : otherwise $R_0 > 1$ for an expanding population. It is even possible that R_0 will be less than one at very low population densities, particularly when success in locating suitable mates is low. When $R_0 = 1$, a steady state or equilibrium density is reached. Denoting this equilibrium density as x_E , the population as a later period can be predicted from the relationship

$$X_{n+1} = X_n - b x_E x_n$$

where b is a constant. The equation can also be expressed as

$$X_{n+1} = (1 - K)X_n$$

in which K stands for the composite unit $b x_E$, K can be used to predict oscillations in populations. If it is negative, the equilibrium will be unstable and large departures from the equilibrium level can be expected. Other possibilities are that of $0 < K < 1$, when oscillation will be damped : when $1 < K < 1$ there will be a series of convergent oscillations around the equilibrium level. When $K > 1$ oscillations will be of increased amplitude, which means that the population will tend to reach

equilibrium level through a series of small oscillations, each of increasing higher amplitude.

C. Periodicity of the reproductive cycle

The term “birth-pulse” has been used to denote seasonally breeding population against “birth-flow” for continuously breeding populations (Caughley, 1967). In birth-pulse population, the well-marked period of abundance is separated by periods of decline and this is clearly related to the phases of reproduction. Consequently, the concept of infinitesimal rate of increase in Lotka’s (1925) model does not properly fit in these situations. However, the value of r or r_m , the intrinsic rate of increase can be calculated by iteration from the equation :

$$\sum L_x e^{-rx} m_x = 1$$

in which m_x is the mean number of live births for each animal of age x . For higher vertebrates x could even be expressed in years.

Since the reproductive phase of higher animals is restricted to a particular period, the value of r for several consecutive years needs to be determined provided the population has a stable—age distribution at that time. Then the appropriate equation for determining will be :

$$r = \frac{(t - \bar{t}) (N - \bar{N})}{(\bar{t} - t)^L}$$

where \bar{N} is the stable age population for each year after conversion to Napierian logarithm. t is time.

II. Variation at population level

D. Competition

It is generally assumed, though not proved in all cases, inter and intra specific competition plays varying role in regulating population size. Theoretically at least, competition between two or more species with the same resource for food, shelter and breeding can make one species dominant, and the others may even perish. Under field conditions, it is indeed difficult to show how competition actually operates, but some broad generalizations are possible from the laboratory investigations of Gause (1934), Crombie (1946),

Park (1948, 1954) and Frank (1962, 1957). Although, according to Birch (1957), competition occurs when a number of animal of the same or different species utilize common resources that are in short supply, even sheer physical interference between animals may lead to competition. Competition may therefore be best defined as the interaction between species that share a common population limiting environmental resource like food or shelter.

One of the earliest mathematical expression to the competition process was given by Volterra (1926). Denoting ϵ_1 and ϵ_2 as coefficient of increase of two species under competition, h_1 and h_2 as constants for food consumption by the two species, and N_1 and N_2 as the numbers of the two species present, the population changes of the two species can be expressed as :

$$\frac{dN_1}{dt} = \epsilon_1 N_1$$

for the first species, and

$$\frac{dN_2}{dt} = \epsilon_2 N_2$$

for the second species. It is natural that each species will remove a quantity of food, $h_1 N_1 + h_2 N_2$, which will bring down the values of ϵ_1 and ϵ_2 , so that,

$$\frac{dN_1}{dt} = N_1 [\epsilon_1 - y_1 (h_1 N_1 + h_2 N_2)]$$

and

$$\frac{dN_2}{dt} = N_2 [\epsilon_2 - y_2 (h_1 N_1 + h_2 N_2)]$$

in which y_1 and y_2 are the constants representing the susceptibilities of the two species to food shortage. It follows that when $\epsilon_1 y_2 > \epsilon_2 y_1$ the second species will approach extinction. Obviously the species showing greater susceptibility to food shortage, that is, first to approach the condition $\epsilon_1 / h_1 y_1$, will be ultimately eliminated in competition with the other species showing less susceptibility to food shortage.

Gause's (1934) competition model was derived basically from

Verhulst—Pearl's logistic equation and is expressed in the differential equations :

$$\frac{dN_1}{dt} = \left(\frac{r_1 N_1 (K_1 - N_1 - \alpha N_2)}{K_1} \right)$$

and

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_1 - \beta N_2}{K_2} \right)$$

where N_1, N_2 = Population size of the two species.

r_1, r_2 = Intrinsic rate of increase of the two species.

K_1, K_2 = Saturation levels of the two species.

β, α = Competition coefficients of the first and second species respectively.

The outcome of the competition can be assessed from the relation between β and α , and the ratio K_1/K_2 and K_2/K_1 . The following combinations are possible :

1. When $\alpha < K_1/K_2$ and $\beta > K_2/K_1$ species 1 wins.
2. When $\alpha > K_1/K_2$ and $\beta < K_2/K_1$ species 2 wins.
3. When $\alpha > K_1/K_2$ and $\beta > K_2/K_1$ then success will depend on the initial population.
4. When $\alpha < K_1/K_2$ and $\beta < K_2/K_1$ then both the species will survive in a state of equilibrium.

Both Volterra and Gause's models have their own limitations in assuming that the decline in growth rate is a linear function of density, and that there is an instantaneous response to changes in the environment. Both considered that, K , the saturation density, cannot be exceeded by N , the population level, at a particular time. It is however known that owing to statistical variation, the theoretical upper asymptote can be exceeded by both single and multiple species populations (Park, 1948). Nevertheless, the two species competition models of Volterra and Gause have even been extended to describe situations where eight different species are competing for common resources (Levin, 1969).

In recent years deterministic models have been particularly effective in describing the complex processes involved in competition. For example, the inter-specific competition models of Landahl (1955) and their modified versions (N.W. Taylor 1967; 1968) have been fruitfully applied to demonstrate the outcome of competition between *Tribolium castaneum* and *T. confusum*. N.W. Taylor's

(1968) deterministic model can indeed be applied to a wide variety of situations involving more than two species and even to intra-specific competition.

Although the effect of competition can be predicted with a measure of certainty from these theoretical models, the final outcome of competition depends greatly on the "properties" of the population itself. This refers in particular to those conditions which have existed long enough to allow the initial population to settle down. Food, or lack of it, does certainly initiate competition, but the toxic substance that accumulate in the media on which the population grows, could also have some inhibiting effect, and in turn, this might lead to competition. This aspect is not considered in the models discussed, though an approximation to the unstable equilibrium, that is likely to develop under such conditions, can be obtained from these models. Equally important is that when two small populations are under competition, the outcome will be equal on the genetic variability (Levin, 1969 ; Lewontin and Kojima, 1960) of the competing species: natural selection is unlikely to have any appreciable effect in deciding the outcome (Park and Lloyd, 1955).

One of the most effective ways of population regulation through intra-specific competition is cannibalism (Sonleitner, 1961). Chapman (1928) and Park (1954) demonstrated that self-limitation of the laboratory population of *Tribolium* occurs mostly due to egg cannibalism and predation of smaller larvae by the larger larvae and adults. Landahl (1955) showed cannibalistic activities could even lead to oscillations, particularly where adult cannibalism is reduced relative to that by larvae, though pupal predation by adults regulates the population more effectively than egg predation by larvae (Young, 1970). Undoubtedly cannibalism as a regulating force in the dynamics of population is of great consequence and can be expressed mathematically in deterministic models (Taylor, N.W. 1967).

As opposed to the deterministic model, Mertz and Davis (1968) have used stochastic models, based on the hypothesis of predator satiation, to explain the significance of cannibalism of *Tribolium castaneum* in population regulation. In a population of the beetle, adult cannibals exist either in a state of satiation or in the process of actual hunting. A satiated adult remains occupied with its prey in a time consuming manner involving attacking, handling and digesting : the adult first gets satiated before going for actual

physical hunting. The rate of satiation during the time interval t to $t+\tau$ is given by the transition probability :

$$P_r = M\tau + O(\tau)$$

in which M expresses the state of satiation. The second transition, that is, the one from satiation to physical hunting, may occur after a time T , following the onset of satiation. This transition can be considered in two ways, i.e. either T is a random variable or as a constant.

In situations where T is a constant, and $T^{(K)}$ is the time consumed until K th attack by a single beetle

$$T^{(K)} = T_H + T_S$$

where T_H is the total time spent in hunting and T_S the time spent in satiation.

In applying mathematical models to actual situations, it is worth noting that in cannibalistic activity, insatiable predators are biologically superior to satiable predators, because the former operates on a prey population irrespective of its size and relative proportions of different stages in the population. Cannibalism may also help maintaining equilibrium densities around the same level, even for species or strains having different reproductive potentialities (Lloyd, 1968), thus suggesting its strong regulatory bias.

Apart from regulating the population, cannibalism has other biological advantage, for the population as well. For example, egg-eating reduces the mortality and increases the developmental speed of the larvae into the pupal stage (Mertz & Robertson, 1970). It is clear therefore that in a population of both cannibals and non-cannibals, the former will be favoured by natural selection, because in more than one way they are more fit than non-cannibals; the faster rate of development of the cannibals due to egg-eating is undoubtedly a sign of fitness and therefore of considerable selective advantage.

E. Predation

Predation is a singularly powerful population regulating factor under a natural setting, and because of its importance, the predator-prey system has been a subject of considerable theoretical and practical interest (Holling, 1961 : Solomon, 1964). In itself,

predation is not a single system, but is made up of a series of sub-systems that are interlocked and interrelated in a causal pathway : the whole system and its interactions also cause oscillations in both predator and prey populations.

The important components of a predatory system (Holling, 1959) are : (1) density of predator and prey, (2) reactions of the prey to predators, (3) density and qualities of alternate food available to the predator and, (4) food preference and efficiency of attack by the predator.

These components may act singly or jointly to influence the whole system. The Lotka-Volterra model on predation, though based on excellent theoretical assumptions, did not consider this and other factors of consequence in predator efficiency. The Lotka (1925) and Volterra (1926) model for competition is :

$$\frac{dN_1}{dt} = r_1 N_1 - K N_1 N_2$$

$$\frac{dN_2}{dt} = K_2 N_1 N_2 - d_2 N_2$$

where N_1 = prey density.

N_2 = predator density.

r_1 = intrinsic rate of increase of prey.

d_1 = exponential death rate of predators.

K_1, K_2 = predation constants.

In an intrinsic cycle of relationship, these equations can be expanded to show that prey density has no effect on the likelihood of a prey being eaten, and predation density will have nothing to do with the likelihood of a predator catching a prey ; these equations also indicate that predators will continue to grow indefinitely. Since the first two assumptions are biologically inappropriate, interpretations of the constants in the equations become difficult. Although using a power series the constants can be expressed as :

$$\begin{aligned} K_1 &= a + bN_1 + CN_2 + \\ K_2 &= a^1 + bN + CN_2 + \end{aligned}$$

they are not powerful enough to explain the asymptotic growth rate of the prey. For such situations, the exponential model of Gause (1934) offers greater efficiency.

Unlike Lotka-Volterra model, Gause's model is based on the assumption that each predator is capable of making a certain number of maximum attacks and that the rate of attack is proportional to the unutilized opportunity for attack :

$$N_A = K (1 - e^{-aNo})$$

where K = number of attacks possible.

N_A = number predated.

No = prey density.

a = instantaneous rate of discovery of a prey.

This model accurately describes the behaviour of the predator but not that of the prey. Much on the same line is Nicholson's (1955) model on predator-prey interactions which assumes that a predator has to make a certain amount of searching for the prey and this exploitation component forms the basis of the Nicholson's model. It is shown that the exploitation rate is proportional to the density of the undiscovered prey, so that,

$$N_A = N_C (1 - e^{-aP})$$

where P is density of the predator. When the predator is active, physical interference during predation is a clear possibility, particularly at high densities. Considering this and the exploitation component, it is possible that (Watt, 1959) :

$$A = ap^{-i}$$

in which A = number of prey attacked by each predator.

P = predator numbers.

a, i = positive constants.

Predators may at the same time respond to changes in prey-densities, either, by (A) a functional response, in which the predator takes more of the prey as the prey population increases until a saturation level is reached, or (B) by numerical response by increasing in numbers either by reproducing or through immigration : several well documented observations on both these phenomena have been reviewed by Solomon (1949, 1964).

The functional response aspect of predation can be mathematically expressed as Holling (1961) :

$$N^A = \frac{Tt aNo}{1 + abNo}$$

which correctly describes functional response curve, though by using the Gause's (1934) model, a similar relationship can also be demonstrated. The parameters used in this equation have already been elucidated. The main assumption is that a fixed interval of time, T_1 , is allowed between successive predation and b is the time required to pick up one single prey.

Predation does not necessarily exterminates the entire prey-population even within a closed ecosystem, because, apart from multiplying simultaneously with its predators, the prey is also capable of avoiding predation. Therefore, while natural selection tends to increase the efficiency of a predator in finding a prey, it does at the same time, favour individual prey capable of escaping predation. The selection force therefore acts in opposite directions, and when these opposing forces are fully functional, the probability of a contact (C) between a predator (P) and prey (p) is :

$$C = K.p$$

where K , is the ability of the predator to effectively discover a prey (Banerjee, 1971).

Under conditions operating in natural populations, the biological and physical parameters could complicate the simple conditions sought in explaining the predator-prey interactions. For example, in a predator-prey system, each species may alternatively become common, rare, common and again rare and so on : such cyclic changes eventually lead to oscillations in the predator-prey system. Moreover, complications of the environment under laboratory conditions could also lead to oscillations in a predator-prey system (Huffaker, 1958). Although the significance of these oscillations in a predator—prey system is a matter of controversy (Holling, 1959), it is worth examining the roots that cause oscillations in both open and closed systems.

Although oscillations in a predator-prey system are derived from the interactions between individuals in competition, cyclic oscillations that do not reflect any form of competition can also exist (Lotka, 1925; Volterra 1926; Nicholson and Bailey, 1935). Although in experimental populations, a two way interaction between predator and prey causes reciprocal oscillations (Huffaker, 1958), they may also develop due to the delay or persistence of the influence of one individual upon another in the population. Even in single species populations, delayed effects of competition for continuous but limited supply of food cause oscillations

(Nicholson, 1945). Moreover, regular oscillations of all animals, and mammals in particular, are not necessarily due to the reciprocating effects of their predators. The regular four year cycle of populations of lemmings in North Europe and Canada, and the ten year cycle of snowshoe hare in Canada, are also reflected in their predators, which are therefore unable to regulate the cyclic changes in their prey populations.

III. Assessment of the regulation in natural populations

I have earlier discussed the biological processes involved in the regulation of the populations, particularly those preventing undue rises in population level. Apart from the biological processes, seasonal changes in weather, food supply, diseases etc. are also major causal factors in population fluctuations. When multiple factors operate simultaneously such fluctuations are extremely irregular. However, the quantitative changes in the abundance of the population from generation to generation can perhaps be best described from the key factors (Varley and Gradwell 1965, 1970) responsible for the greatest part of the variation in fluctuation. The technique, based on graphical correlation, involves computation of a series of age-specific mortalities by subtracting each log population from the log population of the previous generation : these are referred to as κ , and each κ represents a specific mortality factor. The total generation mortality, K , is then computed as :

$$K = k_1 + k_2 + k_3 \dots k_n$$

A series of k 's, one for each generation, gives a complete picture of the courses of population changes over generations. This method enables evaluation of the role of the key-factors for specific periods, and of the causes of mortality at every stage of the life-cycle. This technique has been used extensively (Klomp, 1966a; 1966b) in evaluating the long term population dynamics of the pine looper, and by Banerjee (1979a) in the tropical Bombycid moths.

The technique of determining age-specific mortality by Morris (1963 a, b) is based on a series of regression analyses to find out the influence of previous generation on the current or next generation, plus the recognition of density-dependent mortality factors. After indentifying various mortality factors, a suitable predictive equation is developed. Apart from being comprehensive in covering almost all of the possible mortality factors, the overall regression can be used to predict the population size in successive generations.

The models discussed are overwhelmingly concerned with the mortality aspects of regulation. A better appreciation of the whole population process is possible from an understanding of the temporal relationship between natality and mortality, expressed as the survivorship curve. The numbers of individuals alive at a particular age is plotted against the age, and the resultant shape of the curve indicates the distribution of mortality at that particular age.

However, the more functional aspects of the relationship between birth and death rates in a population is best expressed in the life tables; it is difficult to construct life-tables for tropical insects because of the overlapping of the generations though there are some exceptions (Banerjee, 1979a). Although the life-table is rather specific, it is possible, even within the same species the substances of the table will vary reflecting the characteristics of the niche where the population was sampled. The variation in the life-table of the milkweed bugs (Landahl and Root, 1969), for example, is mostly due to the latitudinal difference in the distribution of the species in different areas. Such variations are likely to occur in many other species.

CHAPTER IV

POPULATION DISTRIBUTION

In last two chapters population processes have been reviewed against the background of time. Since spatial limitation restricts the physical aspects of population growth, an understanding of the variation in the distribution of the animals is a necessary preliminary to the theories of the natural regulation of population. It can be easily visualized that even when a population is in the active phase of growth, lack of a favourable physical condition can restrict the spatial aspect of the growth. As a direct response to varying physical and biological conditions, the animals in an area may be distributed at random, in clumps or in aggregations, or they may even be uniformly distributed. Southwood (1966) and Da Fonseca (1966) have reviewed the more mathematical aspects of animal distribution, but I will deal with only a few major aspects of spatial distribution.

I. The Basic approach

Variance (S^2) and mean (m) are the two major statistical parameters commonly used to describe animal distribution. When, for example, $S^2 > m$ the animals are described as distributed in clumps or aggregations, and when $S^2 < m$ they are uniformly distributed as opposed to a random distribution, when $S^2 = m$.

However, because of ecological heterogeneity, it is more common to have situations where variance tends to be greater than mean, that is, the animals stay aggregated so, that :

$$S^2 = m + K m^2$$

in which the mean (m) and variance (S^2) are the principal parameters, and K the index of aggregation. When K approaches zero, Negative Binomial becomes same as the Poisson series, but when K takes larger values, Negative Binomial becomes a series with variance more than mean.

The value of K may not however remain constant even in the same species. In *Cylindroiulus punctatus* (Leach), K varied between months and according to developmental stages of the animal

(Banerjee, 1967a; 1976), whereas in *Tribolium confusum* the distribution pattern itself changed from aggregation to random and finally to uniformity (Naylor, 1959). Behavioural aspects of aggregation also need consideration (Banerjee, 1971a) in developing the concepts on causes of aggregation.

II. Taylor's Power law

The models described assume variance and mean are independent of each other. In most natural populations, however, the variance is not always independent of mean, rather they tend to increase together. With a large body of data the relationship between mean and variance seems to follow a power law, and the model derived therefrom fits well with a series of distribution from random to highly aggregation (Taylor, 1961, 1965). The relationship is expressed as :

$$S^2 = am^b$$

where S^2 = variance.

a = a constant, largely a sampling factor.

m = mean.

b = a constant, which actually is the index of aggregation.

Using logarithms, the power law can be fitted as a regression equation :

$$\log S^2 = \log a + b \log m$$

Though the parameter 'b' remains somewhat specific, 'a' differs according to sampling procedure, but the variance stays proportional to the same power of the mean. Consequently, the model with a variance stabilizing function is applicable to the same species in environments that differ marginally (Taylor, 1970). However recent studies show that the parameter 'b' does not remain fixed even within the same species, but may vary according to the growth stages of the individuals (Banerjee, 1976). The problem has been reviewed recently (Taylor and Woiwood, 1982).

III. The Logarithmic distribution

The logarithmic series is of particular interest because it describes well the situations where Negative Binomial takes a very small value of K . The logarithmic series distribution (Fisher, Corbett and Williams, 1943) is expressed as :

$$\lambda = \frac{1}{(\alpha + 1)}$$

where λ = expected measure of concentration of the animals.
 $\alpha = Z^k$, with Z species and k is the dispersion parameter.

This series describes well the relationship between number of species and the number of individuals in a habitat. λ can also be used to interrelate the entire sequence of frequency distributions, including Poisson and Negative Binomial series.

IV The significance of distribution patterns

Although animals in natural communities mostly stay in aggregations or clumps, some physical distance, however minute, is maintained by the individuals in these aggregations. Moreover, there is a limit to the number of individuals in an aggregation and this is of considerable survival value (Banerjee, 1967a). For example, concentration of too many individuals at any one spot may cause accumulation of toxic substances hazardous to the animals. Consequently, aggregations are usually made up of number of individuals sufficient enough to support the population in a particular niche. In *Cylindroiulus punctatus* (Leach) aggregations more than 13 individuals were never found and aggregations of one sex were not seen either (Banerjee, 1967a) : the latter is of help for quick location of mates during breeding.

In the sparse populations, spatial distribution is also of consequence in selecting mates (Rohlf, 1969). Clumping obviously has a slight advantage in finding mates in a sparse population, but not so, when the individuals are numerous in a population. These observations however hold good only for higher animals : for smaller and unicellular animals the significances of spatial distribution patterns have been discussed by Buzaz (1970).

V Multispecies distribution and species associationship

The different spatial distribution patterns described earlier, refer to single species populations. Frequently, more than one species may occupy the same biotype or different parts of the same biotype without entering into direct competition. Although such inter-specific associationship is broadly described as coexistence, yet in delimiting communities, the associationship might turn out to be a complex one with subsidiary ramifications. A simplest model (Cole, 1949; 1960) for determining the associationship between species is :

$$C = \frac{ad - bc}{|ad - bc|} \sqrt{\frac{\text{obs } X^2}{\text{max } X^2}}$$

where $\text{obs}X$ is the value of X^2 associated with the observed values of a, b, c, d, the four cells of a 2 x 2 contingency table. $\text{Max } X^2$ is the value of X^2 when a 'a' is as large or small as the marginal total of the contingency table permits. This simple model directly measures association between species, but it is influenced by the heterogeneity of the area sampled (Bray, 1956). Moreover, the index, C, is not independent of the frequency of the species counts in the sampling area (Hurlbert, 1969). This inadequacy is overcome if $\text{Min } X^2$ is subtracted from both the numerator and denominator of the fraction under square root in the equation. This aspect has recently been discussed (Ratcliff, 1982).

We have discussed the association only at species level. A better understanding of the process is obtained if the relationship is extended to quantify the numbers of individuals of each species present in an association. The broken—stick model (MacArthur, 1957 ; MacArthur and Levins, 1967) gives a close approximation to this situation :

$$\frac{N}{S} \sum_{i=1}^r \frac{1}{(s-i+1)}$$

where S = number of species.

N = number of individuals.

i = the intervals between successively ranked species and the rarest.

r = rank in rareness.

This model fits well with bird populations, but in other animals it shows a preponderance of very common and very rare species in the samples. The mathematical aspects of the ecological consequences of comparative abundance of all species found together in a community can be mathematically expressed as :

$$\log N_i(t) = \log N_i(0) + \int_0^t r_i(t) dt$$

where $N_i(t)$ is the abundance of i th species at a time (MacArthur, 1960). However, the rate and pattern of accumulation of different species in communities are not considered here (Banerjee, 1981 ; 1983).

The coefficient of correlation between different species in a habitat can be described in a community matrix (Levins, 1968),

but the members in a community derive their attributes from inter-and intra-specific competition ; the saturation density of the i th species in the community (Vandermeer, 1970) will be :

$$K_i = N_i \sum_{j=i}^m \alpha_{ij} N_j$$

where m = number of species.

K_i = saturation density of i th species.

α_{ij} = competition coefficient between i and j species.

N_i = equilibrium density of the i th species.

The equation is also used to relate several interconnected population parameters to a number of species in a community, though it does not consider the interactions and time-lags in the system at the community level.

Indelimiting the communities, because of the divergent reproductive and physiological attributes of the cohabiting animals, some biological overlapping is perhaps inevitable. This overlap may occur not only between species in a community, but also in the time and energy distribution of various categories of animals in the community. A mathematical model to describe such diversity will have to be very sensitive (Horn, 1966) because the samples used for measuring overlapping will show a wide range of heterogeneity. This index of heterogeneity (R_e) can be incorporated in Horn's model as :

$$R_e = 1 - R_o = \frac{H_{\text{obs}} - H_{\text{min}}}{H_{\text{max}} - H_{\text{min}}}$$

where R_o is the measure of overlap. An example of the construction of the faunal map of the bee *Euglossa* using this index is given by Ricklefs *et al* (1969).

Although the term "diversity" is used in a very general way to describe species association, simple numerical abundance of a particular species in a community is an inadequate description of community diversity (Dickman, 1968). To be biologically meaningful, it has to be sensitive enough to the relative abundance of animals at all trophic levels. One such model is the information theory index of diversity (MacArthur and MacArthur, 1961) :

$$H = \sum P_i \log_e p_i$$

Where p_i is the proportion of the i th species in the total sample. This index shows that some species in a sample are more numerous than the others, but it also gives a better measure of the comparison between biotypes than the species numbers by themselves. In terms of relative productivity (H_p), the original Shannon-Weaver

(1948) index of diversity can also be modified to state $P_i = Pr/PR$ where Pr is the productivity of a particular species, and PR is the total productivity.

The Shannon-Weaver model is ineffective in measuring biomass and relative abundance of a few species in a community but is highly sensitive in terms of species productivity.

The Shannon-Weaver index and other indices of diversity can be criticized on the ground that some of the mathematical assumptions implicit in them are oversimplified (Hairston, *et al* 1968). Using equitability index (Lloyd and Ghelardi, 1964), these difficulties are greatly overcome in coming closer to the actual situation. This concept has been used (Hairston *et al* 1968 ; Pulliam *et al* 1968) to explain resource limitations in specified field situations, as it measures the relative abundances of the species for contiguous, non-overlapping niches. However, being dependent on the species count component of total diversity, its usefulness in comparative statistics is somewhat limited. To overcome this, another measure of diversity, E , (Sheldon, 1969) can be used :

$$E = e^H/S.$$

where H = observed diversity.

e = base of natural logarithm.

S = observed number of species.

e^H = the minimum number of equally common species that could yield the observed diversity H .

This model is more stable than indices of equitability because it is not dependent on species counts.

As opposed to various indices of diversity and equitability, the measure of concentration (Simpson, 1949), also serves as a useful index for comparing degrees of diversity and distribution of animals in different biotopes (Eberhardt, 1969).

Our interest in this section has been to seek mathematical background for the intra and inter-specific associationship, and distributions of species in a habitat or community. The system that interlinks the community and influence its spatial distribution does not remain static. It is, for example, not uncommon to find competitive displacement amongst ecological homologues (De Bach, 1966). In a community, with organisms having different spatial distributions, a system of interlocking cause and effect pathways operates. Once the interlocking process is identified, and the system is understood, much of the ambiguities on the operative side of ecological processes can be removed.

CHAPTER V

POPULATION THEORIES

From the very beginning of the analytical studies on insect populations, theoretical speculations have been made on the processes involved in the natural regulation and oscillations of the animal numbers. Unfortunately the area of agreements on different views has been very little, and on some points, none at all. It is true however that some population theories are purely inductive in nature and are based on imperfect data or on unplanned short-term population studies. And this has been a source of misinterpretation in many cases. We will discuss first some of the basic components of population theories for an over view.

Density-dependent and density-independent factors

Fundamental to the modern concepts of population theories is the operation of either density-dependent and/or density-independent factors.

The term-density-dependent, as accepted by Smith (1935) and Solomon (1957), is derived basically from the idea of facultative factors of Howard and Fiske (1911), who used the term "catastrophic factor" to indicate the effects of climate, which eventually led to the concept of density-independent factors. In a very general way, density dependent factors are identified as those whose severity in depressing population increases as the population numbers increase. Factors operating in any other way are therefore density-independent. Density in this context refers to the number of animals in an unit area or volume or substrate.

Varley (1958) used the term, delayed density-dependent mortality, to indicate the time lags involved in the responses of the predators to prey densities. Milne (1958) identified two types of density-dependent factors : the intra-specific competition for food and living space is perfectly density-dependent as against imperfectly density-dependent factors involving inter-specific relationships like parasitism or predation.

It is indeed difficult at times to draw clear cut distinctions between density-dependent and density-independent factors or

between the various sub-divisions of the former. It is not uncommon either to find a factor acting in a density-dependent manner on one population and independent of density in another (Macfadyen, 1963).

The equilibrium density

Nicholson (1954, 1957, 1958) stresses that insect numbers are regulated fundamentally through subtle operation of the density-dependent factors. Populations remain in a state of equilibrium with environment as integrated groups because of the operation of the density-dependent factors against indefinite population growth. It follows therefore that a self-regulating system operates in the population, and that the animals regulate their own numbers in relation to their own properties and that of the environment. Intrals and inter-specific competitions are of crucial importance in the regulation mechanism because these forces tend to maintain insect populations in a state of balance even in the face of violent environmental fluctuations. The state of balance does not, however, imply that the population will always remain in a steady state : it in fact oscillates around the equilibrium density; which is maintained in conformity with the prevailing biotic and physical conditions.

When however the actions of the external mortality factors are intensified, intra-specific competition is automatically relaxed to compensate for the losses due to the external mortality forces. This, in effect, reduces the effectiveness of the inre-specific destructive forces. Although Nicholson particularly stressed the importance of the density-dependent mortality factors, those independent of density can also act on the population only by modifying the properties of the animals or those of their environment.

The oscillation of the population around the equilibrium density, in Nicholsonian concept, is the system by which the tendency to geometric increase is balanced by density-dependent controlling factors. As the population increases, the intensity of the controlling factor(s) also increases correspondingly to bring down the population to the equilibrium density.

According to Andrewartha (1963) and Watt (1964b), the supposed density-dependence in animal populations can result only in a false negative correlation of the ratio of the successive populations densities (N_{t+1}/N_t) with the intial density (N_t), because population parameters are independent variables with

N_t contributing to both. On the other hand, negative correlations were not found in some temporal series of population densities (Green, 1968). It is possible that the use of random numbers, as done by Watt (1964a), is not valid for testing the null hypothesis of density-dependence.

The principal objection to Nicholson's theory is that it is based essentially on laboratory studies and may not be relevant to the actual changes in natural populations. Moreover, the population stabilization process cannot possibly be generalized to all situations under varied ecological conditions in the natural setting. Although the stabilities of natural communities and populations at different trophic levels have been discussed at length (Watt, 1968), elaborate laboratory and field work is still needed before a functional relationship between stability and diversity can be established (Hairston *et al*, 1968).

The Nicholsonian concept of population equilibrium has also been contested by Richards (1961) who suggests the term "balance" for equilibrium, because the latter is relevant only to relatively vast increases in numbers or to sudden extinctions that are theoretically possible. Besides, by stressing too much on the density-dependent factors, Nicholson appears to have overlooked or underestimated many other associated biological and physical factors of consequence.

Weather and resource

Although Nicholson did not consider weather to be a population regulatory force because of its inability to act in a density-dependent manner, Andrewartha and Birch (1954) and Birch (1957) and Andrewartha (1966) consider weather as of crucial importance in the dynamics of insect populations.

According to them, weather along with the following factors are primarily responsible for the regulation in animal numbers :

1. A shortage of resources.
2. Inaccessibility of the resources relative to the animal's capacity to find them.
3. By a shortage of time when the intrinsic rate of increase is positive. Fluctuations in the value of r may be caused due to the vagaries of weather.

Andrewartha and Birch have objected to the ideas of density-dependent and density-independent factors because they do not

have any practical significance in the context of field population changes. Animal numbers, according to them, are regulated without the operation of the so-called stabilization mechanism of the density-dependent factors.

Through a series of elegant field studies, particularly on *Thrips imaginis* and the grasshopper, *Austroicetes cruciata*, Andrewartha and Birch have shown that weather indeed plays a major role in causing changes in animal numbers. The average density is determined from the relative rates of increase and decrease during favourable and unfavourable weather, as well as from the relative durations of the favourable and unfavourable weather periods. It thus follows that weather can and does act independent of animal densities, though weather may act in a density-dependent manner by interacting with the population numbers and availability of shelter sites (Paris, 1963).

On availability of the food, Andrewartha and Browning (1961) state that animal numbers in an area are regulated by the dispersal abilities of the animals relative to their food. When the power of dispersal is small or limited, much of the food will go undetected : consequently the animals will have patchy distributions. When the dispersal powers are great, relative to the food, both the animals and their food are likely to be rare. The shortage of food therefore results more from exploitation, rather than from intra-specific competition, which Andrewartha and Browning consider to be of little importance.

The concept of extinction level

According to Milne (1957, 1958, 1962), changes in animal numbers, particularly their tendencies to increase indefinitely are checked by the joint actions of the density-dependent and imperfectly density-dependent environment factors. Even if their joint action fails, increase is prevented by the intra-specific competition within the population. Decrease in numbers to a zero level is again prevented by the operation of the density independent factors, and if they fail to be effective at appropriate time, the residual population may ultimately perish. The concept of regulation or control is therefore a state which prevents the increase or decrease in numbers from the theoretical "extinction levels" Consequently, the highest density remains below the level of collective destruction, and the lowest above zero, which by implication, suggests that the population indeed stays in balance with the environment itself. Milne's theory will appear to be synthesis of both Nicholsonian and Andrewartha and Birch's concepts.

Milne suggests that natural enemies in inter-specific competition alone are unable to control population growth because at best they can act in an imperfectly density-dependent manner. The action of intra-specific competition is therefore considered to be automatic and that of inter-specific predation and competition as probabilistic.

However, although intra-specific competition is more or less automatic in action, it does not necessarily prevent expansion or extinction of the population (Clerk *et al*, 1968). Moreover, successful operations of biological control involving density-stabilizing interactions between predator and prey, suggest that under certain conditions natural enemies help reducing the populations. Although to an extent the actions of natural enemies are probabilistic, they do nevertheless serve as important stabilizing forces. Milne's argument is at times difficult to appreciate, particularly in the context of many well known examples of control of economic pests using predators and parasites (Macfadyen, 1963).

The regulatory aspects

Solomon (1964) basically accepts Nicholsonian concept of equilibrium density, but point, out that in practice it would be difficult to distinguish the movements towards and away from the equilibrium level. Though disagreeing with Andrewartha and Birch, that a density-independent factor like weather could be an important regulator of population, Solomon believes that weather may give rise to situations in which competition may occur for a residue of favourable sites. Weather therefore determines which regulatory process should become dominant and modify its intensity :

Solomon (1964) recognizes the importance of natural enemies in the regulation of populations, and distinguishes three steps in the natural control of insects.

1. Regulation by the density-dependent processes, which may be one, or more than one, acting simultaneously. These are exerted in different intensities depending on time and space.
2. Modification of the regulatory processes : the modifying factors may include genetic changes.
3. Imposition of changes in abundance, independent of density.

The feed-back mechanism

Pimental (1961) suggests population growth has its foundation in the evolutionary process and that a genetical feed-back mechanism regulates populations of herbivores, predators and parasites. The mechanism functions through the dynamics of density pressure, selective pressure and genetic changes in a population. In a food chain cycle, the actions and reactions of the interacting populations through genetic feed-back mechanism result in the evolution of a new population, and regulation of the existing population. The genetic feed-back system, competition and environment are therefore interdependent. In animals that are new to a particular ecosystem, stabilizing factors like competition, and environmental randomness are gradually replaced by the feed-back mechanism.

However, in a food chain, the food organisms are not attacked by one particular species, but by a number of species, each in its own way (Milne, 1962). Since the attacking species have different ecological and physiological attributes, it is possible that they would exert opposing selective pressures on the genotypes of the food organisms. Moreover, density-related genetic changes are matters of theory and speculation though genetic composition of the population may change from generation to generation because of the operation of the natural selection (MacArthur and Connell, 1966).

The genetical aspect

According to Chitty (1960, 1965), the numerical self-regulation of the population is caused by the genetically induced changes in the composition of the individuals in the population. It is assumed that animal populations are genetically heterogeneous : therefore both at high and low population densities different genotypes tend to influence the population. Although the theory is based on field observations on voles, in the tent caterpillar, *Malacosoma pluviale*, individuals with different genotypes do exist : the appearance of active and sluggish forms in the population is also genetically regulated (Wellington, 1965). Selective advantages or otherwise associated with this mechanism restrict the excessive expansion of the population.

Changes in the quality of the population with density are quite widespread in natural populations, but the causes are many and perhaps not genetic in all cases (Macfadyen, 1963). It is equally possible that changes in the quality of the populations, implied

in Chitty's thesis, may also result from (1) the variable properties of the animals and (2) effective environmental factors.

The trophic level approach

An interesting approach to population problem has been taken by Hairston Smith and Slobodkin (1960) who consider animal numbers are regulated at their trophic levels. Thus the primary consumers are limited by predators, and the producers, carnivores and decomposers by the shortage of resources. They dismiss weather as a possible controlling factor for herbivores, because, to be a controlling factor, weather has to ensure preadaptation of the animals to it. Watt (1965) maintains that stability at herbivore or carnivore trophic level increases with the numbers of competitor species at that level, and decreases with the number of species that feed on them. Their number also decreases with the proportion of the environment containing useful food.

Some general considerations

Although modern theories on the regulation of insect numbers either stress the importance of density dependent factors like competition, or density-independent factors like weather, these two are not necessarily mutually exclusive alternatives (Horn, 1968). In a very general way, density-dependent forces become operative where population growth is not a linear function of the density, whereas in a density-independent process, a linear function exist between the two. Therefore, if the density-dependent growth rate is plotted against density-independent death rate, the point of intersection will be the theoretical equilibrium.

For most animals, particularly those in the higher taxa, there is a fixed period for rapid multiplication and breeding when generations are quickly built up causing an overall increase in the population. Birth rate during this period also exceeds the death rate. Animals undoubtedly multiply outside this period of peak activity, but at a lower rate. The characteristic environment at the time of optimal multiplication initiates rapid changes in population growth, and other associated activities. The timing will vary for different species, but in a particular biotype, diverse species may become active more or less at the same time; the period of reproductive activity is indeed a recurring feature in the life-systems of all species. Since the weather during the period does not necessarily remain steady, animal numbers and the duration of the reproductive phases may also vary indirectly with

such weather fluctuations as it may affect the physiology of reproduction. The moot point is that even in the face of weather fluctuations, large or small, the period of activity appears with regularity, covering more or less the same length of time under any spatial limitation. Even when the insects exploit the food source at a particular site continuously, population peaks and troughs do recur with precision (Banerjee, 1966a; 1974a; 1980; Banerjee and Kakoti, 1968). The magnitude of these peaks and oscillations may vary, but the regularity is worth noting.

How and in which ways do the seasonal changes in weather affect the existing field populations are not always clear, and it is equally difficult to say which component of the weather is important, and under what conditions. The month to month variation in the numbers of three species of diplopods and a species of red spider mite (*Oligonychus coffeae* Neitner) was correlated with the prevalent weather conditions (Banerjee, 1967b; 1979c) but no valid conclusions could be drawn possibly because of insufficiency of the data.

The seasonal and often well-marked increases in insect and other arthropod populations suggest that the reproductive potentialities of these animals must also be following a seasonality, influenced, as it is, by various climatic and biological factors. Once under the stimuli of favourable conditions, the animals start multiplying rapidly, causing intra-specific competition to become operative at least discreetly. It is equally possible that most animals would avoid competition because the period of their abundance synchronizes well with the abundance of food supply. One important source of competition, food, is thus eliminated. Moreover, most insects have a fairly wide range of food plants, and if one is in short supply, the rest can balance the supply. In a shortage of resource, animals also avoid competition by migrating: dispersal therefore helps animal species to limit their own numbers and avoid consequences of unrestricted competition for food (Wyne-Edwards, 1962). In fact, animal numbers at any habitat never become high enough to induce competition (Solomon, 1957; Banerjee, 1983). Harrison (1964), Caplan (1966) and Ross (1957) did not find any evidence of intra-specific competition in lepidopteras and acrids though different species were utilizing a common food supply while occupying the same niche in the field.

Predation and parasitism are perhaps the greatest controlling forces against unrestricted population growth: in an expanding population, predation rate remains density-dependent at a low

prey density, but independent at high densities (Banerjee, 1971e). No matter in which way the predators and parasites operate, undoubtedly they are of consequences in the regulation of animal populations. The practical importance of natural enemies is fairly well known and well-documented (De Bach 1964).

An absolute increase in their numbers is also prevented by the animals themselves, especially when they are distributed in patches. Since the reproductive potentiality is density-dependent (Watt, 1964b), when population density reaches a critical level, reproductive rate is automatically lowered (Banerjee, 1979b). Conversely, when population density is low as it often happens under indiscriminate predation, the reproductive rate of the surviving individuals increases to make good the loss.

It is perhaps interesting, in a negative way, that in formulating population theories, the fundamentals of insect behaviour were often overlooked or underestimated. Since the basic behaviour patterns are always at the root of physiological or ecological manifestations of population growth, they ought to form the main plank of the theories and mathematical models on population regulation. In constructing mathematical models or developing theories, certain amount of speculation is unavoidable, but a better insight into ecological processes can be obtained if the basic behaviour patterns that influence the distribution and abundance of animals are duly considered (Banerjee, 1971b; Harker, 1961).

The points made can be arranged as :

1. Seasonal fluctuations affect the behaviour and reproductive physiology of the animals.
2. Seasonal variation in animal numbers is a reflection of the variation in reproductive potentialities of the animals.
3. Rapid multiplication under favourable physical and biological conditions leads to population peaks. This period normally coincides with the breeding period of the animals.
4. Dispersal prevents intra-specific competition in natural populations.
5. Predation prevents undue expansion of the population.
6. At low densities reproductive rate increases and vice versa.

The extent and the degree of severity of the environment in its totality therefore influences the regulatory mechanism in a population. The minor cyclic variations in the environment are tackled through appropriate behavioural responses at individual levels. When the fluctuations are severe and persistent, population as a whole responds by dispersing or by rapid growth or decline as the situation may demand. If the conditions are such that only a small fragment of the population can survive, they may produce offspring that will incorporate genetic traits to enable them to withstand the changed environment.

The regulation and adjustment of the populations in the direction of relative stability are the essential elements of a homeostatic system, by which the population is maintained at its operative level inspite of the seasonal fluctuations in environment (Banerjee, 1971c; 1971e). The level to which population should rise is also regulated by this mechanism : it is therefore something more than a simple feed-back system by which the population samples the environment and compensates for its variation. The simple feed-back in population control is provided by competition, but the overall regulation is the outcome of a confounding of both physical and biological environments.

It is indeed difficult to show the regulatory aspects of the changes in the genetic characters of the population, primarily because the genetical processes are extremely slow. However, marked numerical changes in animals can speed up the evolutionary process : it will permit extreme genetic variation during the period of rapid growth, selective elimination when the population is stabilized, and still more when the population declines.

The points raised above are no doubt partly theoretical and may not clear all the ambiguities associated with population regulation. They will at least emphasize that a multitude of environmental and biological factors, and their interactions, are deeply involved in population regulation.

One would certainly agree with Birch and Ehrlich (1967) that in population biology more work is needed to find out the general properties of the populations of single as well as those of more than one species. The answers to the following questions are therefore must for logical follow up of any modern concept of population dynamics :

1. How frequently populations become extinct in nature ?
2. Do most populations have self-regulating mechanisms ?

3. How frequently populations utilize the same limited resources in nature ?
4. What kind of selective pressure does such utilization impose upon each population in nature ?
5. Is great gene flow necessary for differentiations of populations in nature ?
6. How are the community complexity and stability are best defined and measured ?
7. What is the relationship between complexity and stability ?

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