NETAJI SUBHAS OPEN UNIVERSITY

STUDY MATERIAL

POST GRADUATE ZOOLOGY

PAPER - 2
GROUP : A

Ecology, Environmental
Biology and Toxicology

PREFACE

In the auricular structure introduced by this University for students of Post Graduate degree programme, the opportunity to pursue Post Graduate course in Subject introduced by this University is equally available to all learners. Instead of being guided by any presumption about ability level, it would perhaps stand to reason if receptivity of a learner is judged in the course of the learning process. That would be entirely in keeping with the objectives of open education which does not believe in artificial differentiation.

Keeping this in view, study materials of the Post Graduate level in different subjects are being prepared on the basis of a well laid-out syllabus. The course structure combines the best elements in the approved syllabi of Central and State Universities in respective subjects. It has been so designed as to be upgradable with the addition of new information as well as results of fresh thinking and analysis.

The accepted methodology of distance education has been followed in the preparation of these study materials. Co-operation in every form of experienced scholars is indispensable for a work of this kind. We, therefore, owe an enormous debt of gratitude to everyone whose tireless efforts went into the writing, editing and devising of a proper lay-out of the materials. Practically speaking, their role amounts to an involvement in invisible teaching. For, whoever makes use of these study materials would virtually derive the benefit of learning under their collective care without each being seen by the other.

The more a learner would seriously pursue these study materials the easier it will be for him or her to reach out to larger horizons of a subject. Care has also been taken to make the language lucid and presentation attractive so mat they may be rated as quality self-learning materials. If anything remains still obscure or difficult to follow, arrangements are there to come to terms with them through the counselling sessions regularly available at the network of study centres set up by the University.

Needless to add, a great deal of these efforts is still experimental—in fact, pioneering in certain areas. Naturally, there is every possibility of some lapse or deficiency here and there. However, these do admit of rectification and further improvement in due course. On the whole, therefore, these study materials are expected to evoke wider appreciation the more they receive serious attention of all concerned.

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Vice-Chancellor

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NETAJI SUBHAS
OPEN UNIVERSITY

PGZO-2
Ecology, Environmental
Biology & Toxicology

GROUP - A

Part-I : Ecology

Part-II : Environmental Biology and Toxicology

UNIT 1 ❐ Ecology of Population

Structure

1.0. ❐ Introduction

Life table is a table showing the mortality within a population arranged by age groups (cohort). A life table is compiled from the age structure of a population at a particular time. In other words, a life table is basically a table of probabilities dealing with the rate of death and expectation of life at various time intervals over an organism's life span. A clear and systematic picture of mortality and survival in a population is best provided by life table. It is useful device to analyze probabilities of survivorship of individuals in a population, to determine ages most vulnerable to mortality and to predict population growth.

The life table consists of a series of columns, each of which describes an aspect of mortality statistics for member of a population according to age. Figures are presented in terms of a standard numbers of individuals all born at the same time, called a cohort. By convention, the initial number of individuals in a cohort is set at 1000. The column includes x -the unit of age or age level, lx -the number of individuals in a cohort that survive to that particular age level; dx -the number of cohort that die in an age interval x to x+1 (from one age level listed to the next) and qx- the probability of dying or age-specific mortality rate. This rate is determined by dividing the number of individuals that died during the age interval by the number alive at the beginning of the interval. Another column, s, or survival rate may be added. It can be calculated from 1-q. In order to calculate life expectancy, given in column ex, two additional statistics are needed, Lx and Tx. Lx, is the average years lived by all individuals in each category in the population. It is obtained by summing the number alive at age interval x and the number at age x+1, and dividing the sum by 2. Tx is the number of time units left for all individual to live from age x onward. It is calculated by summing all the values of Lx from the bottom of the table upwards to the age interval of interest. Life expectancy, ex, is obtained by dividing Tx for the particular age class x by the survivors for that age, as given in the lx column.

Mortality (dx) can be estimated by determining the ages at death of a large number of animals born at the same time.

1.1 ☐ Types of life table

There are thee basic types of life tables Horizontal, Vertical and Dynamic-Composite.

1.1.1 Horizontal life table

Horizontal life table also called cohort or dynamic life tables, are constructed by following a cohort of individuals, a group all born within a single short span of time, from birth to death of the last member. Construction of such table is most easily accomplished when the species is short-lived (one or two years), so that the generations are discrete.

In this type of life table, the survival of a known group of organisms, called a cohort, is followed from birth to the time when they are all dead. This method is applied to plants and sessile animals that are not very long lived, because thy are to keep track of and resample during their life. It is difficult to apply to animals which disperse because dispersal may be confused with mortalitry. Grant and Grant (1992) constructed such tables for populations of the medium ground finch *(Geospiza fortis)* and the cactus ground finch *(Geospiza scandens)* on Isla Daphne Major in the Galapagos archipelago. They followed four color banded cohorts born in the years 1975 and 1978 until nearly every individual died. Under mentioned table **(Table-A)** provides an example of a, short life table for the cactus ground finch in 1975. The survivorship of males and females is combined.

Table-A. Life table of 1975 cohort of *Geospiza scandens*

Age Class	Number alive each year	Production surviving at start of age x	Production dying between x and x+1	Mortality rate	Mean expectation of further life
0	82	1.000	0.488	0.488	2.63
1	42	0.512	0.207	0.404	3.64
2	25	0.305	0.098	0.301	4.78
3	17	0.207	0.036	0.174	5.79
4	14	0.171	0.000	0.000	5.93
5	14	0.171	0.012	0.070	4.93
6	13	0.159	0.000	0.000	4.27
7	13	0.159	0.000	0.000	3.27
8	13	0.159	0.074	0.465	2.27
9	7	0.085	0.037	0.435	2.79
10	4	0.048	0.000	0.000	3.50
11	4	0.048	0.000	0.000	2.50
12	4	0.048	0.024	0.500	1.50
13	2	0.024	0.000	0.000	1.50
14	2	0.024	0.012	0.500	0.50
15	1	0.012	0.012	1.000	0.50
16	0	0	....	....	....

1.1.2 Vertical, time-specific or static life table

It is constructed by sampling the population in some manner (such as hunting takes or core sampling of trees) and aging the organisms to obtain a distribution of age classes during a single time period (Table-B). This life table involves the assumptions that each age class is sampled in proportion to its numbers in the population and ages at death, that the birthrate and death rate are constant, and that the population is neither increasing nor decreasing. It assumes, for example, that survivors of one year class were survivors from the year before and so on, the same as they would have been if they were a single cohort.

Such assumptions, of course, are false because when data' are so collected, the number of survivors in one year may be greater than the year previous. In this case the data have to be adjusted or smoothed to get rid of this anomaly (see Caughley, 1977).

Table-B Time specific life table for Red Deer on Isle of Rhum, 1975

X	Ix	dx	1000X	ex
Stages				
1	1000	282	282.0	5.81
2	718	7	9.8	6.89
3	711	7	9.8	5.95
4	704	7	9.9	5.01
5	697	7	10.0	4.05
6	690	7	10.1	3.09
7	684	182	266.0	2.11
8	502	253	504.0	1.70
9	249	157	630.6	1.91
10	92	14	152.1	3.31
11	78	14	179.4	2.81
12	64	14	218.7	2.31
13	50	14	279.9	1.82
14	36	14	388.9	1.33
15	22	14	636.3	0.86
16	8	8	1000.0	0.33
Hinds				
1	1000	137	137.0	5.19
2	863	85	97.3	4.94
3	778	84	107.8	4.42
4	694	84	120.8	3.89
5	610	84	137.4	3.36
6	526	84	159.3	2.82
7	442	85	189.5	2.26
8	357	176	501.6	1,67
9	181	122	672.7	1.82
10	59	8	142.2	3.54
11	51	9	164.6	3.00
12	42	8	197.5	2.55
13	34	9	246.8	2.03
14	25	8	328.8	1.56
15	17	8	492.4	1.06
16	9	9	1000.0	0.50

1.1.3 Dynamic-Composite life table

It records the same information as the dynamic life table, but it takes as the cohort a composite of a number of animals marked over a period of years rather than at just one birth period. For example, wildlife biologists may mark or tag a number of newly hatched young birds or newly born young mammals each year over a period of several years. After following the fate of each year's group, they pool the data and treat all of the marked animals as one cohort (see Barkalow et al, 1970). Or biologists may record the ages at death of animals found over a series of years and pool those data to construct a life table. Houston (1982) used this method to construct a life table for Yellowstone elk (Table-C).

Table-C. Dynamic-Composite life table for Northen Yellowstone Female Elk

X	l_x	d_x	q_x	e_x
0	1000	323	.323	11.8
1	677	13	.019	16.2
3	662	2	.003	15.5
4	660	4	.006	13.6
5	656	4	.006	12.7
6	652	9	.014	11.7
7	643	3	.005	11.0
8	640	3	.005	10.0
9	637	9	.014	9.0
10	628	7	.001	8.1
11	621	12	.019	7.3
12	609	13	.021	6.4
13	596	41	.069	5.5
14	555	34	.061	4.9
15	521	20	.038	4.2
16	501	59	.118	3.3
17	442	75	.170	2.7
18	367	93	.253	2.1
19	274	82	.299	1.7
20	192	57	.297	1.2
21+	135	135	1.000	0.5

Source : Adapted from Houston 1982.

Note : Both, the static (time-specific) and dynamic-composite life tables are inaccurate. Mortality and reproduction vary from year to year over which the data are collected. The data reflect standing age distributions; yet the life table is based on a stable age distribution. If age distributions are unstable, populations are changing continuously and the data from which life tables are constructed do not reflect the true nature of the population. In spite of these shortcomings, such life tables may present a reasonable assessment of average conditions in the population, useful to compare life history trends within and between populations.

The life tables described are typical of long-lived species in which generations overlap and in which different age groups are alive at the same time. However, tremendous numbers of organisms have one annual breeding season and generations do not overlap. All individuals belong to the same cohort or age class. Many insects and annual and biennial plants follow this pattern. Some organisms, notably insects, have several stages to their life cycle. In this case, the life table is best divided into developmental stages rather than discrete time intervals. The *lx* values are obtained by observing a natural population over the annual season and by estimating the size of the surviving population at each stage of development from eggs, larvae, pupae and adults. From the records of weather conditions, abundance of predators, parasites, and diseases, one can estimate how many die from various causes.

1.2 ☐ Survivorship and mortality curves

The life table is a very important tool in the analysis of population dynamics. From it, survivorship curves can be derived based on the *lx* column and also mortality curves can be drawn based on the *qx* column. These curves enable to determine the ages at which a particular organism most often dies. This information provides some leads in determining the causes of death and ultimately the processes that affect the population dynamics of a given species. They enable biologists to compare survival between the sexes, between *cohorts* arising in different years, between populations, and between species.

1.2.1 Survivorship Curves

The survivorship curve depicts age-specific mortality through survivorship. It is obtained by plotting the number of individuals of a particular age cohort against time. The usual form is to plot the logarithms of the numbers of survivors (usually on semilogarithmic graph paper) against age. .

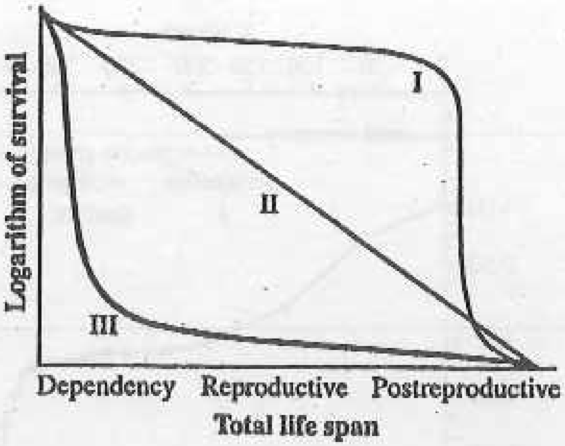


Figure-1. Three basic types of survivorship curves. The vertical axis may be scaled arithmetically or logarithmically. If it is logarithmic, the slope of the lines will show the following rates of change:

Type I, curve for populations in which the survival of juveniles is high and mortality is concentrated among old individuals.

Type II, curve for populations in which the rate of mortality is fairly constant at all age levels, so that there is more or less a uniform percentage decrease in survivorship over time;

Type III, curve for a population in which high mortality is concentrated among juveniles.

Survivorship curves may be classified into at least three hypothetical types **(Figure-1)** (Deevey, 1947). These curves are conceptual models only, against which real-life survivorship curves can be compared. The Type I curve is convex. It is typical of populations whose individuals tend to live out their physiological life span; they exhibit a high degree of survival throughout life and experience heavy mortality in old age. Such a curve is typical of some plants, such as *Phlox drummondii* **(Figure-2)**, and many mammals, such as elk (Figures-3). The Type II curve is linear and typical of organisms with constant mortality rates. Such a cuvre is characteristic of the adult stages of may birds **(Figure-4)**, rodents, and some plants **(Figure-5)**.

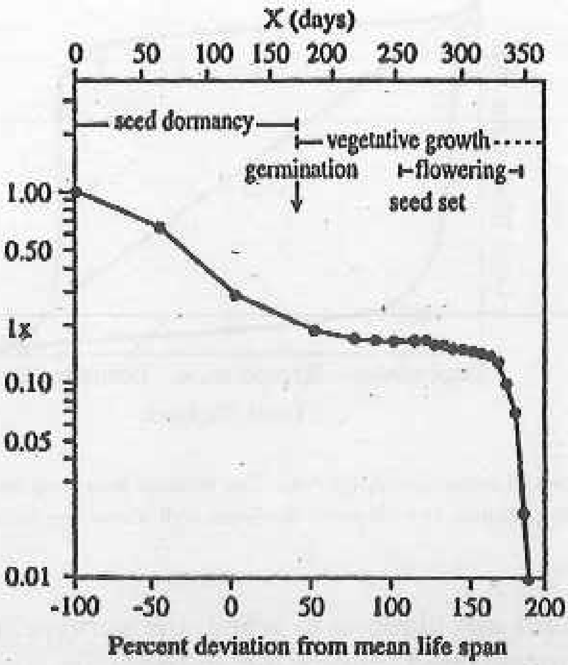


Figure-2. Type 1 survivorship curve for the annual Phlox drummondii at Nixon, Texas (From Leverich and Levin, 1979 : 885).

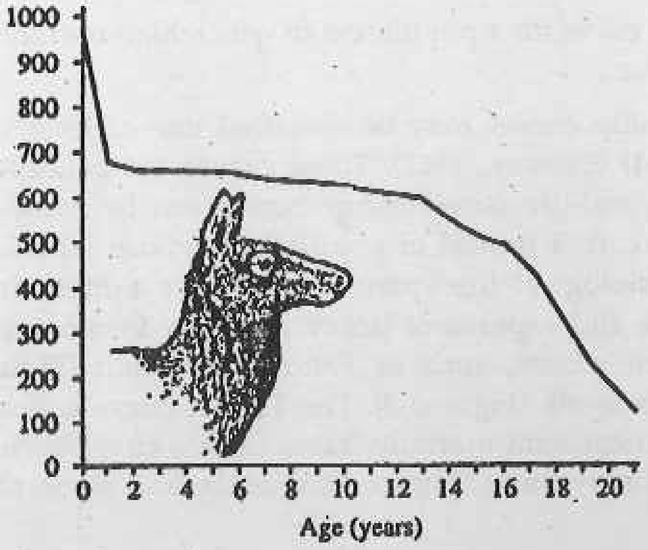


Figure-3. Type I survivorship curve for female elk of Yellowstone National Park.

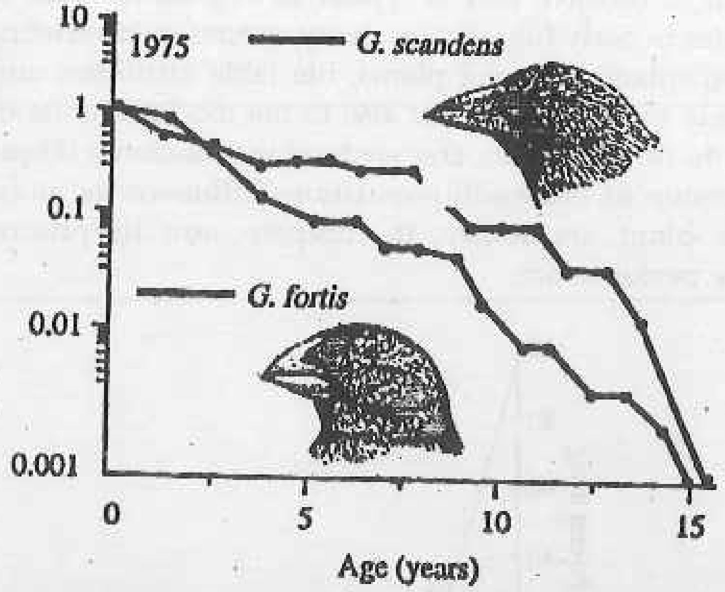


Figure-4. Type II survivorship curve for the 1975 cohorts of the cactus ground finch (*Geospiza scandens)* and the medium ground finch (*G. fortis)* (Adopted from Grant and Grant, 1992:771.)

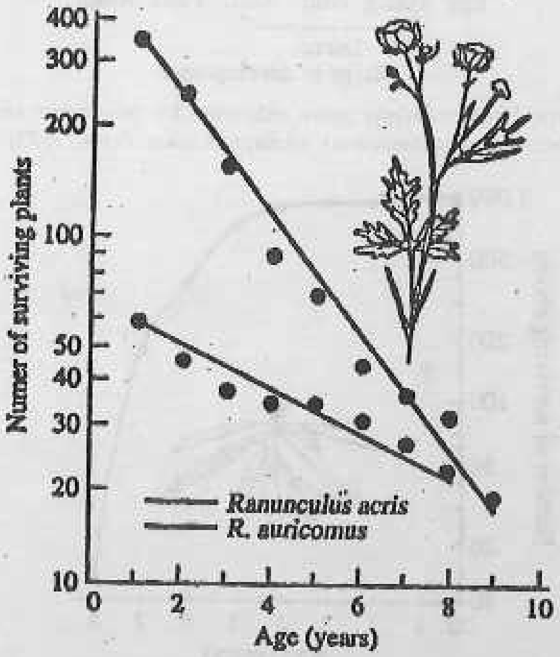


Figure-5. Type II survivorship curves for buttercups *Ranuculus acris* and *Raniculus auricomus.* (From Sarukhan and Harper)

Type-III is concave and is typical of organisms with extremely high mortality rates in early life; such as many species of invertebrates **(Figure-6)**, fish, and someplants. Among plants, life table attributes and survivorship apply not only to individuals but also to the modular units the populations of leaves, buds, flowers, fruits, and seeds, as well as clones **(Figure-7)**. Mortality and survivorship of these sub populations influence the individual growth form of the plant, its ability, to compete, and its photosynthetic and reproductive performance.

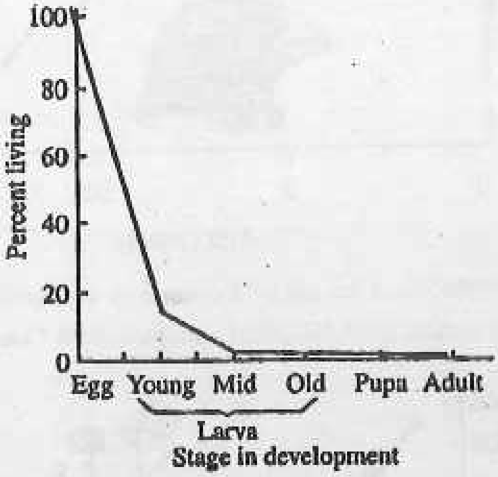


Figure-6. Type I survivorship curve exhibited by the oyster shell scale insect (*Lepidosaphes ulma*). (Adapted from Price, 1975)

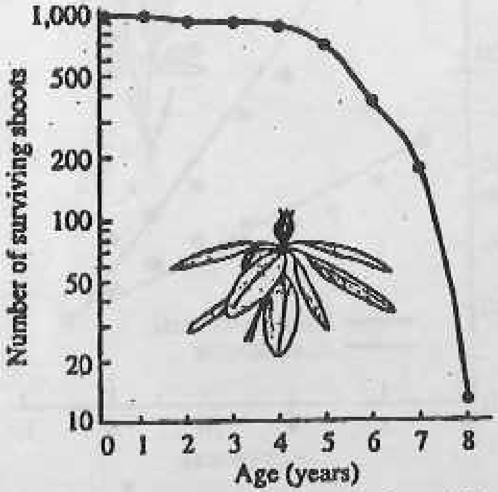


Figure-7. sSurvivorship curve of plant modules : Shoots of *Rhododendron maximum*. The curve is Type-1 (Based on data from McGraw, 1989).

The validity of the survivorship curves depends upon the validity of the life table and the *lx* column. Life tables and thus survivorship curves are not typical of some standard population, but depict instead the nature of the population at different places at different times under different environmental conditions, and assume stable age distribution. Their greatest usefulness rests in the comparison of populations of one area, time, sex, or species with populations of another. For example, **Figure-8** shows the variation in survivorship of the small-mouthed salamander *(Ambystoma texaum)* larvae over several years. It emphasizes the effects of variations in the environment on survivorship. Low survivorship in 1983 and 1984 resulted from severe flooding of the stream habitat. Similarly, survivorship curves can point out the effect of environmental changes on plant populations. Klemow and Raynal (1983) followed the fate of population of the summer annual garden rocket *(Erucastnugallicum)* for five years. Survival of plants that emerged the spring varied markedly with rainfall, drought had a type-II survivorship curve.

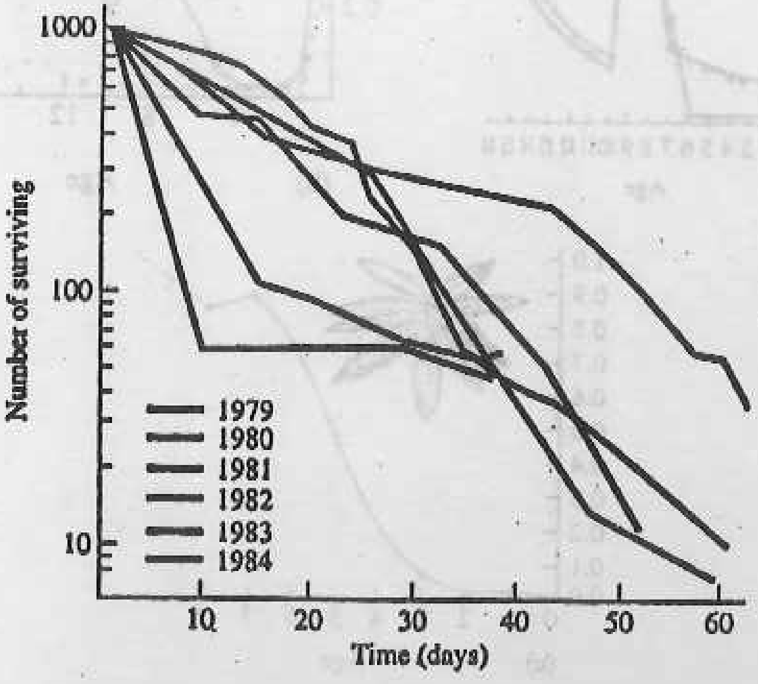


Figure-8. Variation of survivorship in small mouth salamander *(Ambystoma texaum)* larvae over a period of five years. Low survivorship in 1983 and 1984 resulted from severe flooding of their stream habitat. (Pefranka and Sih, 1986:731)

1.2.2 Mortality Curves

If the data are plotted in the qx or mortality rate column of the life table against age, a mortality curve can be obtained. It consists of two parts: (1) the juvenile phase, in which the rate of mortality is high; and (2) the post-juvenile phase, in which the rate first decreases as age increases, then increases with age after a low point in mortality (Figure-9). Most populations have a roughly J-shaped curve.

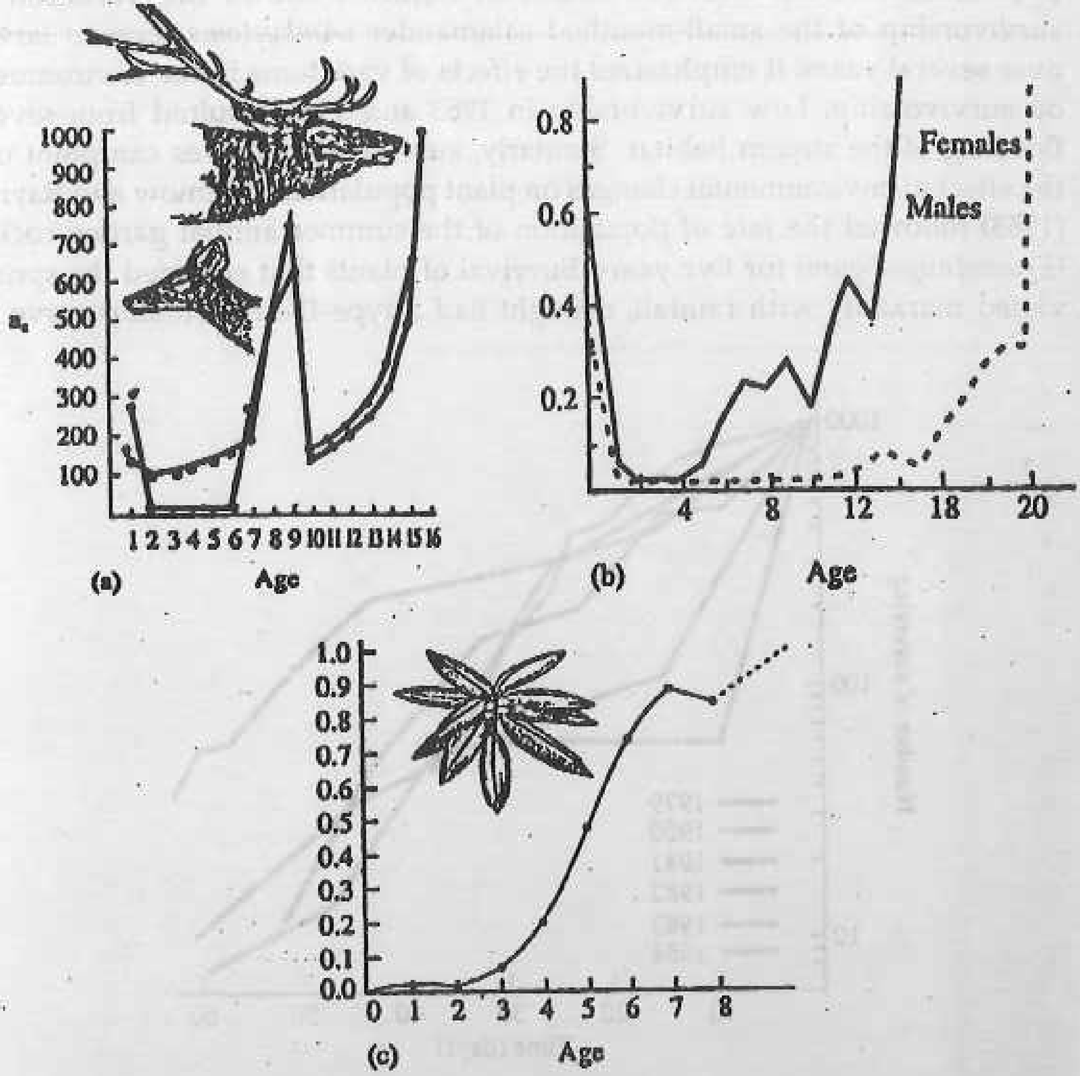


Figure-9 Mortality curves :

(a) The red deer (*Cervus elapus)* males and females. (Data from Lawe 1969)

(b) Elk or wapiti *(Cervus canadensis)* of Yellowstone (From Houston 1982:57). The. mortality curves of the males of these two related species are similar with a sharp peak in mortality in the middle years. The female red deer show a similar peak, but female elk do not.The mortality curves, however, assume a J-shape.

(c) The mortality curve *of Rhododendron* also assumes a strong J-shape, with maximum mortality late in life (Data from McGraw 1989).

Because qx is the ratio of the number dying during an age interval to the number alive at the beginning of the period (or surviving the previous age period), that parameter is in dependent of the frequency of each of the previous age classes. Therefore the parameter is free of the biases inherent in the *Ix* column and survivorship curves. Most life tables of wild populations are subject to bias because the first-year age class is not adequately represented. This error distorts each succeeding *Ix* and dx value. If the first values are inaccurate, all succeeding ones are inaccurate. But if the full values of qx are wrong, the error does not affect the other values. For this reason mortality curves, which indicate the rate of mortality indirectly by the slope of the line are informative.

1.3 ☐ Generation time, net reproductive rates, and reproductive values

Generation time :

The life tables and fecundity schedules drawn up for species with overlapping generations are at least superficially similar to those constructed for species with discrete generations. With discrete generations, the basic reproductive rate (R_0 represents summery describing the overall outcome of the patterns of the survivorship and fecundity.

R_0 describing two separate population parameters was the number of offspring produced on average by an individual over the course of its life; but it was also the multiplication factor that convened an original population size into a new population size. When a cohort life table is available the basic reproductive rate can be calculated using the formula :

$$R_0 = I_x m_x$$

Having made these assumptions, the t, *dx* and *qx* columns were constructed. It is clear, however, that the assumptions are false. There were actually more animals in their seventh year than in their sixth year, and more in their 15th year than in their 14th year. There were therefore 'negative' deaths and meaningless mortality rates. The pitfalls of constructing such static life tables (and equating age structures with survivorship curves) are amply illustrated.

Nevertheless, the data can be useful. Lowe's aim was to provide a *general* idea *of* the population's age-specific survival rate prior to 1957 (when culling *of* the population began). He could then compare "his with the situation after 1957, as illustrated by the cohort life table previously discussed. He was more concerned with general trends than with the particular changes occurring from 1 year to- the next. He therefore 'smoothed out' the variations in numbers between ages 2-8 and 10-16 years to give a steady decline during both *of* these periods. The results of this process are shown in the final three columns *of* Table (vide infra), and the survivorship curve is plotted in Figure-4. A general picture does indeed emerge : the introduction *of* culling on the island appears *to* have decreased overall survivorship significantly, overcoming any possible compensatory decreases in natural mortality a *Carex bigelowii* population. The densities per m' of tillers are shown in rectangular boxes and those of seeds in diamond-shaped boxes. Rows represent tiller types whilst columns depict size classes of tillers. Thin-walled boxes represent dead tiller (or seed) compartments, and arrows denote pathways between size classes, death or reproduction. (After Callaghan. 1976.)

A general relationship that links population size, the rate of population increase, and time but which is not limited to measuring time in terms of generations. Imagine a population]that stans with 10 individuals, and which, after successive interval of time rises to 20, 40, 80, 160 individual and so on. It is referred to the initial population size as N_0. (meaning the population size when no time has elapsed). The population size when no time has elapsed). The population size after one time interval is N_1, after two interval is N_2 and in general after t time interval it is N_t. In the present case $N_0 = 10$, Nl = 20, and therefore it can be presented as N_t = No R

Net reproductive rate :

Because population increase depends mostly on the no. of females in the population, the age specific birth schedule usually counts only the female giving rise to females. The age specific schedule is obtained by determining the mean number of females form each group of females, designated as mx. With help of lx (survivorship column from life table) and age specific mx values, a fecundity table can be constructed and net reproductive rate, R_0 can be derived by their multiplication.

Net Reproductive rate R_0 = lx mx. This will indicate the number of females left during lite time by a new born female.

UNIT 2 □ Population Growth

Structure

2.1 Growth of organisms with non overlapping generations
2.2 Exponential growth, Verhulst-Pearl logistic growth model
2.3 Stochastic and time log models of population growth
2.4 Stable age distribution
2.5 Population growth projection using Leslie Matrix

2.1 □ Growth of organisms with non overlapping generations

The population is defined as a collective group of organisms of the same species (or other groups within which individual may exchange genetic information) occupying a particular space.

Some of the properties of population are density, natality, mortality, age distribution, biotic potential.dispersion and growth form. The study of changes in the relative number of organisms in population and the factors explaining these changes is termed **population dynamics.**

2.1.1 Growth rate and growth rate curve

Growth rate of population is the number of individuals added to the population per unit time and is obtained by dividing the population increase by the time elapsed. The change is abbreviated by writing the symbol Δ (delta) in front of the letter representing the entity changing. Thus if N represents the number of organisms and t represents the time, the standard formula for assessing the population change is

$\Delta N / \Delta t$ Where N= population size and t = time.

For instantaneous rates, the notion is dN / dt

ΔN = the change in the number of organisms.

$\Delta N / \Delta t$ = the average rate of change in the number of organisms per unit time. This is the growth rate.

$\Delta N / N \Delta t$ = the average rate of change in the number of organisms per unit time per organism. This is often called the **specific growth rate** and is useful when population of different sizes are to be compared.

dN / dt = the rate of change in the number of organisms per unit time at a particular instant.

dN / N dt = the rate of change in the number of organisms per unit timeper individual at a particular instant.

(The letter 'd' (for derivative) replaced Δ when instantaneous rates are being considered)

In forms of growth curve, the slope (straight line tangent) at any point is the growth rate.

2.1.2 Growth rate curve and Concept of Carrying Capacity

Population show characteristic patterns of increase, termed population growth form. In absolute numbers, the initial growth period is slow but is followed by a period of rapid increase and then by a slowing down at a upper levet. These shifts in rate can be more readily seen by constructing a growth rate curve. The two major components of growth curve - the period of increase and the period of equilibrium. There is a period of increase in initial phase followed by slow acceleration (lag phase) and then again a period of rapid growth (positive growth phase). The rapid growth portion of the positive ; growth phase is often referred to as the logarithmic growth phase because a straight line would be produced if the data were plotted logarithmically. After this phase, the rate decelerates rapidly at first then more gradually and rather uniformly to nearly zero. There is no change in the population at zero point, it is at the stationary or equilibrium phase. That is, it had reached the maximum numbers that the environment can support, a limit sometimes referred to as the carrying capacity of the environment.

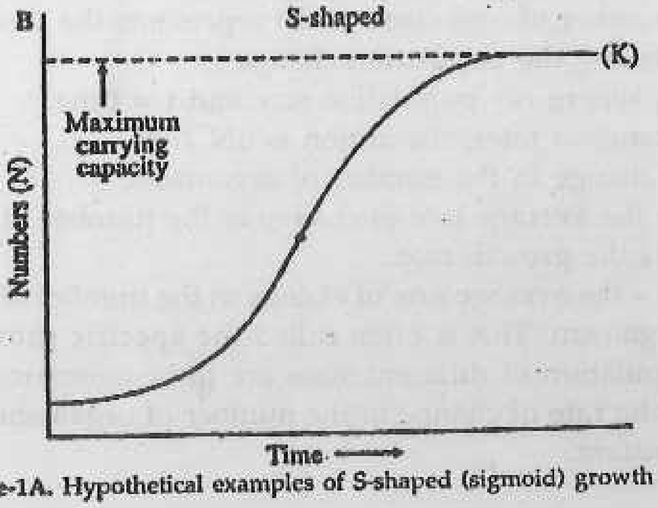


Figure-1A. Hypothetical examples of S-shaped (sigmoid) growth curve.

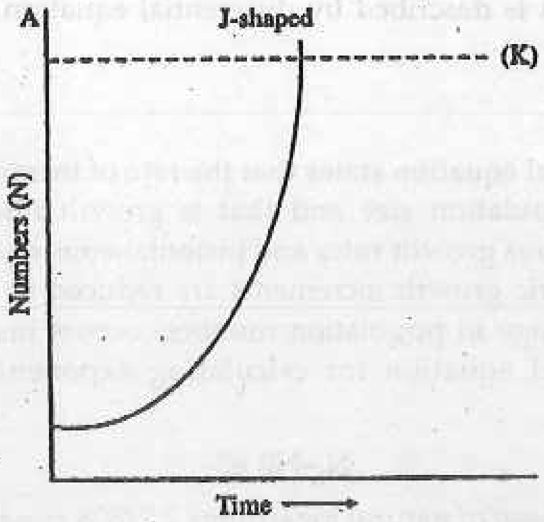


Figure-1B. Hypothetical examples of J-shaped (sigmoid) growth curve

Sigmoid or S -shaped growth form (Fig-1.A.) Population increases slowly at first (positive acceleration phase), then more rapidly(approaching a logarithmic phase) but it soon slows down gradually as the environmental resistance increases in percentage (negative acceleration phase) until equilibrium is reached and maintained.

J-shaped growth form (Fig-1.B.)-density increased rapidly in exponential fashion and then stops abruptly as environmental resistance becomes effective.

2.2 ❐ Exponential growth, Verhulst-Pear l logistic growth model

2.2.1 Exponential Growth : Continuous growth through time

If a population were suddenly presented with an unlimited environment as can happen when a small.number of bacteria, non native plants, or animals are introduced into a suitable but unoccupied habitat, it would tend to expand geometrically. Assuming there were no movement in or out of the population and no mortality, then birth rate alone would account for changes in population numbers. Under this condition, population growth would simulate compound interest a continual increase called **exponential growth.**But growth of populations is tempered by death, so a death rate, must be factored in with the birthrate.

Exponential growth is described by differential equation

$dN/dt = (b - d)N$

or $dN/dt = rN$

This differential equation states that the rate of increase *dN/dt* is directly proportional to population size and that is growth rate *r* (the difference between instantaneous growth rates and instantaneous death rates). The time intervals of geometric growth increments are reduced to zero (Figure-1. C), so theoretically change in population numbers occurs instantaneously.

A more useful equation for calculating exponential growth is the integrated form

$$N_t\text{-}N0\ e^{rt}$$

where *e* is the base of natural logarithms 2.71828 rise the rate of increase, and *t* is the unit of time. This exponential equation is equivalent to the equation for geometric growth.

$$N_t = N_0\ A^t$$

In this equation A (lamda) takes the place of *er*. Provided that the geometric growth rate and the exponential growth rate are equivalents, the two equations will produce the same growth curves, except that the geometric curve will have discrete points. If the populations are increasing, *r* will be greater than 0, and A (lamda) will be greater than 1. If the population remain the same, *r* = 0 and A = 1. If the population has negative growth rate, *r* will have negative exponential growth rate, and A will be between 0 and 1.

The rate of growth at first is influenced by heredity or life history features, such as the age at beginning of reproduction, the number of litters produced during the lifetime of each female, the number of young produced, survival of young, and length of the reproductive period. Regardless of the initial age of the colonizers, the number of animals in the prereproductive age class would increase because of births, whereas those in the older age categories for a time would remain the same. As the young mature, more would enter the reproductive stage and more young would be produced. A J-shaped growth curve is characteristic of many organisms introduced into a new and unfilled environment.

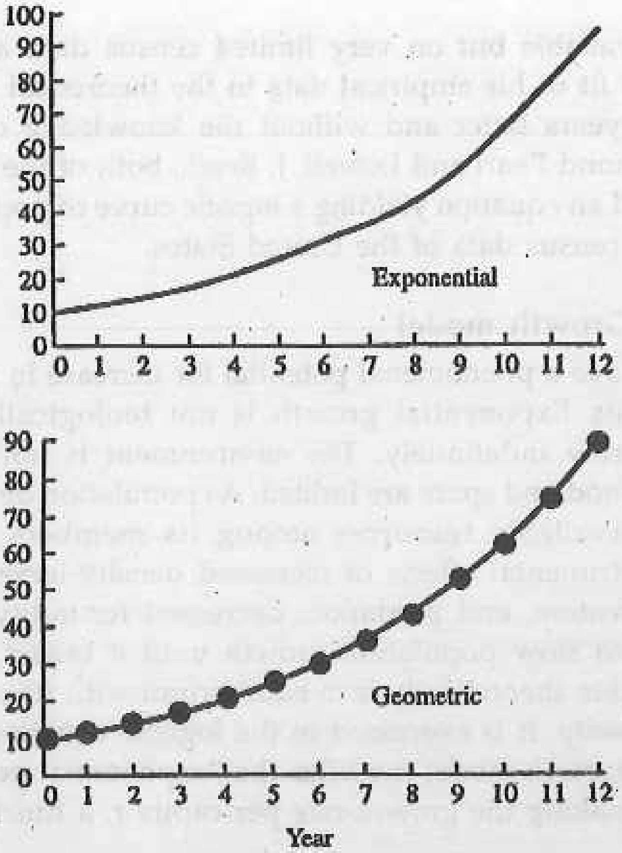


Figure-1C. Geometric growth curve plotted for A=1.20 and exponential growth curve plotted for r=0.186. The curves are similar except that the geometric curve has discrete points

2.2.2 Verhulst- Pearl logistic growth model

A population that is increasing at its intrinsic rate will undergo a geometric increase in population number and will follow the characteristic geometric curve. The geometric increase occurs because more individuals are added to the population, more are increasing at that rate. At each time interval, the number of individuals added to the population will be greater than in the previous time interval.

In 1838, French Mathematician P. E. Verulst advanced an equation that takes into account the fact that the instantaneous rate of growth in a limited environment is retarded by an increase in the number of inhabitants. A plot of Verhulst equation yields a sigmoidal curve which in mathematical version is termed as 'Logistic Curve'. Verhulst then applied his mathematical formulation to available but on very limited census data and observed a respectively good fit of his empirical data to the theoretical curve.

In 1918, 80 years latter and without the knowledge of the Verhulst formulation Raymond Pearl and Lowell. J. Reed., both of the Jhons Hopkins University derived an equation yielding a logistic curve of population growth and applied it to census data of the United States.

2.2.2.1 Logistic Growth model

Organisms have a phenomenal potential for increase in numbers when there are no limits Exponential growth is not biologically realistic; no population can grow indefinitely. The environment is not constant, and resources such as food and space are limited. As population density increases, competition for available resources among its members also increase. Eventually the detrimental effects of increased density-increased mortality from disease, starvation, and predation, decreased fecundity, or both, and emigration-begin to slow population growth until it ceases. This level, at which the population theoretically is in equilibrium with its environment, is called *carrying capacity.* It is expressed in the logistic equation as *K.*

The logistic growth model modifies the "exponential growth equation $dN/dt = r_m N$ by making the growth rate per capita r, a function *of* density, fN. Thus :

$dN/dt = rN$..Eqn-1

and

$r=f/(N)$..Eqn-2

To determine the form of this function, it is assumed that there are sufficient resources *to* sustain a stable population density of K individuals, called the **carrying capacity (Figure-l.D)** *of* the population. The maximum growth rate per capita is equal to r_m, which is the growth rate when there are no effects *of* density (i.e. growth is exponential). When all individuals are identical, each individual uses 1/K of the resources and reduces the maximum growth rate, r_m, by 1/K. Thus, N individuals reduce r_m by *N/K.* This relationship is expressed in the following way :

$r = r_m(l-N/K)$..Eqn-3

This equation shows that the growth rate per capita, r is dependent on the population density (N). In populations where there is a large carrying capacity (K) and N is small, r approximates rm. its value when there are no density-dependent effects. As the population density (N) increases *to* the carrying capacity (K), the value of r steadily decreases until at the carrying capacity it equals zero and the population stops growing. If N exceeds K, then r becomes negative and the population will decline.

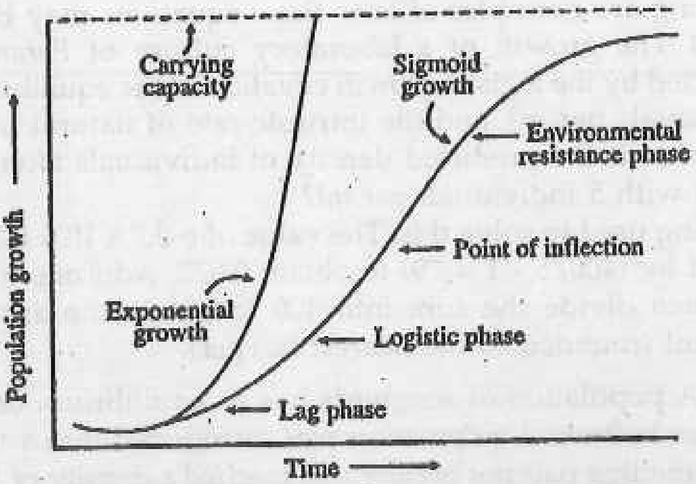


Figure-1D. Graph depicting the various phases of the modified sigmoid growth curve

By substituting Eqn-3, the logistic growth equation is obtained which was first derived by the French mathematician Verhulst (1838), and independently derived by the American demographers Pearl and Reed (1920):

$dN/dt = r_m N - r_m N^2/K$.......................... Eqn-4

Equation 2 is frequently presented in two other equivalent forms :

$dN/dt = r_m N (1-N/K)$ or $dN/dt = r_m N (K-N/K)$.........................Eqn-5

One interpretation of Eqn 4 is that the rate *of* increase *of* the population *(dN/dt)* is equal *to* the biotic potential, i.e. the potential for exponential growth ($r_m N$), minus the resistance to growth that is created by the population itself, i.e. density-dependent effects ($r_m N^2 / K$). This latter term can be considered *to* be a measure *of* intraspecific competition and is one component *of* what Darwin termed the 'struggle for existence.

To express population density as a function of time. Eqn-4 is integrated following the rules of integral calculus to give the following complex equation:

$Nt = K / 1+(K/N_0 - 1)_e \, r_m \, t$...........................,..............Eqn-6

This equation shows that the population density at time $t(N_t)$ is related to the starting population size (N_0), the carrying capacity (K) and the intrinsic rate of natural increase (r_m) in a complex way. However, one intends *to* calculate rm from a logistic growth curve, with knowledge of the population densities at three points (N_o. N_t and *K*). it is easier to do this if Eqn-6 is rearranged to:

$-r_m\ t\ \mathrm{In}\ \{ K- N_t\ /\ (N_tK- Nt\ N_0)\ N_0\}$..Eqn-7

The following are examples of how these equations may be applied.

Example: 1 The growth of a laboratory culture of *Paramecium* was accurately predicted by the logistic growth equation. If the equilibrium density (K) is 400 individuals per ml. and the intrinsic rate of natural increase (r_m) is 0.7 per day. what is the predicted density of individuals after 10 days in a culture started with 5 individuals *per ml?*

Eqn-6 is being used to solve this. The value of e-0.7 x 10 = 0.000912. and this is multiplied by (400/5 - 1 = 79) to obtain 0.072. Add one to this value (= 1.072). and then divide the sum into 400 to obtain the answer of 373 individuals per ml (rounded to the nearest integer).

Example:2 A population of songbirds has an equilibrium density of 31 breeding pairs per hectare. A population was introduced into a new area at a density of one breeding pair per hectare and reached a density of 12 breeding pairs per hectare after 10 years. What is the intrinsic rate of natural increase (r_m) assuming that the population is growing logistically?

Eqn 7 is being used to solve this. Here set $t = 10$. $K = 31$. $Nt = 12$ and $No = 1$. The answer is 0.294 per year.

Example:3 What is the realized rate of increase per capita when there are 12 breeding pairs per hectare in the population in example 2.Eqn-3 is being used to calculate this. Where $r_m = 0.294$ per year, $N = 12$ and $K = 31$. The answer is approximately 0.180 per year. Note that *r* does not appear in Eqns 4 to 7. This is because these equations automatically calculate r from the r_m , N and *K* values.

2.2.2.1 Discrete Generation

Consider each female of a species with a single annual breeding and a life span of 1 year. Let produce R_0 female offspring, on the average which survive to breed in the following year, then

$N_t+_1 =R_0 N_t$

Where

N_t = Population size of females at generation t

N_t+_1= Population size of females at generation t + 1

R_0 = net reproductive rate of number of female offsprings produced per female per generation.

Overlapping Generation :

In populations that have overlapping generations and prolonged or continuous breeding season, population growth can be described more easily by the use of differential equations. Assume for the moment that the growth of the population at time *t* depends only on conditions at that time and not on past events of any kind.

1. Multiplication rate constant : Assume that, in any short time interval *dt*, an individual has the probability *b dt* of giving rise to another individual. In the same time interval, it has the probability *d dt* of dying. If band *d* are instantaneous rates of birth and death, the instantaneous rate of population growth per capita will be

Instantaneous rate of population growth = $r = b - d$

and the form of the population increase is given by

$dN/dt = rN = (b - d)N$

Where

N = population size

t - time

r = per-capita rate of population growth

b - instantaneous birth rate

d - instantaneous death rate

This is the curve of geometric increase in an unlimited environment.

Note, that we can. use the geometric growth, model to estimate the doubling time for a population growing at a certain rate.

$Nt / N0 = e^{rt}$

But if the population doubles, Nt/No = 2. Thus

$2.0 = e^{rt}$

or

$\log_e(2.0) = rt$

$0.69315/r = t$

Where

t = time for population to double its size,

r = rate of population growth per capita

A few values for this relationship are given for illustration

r	*t*
0.01	69.3
0.02	34.7
0.03	23.1
0.04	17.3
0.05	13.9
0.06	11.6

Thus if a human population is increasing at an instantaneous rate of 0.03 per ye, (finite rate = 1.0305), its doubling time would be about 23 years, if geometric increase prevails.

2. Multiplication rate dependent on population size : But populations do not show continuous geometric increase. When a population is growing in a limited space, the density gradually rises until eventually the presence of other organisms reduces the fertility and longevity of the population. This reduces the rate of increase of the population until eventually the population ceases to grow. The growth curve defined by such a population is *sigmoid*, or S-shaped (**Figure-2**). The S-shaped curve differs from the geometric curve in two ways : It has an upper asymptote (that is the curve does not exceed a certain maximal level), and it approaches this asymptote smoothly, not abruptly.

The simplest way to produce an S-shaped curve is to introduce into geometric equation a term that will reduce the rate of increase as the population builds up. It is required to reduce the rate of increase in a smooth manner. It can be done by making each individual added to the population reduce the rate of increase an equal amount. This produces the equation-

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

where,

N = population size
t = time
r = rate of population growth per capita
K = upper asymptote or maximal value of N

This equation states that

$$\left(\begin{array}{c}\text{Rate of}\\ \text{increase of}\\ \text{population}\\ \text{per unit time}\end{array}\right) = \left(\begin{array}{c}\text{Rate of}\\ \text{population}\\ \text{growth}\\ \text{per capita}\end{array}\right) \times \left(\begin{array}{c}\text{population}\\ \text{size}\end{array}\right) \times \left(\begin{array}{c}\text{unutilized}\\ \text{opportunity}\\ \text{for population}\\ \text{growth}\end{array}\right)$$

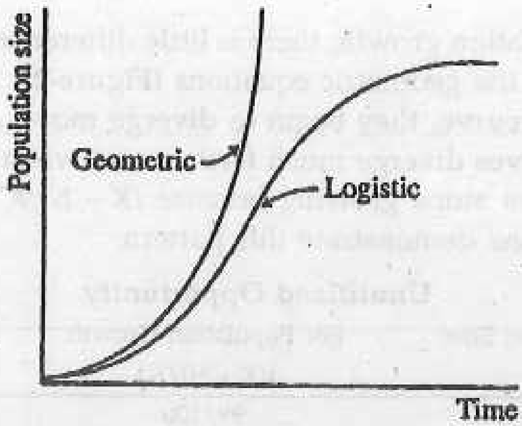


Figure-2. Population growth in an unlimited environment and logistic (sigmoid) grwoth in a limited environment

and is the differential form of the equation for the *logistic curve*. This curve was first suggested to describe the growth of human populations by Verhulst in 1838. The equation was independently derived by Pearl and Reed (1920) as a description of the growth of the population of the United States.

Note that r is the rate of population growth per individual in the population the integral form of the logistic equation can be written as follows:

$Nt.= K/1+e^{a+rt}$

Where

Nt = population size at time t

t = time

K = maximal value of N

e = 2.71828 (base of natural logarithms)

a = a constant of integration defining the position of the curve relative to the origin

r = rate of population growth per capita

Let us look for a minute at the factor $(K - N)/K$, which has been called the unutilized opportunity for population growth. To demonstrate that this factor put the brakes on the basic geometric growth pattern, we consider a situation this:

$K = 100$

$r = 1.0$

N_0 = 1.O (starting density)

Very early in population growth, there is little difference between the curves for the logistic and the geometric equations (**Figure-2**). As we approach the middle pent of the curve, they begin to diverge more. As we approach the upper limit, the curves diverge much farther, and when we reach the upper limit, the population stops growing because $(K - N)/K$ becomes zero. The following calculations demonstrate this pattern:

r	Population Size (N)	Unutilized Opportunity For Population Growth [(K - N)/K]	Rate of Population Growth.(dNZdt)
1.0	1	99/100	0.99z+
1.0	50	50/100	25.00
1.0	75	25/100	18.75
1.0	95	5/100	4.75
1.0	99	1/100	0.99
1.0	100	0/100	0.00

Note that the addition of one animal has the same effect on the rate of population growth at the law and at the high ends of the curve (in this example, 1/100).

The logistic equation can be written in yet another way by rearranging terms:

$\log_e (K-N/N) = a-rt$

This is the equation of a straight line in which the *y* coordinate is loge [(K - N)/ N] the *x* coordinate is time, and the slope af the line is *r*. This relationship can be useto fit a logistic equation to actual biological data (Pearl 1930).

Non Overlapping Generation :

1. Multiplication rate constant Let Ro be a constant. If Ro > 1, the population increases geometrically without limit, and if Ro < 1, the population decreases to extinction. For example, let Ro = 1.5 and $Nt = 10$ when $t - 0$:

Generation	Population Size (N_t)
0	10
1	15 = (1.5)(10)
2	22.5 (1.5)(15)
3	33.75 (1.5)(22.5)

2. Multiplication rate dependent on population size. Populations do not normally grow with a constant multiplication rate as in **Figure-1. A.** Populations that fluctuate little, others that fluctuate in a chaotic manner, and still others that fluctuate in cycles. How can we explain this variety of dynamical behavior? To explain variety of dynamical behaviour like

The simplest way is to assume that the multiplication rate changes as population density rises and falls. At high densities, birth rates will decrease or death rates will increase from a variety of causes, such as food shortage or epidemic disease. At low densities birth rates will be high and losses from diseases and natural enemies low.

On the other way in which the multiplication rate slows down as density increases. The simplest mathematical model is linear: If there is a straight line relationship between the density and multiplication rate, it will be found that the higher the density, the lower will be the multiplication rate **(Figure -1.B).** The point where the line crosses $Ro = 1.0$ is a point of equilibrium in population density where the birth rate equals the death rate. It is convenient to measure population density in terms of deviations from this equilibrium density:

$Z = N - Neq$

where

Z = deviation from equilibrium density

N = observed population size

Neq = equilibrium population size (where $Ro = 1.0$)

The equation of the straight line shown in Figure -B is thus

$Ro = 1.0 - B\ (N - Neq)$

$= 1.0 - Bz$

where (-) B = slope of line

Ro = net reproductive rate

In Figure B : $B = 0.02$ and $Neq = 100$. Basic equation can now be written)

$N_{t+1} = Ro\ N_t = (1.0 - BZ_t)N_t$

The properties of this equation depend on the equilibrium density and, the slope of the line.

Laboratory test of the logistic theory

Many populations have been followed in the laboratory as they increase in size. Gause (1934) studied the growth of populations of *Paramecium aurelia* and *P. csadatum.* He used 20 *Paramecium* to begin his experiments in a tube with 5 cubic centimeters of a salt solution buffered to pH 8. Each day Gause added a constant quantity of bacteria, which served food. The bacteria could not multiply in the salt solution. The cultures were incubated at 26°C, and every second day they were washed with fresh salt solution to remove any waste products. Therefore, Gause had a constant environment in limited space, the temperature, volume, and chemical composition of the medium were constant, waste products were removed frequently, and food was added in uniform amounts each day. The growth of some of Gause's *Paramecium* populations is shown figure-3, In general, the fit of these data to the logistic curve was quite good. The asymptotic density *(K)* was approximately 448 per 0.5 cubic centimeter for *P. aurelia* and 128 per 0.5 cubic centimeter for P. *caudatum* under these conditions.

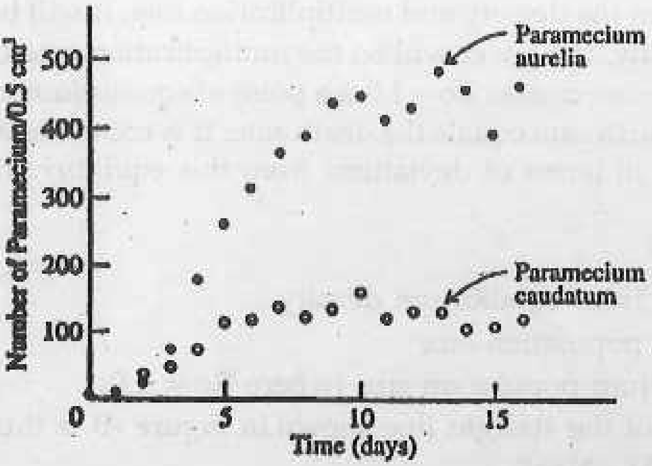


Figure-3. Population growth in protozoans *Paramoecium aurelia* and *P.caudatum* at 260°C in buffered Osterbout's medium, pH 8.0 "One loop" concentration of bacterial food

Field data on population growth

Population growth does not occur continuously in field populations. Many species anal environments show population growth during the favorable season each year. Long-lived organisms may show population growth only rarely, and few populations fill up a vacant habitat in nature the way they do in the laboratory. Same les we have are from situations where animals were introduced anta islands or other new habitats and were then studied as they increased in numbers.

Reindeer have been introduced into many parts.of Alaska since 1891 to replace the dwindling caribou herds in the economy of the Eskimo. In 1911 reindeer were introduced onto two.of the Pribilof Islands in the Bering Sea off Alaska. Four males 1 females were released an St. Paul Island (106 km2) and 3 males and 12 females on St. Gearge Island (90 km^2). The stockings were an immediate success. The subsequent history of these herds is.of interest because the islands were completely undisturbed environments-there was little hunting pressure, and there were no predators. The two herds have had quite different histories an the two islands (Figure-4). The St. Gearge herd reached a law ceiling.of 222 reindeer in 1922 and then subsided to a small herd of 40 to 60 animals. The St. Paul herd grew continuously to about 2000 reindeer in 1938, overgrazed the habitat, and then abruptly declined to only 8 animals in 1950. The ecological differences between the two islands appear to have been very slight (they had the same type *of* vegetation (and the same climate), and no one understands why the two populations behave so differently (Scheffer 1951). It is possible that illegal hunting on St. George Islands was the cause *of* the differences shown in Figure-4.

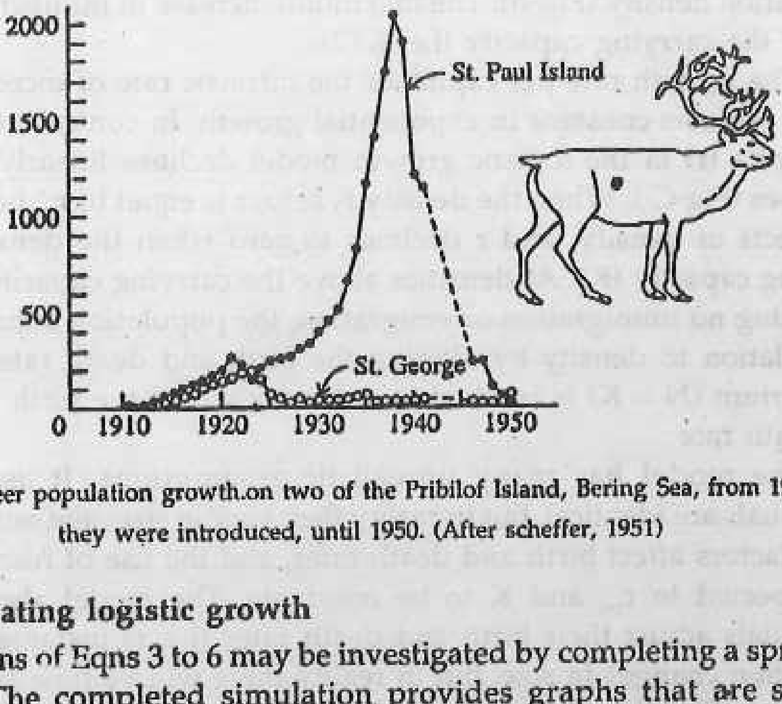


Figure-4 Reindeer population growth.on two of the Pribilof Island, Bering Sea, from 1911, when they were introduced, until 1950. (After scheffer, 1951)

2.2.2.2 Simulating logistic growth

The predictions of Eqns 3 to 6 may be investigated by completing a spreadsheet simulation. The completed simulation provides graphs that are similar to Figs- A to C.

The logistic model of population growth predicts that population sustam a stable carrying capacity (K). The form of growth is S-shaped for populations starting at a density below that of the carrying capacity (Fig. -A) and so it is sometimes called sigmoid growth. The precise shape of the curve depends on the starting density (N_0 and the final density or carrying capacity (K). The steepness of the curve is directly proportional to the value of the intrinsic rate of increase (r_m). Population densities never overshoot the carrying capacity and so the growth curves have a smooth shape. This indicates a perfect adjustment of the per capita (i.e. per individual) growth rate *r* as the density changes.

Simulations show that populations starting at densities above the carrying capacity approach the carrying capacity more rapidly than populations starting at densities below the carrying capacity. This is because the inhibition to population growth (term $r_m N^2 / K$ in Eqn-4) is related to the square of the population density.

An examination of the S-shaped growth curve suggests that the population grows at its fastest rate at intermediate densities. This observation is confirmed when the population growth rate is plotted as a function of population density (Fig-B). The maximum increase in numbers always occurs at half the carrying capacity (i.e. K/2).

The growth rate per capita, or the intrinsic rate of increase (r_m) as it is called, remains constant in exponential growth. In contrast, the growth rate per capita (r) in the logistic growth model declines linearly as the density increases (Fig-C). When the density is zero, r is equal to r_m because there are no effects of density, and r declines to zero when the density reaches the carrying capacity (K). At densities above the carrying capacity, r is negative. Assuming no immigration or emigration, the population adjusts the value of r in relation to density by altering the birth and death rates, and a stable equilibrium (N = K) is reached at a density where the birth rate is equal to the death rate.

The model has many unrealistic assumptions. It assumes that all individuals are identical, but in reality they vary in size, age, sex and genotype. These factors affect birth and death rates, and the use of resources, and it is not expected to r_m and K to be constants. The model also assumes that individuals adjust their birth and death rates (i.e. r) instantaneously as the population changes in size, but in reality there will be time lags to any such response. Finally, it assumes that the environment is constant, but environments change over the course of time and this is another reason why it is not expected r_m and *K* to be constants.

2.3 ▫ Stochastic and time lag models of population growth

2.3.1 Stochastic models of Population Growth

The models discussed so far are deterministic models, which means that given certain initial conditions, the model predicts one exact outcome. But biological systems are probabilistic, not deterministic. Thus the probability is being considered as that female will have a litter in the next unit of time, or the probability that there will be a cone crop' in a given year, *of* the probability that a predator will kill a certain number of animals within the next month. Population trends are therefore the joint outcome of many individual probabilities like this, which has led to the development of probabilistic, or **stochastic models.**

Stochastic models of population growth incorporate the chance effects of genetic viability and extrinsic factors like climate on population dynamics. These are based largely on probability theory. Rather than exactly two offspring, one might assume that each female has a 0.5 probability of giving birth to two offspring, a 0.25 chance of producing three progeny, and a 0.25 chance of producing one.

In a stochastic model, a coin can be flipped to mimic the probability of the outcome. Suppose a head and a tail (in either order) indicates two offspring, two tails imply one offspring, and two heads mean three offspring. Here are the results I got one night:

Outcome of Trial

Mother	1	2	3	4
	(number of offspring)			
1	2	3	3	2
2	3	1	1	1
3	3	1	2	2
4	1	1	3	3
5	3	1	1	1
Total population in next generation if parents die after reproduction	12	7	10	9

Some of the outcomes are above the expected value of 10, and some are below. If the tosses are continued for, say, 50 trials, a frequency histogram can be constructed (**Figure-5**). This histogram gives the likelihood (proportion.) of the observations yielding a certain final population size. The most likely outcome is a final size of 10, just as in the deterministic model. For the geometric deterministic model

if Ro = 2 and. N = 5,

then $N_{t+1} = R_0N_t$

$= 2X5 = 10$

However, with the stochastic model, other outcome possible; for example, all five mothers could have three offspring, for a total population of 15. This is the maximum possible number of offspring, and the likelihood of it happening is small-hence the low proportion of observations- Stochastic models can also be developed for continuous growth. Again, such a model is best explained by referring to the corresponding continuous equation, viz,

$$dN / dt = rN = (B-d)N$$

It can be concluded that, the larger the initial population and the greater the value of *b - d*, the more resistant to extinction the population becomes. In reality, *b - d* is often zero, so *d / b* = 1.0 as time reaches millions of years and, in the limit, approaches infinity. In other words, the probability of extinction is unity, meaning that extinction is a certainty for a population that exists over a long enough time span and is likely to occur more quickly for a small population. Fischer, Simon, and Vincent (1969) maintained that probably 25 percent of the species of birds and mammals that have become extinct since 1600 may have died off "naturally," possibly because of stochastic variation due to a small population, and not because something killed the last remaining individuals. They also suggest that about 30% of birds and 15% of mammals currently are endangered because of such natural causes. These kinds of stochastic effects are particularly important when the conservation of small populations of rare species is at issue. For example, Schaffer and Samson (1985) have predicted that if the effective population size, or the number of individuals that mate within a population, is 50 for grizzly bears, demographic stochasticity alone would can use extinction once every 114 years, on average. A population model of the spotted owl *(Strix occidelltails)* suggests, that demographic stochasticity is likely to extinguish local populations over the short term of decades (Simberloff, 1986b).

Stochastic models introduce biological;Variation into calculations of population growth and are much more likely to represent what is happening in the field. The price paid is complicated mathematics. 5tojChabtic models become more salient as populations get smaHer and so are important in examining conservation. For a population that is in the millions, as arc many pest populations, deterministic models will do.

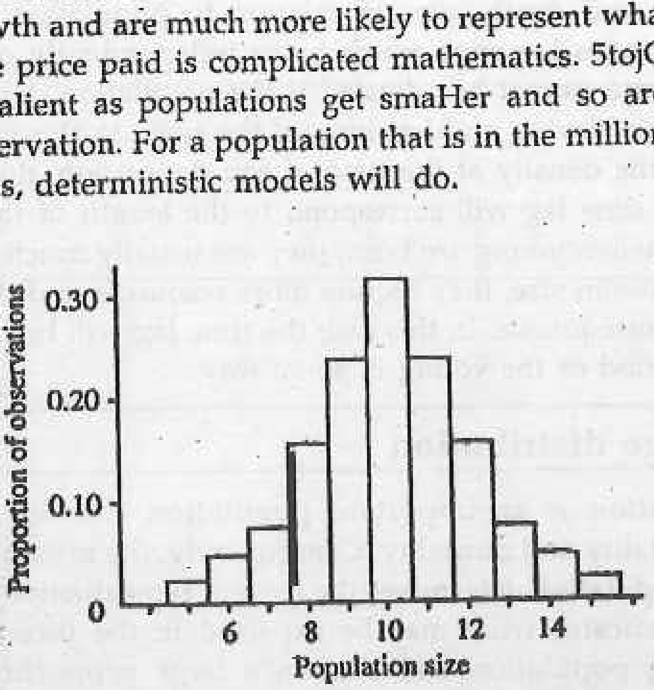


Figure-5. Stochastic frequency distribution of a female population after one generation beginning with five females.In this case the probability of having three female offsprings is 0.25 and probability of having one female offspring is 0.25

2.3.2 Time lags

There are various models to simulate time lags in logistic growth, but one of which is mentioned bellow. The discrete version of the logistic model describes population growth by the following equation:

$N_{t+1} = N_t + r_m N_t \, (1 - Nt/K)$..Eqn-8

If N is subtracted from both sides of Eqn-8 it can be seen that this equation is analogous to the logistic equation of 5, except that there is a built-in time lag of one time step because the population size at time t + 1 depends on the population size at time t. As the time lag is a constant, the response of the model depends solely on the intrinsicrate of increase (r_m).

The logistic growth equation assumes that there is an instantaneous and continuous adjustment of the growth rate as the population changes in density, hence the smooth form to logistic growth curves (Fig-1.A & Fig-1.B.). It seems likely, however, that most populations have time lags in the way that they adjust their birth and death rates in relation to population density. For example, many species lay eggs which hatch independently of the parent, and so the birth rate cannot be adjusted if the population density changes between the times of laying and hatching of the eggs. In this case, the birth rate is related to the density at the time of egg deposition, not the time of hatching, and the time lag will correspond to the length of the incubation period. Similarly, when young are born, they are usually much smaller than adults. As they grow in size, they require more resources and the death rate may adjust as a consequence. In this case the time lag will be related to the developmental period of the young in some way.

2.4 ☐ Stable age distribution

Age distribution is an important population characteristic which influences both natality and mortality. Consequently, the ratio of the various age groups in a population determines the current reproductive status of the population and indicates what may be expected in the future. Usually a rapidly expanding population will contain a large proportion of young individuals, a stationary population a more even distribution of age classes, and a declining population a large proportion of old individuals. However, a population may pass through changes in age structure without changing in size. There is evidence that populations have a "normal" or stable age distribution toward which actual age distributions are tending. Once a stable age distribution is achieved, unusual increases in natality or mortality result in. temporary changes, with spontaneous return to the stable situation

In so far as the population is concerned,.there are three ecological ages, which have been listed by Bodenheimer (1938) as **prereproductive, reproductive, and postrepro-ductive.** The relative duration of these ages in proportion to the life span varies greatly with different organism. Many plants and animals have a very long prereproductive period. Some animals, notably insects, have extremely long prerproductive periods, a very short reproductive period, and no postreproductive period.

Lotka (1925) has shown on theoretical grounds that 'a population tends to develop a stable age distribution, that is, a more, or less constant proportion of individuals of different ages, and that if this stable situation is disrupted by temporary changes in the environment or by temporary influx from or egress to another population, the age distribution will tend to return to the previous situation upon restoration of normal conditions. More permanent changes, of course, would result in development of a new stable distribution.

Representation of population age distribution :

A convenient way to picture age distribution in a population is to arrange the data in the form of a polygon or age pyramid (not to be confused with the ecological pyramids, the number of individuals or the percentage in the different age classes being shown by the relative widths of successive horizontal bars. The upper pyramids in **Figure-6** illustrate three hypothetical.cases: (left) a pyramid with broad base, indicating a high percentage of young individuals; (middle) a bell shaped polygon, indicating a moderate proportion of young to old; and (right) an urn-shaped figure; indicating a low percentage of young individuals. The latter would generally be characteristic of a declining population. The vole pyramids in **Figure-6** show stable age distributions under conditions of maximum rate of population increase (left) and with no growth (right), i.e., natality equaling mortality. The rapidly growing population has the much greater proportion of young individuals.

In general a high ratio of juveniles to adults, as shown in the bottom diagrams in Figure 7-6, indicates a highly successful breeding season and likelihood of a larger population the next year, provided juvenile mortality is not excessive. In the muskrat example (lower right, **Figure-6**) the highest percentage of juveniles (85 per cent) occurred in a population which had been heavily trapped for the previous few years; reduction in total population in this manner had apparently resulted in increase natality for those individuals surviving.

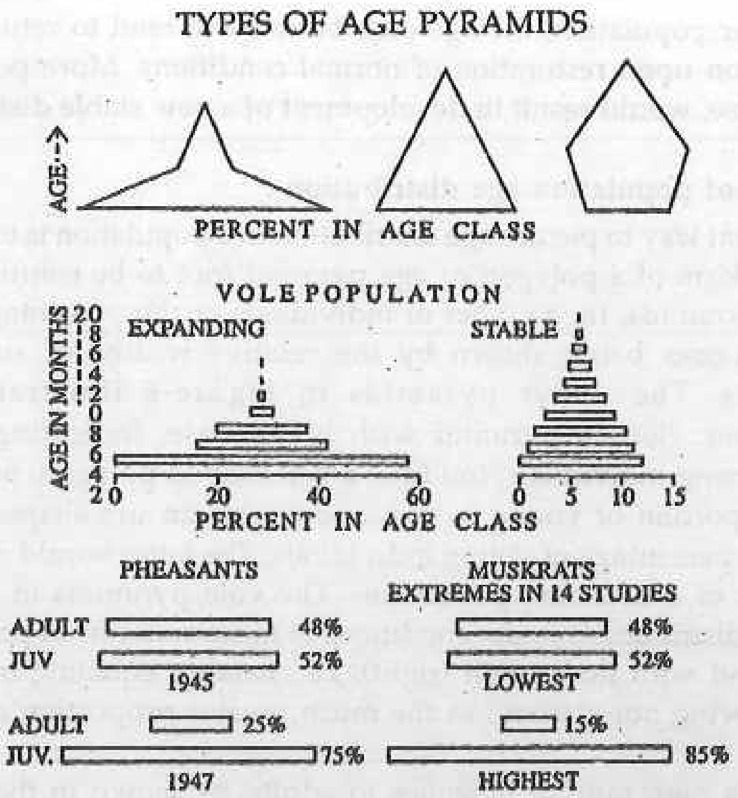


Figure-6. Age pyramids : Upper : Three types of age pyramids representing a large, moderate, and small percentage of young individuals in the population. Middle: Age pyramids for laboratory populations of the vole, *Microtus agrestis* (left), when expanding at an exponential rate in an unlimited environment, and (right) when birth rates and death rates are equal (data from Leslie and Ransom, 1940). Lower: Extremes in juvenile-adult ratios in pheasants in North Dakota (data from Kimball, 1948) and in muskrats in eastern United States (data from Petrides, 1950).

2.5. ❐ Population growth projection using Leslie Matri

One realistic way of estimating population growth was pioneered by Leslie (1945),, who calculated population changes from age-specific birth and survival rates. Such an age-classified model is called a *Leslie matrix*. The essential feature of these models is that the life cycle of the plant or animal is broken down into a series of stages (Figure -7). Each age class is one stage in a simple Leslie matrix. Organisms pass from one, stage to the next with probability *P"*, and they reproduce a number of offspring *Fx*.

In the conventional life table notation :

$$P_x = 1_{x+1}/1_x = (1\text{-}qx) .$$

probability that an individual of age group x will survive to enter age group $x+1$ at the next time interval (of the life table, page 169)

$F_x = b_x s$ = number of female offspring born in one time interval per female alive aged x to $x+1$; these offspring must survive to enter age group 0 at the next time interval.

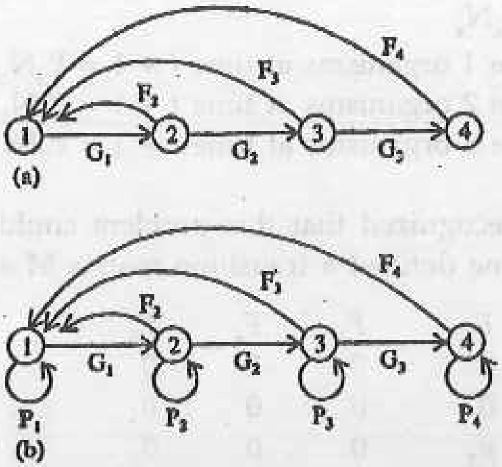


Figure-7. Population projection matrices, (a) The Leslie matrix, or age classified life cycle. Four age classes are shown in this example, with different fecundities (F x) for each age class and different probabilities Ps of surviving from one age to the next, (b) A size- or stage-based life cycle, in which the only added complication is that an individual has a probability Px of remaining in the same life-cycle stage in one time period and a probability G_x of surviving and moving on into the next stage of the life cycle. (After Caswell 1989)

Where,

l_x = number of individuals alive at start of age interval x

b_x = nWllber of births in one time interval per adult female aged x to $x + 1$

s, = proportion of the b_x offspring that are still alive at the start of the next time interval

Begin with a population having specified age structure at time t:

No = number of organisms between ages 0 and 1

N_t = number of organisms between ages 1 and 2

(and so on to the oldest age class)

N_k = number of organisms between ages k and k+ 1 (oldest organisms)

Time units for age are often one year but can be any fixed time unit, depending on the organism. Usually only the female population is considered.

If we assume no emigration and no immigration, the population's age structure at the next time interval is defined as follows:

new age structure

↓

Number of new organisms at

time $t + 1 = F_oN_o + F_1N_1 + F_2N_2 + F_3N_3 + ... + F_kN_k$

$= F_xN_x$

Number of age 1 organisms at time $t + 1 = P_oN_o$

Number of age 2 organisms at time $t + 1 = P_1N_1$,

Number of age 3 organisms at time $t + 1 = P_2N_2$

and so on.

Leslie (1945) recognized that this problem could he cast as a simple matrix problem if one defined a transition matrix M as, follows:

$$M= \begin{bmatrix} F_0 & F_1 & F_2 & F_3 & F_4 & F_5 & . & F_{k-1} & F_k \\ P_0 & 0 & 0 & 0 & 0 & 0 & . & 0 & 0 \\ 0 & P_1 & 0 & 0 & 0 & 0 & .. & 0 & 0 \\ 0 & 0 & p_2 & 0 & 0 & 0 & .. & 0 & 0 \\ 0 & 0 & 0 & p_3 & 0 & 0 & .. & 0 & 0 \\ 0 & 0 & 0 & 0 & p_4 & 0 & .. & 0 & 0 \\ . & . & . & . & . & . & .. & . & . \\ . & . & . & . & . & . & .. & . & . \\ 0 & 0 & 0 & 0 & 0 & 0 & .. & p_{k-1} & 0 \end{bmatrix}$$

Where, $Fx=0$ and Px ranges from 0 to 1. By casting the present age structure as a column vector, we get–

$$\vec{N_t} = \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ N_3 \\ N_4 \\ . \\ .. \\ N_k \end{bmatrix}$$

Leslie showed that the age distribution at any future time could be found by premultiplying the column vector of [illegible] structure by the transition matrix M:

$$MN_t = N_{1+1}$$
$$MNt+1 = Nt+2$$

Lefkovitch (1965) realized that the Leslie matrix was a special case of a more genera stage-based matrix, in which life history stages replace ages. Such a stage based or size-based model is illustrated in Figure-7. One new complexity is added to the age-based model: whereas all individuals of age x increase to age $x + 1$ after 1 unit of time, inl a stage- or size-based model some individuals will remain in the same life cycle stage. We thus have *two* probabilities associated with each stage:

Px= probability an individual will survive and remain In stage- or size-class x in the next time unit.

Gx = probability an individual will survive and move up to the next stage- or size-cl8.ss $x + 1$ in the next time unit

Note that we set the time unit in stage-based matrices to make it impossible for the' organism to jump up two or more stages in one time step.

Table-1 Stage-based Life and Fecundity Tables for the Loggerhead Sea Turtle.*

Stage No.	Class	Size (Carapace Length/ (cm)	Ages (yr)x	Approximate Annual Fecundity Survivor	(No.eggs/yr ship)
1	Eggs, hatchlings	<10	<1	0.6747	0
2	Small juveniles	10.1-58.0	1-7	0.7857	0
3	Large juveniles	58.1-80.0	8-15	0.6758	0
4	Subadults	80.1-87.0	16-21	0.7425	0
5	Novice breeders	>87.0	22	0.8091	127
6	First-year remigrants	>87.0	23	0.8091	4
7	Mature breeders	>87.0	24-54	0.J091	80

**These values assume a population declining at 3% per year. (Crouse et al. 1987).*

Crouse and coauthors (1987) analyzed the dynamics of the loggerhead sea turtle *(Carella carella)*, an endangered species of sea turtle from the Atlantic Ocean off the' southeastern United States to highlight on example of a size based matrix model. Sea turtles have a long life span which can be broken down into seven stages based on size. These stages arc listed in **Table -1** along with the size and approximate age of turtles in each of the stages.

Survivorship varies, with size and only individuals over 87 centimeters long are sexually mature.

The population projection matrix based on this life history takes the form:

$$\begin{bmatrix} P_1 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 \\ G_1 & P_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & p_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & G_6 & P_7 \end{bmatrix}$$

The best estimates of the parameters of this matrix are given in Table-2

Table-2 Stage-class Population Matrix for Loggerhead Sea Turtles

0	0	0	0	4	127	80
0.6747	0.7370	0	0	0	0	0
0	0-0486	0.6610	0	0	0	0
0	0	0.0147	0.6907	0	0	0
0	0	0	0.0518	0	0	0
0	0	0	0	0.8091	0	0
0	0	0	0	0	0.8091	0.8089

Source-Data from course et al (1987).

Given ihis model of population growth for the loggerhead sea turtle,one can ask some interesting questions about how to reverse the population decline of this endangered species. By holding all the life history parameters constant, save one, one can investigate quantitatively the impact of conservation effort. Figure-8 shows the results of increasing fecundity 50 percent or improving survival in each stage of the life cycle. Improving fecundity 50 percent still leaves the population declining. Maximum improvement is achieved by improving the survival of juvenile turtles. At the present time most conservation efforts on sea turtles are focused on protecting the eggs on beaches and conservationists have found that even after 20 to 30 years of protecting nests on beaches, no increase in sea turtles has occurred (Crouse et al. 1987). In fact this is exactly what this model would predict (Figure-8). What is needed for conservation is an improvement of juvenile turtle survival at sea. Much Juvenile loss is caused by turtles being caught in shrimp nets and drowning, and shrimp trawls are now being fitted with a device to stop the capture and drowning of sea turtles (Anonymous 1983).

Stage-based or size-based matrix models have been used extensively for plant populations in which size is a more useful measure of an individual than is age 'Caswell 1989). Matrix models also permit plants to grow or to shrink in size, a useful biological assumption. Populations may increase or decrease geometrically or may show oscillations. These models assume a constant schedule of survival and,reproduction and thus can be applied to natural populations only for short time periods for which this assumption is valid.

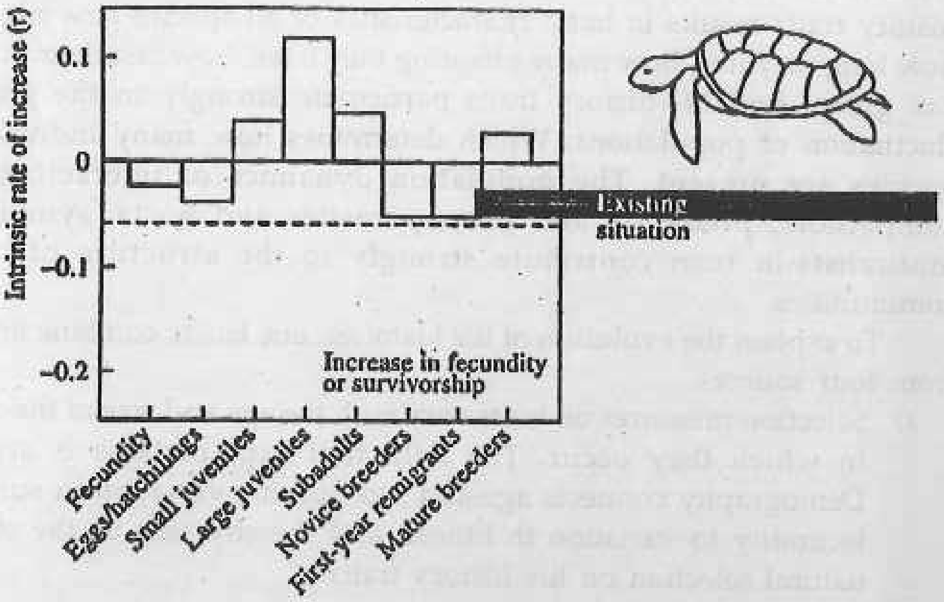


Figure-8. Hypothetical changes in the rate of increase of loggerhead sea turtle populations off the southeastern United States resulting from simulated increases of»50 percent in fecundity or increases in survival to 100 percent for tile stages of the life cycle. The greatest improvement for this endangered turtle would occur by improving the survival of the large juveniles. (From Crovse et al, 1987.)

UNIT 3 ☐ Life history Strategies

Structure

3.1 ☐ Evolution of life history traits

Life-history evolution has important implications for evolution in general. Reproductive success is achieved through life-history traits, mainly survival, age and size at maturity, and fecundity; and variation in reproductive success is necessary for natural selection. Thus understanding variation in life-history traits is one key to understanding natural selection. The evolution of life-history traits results in basic characteristics of all species-how big they are, how long they live, how many offspring they have, how fast their populations can grow. And life-history traits participate strongly in the growth and fluctuation of populations; Which determines how many individuals of a species are present. The population dynamics of interacting species-competitors, predators and prey; parasites and hosts, symbionts and mutualists-in turn contribute strongly to the structure of biological communities.

To explain the evolution of life histories, one has to combine information from four sources.

a) Selection pressures on traits vary with the age and size of the organisms in which they occur. The field that explains this is *demography.* Demography connects age-and size-specific variation in survival and fecundity to variation in fitness, and thereby tells us the strength of natural selection on life-history traits.

b) Life-history traits are influenced by many genes; they are polygenic or quantitative traits. The insights of **quantitative genetics** are important for life-history evolution. Only a certain part of the genetic variation of a trait determines its reaction to selection; this part is the additive genetic variation. The proportion of the total phenotypic variation of a trait that is contributed by additive genetic variation is its heritability.

When heritability = 1.0, the trait has exactly the same value in the offspring as it does in the average of the two parents; when heritability = 0.0, none of the phenotypic variation can be attributed to additive genetic variation, and the trait will not respond to selection. In many species, the heritabilities of life-history traits are in the range 0.05-0.40. Thus most life-history traits that have been investigated could respond to selection.

c) Life-history traits are connected by trade-offs, which exist when a change in one trait that increases fitness is linked to a change in another trait that decreases fitness. The response of life-history traits to a novel selection pressure depends on the strength of the trade-offs present. An improvement in one trait that is linked to high costs in connected traits cannot proceed very far. Important trade-offs include those between the number of offspring and their survival as juveniles, and between reproductive investment and adult survival.

Trade-offs have both a genetic and a physiological component. The genetic component can be expressed as a genetic correlation, which, like heritability, depends on the additive genetic variance of the traits. The physiological component depends on how the organism is constructed and is a mixture of types of connections among traits. Some of those connections are the same for all individuals in a species, have been inherited from ancestors, reflect the phylogenetic history of the species, and differ among taxonomic groups. Other connections among traits vary among the individuals of a species for two reasons: developmental interactions with the environment, which are different for every individual, and variation in the genes that affect the traits involved in the trade-off. Both causes of variation in traits-genetic and physiological-are constrained by fixed effects expressed in development.

d) Traits also need to be understood in phylogenetic context: Phylogenetic effects are the contribution to traits shared by all individuals of a species or clade. They are being thought as 'the development' or 'the physiology' or 'the morphology' of a species or higher taxon. To understand how broadly those traits are shared, and where in the history of the lineage they might have originated, one has to compare them with traits in close and distant relatives. The comparative method can throw light as how much of a pattern to attribute to history and lineage, and how much to attribute to microevolutionary processes

that operated within the local population in the recent past .
The evolution of life history traits involve two parts - an **intrinsic part** (genetics, tradeoffs, phylogenetic effects) and an **extrinsic part** (selection pressures expressed as effects on age- and size-specific mortality and fecundity rates)

3.1.1 Approaches to life history evolution

There are essentially two approaches to the current evolution of life history traits. The first is a **phenotypic approach** , which ignore the possibility that the evolution the optimal phenotype has been presented by genetic constraints such as genetic variation (Maynard Smith, 1978). This approach was first applied to life histories by Lack (1947). The **genetic approach** (de Jong ,1982) considered the effect of selection but this time the way in which the selection will affect gene frequencies. These models are able to make predictions about the directions and speed of genetic change and about equilibrium level of genetic variation, something that phenotypic models are clearly incapable of doing. In other words, phenotypic models can not address questions about gene frequencies. But in attempting to understand why different life histories evolve in different environments, genetic models may add little except intractability to phenotypic models (Charner, 1989a).

3.1.2 Life history traits and survival strategies

Selection pressure resulting from the impact from the physical environments and biotic interactions shape patterns of life history so that each species evolves an adaptive combination of the population traits. Although each species life history is unique, several basic life histories strategies can be recognized and the combination of traits that is characteristic to organisms living in a specified combination can be predicted to some extent.

Stearns (1976) listed four life history traits that are key to survival strategies- 1. brood size (number of seeds, eggs, young or other progeny); 2.size of young (at birth, hatching or germination); 3. age distribution of reproductive effort and 4. interaction of reproductive effort with adult mortality(especially the ratio of juveniles and adult mortality). The following predictive theories have been summarized by Gadgil and Bossert (1970), Stearns (1976), Pianka (2000) and others.

1. Where adult mortality exceeds juvenile mortality, the species should

reproduce only once in life time and conversely where juvenile mortality is higher, the organisms should reproduce several times.

2. Brood size should maximize the number of young surviving to maturity averaged over the life time of the parent. Thus a ground nesting bird may require a clutch size of 20 eggs to ensure a replacement whereas a bird nesting in a cavity or other protected place will have a much smaller clutch size.
3. In expanding population, selection should minimize age at maturity (r-selected organisms will breed at an early stage); in stable populations (at carrying capacity or K-level), maturation should be delayed. This principle seems to hold for human population; in fast growing countries, Child birth being at early age, whereas in stable countries, on average, people postpóne childbearing to a later age.
4. When there is risk of predation, scarcity of resources or both, size at birth should be large; conversely size of young should decrease with increasing availability of resources and decreasing predation or competition pressure.
5. For growing and expanding populations in general not only in the age of maturity minimized and reproduction concentrated early in life but also brood size should be increased and a large portion of energy flow partitioned to reproduction- a combination of traits recognizable as an r -selection strategy. For stable populations, one expects the reverse combination of traits or k- selection strategy.
6. When resources are strongly limiting , breeding begins at an early age.
7. Complex life history enable a species to exploit more than one habitat and niche.

3.2. □ Energy apportionment between somatic growth and reproduction

3.2.1 Energy allocation

Net primary production represents the storage of organic matter in plant tissue in excess of respiration. Plants budget this fixed energy or net income for different uses. A portion is allocated to growth, the buildup of components such as stems and leaves that promote the further acquisition of energy and nutrients (Chapin et al. 1990). A portion goes to storage, for future growth and other functions (Chapin et al. 1990). This storage involves accumulation, reserve formation, and recycling. Accumulation is the increase of compounds that do not directly support growth. These include carbon compounds such as such as starch and fructose, nitrogen as specialized storage proteins, and mineral ions. Reserve formation involves the synthesis of storage compounds from resources that otherwise would be allocated directly to promote growth.

3.2.2 Ecological efficiency of animals

An animal living on only plants is called herbivore and represent second trophic level and that feeds on this animal is at the third trophic level and so on the highest trophic level in the food chain, the top carnivore. An animal can move around and has to select and chase to collect its food, they are much more energy efficient than plant.

The **Lindmann Efficiency** named after the scientist who first developed the calculation, estimates the amount of energy that is passed from one trophic level to the next as a percentage of the total amount available in the lower level.

$$\text{Lindmann Efficiency} = \frac{\text{Respiration + Increase in body weight of higher trophic level}}{\text{Respiration + Increase in body weight of lower trophic level}}$$

Lindmann was the first to try to estimate the ecological efficiency of animals in aquatic systems. His work established a figure of 10% efficiency and this should be regarded as an absolute maximum for endotherms. Endotherms tend to waste energy on heating their bodies and moving around whereas sedentary ectotherms may have high ecological efficiencies.

3.2.3 Law of Thermodynamics

The first law of thermodynamics states that as energy is transferred from one state to another, none is lost; for like matter energy can be neither created nor destroyed but it can be transformed.

The second law of thermodynamics states that as energy is converted from one state to another, the quality of the energy deteriorates as a result of increasing entropy. **Entropy** is the natural progression of energy from a highly ordered form towards a less organized form.

For example the energy added to a food chain in the form of visible light, is energy of very high quality. Light in the visible spectrum has tightly defined predictable wavelengths. The plant after absorving the light for photosynthesis, converts it to store chemical energy, still a high quality energy, but of lower quality than light. If the plant is eaten some of the chemical energy represented by its body is converted into various forms. Some of the energy will never be assimilated by the animal and will be excreted without being digested. Of the food that is digested some will be converted to tissue or fat by the animal but much of it will be used for kinetic energy (movement) or heat. Both the later forms of energy are much lower quality than the chemical energy input. Thus, at every link of food chain, most of the energy is degraded (entropy), leaving less and less high quality energy for each higher trophic level.

The entropy of energy is natural system and it also explains why the largest, most energy-expensive predators are scarce. A large animal requires more energy to keep going than does a small one, the energy requirements of a predator at one trophic level are higher than those of its prey.

3.2.4 Exploitation Efficiency

Proportion between net primary productivity and net productivity (available biomass)

$$\text{Exploitaiton Efficiency} = \frac{\text{Energy ingested by the predators}}{\text{Net production of its food species}}$$

This measurement is advantageous than Lindmann Efficiency for field biologist as they do not have to measure energy degraded in respiration.

3.2.5 Allocation of energy

Once energy has been assimilated by the organism, it will be used either for maintenance, growth, storage or reproduction. Maintenance includes all the basic metabolism of the organism that results in the respiration of carbohydrates such as breathing, heatingi or cooling the body, circulating blood or digesting food. The more active an animal, the higher its energy demand for maintenance. In general, body size, endothermy and metabolic rate are the largest factors governing the amount of energy expended in maintenance.

Growth in some group of animals such as mammals, birds and many insects, is restricted to the young, whereas in other species of trees, crustaceans, reptiles and fish growth continues throughout their life. Consequently in almost all species, the amount of energy apportioned to growth in the young is high, whereas in an adult it is either a lower proportion (continuously growing organism) or zero in case of other organisms.

3.2.6 Energetics of metabolism and movement

A fraction of assimilated food is used for respiration in order to support metabolism and activity. The remainder is incorporated into the animal concerned as secondary productivity and ultimately can be used either in growth or in reproduction.

The relationship are as follows:

Ingestion = Assimilation + Egestion
Assimilation = Productivity + Respiration
Productivity = Growth + Reproduction.

The total amount of energy needed per unit time for maintenance increase, with increasing body mass (Schmidt-Neilsen, 1975). Small animals have relatively high ratio of body surface to body volume, they generally have much higher metabolic ratio and hence have greater energy requirements per unit of body weight than larger animals.

3.2.6.1 Temperature Regulation

Animals that maintain relatively constant internal body temperatures are known as homeotherms. Those whose temperatures vary widely from time to time in tune with the temperature of the environment, are called poikilotherms. Besides an organism that obtains its heat from its external environment is an **ectotherm** (all plants and vast mejority of animals). One that produces most of its own heat internally by means of oxidative metabolism, is known as an **endotherm** (birds and mammals).

An organism could balance its annual heat budget by being entirely passive and simply adjusting its temperature in accordance with the environmental temperature. Such a passive **thermoregulator** is known as **thermoconformer.** Organisms that carefully regulate their internal temperatures are called **thermoregulator or homeotherms** (both ectotherms and endotherms) An intriguing hypothesis for the evolution of homeothermy was offered by Hamilton (1973) who suggested that homeothery is a by-product of advantages gained from maintaining maximum body temperature in the face of an innate physiological design. Ecologically optimal temperatures need not coincide with physiological optimal. It is noted that all homeotherms are endotherms many ectotherms have attained a substantial degree of homeothermy by means of behavioural thermoregulation.

3.2.7 Allocation of energy and reproduction

Allocation of energy to reproduction includes- developing secondary sexual characteristics, forming eggs, sperms, pollens, nurturing a fetus and infants or producing seeds. The expenditure of energy on reproduction is critical to the fitness of the individual and hence of permanent importance.

Reproduction is a physiological process through which perpetuation of race is maintained. The goal of reproduction is to ensure the survival of the genetic lineage. Gense can be passed on through asexual reproduction, in which all the offspring's are exact genetic copies of a single parent or through sexual reproduction in which chromosomes of two parents are segregated and recombined, so that no two offsprings are identical to each other or to either parent.

An organism that reproduces sexually would need only one youngster to maintain an ecological fitness of 1 (because it has 100% of its parents genes). Organisms that reproduce sexually must raise two offsprings to achieve an ecological fitness of 1. Each of the young inherits half of the genes from either parent.

3.2.8 Resource utilization for sexual reproduction-ecological cost analysis

Three basic costs of sexual reproduction must be to overcome-(i) The cost of meiosis, (ii). Cost of recombination, and (iii) Cost of mating.

The **cost of meiosis** can also be thought of as the cost of producing males. There are actually two arrangement here, both relating to the exceptation that half of the progeny will be male. Males do not give birth, thus a female must produce twice as many young as her parthenogenetic counterpart to maintain the necessary numbers of daughters in the next generation.

The **cost of recombination** recognizes that the female has to accept 50% genetic input into her young from a male. The splitting of chromosome in meiosis is far more likely to produce variation than in the chromosome duplication of mitosis. Variation in behaviour, anatomy for physiology may prevent one of the many characters that determine the ecological success of an individual. Consequently, almost all serious variation from j the parents are likely to be immediately fatal to the offspring. The genetic code that determines success frequently result from complex pairing or sequences of genetic information. Chromosomes from the egg and the sperm needed to complete these sequences.

The cost of mating are a significant drain on the female. These are as follows;

1. **The cost of sexual mechanisms** - chemical attractants, sexual organs, flowers and so on all require a substantial diversion of energy from the basic process of building a bigger body or making more young.
2. **The cost of mating behavior** - courtship and the rituals of mating can be time consuming and energy expensive. A parthenogen can spend this time productively feeding or sleeping. Courtship usually involve display fights, calling contests or other showy demonstrations.
3. **Injury inflicted**- by the male mating itself can be dangerous. Males of some species (sea lion) are much larger than the females and can unintentionally injure them. Deliberate injury to the female is understandably rare, because this would reduce her chance of reproducing.
4. **Disease transmission**- any time two creatures come close enough to mate, the increase the probability of transmitting a disease, for example a sexually transmitted disease or skin disease, insect born or pneumonic infection.
5. **The cost of escape from unwanted sexual attention**.- the most females need ones they have been fertilized. The females may find herself pestered by male attention to the extent that she can not feed at time when it is important to maintain or increase body weight.

3.2.9 Limiting factors

Ecologicaly events and their outcome, such as growth, reproduction, photosynthesis, primary production and population size are often regulated by the availability of one or few factors or requisites in short supply, whereas other resources and raw materials present in excess may go partially unused. This principle has become known as the 'Law of the minimum (Liebig,1840). For instance, in arid climates primary production is strongly correlated with precipitation-here water is a 'master limiting factor.

A related concept, develop by Shelford (1931b), is known as the "Law of Tolerance", Too much or too little of anything can be detrimental to an organism. In the early morning, a desert lizard finds itself in an environment that is largely too cold, whereas latter in the day its environment is too hot.

The lizard compensate somewhat, for this by spending most of its time during the early morning in sunny places , whereas latter on most of the activities take place in the shade. Each lizard has definite range of temperature, with both upper and lower limits of tolerance.

3.2.10 Resource budget and principle of allocation

Any organism has a limited amount of resource available to devote to foraging , growth, maintenance and reproduction. The way in which the organism allocates its time and energy and other resources among various conflicting demands is of fundamental interest because such apportionments provide into how the organism copes with and conforms to its environment. Moreover, because any individual has finite resource and energy budgets, its capacity for regulation is necessarily limited. Organisms stressed along any other environmental variable are thus able to tolerate a lesser range of conditions along other environmental variables.

3.2.11 Time, matter and energy budgets

Time, matter and energy budgets vary widely among organisms. For examples, some animals allot more time and energy to reproduction at any instant than do others. Varying time and energy budgeting is a potent means of coping a changing environment while retaining some degree of adaptation to it. Thus many songbirds expend a great deal of energy on terrestrial defense during the breeding seasons but little or none at other times of the year. Similarly, an animal with parental care, an increasing amount of energy is spent on growing offspring until some point when progeny begin to become independents of their parents, where upon the amount of time and energy devoted to them decreases.

An animals time and energy budget provides an explanation how foraging influences reproduction and vice-versa. Foraging and reproductive activities interact in another important way. Many organisms gather and store materials and energy during time periods that are unfavorable for successful reproduction and then expand their resources on reproduction, more suitable time. Lipid storage and utilization systems obviously facilitate such temporal integration of uptake and expenditure of matter and energy. This temporal component greatly complicates the empirical measurements of reproductive efforts.

3.2.12 Energy budget

Growth, reproduction, and daily metabolism all require an organism to expend energy. The expenditure of energy is essentially a process of budgeting. All organisms allocate to growth, reproduction, maintenance and storage. Storage is important but ultimately that energy will be used for either growth maintenance and reproduction.

Two extreme sets of energy allocation are noticed in nature - in some cases most of the energy are invested for building body with a fare minimum are allocated for reproduction. While in other extremes just opposite mode of investment of energy occur. These two extreme cases bring with them some predictable lifestyle consequences.

The plant or animal that allocates most of its energy to reproduction will be small because resources are not being devoted to body size. Those organisms will be vulnerable to attack, Under such circumstances, the best means of defense would be to avoid predators or pathogens by being highly mobile, The solution is to grow fast to a minimum size , invest every component of energy , including the energy reserved for maintaining life in a single reproductive outpouring and then die. In this kind of reproductive strategy, hundred of offsprings are produced because of the chance of high mortality.

Two categories of organisms have been identified - One is **Opportunist** - which constantly invade new areas to compensate being displaced by more competitive species and the other is **Competitor**-just opposite to an opportunist and spend little effort in reproduction.

Attributes	Opportunist	Competitor
Climate needed	Variable and unpredictable	Fairly constant and predictable
Mortality	Often catastrophic	Seldom catastrophic
Population size	Variable through time, seldom reaching carrying capacity disequilibrial	Fairly constant, approaches carrying capacity and equilibrium
Ability to compete	Low	High
Selection favors	Rapid development, early reproduction, small body size, single reproductive effort	Slow development, postponed reproduction, larger body size, repeated reproduction
Length of life	Short, usually < 1 year	Long, usually > 1 year

3.2.13. Energy partition and Optimization : r and k selection

It is important that the pure opportunist or competitor are the extreme of a continuum. I Most organisms exhibit a blend of some opportunistic and some competitive aspects to I their ecology. The ratio of reproductive energy to maintenance energy varies not only with the size of organism and with life history pattern but also with population density and carrying capacity. In uncrowded environment, the selection pressure form species with a high reproductive potential (high rate of reproductive to maintenance efforts). In contrast crowed conditions favour organisms with lower growth potential but better capabilities for using and competiting for scarcer resources (greater energy investment in the maintenance and survival of the individual). These two modes are known as r-selection and k-selection based on r and k constant in growth equation.

Partitioning and allocation of energy among the various activities of an organism reflects balances between advantages and cost of each activity in producing change in rmax, the intrinsic (genetically determined) rate of increase, to enhance survivorship or fitness. The consideration is survival and maintenance of individual (the respiratory component) with additional energy allocated to growth and reproduction (Production component). Large organisms allocate a larger portion of their metabolized energy input to maintenance than small organisms. Natural selection requires that all organisms find on optimum balance between the energy spent on future survival and the energy spent for the survival in the present

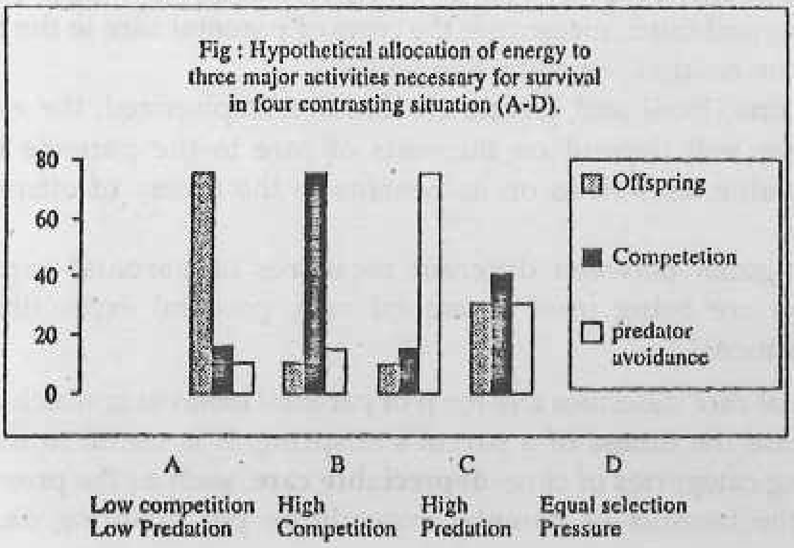


Fig : Hypothetical allocation of energy to three major activities necessary for survival in four contrasting situation (A-D).

1. represents energy expended to cope with competition from other species striving for the same resources.
2. represents energy expended to avoid being eaten (or grazed) by the predator.
3. represents energy expended to produce offspring.

When competition and predation have a low impact, a large part of the energy flow may go for reproduction and production of offspring (A); Alternately competition or antipredators activity may take most of the available energy (B and C respectively). All three demands receive approximately equal allocation in the last case (D).

3.3 ☐ Parental investment and offspring

3.3.1 Types of parental behaviour

All organisms face two fundamental decisions about reproduction. First, they must decide how much of the resources available to them should be spent on reproduction instead of their own continued growth and survival. Second, they must decide how to divide the resources that they allocate to reproduction among their offsprings.

Parental behaviour can be measured at three different levels- First, describing the form, frequency or duration of parental care, for example the number of. times a parent stops feeding to look for predators; Second, measuring the parent's expenditure of energy (or other resources) on caring for its offspring and third, measuring the costs of parental care to the parent's future fitness or residual reproductive value.

As Williams (1966) and Trivers (1972) have emphasized, the evolution of parental care will depend on the costs of care to the parent's residual reproductive value, as well as on its benefits to the fitness of offsprings or other relatives.

To distinguish between different measures of parental care, three different terms are being used - parental care, parental expenditure and parental investment.

1. Parental care describes any form of parental behaviour which appears likely to increase the fitness of a parent's offspring. It is useful to recognize two contrasting categories of care- depreciable care, such as the provision of food, where the benefits of parental expenditure per offspring decline as

brood size increases; and *noti'depreciable* care, such as parental vigilance, where benefits per offspring do not decline with increasing brood size (Wittenberger,1979).

2. Parental expenditure denotes the expenditure of parental resources (including time and energy) on parental care of one or more offsprings.

3. Parental investment refers to the extent to which parental care of one or more offsprings reduces the parent's residual reproductive value. However, there is no reason to distinguish between the costs of parental investment to the parent's subsequent ability to care for, versus produce, young, and today parental investment generally applies to-the costs of parental care to any aspect of the parent's residual reproductive value (Alexander & Borgia, 1979; Gwynne, 1984). **Parental investment** is now being defined as the fitness costs of parental care of *individual* offspring while the total costs of caring for all progeny are designated as **parental effort** which, together with **mating effort** is a part of the **organism's reproductive effort** (Low, 1978; Alexander & Borgia, 1979).

3.3.2 Measuring the costs and benefits of parental care

There is extensive evidence that parental care affects the survival and reproductive success of offsprings. For example, where males guard egg masses, experimental removal of the guarding male often leads to a substantial reduction in egg survival (Simon, 1983). Egg size and neonatal weight are also important in birds, positive relationships between egg size and chick survival are .common (Parsons, 1970; Galbraith, 1988) while1 in mammals, juvenile survival is often closely related to birth weight or early growth (Allden,1970).

In longer-lived animals where generations overlap, parental care commonly extends beyond the point at which offspring obtain their own food (Silk, 1983; Harcourt & Stewart, 1987), For example, in vervet monkeys, mothers help to protect their adolescent and adult offspring from competition with older or more dominant conspecifics , and females with mothers still present in the group have higher reproductive success than those without (Fairbanks & McGuire, 1986). The costs of care to parental fitness are also often substantial. Increased expenditure per offspring almost inevitably reduces the number of offspring that the parent can rear. Experiments on domestic chickens show that (artificial) selection for large egg size reduces the rate of egg production while selection for laying rate reduces egg size (Nordskog, 1977). The costs of egg care can be large, too. In ectotherms where one adult gaurds the eggs, the guarding parent commonly reduces food intake during parental care and may cease feeding altogether (Townsend, 1986).

In endotherms, the energetic costs of egg care include the costs of maintaining eggs temperature. In birds, estimates of the amount of heat transferred to the eggs ranges from 10% to 30% of basal metabolic rate (BMR) in passerines (King,1973), increasing in smaller species with high egg weight to body weight ratios and in species with relatively large clutch sizes (Coleman & Whitlall, 1988). Where parents feed their young after hatching or birth, energy costs are typically high, exceeding those of egg production, incubation or gestation (Robbins, 1983).

3.3.3 The trade-off between the size and number of offspring

The most fundamental type of parental investment is in the resources required to provision the egg.

The Smith-Fretwell model

Smith and Fretwell (1974) quantitative model of the trade-offs between the size and the number of offspring showed how a parent should distribute a fixed amount of resources (M) amongst an indefinite number of youngs. They had in mind a mother whose only investment in her offspring laying and in provisioning the egg so that the only tradeoff involved was between the size and number of eggs.

Suppose the mother produces eggs of size s which survive to maturity with probability *k.f(s)*. The probability of survival has two components, one (f(s)) influenced by parental investment and a second component (k) which summarizes all the other mortality risks that are unaffected by egg size. The number of eggs produced by the mother is simply M/s, the total resources available divided by the amount invested in each individual. The fitness of the mother is thus (M/s).k-f(s), the number of offspring multiplied by their own individual fitness. The optimal egg size is found by maximizing fitness with respect to investment per egg and is f(s)/f 's where the prime refers to the derivative.

The Smith and Fretwell model (Figure-A) reveals a number of interesting properties

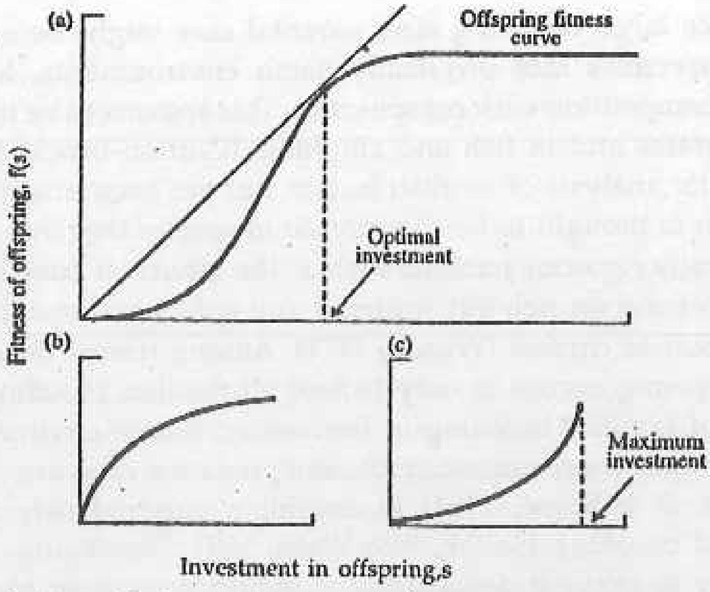


Figure-A. A graphical representation of the Smith and Fretwell model.

(a) The curve describes the relationship between offspring fitness and the resources invested in an offspring. The parent obtains the maximum returns on her investment at the point where a line from the origin is tangent to the offspring fitness curve.

(b) When the offspring fitness curve is always decelerating, the parent is selected to produce the smallest possible offspring.

(c) When the offspring fitness curve is always accelerating, a parent will allocate all resources to a single offspring.

about the trade-off between size and number of offspring (Parker & Begon, 1986; Lloyd, 1987). First, optimal egg size is not influenced by total parental investment in reproduction: total resources (M) do not appear in the expression for optimal egg size. The reason for this rather paradoxical result is that an implicit assumption is made that the fitness of an individual is unaffected by clutch size after the initial provisioning of the eggs. In many animals, egg size and clutch size will both affect fitness and will evolve together (Parker & Begon, 1986).

3.3.4 Distribution of parental care among species

The distribution of parental care raises two fundamental questions. First, why do somespecies show elaborate and protracted care of eggs or offspring while others do not. And second, why are males responsible for care in some species, females in others, and both sexes in a few?

Like large offspring size, parental care might be expected in animals where juveniles face physically harsh environments, heavy predation or intense competition with conspe-cifics. This appears to be the case, both among invertebrates and in fish and amphibia (Clutton-Brock, 1991). Although no systematic analysis of its distribution has yet been attempted, parental care in insects is thought to be commonest in species that live in physically harsh or biotically rigorous habitats such as the intertidal zone or in species whose young depend on rich but scattered and ephemeral resources, such as dung, dead wood or carrion (Wilson, 1971). Among teleost fishes, parental care of eggs or young occurs in only 16% of all families breeding in saltwater, but in 57% of families breeding in freshwater, where environmental conditions are commonly more unpredictable and predation rates are often higher (Baylis, 1981; Gross & Shine, 1981) In amphibia parental care is associated with terrestrial breeding (Salthe, 969; Webs, 1981; Nussbaum, 1985) and may be necessary to prevent desiccation or mould growth or to deter invertebrate predators (Wells, 1981).

3.3.5 Game theory models

Some of the most important questions about parental investment arc those concerning the evolution of male and female care. Since the evolution of care by one sex is likely to reduce its benefits to the other sex (Chase, 1980). Game theory models provide the appropriate framework for analyzing the conditions under which uniparental male care ('sticklehack'), uniparental female care ('duck') and biparental care arc likely to evolve (Maynard Smith, 1977; Vehrencamp & Bradbury, 1984). Maynard Smith's well-known model (1977) assumes that there are discrete breeding seasons; that a female's expenditure on egg laying and on parental care limits the number of young that she can produce; and that care by males and females has the same effects on offspring survival.

Let Po be the probability of survival of eggs that arc not cared for by either parent, Pt be the survival of eggs cared for by one parent and *P2* be the survival of eggs cared for by both parents, such that P2 > PI > Po Suppose that a male who deserts has a chance p of mating again while a female who deserts after egg laying produces V eggs compared with v for a caring female. The pay-off matrix for this game and the four evolutionarily stable strategies (ESSs) that it generates are shown in the following table-

Table: Mayerd Smith (1972) parental care game:

PAY OFF MATRIX	MALE PAY OFF	FEMALE PAY OFF
	Female Guard	Female defects
Female Guard	vP_2/vP_2	VP_1/VP_1
Male defects	vP_1 (l+pVvP_1	VP0(l+p)/VP_0

Evolutionary Stable Strategy

1. Both sexes desert

This requires that: (i) VP_0vP_1, the number of eggs laid by a non-caring female multiplied by their survival exceeds the number laid by a caring female multiplied by their survival, or the female will care, and that (ii) P_0,(I+p)>P_1 the survival of eggs that are not cared for by either parent multiplied by the number of matings achieved by a non-caring male (1+p) cannot exceed the survival of eggs under uniparental care, or the male will care.

2. Female deserts and male cares ('stickleback')

This requires,that: (i) $vP > P_2$, the number of eggs laid by a caring female multiplied by egg survival under uniparental care must exceed the number laid by a non-caring female multiplied by egg survival under biparental care, or the female will care, and that (ii) P_1 >Po(1 + p) egg survival under uniparental care must exceed survival of un cared for eggs multiplied by the number of matings that a non-caring .male can achieve, or the male will desert.

3. Female cares and male deserts ('duck')

This requires that: (i) $vP_1 > VP_0$ the number of eggs laid by a caring female multiplied by egg survival under uniparental care must exceed the number of eggs laid by a non-caring female multiplied by the survival of eggs that are not cared for. or the female will desert, and that (ii) P_1(1 +p] > P2. the mating success of a non-caring male multiplied by egg survival under uniparental care must exceed egg survival under biparental care, or the male will care.

4. Both partners care

This requires that: (i] vP2 > VP!. the number of eggs laid by a caring female multiplied by egg survival under biparental care must exceed the number laid by a non-caring female multiplied by egg survival under uniparental care or the female will desert, and that (ii] $P2>P_1(1+p)$ the number of eggs that survive under biparental care must exceed egg survival under uniparental care multiplied by the mating success of the non-caring male, or the male will desert.

If breeding seasons are continuous so that each individual breeds many times and two parents are less than twice as effective as one at ensuring that their egg survive, either uniparental male or uniparental female care can evolve from no-care (Maynard Smith, 1977).

3.3.6 Influence of gamete size on the mode of caring

Trivers (1972) initially suggested that females should usually be the care giving sex because the costs ,of producing ova' exceed those of sperm. As Dawkins and Carlisle(1976) pointed out, parents of both sexes should decide whether or not to prolong investment on the basis of its likely net benefits in the future (Maynard Smith, 1977). One reason why female care predominates in endotherms is that the large size of eggs (or of neonates in viviparous species) lowers their potential rate of reproduction relative to the rate that can be achieved by males. Where parental care inhibits further reproduction until it is complete, it usually has potentially higher costs to males than to females, with the result that uniparental female care is more likely to evolve than uniparental male care. An additional reason is that most endotherms show internal fertilization, permitting the spatial separation of males and females after copulation.

The importance of the relative rates of reproduction in determining the evolution of parental care *was* first emphasized by Baylis (1981). Baylis (1981) suggested that the faster rates of gamete production by male fish lead to the evolution of predominant *male* care because they cause male fitness to be limited by access to mating partners, with the result that males compete for resources (e.g. nest sites) that will attract females. His model is most relevant to cases when parental care evolves from a non caring ancestor and assumes that unit costs of parental care to males are low in many fish species because males can simultaneously care for multiple clutches and continue to attract females-a situation rarely found in endotherms.

The contrasting consequences of anisogamy in ectotherms and endotherms emphasize that there is no simple relationship between anisogamy and the evolution of parental care. Instead, differences in gamete size and in the rate of gamete production are one of variety of factors that can influence the relative costs of parental care to the two sexes.

3.3.7 Uniparental care in fish

In most teleosts showing external fertilization, parental care only involves males (Figure-B). In the maajority of these groups, male care probably evolved directly from a non-caring ancestor (Gross & Sargent, 1985), the evolution of male (as against female) care in most of these species is thai the costs of care to males arc relatively low (Williams, 1975; Gross & Sargent, 1985). Males can guard large numbers of eggs, contributed by! several females. For example, in some darters, nests commonly contain 2000 or more eggs while females lay around 150 eggs at a time (Gale & Deutsch, 1985). Moreover, in several species, females are attracted by the presence of previous eggs and males prefer to defend nests with fertilized eggs already in them (Unger & Sargent, 1988).

Uniparental *female* care in externally fertilizing fishes appears to be associated either with circumstances where the costs of care to females are unusually low or where the benefits are unusually high (Clutton-Brock, 1991). Uniparental female care is often associated with short breeding seasons or with semelparity, both of which are likely to reduce the costs of egg guarding to females (Perrone & Zaret, 1979; Gross & Sargent 1985).

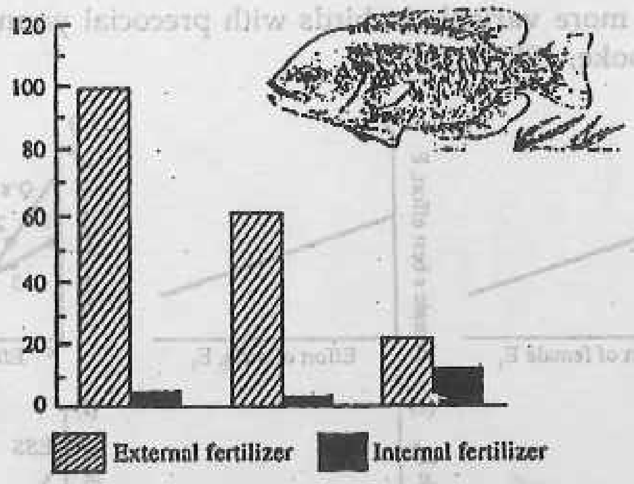


Figure-B. Occurrence of male and female parental care among 181 families of teleost fishes

3.3.8 Stable parental expenditure by males and females

Houston and Davies (1985) showed that where offspring fitness increases as an asymptotic function of total parental expenditure once parental expenditure exceeds some threshold level, each parent should respond to increases in care by its partner by reducing its own expenditure (Figure-C). Conversely parents would be expected to'respond to reductions in care by their mates by increasing their own expenditure. An ESS will be reached when the male's expenditure Em is the male's besl value given that the female expends Er and where Er is the female's best value if the male expends Em (a Nash equilibrium). If curves for Em plotted against Ef and Ef plotted on Em ('reaction' curves) intersect and each has a slope of less than -1, The intersection point should be an ESS for both partners- In such cases, parents should respond to reduction in care by their partners by increasing their own efforts while not fully compensating for the reduction, so that total expenditure is reduced. Where two partners arc making alternative investments in parental care, their expenditures are likely to converge on the ESS through a sequence of smaller and smaller changes. If reaction curves do not intersect or the slope of either is greater than-1, other outcomes arc possible (Chase. 1980; Winkler. 1987). Hutston and Davies' (1985) model begs the question of why biparental care is so common among birds. In many altricial explains, the removal of males reduces the growth rate of cluchs, the survival of nestlings, or the survival of fledglings before-independence. For example, in dark-eyed juncos *Junco hyemális*, experimental removal of males within 2 days of broods hatching had little effect on the survival of chicks to fledging but, after fledging, differences in chick survival increased (Wolf *el al*, 1988). The effects of male removal are more variable in birds with precocial young (Erckmann, 1983; Martin & Cooke, 1987).

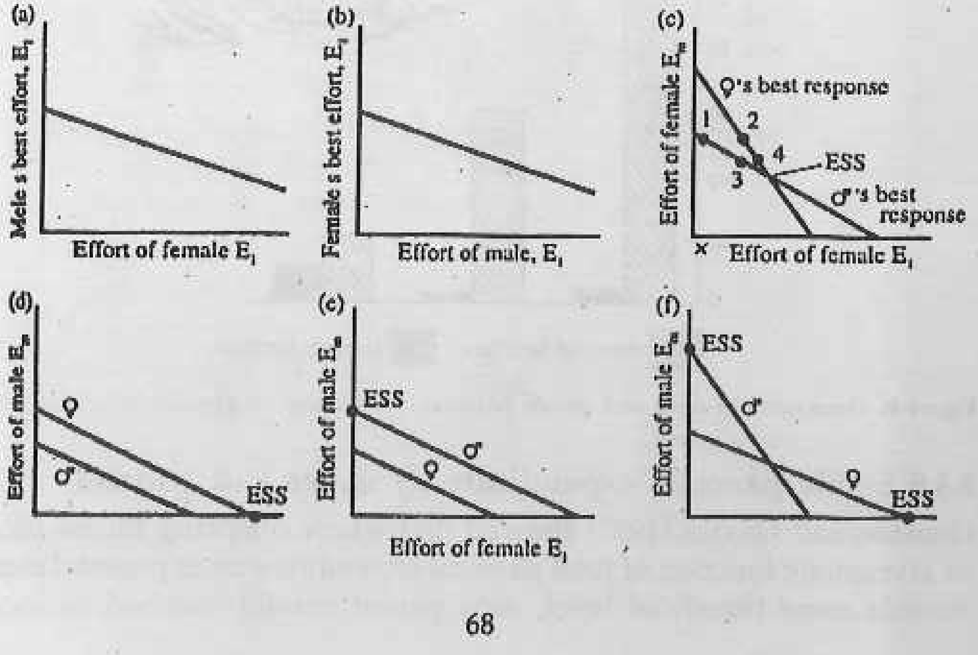


Figure-C. Optimal parental expenditure for males and females plotted against the level of expenditure by the other sex (from Houston & Davies, 1985). (a) Optimal male effort plotted against female effort; (b) optimal female effort plotted against male effort. As both slopes are < -1, when plotted on the same graph (c) they predict an evolutionarily stable strategy (ESS) where both partners care. To see this, suppose the female expends X. then the male's best response is to invest at the level marked 1 on the graph. The female's best response to this level of male investment is found at point 2; the male responds at point 3, the female at point 4, and so on until the ESS is attained. In the ESS, it does not pay either individual to change its effort. Three other possible outcomes were suggested by Chase (1980). In (d) the female curve lies completely above that of the male. Here the ESS is for the female to do all the work. In (e), the male curve lies above that of the female. Here, the ESS is for the male to do all the work. In (f), although the curves intersect, the intersection is unstable and is not an ESS: both 'all female work', or 'all male work' are ESSs.

3.3.9 Conflicts between parents and offspring

There are a number of conflicts that may arise during parental care. The young may demand more resources than the parent is willing to provide or may disagree with their brood mates over the distribution of parental care, and, in species with biparental care, the parents may disagree over their relative-investment in the young. These conflicts are best understood using Hamilton's (1964) theory of kin selection and, in particular, Trivers (1974) extension of the theory to parent/offspring conflict. A trait will be favoured if-(Relatedness) (Benefits (costs) to others)-(Costs (benefits) to actor)> 0

Conflict over the amount of parental investment will affect many aspects of the parent-young relationship (Trivers, 1974). When the youngs are being fed, they will tend to demand more food than the parent is willing to supply. As they grow older, there will be disagreement over the time of termination of parental care. The young wishing to prolong care beyond the parental optimum. Parental aggression against their young towards the end of the period of parental care is characteristic of many birds and mammals and is probably a direct result of parent / offspring conflict over weaning (Trivers. 1974; Lazarus & Inglis, 1986).

Parker and Macnair (1979) and Parker, (1985) model a number of cases of parental retaliation. The results of their studies depend critically on a number of assumptions about the nature of the parental response, about how the costs of solicitation are borne by the brood, and on the social structure of the species involved. In some cases, parent 'wins' or offspring wins are ESSs (i.e. uninvasable by alternative parent or offspring strategies) while in other cases no ESS is possible-gene frequencies cycle indefinitely. However, the commonest solution and probably the most likely result in nature is that the overall evolutionary stable strategy (ESS) is a compromise between the parent and offspring optima.

The work of Parker, Macnair and others have helped resolve some of the early criticisms of the concept of parent-offspring conflict. For example. Alexander (1974) argued that a gene for conflict expressed in the young could never spread as it would reduce the reproductive success of the same individuals when they grew up and became parents themselves. As Dawkins (1976) pointed out, this argument was based on an artificial asymmetry between offspring and parents while explicit population genetic models show the conditions under which parent-offspring conflict can evolve.

3.3.10 Sex allocation and sex ratio manipulation

The evolutionary origin and selective advantages of sexual reproduction remain major unresolved problems in biology (Williams, 1975) An elaborate form of sexual reproduction originated in protists that involved evolution of diploid as well as complex reduction division and production of haploid gametes. This form of sexual reproduction has persisted to the present day through the evolution of more complex organism. The sex ratio is defined as the proportion of male in the population. Fisher's (1930) explained why equal sex ratios are so widespread. Fisher argued that if the population sex ratio is female biased; any gene that led its bearer to produce a preponderance of sons would be selected because these sons would mate with, on average, more than one female: when the population sex ratio is female biased, sons are a more efficient vehicle than daughters for transmitting genes to future generations. However, if the population sex ratio is male biased, sons will mate with, on average, less than one female and a gene that promotes female-biased sex ratios will be favoured. This frequency-dependent selection ceases only when the population sex ratio is at equality, which is thus an evolutionarily stable state. This result applies to the primary sex ratio, the sex ratio at the end of parental investment, and the prediction is unaffected by later differential mortality. A corollary of Fisher's argument is that at sex ratio equilibrium, a parent should be indifferent as to whether he or she invests in sons or daughters: the rate of return (measured in units of parental fitness) is identical for investment in either sex.

Fisher (1930) noted that frequency dependent selection stabilizes the sex ratio of offspring and therefore an equal number of sons and daughters are usually expected. However, sex ratios some time vary from unity. Parasite wasp can have highly female biased sex ratios, offspring sex ratio of many reptiles depend on the brood temperature and ant colonies mainly contrast of females.

Fisher's argument makes a number of assumptions which, when violated, lead to thel prediction of unequal sex ratios (the study of sex ratios, and sex allocation in general,! has resulted). The three dimension that are particularly relevant to the division of the I parent's total investment between the sexes: (i) unequal costs of sons and daughters; (ii) environmental sex determination; and (iii) interactions between relatives.

3.3.10.1 Unequal costs of sons and daughters

If sons and daughters are equally costly to produce, Fisher's argument predicts an equal sex ratio. In fact, when this occurs, the ESS is to invest equally in the two sexes so that the sex ratio will be biased in favour of the cheaper sex. To understand this result, suppose the sex ratio is at equality but that sons cost more to produce than daughters. The reproductive success of sons and daughters will be equal but the gain in fitness through sons is achieved at greater cost than that through daughters: natural selection will thus switch investment towards daughters. When overall investment in the two sexes is the same, the increased cost of sons is exactly counter balanced by their increased reproductive performance as the rarer sex.

A curious example of the consequences of equal allocation in the sexes comes from a group of parasitoid wasps called heteronomous aphelinids (Godfray & Waage, 1990). Female wasps search for two different types of host, one suitable for male eggs and the other for female eggs. In some species, males develop exclusively as parasitoids of moth eggs and females exclusively as parasitoids of homopteran nymphs. It seems likely that for most ovipositing wasps, the limiting investment in reproduction is the time spent searching for hosts. The wasp should thus allocate equal search time to looking for hosts suitable for males and those suitable for females so that the observed sex ratio will depend critically on the relative abundance and ease of discovery of the two host types.

3.3.10.2 Environmental sex determination

Fisher's theory assumes that although the environment may be variable, sons and daughters suffer or benefit in equal measure from this variation. Trivers and Willard (1973) first explored the consequences of relaxing this assumption. Suppose females vary in condition and that this variation is reflected in the quality of the young they rear: for example, females in good condition might rear particularly large young.

Trivers and Willard's suggestion was supported by a series of population genetic models by Charnav (1979) and Bull (1981) who showed that a wide range of phenomena could be explained by this argument, which they' termed environmental sex determination (also called conditional sex expression; Frank, 1987). Among the environmental gradients that have been suggested to influence the fitness of male and female offspring are maternal condition (mammals: Trivers & Willard, 1973), host size (parasitoid wasps: Charnov et al 1989) the number of competitors in a host (nematodes: Charnov, 1982), temperature (reptiles: Charnov & Bull. 1989) and photo period (amphipod: Adams *et al.* 1987).

The consequences of environmental sex determination for the population sex ratio have been unclear and known only for special cases (Bull, 1981; Charnov, 1982). Frank and Swingland (1988) and Charnov and Bull (1989) have now proved that the population sex ratio will always be biased towards the sex produced at the poorer end of the environmental gradient. The actual sex ratio may be very difficult to calculate and may depend on a knowledge of the exact relationship between sex specific fitness and the environmental gradient, but the direction of the sex ratio bias is clear.

Some of the best examples of environmental sex determination come from those parasitoid wasps that lay a single egg per host. Here, the environmental gradient is host size, which correlates very closely with the size of the wasp that eventually emerges from the host. It is argued that females benefit strongly from being large because female size and fecundity are closely correlated; males also benefit from being large but to a lesser extent because mating ability is only weakly correlated with size. As predicted by theory, many species of wasps lay female eggs in large hosts and male eggs in small hosts (Charnov et *al*, 1981; King, 1987).

Many reptiles bury their eggs in the ground and the sex of the offspring depends on the temperatures experienced during development (for example, all crocodilians, many turtles and at least a few lizards; Bull & Charnov, 1989)

There is now good evidence for the effects of environmental sex determination in several species of mammals, although these effects arc strongly modulated by chromosomal sex determination (Clulton-Brock & Albon, 1982). In red deer where there' is great variance in male reproductive success, differences in dominance rank between hinds affect the reproductive success of their sons more than that of their daughters, suggesting that high ranking hinds should produce male calves and low ranking hinds female calves. Data collected over 20 years from the red deer population on Rhum show that high ranking females consistently bias their sex ratio towards male calves while subordinate hinds produce an excess of daughters Clutton- Brock, et al 1984) The mechanism by which the hinds manipulate sex ratio is not yet known.

3.3.11 Concluding remark

Three developments would help to promote the understanding of the evolution of parental care in the future. It is misleading to refer to differential juvenile mortality as sex ratio manipulation unless there is evidence that the parent is responsible for the difference in survival. Considerable emphasis was given on the importance of under! standing the causes of variation in the growth and survival of juveniles.

3.4 ☐ Reproductive strategies -ecology and evolution of sex and mating systems, optimal body size r and k selection

Reproduction is a physiological process through which the perpetuation of the racel is maintained by transmitting genetic characteristics from one generation to another, and! individuals increase the numbers of their progeny. Reproduction is *of* two types - asexual I and sexual. In the former case genetically identical new individuals are formed by thel parents while in the sexual reproduction, recombination of genes allow the gene pool] to become mixed through the -process of combining the haploid gametes (egg and sperm) I to form diploid zygote. Mixing supplies the genetic variability necessary to meet changing selective pressures and to prevent the occurrence of harmful mutation.

Sexual reproduction can be of different types. Bisexual animals pcesses either male or female organs. Some animals pocessing both male and female organs are called **hermaphrodite.** Some hermaphrodites are simultaneous, as earthworms and others are sequential. The later type are one sex when young are developed into opposite sex when mature, as snails.

3.4.1 Evolution of reproductive strategies

Natural selection recognizes only one objective - successful offspring. All living organisms have probably been selected to minimize their own life time reproductive success - they vary greatly in exact mode of reproduction. Some organisms like most annual plants, many insects and certain fish like the Pacific Salmon reproduces only one during their entire lifetime. This mode of reproduction is known as **semalparous.** Most animal and plants are **iteroparous.** the strategy of producing a few large young has a trivial investment in eggs or sperm, but a massessue investment nurturing. Almost entire reproducibility falls on the females to raise the young which has exhibited in its maximum level of mammals.

3.4.2 Matting strategies

Mating strategies are often linked to the kind of parental care system that species employ. Monogamy is a mating system in which males and females form pair bonds, and often both care for the offspring. **Polygyny** is a mating system in which a male mates with several females. The female usually cares for the young while the male attempts to maximize his fitness by mating with as many females as possible. **Polyandry** is a mating system in which a female mates with several males. Males may care for the young while females attempt to maximize their fitness by mating with as many males as possible. And finally, **promiscuity** is a mating system free-for-all, in which either sex may care for the young and both males and females mate with many different individuals (Alcock 2001).

The strategy employed by a male or female also depends on the strategy adopted by the partner. For example, if the female cares for the young, and only a single parent is needed to raise offspring, the male may enhance his fitness by finding new females to mate with. But if the female does not care for the young, the male may enhance his fitness by attending the young himself. This type of conflict can be evaluated by game theory models, in which the different strategies played by the male and female collectively determine the evolutionary fitness gain.

A useful game theory model to resolve such conflict was developed by John Maynard Smith (1977). The model consists of two strategies: care for young (1) or desert young (0), that are chosen by both males and females. Thus, four "games" can be played: (1) both males and females care for young; (2) both males and females desert young; (3) the female cares for young and the male deserts; (4) the male cares for the young and the female deserts. Which of these games should be played depends on several parameters:

Po = the probability of survival of eggs that are not cared for.
PI = the probability of survival of eggs when one parent cares for young.
P2 = the probability of survival of eggs when two parents care for young.
p = the probability of a deserter male finding a new mate.
p′ = the probability of a caring male finding a new mate.
V = the number of eggs laid by a female deserter.
v = the number of eggs laid by a female who cares for her young.

Thus, the model considers the value of parental care by one or two parents; the chance that males mate again; and how parental care affects the number of eggs the female can lay. It can be assumed that $P_0 = P_1 = P_2$, so that the probability of survival of eggs with parental care is never less than the probability of survival without parental care. It can also be assumed that V = v, so that females that care have less energy to allocate towards clutch size. Our final assumption is that p and p′ do not depend on a male's parentage for a given clutch. Given these parameters, the fitness payoff for males and females can be determined as shown in Table 1.

Table-I Fitness payoff Parameters for males and female :

	Female Fitness		Male Fitness	
	Female cares	Female deserts	Female cares	Female deserts
Male cares	*v x P2*	*Vx* PI	*vxP2+ v x P2 x p′*	'Vx PI + V x PIx p′
Male deserts	*v x* PI	*V x Po*	*vxPI+ v x PI x p*	V x Po + V x Po x p′

For example, when both males and females care for the offspring, the female has a reproductive output equal to the number of eggs laid by a caring female (v) times tr probability' of young surviving when two parents offer care (P2). But when a female cares but the male deserts, she has a reproductive output equal to the number of eggs I laid per caring female (v) times the probability of young surviving when a single parent offers care (P_1). When both parents care for young, males have a reproductive output (fitness) equal that of the female (v x P_2), but with the added benefits of remating will another female while still providing care to his first clutch (v x P2 Xp).

The equation v x P_2+ v x P_2 x p′ can be rewritten as v x P_2 x (1 + p′). When the female cares but the male deserts, his fitness is equal to that of a single-parent female (v x P_1) plus the added benefits of remating with another female by deserting his clutch (v x P_1x p), The equation

v P_1+ v x P_1 x p can be rewritten as v x P_1 x (1 + p).

Classification of mating system :

Some animals reproduce without fertilization (pathenogenesis occurs in some invertebrates, fish, amphibians, and lizards), and some are hermaphroditic. But the vast majority of animals must reproduce sexually, a male combining gametes sith a female.

Classification of animal mating systems has been based primarily on how mates are acquired, the number of mates and their monopolization, and characteristics of pair bonds and patterns of parental care (Emlen and Gring 1977; Davies 1991). Promiscuity is the most widespread of animal mating systems and is characterized by short term associations between males and females that generally cease after eggs are laid.

These factors favor a wide range of alternative mating behaviors, in which a subset of the population behaves very differently in attempts to acquire mates. Alternative tactics include forced copulation instead" of providing nutritive courtship offerings, quick and inconspicuous spawning instead of elaborate courtship, and searching instead of defending.

Recently, researchers have focused on variation in female behavior as a critical aspect of many animal mating systems, especially in promiscuous ones. Sometimes, females attempt to copulate with more than one partner. A wide array of ecological factors might affect this behavior. Multiple mating could maximize the benefits of sex by producing highly variable broods of offspring. Alternatively, females might copulate with any male to ensure fertilization and then obtain genes for valuable traits for the offspring by copulating with particular males. Yet another possibility is that females acquire valuable nutrients from males during courtship and copulation.

The behavior of females, in turn, has a powerful effect on the evolution of male behavior. If females copulate with two or more males, fertilization success for anyone male will be reduced. Traits that bias fertilization in a male's favor will be under selection, and a wide variety of such traits have been described in every taxon of animals (e.g., Birkhead and Medler 1998). Males of many taxa defend females during the period before she lays eggs, sometimes fighting off other males or preventing the female from moving about and encountering other males.

Females of some insects have intromittent organs that can remove the sperm of previous males, and in insects and mammals, males produce substances in their ejaculates that block or inhibit insemination by other males.

Such male adaptations to control fertilization appear to influence female success. There is growing evidence that females have evolved mechanisms to prevent males from controlling fertilization completely.

Male and female animals in a variety of taxa, particularly in birds, associate for periods of time far longer than necessary to attract a mate and fertilize eggs. A diverse array of different groupings of males and females is possible. In fish, mammals, and some birds, multiple females can be associated with one male. Such polygynous systems can arise in a variety of ways that represent a continuum of levels of prolonged social association. Access to females may be controlled either directly by defense of a group of females (female defense polygyny) or indirectly by defense of clumped resources that attract more than one female (resource defense polygyny). Female defense polygyny is rare in birds but common in many ungulates where females and young stay in small herds.

In male dominance polygyny, males gather during the breeding season, and females select mates based primarily on male status in the group. These groups enhance male-male competition and lead to greater variance among males in reproductive success. This mating system is often associated with unpredictable resources or resources that are difficult to defend or are highly dispersed. One extreme type of male dominance polygyny is lek polygyny, where males cluster to attract females at a display site (lek), and females visit to mate. Females then leave to rear the young alone, a;d so social associations beyondB copulation are minimal (leks thus are more of a promiscuous system than a polygynousl one). Leks are often found in organisms with long breeding seasons, including speciesl of insects, mouth-breeding fish, bullfrogs, and some mammals and birds.

In scramble competition polygyny, reproductive success is highest for those males thatl are best at finding females rather than at male-male encounters. This mating system is often associated with an extremely short receptive period for females. In the wood frog,! all females in a population are receptive for only one night a year, and male frogs spend} their time finding as many receptive females as possible, rather than defending territory.

In monogamous mating systems, one male pairs with one female for a prolonged period. I Conditions that tend to promote monogamy include young that require much parental! care and conditions where parents can share in parental care. Although less common in I mammals, monogamy is the most common mating system in birds. As an example,! American robins *(Turdus migratorius)* are monogamous, and both parents prepare the nest, I incubate the eggs, and feed the young. Monogamy is apparently favored because the I survival rate of the young and the reproductive success of the parents are highly dependent on the rate of delivery of food to the young.

Polyandry occurs when the female pairs with more than one male per breeding season. This pattern is much Jess common but has been documented in some bird species and several fish species. Control of males may occur directly because of interactions among females, or indirectly by control of resources. In polyandrous fish, fertilization is often external, and males often do all the incubation and brood care. This care, rather than the number of eggs, may be the most limiting factor in the number of successful progeny for a female. In extreme cases, behavioral roles are reversed; females compete for males, and females are often bigger and more brightly colored than males. In the mating system of the jacana *(facana spinosa)*, a large tropical marshland bird in Central and South America, females compete for territories that attract males, which provide parental care to a clutch.

Regardless of social mating system, promiscuity still occurs. In many monogamous birds, males and females frequently copulate outside established pairings, leading to sometimes very high frequencies of extra pair fertilizations. Considerable variation in these frequencies, and in which sex initiates the matings, exists among birds- Such events are likely to be influenced by sexual conflict of various sorts. Explaining this variation is a continuing challenge for evolutionary ecologists.s

3.4.3 Sexual Selection

Choosing a suitable mate is an important prerequisite for successful sexual reproduction. Different types of behavioral manifestation like birds songs in spring, the frogs calling in water bodies, and the clashes among stags in breeding season- all are meant for sex. It has been established that females are more selective in choosing male partners and male must prove their fitness. The result is intense rivalry among males for female attention. The outcome of male rivalry called **intrasexual competition.** Selecting of a fittest mates on specific characteristics during courtship is known as **sexual selection.**

Hypothesis explaining sexual selection :

1. The geneticist R. A. Fischer (1930) tried to provide an explanation on how does sexual selection square with natural selection. He hypothesized that some novel genetic characteristics such as plumage pattern of males become the criteria for female preference. The hypothesis assume that mate competition is male trait and that mate choice is female choice.
2. Trivers (1972) and Maynard and Smith (1956) hypothesized that the basic strategy for both male and female is to ensure their own maximum fitness. Male investment in the sexual process is thought to be minimum as compared to female investment. A male can mate with as many as possible females to achieve maximum fitness supported by innumerable sperm they can produce. By contrast females invest considerably more in reproduction and they become very much selective in choosing fittest mate who will pass on the best genes to the next generation.
3. A Zahavi (1975, 1977) in his handicap hypothesis postulates that the evolution of three characteristics-a **mate handicap**, a **female mating** preference for the handicap and a general viability trait. The handicap is a secondary male characteristic such as bright plumage, that could reduce the males survival. The viability trait is one that affects on individuals ability to survive as by escaping a predator. If a male can carry handicaps and survive, it is proof of a superior genotype. A male with such genotype get more female preference, because their offsprings will carry gene for high viability.

Process of selection :

J. Maynard Smith (1991) has classified the processes of selection into two major types - **intrasexual selection and intersexual selection.**

Intrasexual Selection- This type represents male to male competition for the opportunity to mate with females. Bright or elaborate plumage of male birds and antlers in deer are examples of male supporting structures.

Intersexual selection- represents mostly females choice of male. It is of two types! - the female choice of a conspecific mate and choice between conspecifics. Choice between conspecifics may be of two types- In one the females make a choice based on resources such as territory access to food, which will improve their fitness. The other! choice involve genes only as with many polygamous species. By selecting a male with' exaggerated traits, the female will be acquiring genes for highest fitness.

3.4.4 Lek behaviour and related hypothesis

Extreme examples of genes - only female choice appear in the **lek species.** Usually males compete for females either directly by defending the females or indirectly by defending resources to which females are attracted . In some cases , by contrast, males small territories which contain no resources, often aggregate into groups and put all their effort into self advertisement with visual, acoustic or olfactory displays. Females visit males solely for mating and males provide no parental care . Such mating systems , known as Leks, female often visit several males, before copulating and appear in their choice of mate. Male mating success is strongly skewed with the majority of matings performed by a small proportion of the males on the lek (Bradbury and Gibson, 1983).

Leks have been reported for seven species mammals and some 35 species of birds (Clutton-Brock et al, 1998 ; Oring 1982). This breeding system is thus not common (< 0.2% for mammal speies and < 0.5 % for bird species). Similar mating system occur in some frogs e.g. tree frogs, (Wells et al, 1977) and in some insects (Thronhill and Allcock, 1983) where females visit group of displaying males choose a mate and lay eggs from the display site.

At least three hypotheses have been advanced to explain lek behaviour (Davis, 1991).

1. Female Choice-hypothesis is that female show preference for a court ship area because it is the safest place to male or to forces male to cluster. Leks provide an unusual opportunity for females to choice a male among the displaying males (Bradbury 1981). This advantage holds especially among lekking insects, such as certain tropical *Drosophila m* which females are widely dispersed.

2. 'Hotpot' Model (Bradbury and Gibson, 1983)

Males aggregate on 'hotspot'-an area where encounters with females are potentially high. For example, in some population of topi *Damiliscus kurigwn* males defined small cluster territories in areas of short grassland where groups of female prefer to rest because of improved predator detection (Gosling, 1986) . Hotspot can also occur when females are solitary but have large overlapping ranges (Figure-1). Male settlement to maximize encounter rate with females can lead to aggregation in the overlap region (Bradbury et al. 1986).

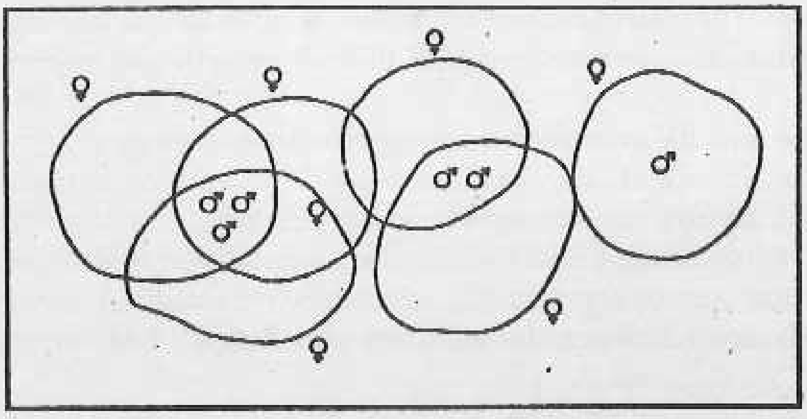


Figure-1. An illustration of Bradhury's hotspot model. Where female have large overlapping ranges, males can maximize their encounters with females by settling in the overlapping zones (hotspots). If male settle in an ideal free manner, then the proportion of males in an area should match the proportion of females so that average male mating success is the same in different areas. In this simple example, six males have settled on six female ranges. Note that once a male has settled in part of a females range, he devalues Ihe whole of that female's range for other males, so male groups are often expected to be separated by a distance of at least the diameter of one female's range.

3. Males aggregate around 'hotspot'

This hypothesis emphasizes an equality of mating success. It revealed a strong hierarchy among the males with the dominant male, in smaller leks at least, displacing all others and leaving no opportunity for female choice. In other words, no visiting females selected an area and mate with the dominant males This situation is very much noted in tropical manakius and birds of aradise.Among these birds one dominant male on the lek may perform over 90 percent of successful copulations (Beehler, 1983). In spite of odds of not mating, males congregate on the lek because by displaying together they draw in females from a larger area. By associating with and congregating about 'hotspots' males with the most effective displays subdominant and satellite may be able to find some mating opportunities. A majority of matings on the lek, however are done by a small percentage of males in the male dominance hierarchy formed in the absence of females.

3.4.5 Parental Energy Budget

The mcst important aspect of reproductive strategy is how organism allocate energy for their growth and reproduction. If organism invest more energy to reproduction, it has less energy to allocate to growth and maintenance. The nonreproductive females devoted as much energy to growth as the reproductive females invested to both growth and reproduction.

Clutch size and its implication in reproductive strategy :

The clutch size of an individual depends on both its reproductive effort and how it I divides the resources between offsprings . Firstly it address how increased reproductive I effort affects the parents , future prospects, in other words on the cost of reproduction. Secondly, it considers how the energy allocation is done between the members and fitness of offsprings.

Clutch size in birds :

Clutch size (number of eggs -or young per reproductive period) in birds seems not only to reflect mortality and survivorship but also to mirror r and k selection. Opportunistic birds (r- strategies) have a larger clutch size than do equilibrium species, as do temperate birds as compared with tropical birds (Odum and Barret, 2005). Clutch sizes among birds vary from 1 or 2 eggs (albatrosses, penguins, humming birds and doves) to as many as 20 among some non -passerines such as ducks and goose. Among birds two reproductive tactics are evident -**nidicolous** and **nidifugous.** Nidicolous chicks are **altrical,** hatching out pink and featherless with their eyes coloured. In sharp contrast chicks of nidifugous are **precocial,** hatching out with their eyes open, fully capable of feeding themselves. Another dichotomy among birds is **determinant** verses **indeterminate** layers. The former has been genetically programmed to lay a fixed number of eggs and can not replace lost eggs where as the later can lay as many as eggs necessary to fill out their clutch, replacing lost eggs as needed.

Each year emperor penguins lay 1 egg, pigeons lay 1 or 2 eggs, gulls typically lay 3 eggs, the Canada goose 4 to 6 eggs, and the American merganser 10 or 11 eggs. What determines clutch size in birds? We must distinguish two different levels of this question-proximate and **ultimate.**

A. Proximate factors explain how a trait is regulated by an individual. Proximate factors that determine clutch size are the physiological factors that control ovulation and egg laying. Proximate factors involve physiological machinery and how it works.

B. Ultimate factors are always selective factors, and ultimate explanations for clutch size differences always involve evolutionary arguments about adaptations.

Note:- Proximate factors affecting clutch size have to do with how an individual bird decodes its genetic information on egg laying. Ultimate factors have to do with changes in this genetic program through time and with the reason for these changes (Mayr 1982). Clutch size may be modified by the age of the female, spring weather, population density, and habitat suitability. The ultimate factors that determine clutch size are the requirements for long-term (evolutionary) survival. Clutch size is viewed as an adaptation under the control of natural selection, and the selective forces that have shaped the reproductive rates of birds.

Natural selection will favor the birds that leave the most descendants to future generations. It is hypothesized that natural selection might favor a clutch size that is the physiological limit the bird can lay. This hypothesis can be tested by' taking eggs from nests as they are laid. Some birds such as the common pigeon, lay a given number of eggs. The pigeon lays 2 eggs; if you take away the first, it will incubate the second egg only. If egg is added it will incubate 3 eggs. But many other birds are indeterminate layers; they will continue to lay eggs until the nest is "full." If eggs are removed as they are laid, these birds will continue laying. This subterfuge has been used on a mallard female, which continued to lay 1 egg per day until she had laid 100 of them. In other experiments, herring gull females laid up to 16 eggs (normal clutch 2-3), a yellow-shafted flicker female 71 eggs (normal clutch 6-8), and a house sparrow 50 eggs (normal clutch 3-5) (Klomp 1970). This evidence suggests that most birds under normal circumstances do not lay their physiological limit of eggs but that ovulation is stopped long before this limit is reached.

The next hypothesis is to address whether the clutch size of birds is limited by the maximum number of eggs a bird can cover with its brood patch. This may be the case for a few birds that lay many eggs. But in many cases, the brooding capacity can be shown experimentally to be larger than the actual clutch size. For example, the partridge in England typically lays 15 eggs, but up to 20 eggs can be successfully hatched (Jenkins 1961). The gannet lays 1 egg but will incubate 2 eggs successfully if one is added (Nelson 1964). Clutch size in most birds is probably not limited by brooding capacity.

One way to think about this problem of clutch size is to use a simple economic approach. Everything an organism does has some costs and some benefits. Organisms integrate these costs and benefits in evolutionary time. The benefits of laying more eggs are very clear-more descendants in the next generation. The costs are less clear. There is an energy cost to make each additional egg. There is a further cost to feeding each additional nestling. If the adult birds must work harder to feed their young, there is also a potential cost in adult survival-they may not live until the next breeding-season. If adults are unable to work harder, there is a potential reduction in offspring quality. A cost-benefit model of this general type is shown in the following **Figure-2.**

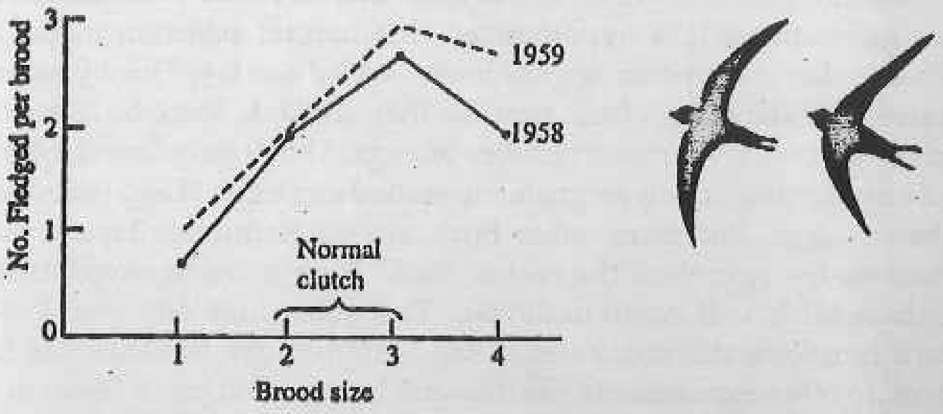


Figure-2. Production of young swifts (Apus apus) in relation to clutch size in England. The normal clutch is two to three; broods were increased to four artificially. Larger broods do not produce more young, and natural selection is stabilizing. (After Perrins 1964.)

Models of this type are called optimality models. They are useful because they help us to think about what the costs and what the benefits are for a particular ecological' strategy.

No organism has an infinite amount of energy to spend on its activities. The reproductive rate of birds can be viewed as one sector of a bird's energy balance, and the needs of reproduction must be maximized within the constraints of other energy requirements. The total requirements involve metabolic maintenance, growth, and energy used for predator avoidance, competitive interactions, and reproduction. In 1947 David Lack suggested that the clutch size of birds that feed their young in the nest was adapted by natural selection to correspond to the largest number of young for which the parents can provide enough food. According to Lack's hypothesis, if additional eggs are placed in a bird's nest, the whole brood will suffer from starvation so that, in fact, fewer young birds will fledge from nests with larger numbers of eggs. A few examples can be cited to test this idea.

Example-1

In England, the swift normally lays a clutch of two or three eggs. What would happen if swifts had a brood of four? Perrins (1964) artificially created broods of four by adding a chick at hatching and found that the survival of the young swifts in broods of four was poor (Figure 2.7). Swifts feed on airborne insects and apparently cannot feed four young adequately, so all the young starve. Consequently, it 'would not pay a swift in the evolutionary sense to lay four eggs, and the results are consistent with Lack's hypothesis.

Example-2

Tropical birds usually lay sm'all clutches, and Skutch (1967) argued that this was an adaptation against nest predators. If the intensity of nest predation increases with the number of parental feeding trips away from the nest, natural selection would favor a reduced clutch size. Hole-nesting passerine birds lay more eggs than comparable species that nest in the open (Slagsvold 1989), and predation rates are much lower for hole-nesting species (Murphy and Haukioja 1986). This suggests that a high risk of predation on the whole brood in the nest is a strong selective factor that reduced clutch size in open-nesting birds, and also favors a shortened nesting period, independent of the ability of the parents to provide food to the nestlings.

Temperature regulation and clutch size :

Temperature regulation is an important component of the development of young birds and may have a bearing on clutch size. Small broods will not have the added warmth of the huddling that occurs in large broods, and consequently much energy may be used by nestlings in small broods just for thermoregulation (Royama 1969). In very large broods, the opposite problem, overheating, may occur. Thermoregulation is another component of reproduction that may place some restraint on clutch size.

Natural selection would seem to operate to maximize reproductive rate, subject to the constraints imposed by thermoregulation, feeding, and predator avoidance. This is called the **theory of maximum reproduction, and Lack's hypothesis** is part of this theory. It is a good example of how stabilizing selection can operate on a phenotypic trait such as reproductive rate. The maximum clutch size is called the **Lack clutch** size.

Lacks hypothesis :

Lack (1947) was the first to propose a functional hypothesis for the evolution of clutch size in birds . He suggested that as clutch (and hence brood) size increased, each of the nestling would receive less food and hence survive less well. As a result, an intermediate brood size might produce the greatest number of survivors. Lack proposed that the population would evolve the most productive brood size (Charnov and Krebs, 1974) which is also referred to as 'Lack' solution (Godfray, 1987). In other words, the optimal clutch size is determined by the trade off between the number and fitness of offspring.

In essence, Lack's hypothesis determines the optimal way of dividing resources by finding optimal clutch size; the optimal investment per offspring follows from this. An alternative approach (Smith and Fretwell, 1974) is to find the optimal investment per offspring, from which follows the optimal clutch size.

Lacks hypothesis has been tested in both insects and birds. In insects the relationship between survival and brood size has been measured and used to predict the most productive! brood size. When only the survival of offspring is taken into account, mean clutch size is consistently less than the most productive brood size

For example, female C *naculatis* beetles typically lay between two and six eggs on I each black -eyed bean while the most productive brood size is about 16 eggs (Wilson,! 1989). Clutch size is also less than the most productive brood size in all even species! parasitoids studies (Charnov and Skinner, 1985).

In birds, Lacks hypothesis has been tested by manipulating clutch or initial rood size I both up and down. If lack hypothesis is correct, any experimental manipulation should I lead to a reduction in the production of young. In collared flycatchers, an experimental increase in brood size led to an increase in the number of young fledging (Gustafsson I and Sutherland, 1988) and similar increase in productivity, measure in forms of fledged young, have occurred in 35 out of 50 studies (Safriel, 1975); so in birds as in insects, the majority of species lay clutches smaller than the most productive brood size.

r-selection and k-selection :

There are obvious broad differences among reproductive patterns in organisms. *Some* species, such as weeds and insects, are small, have high reproductive rates, and live short lives. Others, like trees and deer, are large and have low reproductive rates and long lives. Ecologists call the former r species and the latter *K* species, after the two terms on the logistic equation. Populations o/the former grow rapidly and do not seem to reach or remain at carrying capacity. The populations o/the latter attain and more or less remain around carrying capacity.

The concept of rand AT species originated with MacArthur and Wilson (1967) MacArthur and Wilson considered the former as r-selected because environmental conditions keep growth of such populations the rising part of the logistic curve. Mortality in theses species is largely density-independent. They considered the latter as K-selected because they are able to maintain their densest populations at equilibrium (asymptote) or carrying capacityfAT). *K* species were are able to compete effectively for food and other resources in a crowded environment. Mortality in these species results mostly from density-related factors.

The theory of *r* and K-selection predicts that species in these different environments will differ in life history traits, such as size, fecundity, age at first reproduction, number of reproductive events during a lifetime, and total life span. Species popularly known as r-strategists are typically short-lived. Among species selection favors those genotypes that confer high reproductive rate at low population densities (Figure-3), early and single-stage reproduction, rapid development, small body size, large number of offspring (but with low survival), and minimal parental care.

They have the ability to make use *of* temporary habitats. Many inhabit unstable or unpredictable environments where catastrophic mortality is environmentally caused and relatively independent *of* population density. For them environmental resources are rarely limiting, and they are able to exploit relatively uncompetitive situations. Tough and adaptable r-strategists, such as weedy species have means of dispersal, are good colonizers, and respond rapidly to disturbance.

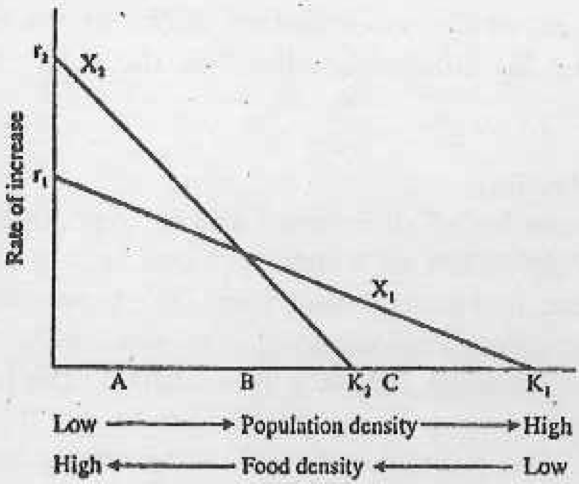


Figure-3. A model of r- and K-selection involving the rates of increase of two genes, X(and X2. Under the environmentall conditions at point A, X2 increases faster than X, and continues to do so up to point C. This population is, r-selected. Under the environmental conditions at point B, Xf increases faster than Xr This population is K-selected. Where the lines cross at point C, r-selection switches to K-selection. (After MacArthur, 1972:228.)

K-strategists are competitive species with stable population of long lived individuals. Among them selection favors genotypes that confer a slower growth rate at low popula"5 but the ability to maintain that growth rate at high densities. K-strategists have the ability to cope with physical and biotic pressures, possess both delayed and repeated reproduction, and have a larger body size and slower development. They produce few seeds, eggs, or young. Among animals, parents care for the young, among plants seeds possess stored food that gives the seedlings a strong start. K-strategists exist in environments in which mortality relates more to density than to unpredictability of conditions. They are specialists, efficient users of a particular environment, but their populations are at or near carrying capacity and are resource-limited. These qualities, combined with their lack of means of wide dispersal, make K-strategies poor colonizers.

Attributes of r and k selection

Attributes	r-selection	k-selection
Climate	Unpredictable	Predictable
Population size	Variable in time	Constant in time
Competition	Lax	Keen
Selection forms	Raid development, Early reproduction, Small body size, Many offspring	Slow development, Delayed reproduction, Large body size,few offspring
Length of life	Short (< 1 year)	Long (>1 year)
Stage in succession	Early	Late (Climax)
Leads to	Productivity	Efficiency

UNIT 4 ◻ Preadation

Structure

4.0 ◻ Introduction

In population interaction most important type of interaction which has dealt in great details is predation. **Predation** is commonly associated with the strong attacking the weak, the lion pouncing on the deer, the hawk upon the sparrow. However, considered more broadly, predation also includes **parasitism**, a case of the weak attacking the strong. In this situation, one organism, the parasitoid, attacks the host (the prey) by laying its eggs in or on the body of the host. After the eggs hatch, the larvae feed on the tissues of the host until it dies. The effect is the same as that of predation.

Another special form of predation is **cannibalism**, in which the predator and the prey are the same species. The concept of predation has been extended still further to include herbivory, in which grazing animals of all types feed on plants. **Herbivores** kill their prey when consuming seeds or the whole plant, or they function as parasites when they consume only part of the plant but do not destroy it. Thus **predation** in its **broadest** sense can be defined as on organism feeding on another living organism, or **biophagy**.

Ecologically, predation is more than just a transfer of energy and nutrients. It represents a direct and often complex interaction of two or more species, of the eaters and the eaten. The numbers of some predators may depend upon the abundance of prey, and predation may be involved in the regulation of prey populations.

4.1 ◻ Models of prey predatory dynamics

In 1925 A. J. Lotka, a mathematician and physical scientist, proposed the first model of predator-prey interactions in *Elements of Physical Biology*. In

1926 the Italian mathematician A. Volterra independently, came up with a similar model.

The Lotka- Volterra model involves paired equations, one for the prey population andl one for the predator population. The prey growth equation has two components, the! maximum rate of increase per individual and the predatory removal of prey from thel population.

$$dN/dt = aN - bNP$$

For the predator population:

$$dP/dt = cNP - dP$$

Where N and P are the densities .of the prey and the predator, respectively, and a I and d are the per capita rates of change in absence of each other, and b and c are the rates of change for prey and predator resulting from the interaction of the two populations.

The Lotka Volterra model is based on a number of under lying assumptions :

(1) in the absence of predation, the prey experiences exponential growth;
(2) the predator population declines exponentially in the absence of prey;
(3) predators move at random among randomly distributed prey;
(4) the proportion of encounters that result in the capture and consumption of prey are constant at all predator and prey densities;
(5) the number of prey taken increases in direct proportion to the number of predators, a linear response;
(6) all responses are instantaneous with no time Jag for handling and ingesting prey; and
(7) energy input to predators is immediately converted to the birth of more predator.

The **Lotka-Volterra** model is depicted graphically in **Figure -A.** The ordinate *P* is the number of predators; the abscissa *N* is the number of prey. The horizontal straight line is the zero growth curve of the prey, and the vertical line is the zero growth curve of the predator. In the area to the right of the vertical line, predators increase; to the left, they decrease. In the area below the horizontal line, the prey increase, and above it they decrease. The circle of arrows represents the joint population of predator and prey and the way it changes. If a point or arrow falls in the region to the left of the vertical line, the prey population is not large enough to support the predators and the predator population declines. If an arrow falls to the upper left, both populations are declining. The predator population decreases enough to permit the prey population to increase, moving the arrow to the lower left. The increase in the prey population now permits predators to increase, and the arrow moves *to* the lower right. As the predator population increases, depressing the prey population, the arrow moves to the upper right. This interaction between predator and prey results in reciprocal oscillations of predator and prey with some time delay in the predator's response. These regular oscillations or cycles will continue.

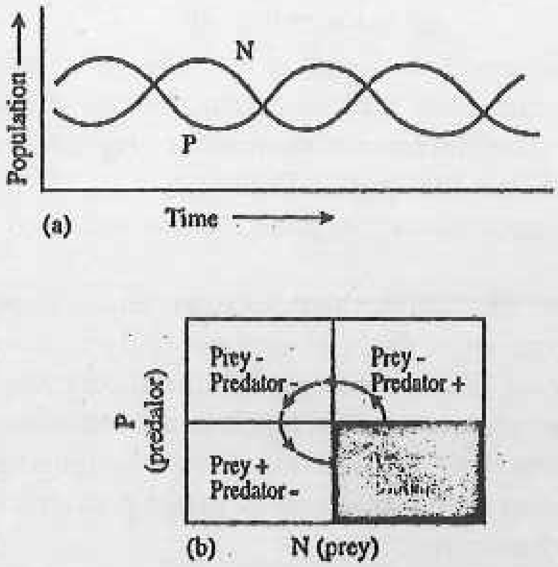


Figure-A. Lotka-Volterra model of predator-prey interactions, (a) The abundance of each population is plotted as a function of time, (b) The joint abundance of species. The zero growth curve or isocline of the predator is vertical and the isocline of the prey is horizontal. They intersect at right angles. A minus sign shows population decline and a plus sign population increase. Predators increase to the right of the vertical line; prey increase below the horizontal line.

A decade later an ecologist, A. J. Nicholson, and a mathematician, W. Bailey, recognized the deficiencies in the Lotka- Volterra model. They developed a model for a hostparasitoid relationship (Nicholson and Bailey 1935). Parasitoids differ from predators in that their attacks. In fact, one host may be attacked many times. The number of parasites reared on the host depends upon the number of attacks, not the number of hosts encountered.

Nicholson and Bailey based their model on a set of assumptions somewhat different from the Lotka- Volterra model.

1. Predators search randomly for static prey uniformly dispersed over a homogeneous landscape.
2. The predators have a constant area of discovery and an insatiable appetite. The predators sample a certain proportion of the prey population. The time element is discrete, not continuous.
3. The generations of both predator and prey have the same time span and are of the same length.
4. Predator mortality is density-independent. The conversion of energy input by thel predator into the birth of more predators is not immediate but delayed by one generation.

4.1.1 Limitations of the model

The equations are based on certain false assumptions

1. Both population have unlimited rate of growth. Neither prey not the predator population inhibits its own growth.
2. Environment is completely closed and homogeneous i.e., prey is randomly distributed and predator also moves randomly in the prey population.
3. Every prey has equal probability of being attacked and every encounter of a predator with prey results into capture of prey. There is no wasted attempt.
4. All responses are instantaneous with no time lag for handling or ingestion of prey.
5. Age structure of both the population is unimportant. Young and old individuals are equally capable of capturing prey or escaping predator.
6. Density dependent mortality of predator or prey is unimportant.
7. Interaction of prey with its food has not been taken' Into consideration.

4.1.2 Different types of interaction between two populations

Organisms do not exist alone in a nature but in association with other organisms of several species in an area will remain unaffected by the presence or absence of other species but in some cases two or more species will interact. Some types of population interactions are summarized bellow.

Analysis of two species population interactions :

Type of interaction	Species-1	Species-2	General nature of interaction
Neutralism	0	0	Neither population affects other
Competition	-	-	Direct inhibition of each species by other, unfavourable of both species
Amensalism	-	0	Unfavourable for species -1, which is affected, No effect on other.
Commensalism	+	0	Favourable for species -1, No effect on other.
Parasitisim	+	-	Favourable for species -1, the parasite (smaller than the host), unfavourable for species -2 (host).
Predation	+	-	Favourable for species -1, -the predator (generally larger than prey) unfevourable for species -2
Photocoperation	+	+	Favourable for both not obligatory.
Mutualism	+	+	Favourable for both obligatory.

0 = No. significant interaction ;
+ = interaction is beneficial resulting into growth ;
- = interaction harmful resulting inhibition.

4.1.3 Competitive Interactions

Competition can be defined as interaction of two species using the same limited resource or harm one another while seeking a resource.

Competitive interactions-are those in which two species negatively influence each other's population growth rates and depress each other's population size.

Based on mechanism of competition, competitive interactions are of following types—

Exploitation Competition occur when populations depresses one another through use of a shared resource such as food or nutrients. Examples include tropical reef fish that graze on the same kinds of algae and desert plants that complete for a limited supply of water.

Interference Competition occurs when an individual or population behave in a way that that reduces the exploitation efficiency of another individual or population. Examples include song birds that maintain well established breeding territories, and out colonies that kill invaders at food patches.

In allelopathy plants engage in a form of interference competition.

Note- Interference competition leaves more resources or population for the winner to consume so it may evolve as an adaptation when exploitation competition is severe.

Pre-emptive competition is a category that has elements of both exploitation and interference. In pre-emptive competition, organisms cbmpete for space as a limiting resource. Examples include birds that use free holes for nesting and intertidal algae that must attach to stable rock surfaces. Unlike food or nutrients that are used exploitatively, space is a renewable resources that is recycled - as soon as organism dies or leaves, the space is immediately available for use by other individuals.

Based on the extent of competition competitive interactions are of two types

A. **Intraspecific competition-** is competition that occurs among members of the samfl species. The logistic equation - $[dN/dt = (b'-d')N]$ is a model of intraspecifiM because competition per capita growth rate diminishes as the population becornfl more crowded.
B. **Interspecific Competition-** is competition between individuals of two or more species

4.1.4 Role of predation in nature

Predation is consumption of one organism (the prey) by another organism (the predator)! in which the prey is alive when the predator first attack it. Whether a predator controls I a prey population or prey population size determines the number of predators has long I been debated by ecologists. Both cases can be true. Let us consider the example of a predator introduced to a habitat in which there are abundant potential prey items. The predators will thrive and increase in number (**Figure-A.a**). After a while, the prey numbers will start to decline. The predator is, therefore, restricting the size of the prey population. We can say that this system is subject to top-down control, because it is the number of predators that will determine the number of prey. Top-down control can be found in numerous systems, such as where grazing sheep and rabbits control plant growth in a pasture, where wolves control deer populations, and in lake ecosystems where large predatory fish may be holding other populations in check. If those large fish are removed, a frequent result is that the populations of smaller fish increase rapidly because they are now free of predation.

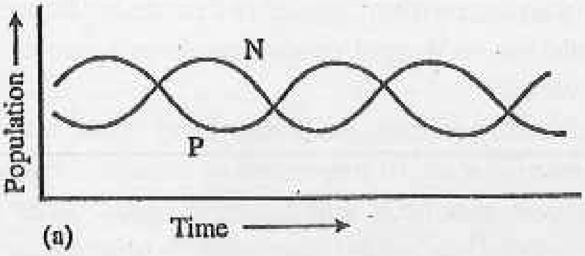


Figure-A.a. a) The abundance of each population is plotted as a function of time

Alternatively, we can think about a world in which populations are driven by limiting resources and the entropy of energy along food chains. Here, we start with a finite pool of resources that are used by the primary producers. The population size of herbivores in this situation may be controlled by the quality of grazing. Predators in this system are seen as limited by the amount of energy in the herbivore trophic level. As herbivore numbers swell, more energy is available to the predators, so their numbers grow. But when the herbivores do badly because of lack of food, disease, or some other factor, the number of predators will fall because of lack of food. This system is being driven by factors at the base of the food chain, with repercussions into the upper trophic levels; thus it is termed a system of **bottom-up control.**

Ecologist investigating processes of competition in the field especially on predation have noticed that predation has had very substantial modifying effect on community structure.

Connell (1961) in his classical studies of the competition for space occurring between the inteftidal branches. *Balanus balaloides* and *Chthamalus stellatus,* identified the very Important role of the predatory gastropod, *Thais lapillus,* in moderating the intensity of competition as well as acting as a limiting factor for *Balanus* at the lower end of its distribution This moderating effect seems a -near-universal property of generalist predators. The role of predatory beetles such as *Ptomaphila lachrymosa* and *Creophilus erythrocephalus* preying upon carrion-feed ing blowfly larvae f) Jelonging to the genera, *Calliphora, Chrysomyia* and *Lucilia,* must reduce fthe intensity of interspecific competition which has been demonstrated to occur among them (Fuller 1934; Ullyett 1950)

Paine (1966) extended the ideas and observations of Connell showing very clearly that certain predators or top predators playa crucial role in maintaining the structure of the food-webs within natural communities. Like Connell, Paine used intertidal communities to support his thesis, comparing selected webs across temperate, subtropical and tropical zones in North America. He identified what he later called 'keystone' predators '(paine 1969), the removal of which led to intense competition within llwer trophic levels and, ultimately, substantial simplification of the food Web concerned.

Predator increase species diversity

Predation leads to the whittling of a prey population, and one might intuitively think that this process threatens the very survival of the prey species. But the converse may be true. It may be that predation is essential for the survival and coexistence of many species. Predation and the continued existence of healthy predator populations may be an integral part of the biodiversity equation.

Predation ensures that the weak and sickly are removed from the prey population. They seldom get the chance to breed, so the breeding stock remains strong. But the predators may have an even more profound effect as they limit the intensity of competition among their prey. To minimize energy expenditure, predators will hunt the most abundant, preferred prey item. Then, as that becomes scarce, they will switch to an alternative. As that prey population declines, the predator will be forced to search for a third type of prey. A diversity of prey populations may be held in check by a single predator.

The explanation is that without predation, one species of barnacle flourished and! displaced some of the mollusks through intensified competition. In turn, this barnacle! was later replaced by two species of bivalve. Competition had been fierce for the limitedl resources on the rock, and without the predator holding the various prey populations in I check, some species had been ousted through competitive exclusion.

Another important insight that arose from Paine's study of the rocky intertidal zonel was that one species may play such a pivotal role that if it were to go extinct the entire community would disappear. Because such a species is disproportionately important to the ecosystem, it was likened to the keystone in an arch. When building a stone arch, the structure was completed by the placement of a wedge-shaped stone in the apex of the arch.

This, the keystone, held all the other blocks in place; if it were removed, the arch would collapse. In Paine's study he suggested the starfish is so important that it be termed a keystone species. A keystone species is now recognized to be broader than just a top predator. A keystone species can occupy any trophic level, but its influence on the local community is disproportionately large compared with its biomass. Removing a keystone species results in a cascade effect that causes all the trophic levels to change-Another realization is that keystone species are essentially local phenomena. In one habitat the starfish is a keystone species, in another the same species of starfish is just an ordinary member of the local community. The starfish, gray wolf, and alligator are examples of predatory keystone species.

Even a primary producer can be a keystone species. In most tropical forests, fruit availability is somewhat seasona; a pattern that results in a glut of fruit production at some times- of tile year and a dearth at others. Animals such as monkeys, chimpanzees, toucans, and hornbills, rely on year-round fruit availability, and when fruit are scarce, their populations are vulnerable to starvation. Figs (*Ficus* species) are fairly unusual rainforest plants in that they produce nutritious fruit throughout the year. During the hungry times for the fruit-eating animals, the difference between survival and extinction is the availability of ripe figs. In these settings, fig trees are considered to be a keystone species.

Predation and ecosystem management

Most nature reserves and remnant patches of natural vegetation are too small to support the predators that feed highest on the food chains. This imbalance may lead to an overabundance of herbivores, leading to overgrazing and environmental degradation. As plans are made to preserve natural areas from development, it is necessary to predict future changes in population densities. For example, it may be necessary to decide if the area would benefit from limited deer hunting to prevent overgrazing of tree seedlings. If hunting is desirable, what is the optimum-number, age, and sex of deer to be removed? Studies of natural predation patterns may lead us to these answers, and they may not accord with the answers preferred by hunters. In terms of reducing deer numbers, it is more important to shoot does than bucks, and shooting a prime male with a fine rack of antlers makes no ecological sense. Perhaps the most important message to conservationists and land managers is that it is possible to change many trophic systems from either the top, the bottom, or for that matter the middle. Before establishing a nature reserve or providing planning permission for a change in land use, it is essential to understand the local systems, their food chains, and predator-prey links.

4.2 □ Optimal foraging theory (patch choice, diet choice, prey selectivity, foraging time)

4.2.1 Introduction

Foraging is an aspect of animal behaviour which is subject to the scrutiny of evolutionary biologist within the general field of behavioural ecology. The aim is to tri to understand how natural selection has favoured particular patterns of behaviour in particular circumstances. Foraging is not just feeding, but it includes searching, capturing food, preparing the food, eating it, moving to other places and so on.

Most animals have the potential to consume a wider range of foods than they actually choose. Evolution usually gives rise to foraging strategies in which animals consume a narrower range of food types than they are morphologically capable of consuming **optimal foraging**. The aim of optimal foraging theory is to predict the foraging strategy to be expected under specified conditions It generally makes such prediction on the number of assumptions—

1. The foraging behaviour of present day animals has been favoured by natural selection and at present most enhances an animal fitness.
2. High fitness is achieved by a high net rate of energy intake (i.e. gross energy intake minus the energetic costs of obtaining that energy).
3. Experimental animals are observed in an environment to which their foraging behaviour is suited or it is a natural environment very similar to that in which they are evolved.

4.2.2 Foraging behaviour

Foraging is the set of process by which organisms acquire energy and nutrients whether the food is directly consumed (feeding), stored for later consumption (hoarding) or given to other individuals (provisioning). Foraging behaviour plays an important role in I evolutionary biology, not only because it is a major determinant of the survival, growth and reproductive success of foragers but also because of its impact on predator avoidance, pollination and dispersal adaptation of potential food organisms (Donald L. Kramer, 2001).

4.2.3 Historical context

Contemporary studies of foraging by evolutionary ecologists are based on the synthesis of two research tradition- both emerging during the 1960s . The ethological approach is illustrated by the research of K. Von Frisch and his associates on honeybee foraging and N. Tinbergen and his group on searching behaviour of birds. The 1970s and 1980s witnessed continued growth in the field of behavioural ecology with the development of new theoritical tools. The most important development during the period was the incorporation of frequency dependence into the study of foraging using game theory (Giraldeau and Caraco 2000). Harper (1982) successfully applied a large scale model of habitat selection called the ideal free distribution (Fretwell, 1972) to local scale competitive foraging of ducks in a park pond . Bernard and Sibly (1981) recognized the inherent frequency dependence of some individuals expectation of the foraging efforts to others (Kleptoparasitism). These developments stimulated many researches to recognize these games among foragers in theoretical and empirical perspectives.

At the start of 21st century, studies on foraging is growing steadily and it includes spatial distribution, predation risk, pollination, seed dispersal etc (Fryxell and Lundberg, 1997).

4.2.4 Basic elements of the foraging process

Foraging cycle and their components :

Foraging is a cyclical activity in which a series of behavioural acts leads to the final consumption of each unit of food. The foraging sequence is divided into functional categories called components **(Table-1)**

For animals that feed on discrete items, whether mobile or not, the "prey cycle" is the basic unit of foraging; this includes search, assessment, pursuit, and handling. Then food items are aggregated, multiple prey cycles occur within a patch cycle comprising patch search and/or travel, patch assessment, and patch exploitation. When foragers return to a fixed location to consume or hoard their prey or to provision other individuals and carry multiple prey per trip, prey and patch cycles can be nested within a central place cycle consisting of travel, loading, and unloading components. Multiple prey, patch, and central place cycles are often nested within a meal or foraging bout cycle, which in some species may include travel to and from a foraging site as well as an obligate period of nonforaging while food is digested.

Although useful in the establishment of a general theoretical and empirical framework for foraging, the division of a continuous sequence into separate components is somewhat arbitrary. For example, in some sit-and-wait predators, handling one prey overlaps with search for the next. Categories may be subdivided, combined, or deleted according to the organism, food type, and question being asked. For example, assessment is often included as part of search, while pursuit can be usefully divided into stalk and attack components.

4.2.5 Measures of Foraging Success

Ideally, evolutionary studies of foraging behavior should use measures of foraging success that are correlated as_ closely as possible with fitness. However, the nutrients and energy obtained by foraging are often allocated simultaneously to survival, growth, and reproduction, making it impossible to examine a single major component of fitness. Thus, comparisons of foraging behavior are based on estimates of the success in gaining food and the costs of doing so, although the quantitative relationships of these measures to fitness are usually unknown.

Net rate of energy gain .is frequently considered the ideal measure of foraging success. Maximizing this rate provides the most energy for fitness-related activities and permits the animal to minimize its foraging time to allow for other important activities.

Table-I Components of the foraging process.

1. The prey cycle -acquisition of individual food items.

1.1. **Search**-leads the forager to come into sensory contact with potential prey and terminates when a prey is detected; for cryptic prey, may be divided into phases in which prey are encountered (potentially detectable) and not-encountered (out of detection distance); may be active (involving movement by the forager) or sit-and-wait (forager not moving during search).

1.2. **Assessment**-leads the forager to pursue or abandon detected prey; may also occur during pursuit and handling.

1.3. **Pursuit-leads** the forager to come into physical contact with detected prey (capture); may include ambush (forager nor moving during pursuit), stalking (approach, often slow, that is difficult for prey to detect), and overt arrack.

1.4. **Handling**-leads to consumption of captured prey; may include food preparation (e.g., killing, removing shell or spines) and ingestion (e.g., grasping, masticating, swallowing).

2. **The patch cycle-foraging on aggregations of prey.**

2.1. **Search**-leads the forager to detect a patch whose location was previously unknown; when movement is between patches of known location, interpatch travel is a more appropriate term.

2.2. **Assessment** -leads the forager to begin to exploit or to abandon a patch.

2.3. **Exploitation**-series of prey cycles (sometimes without additional prey search) that leads to consumption of some or all prey in patch.

3. **The central place trip cyclic-foraging that involves movement between a foraging site and a fixed location to which the forager returns with prey.**

3.1. **Outward trip**-movement from the central place to the foraging site.

3.2. **Loading**-one or mqjj^prey or patch cycles leading to accumulation of a prey load.

3.3. **Return trip**-movement from the foraging site to the central place carrying prey.

3.4. **Unloading**-deposition of the prey load in the central place (may be replaced by handling when prey are consumed rather than stored or provisioned to others at the central place).

4. **The meal/foraging bout cycle-foraging that occurs in more-or-less discrete periods separated by bout of other activities.**

4.1. **IVavel**-movement to a foraging area from a location at which other activities take place.

4.2. **Feeding**-sum of activities in prey, patch, and central place cycles.

4.3. **Processing**-digestion and assimilation of food; although some digestion occurs during feeding and other activities, processing is relevant as a separate category when food consumption is very rapid relative to digestion resulting in a required pause between bouts of feeding; this phase is sometimes called handling in ecological (bur not behavioral) analyses.

4.4. Other activities -not foraging; may overlap with processing.

4.2.6 Foraging decisions

1. A key aspect of foraging behavior is its flexibility. Often, an animal

has the option of continuing what it is doing, switching to an alternative form (or "mode") of the same component or switching to another component altogether. For example, when stalking a prey, a lion may at any moment continue the stalk, switch to direct arrack, or begin to search for an alternative prey.

2. Decision rules are the relationships between foraging decisions and environmental conditions, such as food density, or organismal states, such as the individual's fat level. (Some of the principal foraging decisions are listed. In table -2.)

3. The degree of flexibility in decision making is potentially highly variable. For example, the decision whether to consume a particular type of potential prey could be fixed for an entire species, could vary among populations exposed to different densities of that prey or alternative prey, or could vary within an individual, according to prey abundance and the individual's current handling skills, physical condition, or nutritional needs and so on.

Table-2 Some foraging decisions studied by behavioral ecologists.

1. **Time budget decisions**
   When to start a foraging bout (e.g., relation to time of day, local conditions, internal state)
   When to stop a foraging bout
   When to initiate and terminate controlled interruptions of a foraging bout (e.g., vigilance, grooming)
2. **Spatial distribution decisions**
   Which specific site to search and the sequence in which to visit multiple sites
   When to switch to another site
   How close to other foragers to search (e.g., foraging group size, local density)
3. **Movement decisions**
   Locomotor mode (e.g., fly versus walk)
   Speed and gait of movement
   Duration, timing, and location of pauses during movement (intermittent locomotion)
   Timing and direction of turns and intervals between them
   Specific route

4. **Selectivity decisions (choice)**
   Microhabitat choice (e.g., substrate types, proximity to other foragers)
   Diet choice
   Patch choice
   Behavioral sequence choice: In which order to perform different activities involved in assessment, handling, and patch exploitation
5. **Persistence decisions**
   Whether to continue assessment, pursuit, handling, patch exploitation, or loading versus returning to search
6. **Food allocation decisions**
   Whether to consume or hoard a particular item or ro provision others
   Where to hoard
   Which individual to provision
7. **Defense decisions**
   Whether to defend
   What specific area to defend ` and not defend
   When to patrol and display
   Which intruders to respond to and in which order
   Whether to threaten or attack
   Attack and display decisions (mode, speed, duration)
   (*Note:* Intruders will have a parallel set of decisions with regard to defenders.)
8. **Information acquisition decisions**
   Whether to sample other prey and sites or other foragers
   When to sample
   Which sites to sample and in which order
   How long to sample a particular site.

4.2.7 Foraging games

i) An important part of the foraging environment for many species is the presence of other foragers, of the same and sometimes other species, which can increase or decrease foraging success (Table-3). Such effects are most evident when animals forage in groups, but even "solitary" foragers can affect each other, for example, by reducing prey abundance, alerting prey to the presence of predators, or revealing new food sources by their foraging activity.

ii) Many processes involving interactions with other foragers show density dependence because their occurrence, magnitude, and sometimes direction depends on the number of other individuals present.

iii) Density dependence is often negative, in that some currency of foraging declines with the number of other individuals, but it may also be positive (also known as an *Allee effect)* over at least part of the density range.

iv) Sometimes, social effects may be affected by the proportion of individuals making different alternative decisions. This frequency dependence is an important of social foraging, often in combination with density dependence.

Note:-The basic approach of game theory is to find, from a given set of decision rules. The rule or mix of rules among the interacting individuals such that no individual using an alternative rule would have greater success than the individuals using the established rule or rules. From the perspective of evolutionary genetics, this situation prevents genes for alternative rules from invading the population and is therefore called an *evolutiollarily stable strategy* (ESS)

A fundamental characteristic of social foraging is that the effort of individual foragers creates an opportunity for parasitism of that effort by other foragers. Kleptoparasitisim, however, is not a viable foraging strategy if all foragers are attempting to do it and none are looking for their own food.

Game theory is also relevant to interactions between predators and prey and between Plants and their pollinators and seed dispersal agents.

Table-3 : Social influences on Foraging

1. Changes in food availability.

-Exploitation-removal of food from the foraging area.

-Passive interference (also called prey depression)-reducing foraging rates by making prey less available, for example, by inducing its anti predator defenses.

+ Facilitation-making prey more available, for example, by confusing them or making them more visible while fleeing another forager.

+ Risk reduction-lowering the variance of foraging success by sharing food iscoveries among individuals.

2. **Changes in costs or benefits of search, pursuit, and handling.**

+ **Cooperative hunting**-improved pursuit and handling success or decreased pursuit and handling time by groups.

+ **Increased rate of discovery** of shareable prey or patches by foragers in groups.

- **Scramble** competition-animals foraging in groups may have search areas that overlap with those of other foragers and therefore require more search time to discover the same number of prey; they may have to increase their rate of movement or change other foraging tactics to avoid having other foragers discover or capture the prey first.

3. **Kleptoparasitism**-exploiting the search, pursuit, and handling of others.

+ **For the kleptoparasite,** more potential victims decrease search, pursuit, or handling time by allowing exploitation of prey or patches in which another individual has already invested.

-/+ **For the kleptoparasite,** more kleptoparasites may change food availability and change costs and benefits of foraging as in sections 1 and 2.

- **For the victim,** more kleptoparasites result in increased effort in search, pursuit, or handling as a result of tosingprey or all or part of patches, or additional effort to avoid or defend against kleptoparasites, or reduced success as a result of choosing prey less vulnerable to kleptoparasitism.

+ **For the victim,** more victims can improve defense or dilute the impact of kleptoparasires.

4. **Food defense (also called active interference or interference competition)**-use of aggressive behavior to reduce thatforaging of other individuals on particular prey (food guarding) or specific locations (territoriality).

+ **For the defender,** increased prey availability as a result of reduced exploitation and passive interference by other individuals.

+ **For the defender,** effectiveness of defense may be increased by cooperative defense.

- **For the defender,** costs of defense increase with the number of potential intruders.

+ **For intruders,** foraging in groups can increase access to defended areas or prey by overcoming the defense.

- **For intruders,** decreased access to particular prey or foraging sites as a result of effective defense by other individuals.

- **For intruders,** increased effort or risk of injury to obtain resources by intruding in locations defended by others

5. **Changes in foraging time availability and risk of attack from predators or conspecifics.**

+ **Grouping** can reduce predation risk during foraging; this may permit less time to be spent on vigilance duringthe foraging period or the use of sites that would be too dangerous for a solitary individual.

- **Foraging** in groups may attract more predators, increasing predation risk or reducing the areas that are safe to use.

+/- When **attacks from conspecifics** are a threat, groups may either increase or decrease the risk, depending on the situation.

6. **Foraging information.**

+ **Other individuals** can be used to obtain information about beneficial foraging locations, food types, and foraging techniques.

Information scrounging may reduce the number of accurately informed individuals and provide wrong information.

Note: Minus and plus signs indicate how each process will affect the foraging success of a focal individual as the number of the foragers increases.

4.2.8 Functional response

The Lotka- Volterra equations of predation hint at two distinct responses of predators to changes in prey density. As prey density increases, each predator may take more prey or take them sooner, a functional response; or predators may become more numerous through increased reproduction or immigration, a numerical response. Holling recognized three types of functional response (Figure-A): Type I, ill which the number of prey eaten per predator increases linearly to a maximum at density increases (the Lotka-Volterra

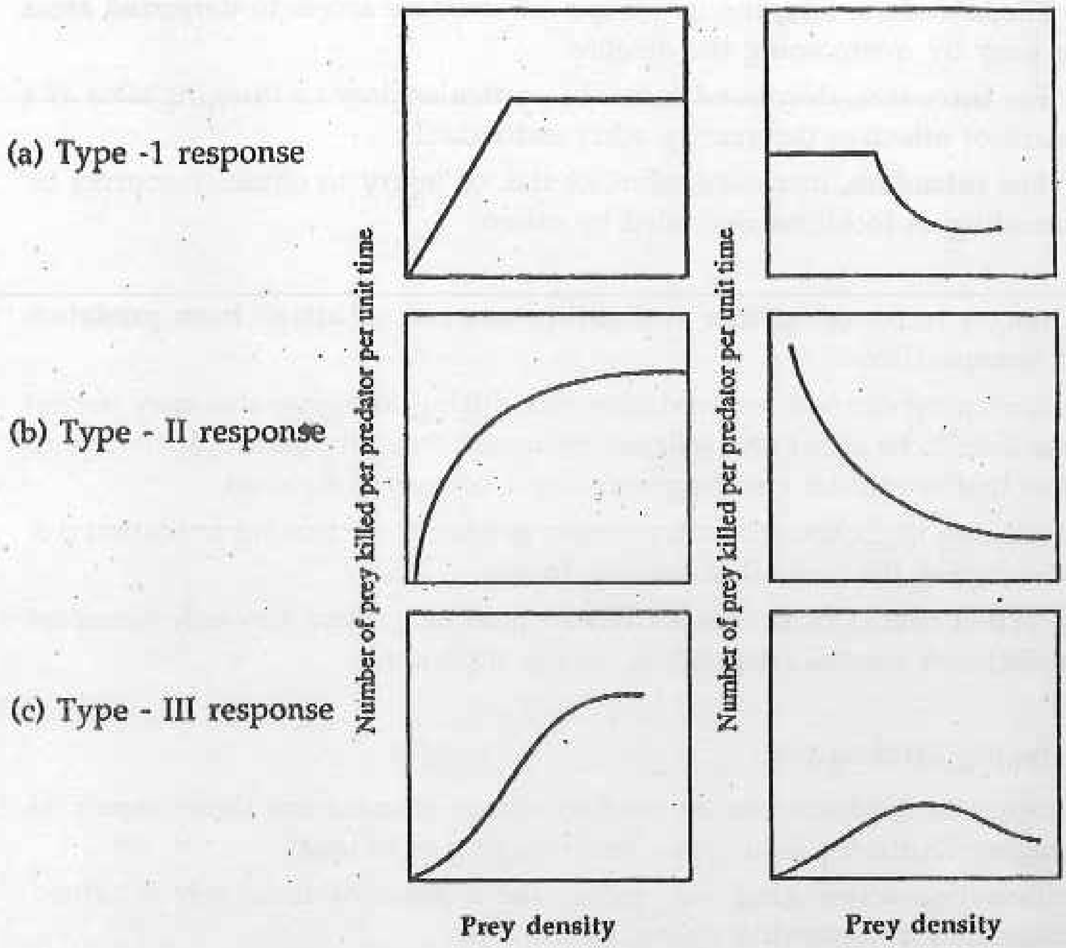


Figure-A. Three types functional response curves, which relate predation to prey density.

- **(a)** **Type-I.** The number of prey taken per predator increases linearly to a maximum as prey density increases. Graphed as a percentage, predation declines relative to the growth of the prey population.
- **(b)** **Type-II.** The number of prey taken rises at a decreasing rate to *D* maximum level. When considered as a parentage of prey taken, the rate of predation declines as the prey population grows. Type II predation cannot stabilize a prey population.
- **(c)** **Type-III.** The number of prey taken is low at first, then increases in a sigmoid fashion approaching an asymptote. When, plotted as a percentage, the functional response still retains some of the sigmoid features, but declines slowly as the prey population increases. Type III functional response has the potential of stabilizing prey populations. (After HoUing 1959.)

assumption), **Type -II** in which the number of prey eaten increases at a decreasing **ratel** toward a maximum value; and **Type III.** in which the number of prey taken is low I at first and then increase in a sigmoid fashion, approaching an asymptote.

Assumed that the well adapted animal would optimize its energy intake, predicted that I the decision to stop feeding in one area and move to the next could be calculated by I knowing how much energy was involved in staying and moving away.

4.2.9 Optimal foraging theory (OFT)

The profitability of hunting by a predator relates to the manner in which its prey is distributed. If prey were distributed in a fine-grained manner, the predator could pick and choose with a search image. Prey, however, are distributed in a coarse-grained manner in patches across the landscape. These patches vary in size and in the quality and quantity of resource, and so the predator must be able to locate profitable patches. This fact gave rise to the concept of the optimal use of patchy environments advanced by MacArthur and Pianka (1966), which later evolved into optimal foraging theory. This theory forms a basis against which actual foraging strategies can be compared.

A foraging animal wants to obtain the most energy from food intake relative to the energy expanded in securing and eating the food. The difference is net energy gain. Its optimal foraging strategy provides a maximum net rate of energy gain, endowing the animal with the greatest fitness. It involves two separate but related components. One is **optimal diet;** the other is **foraging efficiency.**

Response Curve Type-III :

Type III functional response is more complex than Type II. It has been associated wrth vertebrates that can learn to concentrate on a prey when it becomes more abundant, but studies by Hassell et al. (1977) show that Type III is found among invertebrate predators as well.

In Type III response the number of prey taken per predator increases with increasing density of prey and then levels off to a plateau where the ratio of prey taken to prey available declines Because the amount of prey taken is density-dependent, Type III functional response is potentially stabilizing.

The Type III response curve may reflect the acquisition of a search image in some predators, but the same response curve could result from how predators must allocate energy to secure prey (Royama 1970). It is energetically unprofitable for predators to spend time where prey density is low. Predators must discover the most productive way to allocate their hunting time among different prey species of different abundances in different patches. Profitability is measured not by prey density, but by the amount of prey (preferably measured in terms of biomass) that a predator can harvest in a given time. This profitability of hunting is sufficient to produce Type III curves.

4.2.9.1 Optimal diet

Suppose black oilseed (a medium-sized sunflower seed) and white millet (a small seed) are given to winter birds. According to studies of preferred food of winter birds, black oilseeds are preferred by cardinals, house finches, and nuthatches, who extract the meat. The preferred food of mourning doves supposedly is millet, a dose relative of its natural food. After that it was noticed that the doves choose oilseed over the millet. They will not crack the seeds as finches do-their thin pointed bills are not adequate to the task-but will eat them whole. Only after the day's allotment of oilseed is consumed will the mourning doves turn to their supposedly preferred millet.

Obviously, the mourning doves found it energetically more profitable to take large oilseeds, rich in carbohydrates, over small millets seeds. Because of oilseed's larger size. the doves could acquire more energy with less handling time, which meant remaining for a much shorter period in the food patch. When feeding on millet, the doves had to handle many more seeds providing much smaller packets of energy per unit effort. In effect, the doves made an optimal economic decision. They chose larger, more profitable seeds over smaller ones.

According to the decision rules, a consumer should: (1) prefer the most profitable prey (items that yield the greatest net energy gain): (2) feed more selectively when profitable prey or food items are abundant; (3) include less profitable items in the diet when the most profitable foods are scarce; and (4) ignore unprofitable items, however common, when profitable prey are abundant. The mourning doves made all the "right",decisions, but they were operating under ideal conditions unwittingly provided: an abundance of food with a choice of only two items. Natural conditions in which they had to locate food patches that provided much smaller and more diverse prey items might have produced a different outcome.

Davies (1977) studied the feeding behavior of the pied wagtail *(Montacilla alba)* and yellow wagtail *(M.flava)* in a pasture field near Oxford, England. The birds fed on various dung flies and beetles attracted to droppings. They had access to prey of several sizes: large, medium, and small flies and beetles.

The wagtails showed a decided preference for medium-sized prey (Figure-B). The size *of* the prey corresponded to the optimum-sized prey the bird& could handle profitably (Figure-C). The birds ignored small sizes, Although easy to handle, small prey did not return; sufficient energy, and large sizes required too much time and effort to handle.

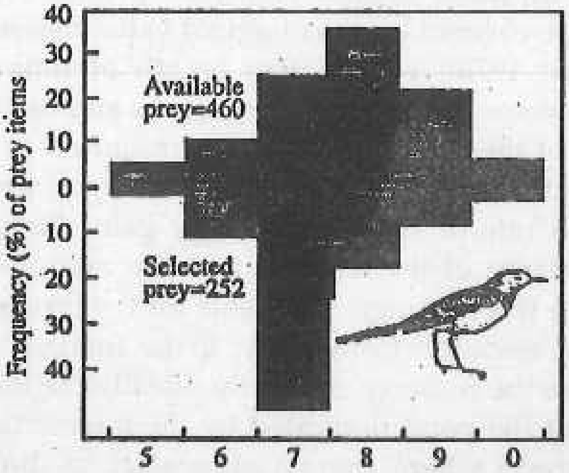


Figure-B. Pied wagtails show a definite preference fur medium-sized prey, which are taken in amounts disproportionate to sizes of prey available in the environment (Davies 1977:48).

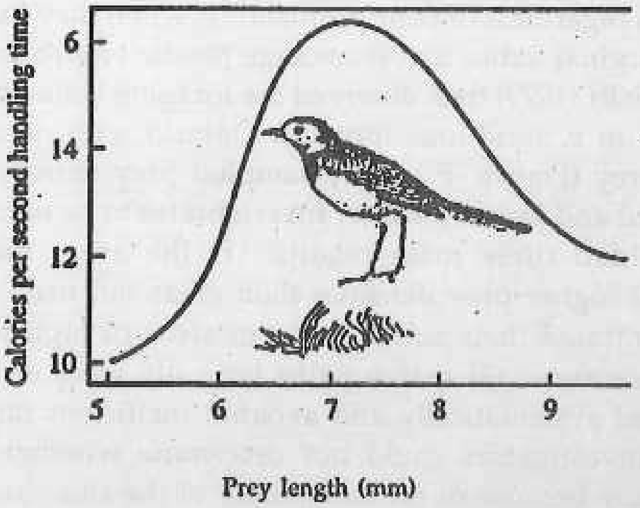


Figure-C Prey size chosen by pied wagtails *(Montacilla alba)* is the optimal size for maximum energy per handling time Small sizes provide too few calories. Large sizes require too much handling time. (Davies 1977:48.)

4.2.9.2 Foraging efficiency

Most animals lie in a heterogeneous or patchy environment. In feeding, they have to concentrate on the most productive *food* patches. This fact has given rise to another set *of* decision rules in optimal foraging theory. The consumer should: (1) concentrate foraging activity in the most productive patches; (2) stay with those patches until their profitability.

These rules are covered by the marginal value theorem (Charnov 1976, Parker and Stewart 1976), which gives length of time a forager should profitably stay in a resource patch before: it seeks another. The length of stay relates to richness of the food patch, the time required to get there, and the time required to extract the resource. When a forager arrives on a patch, it initially has a high rate of extraction energy gain (Figure-D) but as time progress the abundance of the resource and the rate of extraction decline, until on the average it is no longer profitable for the forage remain. Too long a stay depletes the resource. Conversely, if the forager 'eaves a patch too soon, it does not use the resource efficiently. Ideally the forager should leave for another patch at the point (indicated by the intersection of the straight-line tangent **(Figure-E)** where energy gains start to diminish. The model predicts that foragers should remain in a rich food patch longer than in a poor one, and that as travel time between patches increases, it should remain in the patch longer to balance energy loss in travel. Overall the forager should leave all patches regardless of their profitability, when they have been reduced to the same marginal value that is average *for* the environment as a whole.

Zack and Falls (1979) then observed the foraging behavior of free-ranging male ovenbirds in a deciduous forest in Ontario with no control over the birds or their prey (Figure -F). They sampled prey density in the foraging areas of each bird and found the litter invertebrates to be patchily distributed. This study yielded three main results: (1) the areas used *for* foraging consistently had higher prey densities than areas not used for foraging; (2) the birds concentrated their search paths in areas of high prey density and returned to those areas; (3) search paths typically were directional; and (4) the birds foraged systematically and avoided inefficient random searching. However, the investigators could not determine whether the birds were foraging optimally because of the complexity of the situation and the lack of detailed information on prey types. Zack and Falls (1981) concluded.

These and other experimental studies, however, support the hypothesis of optimal foraging up to a point. Much optimal foraging theory concerns mobile animals which forage in areas where food is abundant, leave when searching is no longer rewarding, select the larger and most palatable items of food, leave the poor items until last and travel no farther than necessary to feed. But the theory breaks down with the animals which choose patches in the order of profits or take only optimal food items first and ignore the rest. Such choices may be characteristic of animals foraging in a stable laboratory environment. It is not necessarily the way animals behave in the wild.

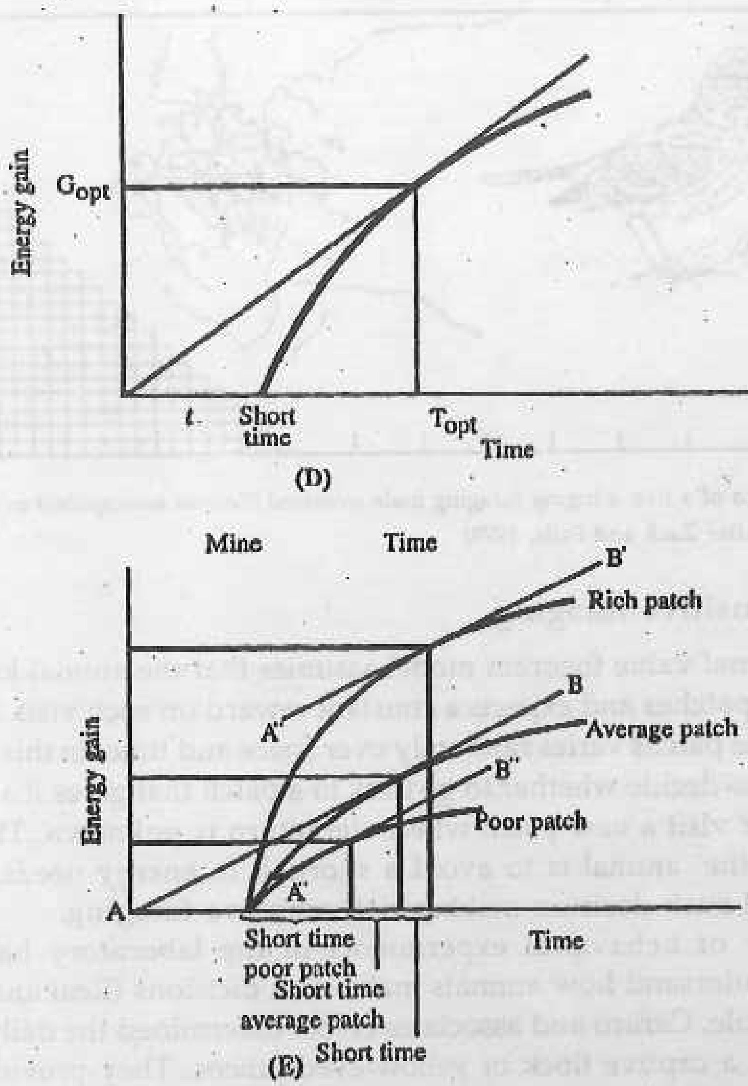
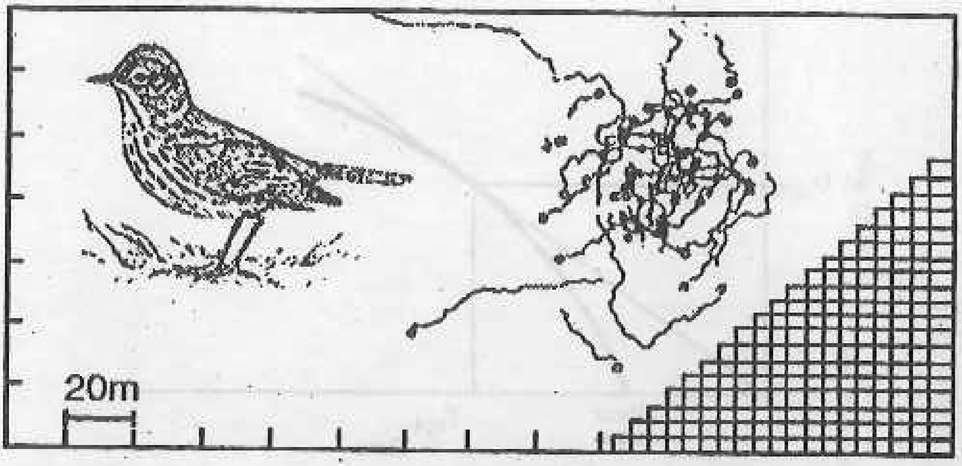


Figure-D & E. The curve represents the cumulative amount of food harvested relative to time in the patch.

Being opportunists, animals will take some less than optimal food items upon discovery and they may quit before food items are reduced to some minimal level. Nor will they pass up certain profitable patches because they do not meet some theoretical expectation. Animals quickly learn where food is and where food is not, and they do not waste much time on a patch after it is depleted. Foragers, however, will stay with a patch as long as the rate of replenishment exceeds the rate of depletion.



Figiire-F. Search path of a free -ranging foraging male ovenbird *(Seiurus aurocapillus)* in a deciduous forest on Ontario (After Zack and Falls, 1979)

4.2.10 Risk-sensitive foraging

The marginal value theorem model assumes that the animal knows Ihe quality of food patches and expects a constant reward on each visit. In reality the quality or the patens varies randomly over space and time. In this situation the animal has to decide whether to go back lo a patch that gives it a constant rate of return or visit a new patch where the return is unknown. The choice is important if the' animal is to avoid a shortfall in energy needs. Animal behaviorists call such decision making **risk-sensitive foraging.**

A number of behavioral experiments in the laboratory have been conducted to undersand how animals make such dicisions (Real and Can co 1986). For example, Caraco and associates (1980) determined the daily energy requirements of a captive flock of yellow-eyed juncos. They provided food (millet) at two feeding stations separated by a partition in their viary cage. The experimenters could manipulate the energy budgets of the birds by depriving the birds of food prior to any trials. In a given experiment one feeding station always offered a constant reward (risk-averse or low risk). The other feeding station offered an unpredictable reward - no seeds half the time; some seeds the other half of the time (risk-prone or constant risk). Thus the birds faced choices between a constant number of seeds and a random number of seeds; but always the mean of the variable reward equaled the mean of the constant reward.

A number of facts have been derived from such experiment.

1. When deprived of rood for one hour in experimental tests and still in a positive energy balance, the juncos avoided risk by preferring the predictable site.
2. When deprived of food for four hours, the birds switched their preference for the variable reward. They changed from being risk-averse to risk-prone.
3. Under energy stress the variable site offered the possibility of providing 50 percent more food than the constant site, whereas the constant site would not provide sufficient food to meet energy needs. Of course, there was the 50 percent risk of finding no food.
4. Nevertheless, in the face of high energy demand, risk-prone behaviour maximized daily survival.

Remark: Animals living in natural conditions face such choices each day. They may start out risk-prone and as time goes on become risk-averse. This behavior has given rise to the expected energy budget rule: be risk-prone if the daily energy budge! is negative: be risk-averse if it is positive (Stephens 1981).

Animal behaviorists undertook several experiments on risk-sensitive foraging in the laboratory in order to find out answers whether laboratory knowledge is applicable in the field.

Cartar (1991) manipulated the energy requirements of the bees by depleting the honey pots or enhancing them with 50 percent sucrose solution. He then censored the foragers from depleted and enhanced colonies visiting the two flower species. He hypothesized that if the bees were risk-sensitive, they should increase their relative use of the more variable huckleberry when the colonies were depleted of energy than when they were enhanced. The bees did so. Because the huckleberry had the higher probability of greater nectar returns, the bees accepted the gamble. They made their foraging decis ons based on the energy requirements of the colony relative to expected intake of energy. Their behavior suggested that the bees were sensitive to the mean and variance of the energy rewards offered by the two plants.

Another, wholly unrelated type of risk-sensitive foraging relates to predation risk. Habitat cover and foraging areas both vary in their foraging profitability and, redation risk. In deciding where it will feed, the forager mu~ balance its energy gains against the risk 0 being eaten. If predators are about, then it may be to the forager's advantage not to visit a most profitable but predator-prone area and 0 remain in a less profitable bui more secure part of the habitat. Ecologists have done many studies on how the presence bf predators affects foraging, mostly in aquatic invertebrates and fish (for a review see Lima and Dill, 1990).

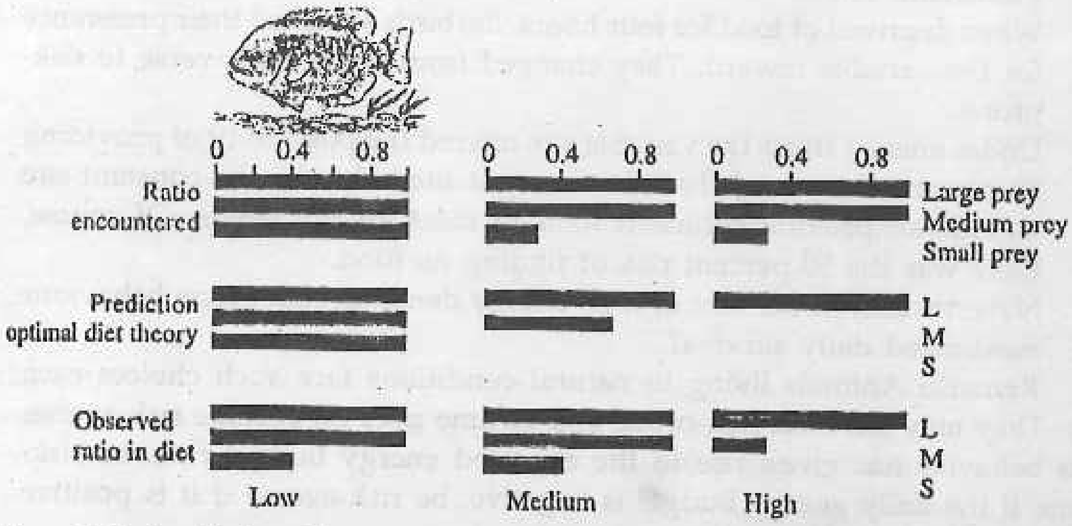


Figure-G. Optimal choice of diet in bluegill sunfish preying on different sizes of *Daphnia*. Histograms show ilic ratio of encounter rules with each size class at three different densities, the prediction of optimal r.ilios in the diet, and observed rat in in the diet Nole the bluegill's preference large prey (Werner and Hall 1974:1048)

4.4 ☐ Terminal questions

1. What is life table? Explain different types of life tables with suitable examples.
2. What are three basic types of survivorship curves? What is a ficundity table? How is it used to obtain net reproductive rate? What is reproductive value?

3. Distinguish between exponential growth and logitic growth. Give the equation for each. In what circumstances might a population be expected to grow in a geomatric fashion and in what circumstances in a.logistic fashion.
4. Explain Verhulst-Pearl logistic growth model with case studies-one from field and one from laboratory studeis.
5. What is the uniqueness of stochastic models of population growth? Discuss this model with suitable example.
6. Discuss the significance of age distribution as an important population characteristic. What are the possibilities of developing stable age distribution.
7. What is the speciality of Leslie Matrix? Discuss diflirent aspects of Leslie Matrix models with suitable example.
8. Explain diffrent aspects of evolution of life history traits. Elucidate the relationship between life history traits and survival strategies.
9. What are the different forms of storage and utilisation of organic matter and energy in the process of growth of organism. Explain ecological efficiency of animals in tiie light of Lindmann efficiency. What is Exploitation efficiency.
10. Briefly discuss the Laws of Thermodynamics with example. Discuss energy budget and partitioning and allocation cf energy for different activities of organisms.
11. Discuss the ecological cost analysis for resource utilization for sexual reproduction.
12. Describe different types of parental behaviour. Discuss the costs and benefits of parental care highlighting Smith-Eretwell Model.
13. Explain the evolution of male and female care with the help of Game Theory Model put forward by Mayerd-Smith (1977)
14. What is evolutionarily Stable Strategy (E.S.S). How one can predict E.S.S based on parental expenditure by males and females. Mention different conflicts those are bring encountered between parents and offspring.
15. Enlist different froms of reproduction in the animal kingdom. Discuss the evolution reproductive strategies highlighting r and k selection strategy. Explain the significance of clutch size in reproductive strategy.
16. What are the different forms of mating system in the animal kingdom.

Explain mating strategy highlighting John Maynard Smith Model (1977)

17. What is sexual selection? Mention its different types. Explain different hypothesis put forword to explain sexual selection.
18. What do mean by Lek behaviour and Lek species? How many Lek species of mammals and buds have so far been reported? Discuss different hypothesis to explain Lek behaviour.
19. Define predation. What is the main difference between predation and parasitism? Enlist different forms of predation. What role do predation play for nature.
20. Discuss Lolka-Volterra model for predation. What are the limitation of this model?
21. What is foraging behaviour. Mention its historical context. Discuss the basic elements of the process.
22. Discuss Optimal Foraging Thoury (OFT) mentioning different functional response and examples.

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UNIT 5 ❐ Competition and Niche theory

Structure

5.0 **Introduction**
5.1 **Intraspecific and Interspecific competition**
5.2 **History of niche concepts**
5.3 **Summary**
5.4 **Terminal question**

5.0 ❐ Introduction

Competition is clearly defined as the interaction of two organisms striving for the same thing. Interspecific competition is any interaction between two or more species populations which adversely affects their growth and survival. Usually competition means exploitation in nature, in which individuals, by using resources, deprive others of the benefits of those resources, from interference competition, in which individuals directly inhibit access to or use of resources by other individuals, often by physical (fighting for example) or chemical means (toxins). Schoener (1983) further subdivided competition into six categories according to its mechanisms.

1. **Consumptive competition,** based on the utilization of some renewable resource.
2. **Preemptive competition,** based on the occupation of open space.
3. **Overgrowth competition,** which occurs when one individual grows upon or over another, thereby depriving the second of light, nutrient-laden water, or some other resource.
4. **Chemical competition,** by production of a toxin that acts at a distance after diffusing through the environment.
5. **Territorial competition,** the defense of space.
6. **Encounter competition,** involving transient interactions over a resource that may result in physical harm, loss of time or energy of theft of blood.

5.1 ☐ Interspecific and intraspecific competition

There have been many studies of interspecific competition among animals. Such studies have been conducted both to determine the mechanism of competition and to gain a better idea for the processes by which natural communities are structured.

Interspecific competition in animals

One of the first experimental demonstrations of interspecific competition in the field resulted from the work of Connell (1961) on two species of barnacles within the intertidal zone of the rocky coast of Scotland. Connell's experiments rank among the classic experiments in ecology both because of the elegance of their execution and because of the importance of their results. Adults of Chthamalus stellatus normally occur on rocks higher in the intertidal zone than those of Balanus balanoides, the more northerly of the two species. Although the vertical distributions of newly settled larvae of the two species overlap broadly within the intertidal zone, the line between the vertical distributions of adults is sharply drawn.

Connell demonstrated that adult Chthamalus are restricted to the portion of the intertidal zone above Balanus not because of physiological tolerance limits, but rather by interspecific competition. When Connell removed Balanus from rock surfaces, Chthamalus thrived in the lower portions of the intertidal zone where they were normally absent. The two species compete directly for space. The heavier-shelled Balanus grow more rapidly than chthamalus, and as individuals expand, the shells of Balanus edge underneath those of Chthamalus and literally pry them off the rock Chthamalus can occur in the upper parts of the intertidal zone because they are more resistant to desiccation than Balanus. So when surfaces in the upper levels are kept free of Chthamalus, Balanus do not invade.

Interspecific competition for space has been demonstrated in a number of other animals. For example, African fish eagles compete with other bird's of prey (raptors) for foraging space in Uganda.

Intraspecific competition in animals

Intraspecific competition is no doubt an important factor in the regulation of animal populations. However, the complicating effects of animal movement and predation make it more difficult to study experimentally in animals than in plants. Simple systems, in which no predators exist, and in which resources are limited to just a few, offer the best opportunity to understand the nature of intraspecific competition in animals. The carabid cave beetles (Neaphaenops tellkampf) of Mammoth Cave, Kentucky, represent one such system.

Griffith and Poulson (1993) undertook a study of intraspecific competition in these remarkable beetles. Cave beetles have no significant predators or competitors, and they represent the only consumer of their single resource, the eggs of a cricketlike cave-dwelling insect *(Hadenoecus subterraneus)*, which they excavate from the moist sand of the cave floor, where they are deposited by the adult crickets. The eggs represent a limiting resource at most times of the year. In addition to the simplicity of the feeding relationships, the internal environment of the cave is so nearly constant that environmental effects on the system are considered negligible.

Based on over 20 years of observations, Griffith and Poulson believed that the beetles competed with one another both by depleting the supply of eggs available to other beetles (exploitation competition) and by actively and aggressively interfering with one another's extraction of eggs from the sand (interference competition). The result of their experiments and observations supported their hypotheses. When beetles were excluded by cages from certain areas of the cave floor, the cricket egg densities there remained high in comparison with similar-sized areas where beetles were allowed to forage. Thus the foraging of beetles had a direct effect on cricket egg abundance. In addition, beetle fecundity (eggc/female) tracked the fecundity of crickets, showing that beetle population growth is directly related to the availability of the limiting resource. In laboratory studies, Griffith and Poulson manipulated the densities of beetles in sand-filled bowls containing a constant number of cricket eggs. They discovered that as beetle density increased, the effectiveness of individual beetle foraging decreased. Beetles in crowded bowls ate fewer eggs and dug fewer and shallower holes. They also took more days to find an egg. These results suggest that mtraspecific competition in the cave beetle is extremely important.

5.2 ❐ History of niche concep t

Habitat refers to the place where an organism or a species population lives, e.g. a pond is the habitat of zooplankton and fish. Soil in a forest floor is the habitat of soil fauna comprising soil insects, their larvae and pupae, microarthropods, some mollusks, annelids, nematodes and protozoa and soil microflora comprising bacteria, fungi and actinomycetes. Habitats may be divided into many types such as terrestrial aquatic, aerial, arboreal and so on. A terrestrial habitat may comprise forest, grassland, agricultural land, tundra, desert and so on. An aquatic habitat may be fresh water, estuarine or marine, or subdivisions of these larger habitats. Air is the permanent or temporary habitat of many organisms. The area of a taxon or species refers to the total geographic range of its movement. The habitat of species comprises the totality of the abiotic factors with which it interacts. The subdivision of a habitat is called a microhabitat. The specific environmental variable in the microhabitat is called microclimate or microenvironment. Joseph Grinnel (1917) coined the word 'niche' to denote the microhabitats where the organisms live. He laid emphasis on the distribution of organisms and their structural peculiarities in relation to microhabitats. Thus he considered the niche to be a subdivision of the habitat and treated it as a distributional unit. Charles Elton (1927) regarded the niche as the fundamental unit of an organism or a species population in the community. It centred around the collection of food, involvement in the intraspecific and interspecific competition, etc, by the organism. This concept of niche emphasizes the occupational state of a species. G. F. Gause, an ecologist said that no two species can coexist with the same ecological niche requirement of food and environmental factors. Thus a niche is different from a habitat. In simple terms, the habitat refers to the place where an organism lives and niche to the activity (functional aspect) of an organism. In other words, habitat refers to the address and niche to the profession of the organism. Kendeigh (1974) considered the niche as a combination of the habitat and biotic interactions of a species for its survival and continuance in a community. For example a lake is the habitat of all types of fish whose niches are different: (a) there may be herbivore, carnivore and omnivore fish depending on their food habits, (b) there may be surface, column and bottom feeders with regard to the distributional patterns, and (c) there may be other kinds of distribution depending upon environmental gradients, such as temperature or pH. Likewise the lake is also the habitat of many species of phytoplanktons but their distribution as regards depth and zone (shallow water zone, neritic zone, etc.) will vary depending upon their differential requirements of ecological factors, such as nutrients, temperature, silica concentration, availability of light, and so on. Thus the niches of organisms vary although their habitat broadly remains the same. Niches may be of different types depending upon the functional attributes of environmental conditions in which the organisms live and reproduce. This concept in its broadest sense includes abiotic and biotic variables and their interactions with organisms; in this case, it is called multidimensional niche.

5.2.1 Types of niches

It is evident from the above discussion that the ecological niche may have three aspects, namely (a) spatial or habitat, (b) torphic, (c) multidimensional or hypervolume. The concept of ecological niche therefore has considerable significance in ecology in terms of the differences between species in the same physical space or at different places, or the same species at more than one location.

5.2.2 Spatial or habitat niche

The spatial or habitat niche is concerned with the physical space occupied by an organism. It is broadly related to the concept of habitat, but differs from it, in the sense that while different species may occupy the same habitat, the activity of each organism may actually be confined to only a small portion of the habitat called microhabitat. O'Neill (1967) discusses the spatial niche giving many examples. He found seven species of millipedes in a maple forest. All species broadly occurred in the same habitat and were detritivores or fed on decomposed materials. Thus they belonged to the same trophic level. But detailed research revealed that each species dominated in its own specific microhabitat, which was different from the others. There were several gradients in the decomposition stage, from the center of the log to the bottom of the leaf litter. These gradients were identified as distinct microhabitats, although the general habitat was the forest floor. A similar examples is that of earthworms occupying agricultural fields, grasslands or forest floors (Dash and Senapati, 1981; Sahu, 1988). In Indian grasslands and agricultural fields some four or five species of earthworms *(Lampito mauritii, Octochaetona surensis, Drawida calebi, Drawidawillsi,* etc.)are commonly found, but the microhabitat requirement of each species is different. Spatial niche separation has also been observed in different species of fungi. Sharma and Dwivedi (1972) found three species of fungi colonizing the decaying parts of fodder grass, *Setria glocci.* Although they occurred in the same general habitat their intensity of occurrence varied depending upon the intensity of fruiting on the upper internode of that grass. Thus the different internodes created different individual microhabitats and harboured different species of fungi.

5.2.3 Trophic niche

This refer to the trophic position (food level) of an organism. For example, in the Galapagos islands in South America, birds belonging to three genera, namely *Geospiza* (ground finches), *Camarhynchus* (tree finches), and *Certhidia* (warbler finches) are found. All these birds live in the same general habitat but differ in their trophic position. One of the tree finches *Camarhynchus crassirostris* has a parrot-like beak and feeds on buds and fruits. The other tree finches *C. heliobates* and *C. pallidus)* are carnivores and feed on insects of different sizes. The ground finches are seed eaters, and the beaks of different species vary according to the type of seeds they eat. Another example is of the two aquatic bugs, *Notonecta* and *Corixa*. Both live in the same pond but occupy different trophic niches. *Notonecta* is predator while *Corixa* is a detritivore. Das and Moitra (1955) elucidated the concept of trophic niche and niche separation in some fishes. They classified *Catla catla* as a surface feeder as it feeds largely on zoo and phytoplankton, *Labeo rohita* as a midfeeder (column feeder) as it feeds largely on phytoplankton and algae and to a lesser extent on zooplankton, and *Cirrhina mrigala, Labeo calbasu,* and *Punitus sophore* as bottom feeders since they largely feed on rotten plant matter and to a lesser extent on plankton in the same aquatic system.

5.2.4 Hypervolume niche or multidimensional niche

The concept of hypervolume or multidimensional niche was developed by Hutchinson in 1965. He recognized two types of niches - (a) fundamental and (b) realized. The fundamental niche is the maximum abstractly inhabited hypervolume, when the species is not competing with others for its resource. If a community is considered to be an aggregate of many environmental and functional variables, then each of these can be taken as a point in a volume of space of infinite dimensions, called the hypervolume or multidimensional space. But an individual or a species normally remains in competition (either interspecific or intraspecific or both) and thus under biotic constraints only a part of the niche is realised by the species. This smaller hypervolume occupied by a species is called the *realized niche.* Thus each species has a *fundamental niche* within a community to which it is adapted in the evolutionary process, but because of competition it occupies a similar niche, namely the realized niche. (Figure. ?? explains this concept. In it zone -C is the competing zone where due to competition, the reproductive success of each species, and hence its chance of survival are reduced. Individuals from populations with overlapping niches, which remain outside the overlapping competitive zone are likely to have a greater survival rate and reproductive success. Natural selection will tend to favour individuals lying in the non-competing zone, and the non-overlapping portions of the niche will also tend to increase in size relative to the overlapping portion of the niche.

Let us consider the following example. Two species -A and B- of earthworms are able to survive and grow in dry soil. A and B can grow successfully if the soil water content is 5-8% and 7-10% respectively. Thus, individuals of both the populations which live in the 7-8% soil water content zone will compete with each other for common resources, and their reproductive success with each other for common success may be less in this overlapping niche zone. It has been found that the amount of niche overlap is usually proportional to the degree of competition for a particular resource. Competition occurs only when a resource is in short supply. The following conditions may arise in respect of niche relationships.

1. Niches may be adjacent to each other but not overlap.
2. The fundamental niche of one species may be completely within the fundamental niche of another species.
3. In a majority of cases, the niches may overlap.

In the first case, competition will be minimized since the niches are different. In the second case there will be severe competition for space, but the species may not compete for food if their trophic niches are but the species may not compete for food if their trophic niches are different. For example, the black and the white rhinoceroses live in the same habitat niche in Africa but their trophic niches are different. The black rhino is a browser and feeds on woody plants while the white rhino graze on herbs and grasses. In the third instance (overlapping niche) there will be an intense competition for space and food. In such a case either one of the species will leave the niche (niche separation) or remain subdued.

5.3 ☐ Summary

On the whole, competition occurs when individuals attempt to obtain a resource that inadequate to support all the individuals seeking it or even if the resource is adequate individuals harm one another in trying to obtain it. The resource completed for can be divided into two types : (i) Raw material such as light, inorganic nutrients, and water in autotrophy and organic food and water heterotrophs; (ii) Space to grow, nest, hide from predators etc. In higher plant this is manifested in spatial patterns, in animals by spatial patterns or movements. It is further noted that............ may be (a) intraspecific - occurring between members of the same population as well as (b) interspecific, occurring between populations of different species. But competition usually takes place between members of the same trophic level.

5.4 ☐ Terminal questions

(a) What is competiton? What is niche?

(b) What are the different types of competition found in nature?

(c) Distinguish between Inter & Intra specific competition. Give source examples.

(d) Give an outline of niche concept with special reference to its ecological significance.

UNIT 6 □ Mutualism

Structure

6.0 Introduction
6.1 Evolution of Mutalism
6.2 Plant pollinator and animal - animal interactions
6.3 Basic models
6.4 Summary
6.5 Terminal question

6.0 □ Introduction

Mutualism is a positive reciprocal relationship between two individuals of different species which results in increased fitness for both parties. Mutualism may be symbiotic, in which the organisms live together in close physical association. There are three types of mutualism viz.

Trophic mutualism,
Defensive mutualism, &
Dispersive mutulism.

Trophic mutualism

Trophic mutualism usually involves partners specialized in complementary ways to obtain energy and nutrients from each other; hence the term trophic. We have seen trophic mutualisms in the symbiotic associations of algae and fungi to form lichens of fungi and plant roots to form mycorrhizae, and of *Rhizobium bacteria* and plant roots to form nitrogen-fixing root nodules. In these cases, each of the partners supplies a limited nutrient or energy that the other cannot obtain by itself. *Rhizobium* can assimilate molecular nitrogen (N2) from the soil; but requires carbohydrates supplied by a plant for the energy needed to do this. Bacteria in the rumens of cows and other ungulates can digest the cellulose in plant fibers, which a cow's own digestive enzymes cannot do. The cows benefit because they assimilate some of the by-products of bacterial digestion and metabolism for their own use (and they also digest some of the bacteria themselves). The bacteria benefit by having a steady supply of food in a warm, chemically regulated environment that is optimal for their own growth. Ants belonging to the tropical group attinae harvest leaves and bring them to their underground nests, where they use them to cultivate a highly specialized species of fungus. These leaf-cutter ants consume the fungus; in fact, it is their only source of food. They also provide a living environment for the fungus, which can live nowhere else in nature. Thus, the organisms are totally dependent on each other. Such mutualistic relationships are extremely stable, especially compared with consumer-resource interactions, because both partners cooperate and are mutually evolved to each other's benefit as well as to their own. Genetic studies indicate that some of these relationships go back more than 20 million years.

Defensive mutualism

Defensive mutualism involve species that receive food or shelter from their mutualistic partners in return for defending those partners against herbivores, predators, or parasites. For example, in marine systems, specialized fishes and shrimps clean parasites from the skin and gills of other species of fish. These cleaners benefit from the food value of parasites they remove, and the groomed fish are unburdened of some of their parasites. Such relationships, often referred to as cleaning symbioses, are most highly developed in clear, warm tropical waters, where many cleaners display their striking colors at locations, called cleaning stations, to which other fish come to be groomed. As might be expected, a few species of predatory fish mimic the cleaners; when other fish come and expose their gills to be groomed, they get a bite taken out of them instead.

Dispersive mutualism

Dispersive mutualism generally involves animals that transport pollen between flowers in return for rewards such as nectar, or that disperse seeds to suitable habitats as they eat the nutritional fruits that contain the seeds. Dispersive mutualism rarely involve close living arrangements between partners. Seed dispersal mutualisms are not usually highly specialized; a single bird species may eat many kinds of fruit, for example, and each kind of fruit may be eaten by many kinds of birds. Plant-pollinator relationships tend to be more restrictive because it is in a plant's interest that a flower visitor carry pollen to another plant of the same species.

6.1 ☐ Evolution of mutualism

Mutualism may have arisen from parasite-host and predator prey relationships or between closely co-existing species with no co-operation or mutual benefit. Evolutionary changes in both partners (co-evolution) have then resulted in both partners benefiting from the relationship, although it is possible for mutualisms to deteriorate into unbalanced exploitation of one partner to the benefit of the other- parasitism. Mutualistic interactions have been central to a number of important steps in the evolution of multicellular organisms. It is also now widely accepted that the origins of the eukaryotic cell have involved the acquisition of prokaryotic symbionts. Both mitochondria and chloroplasts have their origins as free-living prokaryotes and contain circular DNA genomes and other characteristics of bacteria.

6.2 ☐ Plant pollinators

Plant-pollinator relationships may have originated as purely consumer-resource interactions : pollen is an excellent food, and the ovaries of flowers, where seeds develop, are excellent brood sites for insect larvae. Even pure acts of consumption result in some pollen being transferred fortuitously between plants.

Since this pattern began, floral structures have been modified through evolution to increase the efficiency of pollen transfer. Many of these modifications involve offering accessible rewards, such as nectar, that are relatively economical for a plant to produce, and arranging flower parts in such a way that pollen is transferred to the bodies of particular animal visitors. As flower structure becomes more highly specialized, fewer and fewer types of animals fit a flower in such a way that they contact the anthers and transfer pollen efficiently to the stigmas of other flowers. Thus, flower morphology can exclude certain types of flower visitors and increase efficiency of pollen transfer.

Base pollination in orchids

Plant-pollinator relationships are highly developed in the orchid family, with its variety of flower shapes, colors, and smells. The intricate tie between flower and pollinator is exemplified by the orchid *Stanhopea grandiflora* and the tropical bee *Eulaema meriana*. This obligate mutualism is unusual in that

Stanhopea flowers produce no nectar and only male *Eulaema* bees visit them. The flowers are extremely fragrant, and each species of *Stanhopea* orchid has its own unique combination of odors so that its specialist pollinator can find it without confusion. Each type of orchid tends to attract a single type of bee. When a male Eulaema bee visits an orchid, it collects a perfume that it uses to attract female bees. Each bee species uses slightly different scent to attract mates. The male bee brushes part of the flower with specially modified forelegs and then transfers the collected substance to the tibia of its hind leg, which is enlarged and has a storage cavity. In *Stanhopea* a bee enters a flower from the side and brushes at a saclike structure on the lip of the flower and bees often slip when they withdraw from the flower. The orchid fragrances may also intoxicate bees and cause them to lose their footing. When a bee slips, it may brush against the column of the orchid flower, where pollinaria (sacklike structures filled with pollen) are precisely placed so as to stick to the hindmost part of the thorax of the bee. If a bee with an attached pollinarium slips and falls out of another flower, the pollinarium catches on the stigma and pollinates the flower. Thus, flower structure and bee behavior are mutually adapted to increase the efficiency of pollen transfer.

Bird pollination in lobelia

Some of members of the genus Lobelia, particularly those in the subgenus Centropogon, are pollinated by hummingbirds. In some highly specialized species of Centropogon, an exclusive relationship exists with the sicklebill hummingbirds (Eutoxeres), which possess long sickle-shaped bills. The bills of these hummingbirds represent the only structure capable of obtaining nectar from the long, curved flowers of the plants, and thus these hummingbirds are their exclusive pollinators. Unlike other hummingbirds, sicklebills must perch in order to feed. Thus, in addition to the curved flower shape, species of Centropogon that are specialized for pollination by sicklebills have flowers that are more compact and sturdy than close relatives, thus providing a place for the birds to perch.

Because animal pollination is basal within the angiosperms, this type of mutualism must have existed at least since the late Jurrasic. There are exciting times in the study of plant pollinator interactions. As genetic information about plants and animals builds at an accelerating speed, it will allow the design of powerful new tools for experimental studies of interactions. Floral scent, pigments and shape will soon be independently manipulated to test any hypothesis. Phytogenetic information is increasing rapidly for many groups of organisms that are central in plant-pollinator interactions and the availability of robust historical data will allow us to bridge traditional ecological and evolutionary time scales.

Animal-Animal Interactions

The honey guide and the honey badger

An African bird, the honey guide (Indicator indicator), "has formed a remarkable relationship with the ratel or honey badger (Melliovora capensis). A honey guide thet has located a bees' nest leads the honey badger to it. The mammal tears open the nest and feeds on honey and bee larvae, and later the honey guide gets a meal of beeswax and larvae. The honey guide can locate a bees' nest but not break it open whilst the honey badger is in just the opposite situation. The reciprocal link in their behaviour brings mutual benefit.

Shrimps and gobiid fish

Shrimps of the genus Alphens dig burrows, and goby fish (Cryptocentrus) use these as safe sites in an environment that otherwise provides little or no shelter. The shrimp is almost completely blind and, when it leaves the burrow, keeps one antenna in contact with the fish, thereby getting warning of any disturbance for this symbiosis as one element in the ecological divergence in goby fishes). The goby gains a place to live in an environment of sediment containing abundant food. The shrimp gains an optional warning system that allows it to leave its burrow safely for short periods to feed on sediment outside.

Clown fish anemones

A variety of behaviour symbioses is found amongst the inhabitants of tropical coral reefs (where the corals themselves are mutualists). The clown fish (Amphiprion) lives close to a sea anemone (e.g. Physobrachia, Radianthus) and retreats amongst the anemone's tentacles whenever danger threatens. Whilst within the anemone, the fish gains from it a covering of mucus that protects it from the anemone's stinging nematocysts (the normal function of the anemone smile is to prevent discharge of nematocysts when neighbouring tentacles touch). The fish derives protection from this relationship, and the anemone also benefits because clown fish attack other fish that come near, including species that normally eat sea anemones.

6.3 ❑ Basic model

A classic pair of simple equations defines the essence of competition between two species : The Lotka-Volterra equation which describes the population dynamics of two competing species and the terms - al2N2 and - a21Nl represent the negative effect of each species on the population of the other.

$$\frac{dN_1}{dt} = \frac{r_1 N_1 (K_1 - N_1 - a_{12} N_2)}{K_1} \qquad (1)$$

and for the second species

$$\frac{dN_2}{dt} = \frac{r_2 N_2 (K_2 - N_2 - a_{21} N_1)}{K_2} \qquad (2)$$

At first sight we might imagine that an appropriate model for a mutualistic interaction would simply replace the negative contribution from the associated species with a positive contribution so that the presence of each had a positive effect on the growth of the other :

$$\frac{dN_1}{dt} = \frac{r_1 N_1 (K_1 - N_1 - a_{12} N_2)}{K_1} \qquad (3)$$

and for the second species :

$$\frac{dN_2}{dt} = \frac{r_2 N_2 (K_2 - N_2 + a_{21} N_1)}{K_1} \qquad (4)$$

There remains a big question whether any single mathematical model can capture the essence of all mutualisms.

It may not be sensible to bring just two mutualists into the model. The benefits of mutualism, in many of the examples, depend on the presence of one or more other species. For example, the ligume *Rhizobium* mutualism brings its great advantage to the legume when it is competing with some other plant (e.g. a grass) for limited nitrogen from the soil. The ant-acacia mutualism brings advantage to the acacia if it is in competition with other shrubs (the ants prune the competitor), and the interaction is yet more complex because the ants also protect the acacia from herbivores. The dynamics of at least four species (probably more) would need to be built into a model that captured the essence of this situation.

Realistic models of mutualisms may, then, need to involve the dynamics of three or more species and attempts to do this suggest that the presence of a third species (predator or competitor) may stabilize some mutualisms, However, it still unlikely that any single model will encapsulate some property fundamental to all mutualisms, Sadly, each different class of mutualism may demand its own model.

6.4 ☐ Summary

There are many features of the biology of mutualists (particularly those that involve a close symbiotic relationship) that set them apart from most other organisms. They contrast very strongly with aspects of the biology of parasites and with free-living relatives.

1. The life histories of most symbiotic mutualists are remarkably simple (contrasting particularly with the life histories of most parasites).
2. Sexuality appears to be suppressed in endosymbiotic mutualists, especially in comparison with parasites and with free-living close relatives (Law & Lewis, 1983).
3. There is no conspicuous dispersal phase in endosymbionts. Spores from the fruiting bodies of the sheath-forming mycorrhizal fungi are exceptions to this general rule, but these fungi may spend most of their lives in a free-living condition (or as parasites). The contrast between mutualists and parasites is particularly strong : dispersal rules in the population dynamics of most parasites.
4. It might be expected that coevolution of a mutualism would lead to mechanisms that disperse the two partners together. This happens when:
   (a) Young queen ants or scolytid beetles take fungal inoculum with them to found a new colony;
   (b) Fungus and algae are combined in the dispersai unit of many lichens;
   (c) Mycetocyte bacteria are transmitted to the egg in mycetocyte bearing insects.
   (d) Fungi such as the symbiotic (perhaps mutualistic Balansieae : invade and disperse in the seeds of grasses.
5. There seems to be nothing in the life of mutualistic organisms comparable to epidemics amongst parasites. Populations of mutualists seem to have great stability when compared with those of parasites.

6. The numbers of endosymbionts per host seem to be remarkably constant and their population dynamics must have elements of density dependence.
7. The ecological range (and niche breadth) of organisms in mutualistic symbioses appears usually (perhaps always) to be greater than that of either species when living alone. This again contrasts with parasitic symbioses where the host's ecological range is probably usually reduced by the presence of parasites.
8. Surprisingly, species specificity of both partners in mutualisms is often quite flexible-ants and nectarines, algae and fungi in lichens, plants and pollinators, etc. often involve pairs of species that can live mutualistically with several, sometimes many, other partners.

There is no doubt that mutualism and other forms of symbiosis (even commensal isms) have been seriously neglected by ecologists - even more so than parasitisms.

6.5 ☐ Terminal questions

1. Critically evaluate the different categories of mutalism.
2. How mutualism is evolved in nature? Explain -
3. Critically discuss the plant pollinator interaction with examples.
4. Give an illustrated examples of animal-animal interaction.
5. Discuss a basic models of mutualism.

UNIT 7 □ Population Regulation

Structure

7.0 □ Introduction

A population is composed of the individuals of a single species within a given area. An important measure of a population is the number of individuals. From a management and conservation standpoint, it is important to understand the factors that cause population size to change and the processes that regulate those factors.

Continuous population growth can be described by the exponential rate of increase ® in the expressio $Wt = Noe+$. The factor by which a population growth rate of the population (c) c are et interchallangeable in population expressions. The exponential growth rate is the difference between the birth and death rates averaged over individuals (per capita) in the population, (i.e, $r = b - d$). The instantaneous rate of increase of an exponentially growing population is $dw/dt - rN$. Populations may be regulated by factors, called density-dependent factors, whose effects increased as the density of the population increasers. And Density-independent factors are those whose effects are not related to the size of the population.

7.1 □ Population regulation

7.1.1 Population regulation by density dependent factors

The logistic equation has been applied successfully to describe the growth of populations in the laboratory and in natural habitats. It suggests that factors limiting growth exert stronger effects on mortality and fecundity as a population grows. Many things influence rates of population growth, but along density dependent factors, whose effects increase with crowding, can bring a population under control. Of prime importance among these factors are limitations on food supply and places to live, as well as predators, parasites, and diseases whose effects are felt more strongly in crowded than in sparse populations. Other factors, such as temperature precipitation and catastrophic events alter birth and death rates largely without regard to the number of individuals in a population. Such density density-independent factors may influence the exponential growth rate of a population, but they do not regulate the size that the population will attain in the environment. Numerous experimental studies have revealed various mechanisms of density dependence in animals. For example, when a pair of fruit flies is confirmed to a bottle with a fixed supply of food, the descendants of those flies increase in number rapidly at first, but soon reach a limit. When different numbers of pairs of flies are introduced into otherwise identical culture bottles, the number of progeny raised per pair varies inversely with the density of flies in the bottle. This effect results from competition among the larval for food, which caused high mortality in dense cultures. Adult life span also declines, but only at high densities, well above the levels that affect the survival of larval juvenile stages often suffer the adverse affects of densities dependent factors more than adults.

7.1.2 Density-independent regulation of population

The two Australian entomologists, Andrewartha and L. C. Birch, argued that most populations, particularly those of insects and other small invertebrates are influenced primarily by density independent factors, and that periods of favorable environmental conditions for population growth ultimately control the size of a population :

The numbers of animals in natural population may be limited in three ways : (a) by shortage of material resources, such as food, place in which to make nests, etc. (b) by inaccessibility of these materials resources relative to the animals capacity for dispersal and searching; and (c) by shortage of time when the rate of increase r is positive. Of these three ways, the first is probably the least, and the last is probably the most, important in nature. Concerning (c), the fluctuations in the value of r may be caused by weather, predators, or any other component of environment which influences the rate of increase.

7.2 ❐ Population interaction

In general, two species population interact in a variety of ways. The details are given below :

Type of Interaction	Characteristics
1. Neutralism	Neither population affect the other
2. Competition : Direct interference type	Direct inhibition of each species by the others
3. Competition : Resource use type	Indirect inhibition when common resources in short supply
4. Amensalism	Population of one is inhibit but other not affected
5. Parasitism	Population one is prasitize on others.
6. Predation	Population of one type act as predator on others (prey)
7. Commensalism	Population of one type benefits, while other not affectd
8. Proto cooperation	Interaction favourable to both but not obligatory
9. Mutualism	Interaction favourable to both & obligatory

7.3 ❐ Summary

With our general understanding of population equilibrium as a dynamic interplay between biotic potential and environmental resistance (Fig-1), we now turn out attention to some specific kinds of population interactions viz, Predatory - Prey dynamics, Competition, and influence of introduced species.

Biotic potential	Environmental Resistance
• Reproductive rate	• Lack of food or nutrients
• Ability to migrate or disperse	• Lack of water
• Ability to invade new habitats	• Lack of suitable habitat
• Defense mechanisms	• Adverse weather conditions
• Ability to cope with adverse conditions	• Predators
	• Diseases
	• Competitors

Fig.1 : Population equilibrium - relationship of Biotic potential & environmental resistance.

7.4 □ Terminal questions

1. Explain population regulation in nature.
2. Illustrate population interaction processes.
3. States the factors of population of equilibrium.

UNIT 8 ▫ Ecological Modeling

Structure

8.0 Introduction
8.1 Fundamentals of constructing models
8.2 Testing ecological models
8.3 Applications of ecological models
8.4 Summary
8.5 Terminal questions

8.0 ▫ Introduction

Ecology is concerned with the interactions between an organism and its environment (both abiotic and biotic, i.e, other organisms) and the consequence of these interactions, including the change in numbers of individuals in population (single species) or communities (multi-species). In general the primary focus of ecological model is population and community model. An ecological model must be able to describe this change in numbers to varying degrees of accuracy and generality. Such models are phased in mathematical language. For example, instead of the clumsy statement that the number of individuals in a population next year ($Nt + 1$) is given by the number this year (Nt) minus the number of deaths (d) and emigrants (e) from the population plus the number of birth (b) and immigrants (i) we can write :

$$Nt + 1 = Nt - (d + e) + (b + i)$$

This equation can then be manipulated as can any mathematical equation. This leads to a flexibility which goes well beyond a conceptual model phrased in ordinary language.

Mathematical models may also be used to explore the spread of a species in response to global climate change and describe the rate at which this occurs by linking local population dynamics and migration. The application of model, may have profound economic and ecological implications, such as models which indicate the likelihood of success of a biological control agent or suggest the efficiency of a programme of drug treatment.

Mathematical models in ecology can be categorized according to their simplicity, rationale and formulation. It could be simple versus complex, stochastic versus deterministic and so on.

8.1 ◻ Fundamentals of construction models

The complexity of ecology is both its fascination and frustation - it may involve many individuals of various species interacting with a variety of abiotic and biotic factors which themselves may be affected by sets of other factors. All of these factors are likely to change in space and time, often unpredictably. How then can we begin to model these systems? There are two extreme approaches which have been described by various authors. These are as follows :

- General models
- Realistic medels.

In statistical terms we have a dependent variable, e.g. plant or animal change over time, and a series of explanatory variables, e.g, temperature and rainfall. These variables explain a certain percentage of the variance in the dependent variable. The more explanatory variables which can included in this model, the greater the total amount of explained variable in the dependent variable. But the addition of an extra variable may only add small increase in explained variance. We therefore, need to remove all the explanatory variables which do not provide any significant increase in percentage variance explained. We may then be left with, for example, three variables which explain a total of perhaps 70 of the variance. This is likely to be more tractable than our original model with 12 explanatory variables. We can manipulate these variables and explore their effects. We will refer to this as the simplest realistic mode!. Not all ecological models can be simplified in this way but it is important to dry to formulate models which can be simplified according to objective criteria, such as statistically significant gain or loss of explanatory power.

In mathematical models of population or community change over time there are two ways of representing time which have important implications for the way populations or communities are modeled. In the first case time may be considered as continuous, so that, in theory, it can be divided up into smaller and smaller units. In the second case, time is considered to be discrete and indivisible in units of e.g. years. The first case is appropriate to populations of individuals with asynchronous and continuous reproduction, whist the second case is appropriate to populations composed of individuals with synchronized reproduction at regular time intervals. Mathematical equations describing change in time continuous time are differential equations whist equations describing change in discrete time are difference equations. In a deterministic world everything should be predictable. But no ecological system is purely deterministic. There are always some unexpected or unpredictable events, such as strains which may have a strong effect on the dynamics of the target species. These may be entirely random in their occurrence in which case we refer to them as stochastic events.

Construction of the Lotka-Voltera model of predator and pray dynamics

The premise of their preditor-prey models was that of 'two associated species of which one finding sufficient food in its environment, would multiply indefinitely when left to itself, while the other would perish for lack of nourishment if left alone; but the second feeds upon the first, and so the two species can coexist together- Thus Lotka Voltera assumed that prey density (N) increased exponentially (qualified by rl) in the absence of predators :

$$\frac{dN}{dt} = r_1 N \qquad (1)$$

This was made more realistic by assuming that the change in prey density was described by the logistic equation, i.e, the prey population would move towards an equilibrium of K in the absence of predation.

$$\frac{dN}{dt} = r_1 N(1 - N / K) \qquad (2)$$

In presence of predators the rate of change of prey population size with time, dN / dt, is assumed to be reduced in proportion a to the density of predators (P) multiplied by the density of prey (N) :

$$\frac{dN}{dt} = r_1 N - r_1 N(1 - N / K) - \alpha \mathrm{PN} \qquad (3)$$

or

$$\frac{dN}{dt} = r_1 N - r_1 Nt^2 / K) - \alpha PN \qquad (4)$$

Note that r_1/K may be replaced by a single parameter. As we are now modeling a dynamic system in which the predator population density may also fluctuate, we need to develop an equation for dP/dt. Lotka and Voltera assumed that, in the absence of prey, the predator population size would decline exponentially, quantified by $r2$, i.e, they assumed that predator species specialized on one species of prey :

$$\frac{dP}{dt} = r_2 P \qquad (5)$$

In the presence of prey, this decline would be counteracted by an increase in predator density, again in proportion b to the density of predators (P) multiplied by the density of prey (N) :

$$\frac{dP}{dt} = r_2 P + \beta PN \qquad (6)$$

Thus equation 4 and 6 provide a system of two coupled first order nonlinear differential equation.

$$\frac{dP}{dt} = r_1 N - r_1 N_t^2 / K - \alpha PN \qquad (7)$$

$$\frac{dP}{dt} = -r_2 P + \beta PN \qquad (8)$$

This technique is very useful because systems of differential equations may arise in all types of ecological interaction (including the various manifestation of predator-prey interaction, i.e, plant-herbivore, host-parasitoid and host-pathogen; competitive and mutualistic interactions).

8.2 □ Testing ecological models

The testing of ecological models is, in principle, straightforward. The output of a model of, say plant population dynamics should be compared to the observed dynamics in the field. The better the description of the observed dynamics, measured by some objective statistical criterion, the better the model. In practice there are several problems. First, the value for the model components, such as birth rate, may have been taken from the field population against which the predicted dynamics are to be compared and so it is inevitable that model and field will show some agreement. Ideally, estimation of model components should be under aken independently from model testing. Second, there are rarely sufficient field data for statistical testing, particularly where the dynamics are possibly cyclical or chaotic. In these cases we may need a run of population data covering several lifetimes of an average investigator. Often the best we can hope for is that the components of the model, such as birth rate of migration rate, are ecologically realistic and based on careful field measurements. Additionally, dependent on the aim of the model, field or microcosm experiments may complement the modeling. There is a two-way trade between field experiments and ecological models. Not only can experiments be used to parameterize and test the predictions of models and suggest the construction of new models, but also models can be used to indicate the design the field experiments.

No model is perfect. Validation involves studying the error distribution and observing if the errors are consistent. Subsystem validation may be undertaken first, if it is properly defined.

8.3 Applications of ecological models

Models can be used to determine end results of various courses of action and translate questions being asked into predictive answers. Ecological models are very essential for planning for appropriate ecosystem management. However to frame a more realistic model long term ecological parameter evaluation is highly essential.

The Leslie model is a popular one for studying the actual problem of a game (deer, sambhar, rabbit) reserve (20 x 20 Km) forest .in India.

The expression of model can be made as follows :

$a_t \times 1 = A\, a_t$ (i)

at = a tl, ...a t n is the population's age structure at time 't, at', being equal to the number of females alive at time 't' in the age group 'i to i + 1',

at + 1 = a column vector similar to 'a t' but representing the age structure at time 't+1'.

$$A = \left| \begin{array}{ccccc} f_0 & f_1 & & f_{n-1} & f_n \\ Po & O & O & O & O \\ O & P_1 & O & O & O \\ P_1 & O & O & O & \\ O & O & P_{n-1} & O & \end{array} \right|$$

A is a fecundite-mortality matrix where fl is the number of females born at time t of mothers in the age group i to i +1, who will survive up to time t + 1 and PI = probability that a member aged i to i + 1 at time t will remain alive upto time t +1. Equation (i) gives -

$a_t + k = A^k a_t$ after k periods (ii)

and

$A_n = \lambda_n$ (iii)

where λ is an eigenvalue and a is the eigenvector associated with it. Since A is a non-negative irreducible matrix, the Pern-Frobenius theorem tell us that :

(a) the r is a k0 which has a vector with all elements non-negative (the model will always predict a non-absorbed age structure),

(b) λ_0 is the only such eigenvalue of A - the age structure is unique,

(c) λ_0 is not less than any other latent root of A (numerical application) is simple and

(d) Largest row sum $\geq \lambda_0 \leq$ smallest row sum and largest column sum $\geq \lambda_0 \leq$ = smallest column sum.

A non-prolific breeder species may exhibit a fecundity-mortality matrix similar to the one shown below.

Age in years

0-1	1-2	2-3	3-4	4-5	5-6	6-7
0	0	0.19	0.44	0.5	0.5	0.45
0.87	0	0	0	0	0	0
0	0.87	8	0	0	0	0
0	0	0.87	0	0	0	0
0	0	0	0.87	0	0	0
0	0	0	0	0.87	0	0
0	0	0	0	0	0.87	0.8

for which $\lambda_0 = 1.0986 > 1$, which means the population can increase slowly. The intrinsic rate of natural increase (γ) is defined as $c = \log \lambda_0$. The permissible harvesting (H) percentage is $H = 100\ \lambda_{0-1}$

A more profile breeder species, such as rabbit may display an A matrix of the form

$$\begin{array}{ccc} 0 & 9 & 12 \\ \frac{1}{3} & 0 & 0 \\ 0 & \frac{1}{2} & 0 \end{array}$$

For which = 2, which gives a harvesting rate of 50% (H = 100 2 - 1/2). A calculus model gives $N_t = Noe^{rt}$ where N is the population at time t, No is the population in the beginning, γ is the intrinsic rate of increase, and e is the bone of natural logarithm.

The A matrix can be shown as a sum of two matrices :

$$A= \left| \begin{array}{cccccccccc} f0 & fl & f3 & fn & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & P0 & 0 & 0 & 0 & 0 \\ - & - & - & - & 0 & P1 & 0 & 0 & 0 \\ - & - & - & - & - & - & - & - & - \\ - & - & - & - & - & - & - & - & - \\ 0 & 0 & 0 & 0 & 0 & 0 & - & - & 0 \end{array} \right| =F+P$$

Where F represents the input of new members to the population and P represents the transition of members from one age group to another.

The Leslie model can be used for modeling a variety of systems :

(i) spatial distribution of species
(ii) Plant populations
(iii) Animal populations (size, population dynamics etc.)
(iv) Seasonal and random environmental changes
(v) Harvesting

8.4 ❑ Summary

An ecological system represented in a model should be pragmatic in content & scope. The model mus be quantitatively predictive, so that the future behaviour of the system is understood. Model building requires - (a) identification of state variable, (b) factors which influence the state variables, (c) processes which change the state variables, (d) identification of interactions and few process depiction in graphical and mathematical terms, and (e) testing and validation of the model using an independent set of data.

A good model has wide applicability. Although it is generated through observations on one particular system, it should be verified in other systems too. Data for validation should be distinctly different from those used for estimation. If this is not possible, care must be taken to choose a set of data independently from all ranges for testing and validation.

8.5 ☐ Terminal questions

(a) What is ecological model? What are the major objectives of such kinds of model?
(b) Give a brief description about the fundamentals of ecological model.
(c) Distinguish between continuous model and discrete model.
(d) Give an outline of Lotka-Voltera model.
(e) How do you test the ecological model ?
(f) Give an examples of ecological model application.
(g) State the various use of leslie model.

UNIT 9 ◻ Environmental Factors

Structure

9.0 ◻ Introduction

Factors which limit the species to particular habitats are called an **environmental factors**. They are responsible for the growth, distribution, abundance, behavior and ultimate survival of the organisms. Physical and chemical factors collectively form the non-living or abiotic environment whereas living or biotic environment includes inter-relationships with other populations for food, shelter, energy etc. More over there exists an overlaping mechanism between abiotic and biotic factors effective for a particular population in concomitance with time and space.

Any factor that tends to slow down the rate of metabolism or potential growth in an ecosystem is said to be a **limiting factor.**

A factor that controls the survival is said to be a **regulatory factor.**

Law of Minimum

Ecological events and their outcomes, such as growth, reproduction, photosynthesis, primary production and population size are often regulated by the availability of one or a few factors or requisits in short supply, whereas other resources and raw materials present is excess may go partially unused. This principle has become known as the "law of the minimum" (Leibig 1840). As for example in asid climates, primary production is strongly corelated with precipitation (Rainfall). (Fig-9.12) Here water acts a "master limiting".

Law of Tolerance

A related concept, known as "law of tolerance" was developed by Shelford (1913b). Too much or too little of anything can be detrimental to an organism. In the early morning, a desert lizard Finds itself in an environment that is largely too cold, whereas later in the day its environment is too hot. As a result a lizard withstands this environment by spending most of its early morning time in sunny places whereas later its all activities take place in shades. Each lizard has a definite range of temperature, with both upper and lower limit of tolerance.

9.1 Environmental factor—light

Light is the source of life, the most vital and essential abiotic factor without which no life can exist. It is not only a vital factor, but also a limiting one at both the maximum and minimum levels. Sun is the natural source of light and an ultimate source of energy for all activities in the biosphere. The electro-magnetic radiation from the sun supply energy that warms up the earth's surface and the atmosphere to provide a favourable global temperature for the living beings. It is essential for organisms for two quite different reasons:

(i) It is used as a stimulus for the timing of daily and seasonal rhythms or **photoperiodism.**

(ii) It is essential for **photosynthesis** or the production of food for the whole ecosystem.

9.1.1 Solar energy input

Of the enormous amount of radiant energy liberated by the sun (5.6 x 1029 cal./min), only about half a billionth is intercepted by earth. But neither all solar energy reaching the earth does penetrate the atmosphere, nor is the flux reaching the plants and animals constant. However, the flux of solar energy reaching the top of the atmosphere appears to be constant within narrow limits, known as **"Solar Constant".** Their is given an average value of 2g cal mm"2min"' with a probable error of 5%.

Light on land : Variable part of the spectrum of solar radiant energy :

Ultraviolet ← 390 mm — 760 mm → Infrared
Visible spectrum.

Intensity of light depends upon—

1. Angle of incidence : Smaller at low altitude; reduction in light intensity.
2. With the increase of degree of lattitudes, intensity decreases.
3. Intensity is highest when sun on overhead.

4. It also depends on the amount of absorption—
   - (a) Moisture, clouds, dusts.
   - (b) Topography, vegetation, canopy cover
   - (c) "Ozone Umbrella" absorbs UV rays.

5. Intensity also depends on the duration of light exposure, i.e., photoperiod.

Light on water : Water absorbs on scatters enough light to limit the depth at which photosynthesis is possible in aquatic environments. In pure sea water, the energy content of light in the visible part of the spectrum diminishes to 50% of its surface value within 10 meters, and to less than 7% within 100 meters. Water absorbs longer wave lengths more strongly than shorter ones. All intra-red ratiation disappears within the top most meter of water. Short waves of light (violet and blue) tend to be scattered by water molecules and do not penetrate deeply. As a consequence green light tends to predominate with increasing depth. On the basis of light penetration the vertical stratification as follow—

(1) Euphotic (upto 50 m), (2) Disphotic (upto 100 m) and (3) Aphotic (up 200 m).

9.1.2 Biological role of light

Effect on metabolism :

1. Effect is indirect,
2. With the increase of light it increases the heating effect, which in turn increases the enzyme activity.
3. Solubility of salt and minerals increases with the increasing intensity of light. As a consequence, cave dewelling animals face slow rate of metabolism.

Effect on growth and development :

As light influences metabolism, hence also affects growth and development.

1. Normal development of Salmon larvae occurs only under sufficient sunlight, in absence of which there may lake place rapid death of larvae. Where as, in *Mytilus*, larvae in their early stages grow longer in darkness than in light.
2. Under low illumination, development becomes arrested for insects. As in case of Hydrids, if kept in dark, growth is inhibited.

Effect on eye :

The degree of eye development depends on the intensity of light available.

1. Under total darkness, generally eyes are lacking, but if present are non-functional.
2. In case of those animals, who receive less light, then eyes develop as bigger as the nocturnal animal like owl.
3. In animals, living in caves, ***Proteus angulnu,*** and in deep sea fishes, the eyes are absent or rudimentary.
   Where eyes are absent, there develop special organ of senses like tactile organs, special eye, long antennae, finrays etc.

Effect on vision

1. Higher animals including man are able to see various objects only in presence of one or other form of light. Somes fishes, as **Lepomis,** also depends on eyesight for location of their food.
2. Under dim light : dull, overlapped, superposition of image is formed in case of insects.
3. In case of deep sea fishes, fine adjustment between rods and cones and pigments can detect objects even at 500 meter depth.

Effect on pigmentation

1. Cave animals kept in darkness for long time, lack skin pigmentation. When the animals with no colour (like amphibians) are exposed under abundant and prolonged light they develop coloration.
2. In the tropical areas human exhibit dark pigmentation.
3. Pigmentation differ in breeding season, leading to sexual dimorphism.

Effect on locomotion and orientation:

The effect of light is prominent in lower organisms.

1. ***Phototaxis*** : Oriented locomotory movement towards or away from light source.

(a) Towards light source → +ve phototactic,
e.g.—*Euglena, Volvox* etc.

(b) Away from light → – ve phototactic.
e.g.—Earthworm, Cockroach etc.

2. ***Photokinesis*** : When it affects speed of locomotion.

(a) Blind larvae of mussel crabs move faster it exposed to increased intensity of light.

3. ***Photokilokinesis*** : When only a part of the body deviates from the source of light, eg.—larvae of Musca.
4. ***Photopotrotaxis*** : When they are confronted with two equal source of light intensity, still the animal moves along the midline between the sources.
5. ***Phototropism:*** Light directed growth of body parts, flagella of Euglena, polyp of Cnidaria, etc.
6. ***Light compass reaction*** : Movement of animals at a constant angle towards the source of light, e.g.—homing reaction of ants and bees.

Effect on photosynthesis or primary production:

In photosynthesis, light is essential for the formation of organic matter and oxygen from water and carbondioxide :

$CO_2 + 2H_2O + \text{Light Chlorophy} (CH_2O)_6 + H_2O + O_2$

Plants respond differently to variations in the light intensity. They may be divided into **Sciophytes (Shade-tolerant)** and **heliophytes (Shade-intolerant)** species. Sciophytes have lower photosynthetic rate, so as lower growth rate than the heliophytes. Though in both cases, photosynthetic rate increases with the increase in light intensity, as the former cannot promote the process beyond a certain light saturation are poor producer than the later. Heliophytes species do not reach the saturation light even under the brightest sunlight.

This variation in the photosynthetic rate is an attribute of the biochemical pathways. Most plants use C_3 pathway (almost all shade-tolerants), while all heliophytes make use of C_4 pathway (Fig. 9.1). C_4 plants have all the biochemical pathways and they can use either methods to fix CO_2. Therefore, they do not show any light saturation and become more efficient producer than C_3 plants. Some desert succeelents (caetus) make use of a third modification of phytosynthetic pathway, Crassulacean Acid Metabolism (CAM) pathway. They take CO_2 at night and store it as malic acid, which is then used to complete photosynthesis during the day.

Because, photosynthesis requirs light, the depth at which can exist in the ocean and lakes is limited by the penetration of light. Algae are limited to a fairly narrow zone close to the surface where photosynthesis exceeds respiration. This range of depth is called the **Euphotic Zone.** The lower limit of the euphotic zone, where photosynthesis just balances respiration is called the **compensation point.** If algae sink below this point or are carried below it by currents, and do not soon return to the surface of upwelling currents, they die, because they are unable to convert energy by photosynthesis.

Effect on photoperiodism :

The term literally mean the time period between the sunrise and sunset. But from the ecological point of view—it is the "duration of light for which an animal in exposed to". It has a great influence on physiological and behavioral characteristics of organisms— growth, reproduction, metamorphosis and migration of animal. Various reproductive activities of animals have been influenced by the photoperiod as follow—

(a) Initiation of reproductive cycle.
(b) Gonodal maturity.
(c) Egg laying capacity of birds.
(d) Spawning of fish.
(e) Maintaining annual reproductive cycle.

Effects of photperiod have been studied extensively in different groups—fish, amphibia, reptiles, birds and mammals, but the group-bird attracted most.

9.1.3 Types of photoperiodic animals

Animals are differentiated on the basis of two criteria—

1. Difference in photosensitivity.
2. Degree of dependence on photostimulation.

D. S. Farmer (1985) proposed three arbitarily overlappping group—

1. **Primary** : Use day length as a significant environmental component in the control of annular reproductive cycle (ARC), e.g.—temperate populations.
2. **Secondary** : Day length has less significant effect on the ARC. e.g.—Equatorial population—black headed burning munia.
3. **Permissive** : Day length has no significance on periodicity—respond well under exceptional conditions.

But the animals are generally grouped into—

1. **Long day animals** : Sexual activity increases with long day. e.g.—Turkeys and Starlings.
2. **Short day animals** : Activity decreases with long day and vice-versa, e.g.—Sheep, Dear, Goat etc.
3. **Indifferent animals** : No effect of day length, e.g.—Ground squirrel, Guineapig.

Any photoperiodic species when exposed to a long day for a prolonged time, usually loses its responsiveness to the changes in the duration of photoperiod—the species is considered to be **photo-refractory.** When it occurs at the end of breeding phase, is an adaptive mechanism by which animals are prohibited from breeding and ultimately leads to **natural contraception.**

9.1.4 Useful terms

Biological rhythm : The earth typically exhibits a rhythmicity that recurs daily and seasonal changes. As the year progresses the seasons change. The progression of lengthening and shortening days are marked by the flush of new growth and the senescence of the old, by the onset of different life cycle phenomena, by the arrival and departure of migratory birds and so on. These diurnal and seasonal rhythms are driven by the daily rotation of the earth on its axis and its orbiting around the sun.

In plants and animals, the response to light is achieved by light recepters **Phyto-chromes,** eye, **ocelli, stigma** and other photoreceptors. The response achieved is reflected by light synchronised rhythms, which are of 3 types—

1. Seasonal rhythm, 2. Circadian rhythm, 3. Lunar cycle.

1. Seasonal rhythem : Seasonal rhythm involves the ocurence of certain obvious biotic and abiotic events within a definite limited time period of a year. The shedding of leaves in winter, arrival of new leaves in spring, blossoming of flower, ripening of seeds, migration of birds and other biological events that recur with the passage of season and influenced by the interaction of light with temperature and moisture. The study of this seasonality is known as **phenology.**

2. Circadian rhythm : Circadian rhythm are biological rhythms which approximate the period of 24 hours or more accurately, the alternative between day and night. This innate rhythm of activity and inactivity is characteristic of most living organisms except bacteria. The period of circadian rhythm—the number of hours from the begining of a period of activity one day to the begining of activity on the next is called "free-running cycle". The rythm of activity exhibits a self-sustained oscillation under constant conditions.

Plants and animals, including insects, adjust their intrinsic circadian cycle, which can range from about 23 to 25 hours. These rhythms provide a mechanism by which organisms can maintain synchrony with their environment.

The role of the need of light to synchronize the circadian rhythm with the environment can be demonstrated in the laboratory by holding the organism under constant darkness or light conditions to allow the circadian rhythm to drift out of phase with the natural environment. The length of time before this change depends upon the organism and the condition of light and dark. The activity rhythm in rodents and bats may continue for several months, while in many others they fade more quickly.

3. Biological clocks : Circadian rhythms are maintained by some biological clock. Basically it is cellular. In unicellular animals and plants, the clock appears to be located in individual cells, while in multicellular animals it is associated with the brain. In most insects the clock (including the photoreceptors) is located either in optic lobes or in the tissue between the optic lobes and brain. In birds the clock is evidently located in pineal gland, while in mammals it seems to be located in a number of specialized cells (suprachiasmatic nuclei) just above the optic chiasma. To act as a time keeper, the clock must have an internal mechanism with a natural rhythm of approximately 24 hours, which can be reset, by recurring environmental signals (e.g.—changes in the time of down and dusk).

4. Lunar cycle : Quite a good number of organisms set their timing of activity with tidal and Lunar rhythms. The animals inhabiting the intertidal zones, in particular, show rhythms in their behaviour that coincide with cycles of high and low tides. These endogenous timing procesors also exhibit persistent internal rhythms, quite comparable to circadian rhythms. European shore crbas and fidller crabs show this rhythm.

Reproduction in marine animals is restricted a period that bears some relationship to tides. In some of them these rhythmic phenomena occur every lunar cycle 28 days, while in others every semilunar cycle (14-15 days). Some animals time their activity with the lunar cycle of a particular period of the year.

e.g.—The Gruniow (Leuresthes tenuis) swarms in from the sea and spawns 3-4 days after the new full moon, corresponding to the spring tide each month between April and June on the sandy shores of California.

9.2 ☐ Environmental factor—temperature

Temperature is one of the most important environmental factors that has a wide effect on organisms living in a particular environment. Unlike light it is non-directional and has a limiting effect on growth and development of organisms. As a matter of fact temperature is the prime factor determining chemical reaction going in an organism apart from other factors. There are wide range of effects on organisms which are described below :

Temperature range : On the land surface and water bodies, a range of temperature variation can be observed. In terrestrial environment temperature varies greatly as high as about 60°C in warm deserts to as low as -70°C in Siberian atmosphere. Some hot springs show a temperature of about 100°C. In open water bodies, the temperature of the surface do not go below 0°C, so there is a restriction of further cooling of the bottom layer. So organisms can live their safely. Temperature variation may be of 2 type—

1. Duirnal variation : Variation of day and night temperature. As in land environment day and night temperature variation is about 17°C while in desert it is about 4°C. In aquatic system, due to high specific heat of water, the variation is about 1°C.

2. Seasonal variation : Variation of temperature with changing season. In summer, the surface water of a water body may rise at about 21-22°C, whereas it can drop to about 0°C in winter days or may be frozen.

Temperature tolerance : Different organisms can tolerate a range of temperature which may be high or low. Depending upon this tolerance, they are distributed in different geographical areas of the world. Animals can be divided into 2 groups depending on temperature tolerance—

1. Eurythermals : Organisms that can tolerate wide range of temperature fluctuation are called stenothermal organisms, e.g.—cyclops, toad, man etc.

2. Stenothermals : Organisms that cannot survive in wide temperature fluctuation i.e., of narrow limit of temperature tolerance, are called stenothermals. e.g.—many spring tails and tipulids in the Himalyas living at -10° to 0°C and die even at the warmth of a human hand.

9.2.1 Biological role of temperature

1. Effect on metobolism : Temperature is considered to be a limiting factor of growth and development. As we know that metabolic activities depend upon enzyme which again

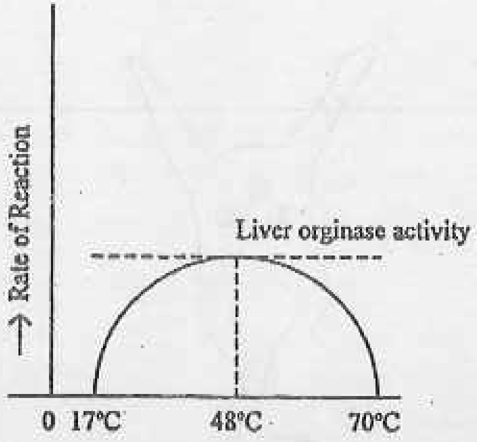


Figure-9.1 Graph illustrating relation between Rate of reaction and temperature

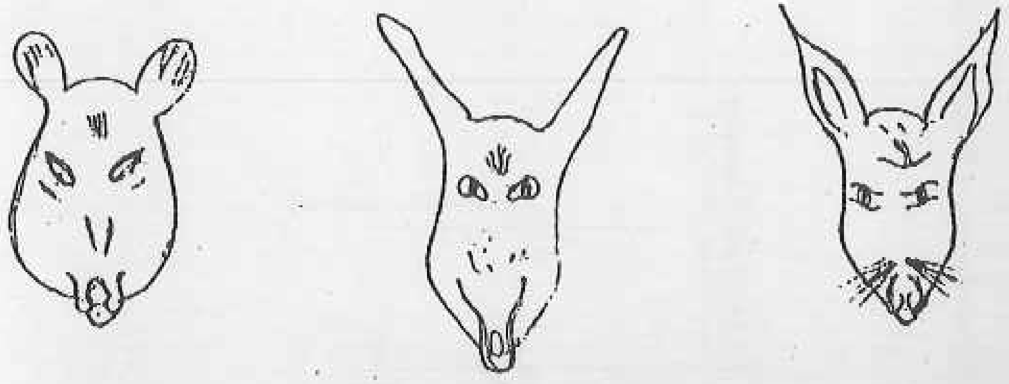
are temperature dependent, so on increasing the rate of metabolism reach a maximum (optimum temperature) after which the enzymes begin to denature and metabolic reaction rate fall. (Fig. 9.1.)
e.g.—**Liver arginase** act upon Arginine of about 17°C and the reaction rate increases gradually to 48°C but after that reaction rate falls automatically.

2. Effect on growth : The size of organs and physiological and behavioral adaptations of organisms vary over their geographical temperature. As a matter of fact, animals in cold region tend to be large (e.g.—polar bears, whates), whilst animals living in hot climate are generally smaller in size (e.g. insectivorus animals)—**Bergman's Rule.**

Again it also has been seen that many species, including tiger, which decreases in size with distance from poles. This is because, animals living in cold climate have to depend upon increased metabolic activity, hence greater body than other climate animals.

The size of external organs of extremities also vary with the environmental temperature they have to tolerate (tails, ears, legs) often appeared to be shorter in cold climate as compared to the hot climate—**Allen's Rule** (Fig. 9.2). Mice reared at 31°C to 33.5°C have longer tails than those reared at 15°C-20°C. In this case, heat escape through body extremities in cold climate is reduced.

The races of birds having relatively narrow and more accuminate wings tend to occupy the cooler region, while those inhabiting areas warmer regions tend to become broader —**Rensch's Rule.**



Arctic fox
Body temperature → 37°C
Env. tem.—0°C

Arctic fox
Body temperature → 37°C
Env. tem.—0°C

Arctic fox
Body temperature → 37°C
Env. tem.—0°C

Figure-9.2 Structural variation in fox species, depending on difference in temperature condition, they thrive

Temperature also affects the morphology of some fishes and is found to exert some influence in the number of vertebrae they possess—**Jordon's Rule.**

3. Effect on development: Temperature induce the development in organisms in poikilotherms. In general incubation period is more rapid in warm temperature, e.g.— Trout eggs develop 4 times faster at 15°C than at 5°C. Chironomic fly requirs 26 days at 20°C for development, of a full generation, 94 days at 10°C and 234 days at 2°C.

4. Effect on pigmentation: Generally light is more important for pigmentation but it is also seen that warmer climatic region, insects, birds and mammals are dancer in colour than the races of the same species inhabiting the cooler and drier climatic condition—**Gloger's Rule.** (e.g.—Reverse effect of temperature in tree frog *Hyla* and the horned toad *Phrynosoma).*

5. Effect on reproduction :

(i) Maturation of gonads, gamete formation and liberation of gametes take place at a specific temperature, depending upon the species. Some species breed througout the year, some in summer, winter or so on.

(ii) **Fecundity** : This is the reproductive capability, i.e., total number of young ones given birth during the life time. Temperature also affects fecundity, e.g.—*Grasshopper* species ***Camnula pellucida*** when reared at 32°C produce 20-30 times more eggs than those reared at 22°C. (Annthakrighman & Viswanathan, 1971)

(iii) **Sex ratio** in some species of animals are determined by environmental temperature. In Copepods, the number of males increase with temperature (Macrocyclops). Daphnids, Rotifers lay parthenogenetic eggs that develop in female at low temperature (5-8°C). At higher temperature (28-30°C) they lay sexual egg that can produce both sexes.

6. Effect on behaviour : In some animal species, eg. *(Daphnia)*, the head shalpe and size changes in different season. This is called **cydomorphosis.** The changes are listed below:

Spring → helmet-like projection
Summer → maximum size of helmet
Winter → disappears.

The prolongation of the helmet has been described as an adaptation to assist in floating since the buoyancy of water reduced with increased temperature (Buoyancy Hypothesis). The helmet acts like a raddar and gives greater stability (Stability Hypothesis).

7. Effect on distribution : Temperature has a definite role in distribution of the animals. Maximum survival temperature of coral is 21 °C, so they are present in tropical and subtropical regions only. Moreover, the lethal limit of temperature also regulate animal distribution.

9.2.2 Impact of temperature on various life processes

Life processes are restricted to the temperatures at which water is liquid : 0°-100°C at the earths surface. Temperature has several opposing effects on life processes. Heat increases the kinetic energy of molecules and thereby accelerates chemical reactions. The rates of biological processes commonly increase between 2 and 4 times for each 10°C rise in temperature throughout the physical range. This factor of increase is called the Q_{10} of a process, and it is estimated by the relationship between the rate of a physiological process; plotted on a logarithmic scale and temperature. (Fig. 9.3)

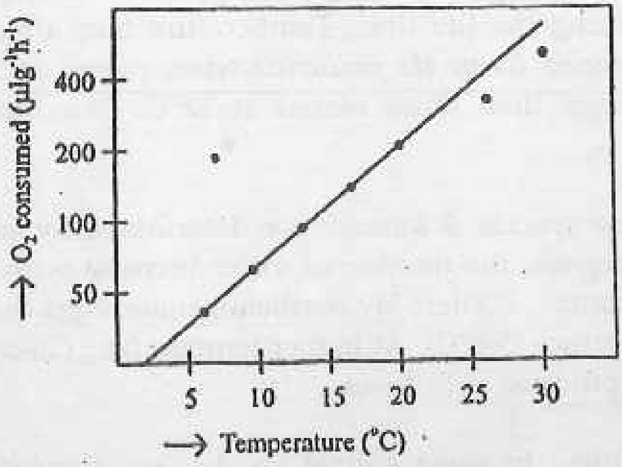


Figure-9.3 The rate of O_2 consumption (log scale) of the Colorado potato bettle as a function of temperature. The rise in O_2 consumption is exponential (Q_{10} = 2.5)

9.2.3 Effects of temperature on photosynthesis

In both C_3 and C_4 plants photosynthesis increases with the increase in temperature upto certain limits. Each plant species has an optimum photosynthetic temperature that often corresponds to the temperature of greatest plant growth. Thus changes in the environmental temperature may cause the onset of unfavourable conditions for the normal life processes of plants. This optimum may be attributed to the activity of the enzyme Ribulose bicphosphate carbonylase/oxygenase (Rubisca) which is responsible for the assimilation of carbon. Rubisco operates more efficiently at temperature below 25°C. Hence, the advantage of C_4 pathway diminishes in cool environment (Fig. 9.4), because this reaction is catalyzed by phosphoenol pyruvate (PEP) carboxilase, which operates more efficiently at higher temperatures. The C_4 plants achieve maximum photosynthesis at about 45°C (i.e., temperatures close to maximum tolerable limit for plants). While C_3 plants at between 20° and 30°C. As a result, C_4 plants predominate is not climates and C_3 plants in cool climate.

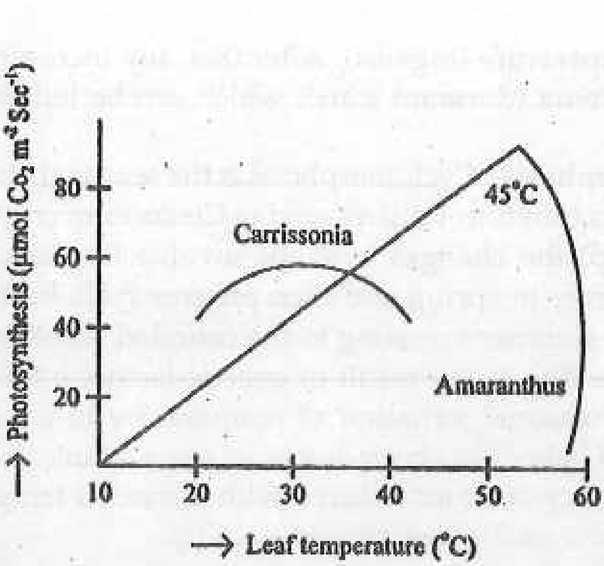


Figure-9.4 Relationship of photosynthesis (measured μ mol m^{-2} sec^{-1}) to leaf temperature in winter active C_3 desert herb *Camissonia caloiformis* and the summer active C_4 desert nest **Amaranthus palmeri.**

9.2.4 Some important terms related with effect of temperature in physiological processes

Cardinal temperature : Every organism has a narrow range of a temperature known as Cardinal temperatures, this range is delineated by a lower minimum and an upper maximum Lethal temperature beyond which the organisms cannot thrive.

Optimum temperature : The range of temperatures in which animal can survive normally, without any abnormalities, is called the **Optimum temperature.** It is about 10-48°C.

Minimum temperature : To proceed all necessary metabolic processes animals require a **lowest effective temperature** at which they can live indifinitely in effective state.

The temperature at which is just possible, is called **survival temperature.**

Just below the survival temperature at which an organism goes into an inactive state, is called **chill coma,** and the organism can survive only if the temperature rises within i a short period.

Maximum temperature : The temperature at which the animal can continue to survive I with its normal functions is maximum temperature or **highest maximum temperature.**

The temperàture (highest) at which survival is hardly possible is called a **Survival** temperature (highest). After this, any increase in temperature can induce **Heat Coma** (dormant state), which can be lethal for organisms.

Cyclomorphosis : Cyclomorphosis is the seasonal changes in body shape found in rotifers (phylum-Rotifera) and in Cladoceran crustaeea. In cladocerans (e.g. *Daphria* sp) the changes in shape involve the head, which is rounded form mid summer to spring and then progressively becomes helmet shaped from spring to summer revesting to the rounded shape by mid summer. The process may be due to the result of genetic-factors interacting with external condition i.e., seasonal variation of temperature in an aquatic system. The prolongation of helmet has been described as an adaptation to assist in floating since the buoyancy of water reduced with increased temperature. The helmet acts like a radder and gives greater stability.

Diapause : Diapause a temporary cessation that occurs in the growth and development of an insect. Insects can enter the diapause state an eggs, larvae, pupae, or as adults. Diapause is frequently associated with seasonal changs in the environmental condition. The insect enter it during the adverse period, and breaking from it when more favourable conditions return. In plants it is called **dormancy**—a resting condition with reduced metabolic rate. This is found in non-germinating seeds and non-growing buds. Temperature here may act as a stimulus, determining another or not the organism start its development at all. Temperature can also interact with other stimuli (e.g. photoperiod) to break the dormancy (e.g. diapause in insect) and thus time the onset of growth.

Thermocline zone : Generally, a gradient of temperature change, but applied more particularly to the zone of rapid temperature change between the warm surface water (epilimnion) and cooler deep waters (hypolimnion) in a thermally stratified lake in summer. It is the zone (Fig. 9.5) where organism can maintain their normal physiological activities. In the ocean this zone of rapid temperature change starts 10-500 m below the surface and can extend down to more than 1560 m. In polar regions the thermocline is generally absent, because the ocean surface is covered with ice in winter and solar radiation is small in summer.

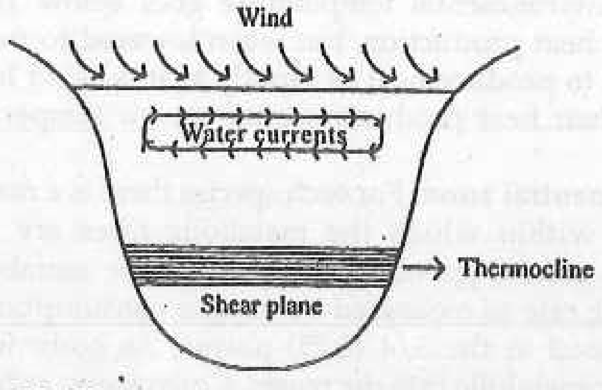
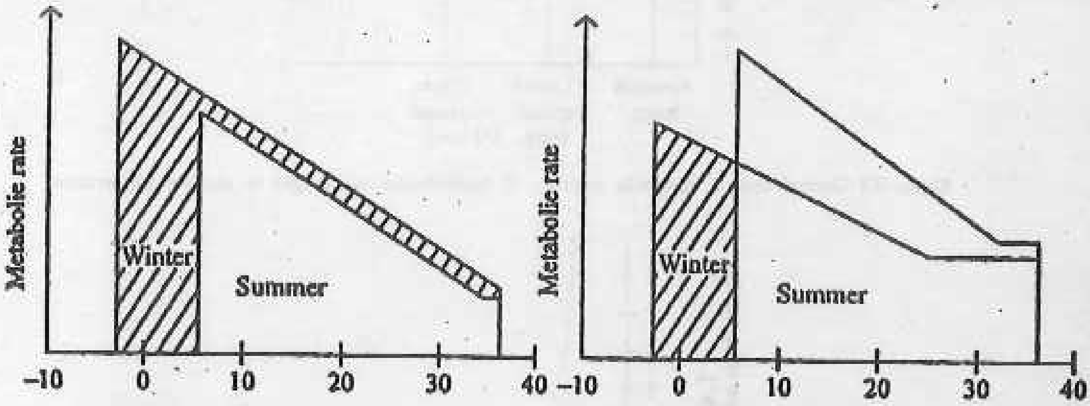


Figure-9.5 Diagrammatic representation of the thermocline plane

9.2.5 Critical Temperature

Within a range of temperature Homeotherms (birds and mammals) can maintain their body temperatures by a change in the insulating thickness of hair, ftir, feathers and fat. Many mammals aquiring a haevier coat of hair (that thins out with onset of warm weather), birds by fluffing their wings withstand with the cold temperature in winter. But during sudden or prolonged cold spells there is a point at which insulation is no longer effective and the animals must maintain body heat by inscreased metabolism (Fig. 9.6). This point is the critical temperature (Fig. 9.7). Tropical birds and mammals increase their heat production when enposed to temperature below 23.5° to



(a)

(b)

Figure-9.6 (a) Metabolic rate increases as the ambient temperature declines in winter (simple metabolic acclimatisation), b) Insulation reduces the metabolic rate in winter and permits tolerance of much lower temperature (simple insulating acclimatisation). (After Smith, 1996).

29°C. If the environmental temperature goes below 10°C, tropical animal must triple its heat production, but when lowered to freezing, the animal is no longer able to produce heat as rapidly as it is being lost. Artie animals do not increase their heat production until the air temperature has fallen to -29°C.

Thermo neutral zone: For each species there is a range of environmental temperatures within which the metabolic rates are minimal known as thermoneutral zone (Fig. 9.6). Outside this zone metabolism increases. The basal metabolic rate as measured by oxygen consumption, is proportional to body mass raised to the 3/4 (0.75) power. As body weight increases, the weight specific metalolic rate decreases. Conversely, as body mass decreases, basal metabolism increases (exponentially with very small body size) (Fig. 9.8).

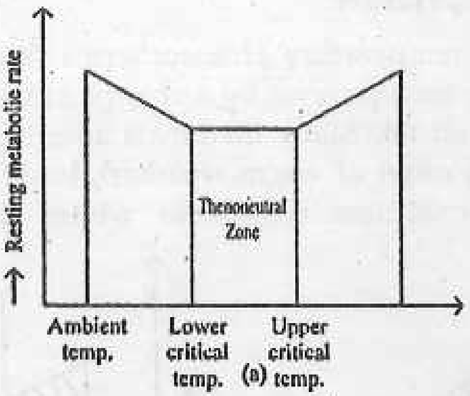


Figure-9.7 General restling metabolic response of homeotherms to changes in ambient temperature

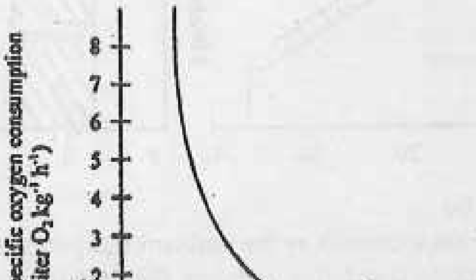


Figure-9.8 Oxygen consumption increases rapidly with decreasing body mass. (Adapted from Smith, 1996)

9.3 ▫ Environmental factor—pressure

Barometric pressure has not been shown to be an important direct limiting factor for organisms, although some animals appear able to detect differences and of course, barometric pressure has much to do with weather and climate, which are directly limiting to organisms.

In the ocean however, hydrostatic pressure is of no importance because of the tremendous gradient from the surface to the depths. In water the pressure increases one atmosphere for every ten meters. In the deepest part of the ocean the pressure reaches 1000 atmospheres.

Pressure changes are many times greater in the sea than in terrestrial environments and have a pronounced effect on the distribution of life. Certain organisms are restricted to surface waters, whereas others are adapted to pressure at great depths. Some marine organisms, such as sperm whales and certain seals, can drive to great depths and return to the surface without difficulty.

Effect on Animal : Many animals can tolerate wide ranges in pressure, especially if the body does not contain free air gas. When it does gas embolism may develop. In general, great pressure are found in the depth of the ocean exert a depressing effect, so that the pace of life is slower there.

Effect on high attitude : As altitude increases the parietal pressure of oxygen decreases. From a sea-level value of 700 mm of Hg, it drops to about 30 mm of Hg at Mount Everest. Now, for haemoglobin to bind with oxygen, needs a PO2 of about 80 mm of Hg. So there are marked reduction in the O2-binding capacity of haemoglobin. Also, it is evident that the PO2 rather than composition of air makes the condition hypoxie (reduced supply of oxygen to the cells).

Mountain sickness : This is caused in high altitudes (above 15,000 ft) due to each of optimum PO2. As there is lesser supply of O2 to the brain, it malfunctions which causer dizziness and nausea accompanied by irritable behaviour.

9.4 ▫ Environmental factor—rainfall

The precipitation in the form of water is called railfiill. Rainfall is largely determined by the weather systems.

When the temperature is less than 0°C, precipitation occurs in the form of snowfall. Frozen rain drops are called as sleet, whereas precipitation in the forms of hard rounded pellets is called as hail.

Moisture laden winds blowing off the ocean deposit most of their moisture on the ocean facing slopes, with a resulting "rain-shadow effect" (Fig-9.9) producing a desert on the other side; the higher the mountain the greater the effect, in general. Thus deserts are usually found "behind" high mountain ranges or along the coast where winds blow from large, interior dry land areas that off the ocean.

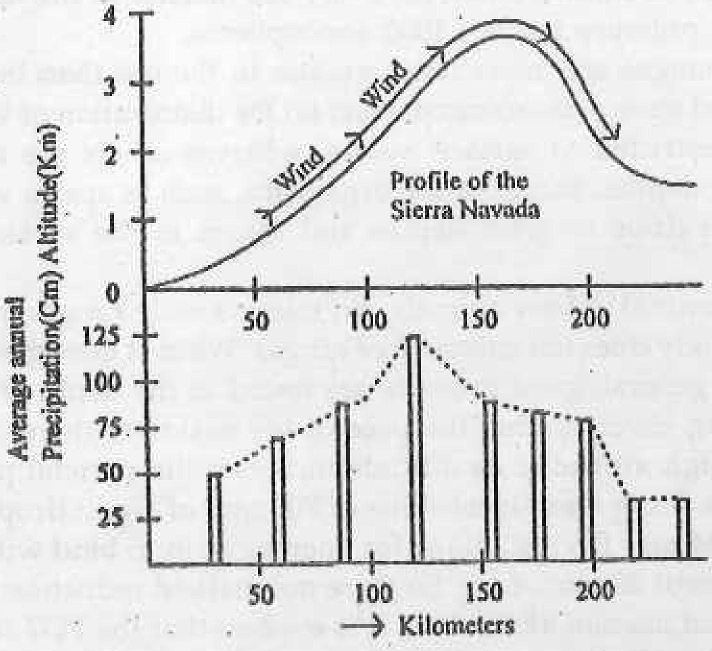


Figure-9.9 Illustration of the "rain-shaddow" effect of the Sierra Navada in Central California

Rainfall tends to be unevenly distributed over the seasons in the topics and subtopics, resulting into well defined wet and dry seasons. In the topic, this seasonal rhythm in moisture regulates the seasonal activities (especially reproduction) of organisms in much the same as the seasonal rhythm of temperature and light regulates temperate zone organisms.

In temperate climates, rainfall is more evenly distributed throughout the year, with many exceptions. Below, there is a rough approximation of the climax biotic communities according to the needs of different amount of rainfall in temperate area :

0 — 10 inches year^1 → Desert
10 — 30 inches year^1 → Grassland, Savanna, or open wood land.
30 — 50 inches year^1 → Dry forest
over 50 inches year^1 → Wet forest

Actually, the biotic situation is not determined by rainfall alone but by balance between rainfall and potential evapo-transpiration, the latter being loss of water by evaporation from the ecosystem.

Humidity : Humidity represents the amount of water vapour in the air. Total amount of water vapour in a unit value of air is called absolute humidity. Weight of water vapour per unit weight of air is called specific humidity. The ratio of actual water vapour in I the air to its water holding capacity at a given temperature is known as relative humidity, Relative humidity can be changed by changing the moisture of temperature.

9.4.1 Effect of rainfall on animals

Variation in rainfall (in turn humidity) affects animal directly or indirectly. Animals of rain forests prefer to live only where the air is saturated with moisture. However, desert animals prefer to live in dry air. Soil moisture also serves as a limiting factor. Desert animals are nocturnal, because relative humidity is high in the night. Most of the animals show their preference towards humidity.

In siver fish, ***Lepisma saccharina*** reproduction occurs when the relative humidity lies between 85 to 90 present. In certain insects and spiders, locomotion and feeding are affected by humidity. Although micro-organisms flourish under moist condition, silk worms do not pupate in moist air. Moisture significantly affects the fecundity and development of insects.

9.4.2 Effect of rainfall on plants

Rainfall controls the geographical distribution of plants. Plants with high water requirments grow in moist places with greater rainfall. They develop suitable adaptations. For example, desert plants open their stomata in the night when the loss of water through transpiration is minimum.

In warm arid regions, water is a master limiting factor, and in absence of run off, primary production is strongly positively correlated with rainfall in a linear fashion (Fig. 9.10). Above about 80 centimeters of precipitation per year, primary production slowly decreases with increasing precipitation and then levels off (asymptotes) (Fig. 9.11)

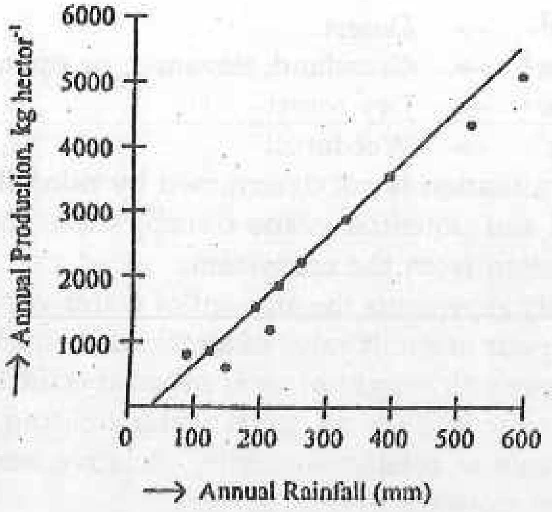


Figure-9.10 An example of strong co-relation between annual rainfall and primary production along a precipitation gradient in a desert region of Namibia. [Adapted from odum (1959) after waiter (1939)].

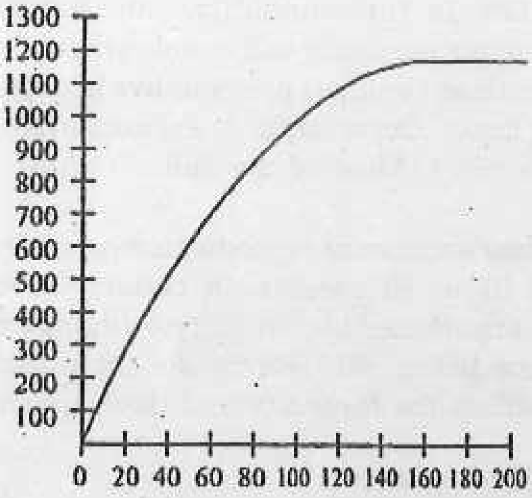


Figure-9.11 Net Primary productivity (above ground) plotted against average annual precipitation, [from Whittaker (1970)]

9.4.3 Adaptation of plants and animals

Plants : 1. Plants have wax-coated leaves that minimise loss of moisture.
2. Some have deep roots that reach the ground water.
3. Leaves when present are thick and very small in number, e.g.—Cactus, desert Shrubs etc.

Animals : 1. Small in size.

2. Remain under cover during the day and come out to feed at night.
3. Have thick external shell that minimises moisture loss due to evaporation.
4. Exerte very concentrated urine,
   e.g. Frogs, Reptiles, Rodents etc.

9.4.4 The combined action of several factors

Two most important factors such as temperature and moisture largely classifies the climate from ecological point of view. There is a number of climatic indices that explain the distribution of vegetation. Like—
(i) Martonne's aridity index (I), which is given by

$$I = \frac{P}{T+10}$$

where, T → Mean annual temperature (0°C)

P → Annual rainfall (mm),

when to calculate for a single month,

$$I = \frac{12p}{t+10}$$

where t → Mean temperature for that month.

p → rainfall for the month.

This index becomes smaller as the climate become arid. The index for July, the season of maximum plant growth and animal activity in the northern hemisphere, has a marked higher value than the annual index.

Example : (ii) *Podisma pedestris*, a borco-alpine species, which is widely distributed in the mountains of Europe, the extreme north of Europe and Siberia. It is stenothermal, but its stonothermy, which varies with humidity, is for more pronounced in a humid climate than in a dry one. So this specie is widely distributed in the drier regions of the southern Alps than the more humid northern Alps. (Dreuse, 1962).

(ii) Gaussen considered that drough conditions establish when the monthly rainfall, P(mm) is less than twice the mean monthly temperature T

(°C). A graph, constructed showing the month on the asscissa and temperature and rainfall on the ordinate, is called a *Pluviothermic graph.*

(iii) Emerger suggested a more complicated formula which would allow for annual variations in temperature. His pluviothermic quotient *(Q)* is given by the formula—

$$Q = \frac{(M+m)\ (M-m)}{100P}$$

where, P -> Annual rainfall (mm)
M -> Mean maximum of the warmest month
m -> Mean minimum of the coldest month.

Different types of Mediterranean climate can be classified using this method, having well marked not and dry seasons. And rainfall in restricted toi the cooler part of the year.

UNIT 10 ☐ Organism-Environment Interactions

Structure

10.0 Introduction
10.1 Resistance
10.2 Tolerance
10.3 Acclimatisation
10.4 Adaptation

10.0 ☐ Introduction

Different kind of organisms are not distributed amongst different kinds of environment. It is therefore, convenient to consider first the variation that exists in environment and could be discussed following—

1. Conditions suitable for life :

Energy obtained by different inorganic transformation (oxidation of methane sulphur compounds, ammonia) powers all the biological activities on earth. These transformations are done by archaebacteria, inhabitants of extremely hot or acidic environment.

However, the mainstream of biological activity are limited by the **efficiency of photosynthetic process and depend on incident radiation.**But incident radiation also determines the physical state of water (i.e. solid, liquid or gaseous) and in turn also determines where and when photosynthesis might occur. Water may be volatilized if radiation is abundant and may be solidified (ice) when radiation is less. Hence ecology of our planet is caught **"between the frying pan and the freezer."**

2. The diversity of organisms and their patchy distribution :

It is not too difficult to imagine a planet like earth is inhabited by one side of organism, The distribution of organisms might be limited to just a tiny subset of the multiplicity of environment or it may range widely over many physical environment if it be eurytherm or could tolerate periods of dessication or could also function when immersed in water. But it could live only where there was liquied water, a source of energy and access to j organic resources for growth and it needs to be self decomposing if died. Otherwise it would exhaust the resource and would be extinct. Such an 'ideal' organism would give the planet an ecology and biogeography. In fact earth is distributed by vartgated from of life that are neither distributed randomly not as a homogeneous mixture over the surface of the globe.

Any sampled area, in the scale of a whole continent contains only a subset of a variety of species present on earth. These restricted patterns of species distribution occur despite the fact that individuals (progeny) of all species are capable of some disposal, which may be on an intercontinental scale (e.g. birds and the seeds of orchids). A great past of science of ecology tries to explain why every type of organisms does not like everywhere. One of the greatest of all ecological generalizations is that : **all species are always absent from almost everywhere.**

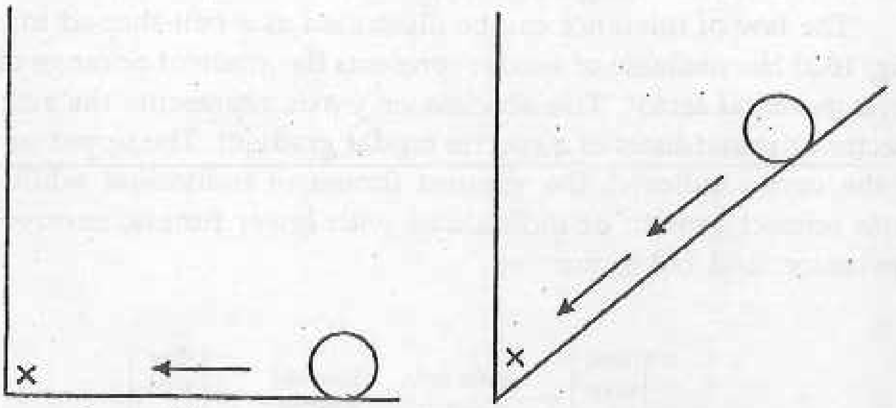
10.1 □ Resistance

Resistance is the ability of a system to withstand of resist variation. It is measured by the degree to which the system is changed from an equilibrium state following a disturbance so resistance describes the ability of a community to avoid displacement from its former state, (Fig 10.1) communities most resistant to change characteristically have a large biotic structure, as trees do, and nutrients and energy stored in standing biomass. A forest community is relatively resistant, which can withstand some environmental disturbances like sharp temperature changes, drough, insect outbreaks etc.

Along with resistance, another factor called **resistance** is there to make a community stable against any environmental perturbation. Resistance is the speed, with which a disturbed system returns to the former or equilibrium state after it has been perturbed and displaced from the former state (Fig 10.1). A rapid return indicates the high resistance and a low return indicates the low resistance.

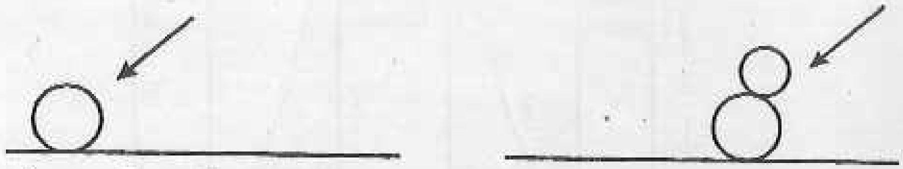
An example :

In the spruce-fir forests of Northern North America under certain environmental conditions, the population of spruce buderorm rapidly increased and escapes the control of predators and parasites. It feeds on blasam fir rapidly and kills them. As a result population of less succeptible spruce-birch increased. But when spruce buderorm population collapse due to shertage of food supply, then again young balsam fir grows back in thick stands with spruce and birch. Thus sometime after the outbreak of buderorm, the system returns to balsam fir. The system is resistent even though some of the interacting populations have low resistance.



Low resilience

High resilience



Low resistance

High resistance

Figure-10.1 Figurative illustration of resistance and resilience

10.2 □ Tolerance

To live in a given environment, an organism must be able to survive grow and propagate, which is very much influenced by different environmental factors. In fact the distribution of various species in their biosphere is dependent on the interaction between different attributes of those organism and the environmental factors to overcome the deletorises effects of these factors.

Tolerance is one of such attributes that allow the individual to withstand the effects of a given range of environmental factor thus enabling a species to survive, grow and reproduce in that environment. To determine the tolerance of organisms to a range of environmental factor, V.E. Shelford (1913) incorporated the idea of law of Tolerance', which states, "**the distribution of a species is controlled by that environmental factor for which the organism has the narrowest range of tolerance".**

The law of tolerance can be illustrated as a bell-shaped tolerance curve (Fig. 10.2) Hie ordinate or x-axis represents the gradient or range of a particular environmental facto*. Trie abscissa or y-axis represents the response of the species or individuals of a species on dat gradient. The upper or middle part of the curve indicates the greatest fitness of individual while descending parts refelect growth of individuals with lower fitness, survive but do not reproduce, and fail to survive.

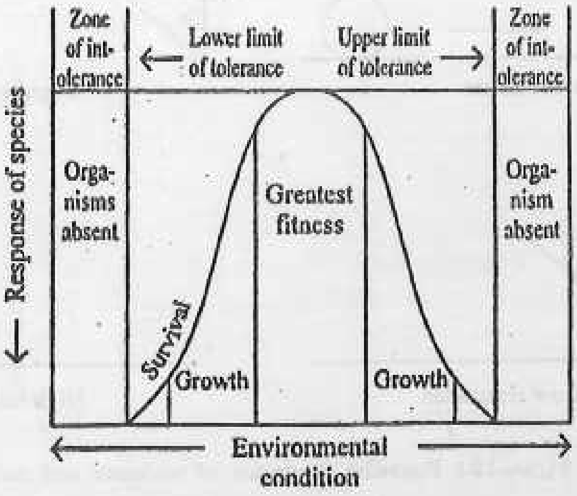


Figure-10.2 The law of tolerance

The adaptiveness of an organism (its growth, survival, life processes) to its environment is exhibited by its ability of function between upper (maximum) and lower (minimum) limits within a range of environmental conditions. These limits are unknown as '**limits of tolerance**', while the range in between two extreme limits are referred to as '**range of tolerance**'. Within this range the rate of various metabolic and other activities gradually increases from the extreme points attaining its peak somewhere near the midpoint, known as **optimum condition.**

As the factor approaches its limit of tolerance, the organism becomes subjected to physiological stress that may result in death at or beyond the limit. Too little of a resource may be harmfull but too much of a good tiling can be just as bad, that is, maximum quantity of a resource tolerated by an organism would limit response as well, thus limiting.

F. F. Blackman (1905) advanced this concept, known as **law of limiting factors**.

The range of tolerance is not fixed but varies with different species. On the basis of relative degree of tolerance, an organism can be designated as—

Steno → denoting narrow or Eury → denoting wide range of temperature tolerance. For instance, the stenothermal thermophilic crustacean, ***Thermabaena mirabilis***, can not withstand temperatures below 30°C, while the eurythermal catterpillars of moth **Lymantria monacha**, can well tolerate temperatures ranging from -10-5°C to 47°C.

Seasonal shifting in tolerance range :

As season and conditions change, individuals may acclimate (short-term alteration of physiological optima) to them and shift the tolerance curves to the right or to the left (Fig. 10.3). For instance fish inhabiting in a pond where water temperature changes from spring through winter. As water warms in spring the tolerance of fish for warmer temperatures gradually increases, at the same time their tolerance for lower temperatures decreases. Similarly, as the water cools in fall and winter, the tolerance for lower temperature increase while just reverse effect occurs for high temperatures.

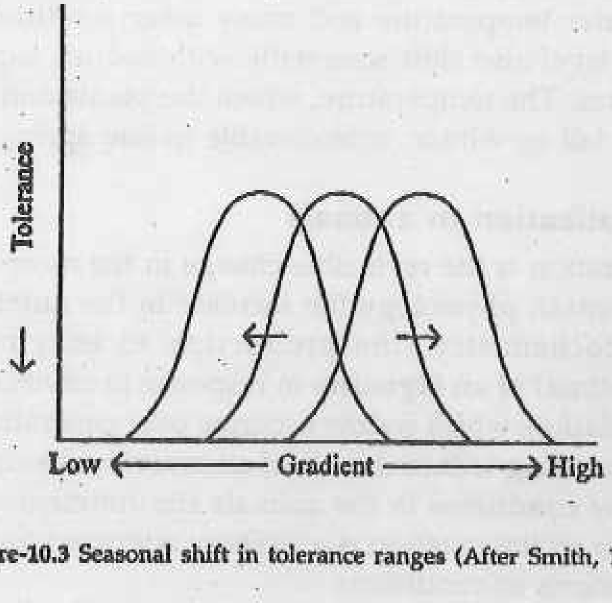


Figure-10.3 Seasonal shift in tolerance ranges (After Smith, 1995)

The stages of the life cycle may differ in their tolorance limits. The young stages are often most sensitive to environmental factors and their limits of tolerance are narrower than those of adults. Thus, the reptiles living at altitudes higher than 1200 m in Alps and pyrenees are viviparous; while below 1200m are all oviparous, since their eggs do not develop at lower temperatures.

10.3 ☐ Acclimatization

Response of the organisms to environmental change fall into general categories : Regulatory, Acclimatory and Developmental responses. Regulatory responses are accomplished more rapidly, while the developmental responses most slowly. Most of the organisms, are not fixed in their tolerance to environmental extremes but are preconditioned by the experience of temperature in their recent past. This process when occurs naturally, it is called **acclimatization,** but when it occurs in laboratory, it is called **acclimation.**

Under natural conditions, however, the environment never differs in just one or two parameters. Many other ones, such as humidity for plants, food availability for fishes etc. are simultaneously involved. The difference in the physiological states that appear after long term exposure to different natural environmental condition is acclimatization. Plants acclimatize to the colder temperatures of fall and winter and fishes acclimatize with seasonal variation of water temperature and many other conditions. As they do so, their tolerance level also shift seasonally with sudden exposure of high and low temperatures. The temperature, which the plants and animals can easily tolerate in late fall or winter, is intolerable in late spring and summer.

10.3.1 Acclimatization in animals

Acclimatization is the reversible change in the morphology (thickening of the fur in winter), physiology (an increase in the number of RBC at high altitude) or biochemistry (the production of enzymes with different temperature optima) of an organism in response to environmental change. In contrast to adaptation, which is slow occuring over generations, acclimatization is more rapid occuring within the life of an individual animal, resulting from exposure to new conditions in the animals environment. Such changes take day to weeks, so acclimatization is a strategy restricted to seasonal and other persistent variations in conditions.

Thus migration up a mountain may lead to acclimatization to low O2 and low pressure. Likewise, during cold winter many birds donot a heavier plumage, providing greater insulation, than they were during the hot summer. The species replace their body feathers in spring and fall; ~ach plumage is suited to the typical conditions of the environment encountered between each moult. This allows the species to retain a similar metabolic rate to meintain their body temperature at varying external temperatures between summer and winter. Although winter acclimatized individuals seen well adapted for both winter and summer climates when at rest, summer activity combined with a winter plumage would quickly produced heat prostration. Adjusting insulation to enhance heat conservation in winter and to facilitate heat dissipation in summer maintains a constant body temperature I at the least possible cost (Reklef's & Miller, 2000).

The measured underlying acclimatory responses may involve neast rate, metabolic rate, and enzyme reaction rate. Animal can make them tolerant to the prevalent environmental condition by employing a variety of enzymes and biochemical systems with different temperature optima. The mechanism of acclimatization and its capacity is not equivalent among all organism for instance, when compared with fish and other ecothermic animals, amphibians appear to have less capacity for acclimatory changes in the amount of efficiency of muscle fibre, less ability to manufacture isoenzymes having greater efficiency in the cold, and less ability to alter enzyme function (Rome, et. al, 1992).

10.3.2 Compounds needed for acclimatory changes

Plants and animals accumulate certain compound to protect their cell (specially cell membrane) during the period of post hardening, from the effects of dehydration. These compounds are mainly free amino acid (especially in plants), low molecular mass polyhydroxy compounds (PHCs) like glycerol. Sugars and sugar alcohols are also needed to protect complex protein and lipid structure from quite extreme dehydration (Franks et al. 1990).

An example :

Insects have been shown to have two strategies that allow survival through low temperatures of winter—

1. Freeze avoiding strategy :

Uses low molecular weight polyhydric alcohols (e.g. glycerol, sorbitol), which prevent the formation of intracelluar ice by depressing both the freezing point and the supercooling point and uses 'thermal hysteresis' proteins to prevent ice-nuclei from forming.

2. Freeze-tolerant strategy :

Involves the formation of polyols, encourages the formation of extracellular ice, but protects the cell membrances from damage when water is withdrawn from the cells. Acclimatization starts as the weather becomes cooler in the autumn and stimulates the conversion of almost the entire glycogen reserve of the animal into polyols.

10.4 ☐ Adaptation

Adaptation is a central concept in biology and one that attracts substantial controvercy. It is often used in several different senses. The most common one is—

(a) any behavioural, morphological or physiological trait that is assumed to be the result of natural selection.

(b) any physiological or morphological feature or from of behaviour used to explain the ability of an organism to live where it does.

(c) a change in physical, physiological or behavioural traits that results from some current environmental pressure, such as adapting to a change in temperature.

- It is used to mean some properties of animals that they prossess to survive in a particular environment (e.g. fishes are adapted to live in water), but nothing says about how the properties were acquired. In contrast, it also can be said dat, those properties for the particular environment constrain those animals to live in dat only and exclude then from other environmental type.

- For an **evolutionary ecologist**,adaptation implies for the forces of natural selection that have affected the life on an adapting induviduals ancestors and so have moulded and specialized its evolution. Here adaptation means that genetic change has occured.

- In contrast, for an **eco-physiologists** the word accounts that individuals of a given species have themselves had some prior experience (e.g. being cold hardened) that make life in their particular environment possible. Here adaptation in non-genetic, but is phenotypic change.

According to Begon et al. (1996), it is a "word that has so many contrasting meanings, does not contribute much precision to science but all the meanings imply something about the way in which organism match their environment." The word adaptation implies the way that organisms react to present circumstances or prepares them for future through some forward planning and design but in truth, their character or properties are entirely consequence of the past, as they reflect the success and failures of ancestors. So the word **Adaptation (exaptation)** comes out, which indicates that the aptness (match) of organisms for their environment is a product of their past rather than a programme for the future. The prefix 'ab' emphasizes that the heritable characteristics of an organism are consequences of the past and not anticipation of the present or future.

Different aspects of adaptation :

(1) It is often used as a term for the characters or traits observed in animals that are the result of selection. As for example, presence of haemoglobin might be said to be an adaptation for greater O_2 carriage in blood.

(2) It might be defined as a process by which natural selection adjusts the frequency of genes that code for traits affecting fitness (the numebr of offsprig surviving in succeeding generations). For instance increased the concentration may be seen as an adaptation to hypoxic environments. In this sense adaptation is an extremely slowly occuring irreversible process but can occur very quickly in extreme environments or in cases where selective pressure from human interferences are strong.

(3) Adaptation is also used to describe short term compensation changes in response to environmental disturbances. This kind of change is the outcome of **phenotypic plasticity.** Where pre-exciting traits are differentially expressed an appropriate to the local conditions. So a trait is considered as adaptation only when it has been evolved in such a way that make it more effective at its task, which in turn increase its fitness.

UNIT 11 ☐ Stress Physiology

Structure

11.1 ☐ Basic concepts of environmental stress and homeostasis

11.1.1 Introduction

Environment is surrounded by many organisms, which continuously interact with its biotic and abiotic factors. All these interaction allow the organisms to survive in its particular enviornment. Environment is extremely variable and impose so many stresses upon its inhabitants, through variation in the biotic and abiotic factors, which may be as follows—

1. Stress by abiotic factors : Abiotic of environment mainly includes ot physical and chemical factors, (e.g.-light, temperature, PH, Humidity, pressure etc). A little variation of these factors form their optimum level can cause physilogical stress among organisms. Since life first evolved in themally and osmotically relatively stable sea and from very begining to work in this stable marine environment all cellular machinary was basically selected. So environmental abiotic stress can be seen from the view point that how much il has been diverged from those starting point. The case in the survival of organisms thus depends on the extreme conditions of its environment As life is relatively easy in cool sea, somewhat tricky in seasonal pond, while extremely difficult in hot desent. Other extreme environments include polar region, alpine zones, hyper saline lakes, not springs and deep sea hydrothermal vents.

2. Stress biotic factors : Biotic factors of environment such as inter and intra specific interaction, habitat modification impose direct or indirect effect of stress among one or more organisms living within the some species or different species. Unlike abiotic stress, biotic stress works in opposite direction. In case of easy habitats, inhabitants may experience large and intense stressful condition due to increased composition and predation pressure.

However, both kids of stresses may be disadvantageous for an organism, causing it to expend more energy for survival wheather in physiological regulation, or avoidance tactics, or competitive or defensive activities.

11.1.2 Stress in organisms

By definition stress is the non-specific (physioiogical) response of the body by any demand made upon them.

Competition for anything give rise to stress. Here adrenal gland is the effector organ. The entire reaction can be divided into three phases,

(i) First there is shock ; the moment there is a shock, there is depression. After that there is a counter-shock, the body will try to counter act. These two aspects i.e. the shock and counter shock will together constitute the alarm reaction. This is the first phase of the stress reaction.

(ii) The second phase is the stage of resistance when stimulation of adrenal activity takes place, i.e. increase in the adrenal weight to increase the adrenal secretion, (anti stress hormone—cortisol)

(iii) If the second stage fails to resist the body from stress, then the third phase or the stage of exhausion access. Here body will be unable to adjust and ultimately death occurs.

The whole stress reaction, the three phases are collectively called as the General Adaptation sysdrome (GAS) (Fig-11.1). It is also referred to as the Hans Selye's concept of stress.

The callular stress response : The cellular stress response entails the rapid synthesis of a suite of proteins that are involved in protecting organisms from damage as a result of exposure to a wide variety of stressors of environmental concern, including heavy metals, organic compounds, and UV light. A subset of these stress protins are heat inducible and part of the classical heat shock response, whereas other stress protiens that are more stressor specific can be included in the broader "stress response".

Four major heat shock protein families of 90, 70, 80 and 16-24 UDA are most prominent and frequently referred to as hsp 90, hsp 70, hsp 80 and the low molecular height (LMW) hsps, respectively. The term 'stress protein' is commonly used as the induction of these protein occur in response to many other types of enviromental stressors.

Molecular Chaperones: Stress 90, stress 70 and cpn 60 (60 UDA family, refered as chaperonin 60) are molecular "chaperones" that under normal conditions direct the folding and assembly of other cellular proteins.

Function : These stress protein are involved in regulating the kinetic partitioning between protein folding, translocation, reactions and protect aggregation. Under adverse environmental conditions, the synthesis of stress 90, stress 70 and cpn 60 increases and they take the role of repairing denatured proteins and protect cellular protein from environmentally induced damage.

11.1.3 Homeostasis

Homeostasis is a physiological process which makes an individual able to maintain constant internal conditions such as body temperature, water balance, pH and amount of salts in fluids and tissues against the variation in external environment. Though all organisms exhibit homeostasis in response to some degree of environmental variation, occurance and effectiveness of it varies.

Homeostasis involves the flow of external environmental information into a biological system with a homeostatic device to immediately cope with that changing environment. This device can be compared with a thermostat that controls the furnace. When a room temperature becomes too low a temperature sensitive on the thermostat turns on the furnace and alter the room is sufficiently hot it turns the furnace off. It is called **negative feedback.**

But if the thermostat fails to turn off the furnace after sufficient heating of the room, then the furnace continues to burn, temperature rises and execssive heat from the furnace sets fire, which spread- through the building and surroundings. This movement is called **positive feed back.**

11.1.4 Mechanism of homeostatic action

All organisms maintain some sort homeostasis in their living system, like, as body respond when environment temperature sharply drop, (fig-11.2) The normal temperature for human is 98.6°F (37°C). When environmental temperature drops, seneory mechanism in the skin detects it and send a mechanism in the skin detects it and send a message to the hypothalamus of the brain. When in turn send mesage to higher brain centers, thai cause voluntary actions like putting a close or come close to heat. Hypothalamus also send message to autonomic nervous system that produce heat through shievering. It stimulates the adrenal gland to release epinephrine hormone in blood stream which elevates the cell metabolism causing conversion of liver glycogen to glucose. At the same time hypothalamus stimulates pituitany gland to release thyroid stimulating hormone (TSH), which acts on thyroid gland to increase release of thyroxine hormone. Both these hormones stimulate body cells to increase their respiratory activity, thus produce heat.

Changes in the adrenal weight in stress induced rat

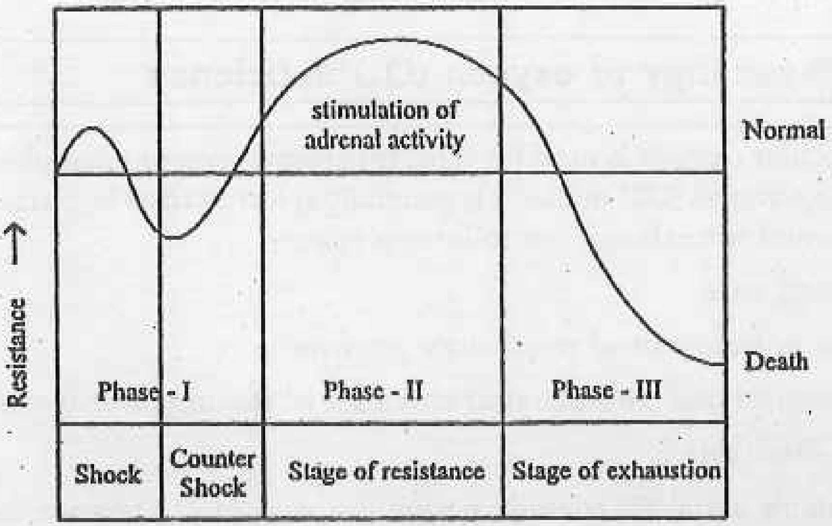


Fig 11.1 Hans Sely's concept of Stress of General Adaptation Syndrome (GAS)

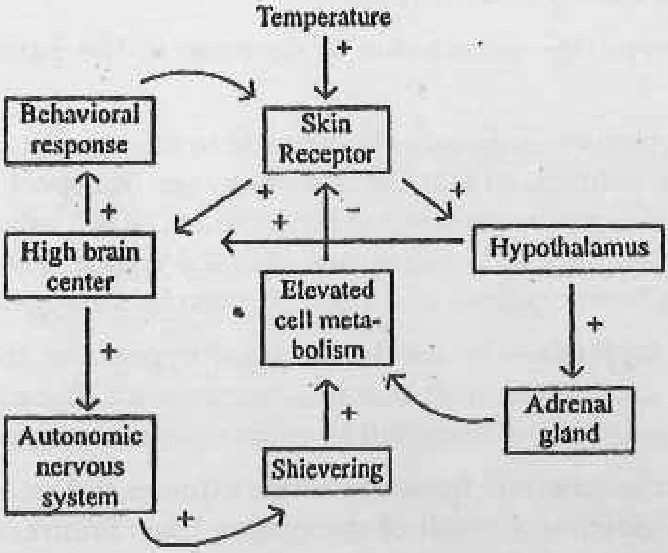


Fig. 11.2 Homeostatic control of body temperature (From smith, 1996)

In extreme enviornmental temperatures homeostasis mechanism breaks down. If Ihe temperature falls very low, homeostatic mechanism is unable to produce more heat to maintain constant internal body temperature. But if the temperature grows very hot Ihe body can not lose heat fast to hold the normal temperature.

11.2 □ Physiology of oxygen (O_2) deficiency

Molecular oxygen is used for most organisms (except anaerobes) to live. Decrease in Oxygen (O2) in blood is generally referred to as hypoxia. Oxygen supply needed to maintain the following roles—

Physiological role :

i) Helps in transport of respiratory pigment.

ii) Anatomical and physiological character of the organ of respiration.

Environmental role :

Maintains aerial O_2 content, partial pressure of O_2, temperature, CO_2, salinity etc.

Types of Hypoxia :

Hypoxia is mainly of four types—

a) **Hypoxia hypoxia**—Occurs due to decrease in the partial pressure of oxygen.

b) **Anemic hypoxia**—Occurs due to decrease in the amount of haemoglobin in anemic condition, so that the rate of oxygen transport through blood is effected. Again, Ihe presence of nitric oxide (NO), Carbon-mono-oxide (CO), Sulfonamides in blood causes anemic hypoxia. These compounds reacts with haemoglobin, as a result it decreases oxygen transport.

c) **Histotoxic hypoxia**—Occurs due to toxic hypoxia at the tissue level, when they arc treated with cyanide, narcotics etc. Because in this case tissue and cells of the body tail to utilize oxygen properly.

d) **Stagnant or isocheimic hypoxia**—Occurs due to reduced blood flow in artery and view, as a result of congestive heart failure, surgical shock etc. So that tissue cells can not get proper oxygen supply though O2 saturation and it total volume in blood is normal.

Example of Hypoxic environment :

1. High altitude :

As altitude increases the partial pressure of oxygen decreases. From a sea-level value of about 700 mm Hg, it drops to about 30 mm of Hg a top Mount Everest. Now, for haemoglobin to bind with oxygen, needs a PO_2 of about 80 mm of Hg. So there are marked redaction in the O_2 binding capacity of haemoglobin. Also, it is evident that Ihe PO_2 rather than composition of air makes the condition hypoxic (Fig-11.3)

2. Mountain Sickness :

This is caused in high altitudes (abopve 15,000 ft) due to lack of optimum PO2. As there is lesser supply of O2 to the brain, it malfunctions which causes dizziness and nausea accompanied by irritable behaviour.

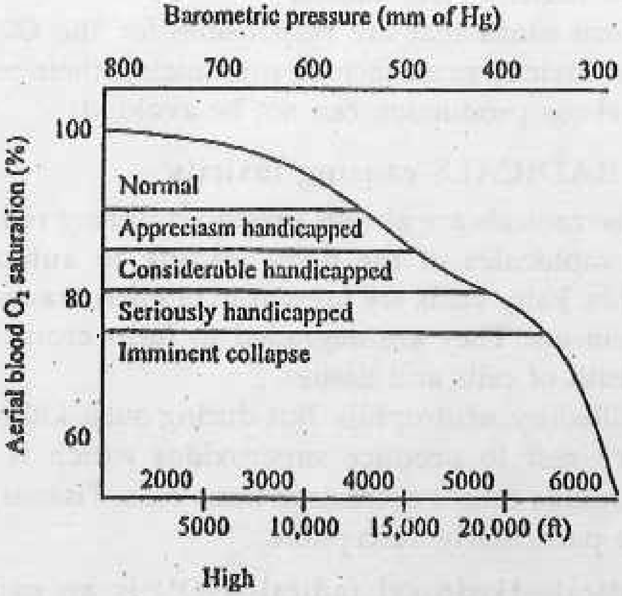


Fig 11.3 : Effect of hypoxiii on the individuals breathing at various altitudes.

11.3 ❐ Oxygen toxicity

The atmosphere of planet earth was unaerobic until the advent of production of oxysen (O_2) through photosynthesis. But a defense was required against the considerable toxicity of this paramagnetic gas (O_2). Those organisms could develop requisite defence could get the benefit and gave rise to enormous variety of aerobic life forms on earth. But those could not throw challange of O_2 toxicity, evolved into the sensitive microscopic anaerobes.

Molecular oxygen is not dangerous to the body. But O_2, because a reactive element may form various Reactive Oxygen Species (ROS) and free radicals at high pressure. Free radicals have a tendency to bind with various substances initiating some life threatning chain reactions.

11.3.1 Examples of ROS and free radicals

i) Superoxide anion free radical (O_2)
ii) Hydrogen Peroxide (H_2O_2)
iii) Hydroxyl radical (OH^*)—free radical
iv) Peroxyl radical (ROO^*)—free radical

These are informations that are responsible for the O2 toxicity, and defense against that toxicity must include minimizing their production and eliminating those whose production can not be avoided.

11.3.2 ROS and RADICALS causing toxicity

Some ROS/free radicals are always produced during reduction O_2 The ROS attacks lipid molecules of the body leading to autooxidation and peroxidation of lipids. Fatty acids are present in biomembranes, nuclic acids, haemoglobin, protein etc. They are degraded to form erotic lesions which cause ultimately death of cells and tissues.

Bacteria are killed by neutrophils. But during such killing neutrophils undergo respiratory rest to produce superoxides which is catalyzed by NADPH. This superoxide causes necrosis in these cells. Tissues such as heart, brain, lungs etc are particularly susceptible.

Hydroxyl radical—Hydroxyl radical (HO^*) is an extra ordinarily powerful oxidant, I which attacks most organic compounds at diffusion limits rates (EZAPSKI, 1984). First I encountered during studies of the effect of ionizing radiation on mater, it can also be I produced by the reduction of H_2O_2 by cations such as Fe (II) or Cu (I)

Reaction : $Fe\ (II) + HOOH \quad (Fe\text{-}OOH)^+ + H^+$ ... (1)
$(Fe\text{-}OOH)^+ \quad (FeO)^2+ + OH^-$ ... (2)
$(Fe\text{-}O)^{2+} \quad (Fe\text{-}OH)^{3+}$ ... (3)
$(Fe\text{-}OH)^{3+} \quad Fe\ (OH) + HO^*$ ... (4)

11.3.3 Potection from ROS and Free Radicals

There are many 'Scavenger Enzymes' which removes these molecules, eg, Superoxide dismutase, catalase the Moreover, there ore also many molecules which remove or decrease the harmfulneSvS of these elements. These are known as antidoxidants. eg-tocopherol..

Cu Zn SODs : These enzymes have Cu and Zn at their active sites. The copper undergoes valence changes during the catalytic cycle while the Zn is thought to play a mainly structural role. Cu Zn SODs are found in cytosols of cells, periplasm of gram negative bactiria and exacellular spaces of mammals.

MnSODs : These enzymes contain on Mn (III) per subunit. Viologens, and a host of synthetic dyes are in this category.

FeSODs : Its defense against O_2^- in **E. Coli** is specific for the metal it contains.

11.3.4 Defense against H_2O_2

The catalase, which dismute $2H_2O_2$ into $O_2 + 2H_2O_2$ and the peroxidases, while use diverse reductants to reduce H_2O_2 to $2H_2O$, are the enzymes that deal with H_2O_2.

Catalases : Mammalian catalases are homotetramerice ferriheme containing enzymes. These enzymes are more efficient even dealing with relatively high concentration of H_2O_2, because their Km for H_2O_2 lies in the millimolar range. Mammalian catalase can also act as peroxidase towards a few small molecules such as methanoi, ethanol, nitric and formate. Thus it can use H_2O_2 to oxidise these substrates, which are small enough to gain access to the heme iron.

Peroxidases : These are enzymes that use a variety of elrctron donors to reduce H_2O_2 to $2H_2O$. Thus, yeast cotains a cytochrome C peroxidase, plants contain ascorbute peroxidase as well as peroxidase acting on a variety of phenots and amines. The principal in mammals in glutathione peroxidase.

UNIT 12 □ Environmental Health Problem

Structure

12.0 Introduction
12.1 Environmental health in relation to water quality
12.2 Environmental health in relation to air quality

12.0 □ Introduction

The environment is a complicated interacting sum total of all the components of atmosphere, hydrosphere and lithosphere and the variety and variability of life forms thrive therein within a climatic regime to maintain the natural balance (i.e., equilibrium in the effective cycling of nutrient materials with the involvement of efficient energy transformations involving living and non-livings compartments of the nature). Such interactive sum total can very well be recognized from tiny microcosm to global scale. As the human society became more and more civilized and thereby, away from nature for their livelihood, the word 'environment' got a new dimension. Human society in the civilized world is more concerned about their environment, where the interpretation of the *interacting sum total* is entirely anthropocentric while the word 'nature' includes human as one of the living components amongst many. Civilized humans have altered different components of the nature in many ways and have added many man-made compounds, foreign to nature (xenobiotics). Very high input of solid, liquid and gaseous wastes from different human activities have disturbed the material cycling and energy flow. All human communities throughout history have produced wastes. Historically, disposal of wastes was easy and convenient as most communities were small and centered basically upon the natural produces for subsistence. An enormous change resulted from the *industrial revolution* -a turning point for modern society in terms of handling the immediate environment. Later the *green revolution* added strange chemicals in the form of chemical fertilizers, weedicides and pesticides to environment that interfered with the living systems. At this time humans routinely use nearly 70,000 chemicals for a variety of reasons as per demand of the civilized society. The rate of introduction of new substances is in the order of 200 -2000 compounds per year to solve growing demands of civilized human society. All chemicals, whether man-made or natural, can both be beneficial and harmful to humans. Dose and length of exposure are crucial factors. 16th Century physician

Paracelsus elaborated: *All substances are poisons. There is none which is not a poison. The right dose differentiates a poison from a remedy.* Further, the net effect of more than one chemical can be antagonistic (the chemicals cancel, either fully or partially, each other's effects), additive (the effects add together) or synergistic (the effect is greater that additive). Therefore, the working arena of environmental pollutants and human health is very vast. This chapter will address briefly the major pollutants that concern human health for focusing students to pollution problems and to build up dissenting opinions on major environmental issues. In the foregoing sections, we will examine pollution of air and water separately which is often the easiest way to analyze environmental pollutions and their effects on human health. However, it must be mentioned at the out set that a specific pollutant may contaminate all three spheres (atmosphere, hydrosphere and lithosphere) and generally move around among all three.

12.1 ☐ Environmental health in relation to water quality

Life without water is unimaginable. Despite such inevitable necessity, human activities have greatly affected the waters around us. Different kinds of natural water sources like freshwater (wetlands, ponds, lakes, streams, rivers), estuaries, marine and even the groundwater are receiving - anthropogenic wastes. Right from the on set of human civilization, which only started beside rivers and large lakes, wter-bodies are being used as shock absorbers due to the excellent self-purifying capacity of natural waters. Further, the behavior of the pollutants is different in these varied kind of waters, fresh or brackish water, surface or ground water. An organic pollutant discharged into surface water may be evaporated or may be degraded by microbial activity and or by oxygen and sunlight. The same compound when contaminates ground water, may become a long-term contaminant, as hardly any means are available in the underground situation to degrade that compound. Metals are natural components of marine waters and a small increase in metal concentration may not be noticeable while the same amount may cause serious problem in freshwater where metal concentrations are normally low.

Liquid wastes from domestic activities such as kitchen, toilet and other household wastewaters (Municipal wastewater) are in most cases discharged untreated directly into a river or into a large water body near the locality. Pollutants of surface runoff and storm water vary according to the nature of land over which it flows. The runoff from agricultural land is contaminated with pesticide residues and remains of inorganic fertilizers while runoff from urban areas mainly contains biodegradable pollutants. Industrial sites may contribute to varied types of pollutants like heavy metals, acids and various inorganic compounds. All these contaminants of the runoff heavily contaminate our natural surface water and groundwater resources, and thereby, aquatic organisms and human health are adversely affected. Both small-scale and large industrial activities produce wastewaters contaminated by a variety of organic and inorganic chemical pollutants (Industrial wastewater). Almost all the rivers of India, at least in certain stretches, are receiving industrial wastewaters that are heavily polluting the aquatic environment. Effluent discharges from different industries on either side of the river Ganga have made the water critically polluted. Even the marine environment is not spared. Either directly or indirectly, via the river systems, marine ecosystem receives industrial wastes. Presently most of the coastal waters are under the pollution threat from the effluents of coastal prawn-culture farms and fish processing industries. Most components of industrial effluents are toxic to ecological systems even in low concentrations and many are non-biodegradable. Another j notable pollutant from the industries is the hot water. Many industries including power plants and oil refineries use water as coolant for the machinery. Waste hot water, having 8 - lOoC higher temperature than the intake water, is released into the natural aquatic ecosystem causing *thermal pollution*. The disposal of hot wastewater in lakes or rivers increases the natural water temperature, decreases the dissolved 02 content and adversely affects the aquatic community. Capsized oil tankers, offshore oil mining and oil exploration operations and oil refineries can contribute to oil pollution of marine ecosystem (oil spill). An oil spill is the accidental discharge (however, may be deliberate in war situations) of petroleum in oceans or estuaries. In addition to economic loss and adverse aesthetic effects of oil covered coastal region, the significant ecological effect is the death of plankton, fish and marine birds. Oil spills are also immensely harmful to coral reef and can drastically damage the marine local biodiversity. Marine harvesting using deep-sea fishing trawlers, equipped with sophisticated capture devices, harvest economically important marine organisms (fish, mussels, cuttlefish, turtles, etc.)- Even whaling business is still in operation in certain countries. Such uncontrolled industrial exploitations of marine resources severely damage the ecosystem. Indiscriminate harvesting of ornamental corals and marine algae can also be detrimental for marine ecosystem. Excessive tourist aggregations in many popular beaches pollute the coastal water by pathogens. Marine poly-metallic nodule harvesting *(deep-*

sea mining) from the depth of 5000 m disturbs the marine benthic community. Poly-metallic nodules are rich in manganese (30 - 40%) and also contain small amounts of other commercially important metals like nickel and cobalt. Seabed mining operations using massive vacuum cleaning machines stir up deep marine sediments that can choke the gills and other filtering structures of marine organisms and may cause serious damage to deep-sea trophic web.

Water quality is degraded by six major conventional pollutants like biochemical oxygen demand BOD), nutrients (mainly phosphates and nitrates), suspended solids, pH, oil and grease and pathogenic microorganisms. United States Environmental Protection Agency (US EPA)have branded 126 priority pollutants of special concern including benzene, toluene, polychlorinated biphenyls (PCBs), polycyclic aromatic hydrocarbons (PAHs) and hosts of metals/metalloids (specially, arsenic, cadmium, lead, mercury, nickel, copper, and zinc). The third non-conventional category includes colour, heat, ammonia, chlorine, fluoride, iron and total phenols. Some of the well-documented degradations of water quality that have affected human health are discussed hereunder.

Table 1. Maximum limit acceptable for drinking water quality parameters

Parameters	Acceptable limit
PH	6.5 to 9.0
DO mg L^{-1} (% Saturation)	4.0 (60-140)
BOD_5^{20} mg L^{-1}	Below 3.0
Conductivity uS cm^{-1}	<4000
(NO_2+NO_3)-N mg L^{-1}	<15
Suspended solid mg L^{-1}	<100
Fecal Coliform, MPN per 100 ml	<2000 per 100 ml
Bio-assay (Zebra Fish)	No death in 2 days
Arsenic mg L^{-1}	0.010
Aluminum mg L^{-1}	0.20
Silver mg L^{-1}	0.01
Lead mg L^{-1}	0.015
Barium mg L^{-1}	2.0
Chromium mg L^{-1}	0.1
Mercury mg L^{-1}	0.002
Copper mg L^{-1}	1.3
Zinc	5.0
Uranium	0.030

Excess Nutrients : Excess inorganic fertilizers, detergents, surfactants and biocide residues are contaminating our soil as well as surface and groundwater resources. Inorganic nutrients, like phosphorus and nitrogen, reach the aquatic ecosystems and accelerate *eutrophication*. Excess nutrients promote excessive growth of tolerant, high yielding algae (*algal bloom*), especially the blue-green algae in freshwater (108-109 Cells L-l) and dinoflagellates.in marine situations (103 - 104 Cells L-l). In freshwater blue-green algal bloom inhibits the growth of other algae. Herbivore fish and other animals detest blue-green algae as they make the environment toxic.

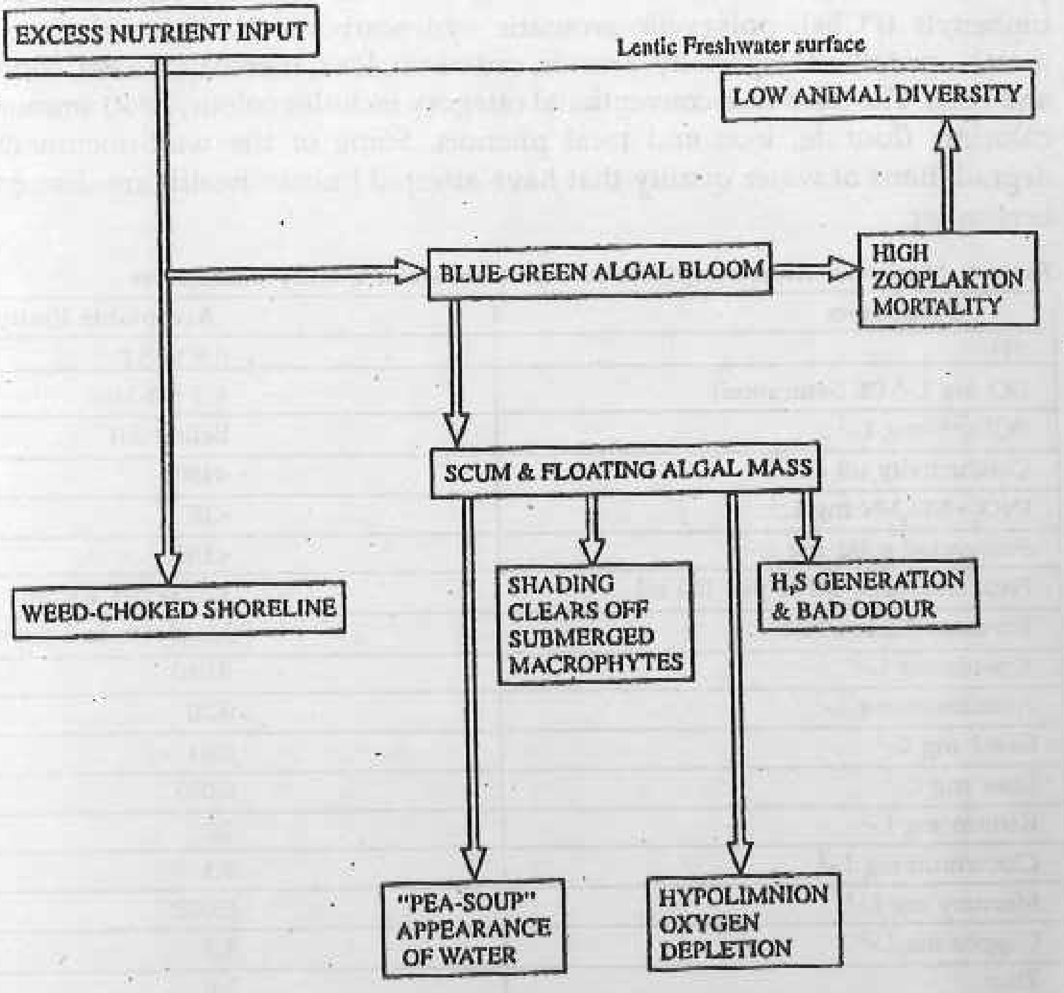


Figure-1. Nutrient enrichment and consequent changes in food web

Aquatic animals die in this toxic environment. This process of nutrient enrichment and consequent loss of aquatic species diversity is the greatest *paradox of nutrient enrichment* and the processes that usher such situation are referred to as eutrophication. In a natural process a large lake after a few hundred years will turn into a shallow eutrophic bog *(natural eutrophication)* but anthropogenic activities are making such natural processes faster (cultural eutrophication). Consequent changes in freshwater bodies in eutrophication are depicted in Table 2 and Fisure 1.

Table 2. Comparison of oligotrophic and eutrophic situations in lentic freshwater bodies.

Oligotrophic	Factors	Eutrophic
High	Phytoplankton Species Diversity	Low
Low (<10ug L^{-1})	Phytoplankton Production (Biomass As Mean Chlorophy 11 a)	High (l5-40ig L-l)
Chlorophyceae & Bacellariophyceae	Phytoplankton Dominant Groups	Cyanophyceae
Predominant	Submerged Macrophytes	Negligible or Absent
Low Organic Matters	Soil-Water Interface	High Organic Matters
Low	Bottom Water Decomposition	High
Oxic (>5.0 mg L^{-1})	Hypolimnion Oxygen	Hypoxic (>0.1 <2.0 mg L-l) to Anoxic (<0.1 mg L-l)
Normally Saturated	Epilimnion Oxygen (Day)	Super Satrated
Low	Bacterial Biomass	High
Deep With Poorly Developed Littoral Zone & Emergent Plants	Depth	Shallow with Well Developed Littoral Zone with Emergent Macrophytes
Low (<700 ug L^{-1})	Mean Inorganic N	High (1900 ug L^{-1})
Low (<10 ug L^{-1})	Mean Total P	High (80 ig L-l)
High (>3.0 m)	Transparency (Secchi Disk Depth)	Low (1.5 - 3.0 M)

Marine coastal ecosystem is also under the threat of organic pollutants from coastal aquaculture industries and agricultural runoff. Marine toxic algal bloom causes significant public health problems. Man is exposed principally to the naturally occurring toxins produced by harmful algae through the consumption of contaminated seafood products. Most significant health problems are caused by harmful algae are: *Amnesic Shellfish Poisoning (ASP), Ciguatera Fish Poisoning (CFP), Diarrhetic Shellfish Poisoning (DSP), Neurotoxic Shellfish Poisoning (NSP) and Paralytic Shellfish Poisoning (PSP)*. Each of these syndromes is caused by different species of toxic algae that occur in various coastal waters of the world (Table 3).

Table 3. Excess nutrients in coastal regions cause bloom of toxin-producing organisms and usher severe human sufferings affecting the food chain.

Poisoning	Causative Agent	Toxin Produced	Major Sufferings
Amnesic Shellfish Poisoning (ASP)	Pseudonitischia sp	Domic Acid	gastrointestinal and neurological disorders;
Ciguatera Fish Poisoning (CFP)	Gambierdiscus toxicus, Prorocentrum spp., Ostreopsis spp., Coolia monotis, Thecadinium sp.and Amphidinium carterae	Ciguatoxin/ Maitotoxin	CFP produces gastrointestinal, neurological, and cardiovascular symptoms. Generally, diarrhea, vomiting, and abdominal pain occur initially, followed by neurological dysfunction including reversal of temperature sensation, muscular aches, dizziness, anxiety, sweating, and numbness and tingling of the mouth and digits.
Diarrhetic Shellfish Poisoning (DSP)	Dinophysis sp.	Okadaic Acid	DSP produces gastrointestinal symptoms, usually beginning within 30 min

			to a few hours after consumption of toxic shellfish and causes diarrhea, nausea, vomiting, abdominal cramps, and chills. Recovery occurs within three days, with or without medical treatment.
Neurotoxic Shellfish Poisoning (NSP)	Gymnodinium breve	Brevetoxins	NSP produces an intoxication nearly identical to that of ciguatera. In this case, gastrointestinal and neurological symptoms predominate. In addition, formation of toxic aerosols by wave action can produce respiratory asthma-l ike symptoms.
Paralytic Shellfish Poisoning (PSP)	Alexandrium spp., Gymnodinium catenatum, Pyrodinium bahamense	Saxitoxins	PSP, like ASP, is life threatening. Symptoms are purely neurological and their onset is rapid. Symptoms include tingling, numbness, and burning of the perioral region, ataxia, giddiness, drowsiness, fever, rash, and staggering. The most severe cases result in respiratory arrest within 24 hours of consumption of the toxic shellfish.

Excess nitrogen containing fertilizers release nitrous oxide (N2O) and ammonia (NH3) gases. Excessive dependence on inorganic fertilisers also affects our drinking water. Excess N-fertilisers contaminate surface and ground water and can build up in drinking water. Nitrate in drinking water causes blue-baby syndrome in infants, especially in the bottle-fed babies (usually less than six-month old). Excess nitrate in drinking water is dangerous for human health and may be fatal for infants. It reacts with haemoglobin and forms non-functional *methaemoglobin* that impairs oxygen transport. This is called *methaemoglobinemia* or *"blue-baby syndrome"*, a form of hypoxia. Inside the stomach the nitrate is reduced to nitrite and is readily absorbed in the blood and reacts with haemoglobin. Methsemoglobin is formed when Fe2+ is oxidized to Fe3+ which is incapable of carrying oxygen and has a bluish colour which imparts a cyanotic colour to tissues. The gut of newborns has a higher pH and a higher load of *E. coli* bacteria than that in adults. Bottle-fed babies consume extraneous water and if that water contains nitrates, the infant gut conditions readily promote the conversion of nitrate to nitrite that affects the oxygen-carrying capacity of the baby. Since 1945, about 2000 cases of methaemoglobinemia have occurred worldwide. Incidentally, breast-fed babies seldom suffer from methaemoglobinemia as they do not directly consume extraneous contaminated water. US EPA has established a maximum contaminant level of lOmg N03-N L-l as the threshold for safe level for drinking water while WHO recommended that as 11.3mg N03-N L-l.

Arsenic : In fact, arsenic is not a metal, but rather a semi-metal or metalloid; however, metal-processing operations and fossil fuel burning are the major sources of arsenic. Scientists have also pointed out that indiscriminate use of sub-soil water and massive increase in the use of detergents for domestic and industrial purposes have increased arsenic contamination of drinking water sources. Like a number of metals, arsenic continues to build up in the environment. Except occupational exposures, most human exposure is through food and water. Fortunately much of the arsenic in food may not be bioavaUabie. Some waters contain naturally high levels of arsenic and pose a chronic risk to those drinking such water. Chronic arsenic inhalation with lung cancer and chronic arsenic ingestion is associated with skin cancer besides many other pathological manifestations like liver and spleen enlargement, diabetes, goiter, liver cirrhosis etc. Chronic exposure initially causes black spots (spotted melanosis) on palm and sole and is referred to as *black foot disease.* Later the spots develop on chest and back and with the length of exposure white spots (leucomelanosis) develop; skin becomes dry, rough, hard and nodulous especially on palm and sole (keratosis is the typical indication of severe toxicity in arsenicosis).

Mercury : A serious mercury-poisoning event (Minamata disease) resulted from consumption of mercury-contaminated fish in Japan. The whole episode started in early 1930s and continued till late 1960s when Chisso Corporation of Tokyo discharged mercury-contaminated effluent into

Minamata Bay. Mercury was converted to methylmercury by the microorganisms in the bay which was concentrated in fish through food chain and finally to humans. His form of mercury is lipophlic and easily accumulated from water column by the fatty tissues of biota. Methylmercury is much more toxic than elemental mercury; furthermore, unlike inorganic forms of mercury, which are poorly absorbed in human gastrointestinal tract, about 90% of methylmercury is absorbed. Most Minamata Bay fish had methylmercury levels ranging from 9 to 24 ppm and in some cases as high as 40 ppm whereas fish with less than 0.5 ppm of mercury is only considered to be safe to consume in any amount. For nearly thirty years as many as 200,000 people were adversely affected and thousands suffered chronic disease and hundreds died from eating contaminated fish of Minamata Bay. The early problems were noticed in local animals, such as the birds failed to fly correctly and used to drop from the sky into the sea, many marine organisms died or became disoriented and sluggish and cats of the locality died in convulsions. In the later years, the local people especially children were observed to suffer and many died from a strange disease (now named as Minamata disease) that affected the central nervous system resulting in convulsion, staggering and excessive salivation. However, as an interesting side-effect, it was noted that pregnant women suffered less than others, although their newborn children usually suffered from neurological disorders. Since a portion of the mercury ingested by the pregnant women was passed into the foetus, carrying women suffered less. Mercury exposure usually causes numbness of limbs, lips and tongue, deafness, blurring of vision and mental derangement.

Cadmium : Cadmium is released by mining and smelting operations and by fossil fuel combustion, especially coal. Nickel-cadmium (Nicad) rechargeable batteries are significant source of cadmium in the solid wastes. Polyphosphate fertilizers and sewage sludge too contribute to cadmium build-up in agricultural soils. Shellfish concentrate cadmium and consumption of scallops and oysters from contaminated waters can be a major source of exposure for people who eat these. Fish, however, concentrate cadmium to a lesser extent and are a lower source of exposure. Cadmium exposure causes another disease called *Itai-Itai* (a painful disease of bone and can result in liver and lung cancer). The most notorious human poisoning with cadmium occurred among poor elderly Japanese women who suffered from kidney damage and severe bone damage that left their bones brittle and painful (hence the name *itai-itai* or *ouch-ouch* or pain-pain). The rice these women consumed was grown in fields near factory engaged in smelting operations and the soil of the region contained cadmium levels up to 10 times those found in other soils. Cadmium gets accumulated in pancreas, liver and kidneys and can inhibit different enzymatic reactions.

Environmental Estrogens : Estrogens are hormones naturally formed by the females. These are carried in the bloodstream to the responsive target tissues where they stimulate and maintain changes to be a female of the species. Estrogens are also required in very small amount by the males. Agents that mimic natural estrogens are referred to as *environmental estrogens* or *xenoestrogens*. However, an environmental agent that can mimic one or more hormones is called an *endocrine disrupter,* a term much broader than xenoestrogen. Chemicals or other environmental agents that show estrogenic properties can be either natural or synthetic. Anthropogenic industrial chemical agents which are proved to have estrogenic properties are pesticides like Dichlorodiphenyltrichloroethane (DDT), Kepone, dieldrin etc., Dioxins and furans, Poly-chlorinated biphenyls (PCBs), Polycyclic aromatic hydrocarbons (PAHs), and plastic degradation products. These chemicals can mimic or partially mimic estrogens. However, unlike PCBs and DDT, dioxins have anti-estrogenic properties in some situations. DDt was the first chemical implicated as having adverse effects on animal reproduction. In some bird species it thinned egg shell. It also affected population size in birds whose egg shells were not thinned. A major population drop seen in Western Sea Gull was attributed to DDT exposure. Many so-called lesbian gulls shared nests with other females and produced eggs that contained males with feminized reproductive tracts. Male gulls showed feminine characteristics and some were sterile. When minks were fed with fish contaminated with PCBs, many abnormalities in reproduction were noted. The greatest route of human exposure to PCBs is fish consumption. Dioxins are a family of chlorinated chemicals related to PCBs. They have powerful biological effects and can interfere with the function of a number of hormones. Pregnant rats that were given one tiny dose of the most toxic dioxin, 2,3,7,8-tetrachloro-/. j-dioxin, produced male offspring that showed reduced sperm production and other adverse effects. Like PCBs, dioxin concentrates in sediments, from which they are taken up by invertebrates that are subsequently eaten by fish. Birds and mammals, including humans, are exposed when they eat contaminated fish. The PAH family of chemicals is relagted to PCBs and dioxins, but does not contain chlorine. PAHs are known human carcinogens and some show estrogenic properties. These are also environmentally persistent substances that bioaccumulate in animal fat. It is probable that thousands more chemicals with estrogenic or other hormonal properties will be identified. For these chemicals more and more human females are suffering from breast cancers and endometriosis. Another major concern is that environmental estrogens are associated with declines in sperm production in mammals including human males. Prostrate and testicular cancers, especially in young men, are attributed to the environmental endocrine disruptors.

12.2 □ Environmental health in relation to air quality

Air with an unnatural load of any gas or particulate matter (i.e., suspended aerosols composed of solids and liquids) may be harmful to life and property. Air can very well

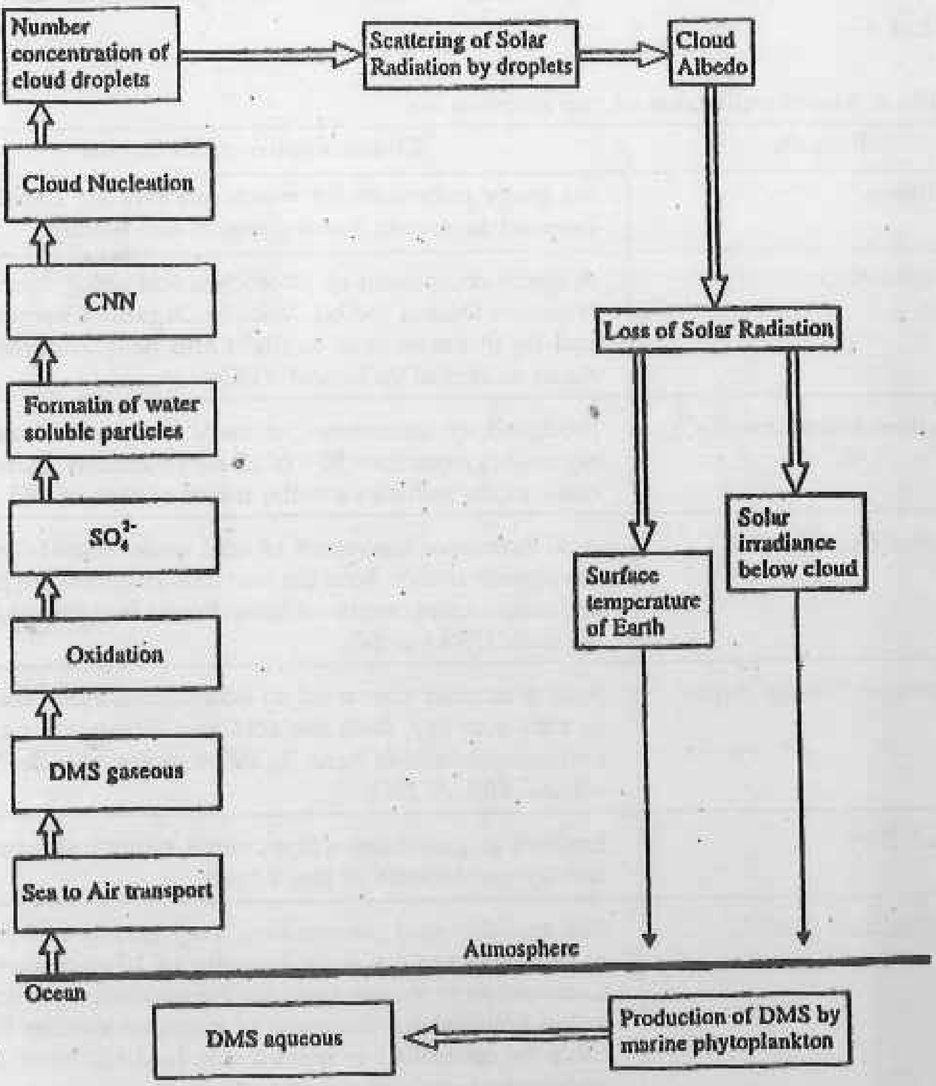


Figure-2. Dimethylsulfide (DMS) Cycle, Ocean-Atmosphere Exchange be polluted by a number of natural sources like pollens from flowers, winds eroding dust, smoke from forest fires and volcanic ash and smoke that are emitted in to the *troposphere* (lower atmosphere that extends from earth's surface to a height of about 10 - 15 km, depending upon latitude and season of the year) and *stratosphere* (upper atmosphere that extends from *tropopause*, the upper limit of the troposphere, upward to a height of about 50 km. *Ambient air* is referred to the outside air that is free to move, i.e., the open air around us (Figure 2). Ambient air pollution is therefore the ground level or tropospheric pollution. Major classes of ambient air pollutants are shown in Table 4.

Table 4. Major pollutants of the ambient air.

Pollutants	Characteristics or examples
Criteria	Six major pollutants for which ambient air standards have been set to protect human health and welfare.
Ozone (O_3)	A major component of photochemical smog formed from Nitrogen Oxides (NOx), Volatile Organic Chemicals (VOCs) and O_2 in presence of sunlight and heat. Automobiles are a major source of NOx and VOCs.
Carbon Monoxide (CO)	Produced by combustion of fossil fuel and biomass, CO represents more than 50% of all air pollutants. In metropolitan cities motor vehicles are the major source of CO.
Sulfur Dioxide (SO_2)	Acid precursor converted to acid under moist conditions or to sulphate in dry. Both the acid and sulphate are particulates and major components of haze. Fossil fuel burning produces the bulk (75%) of SO_2.
Nitrogen Oxides (NOx)	Acid precursor converted to acid under moist conditions or to nitrate in dry. Both the acid and nitrate are particulates and components of haze. In cities motor vehicles produce around 60% of NOx.
Lead (Pb)	Emitted as particulates from metal mining and processing and by combustion of fossil fuels.
Particulates (PM10)	Size and chemical composition, vary greatly and particulates of most concern are with diameter of 10 micrometer or less. Combustion processes generate the maximum particulate load in the ambient air. Emission of particles smaller than PM10 could be controlled to meet a standard (EPA) of 150 micrograms per cubic meter of air.

Pollutants	Characteristics or examples
Hazardous air Pollutants (HAPs)	The 189 haps do not have ambient air standards. Instead, emissions controls air used. About 70% are also vocs.
Organic Inorganic	Examples are benzene, formaldehyde, vinyl chloride etc. Examples are asbestos and metals (Cd, Cr, Hg, Ni etc)
VOCs	Organic chemicals that evaporate easily. Some significantly contribute to smog. People are exposed to vocs in home from paints, solvents, aerosol sprays, deodorants and cosmetics

Anthropogenic activities have vitiated our ambient air with a number toxic gases and particles and enter the atmosphere from fixed (such as large factories, electrical power plants, mineral smelters and different small-scale industries etc.) and mobile (transport vehicles moving by road, rail or air) sources. The United States USEPA classifies air pollutants into two broad categories, *viz.*, primary (five types of primary air pollutants for regulatory purposes are carbon monoxide (CO), hydrocarbons (HCs), sulphur dioxide (SO2), nitrogen oxides (NOx) and paniculate matters) and secondary air pollutants. Earth's environment has been undergoing significant changes due to increasing human population and its activities, especially during the last century. Increased resource consumption by people, depletion of fossil fuel reserves and the large scale changes in land cover and land use are having a large impact on the global environment. The most significant changes brought about by man made activities are the increase in concentration of carbon dioxide and other greenhouse gases in the atmosphere and depletion of stratospheric ozone layer. We now know that any change of ozone in the stratosphere or gain in greenhouse gases in the lower atmosphere may lead to global climate change. The increase in concentration of greenhouse gases as affected by human activities (based on Third Assessment Report, IPCC 2001) is given in Table 5. These environmental changes, occurring on a global scale, may affect biodiversity, quality of food, water resources, land resources as well as human health.

Table 5. The increase in concentration of greenhouse gases as affected by Human activities (based on Third Assessment Report, IPCC 2001).

Greenhouse gases	Sources	Pre-industrial Concentration (1750-1800)	Concentration in 1998	Atmospheric life time in yrs.
Carbon dioxide (CO_2)	Fossil fuel burning Deforestation	280 ppm	365 ppm	5-200 yr
Methane (CH_4)	Agriculture Landfills	0.700 ppm	1.745 ppm	12 yr
Nitrous oxide (N_2O)	Agriculture and combustion	0.270 ppm	0.314 ppm	114 yr
Chlorofluorocarbons (CFCs)	Refrigerants Air	Zero	282 ppt	45-260 yr
Hydrofluorocarbons (HFC)	conditioning Foam blowing			

Recent large scale use of polythene carry-bags, plastic sheet, pet-bottles and other polymer materials not only prevent air and water entry into the soil and adversely affect soil organisms, when burnt, these materials produce toxic carcinogenic gas containing *Dioxins.* Combustion of medical wastes and municipal solid wastes containing polythene garbage is the source of 95% of dioxin in the environment. Once emitted to the atmosphere, the dioxin particulates drift onto water and land.

Photochemical Smog : The most general definition of *smog* is visible air pollution. The word was first used in 1905 to describe the combination of smoke and fog that sometimes totally obscured visibility in London. However, scientifically speaking, the word *smog* refers to the secondary pollutants that are produced in presence of sunlight *(Photochemical smog).* Secondary pollutants are formed during chemical reactions between primary air pollutants and other atmospheric constituents, such as water vapour. Photochemical smog of traffic congested metropolitan cities where solar radiation is very intense is a modern day problem worldwide. Automobile exhausts contain HC and NO and these play an important role in ozone (O3) formation in urban environment. A simplified set of some of the photochemical reactions involved in smog formation is as follows:

$N_2 + O_2 \rightarrow 2NO$ (inside engine)
$2NO + O_2 \rightarrow$ (in atmosphere)
NO_2 + UV radiation $\rightarrow NO + O$
$O + O_2 \rightarrow O_3$
$NO + O_3 \rightarrow NO_2 + O_2$
$HC + NO + O_2 \rightarrow NO_2$ + Peroxyacetyl Nitrate (PAN)

Photochemical smog is composed mainly of O_3, peroxyacetyl nitrate (PAN) and NOX. Favourable conditions for O_3 formation include air temperature exceeding 32°C, low winds, intense radiation and low precipitation. Unfortunately almost all major metropolis of India provide such suitable conditions for most part of the year. Photochemical smog is often referred to as *brown air* where solar radiation is intense. Smog formation in the areas or seasons of less solar radiation is not complete and the air is referred to as *grey air.*

Smog ozone may damage plant as well as animal life. In plants the main damage occurs in leaf. Ozone aggravates lung diseases in humans. Several plant species are also very susceptible to PAN in smog. PAN damages chloroplasts and thus the photosynthetic efficiency and growth of plants are reduced (Figure 3). It also

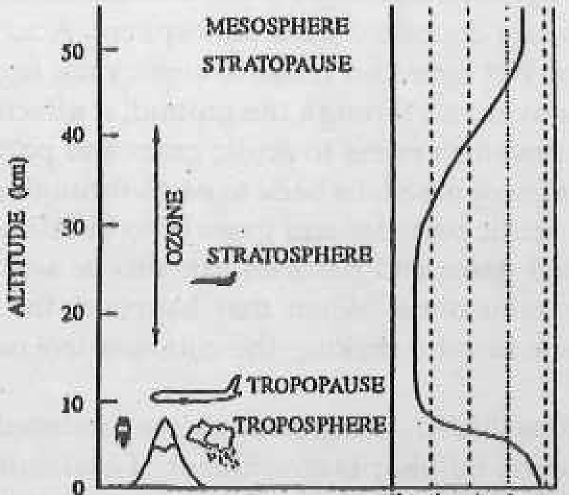


Figure-3. Upper and lower atmosphere showing ozone and temperature distribution inhibits electron transport system and interferes with enzyme systems that play important role in cellular metabolism. In humans. PAN causes acute irritation of eyes and headache. O_3 also irritates the eyes, nose and throat and lungs and decrease the ability of the lungs to function optimally, Ozone in respirable air impairs the normal functioning of liings because it inflames the cells that line the respiratory tract. Other health hazards include an increase asthma attacks, increased risk of infection and reduction in heart and circulatory functions. EPA set standard for O_3 in ambient air is 0.12 ppm. Ozone is an oxidizing pollutant and corrodes the heritage building surfaces; damages marble statues and other cultural assets.

Ozone may be either hazardous or beneficial, depending largely on its location. For example, it is hazardous as an oxidant in smog within the lower troposphere, while in the ozone layer in stratosphere it is beneficial because it absorbs biologically harmful UV radiation.

Acid rain : Acid rain is a broad term used to describe several ways that acids fall out of the atmosphere. A more precise term is acid deposition and it must be noted that it refers to only one type of pollutant deposited from the atmosphere; the term *atmospheric deposition* better describes actual conditions. Not only acids, but many other substances, including metals and organic pollutants, are deposited from atmosphere. Acid deposition has two parts: wet and dry. *Wet deposition* refers to acidic rain, fog, and snow. As this acidic water flows over and through the ground, it affects a variety of plants and animals. *Dry deposition* refers to acidic gases and particles. About half of the acidity in the atmosphere falls back to earth through dry deposition. The wind blows these acidic particles and gases onto buildings, cars, homes, and trees. Dry deposited gases and particles can also be washed from trees and other surfaces by rainstorms. When that happens, the runoff water adds those acids to the acid rain, making the combination more acidic than the falling rain alone.

Nitrogen oxides (NOX), VOCs and SO_2 are produced by the combustion of coal and petroleum. Sulphur is constituent of coal and oil while NOX are produced as by-products of high-temperature furnaces and internal-combustion engines. Lightning also produces NOX naturally. These gases are highly reactive in air. They rapidly oxidize to acids (sulphuric or nitric), which quickly dissolve in water and wash out as acid rain. Normally rainwater is always slightly acidic (pH 5.5 - 6.5) because water and CO_2 combine in air to form a weak acid. Acid rain, however, often have a pH less than 4.0. As it will be discussed in detail in the following section, Dimethylsulphide released by marine phytoplankton bloom can also cause acid rain.

Acid rain damages building materials and furnishing fabrics. Our heritage monuments (such as Taj Mahal at Agra) are threatened by the corrosive action of acid deposition. Low pH environment releases many toxic metals and trace elements in excessive amount, which may have dangerous effects on biological world. Acid precipitation adversely affects the aquatic and soil ecosystem. Most plankters, molluscs and fish fry cannot tolerate pH below 5.0. Calcareous shell formation in molluscs is impaired in lower pH. Low pH conditions also damages soil microbial community and thereby, nutrient cycling is disturbed.

Changes in CO_2 concentration : If the concentration of atmospheric CO_2 available to plants increases, plants may be able to increase their rate of photosynthesis and thus grow more. This response of plants to elevated concentrations of CO_2 is known as the *Carbon dioxide fertilization effect.* Numerous CO_2-enrichment studies suggested that growth of many plants could increase about 30% on average with a doubling of the atmospheric CO_2 concentration, in the short-term (up to a few years). This increase in crop yield occurs under favourable conditions of water, nutrients, light and temperature. However, under natural conditions, this increase may not be realized as the plants grow under various limiting environmental conditions. Many studies have indicated that there would be a decrease in world food production not withstanding the CO_2 fertilization effect. As the plants open stomata to allow entry of CO_2, they also lose water vapour through the same passage; therefore, if the subsoil water is in short supply, excess CO_2 alone would be of no help in increasing primary productivity.

Changes in global temperature : The gaseous layer over the earth's surface acts like a window glass pane. It allows considerable portion of solar radiation to enter right up to the earth surface but restrict the degraded heat waves to escape. Terrestrial heat wave radiation is largely the long-wave radiation encompassing the spectrum from about 3.0 - 100.0 mm. The gaseous mantle over globe, however, permits escape of a portion of long-wave energy (spectrum from about 8.0 - 11.0 mm) to space. This regulatory adjustment controls the escape of heat wave from the earth's surface to outer space and thus forms a blanket over the earth to keep it warm and hospitable. The phenomenon is referred to as *greenhouse effect* (comparable to the glass-enclosed greenhouse that allows suitable temperatures for the growth of tropical plant species in temperate environment). Without the warming by the natural greenhouse effect, the earth would be about 33°C colder than its present mean temperature of about 15°C. Carbon dioxide is by far the most abundant and important atmospheric trace gas contributing to the natural greenhouse effect. In addition to CO_2, the other main *greenhouse gases* are CH_4, N_2O, chloroflurocarbons (CFCs) and also water vapour.

The thermal insulation over the earth's surface is becoming more and more effective as the concentration of different greenhouse gases, especially the CO_2, has increased many folds due to urbanization, deforestation and different industrial activities during the past centuries. The consequent increase in the global mean temperature is referred to as *global wanning*. It is been predicted that increased global warming by greenhouse gases may add about 1°C to the global mean temperature by the year 2025, and about 3°C by the end of the twenty-first century. Although there is much uncertainty in the predicted warming, but it is of serious global concern as warming could have major long-term consequences for the life on earth. The temperature rise may not only affect distribution of species but can also expedite extinction process for many. Global warming would also change the global wind flow, oceanic waves and precipitation patterns; in a word global climate would be seriously affected. Warming process may melt more polar ice deposits adding more water to the oceans raising the sea level. With the rise in the sea level, coastal cities and island-countries are under the threat of inundation. Major ocean circulation systems are already showing signs of being affected by the rise in atmospheric temperatures. The cyclical shift in Pacific Ocean currents, "El Nino" results in massive warming in the mid-Pacific and a warm shet of water crawling up the west coast of North America and pushing away the normal cold current that flows from Alaska. An El Nino year is characterized by dryer, warmer conditions in the Pacific Northwest and much wetter conditions throughout much of California and the Southwest. Major El Nino events, such as the ones in 1982-1983 and 1997-1998, cause substantial flooding. El Nino events have increased in frequency and intensity, and it is predicted that by the year 2050 the "normal" state will resemble "El Nifio-like" conditions.

The recent warming trends and the predicted global warming have effects on weather and climate, rise in sea level and shift in the range of distribution and phenology of organisms. In the past several decades, the global mean temperature has increased by approximately 0.6°C since the late

19th century. Climate changes from late 1960s caused an increase in precipitation (0.5 to 1%) during autumn and winter mostly in the northern hemisphere. In the subtropics, precipitation has decreased by 0.3% per decade. Further, the frequency of extreme events (e.g. droughts, floods etc.) may increase substantially for the rise in average global temperature.

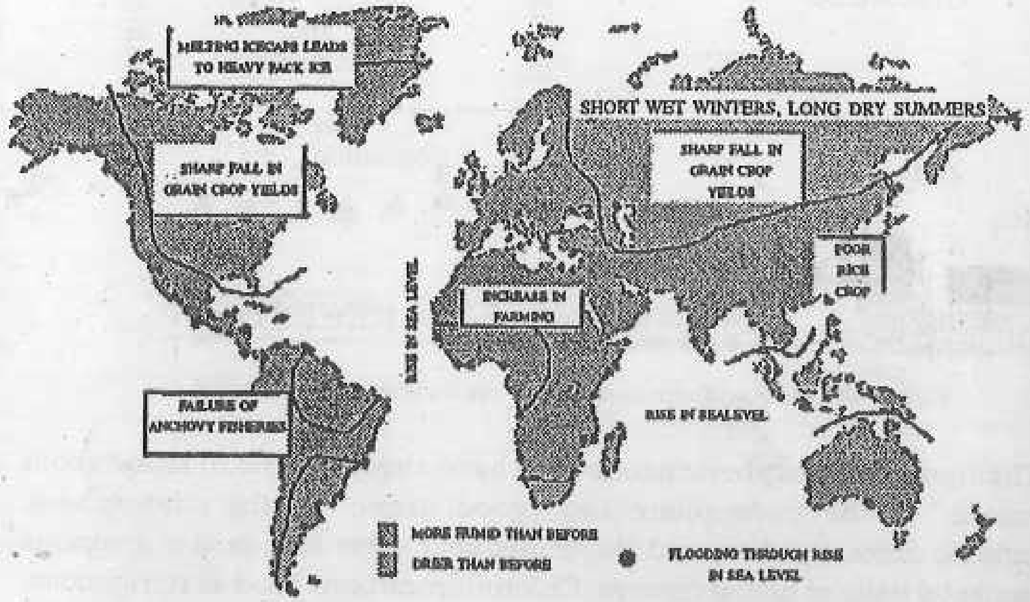


Figure-4a. Consequences of global warming
(a) What might happen if the earth's surface temperature increased, on average by 1°C

Each plant or animal species occurs in a specific range of temperature. The global warming is likely to shift the temperature ranges and therefore would affect altitudinal and latitudinal distribution pattern of organisms. With increasing global warming many species are expected to shift slowly pole ward. So if temperature were to increase by 3oC, species distribution may shift by about 500m up mountain-side (Figure 4).

The global warming may contribute to sea level rise for the thermal expansion of ocean as it warms, melting of glaciers, changes in the mass of Antarctica and Greenland ice sheets and changes in terrestrial water storage. It is currently estimated that about half of the world's population lives in coastal zones. Sea-level rise is projected to have negative impacts on human settlements, tourism, freshwater supplies, fisheries, exposed infrastructure, agricultural and dry lands, and wetlands.

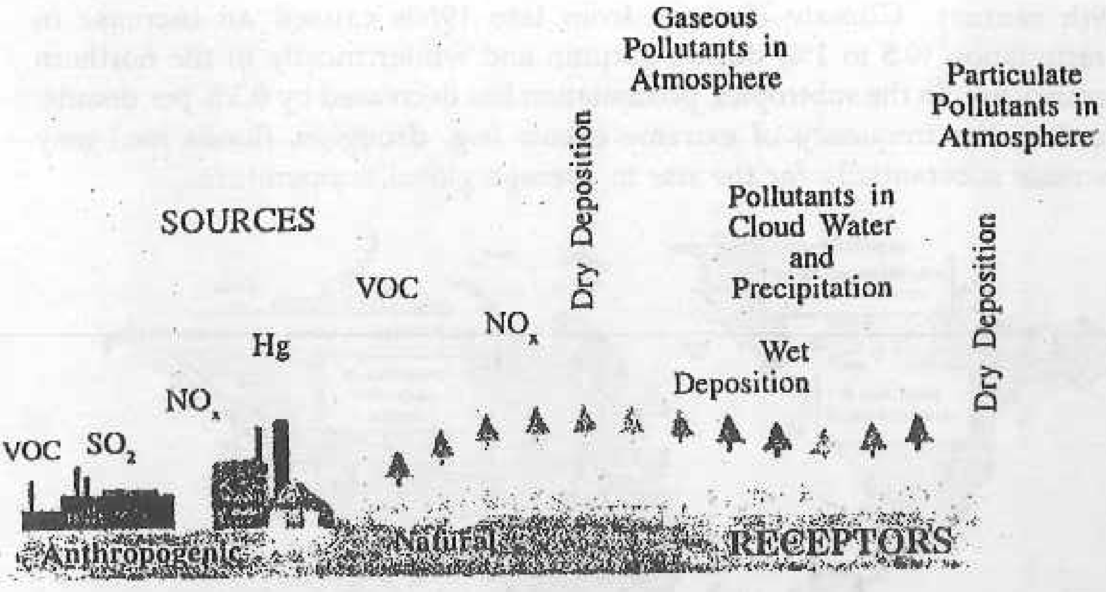


Figure. 4b. How acid rain is caused by the aumospheric pollutants

Changes in stratospheric ozone : We have already come to know about "bad ozone" of the troposphere and "good ozone" of the stratosphere. Stratospheric *ozone depletion*, and the consequent *ozone hole*, is also a serious environmental issue of global concern. Chloroflurocarbons used as refrigerants, propellants in aerosol spray cans and cleaning compounds etc. escape to the upper atmosphere and catalyze the destruction of stratospheric O^ molecules. Nitric oxide (NO) and hydroxyl ions (OH-) also cause O3 depletion. Of these catalysts, CFCs are entirely anthropogenic (negligible is released from volcano vents) and serious attempts are to be taken to phase out the production of CFCs to protect our O_3 shield. Methyl chloride and methyl bromide are also O_3 depleting chemicals, but marine organisms and forest and grassland fires are estimated to release 5 million tons as compared to only 26,000 tons from human activities. Stratospheric O_3 layer absorbs UV radiation (classed as UV-A, UV-B and UV-C), and thereby, the amount of biologically harmful UV (especially UV-B) light striking the earth's surface is reduced. In humans, increased UV-B increases the incidence of cataract, skin cancer including melanoma. Plant growth may also be adversely affected. For each 1% increase in UV-B radiation reaching the earth, nearly 2% increase in nonmeianoma skin cancer will occur. Marine phytoplankton has declined in areas near Antarctica where a temporary decrease in O_3 concentration is measured each year. The decline of phytoplankton is thought to be due to increased amounts of UV that are reaching surface waters. Around 40% of stratospheric O_3 layer above Antarctica is depleted forming a very thin layer of O, of the size of the United States. This is referred to as *ozone hole.* The high incidence of skin cancer in Australia is directly related to this ozone depletion. Thinning of ozone layer and depletion in ozone concentration regularly occurs during Antarctica Spring. During the polar winter, Antarctica stratosphere is isolated from rest of the stratosphere by swirling winds. These winds circulate about the pole creating the *Polar Vortex.* Such polar vortex is also formed over the Arctic. Because of its extreme isolation, temperature inside the polar vortex drop as low as -80 to -90°C.Conditions of the Antarctica winter and spring that favours ozone destruction are:

- The polar stratospheric clouds at low temperature provide surfaces for the reaction of free chlorine to occur.
- The ozone depleting reactions are very fast. Chlorine attacks ozone molecules under simultaneous co-occurrence of sunlight and freezing conditions in the early spring of Antarctica.

As a result, the losses of ozone also occur over the Antarctica. The loss of ozone also occurs in the Arctic in the springtime. The Arctic stratosphere warms faster in the spring, leaving less time for the critical over lap between cold and sunlight, necessary for ozone depletion. The polar vortex over Arctic is not as tight as over the Antarctica. Thereby, the losses of ozone over the Arctic are lower (5 to 10%) compared to that over Antarctica (50 to 66%). The thinning of ozone layer causes increase in the ultraviolet radiation reaching the earth surface. In humans, increased ultraviolet radiation increases the incidence of cataract, skin cancer including melanoma. Excess exposure of ultraviolet radiation may cause diminished functioning of immune system in human beings. Elevated levels of ultraviolet radiation affect photosynthesis as well as damage nucleic acids in living organisms. Ultraviolet radiation inhibits photosynthesis in most phytoplankton as they may penetrate through the clear open ocean waters. This in turn can affect the whole food chain of organisms that depend on phytoplankton, such as zooplankton, krill, squids, fish and whales.

Dimethylsulphide : Oceans, Atmosphere and Climate :

Dimethylsulphide [DMS; Thiobismethane Methylsulphide C_2H_6S / (CH3)2S], emitted by marine phytoplankton, is the second most important source of atmospheric sulphur, after anthropogenic SO_2. Nutrient enrichment through coastline causes marine phytoplankton bloom intensifying the process of DMS release to atmosphere. In the ocean DMS is produced through a web of biological interactions (Figure 5). Certain species of phytoplankton in the upper ocean synthesize the molecule dimethylsulphoniopropionate (DMSP), which is the precursor to DMS. When phytoplankton cells are damaged, for example by grazing zooplankton or viral lysis, they release their contents into the seawater. Bacteria and phytoplankton are involved in degrading the released algal sulfurous compound DMSP to DMS and other products. While many algae do produce high concentrations of DMS, for example prymesiophytes and dinoflagellates, including many bloom forming taxa e.g. *Phaeocyslis, Emiliania,* and *Alexandrium,* lesser amounts are found in other phytoplankton. Some species of the larger ocean plants, the seaweeds, for example *Viva fenestra* and *Polysiphonia hendryi,* also have the enzyme to convert DMSP to DMS. In the atmosphere, DMS is transformed into condensable acidic sulphur products and, through gas-to-particle conversion, it becomes the most important natural source of atmospheric sulphate aerosols. DMS is the dominant sulphur trace gas in seawater and its sea-to-air emission is a key pathway in the global sulphur cycle, whereby sulphur is transported

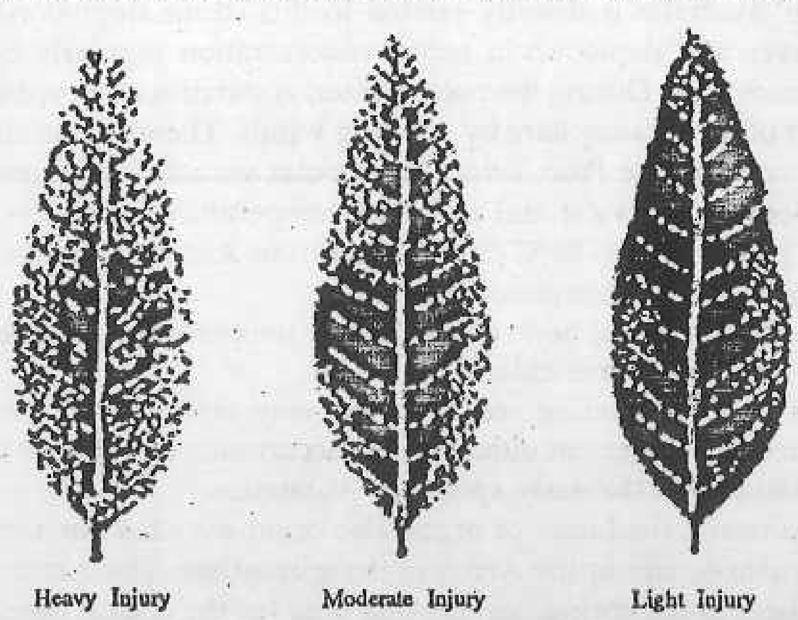


Figure-5. Milkweed leaves with different grades of ozone injury from the sulphur-rich marine environment to the relatively sulphur-poor land surface. Salt marshes have also been identified as one system with a high area-specific sulphur emission. DMS and hydrogen sulphide "(H_2S) constitute the bulk of the flux from salt marshes, with DMS predominating in vegetated areas of the marsh. As H_2S is a product of anaerobic decomposition in sediments, it has been assumed that other sulphur gases emitted from salt marshes also originate from decomposition in sediment processes. It has also been suggested that DMS and DMSP in salt marshes arises primarily from physiological processes in leaves of higher plants. DMS is a climatically important component of global biogeochemical cycles, through its role in the sulphur cycle. Changes in ultraviolet (UV) radiation exhibit both positive and negative forcings on the dynamics of production and turnover of DMS and its precursor DMSP. An inverse relationship is observed between UV radiation and atmospheric DMS associated with extreme changes (defined as the greatest 5%) in daily UV, independent of changes in wind speed, sea surface temperature, and photosynthetically available radiation (PAR). It has been suggested that variations in algal production of natural gases play an important role in moderating our climate through their aerosols' effect on backscattering solar radiation and in cloud formation. A portion of the DMS diffuses from saltwater to the atmosphere. Once it is transferred to the atmosphere the gaseous DMS is oxidized to tropospheric sulfate aerosols, and these paniculate aerosols act as cloud condensation nuclei (CCN), attracting molecules of water. Water vapor condenses on these CCN particles, forming the water droplets that make up clouds. Clouds affect the Earths radiation balance and thereby greatly influence its temperature and climate. DMS represents 95% of the natural marine flux of sulfur gases to the atmosphere, and scientists estimate that the flux of marine DMS supplies about 50% of the global biogenic source of sulfur to the atmosphere. A key process in the sulfur cycle is the transfer of volatile sulfur compounds from the sea to the land via the atmosphere. Because the sulfate aerosols function as CCN. DMS has a significant impact on the Earth's climate. DMS may influence both the hydrologic cycle and the global heat budget through its part in cloud formation, and may alter rainfall patterns and temperatures. DMS is part of the Earth's ocean-atmosphere feedback loop, a climate stabilizing mechanism, moderating temperatures on Earth. A direct link between sea surface temperature and atmospheric DMS over a large area in the southern Indian Ocean has been established. It has been estimated that an increase in temperature would increase the atmosphere's DMS concentration and have a negative feedback on the original warming. Plankton production of DMS and its escape to the atmosphere is believed to be one of the mechanisms by which the biota can regulate the climate.

International initiative for mitigating global change : In the case of climate change, large-scale problem-solving strategies are needed to mitigate the crisis. There is no ready solution for climate change due to accelerated release of greenhouse gases. Existing sources of accelerated input of carbon must be eliminated and carbon sinks should be increased wherever possible. A slower rate of climate change will surely result over the coming centuries and there by ecosystems and humans will be provided with more time. The largest emitter of greenhouse gases is the U.S., with about 25% of global emissions created by <5% of the world's populations. Because carbon and other greenhouse gases are emitted primarily from automobiles and industrial activity, climate change is also an economy issue. Without coordinated efforts by other countries, a reduction in U.S. emissions would be made up rapidly by the increases in emissions from developing countries if they follow the same industrialization pathway as the U.S. Therefore, the most useful means of lowering the rate of greenhouse gas emissions is to coordinate the actions of many countries, implementing policy reforms at national and international levels simultaneously. Climate policy differ form other environmental issues because of its global scale and because of its implications in economic adjustments. In sequel of the Vienna Convention for the Protection of Ozone Layer, the most relevant is the Montreal Protocol (1980); world leaders meet to sign an agreement designed to gradually phase out the production and use of chemicals that destroy stratospheric ozone. The Montreal Protocol has been widely judged as a success. Most nations have ratified the treaty, which called for the step-wise elimination of the ozone-depleting chemicals used in the industries. The atmospheric concentrations of these chemicals have been greatly reduced and positive effects in the stratosphere are already apparent. Rio Convention (1992), also known as Earth summit, was convened by the United Nations Conference on Environmental and Development (UNCED) in Rio de Janeiro, Brazil. A total 154 nations signed the UN Framework Convention on Climate Change (UNFCCC), which looked forward to reduction of emission of greenhouse gases and Developed nations (also known as Annex 1 countries) would be asked to make larger reduction that developing nations. Next landmark agreement came from the third Council of Parties

(COPs) meeting in 1997, popularly known as Kyoto Protocol; delegates in Kyoto, Japan took initiatives to reduce emissions of greenhouse gases more quickly than it was framed in Rio convention. Global emission levels should be 5% less than 1990 levels by 2012. The Kyoto Protocol is an outgrowth of the UNFCCC designed to provide specific targets for reductions, reporting of emissions levels and creation of enforcement mechanisms to ensure that greenhouse gas emissions targets were met. More than 141 nations have ratified the Kyoto Protocol as of February 16, 2005, when the treaty went in force. The UN World Summit on Sustainable Development (UNWSSD, 2002), Johannesburg, South Africa, followed up on issues raised by the Rio de Janeiro summit (hence the conference's alternate name Rio+10). UNWSSD has emphasized special attention to finding means to create climate-friendly development and suggested appropriate steps for alleviating poverty, and providing safe drinking water and shelter as well as to reduce the risks of global warming. Beyond these international efforts, many corporations are making changes on their won. In the petroleum industry, major voluntary shifts in corporate strategy have been taking place, reflecting the influence of public opinion and the future profitability of alternative energy sources.

UNIT 13 ❑ Environmental Laws and Ethics

Structure

13.0 **Introduction**

13.1 **Environmental ethics**

13.2 **Environmental laws**

13.3 **Environmental acts of India**

13.0 ❑ Introduction

The thought of protection to our environment has gained much importance in the recent years for sustainable economic and social progress in our country. In ancient India; protection and conservation was in the essence of Vedic culture where trees and wildlife were given much religious importance. *Rigveda,* told about the nature's potentiality in controlling climate, increasing fertility and improving the quality of human life. The *Atharvaveda* also envisaged the trees as abode of Gods and Goddesses. In medieval India too nature got special attention of the *Mughal* emperors as many of them were great nature lovers; however, they did not pay much need to the conservation of the wealth of nature. Barring a few ceremonious species of trees, the 'royal trees', the moghul rulers used to exploit nature for recreation and economy. But they made significant contribution to the nature conservation by establishing magnificent gardens, fruit orchards, and vast green public parks around their palaces and their headquarters. Fresh inland waters were much cared by these emperors. During Akbar's regime unnecessary killing of birds and beasts were prohibited on religious principles. Moghul miniature paintings are the excellent depiction of the nature and natural wealth of the era and serve much information on biodiversity of that time. We found the most paradoxical approach towards the natural wealth during the British India. Both Indian provincial rulers/Maharajas and the British rulers indiscriminately fell trees and hunt thousands of wildlife. However, this is the period of marked beginning of conservation of forest wealth with administrative steps like formation of forest policy and the legislation to implement the policy decisions. The systematic management of forest resources began with the appointment of the first Inspector General of

Forest in 1864 for exploration of forest wealth, demarcation of wildlife reserves, protection of forests against fires etc. The first Forest Policy was enacted in 1894 with two major focuses: firstly, permanent cultivation was to come before forestry and secondly, public benefit was the sole object of forest administration. Therefore, the policy suffered from the deficiencies in conservation outlook and was revised in 1927 to include such intentions. After the independence of India from *British Raj*, there was no precise environmental policy in the early days but the concerns for environment protection were reflected in the national planning processes and forest policy. The ever-increasing awareness for the management of environment in the global scale has its own course of evolution and that influenced the Indian scene for strengthening legal framework for environmental protection.

13.1 ☐ Environmental ethics

Environment is being exploited by mankind to fulfill their unending need for food, shelter and comfort. Indiscriminate slaughtering of wildlife for pleasure, myth and economy has posed a serious threat to our biodiversity though we have no ethical right to disregard the intrinsic values of biological resources. Ethics is a branch of philosophy that deals morals and values and such understanding helps one to decide whether an action is good or bad in a frame of reference. Environmental ethics speaks about the moral relationship between human and the nature. A balance should be maintained between the environment-based needs and interests of mankind and their responsibilities towards the nature. Such ethical approaches lead to the establishment of different principles that serve to protect our natural resources to produce "the greatest good for the greatest number for the longest time". To prevent environmental degradation, a biocentric ethical standpoint must have to be adopted as it regards the inherent values of natural world, regardless of its potential for human uses, against the anthropocentric viewpoint. Environmental ethis say us :

1) The well-being and flourishing of human and nonhuman life on Earth have values (inherent worth; intrinsic value; inherent value) in themselves which are independent of the usefulness of the nonhuman world for human purposes.
2) Richness and diversity of life forms contribute to the realization of these values and are also values in themselves.

3) Human are just one of the members of Earth's living community (biotic community) like all other living beings and they have no right to reduce this richness and diversity except to satisfy vital needs.
4) The flourishing of human life and cultures is compatible with a substantial decrease of the human population. The flourishing of nonhuman life requires such a decrease.
5) Policies must therefore be changed. The changes in policies affect basic economic, technological structures. The resulting state of affairs will be deeply different from the present.

Such principles are now recognized as "deep ecology." Deep ecology is an environmental movement initiated by a Norwegian philosopher, Arnie Naess, in 1972. He coined the term "deep ecology" and helped to give it a theoretical foundation. Deep ecology portrays itself as "deep" because it asks deeper questions about the place of human life, who we are. Deep ecology is founded on two basic principles: one is a scientific insight into the interrelatedness of all systems of life on Earth; together with the idea that *anthropocentrism* -human-centeredness - is a misguided way of seeing things. The second component according to Arnie Naess is the the need for human self-realization. Instead of identifying with our egos or our immediate families, we would learn to identify with trees and animals and plants, indeed the whole ecosphere. In contrast **Eco-feminism** says that the real problem isn't anthropocentrism but androcentrism man-centeredness. They say that 10,000 years of patriarchy is ultimately responsible for the destruction of the biosphere and the development of authoritarian practices, both socially and environmentally.

13.2 ☐ Environmental laws

13.2.1 Statutory laws

Though statutory control of environmental pollution in India is not of resent origin but the concerted legislative activity started after 1970 with the enactment of some specific legislations dealing exclusively with pollution problems. Before that we had some zoo legislations dealing with various aspects of environmental protection. Statutory environmental laws written and agreed upon by legislative bodies are passed for protection and management of natural resources. Various Government agencies work on the details like setting of standards, pollution control requirements and resource management. According to Statutory laws various enforcing agencies are given the authority to take Iega"l actions by pin-pointing polluters and to take them to the court to face criminal charges and possible jail sentences.

13.2.2 Common laws

These oldest sources of our environmental laws were introduced in India by British rulers. Common laws are applied by virtue of Article 372(1) of the Constitution, unless it has been modified or replaced by legislations in India. The basis of the applications of common laws is "justice, equity and good conscience". A common law is a body of unwritten rules and principles derived through hundreds of years of legal decisions which attempts to balance competing societal interests. For example, a factory that generates annoying noise may be brought to the court by the neighbouring inhabitants with a complaint that the factory is a nuisance and the activity could be stopped through an injunction.

13.3 Environmental acts of India

Protection of Physical environment has assumed importance in India since 1972. In order to achieve this objective, the Government of India has passed a number of Acts. Such Acts are -

1) The Water (Prevention and Control) Act, 1974
2) The Air (Prevention and Control) Act, 1981
3) The Environment (Protection) Act, 1986
4) The Coastal Regulation Zone Notification under EPA, 1986
5) The Biological Diversity Act 2002 and Rules 2004
6) National Environmental Policy 2004 (Draft Proposal)

13.3.1 Water (Prevention and Control of Pollution) Act, 1974

The water (Prevention and Control of Pollution) Act, 1974, deals with the problem of water pollution comprehensively at national level. The Act was enacted under article 252 (1) of the constitution, which provides power to the union government to legislate on matters of state list, where two or more state legislatures consent to a central law.

Objectives :

The objectives of the act are to 'Prevent and Control, water pollution and also maintain and restore the wholesomeness of water. It defines the term 'Pollution' as any contamination of water or alteration of properties of water, discharge of sewage or trade effluents or any other substances (liquid, solid or gaseous) into water (directly or indirectly) to create nuisance or injurious to life or human health, plants, animals, aquatic organisms etc. The act provides for establishing a Central or State Boards and joint boards for the accomplishment of the objectives of legislation.

Merits :

1. The act provides a comprehensive scheme for the prevention and control of pollution except for the standards for the regulation of pollution but the central and State Boards are given wide powers to decide heir own standards and regulations for the local needs.
2. This act prohibits disposal of noxious, poisonous and polluting matter into streams or wells or onto the lands in excess of standard established by State Board.
3. A person must obtain consent from the boards through an application before the establishment of any industry, operation or process which may result in disposal of sewage trade effluent into a stream. The consent by the boards will be given only after a thorough enquiry in the prescribed manner.
4. Persons who have been releasing water pollutant, without meting the consent requirements of Section-25, penalties are imposed for contravention of the provisions of sections 24, 25 and 26. Persons will be punished for the violation of the provisions of section 24 with imprisonment of one year and six months or which may extend.
5. The oards will take emergency measures, if the cause of pollution of well or stream is an accident or unforeseen act or event.
6. One significant and remarkable achievement of the 1988 amendment of water act is the incorporation of a provision for citizen's suit in section 49 of the act; citizens may file criminal complaints against offenders after 60 days, notice to the board.

Demerits :

1. Definitions of some important terms like 'pollutant', 'discharge of

pollutant', 'toxic-pollutant' etc. are not provided in the act.

2. This act includes a definition of stream but not an 'estuary' as stream may be covered under the 'river' or 'sea' or 'tidal waters'. So it is needed to add estuary in a suitable place.
3. The act has the provision for the establishment of central, state and joint boards but there is no adequate representation of the members of social groups and lawyers.
4. In making consent orders by state boards, there is no public participation in decision making process under the act.
5. Provisions for fixing up standards of quality and targets for eradication of pollution are absent from the act; just like public participation in fixing up these.

13.3.2 The Air (Prevention and Control) Act, 1981

The Air was passed by the Parliament to implement the decisions taken at the United Nations Conference on Human Environment held in Stockholm in June, 1972, to take steps for the preservation of natural resources of the earth, which mainly include preservation of the quality of air and control of air pollution. This act contains the Government's explanation of the contents and scopes of the land and its commitment and concern for the ' detrimental effects' of air pollution on the health of the people and also on animal life, vegetation and property. It extends to the whole of India.

Objective :

The Air Act defines air pollution as " Presence in the environment of any air pollution", where the term 'air pollutant' means "any solid, liquid or gaseous substances including noise present in the atmosphere in such concentration as may be or tend to be injurious to human beings or other living creatures or plants or property or environment". Thus the act considers their common and important sources of emission like industrial plants and automobiles.

Merits :

1. The act provides for an enforcement machinery in the from of environment and Sate Air Pollution Board in their respective geographical jurisdiction.
2. The Central Board for the prevention and control of water pollution constituted under section 3 of the water (Prevention and Control of

Pollution) Act 1974; also perform the function of the Central board for the prevention and control of air pollution under this act.

3. The main functions of Air Pollution Boards are to improve the quality of air and to prevent and control air pollution in country.
4. These boards collect and disseminate information relating to air pollution and plant comprehensive programme to fight with.
5. For the control of industrial pollution, the act prohibits the establishment or operations of any industrial plant in air pollution are by any person with previous consent of the state board.
6. The state board is viable to cancel the already given consent even before the expiry of granted period if conditions to consent order are not fulfilled.
7. This act puts restriction on any person carrying an industry on air pollution control area, not to allow emission of air pollutants in excess of standards put forward by state board.

Demerits :

1. It does not tell about "Pollution through medium of air". Emission of noxious odours (leather industry), right protection caused by high industry sign boards, neon advertisement etc.
2. The act does not provide any concrete policy guidance in its provisions but simply emphasis upon the purposes, constitutions and function of board.
3. Prevention and control of air pollution under this acts has given as a secondary duty to the (water) pollution boards. So there remains a chance to underrate the control of air pollution by the board than its primary function.
4. The air act after it amendment in 1987 has adopted a new stand that an ordinary citizen given the right to file a complain in court against a polluting unit or polluters in his individual capacity, called as *Citizen Suit* is rendered ineffective by requirement of sixty days notice which gives a long enough time to escape viability under the act.

Apart from such drawbacks the Air Act is a good piece of legislation and right path in the direction to fight against air pollution.

13.3.3 The Environment Protection Act, 1986

The Environment (Protection) Act, 1986 passed in the wake of Bhopal tragedy and decisions were taken at the United Nations Conference on the Human Environment held at Stockholm in June, 1972, in which India participated to take appropriate steps for the protection and improvement of human environment and the prevention of hazards to human beings, other living creatures, plants and property etc. It constitutes an 'Umbrella' legislation that provides a framework for Central Government for co-ordination of the activities of various central and state authorities established under the water and air act.

Objectives :

The chief objective of the act is to provide for the protection and improvement of environment and for matter concerned therewith. The act defines 'environmental pollution' as presence in the environment of any 'environmental pollutant' (solid, liquid or gaseous substances) which in such concentration may be or tend to be injurious to environment. Standards for the quality of environment in its various aspects and standards for emission or discharge of environmental pollutants from various sources have been laid down under the act. For the prevention accident which may cause environmental pollution, procedure and safeguards along with remedial measures have been put down under this act. This act provides protection for handling of hazardous substances which are likely to cause environmental pollution.

Merits :

1. The act speaks our hazardous industries and environmental disasters.
2. Definition of pollution is not only restricted to air and water but also include noise.
3. Restriction of areas in which any industries, operations or processes shall not be carried out or shal! be, but with certain safeguards.
4. Establishment or recognition of environmental laboratories to carry out various environmental functions.
5. Collection and dissemination of information on environmental pollution.

Demerits :

1. All power and authority is vested on Central Government excessive centralization could become major hurdle for efficient execution of the act.
2. General draw backs of the act are reflected on
   (a) narrow area of operation
   (b) weak citizen suit provisions
   (c) absence of any provision saying an individual's right to ask a defaulter for damages.
   (d) tax provisions relating to fixing of liability or corporate officials.
3. Problems created by nuclear power plants are not included under this act and also no regulation prohibiting import and marketing of chemicals banned, (e.g. - DDT).

13.3.4 The Coastal Regulation Zone Notifications under EPA 1986

The principal notification was published in the Gazette of India dated, the 19th February 1991 and the latest amendment on 3cd October 2001. Notification was made under section 3(1) and section 3(2) (v) of the Environment (Protection) Act, 1986 and rule 5(3) (d) of the Environment (Protection) Rules, 1986 declaring Coastal Stretches as Coastal Regulation Zone (CRZ) and regulating activities in the CRZ. The notification provided coastal area classification and development regulations, guidelines for development of beach resorts/hotels, regulations on industries, operations and processes in the CRZ and list of petroleum products permitted for storage in port areas.

The Notification empowers the Central Government to declare the coastal stretches of seas, bays, estuaries, creeks, rivers and backwaters which are influenced by tidal action (in the landward side) up to 500 metres from the High Tide Line (HTL) and the land between the Low Tide Line (LTL) and the HTL as Coastal Regulation Zone. For the purposes of this notification, the High Tide Line means the line on the land up to which the highest water line reaches during the spring tide and shall be demarcated uniformly in all parts of the country by 'he demarcating authority so authorized by the Central Government in consultation with the Surveyor General of India. The distance from the High Tide Line shall apply to both sides in the case of rivers, creeks and brackish waters and may be modified on a case by case basis for reasons to be recorded while preparing the Coastal. Zone Management Plans.

However, this distance shall not be less than 100 metres or the width of the creek, river or backwater whichever is less. The distance up to which development along rivers, creeks and backwaters is to be regulated shall be governed by the distance up to which the tidal effect of sea is experienced in rivers, creeks or back-waters, as the case may be, and should be clearly identified in the Coastal Zone Management Plans.

13.3.4.1 Classification of coastal regulation zone

For regulating development activities, the coastal stretches within 500 metres of High Tide Line on the landward side are classified into four categories, namely:

Category I (CRZ-I)

(i) Areas that are ecologically sensitive and important, such as national parks/marine parks, sanctuaries, reserve forests, wildlife habitats, mangroves, corals/coral reefs, areas close to breeding and spawning grounds of fish and other marine life, areas of outstanding natural beauty/historically/heritage areas, areas rich in genetic diversity, areas likely to be inundated due to rise in sea level consequent upon global warming and such other areas as may be declared by the Central Government or the concerned authorities at the State/ Union Territory level from time to time.

(ii) Area between the Low Tide Line and the High Tide Line.

Category-II (CRZ-II)

The areas that have already been developed upto or close to the shoreline. For this purpose, "developed area" is referred to as that area within the municipal limits or in other legally designated urban areas which is already substantially built up and which has been provided with drainage and approach roads and other infrastructural facilities, such as water supply and seweage mains.]

Category-III (CRZ-III)

Areas that are relatively undisturbed and those which do not belong to either Category-I or II . These will include coastal zone in the rural areas (developed and undeveloped) and also areas within municipal limits or in other legally designated urban areas which are not substantially built up.

Category-IV (CRZ-IV)

Coastal stretches in the Andaman & Nicobar, Lakshadweep and small islands, except those designated as CRZ-I, CRZ-II or CRZ-III.

13.3.4.2 Prohibited activities in CRZ

The following activities are declared as prohibited within the Coastal Regulation Zone, namely :

(1) setting up of new industries and expansion of existing industries, except those directly related to water front or directly needing foreshore facilities;

(2) manufacture or handling or storage or disposal of hazardous substances as specified in the notifications of the Government of India in the Ministry of Environment and Forests,

(3) setting up and expansion of fish processing units including warehousing (excluding hatchery and natural fish drying in permitted areas);

(4) setting up and expansion of units/mechanism for disposal of waste and effluents, except facilities required for discharging treated effluents into the water course with approval under the Water (Prevention and Control of Pollution) Act, 1974; and except for storm water drains;

(5) Discharge of untreated wastes and effluents from industries, cities or towns and other human settlements. Schemes shall be implemented by. the concerned authorities for phasing out the existing practices, if any, within a reasonable time period not exceeding three years from the date of this notification;

(6) dumping of city or town waste for the purposes of land filling or otherwise; the existing practice, if any, shall be phased out within a reasonable time not exceeding 3 years from the date of this notification;

(7) dumping of ash or any wastes from thermal power stations;

(8) land reclamation, funding or disturbing the natural course of sea water with similar obstructions, except those required for control of coastal erosion and maintenance or clearing of waterways, channels and ports and for prevention of sandbars and also except for tidal regulators, storm water drains and structures for prevention of salinity ingress and for sweet water recharge;

(9) mining of sand, rocks and other substrata materials, except those rare minerals not available outside the CRZ areas;

(10) harvesting or drawal of ground water and construction of mechanisms within 200 m of HTL; in the 200 m to 500 m zone it shall be permitted only when done manually through ordinary wells for drinking, horticulture, agriculture and fisheries;

(11) construction activities in ecologically sensitive areas as specified in Annexure-I of this notification;

(12) any construction activity between the LTL and HTL, except facilities for carrying treated effluents and waste water discharges into the sea, facilities for carrying sea water for cooling purposes, oil, gas and similar pipelines and facilities essential for activities permitted under this notification; and

(13) dressing or altering of sand dunes, hills natural features including landscape charges for beautification, recreational and other such purpose, except as permissible under the notification.

13.3.4.2 Regulation of permissible activities

All other activities, except those prohibited in para 2 above, will be regulated as under:

(1) Clearance shall be given for any activity within the Coastal Regulation Zone only if it requires water front and foreshore facilities.

(2) The following activities will require environmental clearance from the Ministry of Environment and Forests, Government of India, namely :

  (i) construction activities related to defence requirements for which foreshore facilities are essential (e.g. slip-ways, jetties, etc.);

  (ii) operational constructions for ports and harbours and light houses requiring water frontage;

  (iii) thermal power plants (only foreshore facilities for transport of raw materials facilities for intake of cooling water and outfall for discharge of treated waste water/cooling water);

  (iv) all other activities with investment exceeding rupees five crores.

(3) (i) The coastal States and Territory Administrations shall prepare, within a period of one year from the date of this notification, Coastal

Zone Management Plans identifying and classifying the CRZ areas within their respective territories in accordance with the guidelines;

(ii) Within the framework of such approved plans, all development and activities within the CRZ other than those covered in para 2 and para 3(2) above shall be regulated by the State Government, Union Territory Administration or the local authority as the case may be; and

(iii) In the interim period till the Coastal Zone Management Plans mentioned in para 3(3) (i) above are prepared and approved, all developments and activities within the CRZ shall not violate the provisions of this notification.

13.3.5 The Biological Diversity Act 2002 and Rules 2004

India's population, in particular tribal and traditional communities - farmers, fishermen and indigenous people, is heavily dependent on biodiversity and biological resources for their survival and livelihoods. India's biodiversity is severely threatened; wildlife populations, traditional cultures, geological cycles, and a range of other attributes are being destroyed. There are a variety of reasons for this, including increasing exploitation of biological resources for trade both at national and international levels. The Biological Diversity Act 2002 is a law meant to achieve three main objectives :

- The conservation of biodiversity;
- The sustainable use of biological resources;
- Equity in sharing benefits from such use of resources.

Its key provisions aimed at achieving the above are:

1. Prohibition on transfer of Indian genetic material outside the country, without specific approval of the Indian Government;
2. Prohibition on anyone claiming an Intellectual Property Right (IPR), such as a patent, over biodiversity or related knowledge, without permission of the Indian Government;
3. Regulation of collection and use of biodiversity by Indian nationals, while exempting local communities from such restrictions;
4. Measures for sharing of benefits from the use of biodiversity, including transfer of technology, monetary returns, joint Research & Development, joint IPR ownership, etc.;

5. Measures to conserve and sustainably use biological resources, including habitat and species protection, environmental impact assessments (EIAs) of projects, integration of biodiversity into the plans, programmes, and policies of various departments/sectors;
6. Provisions for local communities to have a say in the use of their resources and knowledge, and to charge fees for this;
7. Protection of indigenous or traditional knowledge, through appropriate laws or other measures such as registration of such knowledge;
8. Regulation of the use of genetically modified organisms;
9. Setting up of National, State, and Local Biodiversity Funds, to be used to support conservation and benefit-sharing;
10. Setting up of Biodiversity Management Committees (BMC) at local village level, State Biodiversity Boards (SBB) at state level, and a National Biodiversity Authority (NBA).

Biological Diversity Rules (15 April, 2004) under the Biological Diversity Act 2002 were framed to strengthen the provisions on conservation, sustainable use, and equity. The Biodiversity Rules are the executive orders made by the Government in order to carry out the purposes of the Act (Section 62) . The Rules among other things outline the procedures to be followed for access to biological resources (wild plants and animals, crops, medicinal plants, livestock, etc) , their commercial utilization, transfer of rights of research, and intellectual property rights related to biodiversity. From the point of view of local communities, it is important to understand the process of allowing access/ utilization of bioresources and also the role of communities.

Keeping this in mind some provisions are made that are directly relevant to local communities, the most critical of them being the Biodiversity Management Committee (BMC). Section 41 of the Act states :

"Sec 41(1) *Every local body shall constitute a Biodiversity Management Committee within its area for the purpose of promoting conservation, sustainable use and documentation of biological diversity including preservation of habitats, conservation of land races, folk varieties and cultivators, domesticated stocks and breeds of animals and microorganisms and chronicling of knowledge relating to biological diversity".*

Under the Biodiversity Rule, Sec 22 expands on constitution and role of BMC and states that every local body shall constitute a BMC within its area of jurisdiction. The main function of the BMC is to prepare People's

Biodiversity Register (PBR) in consultation with local people. The Register is supposed to contain comprehensive information on availability and knowledge of local biological resources, their medicinal or any other use or any other traditional knowledge associated with them. The other functions of the BMC are to advise on any matter referred to it by the State Biodiversity Board or Authority for granting approval, to maintain data about the local vaids and practitioners using the biological resources.

Shortcomings of the Act/Rule :

Some of the critical problems both from the Act and Rules are:

1. It exempts those plants that are registered under the Protection of Plant Varieties and Farmers' Rights (PVPFR) Act, 2001. Such an exemption means that the progressive provisions listed above, many of which are absent from the PVPFR Act, would not apply to plant varieties registered under PVPFR Act .
2. It does not provide citizens the power to directly approach the courts; such power is restricted to an appeal in the High Court against any order by the NBA or SBBs.
3. It is requiring only "prior intimation" to a SBB for the commercial use of bioresources, rather than permission from the NBA as in the case of foreigners.
4. It does not fully empower local communities, to protect their resources and knowledge from being misused, or to generate benefits (except charging collection fees).
5. It has very weak or no representation of local community members on the State Biodiversity Boards or National Biodiversity Authority.
6. The power of declaring a Biodiversity Heritage Sites lies with the state government (Article 37 of the Act): It is important that the heritage sites should be designated only after consultation and moreover consents of the affected communities.

Several organizations and people feel that the basic framework of the Act is problematic, since it accepts intellectual property rights on biodiversity, could be used to further commercialize biodiversity, and does not truly empower communities. Others feel that the Act provides some potential for checking biopiracy, achieving conservation, and facilitating community action. They stress that a combination of strong rules, and amendments related to the above points, would help strengthen this potential.

13.3.6 National Environment Policy, 2004

National Environment policy deals with India's environmental crisis like deregulation of forests, pollution of water and air, poisoning and erosion of soil, exposure of millions of people to toxic substances, displacement in the name of "development" and the threat of extinction of animal and plant species. In August 2004 the Government of India put on a draft- National **Environment Policy (NEP)**, where several measures have been taken into account to fight over those

Objectives :

It describes the key environmental challenges facing the country, and their causes and impacts and put forward a set of objectives, which are —

1. Protection and conservation of critical environmental resources.
2. Ensuring equity between and within generations in the use of natural resources.
3. Integrating environmental factors into economic and social development.
4. Achieving efficiency in resource use and governance.
5. Enhancement of resources for environmental conservation.

For the proper realization of these objectives through various strategic interventions by different public authorities at central, state, local governmental levels, unambiguously stated principles are needed, which are —

1. Human beings are at the **center of sustainable development** concerns.
2. The **right to development** must be fulfilled so as to equitably meet developmental and environmental needs of present and future generations.
3. Environmental protection is an **integral part** of the development process.
4. Lack of full scientific certainty shall not be used as a reason for **postponing cost-effective measures** to prevent environmental degradation, in case of threats of irreversible damage to resources.
5. **Economic efficiency** requires that the service of environmental resources be given economic value and such value to be given economic values of other good and services.
6. **Equity or justice** requires that human beings cannot be treated differently based on irrelevant differences between them.

7. **Civil liability** for environmental damage would deter environmentally harmful action and compensate the victim for that.
8. The state is not an absolute owner; **public trust doctrine** will be made.
9. **Decentralization** refers transfer of power from a central authority to state and local authorities.
10. **Prevention act** is better to prevent environmental damage rather than restoring degraded environmental resources.

Merits :

(i) The draft NEP contains a number of strong points. It makes fair assessment of the institutional, policy and other failings. For instance, it rightly points to the fact that the government has been responsible for the alienation of tribal and other communities from their common lands, thereby undetermiriing the sophisticated traditional systems of resource management that these communities practiced.

(ii) It also points to macro-economic policies, such as subsidies on chemicals that cause ecological damage.

(iii) It stresses the need for a flexible, evolving environment policy. Among the principles and methods it suggests for dealing with the environment, are the precautionary principle under which action can be taken even in the absence of conclusive scientific proof of environmental damage caused by the project; equity in the way benefits are derived from natural resources; decentralized, participatory process, and the doctrine of public trust by which the government is not the absolute owner of natural resources but holds them in trust for public goods.

(iv) Several important strategies are laid out, including a review of economic policies that lead to environmental destruction, establishing stronger regulatory mechanisms, facilitating partnerships between communities, official agencies, NGOs and private parties safeguarding ecosystems and species that are of "incomparable value", promoting organic farming, using economic instruments to stop polluting and destructive activities and integrating the economic value of natural resources into budgets and plans.

Demerits :

The NEP has a number of basic flaws which will undetermine the ability of the government, as other actors, to get to the root of the problem and arrive at sustainable solutions. The following key of elements is essential for a national level policy on environment.

(i) The draft NEP does not challenge the fundamental nature of the current model of 'development' even though it is now widely recognized that this model at the heart of environmental destruction. This model makes a holy cow of unlimited 'economic growth' (instead of more holistic process according importance to human welfare and well being) and in the process treats nature (are people) commodities. It does not recognize nature as the basis of all human activities, and instead relies on essentially technological solutions to problems that are fundamentally social or political in nature. For instance, its emphasis is on increasing food production through artificial inputs whereas the real problem is not quantum of food produced but the unequal control over its production and distribution.

(ii) A long-term plan for the use of land and water resource is a dire necessity. Many governments have promised it, but none has developed one yet. With a new government, with a fresh mandate in place, this is a great opportunity to move towards a long-term policy. This would include a plan to map out areas where for ecological cultural/social reasons; land use should not be changed for any reason.

(iii) The draft implies that the current level of governing natural resources has failed. But it does not offer a new alternative. It talks of decentralization, of 'partnerships' amongst various sections of the society, and of specific elements like public access to information. But what is needed is an overall vision of how natural resources will be governed, who should take decisions at what stage and how will current institutions of governance change.

(iv) This relationship includes ethical, cultural, spiritual and material dimensions. Other than the material dimensions, the other dimensions are missing from the draft of NEP. This is strange, given that these dimensions have been an integral part of Indian tradition.

(v) The draft NEP lays emphasis on tne critical role of the natural environment in economic activity. It does not, however, asset that a healthy environment (including access to fresh air, clean water, healthy food, and natural surroundings) is a fundamental human right. Such a right is increasingly being recognized in many countries.

The process of developing the NEP has been flawed. The claim that the draft NEP was "Prepared through a process of extensive consultation with experts, as well as diverse stakeholders", highly disputable. On September 3, nearly 70 prominent environmentalists and environmental groups in the country signed an open letter to the Ministry of Environment and Forests (MoEF), in which they asserted that the draft NEP has been developed is an extremely non-participatory manner. The draft is available only on a website, and only in English, which means the local communities and most community based NGOs continue to remain outside the consultation process.

মানুষের জ্ঞান ও ভাবকে বইয়ের মধ্যে সঞ্চিত করিবার যে একটা প্রচুর সুবিধা আছে, সে কথা কেহই অস্বীকার করিতে পারে না। কিন্তু সেই সুবিধার দ্বারা মনের স্বাভাবিক শক্তিকে একেবারে আচ্ছন্ন করিয়া ফেলিলে বুদ্ধিকে বাবু করিয়া তোলা হয়।

—রবীন্দ্রনাথ ঠাকুর

ভারতের একটা mission আছে, একটা গৌরবময় ভবিষ্যৎ আছে, সেই ভবিষ্যৎ ভারতের উত্তরাধিকারী আমরাই। নূতন ভারতের মুক্তির ইতিহাস আমরাই রচনা করছি এবং করব। এই বিশ্বাস আছে বলেই আমরা সব দুঃখ কষ্ট সহ্য করতে পারি, অন্ধকারময় বর্তমানকে অগ্রাহ্য করতে পারি, বাস্তবের নিষ্ঠুর সত্যগুলি আদর্শের কঠিন আঘাতে ধূলিসাৎ করতে পারি।

—সুভাষচন্দ্র বসু

Any system of education which ignores Indian conditions, requirements, history and sociology is too unscientific to commend itself to any rational support.

–Subhas Chandra Bose

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NETAJI SUBHAS OPEN UNIVERSITY

STUDY MATERIAL

POST GRADUATE ZOOLOGY

Paper : 2
Group : B
Units : 1-18

Ethology & Evolution

PREFACE

In the curricular structure introduced by this University for students of Post-Graduate Degree Programme, the opportunity to pursue Post-Graduate course in subject introduced by this University is equally available to all learners. Instead of being guided by any presumption about ability level, it would perhaps stand to reason if receptivity of a learner is judged in the course of the learning process. That would be entirely in keeping with the objectives of open education which does not believe in artificial differentiation.

Keeping this in view, study materials of the Post Graduate level in different subjects are being prepared on the basis of a well laid-out syllabus. The course structure combines the best elements in the approved syllabi of Central and State Universities in respective subjects. It has been so designed as to be upgradable with the addition of new information as well as results of fresh thinking and analysis.

The accepted methodology of distance education has been followed in the preparation of these study materials. Co-operation in every form of experienced scholars is indispensable for a work of this kind. We, therefore, owe an enormous debt of gratitude to everyone whose tireless efforts went into the writing, editing and devising of a proper lay-out of the materials. Practically speaking, their role amounts to an involvement in 'invisible teaching'. For, whoever makes use of these study materials would virtually derive the benefit of learning under their collective care without each being seen by the other.

The more a learner would seriously pursue these study materials, the easier it will be for him or her to reach out to larger horizons of a subject. Care has also been taken to make the language lucid and presentation attractive so that they may be rated as quality self-learning materials. If anything remains still obscure or difficult to follow, arrangements are there to come to terms with them through the counselling sessions regularly available at the network of study centres set up by the University.

Needless to add, a great deal of these efforts is still experimental-in fact, pioneering in certain areas. Naturally, there is every possibility of some lapse or deficiency here and there. However, these do admit of rectification and further improvement in due course. On the whole, therefore, these study materials are expected to evoke wider appreciation the more they receive serious attention of all concerned.

Professor (Dr.) Subha Sankar Sarkar
Vice-Chancellor

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PGZO-2
Ethology & Evolution

Unit 1 ❑ Introduction to Ethology

Structure

1.0 Introduction
1.1 Ethology as a branch of biology
1.2 Animal psychology—classification of behavioral patterns, analysis of behaviour (ethogram)

1.0 Introduction

Ethology literally means ‘character study’ .It developed from the works of A. Vesalius (1543) and Darwin and Wallaces’ theory of evolution. From their studies it is evident that neurobiology, physiology and psychology are very much involved with the study of ethology. In seventeenth century, the word ‘Ethology’' was used in human ethics and by middle of nineteenth century this term was used inrespect of living organisms in the ecological sense rather than in behavioural sense (Grier, 1984). In 1940’s the term ethology was widely used in the study of animal behaviour. Ethology deals with the study of species specific patterns of animal behaviour under natural conditions with little emphasis on learning. On the other hand, comparative psychologists paid much attention to the principles of associated learning under laboratory conditions using certain experimental designs and biostatistical methods. They concentrated more on the learning behaviour of man and other vertebrates like pigeons, dogs, rats and other rodents etc. Parallel to this neurobiologists provided understanding of the functional units of behaviour by making observations on proximate mechanism of nervous system. The causes of behaviour were explained by physiological psychologists, Maier and Schmeirla (1935) in their book ‘Principles of Animal Psychology and Ethology’. Following confrontations, ethologists and psychologists are now very close to each other concerning the thought and results because behaviour may be defined as the observable act of animals (Grier, 1984) which is dependent on ecology and sociobiology on the one hand and neurobiology on the other.

However, whatever be the controversy ethology was brought into the fore-front in 1972 when ethologists Konard Lorenz, Niko Tinbergen and Karal von Frisch (Fig. 1.1) were honored by award of Nobel Prize.

Fig 1.1 : Ethology's three Nobel prize winners : (a) Konrad Lorenz (photograph by H. Kacher, (b) Niko Tinbergen (photograph by B. Tschanz) and (c) Karl von Frisch (photograph by M. von Frisch).

1.1 Ethology as a branch of biology

Ethology is defined as the biology of behaviour. It helps us to understand why an animal exhibits certain behaviour patterns under certain circumstances. Since biology involves with the study of life processes of an organism or group, behaviour of an animal, like its structure, is the result of natural selection. Perhaps more often than not, structure and behaviour evolved together, structure influencing behaviour evolved together, structure influencing behaviour, and behaviour in turn influencing the development of the structure. To respond to the environmental changes, physical and social, the animal must first receive a stimulus from the environments through its sensory system—sight, taste, smell, touch and hearing. From here the stimulus is transmitted to the motor organs, the muscular system, and the type and development of motor organs determine the manner in which the animal is able to respond to its environment. Thus how an animal perceives and reacts to the world is limited by what its eyes are built to see, its ears designed to hear, and its organs to taste, hear, and smell are designed to respond to respective environmental stimuli. Because of this, the world appears different to other animals than it appears to man. What'is visible and important to other animals may be unperceivable to man. Thus, it appears that the functions of an organ is dependent on the structure of the same. Therefore, structural peculiarities of an organism play significant role in assuring the targeted function. Since the structural components of an organism are determined by the biology of the individual concerned then the behaviours exhibited by the said organism by using these structures are very much dependent on the same. That is, ethology is the functional aspect of biology. In other words, ethology is a branch of biology.

1.2 Animal psychology—classification of behavioural patterns, analysis of behaviour (ethogram)

How behaviour does develop is a vital question to all ethologists. It is argued that the behaviour is initiated by psychology of the animals concerned. Edward Thorndike (1874—1949) used the puzzle box to perform a series of task-learning experiments, using cats as test subjects. A cat was placed in the box, which was fastened shut; by manupulating a shuttle-lever, the cat could open the door and obtain a reward placed outside the box. From these experiments Thorndike concluded that much of the animal learning takes place by trial and error and that rewards are critical component of learning processes.

During 1930—1960 comparative psychology was dominated primarily by theories of learning and secondarily by work on development. Thereafter truly broad-based comparative work came into the sight. Dewsbury (1984) characterizes the subject matter of current comparative psychology as involving the study of either behaviour patterns that are closely tied to work on learning, motivation, or physiological psychology, on species other than those commonly used for such studies, or both. For comparative psychologists, the primary emphasis has been on 'how' questions about the mechanisms that underlie observed behaviour patterns occur. One way to begin research in comparative psychology is by identifying and characterizing the classes of behaviour patterns in two or more species. A second way to begin is by selecting a species that is the most appropriate for investigation of a particular problem. However, too much emphasis on a single species limits the generality of the conclusions we may draw (Beach 1950, Hoods and Campbell 1969; Lockard 1971; Dewsbury 1984).

Both the ethological and psychological perspectives have a great deal to contribute to the investigation and understanding of animal behaviour. Because, both 'how' and 'why' questions must be tested, an integrated approach that combines the methods of each discipline provides the best total analysis of behaviour. During the last decade there has been a great deal of sneurgism between scientists approaching proximate (how) and ultimate (why) questions (Drickamer 1998; Dewsbury 1999). The integrated discipline that is emerging involves combining laboratory and field approaches to study simultaneously internal mechanisms of behaviour, their ecological significance, and their evolutionary origin.

The systematic study of the function and evolution of behaviour, called *ethology*, is now a little over a century old. One of its most important principles is that behavioural traits, like anatomical and physiological traits, can be studied from the evolutionary viewpoint. For example, C.O. Whitman (1842--1910) made extensive observations of display patterns, which he termed instants, in various species of pigeons. Whitman found that he could use displays (patterns of behaviour exhibited by animals that function as communications signals) to classify animals according to similarities and differences in behaviour. The ethogram, an inventory of a species, has been a starting point for many ethological studies. After making observations of an organism's behaviour, ethologists then formulate specific questions about the adaptativeness and function of particular behavioural patterns. A student of Whitman, Wallace Craig (1876 —1954), defined two key categories of behaviour patterns from his work with doves and pigeons. The first category includes the variable actions of an animal, such as its searching behaviour to find food, a nest site, or a mate; these are called *appetitive behaviour*. The second category includes stereotypical actions that are repeated without variation, such as the act of mating or the killing of prey; these are called *consummatory behaviour*. Ethologists of 1940's and 1960's have broken down any behaviour in nine patterns like (i) eating (ii) shelter-seeking, (iii) agonistic; (iv) reproductive, (v) epimeletic, (vi) et-epimeletic, (vii) eliminative, (viii) mutual-mimicking, and (ix) investigative behaviour. Modern ethologists tend to retain of some the categories, to modify some and to discard others. Thus, now-a-days, behaviour is categorised as (i) communication and releasers, (ii) motivation and drive, (iii) biorhythms, (iv) instinct and learning, (v) genetic and evolutionary, (i) evolutionary, (vi) agonistic, (vii) reproductive and parental and (viii) social behaviour.

After making observations of an organism's behaviour ethologists then formulate specific questions about the adaptativeness and functions of particular behavioural patterns. The ethogram, an inventory of the behaviour of a species, have been a starting point for many ethological studies.

Unit 2 ☐ Innate behaviour

Structure

2.0 Introduction to innate behaviour

- Early research in the field of animal behaviour—notably by Nobel Prize winners Karl von Frisch, Konard Lorenz, and Niko Tinbergen—focused on behavioural patterns that appeared to be instructive or innate.
- Because behaviour is often *stereotyped* (appearing in the same way in different individuals of a species), these early researchers argued that it must be based on preset paths in the nervous system. In their view, these paths are structured from genetic blue prints and cause animals to show essentially the same behaviour from the first time it is produced throughout their lives.
- These researchers based their opinions on behaviour such as egg retrieval by geese. Gesse incubate their eggs in a nest.
- If a goose notices that an egg has-been knocked out of the nest, it will extend its neck toward the egg, get up and roll the egg back into the nest with a side-to-side motion of its neck while the egg is tucked beneath its bill.
- Even if the egg is removed during retrieval, the goose completes the

behaviour, as if driven by a programme released by the initial sight of the egg outside the nest.

- According to ethologists, egg retrieval behaviour is triggered by a *sign stimulus* (also called a *key stimulus),* is the appearance of an egg out of the nest; a component of the goose's nervous system, the *innate releasing mechanism* provides the neural instructions for the motor program, *or fixed action pattern.*
- More generally, the sign stimulus is a 'signal' in the environment that triggers a behaviour. The innate releasing mechanism is the sensory mechanism that detects the signal, and the fixed action pattern is the stereotyped act.
- One interesting aspect of sign stimuli is that they are often not very specific; in some situations, a wide variety of objects will trigger a fixed action pattern. For example, goose will attempt to roll baseballs and even beer cans back into their nests. Moreover, once the objects are in the nest, the goose recognizes that they are not eggs and removes them!
- A similar example is provided by a male stickleback fish. During the breeding season, males develop bright red coloration on their undersides. Territorial males react aggressively to the approach of other males, performing an aggressive display and even attack. Niko Tinbergen observed a male stickleback in a laboratory aquarium displaying aggressive posture when a red fire truck passed by the window. He realized that the red coloration was the sign stimulus. Subsequent experiments revealed that males would respond to many unfaithful models as long as the models had a red stripe.
- This phenomenon is taken one step further by what are termed *supernormal stimuli.* Given a choice between two sign stimuli, one of normal size and the other much larger, many animals will respond to the larger of the two. Thus, geese given a choice of a normal goose egg and one the size of a volleyball will choose to roll the bigger one back to the nest. Why supernormal stimuli exist is not always clear. One aspect to keep in mind, however, is that in many cases, supernormal stimuli do not occur in nature. Thus, geese may prefer eggs the size of volleyballs, but they never encounter eggs of that size. It may be that geese have evolved to respond to the larger

object so that they will attend to eggs, rather than smaller, circular rocks. As a result, natural selection may have found the evolution of a preference for larger objects. This general response may lead to unexpected outcome in experiments but probably doesn't often lend to maladaptive behaviour.

There are many striking examples of behaviour appearing apparently normally in animals whose experience is distinctly abnormal. A case in point was shown by experiments carried out by Janet Kear on ducklings which she had reared by hand from the egg. Most duck species nest on the ground, but some of them, such as the wood-duck, do so in holes far up in trees from which the fledglings have to leap to the ground beneath. Fortunately they are light and fluffy when they do so and as a result, they bounce and run off rather than suffer multiple fractures. Kear tested chicks of various species on a visual cliff. In the apparatus the animal is placed in the centre and can move either to one side where there is a drop looking like a cliff beneath the glass or to the other where the floor is immediately under the glass so that it looks shallow. The behaviour of the ducklings was appropriate to their normal nesting place. Tree-nesters did not avoid the deep side of the cliff but, if they moved that way, they would leap as if casting themselves into space. On the other hand, the ground-nesters tended to move to the shallow side rather than the deep one, suggesting that they avoided heights. Interestingly, if they did move to the deep side their behaviour was quite different: they pushed off with both feet as they would when moving out from the edge of a pond!

Being hand-reared, these young birds had no opportunity to learn the actions they showed form others or from earlier experience with ponds or with cliffs. Many ethologists would therefore have used this evidence the argue that the behaviour must be innate because it develops despite deprivation of opportunities for learning, and the main motivation for carrying out such experiments has often been to discover whether behaviour is 'innate' or 'learnt'. Sometimes, as with the duckling, behaviour develops normally even though the animal is reared in a very *impoverished environment.*

Another good example here is the hoarding behaviour of squirrels whereby, even in captivity, they will bury nuts underground to form stores which they eat later when food is scarce. If such an animal is raised on a liquid diet, so that it never experiences nuts, with masses of this food available the whole time, so that it never needs to hoard, and on a bare floor so that digging is impossible, the first time it encounters nuts and earth it still digs a hole and buries them.

By contrast with these experiments, others have shown behaviour patterns to be radically altered unless particular experiences are available. If a young dog is reared in total isolation from all others, in a chamber in which it can be fed and cared for without contact with even its human caretakers, it turns into a strange animal, apparently careless of its own welfare. It will put its paw in a fire and singe it and it will repeatedly approach an object that gives it an electric shock. This is quite unlike a normal puppy of the same age, which hastily withdraws from such painful experiences. Furthermore, the normal puppy will yelp when hurt, whereas the one that had been isolated behaves as if it did not even feel pain. Clearly its deprivation has led to a drastic alteration in the way its behaviour developed. In another example, to which we will return later, a young male chaffinch reared out of earshot of all birds of its species has been found to develop a very simple and unstructured song quite unlike that of a normal adult. If he is defended as well, so that he can not even hear his own efforts at singing, the song he produces is even worse, being little more than a screech.

These Kaspar Hauser experiments vary enormously in what they actually deny the animals. The isolated chaffinch cannot copy song from other birds, but he can practice singing, if deafened he can still practice, but cannot hear the outcome. The hoarding squirrel has had experience of neither nuts nor earth so its deprivation is more extreme; it can not copy from others, it cannot learn for itself, not can it practice digging in earth, though it can carry out the movements concerned on the bare cage floor. In many cases it has proved very difficult to deny animals all the experiences one might think likely to be relevant. Finches with no hay that they can use for nest building will carry seed, latency, faeces and feathers to their nest site. Some bizarre behaviour results when the feathers used are still attached to themselves or to their mates. A bird may have to walk rather than fly to its nest site because it is holding its own wing in its beak as nest material; after carefully placing the wing in a corner of the nest it will then fly down, pick the wing up again and struggle back to the nest with it!

2.1 A false dichotomy

To ethologists such as Konrad Lorenz, deprivation experiments were the main evidence used in deciding whether or not particular aspects of behaviour were innate. But the examples mentioned above point to a problem in interpreting these experiments : it is almost impossible to tell exactly of what one has deprived the animal. This difficulty was one of those pointed out forcefully by a leading critic of Lorenz's theories, the American psychologist Danny Lehrman. The points he raised deserve discussion here because they were very influential in leading to current views of behaviour development. They fall under three main headings.

2.2 Criticism of the deprivation experiment

Lehrman argued that deprivation could show where experience was important but not where it was not. Thus the chaffinch which sings abnormally after being isolated shows that hearing the song of others is essential for normal song development. But the bird that builds a normal nest the first time it encounters hay may have had many experiences, form grooming its own feathers to husking seeds which could have contributed to its nest building capability. Sometimes the strangest and most unexpected experiences turn out to be important. Thus baby rats will not urinate for the first time unless thin genital area is stimulated, normally this occurs because their mothers lick them soon after they are born, but if they are isolated before this occurs they will swell up until their bladders burst. Given the existence of such unlikely influences, it is rash to assume that a simple deprivation experiment has removed all the experience that may be relevant.

2.3 Criticism of viewing learning as the only environmental influence

The environment has many influence on animal development to which it would not be appropriate to apply the word learning. The example of the baby rats can also be used to illustrate this point. Though the young rat is stimulated to start urinating, no one would suggest that it has learned to do so.

2.4 Criticism of viewing behaviour

The discovery that many unexpected factors can influence behaviour has led ethologists to examine the development of behaviour much more carefully and to avoid making sweeping statements about how this or that behaviour pattern is innate' or 'inherited'. These words suggest that the behaviour is absolutely fixed and that it would develop in exactly the same way no matter what environment the animal found itself in.

Unit 3 ❒ Perception of the environment

Structure

3.0 Introduction

Broadly speaking perception of the environment by an animal is reflected through their communication system. In a communication system one is the sender and other is the receiver. The following methods are adopted by the animals for chief communication purposes: (i) mechanical; (ii) electrical; (iii) chemical; (iv) olfactory; (v) auditory and (vi) visual.

3.1 Mechanical

A number of points of information are transmitted by tactile communication which is more developed in social interactions of many invertebrates like that seen in the blind workers of some termite colonies. The tactile communication is highly developed in monkeys where one monkey grooms another by touching and passing some information. Cockroaches and lobsters have long 'feelers' which help them to know each other in their sex act. Few animals have machine receptors by which they know some mechanical disturbances in air or water around them. Pond-skaters ascertain the sex of other adults by producing ripples on the water surface. The blind fishes know the presence of other fishes in the group by creating mechanical disturbances in the water through their lateral line organs. The tactile communication is highly developed in monkeys where one monkey grooms by touching and passing some information.

3.2 Electrical

Electric sense is a kind of 'sixth sense'. It is seen in many animals who live dim light and are poor in vision. Many lower animals are able to orient themselves in artificial electric fields, but little is known about the sensory basis of this behaviour. A number of species of fish make use of electrical sensitivity in their normal orientation and communication, and scientists know a considerable amount about their electrosensory systems. Sensitivity to magnetic fields has also been domesticated in a number of animals. Certain bacteria, for example, orient toward magnetic North and will respond to a magnet in the laboratory. Examination by electron microscope reveals that these bacteria have chain-like structure containing crystals of magnetite, which have also been found in the abdomen of honey-bees and in the pigeon retina. The bacteria in the northern hemisphere follow the declination of the earth's magnetic field and this steers them down into the anaerobic mud, their normal habitat. Those in the southern hemisphere have the polarity reversed. Magnetically directed behaviour has been studied also in bees and pigeon and some researchers have claimed that humans are sensitive to magnetic fields.

Fishes use electricity in three principal ways :

(a) The so-called 'strongly electrode fish' such as the electric ray *(Torpedo* sp.) and electric eel *(Electrophorus electricus)* produce electric shocks capable of stunning prey but may not possess an electric sense.

(b) Electrosensitive fish such as the dogfish *(Scyliorhinus)* and sharks do not produce electricity. Dogfish are capable of detecting prey, even when buried in sand, by the local distortion of the earth's electric field. The sense organs responsible are the ampullae Lorenzini, which are distributed widely over the body surface, especially near the head.

(c) The so-called 'weakly electric' fish (Gymnotidae and Mormyridae) generate their own electric fields and are sensitive to electrical changes in the environment.

These fish are usually nocturnal and live in turbid water where vision is not practicable. They have two types of electrosensitive receptor : *ampulla* receptors, which respond to slowly changing electric fields; and *tuberous* receptors, which only respond to rapidly changing fields. Some species possess only one type of receptors; others have both. They generate weak electric fields by means of electric organs, which are modified muscles or neuronal axons. The electrical discharges typically are pulsed at up to 300 pulses per second. Some fish can vary the pulse rate as a means of communication with other fish or as a part of a jamming avoidance response designed to reduce interference from the fields generated by other members of the species. In other words when one fish is subject to electrical interference from another fish it can change its pulse rate to reduce the interference. The electo-receptors are also used to locate objects in the surrounding water by the distortions they cause in the electric field. Some fish, like *Gymnarchus,* can discriminate (Fig. 3.1) between good and poor electrical conductors such as a metal rod and a plastic rod.

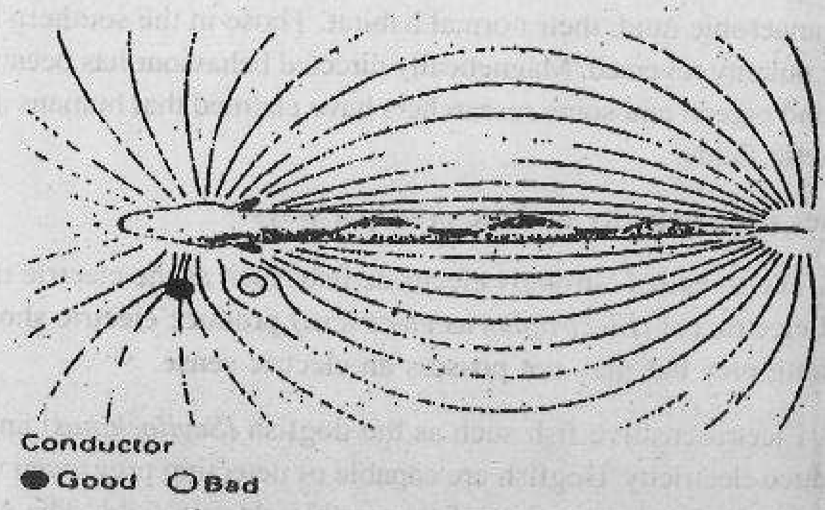

Fig 3.1 : The electric field of *Gymnarchus*. The field on the animal's right is undistorted. The field on the left is distorted by a good conductor (black) and by a poor conductor (white). The animal can detect the presence of these two objects by sensing the effects they have on the electric field.

33 Chemical

Orientation with respect to the source of some chemical diffusing in air or water, called *Chemotaxis*, is almost universal. Chemotaxis makes possible some behavioural performances that seem amazing to 'non-olfactory, creatures like ourselves. For example, *Paramecium* back-and-turn if they happen to swim into a region containing a noxious chemical. Chemoreception is the capability of identifying chemical substances and detecting their concentrations. It exists even among very primitive forms of life. In a technical sense, virtually every nerve cell is a chemoreceptor in that it reacts specifically to substances released by other nerve cells. The mechanisms of chemoreception involve the recognition of specific molecules by receptor sites on cell membranes. Exteroceptors detect the presence of chemicals in the external environment while interoceptors detect substances circulating in the body fluids, such as carbon dioxide, nutrients and hormones. Chemical substances when come in contact with the taste organ only then it is possible to feel the taste of the substance concerned. In many animals there is a neurological distinction in that some nerves are concerned with olfaction, or the detection of low concentrations, while others convey *gustatory* messages from different receptors specialized for detecting high counteractions of chemicals. In blowfly, chemoreceptors on antennae detect small quantities of airborne substances, and chemoreceptors on the tarsi (feet) are capable of detecting salt, sugar and pure water.

3.4 Olfactory

Olfactory signals or pheromones as they are usually called might seem to have very few advantages. Smells diffuse only through the environment, their speed and direction of travel being highly wind dependent and they can carry very little information, for after one smell is released time must elapse for it to disperse before another signal can be employed. However, these are situations where pheromones are ideal. A small animal such as moth could not be seen or heard from more than 100 meters or so away, no matter how brightly coloured or noisy it was. Yet the male of some moth species can detect the pheromone produced by the female several kilometers away. The chemical involved is a small molecule so that it diffuses rapidly, yet large enough that its structure can be species-specific; the male need only sense a few molecules to start moving upwind to where to ; female waits for him. Moths (also in many other insects) have various types of olfactory sensilla (Fig. 3.2). Thus usually have numerous minute pores in the surface, which terminate fluid-filled tubules. Dendrites of the receptor cells extend ; into the sensilla and the receptor exons travel directly to the brain. Airborne, pheromone molecules enter the pores of the sensillum and pass through the pores into the fluid-filled interior, where they come into contact with the receptor

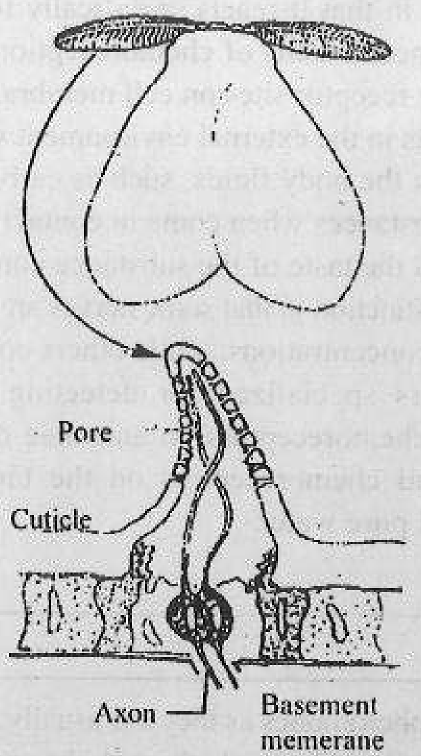

Fig 3.2 : Schematic diagram of the olfactor sensillum of a moth.

membranae. In vertebrates the olfactory receptors are primary sensory neuron with dendrites that extend as cilia into a mucous layer (Fig. 3.3). The axons of these neurons go to the olfactory bulb where they synapse with secondary neurons whose axons form the olfactory tract that enters the forebrain.

Pheromones continue to signal even when the animal is not there. Man) mammals have different scent glands which they use for various purposes.)

Territorial species often mark the boundaries of their range as a signal to others that the area is occupied. They may do this with special gland, or with scents in their urine or faeces, and a wealth of information can be contained in such signals. The potential intruder may glean, for example, not only where the territorial boundary is, but which individual is occupying it, what reproductive state he is in and even, by sensing how fresh the mark is, how long ago it was that the owner of the territory last went by. Thus, though olfaction might seem to us the poor sister of the senses as far as communication is concerned, its very persistence and slowness of dissipation make it adapted for uses of its own for which the other sense would be of battle use.

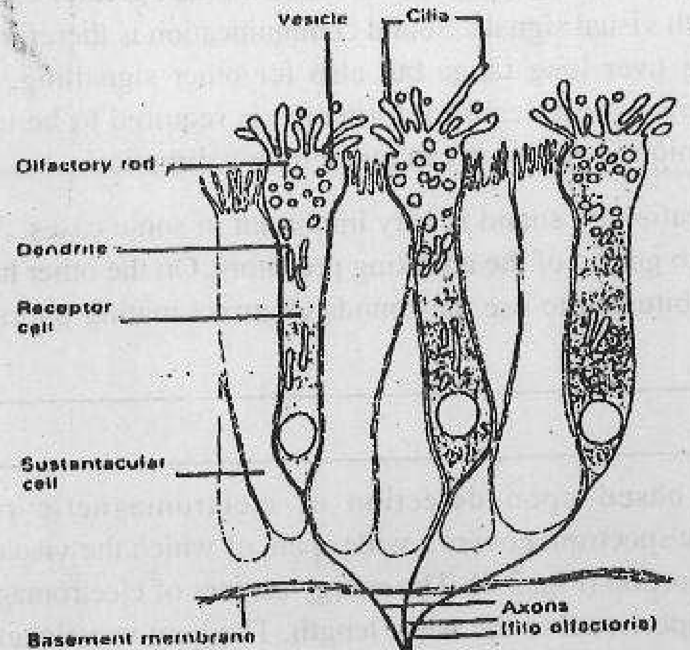

Fig 3.3 : Schematic representation of the olfactory mucosa of a rabbit. Three receptor cells are surrounded by supporting cells.

3.5 Auditory

Sound results from minute changes in pressure that originate from a vibrating source within a medium such as air or water. The receptors that detect sound are basically mechanoreceptors that show rapid adaptation and that are thus sensitive to vibration. The auditory systems of animals, though diverse, have certain features in common. There is peripheral device for convenient sound pressure to vibratory motion. Sensory receptors convert this motion into nerve impulses that can be decoded by the central nervous system. There are many properties of sound to which an animal might respond. The extent or amplitude of the waves determines the intensity or loudness of the pierced sound. In air, sound travels at about 340 meters per second. Sound communication has the merit that a great deal of information can be transmitted very rapidly. The pattern of frequency in time which codes this information can be changed with great speed so that one signal can allow quickly on the heels of another to a much greater extent than would be possible with visual signals. Sound communication is therefore ideal not only for advertising over long range but also for other signalling, such as in our language, where a great deal of information is required to be transmitted very rapidly. It is unique because it can move in any direction.

Communication by sound is very important in some cases. An alarm call is very effective to get rid of the attacking predators. On the other hand advertising animals are habituated to use the sounds to attract mating partners.

3.6 Visual

Vision is based upon detection of electromagnetic radiation. The electromagnetic spectrum covers a wide span, of which the visual spectrum is a very small proportion (Fig. 3.4). The energy content of electromagnetic radiation is inversely proportional to the wave length. The long wavelengths contain too little energy to activate the photochemical reactions that form the basis of photo reception. The short wave lengths contain so much energy that they damage living tissue most of the short-wave radiation from the sun is absorbed in the ozone layer of the atmosphere and it is doubtful that life could have evolved on earth if this had not been the case. All photobiological responses are confined to a narrow band of the spectrum between two extremes.

The pigment present in the photoreceptor cells is bleached by the action of light. The bleaching involves changes in the shape of the pigment molecules. The bleaching process leads to electrical changes in the receptor membrane that

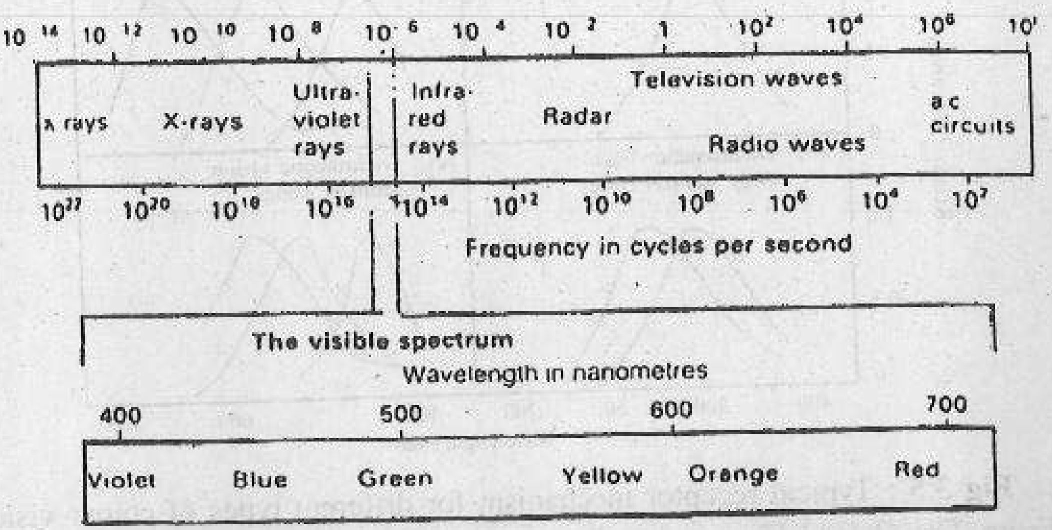

Fig 3.4 : The electromagnetic spectrum (above) wavelengths in metres, with the visible portion enlarged (below).

are not fully understood. The photoreceptors are of two types, called rods and cones. The rods are more elongated than the cones.They are very sensitive to low levels of illumination and have only one type of photopigment, called rhodopsin. Rod vision is therefore colourless. Many rod cells are connected to the single ganglion cell. Consequently, single fibre in the optic nerve receives information from many rods, an arrangement that increases sensitivity at the expense of acuity. Rods are predominant in nocturnal species where sensitivity is at a premium. Cones provide sharp vision. Cones may be of more than one type, the photopigments absorbing in different parts of the spectrum.Cones thus provide the basis for colour vision. Cones are most sensitive to the wave lengths that are most strongly absorbed by their photopigments. Vision is monochromatic when there is only one active photopigments. This is the case with twilight vision in humans when only the rods are operating (Fig. 3.5). Vision may be dichromatic when two photopigments are active as in grey squirrel. In the visual systems where three receptors are involved trichromatic vision is developed. This sort of vision is found in many spices.including humans.

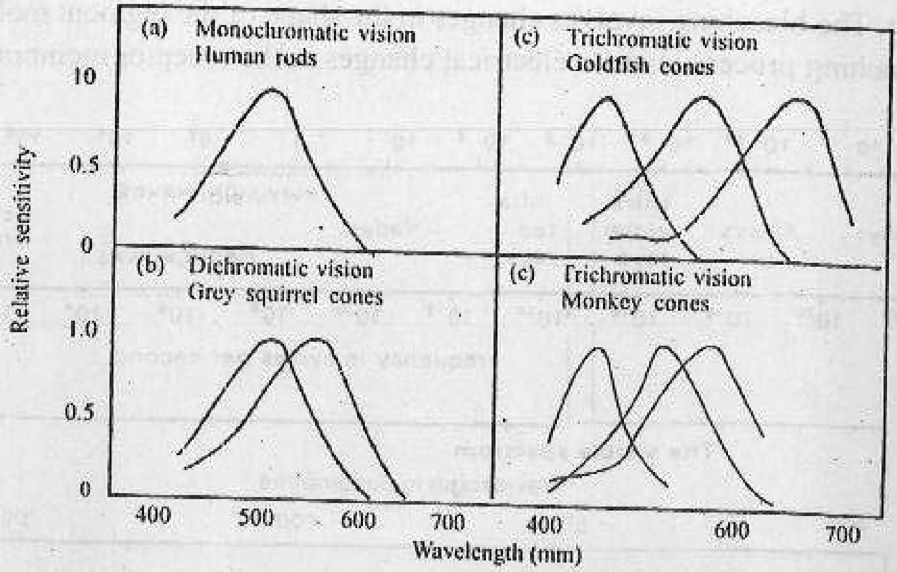

Fig 3.5 : Typical receptor mechanism for different types of colour vision (From *The Oxford Companion to Animal Behaviour*, 1981).

Changes in posture and colour are the main ways that animals communicate through the visual channel. Vision is the most important sense and by predators that hunt by day, for it is the best for location and homing in on, prey. So, this is not an ideal sense for animals that use it in advertising for mates. Also, in dense forest it is not that much effective. Moreover, small animals could not be seen from a distant place. However, this signal is very much helpful in short range communication i.e., between mates or between rivals in territorial boundary.

Unit 4 ☐ Behaviour and Neural Mechanisms

Structure

4.1 Introduction

The survival of all animals depends on their ability to solve all the problems encountered by them. The problems like food foraging, antipredator defence, mate selection etc. are solved by different patterns of behavioural activities. The aim of this section is to link between nervous system and such behaviour. The job of nervous system can be divided into three components: (i) The reception of sensory information from the environment, (ii) the processing of this information and making of decision, and (iii) the motor response to that information. The general plan of functioning of nervous system is same in all nervous system intensive animals. Through natural selection nervous systems have been shaped by the demands of constrains imposed to different animals differently. A toal can recognize which one is food and which one is non-food. A little skate can differentiate the electric field produced by its own breathing movement and electric field produced by the movement of its prey. These are just few examples we will discuss in this section taking nervous system as proximate factor. Although, we will focus on mechanism, we will also consider the ultimate cause or euolutionary significance or adaptive value of such nervous system oriented behaviours.

4.2 Nervous system and development of instinctive and learning behaviours

The ethologists labeled an instinctive behaviour a *fixed action pattern* or FAP The key component that activates FAP is called *sign stimulus or a releaser* (if the sign stimulus is a signal from one individual to anthor). The hypothetical neural mechanism that receives sensory input from sign stimulus and activates the FAP is labeled as *innate releasing mechanism*. Learning behaviour also needs a specific pattern of nervous system. All kinds of learning needs a well organised sensory receptor systems as well as an effective motor system for the manifestation of the same. The interrelationship between nervous system and instinctive and learning behaviour may be illustrated as follows.

Instincts	**Learning**
All individual of a species	An individual of a species
↓	↓
Genome + environment	Genome + environment
↓	↓
Developmental system	Developmental system
↓	↓
Neural networks relating to innate releasing mechanism	Neural networks relating to learning mechanisms
↓	↓
Fixed action pattern of behaviour (instinctive behaviour)	Learned changes in behaviour (learning behaviour)

The following examples of male and female behaviour in rat can help us to understand the whole process.

The male and female behaviour arises from an interaction between rat's genetic makeup and its environment. The basic pattern is laid out by sex-chromosomes leading to the production of testis in embryonic males and ovaries in females. The embryonic testis of male secretes testosterone, while the female's ovarian cells donot. The hormonal differences activate a developmental mechanism that provides male a masculinized brain capable of male-behaviour, and feminized brain with female behaviour. The hypothesis that testosterone is an internal signal that changes the developmental pattern modifying receptors in nervous system. There are experimental evidences that if a small amount of testosterone is injected into a new born female rat, it will attempt to copulate with other females after adulthood. Her nervous system (brain) became masculinized as a result of exposure to testosterone early in life. Conversely, if one removes the testosterone producing gonads from new-born male rat, it will develop female-like brain and may produce female like behaviour in adulthood if it receives proper amount of estrogen in adulthood. After the development of such instinctive behavioural pattern the same may be modified by learning. The process of learning is directly associated with the advancement of nervous networks. The mammals having most advance type of nervous system possess the faculty of learning uniuely.

4.3 Nervous system as the proximate causes of some behaviour

The role of nervous system as the proximate causes of some behaviour can be understood in the study of the following examples :

4.3.1 Aplysia learning behaviour and synaptic changes

The sea hare *Aplysia* moves across the oceanic battom in order to forage on seaweeds. During such foraging its siphon is extended and gills are spread out on the dorsal side. The gills are partly covered by mantle sheet, which terminates in siphon. Such siphon is a fleshy tube through which *Aplysia* can expel out excess seawater and wartes when siphon is disturbed the mantle sheet with gills are withdrawn into the mantle cavity. It is a defence response, called the gill-withdrawal reflex.

The gill-withdrawal response can be modified by experience, that is, through learning. The forms of learning have been studied here are *habituation* and *sensitization.*

Habituation : The habituation occurs when an animal learns not to respond to a repeated stimulus that proves to be harmless. The habituation form of learning is adaptive because it saves energy ignoring irrelevant, harmless stimulus. The demonstration of habituation may be done disturbing the siphon by touch or a brief jet of seawater. After 15 such stimuli at 10 minutes apart, the reflex response becomes half of their initial value. A diagram of the neural circuitry for gill-withdrawal reflex is as follows :

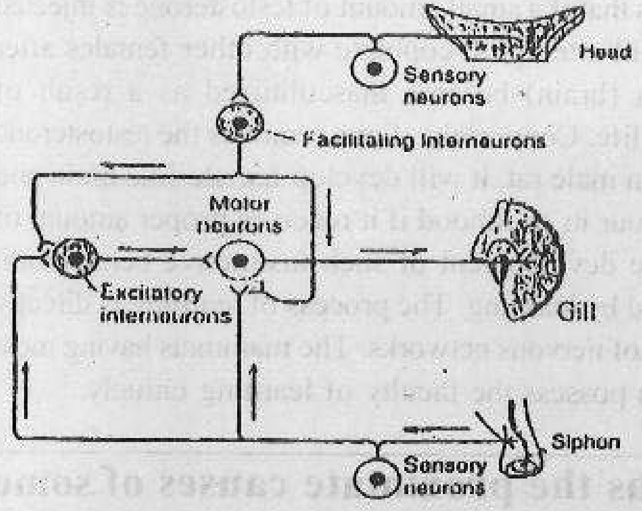

Fig 4.1 : Neural circuitry for habituation and sensitization of the gill-withdrawal reflex in *Aplysia.*

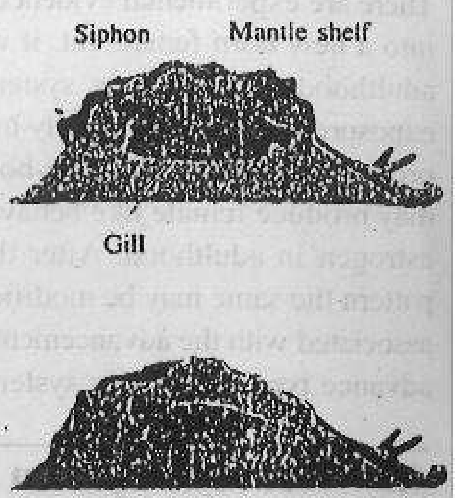

Fig 4.2 : The gill-withdrawal reflex in the sea hare, *Aplysia.* The gills, mantle shelf, and siphon are drawn here as if the animal were transparent. Normally, the gills are spread out and are only partially protected by the mantle shelf. The siphon, through which water is drawn in over the gills and excess water is expelled, is extended so just the tip is visible when the animal is seen from the side (a). It the siphon is touched, the gills, mantle shelf, and siphon are withdrawn into the mantle cavity (b). The gill-withdrawal reflex can be modified by learning.

The habituation occurs because the sensory neuron releases less neurotransmitter as a result of repeated harmless stimuli. This, in turn, results in fewer action potentials in motor neuron for gill withdrawal. The reason is that calcium channels become less effective because of repeated harmless stimuli. So, they allow less Ca^{++} into axon terminal. Calcium ions are needed for the synaptic vesicles to fuse with the presynaptic membrane. The changes in synaptic functioning during habituation is as follows :

Habituation of gill withdrawal response :

Repeated stimulation of sensory neuron from siphon of ***Aplysia***

↓

Less effective calcium channels in axon terminals of sensory neuron

↓

Decreased Ca^{++}inflow

↓

Decreased neurotransmitter release by sensory neuron

↓

Decreased firing rate of gill motor neuron

Sensitization : In second form of learning in ***Aplysia*** regarding gill-withdrawal response is *sensitization.* The gill-withdrawal reflex becomes stronger when a stimulus that causes gill-withdrawal is preceded by a strong, noxious stimulus, such as an electric shock anywhere on *Aplysia's body.* Sensitization also involves changes in the functioning of synapses. In this case the rate of release of neurotransmitter from axon terminal of sensory neuron is increased. Thus, it increases the rate of firing of motor neuron. Sensitization requires a facilitating interneuron. These interneurons release *serotonin* onto the axon terminal of sensory neuron. Serotonin increases intracellular concentration of second messenger, in this case, cyclic adenosine monophosphate (CAMP). CAMP causes the closing of certain types of k^+ channels of neuronal cell membrane. This keep k^+ inside the cell and causes sensory neuron depolarized allowing additional Ca^{++} to enter the cell. The raised Ca^{++} levels cause more neurotransmitter to be released. The entire event may be depicted as follows:

Strong, noxious stimulation to skin stimulates sensory neuron from skin.

↓

Stimulates facilitating interneuron that synapses on the axon terminal of sensory neuron from skin.

↓

Release of serotonin from facilitating interneuron.

↓

Increased CAMP level at axon terminal of sensory neuron from skin.

↓

CAMP causes closing of certain type of k^+ channel and k^+ increases in cell. prolonging depolarization of sensory neuron.

↓

More Ca^{++} enter than normaly entering the axon terminal.

↓

Increased release of neurotransmitter by sensory neuron.

↓

Increased firing rate of gill motor neuron.

4.3.2 Neuromodulators and Leech feeding behaviour

The European leach *(Hirudo medicinalis)* feeds on blood of animals, mammals in particular. A hungry leech usually rests at the water's edge: It senses a prey, it begins to swim in an undulating fashion in the direction of the target. Once the leech reaches the target, it tries to search out warm region of the animal body. When a warm region is reached, the leech bites with its three jaws. It flows blood from the wound, ingestion begins. Rhythmic contractions of the muscular pharynx pump blood into the crop for next half hour or so. Then the leech enormously distended and detaches from its host.

Charles Lent ***et al*** (1989) demonstrated that **serotonin** modulates the physiology and pattern of behaviour associated with feeding in leeches. Bathing leeches in serotonin (a method that does not cause injury to leech, therefore, preferable to the method of injecting serotonin) produces profound effect on feeding behaviour. A serotonin bath reduces the time of swimming toward potential prey, increases the frequency of biting by 40%, and pharyngeal contraction by 25%, and increases the volume of ingested blood. It needs to be noted that though the action of serotonin in feeding behaviour is activational, it inhibits the leech's sexual behaviour. The modulatory effects of serotonin in leech are summarized below .

Effect of serotonin in leech

Activational effect on :

(i) biting
(ii) pharyngeal pumping of blood
(iii) salivation
(iv) mucus secretion
(v) swimming pattern
(vi) cardiac pattern

Inhibitory effect on :

genital organs

Functionally, neuromodulators appear to be intermediate to classic neurotransmitters and hormones. Whereas neurotransmitters are released at specific synapse and hormones are broadcast throughout the body via blood stream, neuromodulars are released in the general vicinity of the traget tissue. It is difficult to establish the specific point at which a neurotransmitter becomes a neuromodulator, and a neuromodulator a hormone. For examples, dopamine acts as neurotransmitter at some synapses, and as modulators at others.

4.4 Specialization for perception of biologically relevant stimuli : sensory processing

Animals encounter wide variety of stimuli from its environment. The job of an animal's sensory system is not to transmit all available information, but rather to be selective and prodive only information that is vital to the animal's survival and reproductive success. How does an animal's nervous system enable it to select important stimuli and to ignore irrelevant ones? Here we will discuss the selective filtering action of nervous system in the little skate and common toad.

4.4.1 Stimulus filtering in the little skate

The little skate ***(Raja erinacea)*** has specialized receptors and brain structure that are capable of detecting and analyzing different types of electric fields. This specialized sensory ability of skate is called **electroreception.** There are two general categories of electroreception, **active and passive.** The electric fish of Africa **(Mormyriformes)** and south America **(Gymnoriformes)** have electric organ to generate electric field around their body water—this is called **active electroreception.** Electric fish has two types of electroreceptors, called ampullary and tuberous receptors. Little skates do not have their own electrical field generated by their own electrical organ. Instead skates respond to electrical field

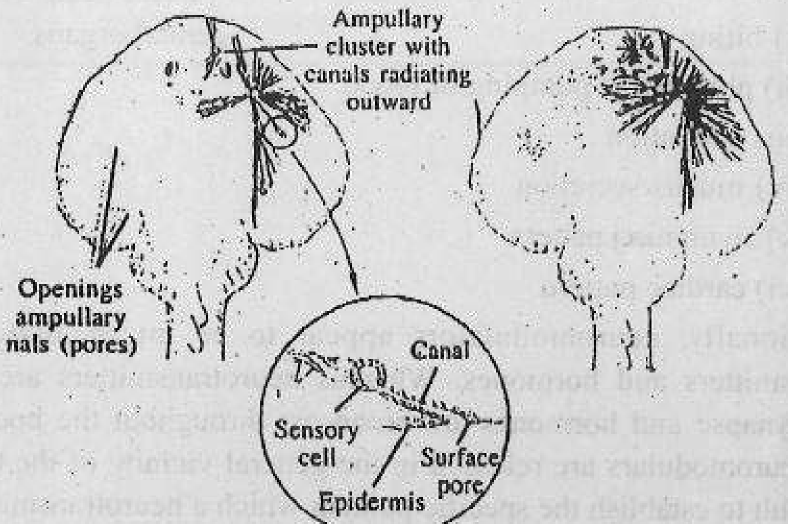

Fig 4.3 : Distribution of canals and ampullary clusters in the thornback ray, a relative of the little skate, (a) Dorsal surface, (b) Ventral surface, (c) A single ampullary organ. Elasmobranch fish such as skates and rays use electroeception to locate prey—note the concentration of receptors on the ventral surface, especially around the mouth, (a and b : Redrawn from Montgomery 1984.)

in their environment such as those field produced by preys or the earth's magnetic field. Such type of electroreception is called **passive electroreception.** Animals with this system have only one type of receptor, called ampullary organ. In case of elasmobranchs. ampullary organ is called **ampullae of Lorenzini.** The ampullae of Lorenzini of the little skate are distributed in clusters over the head and pectoral fins (Fig 4.3). Eighty percent of the receptors are distributed on the ventral surface of the body and are densely in the snout area. One problem faced by skates, as well as by other same animals having electrosensory systems, is how to deal with self-generated 'noise'. The skate's respiratory movement can generate weak electrical field. This self-generated electrical field can interfere with the detection of extrinsic electrical signal produced by prey.

The filtering of irrelevant electrical information (generated by respiratory movements) is done in the following ways.

First, all receptors distributed on both sides of the body respond equally. Second, as a result of peculiar type of synaptic connections with the central nervous system, the signal from one side of body is excitatory, whereas that from other side is inhibitory. As a result of this arrangement, the equal and opposite signals essentially cancel each other out. Thus the neural mechanism allows the skate to focus on biologically relevant electrical stimuli associated with prey animals only.

4.5 Hormonal control of behaviour

Hormones affect behaviour in two fundamental ways; **organizational and activational** effects.

In organizational effects of hormome, hermones act as proximate factor during an organism's development. It produces relatively permanent changes in the organism's nervous system and other tissues. For example, the sex differentiation and pattern of growth for body tissues. In **activational effects,** hormones act as triggering influences on the expression and performance of behaviour patterns in adulthood.

4.5.1 Examples of organizational effect of hormones on behaviour

Studies of quail, zebra finches, rats, guineapigs, mice and rhesrus monkey have provided clear evidence that certain hormones have impact on sex differentiation during early development. Now, let's consider some examples of hormonal impacts on organization effects on behaviour and related processes.

4.5.2 Sexual behaviour of rat

If a male neo-natal rat is castrated within the first four or five days of his birth, he will not show normal sexual behaviour as an adult. It a neonatally casterated male rat is given the normal doses of estrogen and progesterone of adult female he will exhibit female sexual behaviour, such as, the **lordosis posture.** By lordosis postures, a receptive female permits a male to mount and intromit. It is characterised by shifting the tail to one side, raising hindquarters, lowering the abdomen (Fig 4.4). If we select an adult castrated male rat to give estrogen and progesterone, he will not show female sexual behaviour. Neonatal female rats if treated with androgen within first four or five days after birth it exhibits male like sexual behaviour Similar studies have been made on guineapig and rhesus monkey.

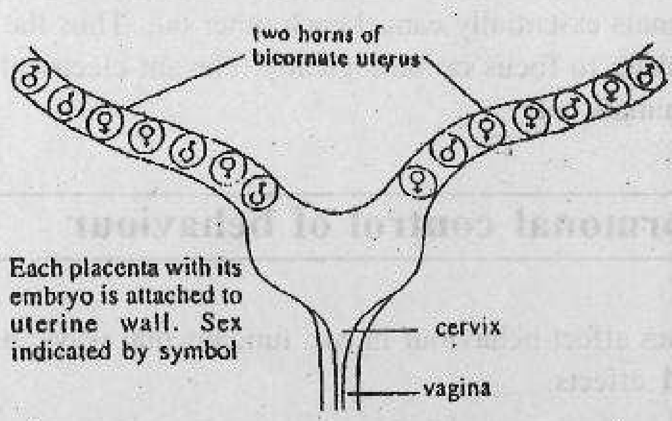

Fig 4.4 : Rat uterus. Both rats and mice have bicornate uteri. The often numerous fetuses of a pregnancy are arranged sequentially in each of the two horns of the uterus as shown here for the rat. Pups of one sex may by positioned between two pups of their own sex between two of the oposite sex, or between fetuses of opposite sexes. The location of female next to a male fetus results in masculinization of the genetic female.

The intrauterine position of a female fetus in rats and mice can influence her genital morphology and sexual behaviour. Both species have bicornate uteri fetuses are arranged sereially in each arm.of the uterus (Fig. 4.4). Thus, feture of one sex can be positioned between two other fetuses of the same sex, between two of the oppositve sex, or between two fetuses of opposite sexes. In rat and mice testicular androgens are released late in gestation. The female fetus in utero could be masculinized by exposure to testosterone from adjacent male fetuses if present. It is evident that **anogenital distance** (measurement of distance between the anal opening and the genital opening) is a reliable measure of androgen exposure. For rats and mice, anogenital distance for female fetus positioned between male fetuses are larger than females positioned between two female fetuses in utero. The rat females that have been masculinized due to in-utero position show more malelike mounting behaviour.

4.5.3 Examples of activational effects of hormones on behaviour

In adulthood, steroid hormones produce activational effects on sexual behaviour in male and female rats. Female rats with high blood levels of estrogen and progesterone display feminine sexual behaviour in the presence of a sexually active male. This type of behaviour rarely occurs when the levels of these ovarian hormones are low in blood stream. In fact, an adult female with removed ovary will not copulate unless she receives injections of estrogen and progesterone. Similarly, removal of testes in adult male eventually eliminates copulatory behaviour, unless he is given injection of testosterone. Results from researches indicate that the presence or absence of testosterone influenced aggressive behaviour in birds, mammals, if ring doves, roosters, mice rats, cats. Intact male birds and mammals show more aggression behaviour like fighting than castrated animals of the same species.

4.5.4 Influence of hormones on reproductive behavioural sequence in Ring doves

- A male ring dove bagins courtship display shortly after being placed with a receptive female. The failure of castrated male to court female indicates the importance of continuous supply of androgens for the initiation of the reproductive cycle.

- Male courtship stimulates release of FSH from pituitary in the female dove. FSH, in turn, stimulates follicle development in the ovaries. The follicles secrete estrogen, which affects uterine growth and development.

- Within a day or two, the birds begin nest construction, during this phase they capulate and continually add nesting materials to their nest.
- The presence of a nest stimulates the production and secretion of progesterone in femles. Progesterone promotes inculation behaviour after eggs are laid. Egg laying is activated partially by secretion of LH by the females pituitary.
- Under the influence of the presence of eggs in the nest and as a result of stimulation from incubation behaviour, both the sexes secrete prolactin. Prolactin acts to inhibit FSH and LH sécretion, and all sexual behaviour ceases.
- Prolactin stimulates crop development and production of **crop milk** (a nutrient rich fluid in the crop). The parents feed hatchlings with crop milk.
- During next ten to twelve days the prolactin level gradually drops down, as well as feeding behaviour gradually ceases.
- As prolactin decreases, the pituitary secretes FSH and LH, the same pair of doves again starts courtship, and the whole sequence repeats again.

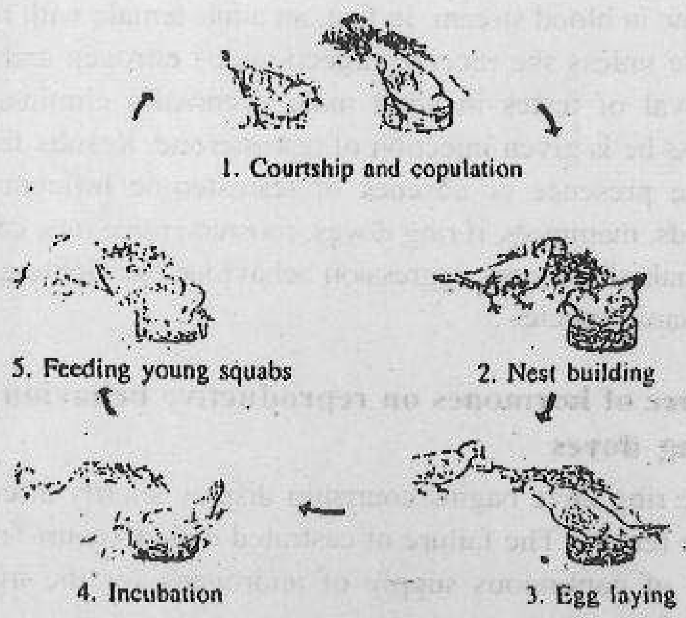

Fig 4.5 : Reproductive behavior cycle of the ring dove. This cycle provides an example of indirect environmental determinants of behavior. The sequence involves (1) courtship and copulation, (2) nest building, (3) egg laying, (4) incubation, and (5) feeding crop milk to the young squabs after they hatch. The cycle then repeats.

Unit 5 ❒ Genetic and Environmental Components in the Development of Behaviour

In humans, identical twins are genetically identical. It is obvious that most sets of identical twins are raised in the same environment. Therefore, it is not possible to determine whether similarities in behaviour result from their genetic similarity or from experiences shared as they grew up. Experimental studies on the twins separated at birth revealed many similarities in personality, temperament, and even leisure-time activities, even though the twins had often been raised in very different environments. These similarities indicate that genetics plays a role in determining behaviour in humans.

Young birds of some species begin to follow their mother within a few hours after hatching, and their following response results in a bond between mother and young. However, the young birds' initial experience determines how the imprint is established. Konrad Lorenz showed that birds will follow the first object they see after hatching and direct their social behaviour toward that object. Lorenz raised geese from eggs, and when he offered himself as a model for imprinting the goslings treated him as if he were their parent, following him dutifully.

Grohmann, in a classic experiment, reared a group of pigeons in tubes so that they could not move their wings. Another group of the same age was allowed to develop without restraint. When the unrestrainted pigeons had reached the stage at which they could fly satisfactorily, those that had been restrained were freed.Grohmann discovered that they also were able to fly immediately upon being released.

Thus, it appears that the geese and pigeons responded in respect to the conditions in which they were exposed. Therefore, the impact of environment on the development of these behaviours could not be ruled out.

From these examples it is clear that both genetical and environmental components are prerequisite for the development of behaviour. Because, if any one factor of the two would have been enough to provide the expected result then the behaviour manifested by the human twins maintained under diffrent environmental conditions would not have been different. Likewise the geese would have been failed to follow the first object they saw when they hatched if the imprinting was not influenced by the hereditary factor. Similarly, the restrained pigeons find no problem to fly at the same time along with the unrestrained individuals.

'The question whether the nature or the nurture, the genotype or the environment, is more important in shaping man's physique and his personality is simply fallacious and misleading. The genotype and the environment are equally important, because both are indispensable. The question about the roles of the genotype and environment in human development be posed thus : to what extent are the differences observed among people conditioned by the differences of their genotypes and by the difference between the environments in which people were born, grew and were brought up?' (Dobzhansky, 1964). These statements are very much applicable to most of the animals too. It is said that the behaviour patterns in organisms are 'blueprinted in the genes'. An important point to appreciate here is that natural selection has only determined how development should take place in the normal environment of each species. Thus a behaviour pattern may appear extremely fixed and constant in all individuals of a species because their genes interact with that environment to ensure that this is the case. However, moved to another environment, different from any the species has encountered before, the result may be quite different. Natural selection can not ensure that the genes will interact with any environment to give the same result; it can only give the right outcome in environment in which it has had a chance to work.

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Unit 6 □ Communication

Structure

6.0 Introduction

Wilson (1975) defined biological communication as an 'action on the par of one organism (or cell) that alters the probability pattern of behaviour ir another organism (or cell) in a fashion adaptive to either one or both the participants'. The word **adaptive** means the signal or response is to some extent genetically controlled and under the influence of natural selection.

Smith (1984) defined communication as 'any sharing of information'. The sociobiological view of communication considers that natural selection acts primarily at the level of the individual. Thus, communication is a means by which the sender manipulates others for his or her own benefit. The receiver may benefit or may be harmed.

6.1 Signals and its role in communication

A **signal** is the physical form in which a message is coded for transmission through the environment. Some signals are **discrete** (digital) but others are **graded** (analog). For example, zebras communicate hostile behaviour by flattering their ears and communicate friendliness by raising their ears (discrete signals). The intensity of aforesaid emotions are indicated by the degree to which the mouth opens (graded signal) (Fig. 6.1).

Two or more signals can be combined to form a **composite signal** with a new meaning. In zebras the meaning of the open mouth depends on whether the ears are forward (friendly) or backward (hostile). Animals can convey additional information with a limited number of displays by changing the **syntax,** or sequence of displays. For example, the two signals A and B would have different meanings depending on whether A or B came first. The same signal may have different meanings depending on the **context.** For example the lion's roar can convey as a spacing device for neighbouring prides, as an aggressive display in fights between males; or as a means of maintaining contact among pride members. The communication about communication is called **metacommunication.** We can see good examples in play behaviour.

canids such as, dogs and wolves precede play with the play bow. Monkeys communicat play behaviour through a relaxed, open mouthed face.

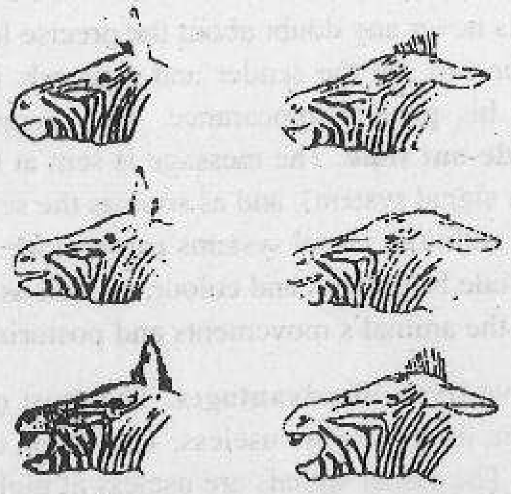


Fig 6.1 : Composite facial signals in zebras. Ears convey a discrete signal. They are either laid back as a threat or pointed upward as a greeting. The mouth conveys a graded signal and opens variably to indicate the degree of hostility or friendliness.

6.2 Channels of communication

The sensory channels are the physical forms used to transmit signals from sender to receiver. Communication can involve any of a variety of sensory channels—vision, audition, chemical, touch, and electrical fields. The characteristics of different sensory channels are as follows :

Table 6.1 : Characteristics of different sensory channels for communication

	Type of Signal				
Feature	**Visual**	**Auditory**	**Chemical**	**Tactile**	**Electrical**
Effective distance	Medium	Long	Long	Short	Short
Localization	High	Medium	Variable	High	High
Ability to go around obstacles	Poor	Good	Good	Good	Good
Rapid exchange	Fast	Fast	Slow	Fast	Fast
Complexity	High	High	Low	Medium	Low
Durability	Variable	Low	High	Low	Low

6.2.1 Vision

There are two important properties of visual signals. First is visibility of localization of sender and receiver. For example, when a male is displaying to attract a mate, there is never any doubt about the precise location of sender and receiver. The receiver can see the sender and responds in terms of his exact location, as well as his general appearance. The second property is **rapid transmission** and **fade-out time.** The message is sent at the speed of light (as it is a light dependent signal system), and as soon as the sender stops displaying the signal is gone. In addition, visual systems can provide a enormous varieties of signals. These include brightness and colour, as well as spatial and temporal pattern (produced by the animal's movements and posturing).

Visual signals have some **disadvantages.** The most obvious is that if the sender can not be seen, its signals are useless. The vision can be blocked by all sorts of obstructions. The visual signals are useless at night or less illuminated places (including the depth of the sea), except for light producing species. Furthermore, visuals power is confined within the visual range of a particular species, beyond this range of vision all kinds of singnals are useless. So, distance is an important factor.

6.2.2 Audition

Sound signals have number of advantages. They can be transmitted over long distance. Although sound signals are transmitted at a slower speed then light, it is still a rapid means of sending a message. After the message has been sent, the signal disappears without a trance. Sound signals have an additional advantage as it can convey message in limited vigibility, such as at night, in water, or in dense vegetation.

6.2.3 Chemical Communication

The chemical senses, smell and taste information may be transmitted by chemicals over long distance, especially when assisted by currents of air or water. The rate of transmission and fade-out time are slower than the visual and auditory signals. Demanding on the nature of function, this may be an advantage. For example, the demarkation of territorial boundaries, a durable, odoriferous signal is more efficient, because, if remains after the signaler has gone. Furthermore, chemical signals can be used in situations where visibility is limited. The detection of chemical signal depends on the quantity of chemicals emitted. It is difficult to locate a chemical signaler than one using visual or auditory-signals.

Chemical signals can be varied to serve different functions. For example, odoriferous pheromones are involved in mate identifications attraction, spacing mechanism, or alarm devices. Bronson (1971) suggested that pheromones in mice can be classified by function.

Priming pheromones : • Estrus inducer • Estrus inhibitor • Adrenocortical activator.

Signaling pheromones : • Fear substance • Male sex attractant • Female sex attractant • Aggression inducer • Aggression inhibitor.

Many of the substances produced by mammals function as a means of staking out territories or home ranges.

6.2.4 Touch

Short ranged communication in the form of physical contact is used by many animals. In some arthropods antennae covered with sensory receptors are used in such communication system. Antennae are used in such commuonication system. Antennae are used by sub social insects, such as cockroaches and by social insects, such as bees.

Perhaps, the most wide spread use of tactile stimuli occurs during copulation. In many rodents, stimulation of back end of an estrous female produces typical posture of lordosis. In some mammals vaginal stimulation induces ovulation.

6.2.5 Electric field

Two groups of tropical fresh water fish produce electrical signals used in both orientation (electrolocation) and communication. These groups are the knife fish (gymnotid) of south America and elephant nose fish (mormyrid) of Africa. The electrical signals are generated by electric organs that are derived from muscle in most species, but in one family of gymnotids they are derived from nerve.

Now let us consider the characteristics of electrical signals. When an electric organ discharges an electrical field is created in the water. It also disappears when the discharge stops. As a result, electrical signals are ideally suited for transmitting information that fluctuates quickly, such as aggressive tendencies.

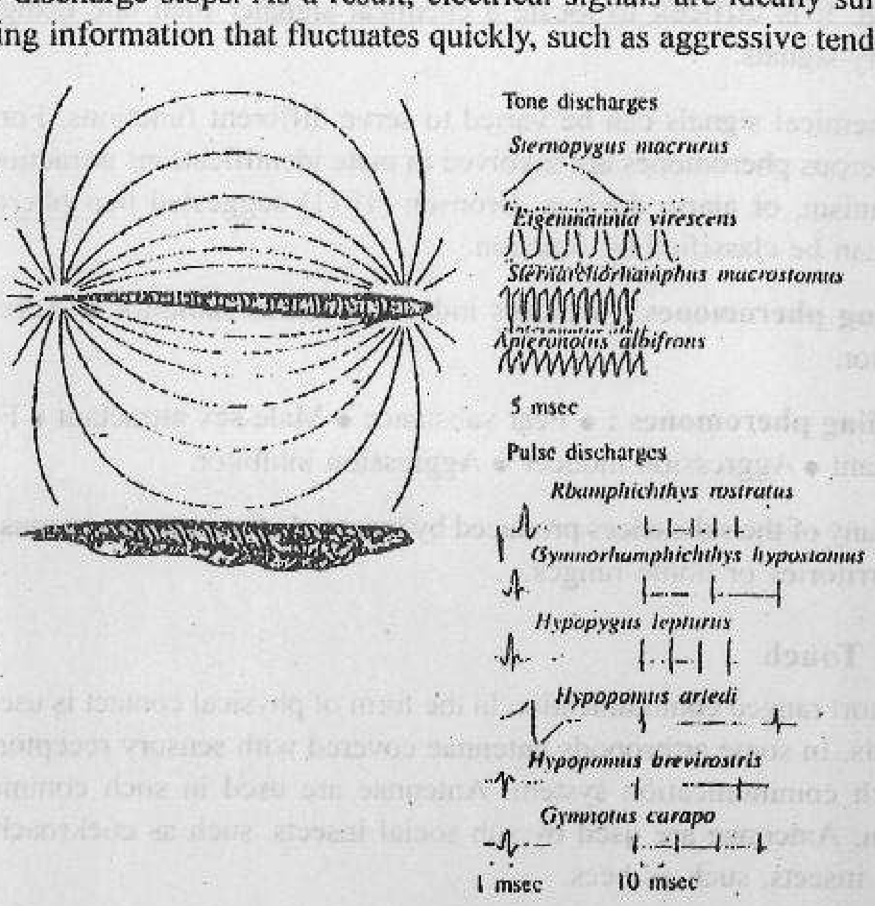


Fig 6.2 : (a) Discharges from an electric organ create an-electrical field around a weakly electric fish that is used as a communication signal. The signal can be varied by altering the shape of the electrical field, the waveform of the electrical discharge, the discharge frequency, and the timing patterns between signals from the sender and receiver, as well as by stopping the electrical discharge, (b) Some species of weakly electric fish produce electrical signals with a delay between each pulse, and others produce a continuous "buzz" of signals. (From Hopkins 1974.)

An electrical signal does not propagate away from the sender, but exists as an electrical field around the sender. Since, the electrical signal is not propagated, its wave form is not distorted during transmission. As a result the wave form of electrical field may be taken as a reliable indicator of the sender's identity.

Discharge from an electric organ create an electric field around a electric fish that its used as a communication signal. The signal can be varied by altering the shape of the electrical field, the wave form of the electrical discharge, the discharge frequency, and the timing patterns between signals from the sender and receiver, as well as by stopping the electrical discharge. Some species of weakly electric fish produce electrical signals with a delay between each pulse, and others produce a continuous "buzz" of signals (Fig. 6.2)

6.3 Species specificity of songs

Communication is an **important** adaptive behaviour for the survival of the species. Intraspecific communication helps in sexual reproduction, prarenting offsprings, alarming dangers and other such actions. The relationship between sexual behaviour and the maintenance of species identity is obvious among animals. The insects, like ***Drosophila*** sp. and mammals like humpback whale ***(Megaptera novaezangliae)*** and some birds have some specific **song pattern** by means of which they can announce their territory or convey message to their potential mates. Such song patterns are highly species specific. Some song patterns are discussed below,

6.3.1 Song and group cohesion across long distance

Payne and McVay 1971 analyzed songs of humpbacked whale ***(Megaptera novaeangilae)***, which are varied, occur in sequences of seven to thirty minutes'

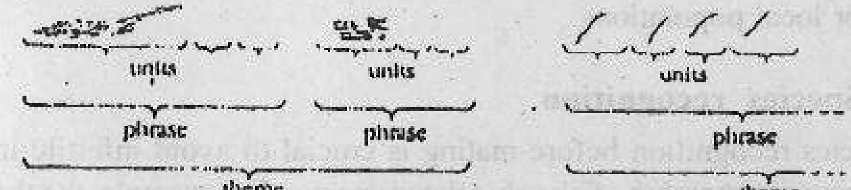


Fig 6.3 : Song of humpback whale. The song of a humpback whale can be broken up into units, phrases, themes songs, and song sessions. Each whale sings its own variation of the song, which may last up to a half hour.

duration with repeated manner. The songs have a great deal of individuality.' Researchers have not yet ascribed a clear function to these sounds. They may-serve to maintain group cohesion across thousands of miles. (Fig. 6.3)

6.3.2 Individual recognition and song

Indigo buntings ***(Passerina cyanea)*** produce a complex song that is quite variable. Most of the phrases are paired (sweet-sweet, chew-chew ....). Emlen (1972) analyzed the song pattern, and discovered the significance of the song. Past of the song sequence was species-specific, communicating the message, "I am an indigo bunting", and another part was variable from individual to individual. Therefore, such type of song pattern is useful to identify both the species and individual performing the song.

6.3.3 Neighbour recognition and song

Falls and Brooks (1975) studied that white-throated sparrow male can recognize neighbours individually or as a class.

6.3.4 Deme (local population) recognition and song

Local dialects in bird song have been demonstrated for a number of geographically separated populations of white crowned sparrows. Females from one population perform compilation-solicitation displays when they hear songs of males from their own population, but rarely do so when they hear songs from another population. This tends to lead to mating with members of locally adapted dames or local populations.

6.3.5 Species recognition

Species recognition before mating is crucial to avoid infertile mating and energy between member of closely related species. For example, the three species of picture winged Hawaiian ***Drosophila*** (Fig. 6.4) have completely different types of song pattern. Their sound producing mechanisms differ radically from those of main land populations.

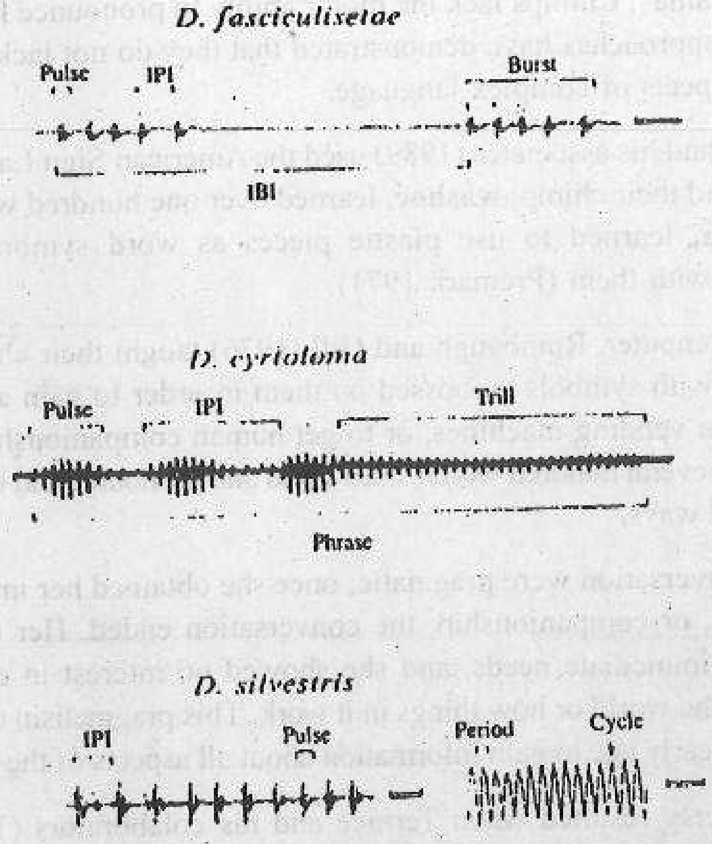


Fig. 6.4 : Song of Drosphila.

6.4 Language acquisition

Communication using unique language pattern has provided a clear-cut separation of humans from other animals. **True language means both the use of symbols for abstract ideas and the understanding of syntax, so that symbols convey different messages depending on their relative position.**

6.4.1 Language acquisition in Chimpanzees

Some researches indicate that there is a potential of chimpanzees *(Pan troglodytes)* to learn language. Hayes (1951) demonstrated that chimp can use human language. Its vocabulary consisted of only a few simple words, such as "cup" and "mama". Chimps lack the motor ability to pronounce human sounds, but different approaches have demonstrated that they do not lack the ability, to learn other aspects of complex language.

Gardener and his associates (1989) used the American Sign Language (ASL) for the deaf and their chimp, **washoe**, learned over one hundred words. Another chimp, **Sarah,** learned to use plastic pieces as word symbols and could communicate with them (Premark 1971).

Using a computer, Rumbaugh and Gill (1976) taught their chimp, Lana, to press buttons with symbols embossed on them in order to gain access to food and drink from vending machines, or to get human companionship. She had a vocabulary of several hundred words, used verbs and pronouns, and could anemble words in novel ways.

Lana's conversation were pragmatic; once she obtained her immediate goal of food, drink, or companionship, the conversation ended. Her curiosity was related to her immediate needs, and she showed no interest in extending her knowledge of the world or how things in it work. This pragmatism contrasts with language at an early age to.gain information about all aspects of the environment.

A controversy resulted when Terrace and his colaborators (Terrace et al. 1979) asserted that chimps could not really create sentences. They worked with their own chimp, Neam Chimpsky (Nim for short, named after the famous linguist Noam Chomsky), and also reanaglyzd the videotapes and films made by other investigators. Nim mastered a respectable vocabulary of sign language words and, like other chimps, used them to convey information to another individual. Nim did use two-sign combinations that were syntactically consistent; he signed the correct "eat banana", for example, more often than "banana eat." But he was apparently initiating his teachers' previous uttarances or responding to other cues, rather than creating sentences of his own. The Gardners sain in response that Nim was trained in an environment unlikely to produce spontaneous behavior and that the film segments of Washoe that Terrace analyzed were too short to demonstrate the complexity of communication (Marx, 1980).

The Rumbanghs questioned whether Lana and her successors, Austin and Sherman, were using symbolic representation in the same way that humans do

Savage-Rumbaugh et. at. 1980). Symbolyzation means the use of arbitrary symbols to refer to objects and events that are removed in time and space. Although chimps may learn to string words together in social interaction routines to attain goals, this accomplishment is not proof that they can do more than associate a word with an object — that is, their language learning does not demonstrate a referential relationship. However in another paradigm, Sherman and Austin learned how to request tools from one another in order to obtain food that they then shared (Savage-Rumbaugh 1986). Thus, if Sherman was shown a container of food that required a wrench to open, he would punch the appropriate symbol on his keyboard. Austin than knew a wrench was needed rather than some other tool, and would hand it to Sherman, who could then obtain the food. This example appears to be a case of symbolic communication between two nonhumans.

Unit 7 ❐ Ecological Aspects of Behaviour

Structure

7.0 Introduction

In recent years scientists tried to relate ecology with the behaviour of organisms. Accordingly a new branch of behavioural science known as ecoethology or behavioural ecology which is particularly concerned with the behaviour of an organism and its relationship and with the living and non living components of its environment. The major aspects of ecoethology now deal with different attribute like habitat selection, food optimization, aggression, territory defenses, dispersal, host-parasite interactions etc. A comprehensive account of all these aspects is given below.

7.1 Habitat selection

A habitat is defined as any part of the biosphere where a particular species can live, either temporarily or parrnanently (Krebs, 2001). The planet earth possesses a mosaic or patchwork of such habitats having a non-random or uniform distribution of organisms. This is because some organisms do not occupy all their available potential habitats even though they could have physically able to dispers into the unoccupied areas.

Habitat selection is a specialized behaviour of an organism and refers to the choice of a place to live. In a particular environment habitat selection is quite a discernible event. But some species can not adapt quickly when habitat changes. Thus they inhabit only a portion of their potential range. This particular behavioural aspect is regarded as one of the most poorly understood eological processes because of the following attributes :

(i) What are the reasons for the presence or absence of a species in a particular habitat (distribution pattern)?

(ii) What are the exact reasons for choice of a particular breeding sites and why so many animals disperse from their brith place.

(iii) How dispersal ability, interactions of other organisms and physico-chemical factors restrict hapitat use?

(iv) Whether the fundamental niche is really often much larger than the realized niche?

[a fundamental niche is a multidimensional space occupied by a species in an ideal condition without having any competition while the realized niche in the space occupied by species under real world conditions involving competitions, predations and diseases].

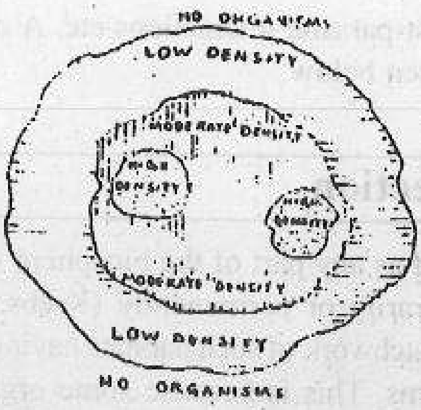


Fig 1: A typical relationship between the spatial distribution and density of a species. High density areas have optimal habitats and are surrounded by saboptimal habitats with lower densities, source : Drickmar, L.C. et.al. 2002.

7.1.1 Different aspects of habitat selection

Two broad aspects of habitat selection have been suggested by Krebs (2001). These two approaches.

(a) **The proximal approach** : This suggests habitat choice as a consequence of behavioural mechanism and

(b) **The ultimate or evolutionary approach** : It suggests the adaptive reasons for habitat choice and also the evolutionary significance of the associated behaviour.

Remark: Animals in most cases use their behavioural mechanisms to select their habitats and consequently individual movements become an essential component of the resulting habitat selection. But an opposite situation is found in case of plants owing to their apparent inability to move from one habitat to another, seeds or spores reach in different habitats through dispersals whether they will either survive and grow or will just die.

7.1.2 Factors associated with habitat selection

The following determinant factors govern habitat selection.

1. Inherited experience and leaning : Several experiments suggest that the genetic manipulation to respond to certain stimuli can be altered by habitat imprinting or early experience. This phenomenon is normally noticed in migratory vertebrates. The migratory birds usually return back to their birth place for nest building and breeding and this produce young at particular intervals. This condition is known as interoparity. However, some organisms produce offsprings only once in their life time—and the condition is known as semelparity. Haser *et al* (1978) demonstrated that salmon hype of fishes, after feeding in the open ocean for serveral years, normally return to the same upstream spawning bed where they were hatched. The olfactory system of these fishes is programmed to respond to **unique odours of the home stream** during their early life (Drickamer, 2002).

2. **Heredity :** Hereditary basis of habitat selection is quiter common among several groups of invertebrates like arthropods (crustaceans and insects), molluscs etc. Some examples include background matching by moths and butterflies in their specific host plants before egg laying, differential habitat preference by ***Drosophila*** larvae etc.

3 **Tradition :** This important behaviour is also common among certain vertebrates and normally passes from one generation to the next through the process of learning. Many species of waterfowl have specific transitory staying places within their migration route. These areas are, used year-after year for resting and feeding during migration from breeding grounds to winter grounds.

7.2 Factors restricting habitat selection

When a species occupies an area and evntually reproduces there, the required conditions will be definitely in its favour. This favourable conditions will help it to compete with other speeies successfully. Behavioural scientists have suggested a useful way to identify the factors affecting the distribution of species and the best way to do that is to determine why it is absent from a place. Krebs (1985) in his earlier work has suggested a methodological approach for studying the geographical distribution of a species. He considered four basic interacting factors with the involvement of behaviour in each category.

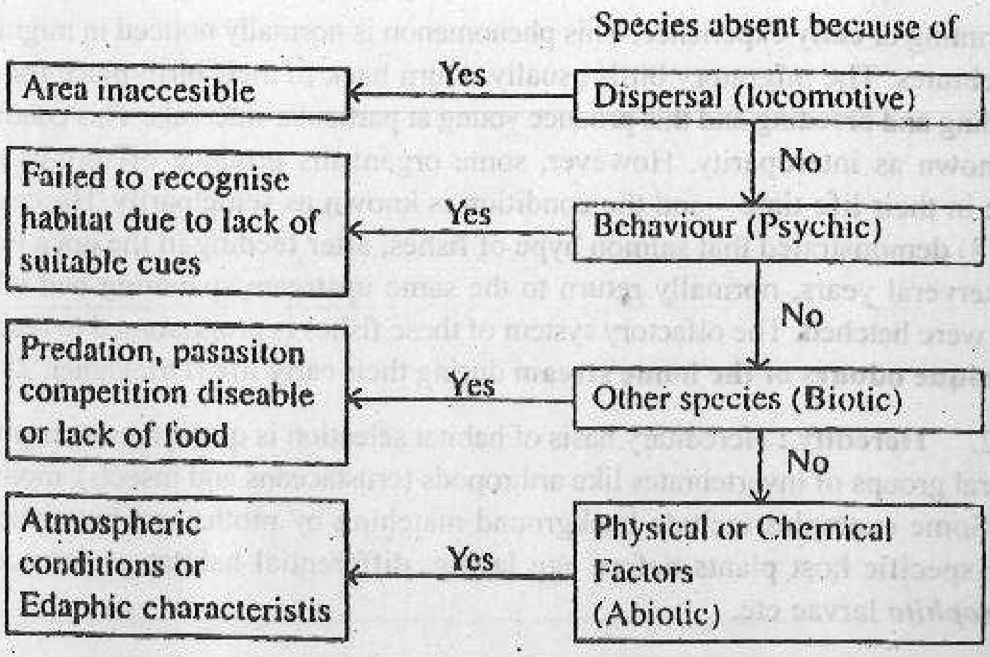


Table 7.1 : Krebs' Species distribution analysis.

7.2.1 Theory of habitat selection

According to Rosenzweig (1985) no single general theory of habitat selection is currently accepted. However, two earlier theories, explainng habitat selection may be mentioned here.

1. Optimal foraging theory : Mac Arthur and Pianka (1966) proposed this theory. This theory predicts that which habitat patch an animal should select and when to leave that patch for another suitable habitat in order to obtain maximum benifit at a minimum cost. One of the major factors for this type of habitat selection is food (energy) although nesting site or mate selections are also equally important factors. .

2. Ideal free distribution : This second approach, proposed by Fretwill and Lucas (1970), predicts about the conditions by which organisms distribute themselves in such a manner so that they can have the highest possible fitness. And for this purpose the animals must have the following :

(i) Complete and accurate knowledge about the distribution of resources ideal).

(ii) They would be passive toward one another.

and (iii) Can more to the best possible site (free).

When the organisms settle in their habitats they get the best resources and consequently their density increases. Gradually they will occupy the less desirable areas and all have the same fitness due to the absence of intraspecific competition.

Anti-predator defenses : In any stable ecosystem, harbivore-carnivore systems involve interactions between the second and third trophic levels. These interactions influence the fitness of both predators and prey. The various species in this system have developed different anti-predator defense strategies.

Defense strategies : Different 'prey' animals have evolved different defensive strategies ranging from chemical defenses to simply overwhelming the predators. The sole aim of all these strategies is affect the 'diet-eath' of the predators and also to minimize the predators ability to secure prey. Various methods are:

(i) Chemical defense :

Several groups of arthropods, fishes, amphibians and snakes produce chemical substances repel predators. The active components in the defensive secretions of many arthropods include saponins, glossypol etc.

(ii) Warning colouration and mimicry :

Some animals also possess warning colouration that send warning signals to would be predators. The black and white stripes of the skunk, bright orange colour of the monarch butterfly, yellow and black colour of many bees and wasp's send danger signals to their predators.

Besides warning colouration, some animals evolved a mimetic or false warning colouration similar to their habitats. Two very popular types of mimicry are —

(a) ***Batesian mimicry*** : Proposed by H.W. Bates (1896). He described that some edible (palatable) species develop resemblances (mimic) to an inedible one (model). Once the predator has learnt to avoid the models, it avoids the mimic also.

(b) ***Mullerian mimicry*** : Described by Fritz Muller (1879). This is a less common type of mimicry where one unpalatable or venomous species mimics another. Such mimicry is advantageons to both.

(iii) Cryptic colouration :

Another important anti-predator defense that makes locating prey more difficult certain colour patterns and behaviours euolved by prey enable them to hide from the predators. Such cryptic colourations involve patterns, shapes, postures, movements and behaviours that make the prey less visible. Cryptic colouration is common among fishes, reptiles and many ground nesting birds.

(iv) Flashing colouration :

This is another type of anti-predator strategy often associated with cryptic colouration. Certain butterflies, grass hoppers, birds and ungulates especially white tailed deer display flashing colour in the form of extremely visible patches when disturbed. This flashing colour distracts and disorient the predators. When the animals having flashing colouration come to rest, the bright or white colours vanish and the animals blend perfectly into their surrounding.

(v) Armor and weapons :

One of the most effective means of defense developed by animals like molluscs, armadillos, turtles and certain beetles. All have such hard armor coats or shells. Porcupines, hedge hogs and echidanas have quills (modified hairs) which effectively drive away predators.

(vi) Behavioural defense :

An important behavioural defense is the alarm calls produced by the prey animals during the sighting of a potential predator. However, it is not clearly known whether the alarm call is altruistic or selfish type. Another type is group living. This behaviour reduces the chances of possible predator activity'and is also known as attack—abatement effect.

(vii) Predator satiation :

This is another unique defense mechanism by means of which the timing of reproduction is manipulated in such a way so that most of the offsprings are produced in a very short period of time. The major advantage is the synchronization of births to reduce predation on the new born. Reduction of predatory activites occurs in three ways.

(a) breeding aduths collectively defends the yong .

(b) interference with the predators ability to pickout a prey individual; and

(c) maintaining a high production rate so that the predators can take only a fraction of them.

Conclusion :

Habitat selection have an impact above the level of the individual affecting population structure and even the formation of new species. However, such mechanism has yet to be established and needs further, probes.

7.2.2 Aggression

Moyer (1976) defined aggression as a complex behaviour that appears to be intended to inflict noxious stimulation or destruction on another organism and is not a unitary concept. However, the act of aggression is precisely described as agonistic behaviour and includes all aspects of conflict like threats, submission, chases and physical combat excluding predatory aggression. Moyer (1976) listed the following different forms of aggressive behaviours —

i) Teritorial — Exclusion of others from the same physical space.

ii) Dominance — Control of the behaviour among conspecific groups due to previous encounters.

iii) Sexual — Use of threats and physical punishment, usually by males for obtaining and retaining males.

iv) Parental — In the presence of newborn, usually by the females.

v) Parent-offspring — Disciplinary action by parents against offsprings.

vi) Predatory—Act of predation and cannibalism.

vii) Anti-Predatory—Defensive attack by prey or predators.

7.2.3 Homing

Several species of animals, either migratory or simply foraging within the home range, usually return to their nest site or den. This process is called homing. Several groups of molluscs especially *Chitons* use the most direct method of homing with the help of a chemical trail. Any disruption to this trail often lead to confusion. It has been observed that they vigorously search the area of disruption during return journey. This kind of coordinated actions, however, are not so well pronounced in other groups.

7.2.4 Territoriality

Territory is an area exclusively occupied by an organism or group and is avidly defended by them. Its allied form is home range—the area used habitually by an animal or group, in which the animal spends most of its time. The area of heaviest use within the home range is the core area. In all these areas, the organisms normally maintain a minimum distance between the members of the same species. This phenomenon is called individual distance. The behavioural mechanism of animals associated with the maintenence of a territory or home range is called territoriality.

Territorial mechanisms are quite common among animals who spend much time petrolling the boundaries of their space and show specific behaviours like singing, visiting scent posts or making other displays. The most common display is the tendency to respond less aggressively to neighbours than the total strangers. This behaviour is called 'dear enemy' phenomenon.

The reason behind the establishment of a territory by an organism is not very clear. Brown (1964), however, suggested a probable reason known as economic defendability. It probably accurs when costs of living (energy expenditure) are overwighted by the benefits (access to resource).

7.2.5 Dispersals

It may be defined as a more or less permanant movement of an individual from an area like the movement of a juvenile away from its place of birth. But it becomes somewhat a problemetic issue since animals have to decide about whether to remain or return at the natal site (emigration) or to disperse to other breeding site (immigration).

In most species of birds and nammals, members of one sex tend to disperse, while members of other sex are **'philopatric'** i.e. breed near the place where they were born. Male mammals usually disperse while the female perching birds who are mostly monogomous normally disperse (Greenwood, 1980).

Causes of dispersals

It can be explained at the following levels

i) ***At the proximate level:*** Individual may be forced out by the parents or other residents or it may respond involuntarily to increase in testosteron levels associated with sexual maturation.

ii) ***At the ultimate level:*** It suggests the long term evolutionary causes of dispusal. When an individual fails to disperse, it will have a lower reproductive success because its offsprings will be compelled to inbreed and therefore will be less viable. Natural selection would then favour the dispersers.

7.3 Host-parasite relation

Hosts are homes (habitats) for parasites and parasites exploit every conceivable habitat on and within them—showing extreme specialization for resource exploitation. Thus parasitism is a situation in which two organisms live together, but one derives its nutrition at the expense of the other. Parasites exhibit a tremendous diversity in the ways they exploit their hosts. They may parasitize plants or animals or both.

Parasites may be ectoparasites living outside the body of the host or endoparasite living within the body of the host. On the basis of size parasites may be microparasites like viruses, bacteria and protozoans or macroparasites like worms, the platyhelminthes, acanthocephalans, roundwarms, flukes, lice, fleas, mites and fungi.

All parasites reach a stage in their life cycle within the host's body when they can not develop further. On this basis a host may be classified into—

a) ***Definitive host:*** an organism in which the parasite becomes an adult and reaches maturity.

b) ***Intermediate host*** : the organism which harbours only some developmental phase of the parasite.

7.3.1 Parasitic transmission

Most successful parasitic transmission occurs when the population of potential hosts is dense, particularly if the parasites depend upon direct contacts among hosts. In animal population (other than humans) rapid spread of parasitic diseases especially in dense population is called **epizootics.** In human the same phenomenon is called **epidemics.**

7.3.2 Host—parasite relations

The relationship between hosts and parasites is best understood by mathematical models. These models suggest the intricate mechanism of prey—predator interrelationships involving the following parameters :

(i) parasite density within the host
(ii) density of the host
(iii) proportion of parasites in the transmissive stage
(iv) rate of production of eggs and subsequent life stages, and
(v) influence of the parasites on the host survival.

7.3.3 Special type of parasitism

At least two specialized typical parasitism also occur in nature. These are (i) Brood parasitism and (ii) Klepto parasitism.

(i) Brood parasitism

Here one organism depends upon the social structure of another to rear its young. This brood parasitism may be temporary or permanent, facultative or abligatory, inter or intraspecific. Brood parasitism frequently occurs among ants, wasps and birds.

(ii) Klepto parasitism

It involves the piracy of food by one individual from another. It is most conmon among organism where potential hosts are aggregated in large breeding colonies and feeding groups Birds like hawks, gulls, skurs waders are good examples.

From the eco-ethologcal stand-point, kleptoparasitism is energetically profitable for the parasites but adversely affects the foraging behaviour and enngy budgets of the hosts.

Unit 8 ❒ Social Behaviour

Structure

8.0 Introduction

We can define a **society** as a group of individuals of the same species that is organised in a cooperative manner extending beyond sexual and parental behaviour and well call their behaviour **social behaviour.** The study of social behaviour involves aggregations or group diving cooperative behaviours and eusocial organization of animal societies. In this chapter we will discuss the nature of aggregations cooperative behaviours like altruism, group selection and organization of insect and primate societies.

8.1 Aggregations

The animals live at least part of their life in a group, but the details of their behaviour vary tremendously. Some species barely tolerate conspecifics, and get together only briefly for mating, others live in groups but show no cooperations. Others spend every moment of their lives in cooperative interations with conspecific. The term **group or aggregation** does not imply any particular form of special behaviour or cooperation: the type of cooperation involves pairwise, is called **dyadic interactions.** In these dyadic interactions, two individuals interact in such a way that,the fitness of each is affected by both its own action and the action of the partner. Cooperation can also occur in **polyadic interactions,** that is, interactions that involve more two individuals. One example of polyadic interactions involving cooperation is **coalition behaviour,** which is typically defined as a cooperative action taken by at least two other individuals or groups against another individual or group. When coalition exist for long period of time, they are often referred to as **alliances.** The pattern of aggregations, or groups are called differently in different animals. For example, schooling or shoaling in fishes, flocking in birds and herding in mammals.

8.1.1 Schooling in fishes

Shoaling—sometimes referred to as schooling is a measure of group cohesiveness **motion.** It can be accounted as an **antipredator defence behaviour** in fishes in addition to the potential **hydrodynamic and foraging benefits.**

When a predator is sighted, schooling fish often increase "effective group size" and adopt following antipredator tactics.

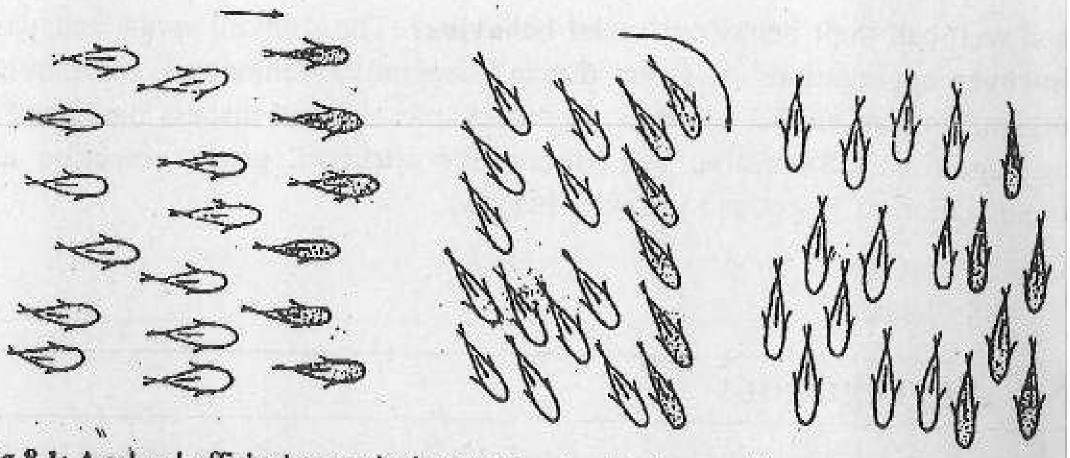


Fig 8.1: A school offish changes its leadership when it changes direction. The leaders at th left (stippled) are shifted to the flank when the school makes a 90° turn, as shown i sequence in the center and at the right (Modified from Show, 1962).

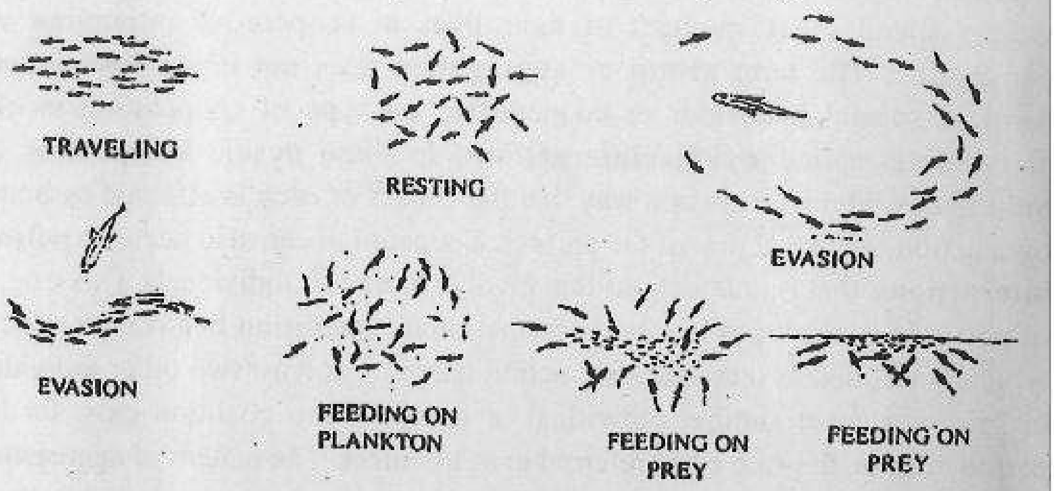


Fig 8.2 : In open water members of fish schools change their alignments according to conditions in the environment. In general, organization declines and behavior is individualized when the fish rest or feed (Modified from Radakov, 1973).

- **Fountain Effect** : Schools, maximize their speed, split around a predator, and then reasemble behind the predator.
- **Trafalgar Effect**: In tight groups, the information about a predator spreads from individual to individual more quickly than in loose school. Trehene and Foster (1981) coined the term "Trafalgar Effect" because it resembled the quick transfer of information through the use of battle signals followed by Lord Nelson at the battle of Trafalgar.

- **Flash expansion :** Tightly packed schools of fish "explode" with fish quickly swimming off in all directions. This can temporarily confuse a predator and allow for escape.

- **Confusion effect :** Schooling fishes often confuse predator by moving around in a erratic patterns within group making it difficult to home in on a single target by the predator. This effect differs from flash expansions in that the school remains in a single group.

- **Predator inspection :** Here, a few individuals break away from a school, approach a predator to gain information, and then return to school, where this information may be spread across individuals.

Evolution of schooling in fishes : ***a cash at study***—The American icthyologist C. P. Haskins (1957*1* conducted a unique study on the effect of predator and schooling in guppy *(Poecilia reticulata)*. Generally speaking guppies from high predation sites school more tightly and in greater number than guppies from low-predation sites. Further **more,** fish from high predation sites inspect a predator less closely than their low-predation counterparts.

At high predation site swimming in large groups provide more protection than swimming in small groups. In the early 1990s, Anne Magurran and her colleagues fortunately observed some natural incidents on the evolution of antipredator behaviour in guppies. This study was the follow-up of the study conducted in 1957 by C. P. Haskins. Haskins transferred 200 guppies from a fish predation site (in the Arima River) to a low predation site (in the Turure River). Magurran realized that after 33 years it was a golden opportunity to examine natural selection on antipredator behaviour on schooling of guppies. If natural selection, via predation pressure, shapes schooling behaviour as an antipredator response, then the lack of predation pressure in the Turure should have led to selection for weakened schooling behaviaur in guppy descendants studied in the 1990s. Magurran and her associates sampled numerous sites in the Turure and examined both the behaviour and genetic composition of fish of these sites. Genetic analysis suggests that the fish transferred from Arima River back in 1957 had spread all arounds the site in the Turure River. Because of strong natural selection pressures, the descendents of Arima River fish evolved schooling in

Turure River more similar-to guppies at low predation sites than their ancestral site of Arima River with strong predation pressure.

8.1.2 Flocking in birds

Studies reveal that two environmental influences on group size or flocks are **food and predators.**

8.1.2.1 Avoiding predation

Living in group might help an individual to avoid becoming a meal of a predator. This could happen in the following ways :—

(a) Increased vigilance: The goshawks are potential predator of pigeons. The hawks are less successful in attacks on large flocks of pigeons mainly because the birds in a large flock take to the air when the hawk is still some distance away. If each pigeon in the flock occasionally looks up to scans for a hawk, the

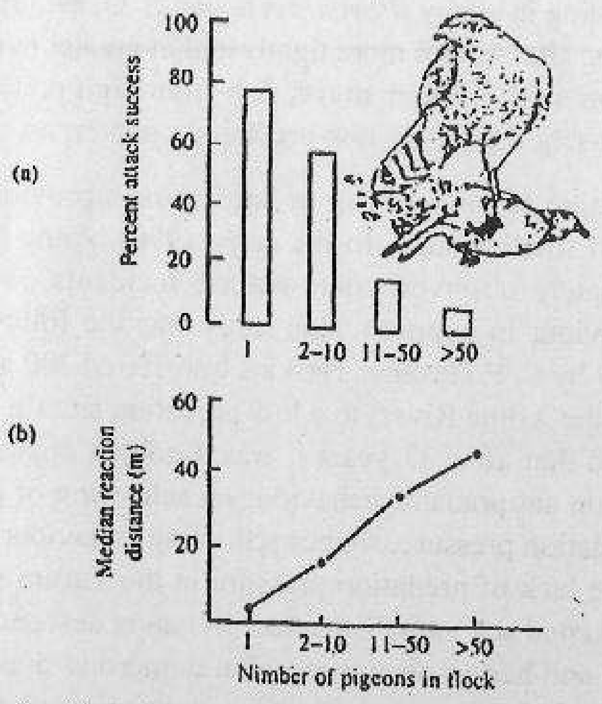


Fig 8.3 : (a) Goshawks *(Accipiter gentilis)* are less successful when they attack larger flocks of wood pigeons *(Columber polumbus)*. (b) This is largely because bigger flocks take flight at greater distances from the hawk. The experiments involved releasing a trained hawk from a standard distance. From Kenward (1978).

bigger the flock the larger the chances to be alert when the hawk looms over the horizon (Fig. 8.3 a, b). The way in which vigilance changes with flock size depends on how individuals in the group spend their time. In ostrich flocks, it is found that each individual spends a smaller portion of its time scanning in group than when lives alone. Therefore, each bird in the flock has more time to feed and enjoy greater protection from approaching lions (a potential predator of ostrich).

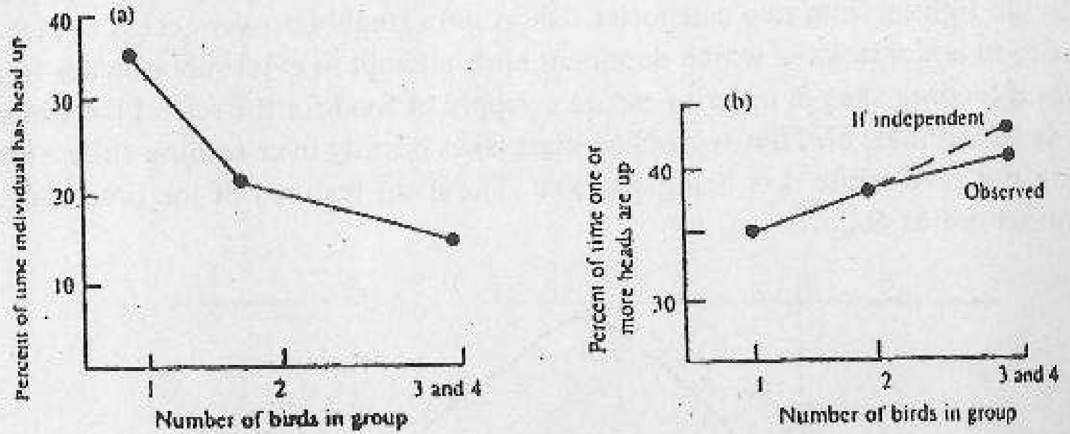


Fig 8.4 : Vigilance in groups : - (a) An ostrich *(Strmhio camelus)* spends a smaller proportion of its time scanning for predators when it is in a group. (b) The overall vigilance of the group increases slightly with group size (solid line), as predicated if each individual looks up independently of the others (broken line). (From Bertram; 1980).

(b) Dilution an cover : By living in large group each individual dilutes the impact of successful attack by a predator because there is a good chance that another member will be the victim. Although there is only a slight increase in vigilance with increasing group size in ostriches, the chances that any one individual will be eaten during an attack by lions decreases rapidly with group size, because the lions can kill only one ostrich per successful attack.

8.1.2.2 Time budget and the optimal flock size / group size : ***A case study of yellow-eyed Junco:*** Ron Pulliam (1976) and Tom Caraco (1979) have used time as a currency and developed a model of optimal group size based on the time budget. The model is used to illustrate the factors influencing winter flocks of small birds. The survival of birds in flock is considered to be dependent on two main risks, **starvation and predation.** The time budget is divided into three types of behaviour associated with these risks : scanning for predators, feeding and infighting for food. The three activities in the time budget are assumed to be mutually exclusive, that is a bird can not, for example, scan and feed at the same time. In order to scan it has to point its head upwards, while picking involves facing forwards the ground. The scanning for predators takes precedence over feeding, since failing to see an approaching predator is more dangerous than failing to eat a seed. Dominant birds give higher priority to satisfying their daily energy requirement than to eviction of subordinates. **Pulliam and Carago** divide fighting into two categories : short term stuabbles over access to pieces of food and attacks in which dominant birds attempt to evict subordinates from good feeding sites in order to ensure a supply of food for the rest of the winter. For subordinate bird the aggression must takes priority over feeding since a bird can not feed while it is being attacked. The main features of the time budget model are as follows :

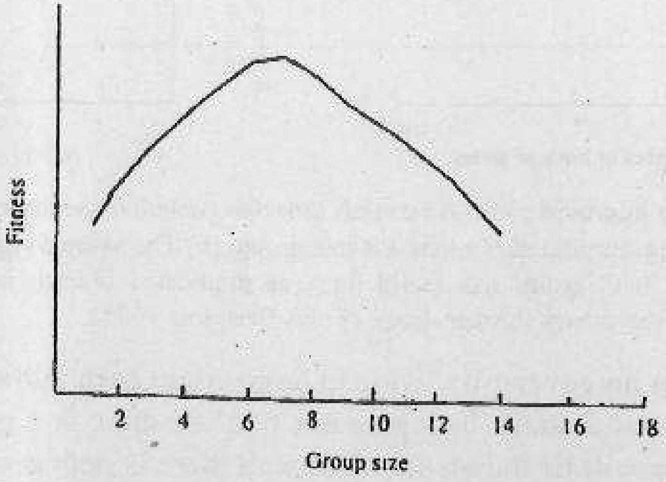


Fig 8.5 : Sibly's model of optimal and stable group size. Each individual join the group that maximizes its fitness, so that the optimal size of seven is not necessarily stable—it will be joined by solitary individuals for example. Alo Sibly (1983).

(1) The proportion of time spent of scanning by an individual is assumed to decrease with increasing group size. The basis for this assumption to that a given level of vigilance can be maintained with less scanning time per individual as group size increases.

(2) As group size increases, and encounters between birds become more frequent the proportion of time spent in aggression increases.

(3) The time spent in feeding is, therefore, maximum in flocks of intermediate size. Using this time budget model the optimum flock size can be measured in different conditions as follows :—

(i) If the only benefit of flock living is to increase the time available for feeding while maintaining a certain level of vigilance, the optimal flock size is the one indicated in the Fig. 8.6a.

(ii) If the benefits of flocking such as dilution and increased vigilance for predators, the optimal flock size may be larger than the one shown in Fig. 8.6b. However, the picture is probably more complicated than Fig. 8.6c, because the optimal flock size may be different for dominant and subordinate birds. Dominant birds obtain a long-term benefit from evicting subordinates, so they should prefer to be in smaller groups.

In order to test whether time budgets influence flock size in the way suggested by the model. Caraco *et. al.* predicted the effect of various environmental changes on flock size. The predictions are as follows :

1. As average daily temperature increases, the dominant bird should have more time to evict subordinates because they can satisfy their energy requirements more rapidly. Flock size should therefore decrease. This prediction was supported by observation on winter flocks of yellow eyed juncos in Arizona by **Caraco** *et al*(1980).

Evolution of group living or flocking in weaver birds : John Crook (1964) studied about 90 species of weaver birds in order to a certain the evolution of flocking in birds. Crook's approach was to search for correlations between the social organization and the species' ecology. The ecological variables he considered.were the type of food, its distribution and abundance, predators and nest sites. His analysis shows that weaver birds fell into three broad categories :

(1) Species living in the forest tended to be insectivorous, solitary feeders, defend large territories and build cryptic solitary nest. They are monogamous, and males and females have similar plumage.

(2) Species living in the savannah tended to eat seeds, feed in flocks and nest in tight colony' in bulky conspicuous nests. They are polygamous

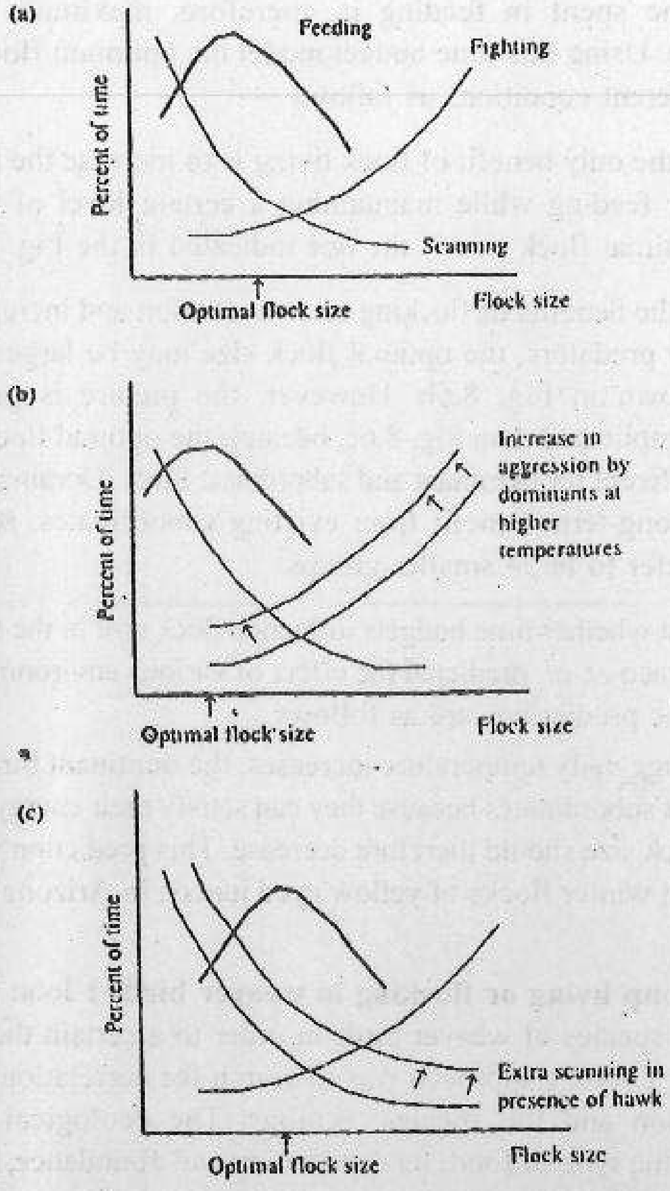


Fig 8.6 : A model of optimal flock size (a) As flock size increases birds spend more time fighting and less time scanning. An intermediate flock size gives the maximum proportion of time feeding, (b) At higher temperatures (or when food is more plentiful dominant birds can afford to spend more time attacking subordinates. The optimal flock size the average bird therefore decreases, (c) When predation risk is increased by flying a hawk over the flock, the scanning level should go up and the optimal flock size is increased. Harval and Pulliam (1976) and Caraco et.at. (1980).

and there are sexual dimorphism in plumage, the males being brightly coloured and the females rather dull.

(3) The species with intermediate ecology have an intermediate social organization, nesting in loose colonies and feeding in flocks.

Crook invoked **predation and food** as the main selective pressures that have influenced the evolution of social organization. His argument was as follows:

1. In the forest insect food is dispersed. Therefore, it is best for birds to feed solitarily and defends their scattered food sources as a territory. Because the food is difficult to find, both parents have to feed their young and therefore stay together as a pair throughout the breeding season. Both must have to be dull coloured to avoid attracting predators. Cryptic nests decrease their vulnerability to predation.
2. In the savannah seeds are patchy in distribution and locally super abundant. It is easy to find patches of seed .being in a group, because groups are able to cover a wider area in their search. Furthermore the patches contain so much food that there is little competition within the flock for food.

In open country the birds can not hide their nests and so they seek safety in protected sites, such as spiny' acacia and date trees. Nests are bulky to provide thermal insulation against the heat of the sun. Many birds nest in the same tree. Within a colony, males compete for nest sites and those defend the best sites attract several females while males in poorer parts of the colony fail to breed. Because of abundant food supply the female can feed the young by herself and so the male is emancipated from parental care and can spend most of his time by attracting more females. This has favoured evolution of polygamy.

(3) Supporting evidences for this inter pretation comes from species with intermediate ecology. The grass land seed-eaters have patchy food supplies so group living is favoured in efficient food finding. However, in grassland the nests are vulnerable, so predation favours spacing out. The result is compromises, these species have an intermediate social organization, nesting in loose colonies and feeding in flocks.

These results show how food and predation may be important in determining flocking pattern in weaver birds.

8.1.3 Herding in mammals

The herding in mammals generally centers around the following factors : (I) Reproductive behaviour, (II) Antipredator defence, (III) Social grooming etc.

(I) **Reproductive behaviour and herding :**—*A case study in lions :* Reproductive behaviour influencing herding in lions includes mate aquisition, raising young etc. Lions live in a **pride** consisting of between 3 and 12 adult females, 1 to 6 adult males and several cubs. The group defends a territory in which it hunts for prey. Within a pride all the females are related, they are sisters, mothers and daughter, cousins and so on. All were bran and reared in the pride and all stay there to breed. For males, life is very different. When they are three years old, young related males (sometimes brothers) leave their natal pride. After a couple of years as monads they attempt to take over another pride from old and weak males. After a successful take over they stay in the pride for breeding for 2 to 3 years before they, in turn, are driven out by new males. The lions pride, thus consists of a permanent group of closely related females and a smaller group of separately unrelated males present for a shorter time.

Within a pride all the adult females tend to come into oestrus in about the same time. The mechanism or causal explanation may be the influence of an individual's pheromones on the oestrus cycle of other females in pride. The function of oestrus synchrony in lions is that different mother breed at the same time, and cubs born synchronously survive better. This is because there is a communal suckling. In addition, with synchronous births there is a greater chance that a young male will have more brothers when it leaves the pride lead a all-male group-life. This will increase the chance of successful pride take over by them.

(II) **Herding in Indian elephants** : Indian elephants live in matriarchal society where the oldest female is the leader. Males leave their-natal families after attaining puberty and then lead more or less solitary lives. They forms transient associations with other males or herds of females they may take over.

Elephant populations are composed of several **clans** and solitary males. Clans are group of elephants, mainly adult females and their offsprings, which may be related to each other. Different clans or members of different clans, however, do not associate with each other. Though associations between clans has been recorded in African elephants.

Clans basically represent large extended families. It should be pointed out that within the clan all members do not associate with each other equally. Some develop special affinities with each other more frequently than with other members of the clan. It is defined as **bond groups** that are actually made up of several family units with special bond between them. These family units comprising adult females and their dependent offsprings are seldom seen apart from each other. The birth of sibling is momentous occasion to the female calf. She adjust to the weaning quickly and play a role of an allomother. This behaviour helps the young females to develop the trait required to be successful mother in later life. At times. Adult females who do not have calves of their own and act as allomother, but this not common. By and large sub adult females play the role of allomother. Females calves continue to live and grow in their natal bond group till they become adults and have family units of their own. They may in fact spend their entire lives in such a group. Ecological stress may sometimes lead to competition for resources between the adult virgin females and their mother or with other bond group members and this could force her to leave the bondgroup.

Unlike females, male calves look upon the arrival of a sibling as competitior. They do not take to weaning and often the mother has to use force to weaning them away. Once weaned males take absolutely no interest in their sibling and contribute nothing to the family. Males reaching the age of nine or ten they are already two big to defend any predator like tigers. Around now they are able to free themselves of the dependency of group bond or clans. Nevertheless, not all contact with the clan was broken as young males continue to return to their natal clan of ten. By the age of 15 male association with the natal clan is irregular at best. Without a doubt, the matriarchal society is the key to the survival of elephants.

(III) Herding in African Ungulates: Jarman (1974) considered 74 species of ungulates. The species were grouped into five ecological categories (Table—8.1). The major correlate of diet and social organization of body size. Small species have higher metabolic requirement per unit weight and need high quality patches of food. These trend occur in the forest and are scattered in distribution, so the small speeds are forces to live a solitary life. At the other extreme, the largest species eat poor quality food in bulk and graze less selectively. It is not economical to defend such food supplies and these species wander in herds. In these herds there is potential for the strongest males to monopolize several females by defending a **harem.** When predator came along these species cannot hide on the open plains and so either flee or rely on safety in members of the herd.[1] Ungulates of intermediate size show aspects of ecology and social organization in between these two extremes.

Table 8.1: Table showing body weight, diet and herd size of different grade of species

Grade	Body weight (kg)	Diet	Herd size
I	3—60	Selective browsing, fruit, buds	1 or2
II	20—80	Selective browsing or grazing	2 to 12
III	20—250	Graze or browse	2 to 100
IV	90—270	Graze	150 to 1000
V	300—900	Graze unselectively	1000 or more

8.2 Group Selection

The change in allele frequency in a ponmictic population disrupting Hardy-Weinberg eqilibrium is the usual measure of evolutionary change of microlevel. One of the important parameters introducing such change of allele frequency is **natural selection.** What does selection act upon—single gene and its alleles, individuals, groups or whole species? Natural selection sees the individual organism and its phenotype. It is the organism as a whole that survives and reproduces. Because of this, Charles Robert Darwin and many people consider the individual as the unit of selection. Another view is that the gene and its alleles are best considered as the unit of selection. Groups may also be considered to be selective units. **According to E.O. Wilson (1980) selection can be said to operate at the group level, and deserves to be called group selection.** Just above the level of the individual we can delimit various group : a set of sibs, parents and their offsprings, a close-knit family, an entire breeding population and so on. If the selection affects the frequency shared by common descent in relatives (related by atleast the degree of third cousin) ; the process is referred to as **Kin Selection.** At higher level an entire breeding population may be the unit, so the populations (demes) possessing different genotypes are extinguished differentially, or disseminate different numbers of colonists, such type of selection may be called **interdemic (or overpopulation) selection.** The theory of kin-selection will be discussed later on. let us consider the process **of interdemic (interpopulation) selection.**

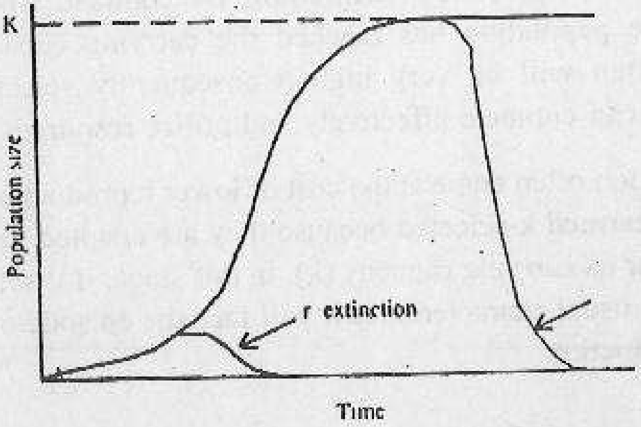


Fig 8.7 : Extinction of a population probably most commonly occurs at an early stage of its growth, particularly when the first colonists are trying to establish a foothold (*r* extinction), or after the capacity of the environment has been reached or exceeded and a crash occurs (*k* extinction). The consequences in evolution are potentially radically different. (From Wilson, 1973).

8.2.1 Interdemic (interpopulation) selection

Species often exists as a network of distinct populations that interact with each other by exchanging individuals. Such network of populations is termed **metapopulations.** Such papulation usually occur in areas in which suitable habitat is patchily distributed and separated by intervening stretches of unsuitable habitat. At any moment of time a given patch may contain a population or not; empty patches are occasionally colonized by immigrants that form new populations, while old papulations occasionally become extinct leaving an empty patch. In considering interdemic selection, it is important to distinguish the timing of the extinction event in the history of population (Fig. 8.7). There are two moments at which extinction is most likely at the very beginning, when the colonists are struggling to establish a hold on the site, and soon after the population has reached the carrying capacity of the site, and is in most danger of crashing from starvation or destruction of habitat. The former event can be called **r-extinct** L and the latter **K-extinction.** At the initial stage of colonization in an empty patch, the population is far below the carrying capacity, resources are abundant, cost of reproduction is low. Selection here favours individuals with the highest reproductive rates (r), such populations are termed **r-selected.** In this stage the extinction of colony is called **r-extinction.** By contrast, when resources are limited, and the papulation has reached the carrying capacity, the cost of reproduction often will be very high. Consequently selection will favour individuals that can compete effectively and utilize resources efficiently.

Such adaptation often come at the cost of lower reproduction rates, and such populations are termed k-selected because they are adapted to thrive when the population is near its carrying capacity (k). In this stage, if k-selected population deviates from its usual characteristics it will face the episode of extinction, and it is called k-extinction.

8.3 Theory of inclusive fitness

Darwinian fitness can be achieved through personal reproduction and care (parental care), and **Kin selection.** The term **Kin selection** was originally defined by John Maynard Smith to account the effects of both parental aid given to **descendant Kin (offspring)** and altruism directed to **non-descendant kinds (relatives other than offsprings).** The term **Kin selection** is, however, currently used very widely by biologists as a synonym for altruism directed to close relatives other than offsprings.

Altruism is a self-sacrificing behaviour. When an animal increases fitness of its close relatives at the expense of its own fitness, it can be said to have performed an act of **altruism.** The self-sacrifice for the well being of own offsprings through parental investment is **altruism** in the conventional sense, but not in the strict genetic sense, because individual fitness is measured by the number of surviving offsprings.

The components of selection and fitness have been shown in the following figure.

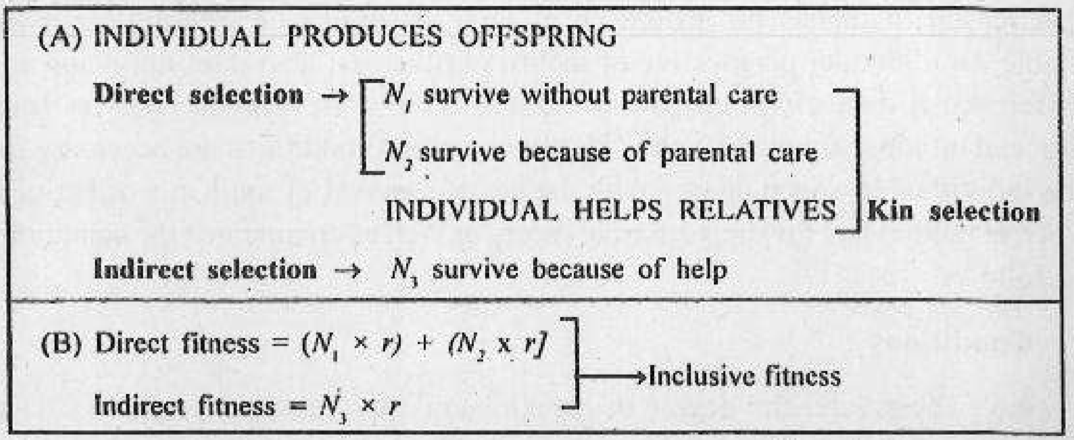


Fig 8.8 : The components of selection and fitness. (A) Direct slection acts on variation in individual reproductive success. Indirect selection acts on variation in the effects individuals have on their relatives' reproductive success, (B) Direct fitness is measured in terms of personal reproductive output, indirect fitness is measured in terms of genetic gains derived by helping relatives reproduce. Inclusive fitness can be considered the sum of the two measures and represents the total genetic contribution of an individual to the next generation (After Brown).

The **direct selection** acts on variation in personal reproductive success. **Indirect selection** acts on variation in the effects individual have on their close relative's reproductive success. **Direct fitness** is measured in terms of personal reproductive output, and **indirect fitness** is measured in terms of genetic gains derived by helping relatives reproduce. **Inclusive fitness** can be considered the sum of the two measures (both direct fitness and indirect fitness), and represents the total genetic contribution of an individual to the next generation through the production **of reproductives** (able offsprings to reproduce).

8.3.1 Kin relection and Hamilton's rules on the evolution of altruism

Usually, alleles of the genes remain in the gene pool of a species. By common ancestry the genes are not found exclusively in the genome of an individual itself, but also in the genomes of their close relatives or kinds with a greater probability. In the case of sexual diploid organisms, half of the genetic traits of the offspring comes from the random meiotic shuffle of the genome of each parent before fertilization. For this reason, each allele possesses an average probability of being found simultaneously in two siblings, which coincides with the probability of being found simultaneously between a parent and each one of its offspring. For this reason, it makes no difference of own offsprings or siblings are made viable. In a broader perspective of inclusive fitness, it also does not make any difference if own offsprings (descendant kins) or offsprings of relatives (non descendant kins) are made viable. However, certain conditions are necessary for the individual to spend energy with the act of survival of the Kin's offsprings. W.D. Hamilton had given us a formal theory as well as enumerated the conditions as follows :

Conditions :

- The greater the degree of genetic similarity between two individuals, the greater the probability that an allele may be shared by two individuals.

- The greater the increase in fitness for the benefited per unit of cost for the performer of the altruist act, the greater the possibility that the gene codifying for this altruistic act will be popagated.

Hamilton's Rule :

Hamilton's rule states that **an altruistic trait can evolve through Kin Selection, if the number of offsprings gained by the recipient of altruistic act, multiplied by the altruist's genetic relatedness to those gained, is greater than the number of offspring lost by the donor of altruist act (which can be achieved by personal reproduction), multiplied by the altruist's relatedness to those lost.**

The entire scheme has been depicted in the following —

- Benefit (b) = $n_1 \times r_1$

  n_1 = number of offsprings of the relative reared by the altruist.

  r_1 = genetic relatedness to the offsprings of the relative.

- Cost (C) = $n_0 r_0$

  n_0 = probable number of offsprings would have been produced by the altruist, if not engaged in the altruistic act.

r_0 = genetic relatedness of the altruist to its own offsprings, if produced.

Rule I

$$\frac{b}{c} > \frac{1}{r}$$

b = benefit to the recipient, C = cost to the donor, r - genetic relatedness between donor and recipient of altruistic act.

This rule is useful to predict when an individual will be selected to sacrifice its own reproductive life to help its relatives.

Rule II

$$n_1 r_1 > n_0 r_0$$

n_1= number of relatives reared,

r_1 = genetic relatedness to relatives.

n_0 = number of offspring reared.

r_0 = relatedness to offsprings.

This rule is useful to predict when a sterile individual who rears relatives will be selected over a fertile individual who rears its own offsprings.

8.3.2 Calculation of the coefficient of relatedness (r)

r is the probability that a gene in one individual is an identical copy, by descent, of a gene in another individual.

Calculation of 'r' in diploid system :

General method

Draw a diagram with the individuals concerned and their common ancestors, indicating the generation links by arrows. At each generation link there is a meiosis and so a 0.5 probability that a copy of a particular gene will get passed on. For L generation links the probability is $(0.5)^L$. To calculate r, sum this value for all possible pathways between the two individuals.

$r = \Sigma\ (0.5)^L$.

Specific examples

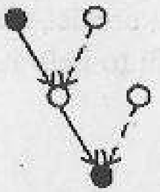
These diagrams show calculations of *r* between two individuals represented by solid circles, other relatives are indicated by open circles. The solid lines are the generation links used in the calculations; the dotted lines are the other links in the pedigrees :

(a) Parent and offspring

$r = 1(0.5)^1$

$= 0.5$

(b) Grandparent and grandchild



$r = 1\ (0.5)^2$

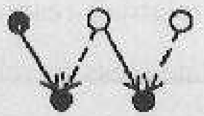
$= 0.25$

(c) Full sibs (brother, sister)

$r = 2\ (0.5)^2$

$= 0.5$

(d) Half-sibs



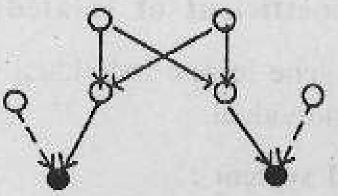
$r = 1\ (0.5)^2$

$= 0.25$

(Identical genes by descent can be inherited by two pathways, either mother or father)

(Identical genes by descent can only be inherited from one parent)

(e) Cousins



$r = 2(0.5)^4 = 0.125$

Table : Coefficients of relatedness (r) for descendant and non-descendant kin in diploid system.

r	**Descendant kin**	**Non-descendant kin**
0.5	Offspring	Full siblings
0.25	Grandchildren	Half-siblings
		Nephews and nieces
0.125	Great-grandchildren	Cousins

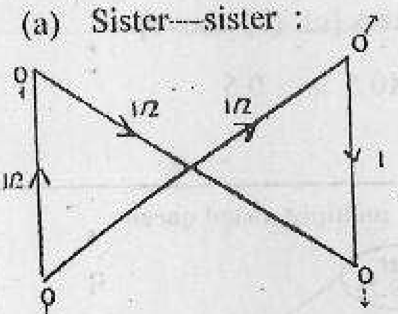
■ *Calculating coefficients of relatedness, r, in haplodiploid system.*

General point : Males develop from unfertilized eggs and so are haploid, ll of a male's sperm are genetically identical so the probability of sharing a copy of gene via the father is 1. Females develop from fertilized eggs and so diploid; the probability of sharing a copy of a gene via the mother is 0.5, because of meiosis.

Method : Draw out a pedigree, linking the two individuals through their recent common ancestors. To determine the coefficient of relatedness between individual A and individual B, draw arrows along the pathways, pointing from A to B. Indicate on each link in the pathway the probability that a copy of a gene will be shared.

Examples :

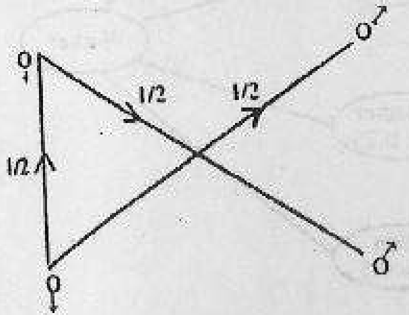
(a) Sister—sister :



Half of a female's genes come from the father; the probability that a copy of one of these is shared with the sister is 1. The other half come from the mother; the probability that a copy of one of these is shared is 0.5.

Via mother = (0.5 x 0.5) + Via father = (0.5 x 1)r = 0.75

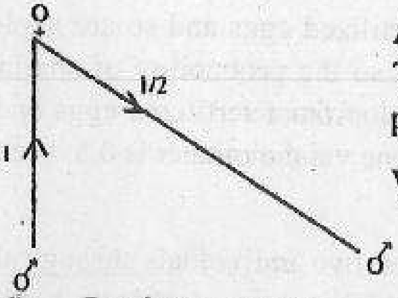
(b) Sister—brother :



A female is linked to her brother only via her mother, as her brother develops from an unfertilized egg. Half of her genes come from her mother; the probability that a copy of one of these is shared is 0.5. The other half come from her father; the probability that a copy of one of these is shared is zero.

Via mother (0.5 x 0,5) + Via father (0.5 x 0)r = 0.25

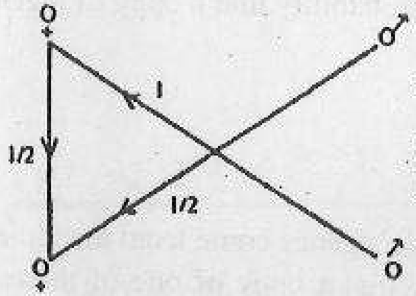
(c) *Brother—brother*



All of male's genes come from his mothe
There is a 0.5 chance of sharing a copy of
particular gene with his brother.

Via mother (1 x 0.5) r = 0.5

(d) *Brother—sister :*



All of a male's genes come form his mothe
There is a 0.5 chance of sharing a copy of
particular gene with his sister.

Note the asymmetry in relatedness betwee
brothers and sisters [cf. (b) above].

Via mother (1 X0.5)r = 0.5

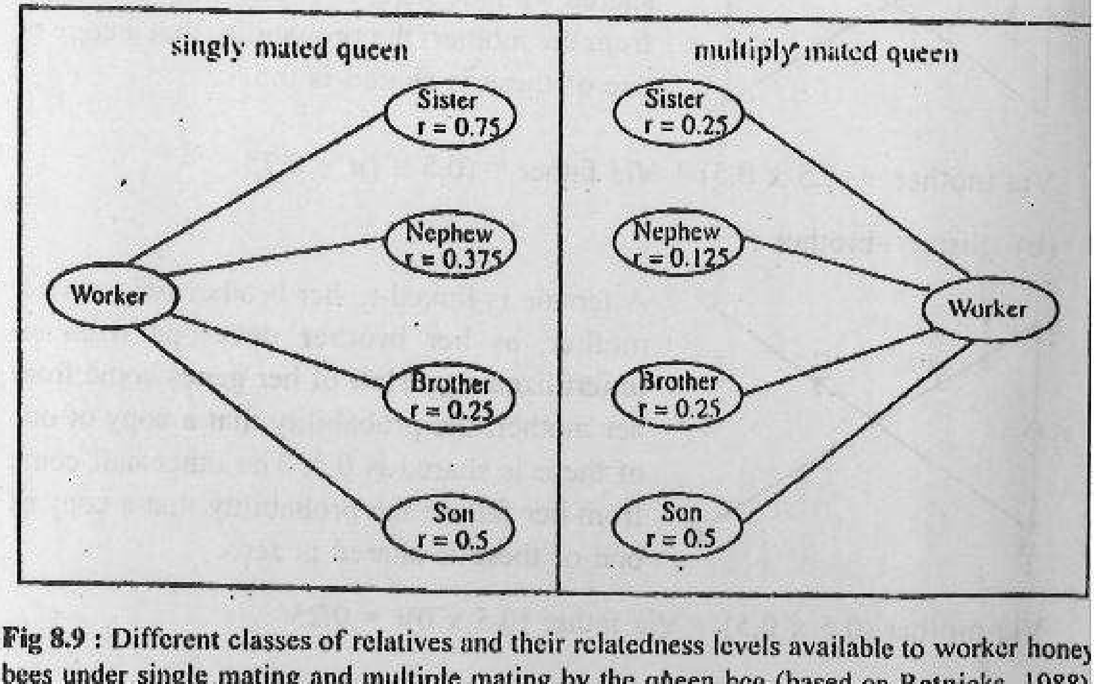


Fig 8.9 : Different classes of relatives and their relatedness levels available to worker hone bees under single mating and multiple mating by the qûeen bee (based on Ratnieks, 1988)

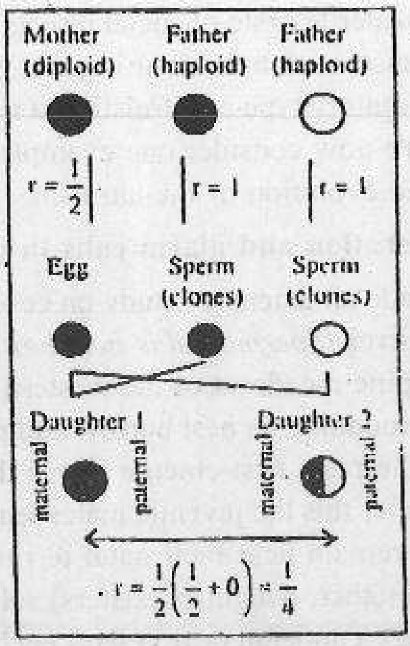


Fig 8.10 : Genetic relatedness under haplodiploidy with multiple matching. Notice that the genetic relatedness between half sisters is 0.25.

Table : Degrees of relatedness between close relatives in a haplodiploid species [(1) in single mating system, (2) multiple mating system]

(1)		Mother	Father	Full-sister	Brother	Son	Daughter	Niece or nephew (via sister)	Half-sisters
	Female	0.5	0.5	0.75	0.25	0.5	0.5	0.375	—
	Male	1	0	0.5	0.5	0	1	0.25	—
(2)	Female	0.5	0.5	—	0.25	0.5	0.5	0.375	0.25
	Male	1	0	—	0.5	0	1	0.25	0.25

8.3.3 Examples of altruism between close relatives

The functions of sterile castes in social insects provide good examples of extreme altruism. The sterile workers are altruistic in another way because they rarely reproduce themselves, but instead help others in the nest (mainly few fertile males and single queen) to produce offsprings.

The act of altruism in sterile caste of social insects is an example of extrem altruistic behaviour, because, such behaviour is genetically and developmentall predetermined. Such obligatory type of altruistic act may or may not follow th rules of kin selection. We now consider one example where kin selection ha been a major force in the evolution of the altruism.

■ Example : Cooperation and alarm calls in ground squirrels

Paul Sherman has made an extensive study on co-operation and alarm call of Belding's ground squirrel *(Spermophilus beldingi), a* diurnal social roden which inhabits the subalpine meadows of the western United States. A femal establishes a territory surrounding its nest burrow and produces a single litter o 3 to 6 young per year. The pups first emerge above the ground at the time o weaning, and then soon after this the juvenile males leave the territory while th juvenile females tend to remain near their natal territory. Sherman found tha closely related females (mother, daughters, sisters) seldom fought for burrow and territories. Indeed they cooperated to defend each other's youngs agains infanticidal members of the same species. Eight percent of all young born wer dragged from their burrows and killed by other non-related ground squirrels Such altruism in form of co-operation among close relatives, in contrast t conflict among unrelated individuals, could be well explained by the theory o kin selection.

The young females who had yet to produce their own young gave alarm call to warn their mother and sisters of the approach of a predator. The alarm caller may suffer a cost for giving the alarm, because they are more likely to b attacked by the predator. Others, however, benefited from the early warning an are more likely to escape.

■ The haplodiploidy hypothesis : the evolution of sterile forms an their altruistic behaviour in social insects

Darwin introduced the idea of natural selection operating at the level of th family rather than of the single organism. If some of the individuals of th family are sterile and yet important to the welfare of fertile relatives, as in th case of honey bees and wasps colonies, selection at the family level is inevitable Here the entire family serving as the unit of selection, and the production o sterile but altruistic offsprings has been adaptive by natural selection.

W. D. Hamilton was the first to fully appreciate the significance of special genetic make up of hymenoptera to form sterile castes. The special feature is haplodiploidy : males develop from unfertilized eggs and are haploid, while females develop from normally fertilized eggs and are therefore diploid. A haploid male forms genetically identical sperms, this means that each of his daughters receives an identical sets of genes to make up half of her total diploid genome. With a diploid father, a daughter would have a 50 percent chance of sharing any particular one of his genes with her sisters, but with a haploid father she is certain to share all of them. The other half of genes come from her diploid mother, so she has a 50 per cent chance of sharing one of her mother's genes with a sister. Now the total degree of genetic relatedness between sisters is 0.5 + (0.5 x 0.5) = 0.75. In other wards, because of haplodiploidy in singly mated system full sisters are more closely related to one another than her parents and offerprings in a normal diploid species. .

Hymenopteran queens are diploid and are therefore related to their sons and daughters by the gentic relatedness value (*r*) of 0.5 only. A female worker can therefore make a greater genetic profit by rearing a reproductive sister (queen), instead of producing her own offsprings becoming fertile. By contrast, in the termites in which both males and females are equally related to their siblings, both sexes may become sterile workers. The cautionary note is that the simple calculations of relatedness hold true only if the colony is formed by a single queen who has mated once. If two workers do not share the same father (half-sisters), they are related by only 0.25. In honey bees, the queen may mate up to 20 times with different males, but the workers are able to discriminate between sister (in real sense, half sisters) that are only related with '*r*' value of 0.25 oly and rear them faithfully.

8.4 Reciprocal altruism

Reciprocal altruism is an altruistic interation between genetically unrelated animals. In this behavioural pattern both participants will gain, if the benefit of an altruistic act to the recipient is greater than the cost of the actor subject to the condition that the altruistic act will be reciprocated at some later date. For example.

A helps B today and then B helps A tomorrow. The problem for its evolution in animals is the possibility of cheating. We will explore the conditions under which reciprocity can be evolutionarily stable by using a simple model called the **Prisoner's Dilemma.**

The **Prisoner's Dilemma Model** : This is an elegant model to illustrate the problems of achieving co-operation in animal societies. Imagine two players in a game who have the choice of cooperating or defeating (being selfish). The payoff matrix is given in the following table with some imaginary numerical values. The values represent the gain in fitness from the interactions.

Imagine a scenario in which two criminals are caught and jailed. The police have good evidence that the men committed a crimes, but they are suspected of a more serious crime. They are questioned separately in different places. Each prisoner has the choice to either cooperate with the other by denying the major crime, or they may defect and accuse the other of the major crime. If both prisoner cooperate (neither acauses the other), the each get a reward R, and pay the penalty only for the minor crime. If both defect (accuse on each other), they each get a punishment, 'P', and have to pay for major crime. If one cooperates and one defects, the defector is set free and gets the best possible reward, T' (the temptation to defect). The prisoner that cooperates when the other defects the sucker's pay off of 'S', because he pays the price for both crimes. The exact values of the pay offs don't matter as long asT > R > P > S, as illustrated in the pay off matrix.

What should a prisoner do? Let us examine it through the analysis of pay off matrix. In a single round of game, player A's best strategy is to defect regardless of what player B does. If player B cooperates, T > R, and if player B defects, P > S. The same logic applies to player B.

Fig 8.11 : The pay off matrix for player A and B in the prisoner's dilemma

	Player B	
Player A	Cooperation	Defection
Cooperation	R = 10	S = 0
Defection	T= 12	P = 2

The imaginary numbers shown are the years saved off of a maximum prison sentence of 12 years (2 years for the minor crime and 10 years for the major crime). The exact values are not important, as long as T > R > P > S.

However, both the players will do worse if they both defect rather than if they both cooperate (R > P). Hence the dilemma. Therefore, players are predicted to defect when they play a single round game even though pay offs are lower than if the cooperated. What happens when individuals play multiple rounds of the game with they same opponents. After conducting an international computer tournament on the problem the best strategy has been ascertained as **"tit-for-tat"**. In this strategies one player cooperates on the first move and than does whatever the other player did on the preceding moves. Axelrod and Hamilton argue that this strategy is evolutionarily stable and that it shows how cooperation based on reciprocity could get started in an asocial group.

Reciprocal altruism is most likely to evolve if—

(i) Doner must be able to recognize cheats, and refuse to feed previous recipients who fail to reciprocate.

(ii) Sufficient repeated pairwise interactions so that there are interchanges of role and therefore net benefits to all donors.

(iii) The benefit of receiving aid must outweigh the cost of donating it.

❑ Example of reciprocal altruism: regurgitation of blood by vampire bats

Wilkinson (1984) studied a population of individually marked vampire bats *(Desmodus rotimdus)*, in Costa Rica. Bats quite often failed to obtain a blood meal during the night and they then begged for blood meal from other roost mates in the day time. In an experiment, it was found that 5 out of 8 bats captured in the evening before feeding and released into the roosts at dawn were subsequently given blood by a well-fed individual in the roost. By contrast, none of 6 bats captured and released after feeding successfully were given a blood meal.

Wilkinson discovered that regurgitation occurred only between close relatives or between unrelated individuals who were perennial roost mates. Such reciprocity has got a evolutionarily stable status as it fulfills all the aforesaid conditions for evolution of reciprocal altruism.

8.5 Social organization in insects

The truly social insects or eusocial insects include all of the ants, termites, and more highly organized bees and waspes. These eusocial insects must include the following traits :

(1) Individuals of the same species cooperate in caring for the young (broods).

(2) There is a reproductive division of labour, with more or less sterile individuals working on behalf of fecund nestmates.

(3) There is an overlap of at least two generations in life stages capable of contributing to colony labour, so that offsprings assist parents during some periods of their life.

These are the qualities by which we can define **eusociality.** The social evolution has been shown in the following table. In the **parasocial** sequence, adults belonging to the same generation assist one another to varying degrees. At the lowest level, they may be called **communal,** which means that they cooperate in constructing a nest but rear their brood separately.

Table : The degrees of sociality in the insects, showing intermediate parasocial and subsocial states that can lead to the highest (eusocial) form of organization.

	Qualities of sociality		
Degrees of sociality	**Cooperative brood care**	**Reproductive castes**	**Overlap between generations**
Parasocial sequence			
Solitary	—	—	—
Communal	—	—	—
Quasisocial	+	—	—
Semisocial	+	+	—
Eusocial	+	+	+
Subsocial sequence			
Solitary	—	—	—
Primitively subsocial	—	—	—
Intermediate subsocial I	—	—	+
Intermediate subsocial II	+	—	+
Eusocial	+	+	+

The next level is quasisocial. in which brood are attended cooperatively, but each female still lays eggs at some time of her life. In the **semisocial state,** quasisocial cooperation is enhanced by the addition of a true worker caste, in other words, some members of the colony never attempt to reproduce. Finally, when semisocial colonies persist long enough for members of two or more generations to overlap and to cooperate, the three basic qualities are complete, and such species are referred as eusocial species (or colony). Once a species has crossed the threshold of eusociality, there are two complementary means by which it can advance in colonial organization : through the increase in numbers and degree of specialization of the worker castes, and through the improvement of communication system by which colony members coordinate their activities.

■ Why is eusociality so prevalent in the hymenoptera?

Hamilton proposed a hypothesis known as haplodiploidy hypothesis in favour of the Explanation of eusociality in hymenopteran insects.

The Haplodiploidy hypothesis :

William Hamilton noted that hymenoptera have an unusual genetic system called haplodiploidy and argued that this predisposes them to eusociality.

Background on haplodiploidy :

- Males are haploid (one X chromosome) and develop from unfertilized eggs.
- Females are diploid (two X chromosomes) and develop from fertilized eggs.

→ As a result of haplodiploidy, females are more closely related to their sisters (full-sibs) than they are to their own offspring.

Summary of relatedness under haplodiploidy	**Female**	→	**Sister**	$r = 3/4$
	Female	→	**Daughter**	$r = 1/2$
	Female	→	**Son**	$r = 1/2$
	Female	→	**Brother**	$r = 1/4$

The Haplodiploidy Hypothesis States :

Females will maximize their inclusive fitness by giving up their direct fitness (production of their own offspring) in favor of investments in indirect fitness (production of sisters).

- In other words, in haplodiploid organisms a female's alleles will increase faster in the population when she invests in the production of sisters rather than her own offspring!

■ **Testing the haplodiploidy hypothesis :**

Sundstrom and co-workers determined the sex ratio of reproductive offspring in the wood ant, *Formica exsecta.*

- They found that queens laid a roughly equal number of male and female eggs but that sex ratios were heavily female-biased at hatching.
- They hypothesized that workers (all female) are able to determine the sex of eggs and that they selectively destroy male offspring.

→ In general, female'-biased sex allocation is widespread in eusocial Hymenoptera, indicating that haplodiploidy has a strong effect on how workers behave.

Question : Is haplodiploidy the reason why so many hymenopterans are eusocial?

■ **The haplodiploidy hypothesis and Sex Ratio evolution :**

- Queens are equally related to their sons and daughters, $r = 1/2$, and should invest equally in both.

  —Predict queens to favor 1 : 1 sex ratio of reproductive offspring,
- Female siblings (full-sibs) are related to sisters at $r = 3/4$ and to brothers at $r = 1/4$.

  —Predict female workers to favor a 3 : 1 female biased sex ratio of reproductive offspring.

→ The fitness interest of queens and workers are not the same!

Question : Do queens or workers control the sex ratio of reproductive offspring?

■ **Does the hapiodipioidy hypothesis explain eusociality?**

- Researchers used to believe that the answer was yes.

- Now most researchers conclude that the answer is no.

  → We will consider three reasons why not...

■ Why haplodipioidy doesn't explain eusociality

1. The prediction that workers favor the production of sisters over their own offspring assumes relatedness between sisters, $r = 3/4$, is greater than between mother and offspring, r - 1/2.

- These relatedness values assume that all workers in a colony have the same father and so are full-sibs.

In many species, however, this is apparently not true—

- For example, in the honey bee a queen mates an average of 17.25 times before founding a colony.

- With so many fathers, relatedness among workers is often $r = 1/3$, less than $r = 1/2$ for mothers / offspring.

■ **Why haplodiploidy doesn't explain eusociality**

2. In many species, there is more than one queen per nest.

- For example, in invasive populations of the red fire ant, *Solenopsisinvicta*, colonies typically have multiple queens.

- Why haplodiploidy doesn't explain eusociality

3a. Many eusocial species are not haplodiploid, example termite, naked mole rats.

3b. Many haplodiploid hymenoptera are not eusocial, example, Pompilidae, mutilidae.

Table : Primitive (or at least relatively simple) social traits in *Bombus* compared with the more advanced traits found in the highest social bees, the honey bees of the genus *Apis* and the stingless bees of the tribe meliponini. (From Wilson, 1971).

Bombus	***Apis and Meliponini***
1. Queens and workers differ morphologically to a slight degree, and intermediates are common.	1. Queens and workers are morphologically very different from each other, and intercastes are normally absent.
2. The life cycle is annual, at least among the majority of species; new colonies are founded by single queens, and the mature colony size is small.	2. The life cycle is perennial, new colonies are started by swarming, and colony size is moderate to very large.
3. The queen maintains reproductive dominance by aggressive behavior, and the workers tend to behave toward one another in the same way. Workers. Occasionally steal eggs from one another and the queen.	3. The queen maintains reproductive dominance by pheromones, at least in *Apis*, and aggressive behavior is muted or absent. Egg stealing is unknown except as a ritual form of eating by the meliponine queens.
4. The larvae are often reared in groups and must compete with other larvae for food placed indiscriminately in their vicinity.	4. The larvae are reared in separate cells on the brood comb, which greatly increases the chances for individual attention on the part of the nurses and control of caste determination.
5. The larvae are fed with raw pollen and regurgitated mixtures of pollen and honey.	5. In *Apis*, larvae are fed at least in part with special food manufactured by the mandibular and pharyngeal glands.
6. The adults rarely regurgitate food directly to other adults or try to groom them.	6. Both grooming and direct transfer of food by regurgitation are very frequent and, in the case of *Apis* at least, known to play an important role in communication and regulation.
7. The queen regulates colony growth by building all of the egg cells herself and laying in them, following the same behavior patterns by which she initiates the colony.	7. The queen plays no direct role in colony growth or in the construction of the brood combs. The workers determine these matters and are subject to much more feedback from the environment outside the nest.
8. Temporal division of labor is weakly developed.	8. A temporal division of labor is strongly developed, in which the young adult worker first engages in brood care (or nest work), then nest work (or brood care), and finally in foraging in *Apis*, at least, this progression is associated with orderly changes in the exocrine glands.
9. Chemical alarm communication is lacking.	9. Chemical alarm communication is well developed and involves pheromones apparently especially evolved for the purpose.
10. Recruitment among workers is lacking.	10. Recruitment is well developed and mediated by special assembling or trail pheromones, in Apis there is also a symbolic waggle dance.

Table : Basic similarities and differences in social biology between termites and higher social hymenoptera (wasps, ants, bees), Similarities are due to evolutionary convergence. (From Wilson, 1971).

Similarities	Differences	
	Termites	Eusocial Hymenoptera
1. The castes are similar in number and kind, especially between termites and ants.	1. Caste determination in the lower termites is based primarily on pheromones, in some of the higher termites it involves sex, but the other factors remain unidentified.	1. Caste determination is based primarily on nutrition, although pheromones play a role in some cases.
2. Trophallaxis occurs and is an important mechanism in social regulation.	2. The worker castes consist of both females and males.	2. The worker castes consist of females only.
3. Chemical trails are used in recruitment as in the ants, and the behavior of trail laying and following is closely similar.	3. Larvae and nymphs contribute to colony labor, at least in later instars.	3. The immature stages (larvae and pupae) are helpless and almost never contribute to colony labor.
4. Inhibitory caste pheromones are similary in action to those found in honeybees and ants.	4. There are no dominance hierarchies among individuals in the same colonies.	4. Dominance hierarchies are commonplace, but not universal.
5. Grooming between indiduals occurs frequently and functions at least partially in the transmission of pheromones.	5. Social parasitism between species is almost wholly absent.	5. Social parasitism between species is common and Widespread.
6. Nest odor and territoriality are of general occurrence.	6. Exchange of liquid anal food occurs universally in the lower termites, and trophic eggs are unknown.	6. Anal trophallaxis is rare, but trophic eggs are exchanged in many species of bees and ants.
7. Nest structure is of comparable complexity and, in a few members of the Termitidae (e.g., *Apicotermes, Macrotermes),* of considerably greater complexity. Regulation of temperature and humidity within the nest operates at about the same level of precision.	7. The primary reproductive male (the "king") stays with the queen after the nuptial flight, helps her construct the first nest, and fertilizes her intermittently as the colony develops; fertilization does not occur during the nuptial	7. The male fertilizes the queen during the nuptial flight and dies soon afterward without
8. Cannibalism is widespread in both groups (.but not universal,		

8.6 Primate social organizations

In 1932 Solly Zuckerman proposed in "The Social Life of Monkeys and Apes" that the binding force of primates society is sexual attraction. He believed that the uninterrupted sexual life of monkeys, apes and man is the prime force of social organization in primates. Zuckerman's theory is proved wrong. It was disproved by the field studies of primate biology that began to flourish in the late 1950's. The primates have been found to possess distinct breeding seasons. Many of the fine details of social interaction have proved not associated with the reproductive behaviour. The nonsexual phenomena associated with the social organization of primates are (i) presence or absence of territory, (ii) the strategy of defense against predators, (iii) level of intelligence due to large size of brain etc. The scheme presented in the Figure 8.12 postulates certain basic primate qualities to be evolutionary prime mover of social organization.

The basic systems of mammalian reproduction and heredity are ultraconservative. Consequently the reproductive and genetic systems are inertial in their effects.

There is a tendency for males to be polygynous and aggressive toward one another, although pair bonding and pacific associations are permissible. Where long term sexual alliances are not the rule, the strongest and most enduring bonds are between the mother and her offerprings, to an extent that the **matrilinies** can be said to be the heart of the society. Mothers are the principal socializing force in early life. Their influence may even extend to later generations. The second class of ultimate determinants of primate social behaviour consists of the basic **postadaptive traits.** The vast majority of arboreal animals (insects to squirrels) are small and have no difficulty moving through the canopies of trees. However, most primates are unusual in being large arboreal animals. The physiological consequence of this adaptive trait are supportive toward social organization. Being large size arboreal and diurnal they possess the following adaptive features :

(1) Increased manipulative skill and improved vision have increased the level of intelligence.

(2) Greater reliance on visual and auditory communication and reduction of chemical communication are contributory toward increased repertory and composited form of graded signals.

The aforesaid adaptive features consequently result into :

(1) Prolonged socialization and increased in complexity.

(2) Behavioural flexibility, and more variable social organization.

(3) Conducive alliances and complex social strategies.

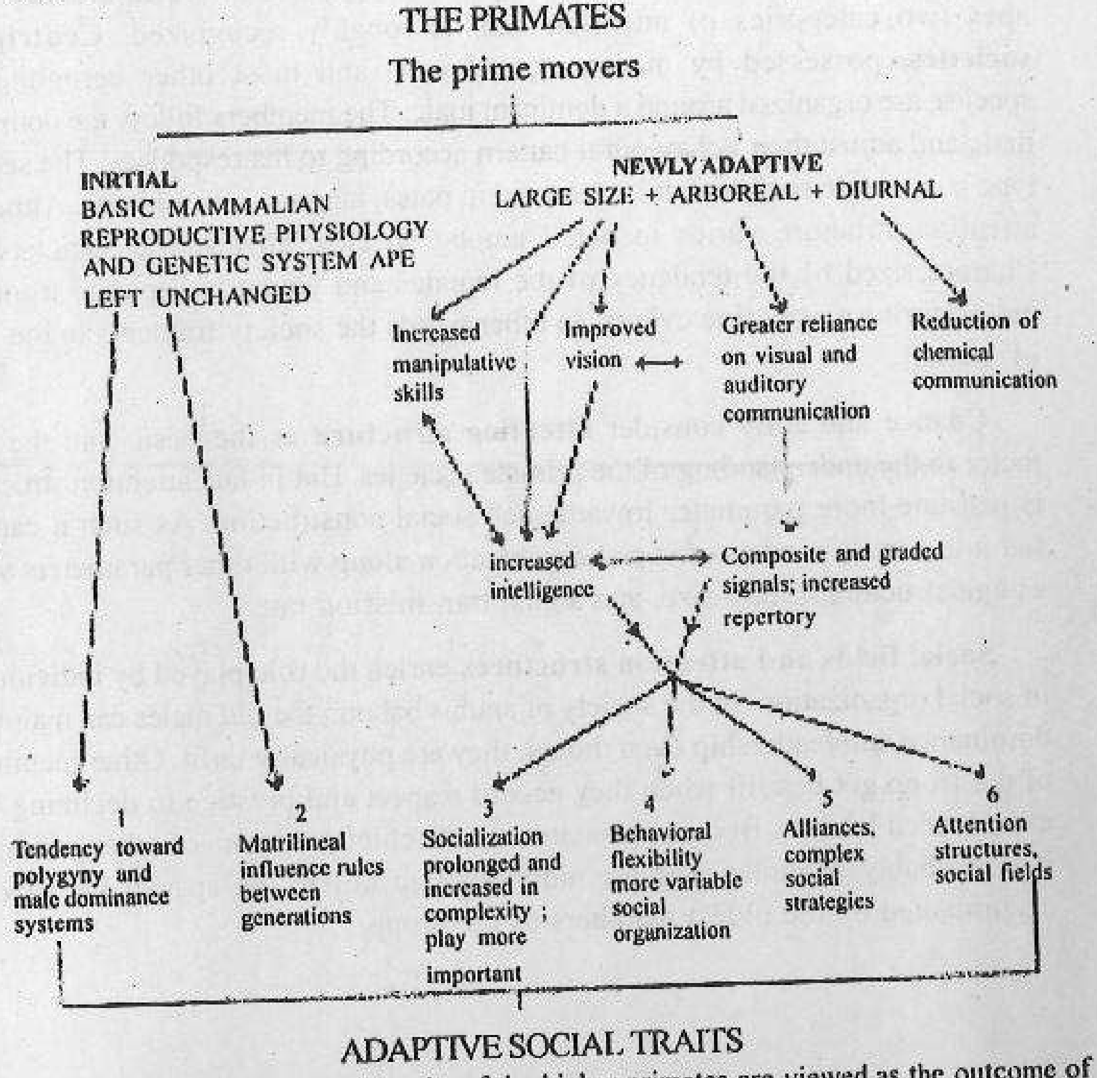


Fig 8.12 : The distinctive social traits of the higher primates are viewed as the outcome of conservative mammalian qualities ("inertial" forces) and adaptation to arboreal life. Even phyletic lines that are now terrestrial have retained the evolutionary advances made by their arboreal ancestors.

In addition to the aforesaid adaptive features of social organization, the primates can evaluate the behaviour of many individuals within the society simultaneously. The animal lives in a **social field** in which it responds to multiple individuals simultaneously. Chance (1967) and Chance and Jolly (1970) have conceptualized the organization of individual social field in terms of the **attention structures** of whole societies. Among the species of Old World monkeys and apes two categories of attention can be roughly recognized. **Centripetal societies,** possessed by macaques, baboons, and most other ceropithecoid species, are organized around a dominant male. The members follow the dominant male and adjust their behavioural pattern according to his responses. The second type is **acentric societies,** it is observed in pates, langurs, and gibbons. Although attention structure varies in detail among species, all acentric societies are Characterized by the tendency of the females and young to separate from the males during aggressive events. In other words the society framents in the face of crisis.

Chance and Jolly consider **attention structure** as the basic and the key factor to the understanding of the primate societies. But in fact attention structure is just one more parameter toward such social construction. As such it can be fed into certain models of social organization along with other parameters such as age structure, group size, and signal transmission rate.

Social fields and attention structures enrich the role played by individuals in social organization. In the society of anubis baboon the old males can maintain dominance and leadership even though they are physically unfit. Other members of the troop get benefit when they accord respect and prestige to declining but experienced leaders. Because primates are the chief predators of other primates, it is probably advantageous for individuals to utilize the special knowledge accumulated by the oldest members of the group.

Unit 9 ☐ Reproductive Behaviour

Structure

9.0 Introduction

Reproduction and its related behavioural traits create a environment of social interactions. Especially, the mode of sexual reproduction results conflict and competition among individuals of a particular species. In this chapter the important components of sex and reproductive strategies will be discussed along with their related functions like sexual selection, courtship, parental care etc.

9.1 Definition and types of sexual reproduction

Sexual reproduction always involves free haploid gametes, on the contrary asexual reproduction is always agametic phenomenon. Sexual reproduction, in turn can be classified as biparental panmixis reproducing diploid type of organism by means of fertilization or fusion of male and female gametes, and uniparental parthenogenesis-producing haploid organism by means of a single female gamete. In the most micro-organisms, fungi and algae the sexes are anatomically similar and the gametes are all of the same size called **isogamy.** I higher sexual organisms one sex produces few large, sessile, less energeticall and developmentally active gamete, called female gamete or ovum. On the contrar other sex produces many relatively small, motile, energetically cheap gamete— called male gamete or sperm. This difference in gamete size, called **anisogamy** Both the male and female gamete producing organs or gonads may be present i the same organism, called **monoecious or hermaphrodite,** or with separat male and female individuals, called **diecious or gonochoris.** Hermaphrodit animals (e.g. snails) may develop both the male and female gonads anatomicall simultaneously but functionally either maleness or femaleness at a time, sinc they perform cross fertilization. On the other hand some hermaphroditism i sequential in which case first one sexual function appears then the other. Whe male sex is followed by the female sex in the same individual, it is calle **protoandrous** (e.g. some echinoderms), and when female sex is followed b male sex sequentially in the same individual, it is called **protogynous** (e.g. some fishes—coral reef fish *Anthias squamipinnis*). Parthenogenesis is a specia type of sexual reproduction, in which organism develops with a definite sex from an unfertilized female gamete. When haploid males are developed by parthenogenesis, it is called **arrhenotoky** (e.g. gamasid mites, honey bee). On the contrary, when haploid females are formed, it is called **thelytoky** (e.g. oribatid mites).

9.2 Evolution of sex

Every thing evolving in the biological world must have a good adaptive value in time and space, otherwise it will be simply washed out in due course of time. The adaptive value of a strategy is determined by estimating its costs and benefits in terms of **Darwinian fitness or reproductive fitness.** Now, let us discuss— why is sexual reproductive strategy so wide spread? The cost of sexual reproductive strategy should be compared with the asexual reproductive strategy. Comparison is given as follow:

Cost

Asexual reproductive strategy	Sexual reproductive strategy
(1) One organism maximizes its genetic contribution to offsprings by creating cloning of itself.	(1) Genotypes are broken up at meiosis and the genes combined with those of the another individual during fertilization. This results 50% reduction in transmission of genes to the next generation, which is known as **cost of meiosis.**
(2) One offspring is sufficient to pass the same number of genes to the next generation.	(2) A female would have to produce two sexual offsprings to pass the same number of genes to the next generation.
(3) The cost of courtship and mating is nil.	(3) The cost of courtship and mating is high-energy consuming.
(4) The cost of producing male is absent.	(4) The cost of producing male is high. Since, most of the sperms are useless, and some of the males never even fertilize single egg, from this point of view males waste resources.

Benefits of sexual reproductive strategy :

Going through the aforesaid comparison one might expect that asexual species will replace the sexually reproducing organisms, instead of, the real picture is reverse. So, let us. discuss the possible benefits of sexual strategies over asexual strategies in favour of evaluation of sexually reproducing organisms.

Benefits of sexually reproducing organisms :

(1) **Faster evolution** : Fisher (1958) first pointed out that sexually reproducing organisms can evolve faster in heterogenous changing habitat. Since the rate of evolution is the function of the degree of genetic variations through genetic recombination and mutations in sexually reproducing organisms such variations are produced.

(2) **Muller's ratchet** : A second advantage was noted by Muller (1964) and

known as **Muller's ratchet.** In asexually reproducing organisms if there is deleterious mutation, it will be transmitted to all its offsprings. Only this type of mutation can be edited out by means of **reverse mutation,** which is an unlikeh event. Thus the ratchet turns on notch each time a deleterious mutation occurs, and such mutations accumulate in the population. On the contrary, in sexual organisms recombinations between two individual with different mutations could produce offsprings with neither mutation. In this way the harmful mutation can be edited out of the population. It is evident from the aforesaid discussion that the **faster evolution and elimination of mutation** from the **gene pool** of a population are the main advantages of sexual reproduction.

9.3 Evolution of differences in sex roles

The differences in sex and sex role are the major characteristic features of sexually reproducing organisms. The sexual dimorphism in the form of male and, female sexes and their corresponding features can be tabulated as follow :

Male	Female
(1) Males are those individuals that produce the smaller, motile male gametes,, usually no more than a set of genes in a package. Just large enough to contain the energy needed to drive the male's DNA to an egg.	(1) Females are the sex that produces larger gametes. The eggs are non-motile in nature.
(2) Male gametes are good at fertilizing female gametes, having good fertilizing devices.	(2) Gametes developed better after being fertilized having good developmental devices.
(3) In general, males make less **parental** investment than famale.	(3) Usually, females make larger parental investment than male.

The difference between the sexes in respect to size and function of the gametes each donates to an offspring can be expressed as a difference in **parental investment.** Robert L. Trivers invented this term to emphasize the trade-offs for parents that make contributions to offspring. **Parental investment includes time, energy and risks**

that a parent invests in one or a **clutch of offsprings that reduces the chances that the parent will have more offsprings in the future.** On the plus side, parental investment may increase the probability that an existing offspring will survive to reproduce. But this fitness benefit may come at the cost of the parent's ability to generate prospective additional offsprings in the future.

This is to be noted, that this **theory of parental investment** is applicable solely to **iteroparous organisms,** (Those that have their young at intervals throughout the breeding life. Such as birds, mammals etc.). On the other hand this theory can not be applied to **semelparous breeders,** those that have their offsprings all at once in the whole life. Such as semelparous insects (Butterfly, Moths), fishes like salmon.

Primary sex ratio : The sex ratio at the time of fertilization of female gametes is called **primary sex ratio.**

Secondary sex ratio : The sex ratio at the time of birth or hatching is referred to as **secondary sex ratio. The primary and secondary sex ratio always approximizes 1:1.**

Operational sex ratio : The sex ratio available at the time of mating is referred to as **operational sex ratio.** The operational sex ratio may deviate from **primary and secondary sex ratio.**

This deviation from 1 : 1 ratio can have large impact on the mating system, since members of the abundant sex will compete for access to the scarcer sex.

Reasons for shift in operational sex ratio :

The probable causes for change of sex ratio from primary equal ratio (1 : 1) to an uequal operational sex ratio, may be as follows.

- **Physiological cause** : Owing to differential immune system in sexes, one sex may be proned to some sex specific microbial diseases than other. This type of immunological aspect may result into the change of sex ratio. In mammals, sometimes it may cause such shift of sex ratio.

- **Behavioural cause** : Sex biased infanticide, siblicide are more important behavioural cause of sex ratio change. In primates and carnivorous mammals' (Lion, Cat) male infanticide by intruder males affect the sex ratio. In honey bee male siblicide also responsible for such change.

Manipulation by parent :

In bees and wasps, especially in honey bee, the queen can manipulate the se ratio by manipulating the fertilization of female gametes. The queen mates with several male and reserves sperms in its 'sperm pocket' or **spermatheca.** At the tim of egg laying in brood cells it can release sperm and fertilize some eggs producing diploid females and haploid males parthenogenetically.

Temperature and sex ratio : In some species, sex determination is temperatun dependent. In reptiles, ambient temperature influences the sex ratio. The red eared slider turtle *Trachemys scripta* eggs when incubated at 20°C-29°C, they produce maximum males.

Dispersal and sex ratio : The dispersion of one sex-group from its **natal place** may affect the sex ratio locally. Among birds, usually females are the main dispersers and males are **philopartic** i.e., remain confined to their natal place.

On contrary, males are the main dispersers in mammals (e.g. all male herd of lions and elephants). So, due to sex biased dispersion the sex ratio of local population may be male dominated or female dominated.

- **Local mate competition and sex ratio :**

The parasitoid wasp *Nasonia vitripennis,* lays eggs in the pupal stage of blow fly. Developing wasps feed on the pupa, and the developed flightless males mate with the females developed from the natal clutch. Since, male sibs try to mate with the same sisters, it is called **local mate competetion.** From evolutionary point of view, the breeding system among close relatives makes little sense, because this lowers inclusive fitness. In such situation the operational sex ratio is female biased.

- **Maternal health or Bateman gradient and sex ratio :**

According to a model based on maternal health condition proposed by Trivers and Willard (1973) called Bateman gradient sets the stage for possible deviation from 1 : 1 sex ratio. The model assumes the mothers in the best physical condition produce healthier offsprings that are more able to compete for mates and other resources. For example, male Antarctic fur seal pups are heavier, grow faster and weigh more at 60 days than their sisters. Trivers and Willard (1973) argue that reproductive success of male offsprings should be high if their mothers are in good health, but low, perhaps zero, if their mothers are in poor shape.

9.4 Mating systems

The male biased or female biased operational sex ratio may set the stage for different types of adaptive mating systems as reproductive strategies. The different types of mating strategies can be tabulated as follows.

Mating systems	Characteristics
(1) Monogamy	(1) It refers to bond during mating between one male and one female at a time. Neither sex is able to monopolize more than one member of the opposite sex.
(2) Polygamy	(2) It incorporates all multiple-mating and **nonmonogamous** mating systems.
(3) Polygyny	(3) It refers to bond between one male and more than one females in single breeding period.
(4) Polyandry	(4) It refers to bond between one female and more than one male at a time.
(5) Promiscuity	(5) It refers to the absence of any prolonged bond and to multiple mating by at least one sex.

- **Monogamy and its adaptive value :**

When the habitat contains scattered ecological resources or scarce nest sites, monogamy is the most likely strategy. The formation of long term pairing also seems advantageous, because less time is needed to spend finding a mate during each breeding season. Long-lived birds, such as sea gulls that breed with former mates have higher reproductive success. Probably because of less aggression between rival mates and better synchronization of sexual behaviour.

- **Polygyny and its adaptive value :**

The males usually during their breeding season can produce sperm continuously, which is an astronomically large figure. Owing to such physiological potential, one male can fertilize several egg clutches in different breeding females. This type of polygynous strategy may be practised at the availability of frequent females. The polygamy may be of the following types :

(1) Resource-defense polygyny :

Males defend areas containing the feeding and nesting sites important for reproduction, and a female's choice of a mate is influenced by the quality of the male and its resource of the territory.

Thus, some males with good territorial resource may get two or more mates while others get none. For example, male walnut flies defend sites that are used by females to lay eggs.

(2) Female-defense polygyny :

It occurs when females are gregarious for reasons unrelated to reproduction. Some males, monopolize females and exclude other males from their **harems.** In many species of seals, the females gather on a particular site to give birth, and they mate soon after. The females are gregarious because there are a limited number of suitable breeding sites, and the male monopolize the females for breeding.

(3) Male-dominance polygyny :

If males are not involved in parental care, and have little opportunity to control resources or mates, **male dominance** polygyny may occur. If female movements or their areas of concentration are predictable, the males may concentrate in these areas advertise their quality and courtship signals. These areas where males congregate and defend small territories in order to attract and court females are called **lek**. For example, the males of baya weaver birds *(Ploceus phillipinus)* congregate on tree and display their quality through the well formed nests in order to attract prospective mates.

(4) Scramble polygyny :

In this case, male actively search for mates without overt competition. Female wood frogs *(Rana sylvatica)* congregate in small temporary ponds, often during a single night in early spring. Large number of males rush about attempting to mate with fecund females, sometimes dislodging weaker, already mating males.

Polyandry : In polyandrous systems, females control access to more than one male. Because female investment in eggs exceeds that of males in sperm. The lionesses are polyandrous, because paternity uncertainty may protect the cubs from infanticide by the adult males of the pride. The honey bee queen is polyandrous, and collects large number of sperms in her spermatheca from several males to fertilize large number of eggs. In honey bee society, usually drones/males die after mating and sperm transfer, but queen/fertile female is long-lived and iteroparous in breeding habit.

9.5 Courtship mating behaviour

The courtship refers to the behavioural interaction between male and female usually before the act of mating. **De Morris** defined courtship as the heterosexual **communication system leading to consummatory sexual act. It is often called species stereotyped and instinctive in nature.**

Varied activities forms a part of the courtship behaviour and has a specific function in form of display. One of the most important functions of displays is to attract and bring potential mates at the right time in order to mate. Once a male and female have come together, the male commonly displays and his behavioural pattern may make female sexually receptive.

The success of courtship depends on the fulfillment of four major functions :

(1) Mate finding (2) Persuation (3) Synchronization and (4) Reproductive isolation.

(1) **Mate finding :** In animals mate finding is a highly organised process, which involves one or more of the channels of communication such as olfactory, optic, auditory and tactile devices. In birds, specific calls and songs are helpful in mate finding. In insects, pheromone related chemical interactions are useful in attracting their mates. Fire flies and many of the deep-sea dwelling animals could detect their mates by means of specific light of light producing organ.

(2) **Persuation** : In some group, meeting of male and female leads almost immediately to mating. But in other groups after locating a potential mate, the next hurdle for the male is to bring the female in proximity and make her sexually receptive. In some cases, the female attacks the male and eats him (e.g. some mantis spiders). In these case, male courtship behaviour may serve not only to stimulate the female sexually receptive but also to suppress her non-sexual trophic behaviour.

(3) **Synchronization** : The occurrence of a same motivation in different individuals at the same time leading to a specific interactive behaviour is called synchronization. Precise synchronization of male and female courtship behaviour is most important factor in reproduction.

(4) **Reproductive isolation** : The correct and precise follow-up of the process of mate finding, persuation and synchronization results reproductive isolation, which preserves the species uniqueness.

◆ **Some examples of courtship :**

(1) Courtship and mating behaviour of *Drosophila sp* :

Mating behaviour *of Drosophila* consists of species specific fixed action pattern. Such patterns are known as courtship displays and involve a number of elements or signals which are performed sequentially. The visually observable courtship signals and orientation movements of both sexes are performed by specific movement of body.

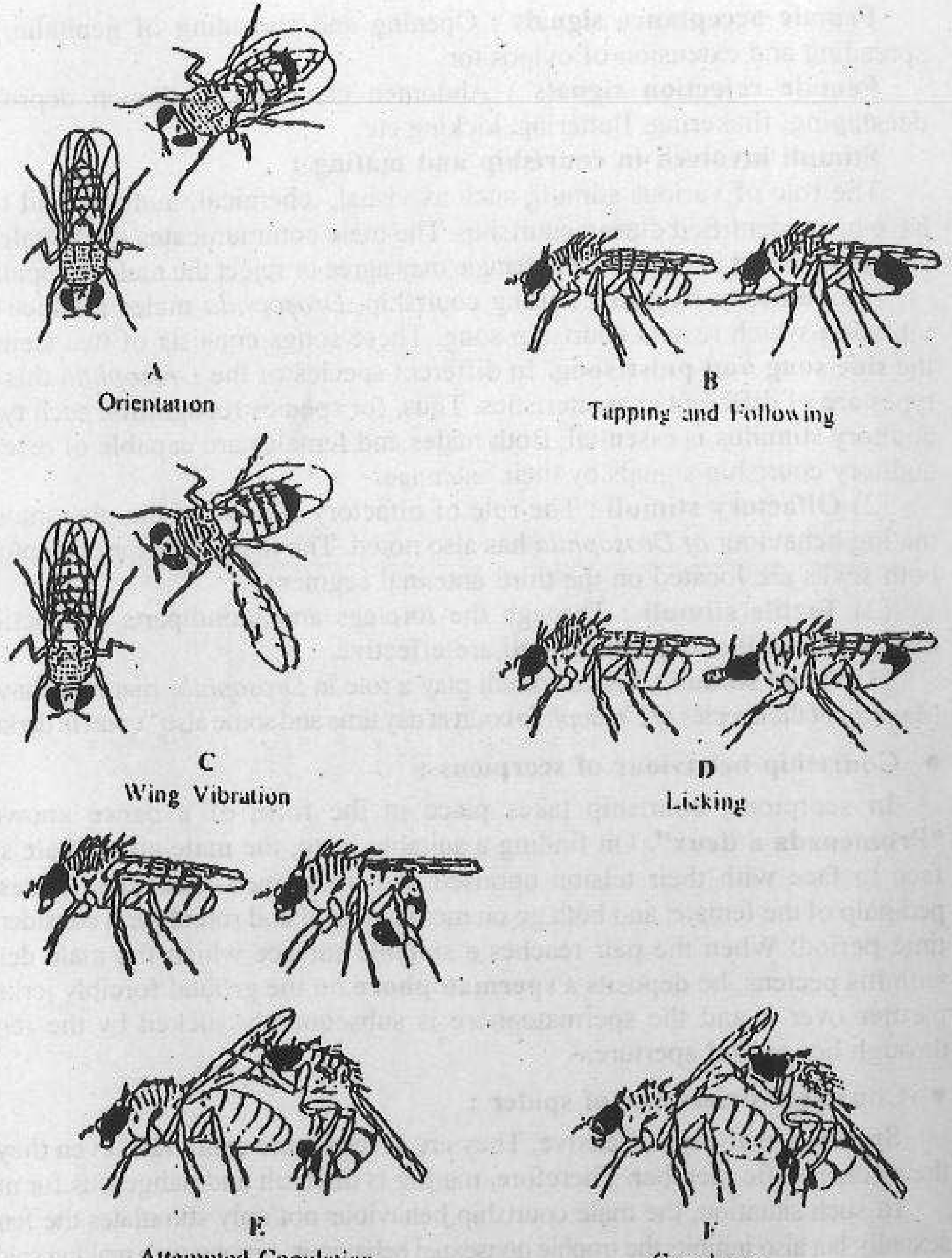
Courtship behaviours that normal sexually mature male performs in response to virgin female.

Male actions are of two types :

(1) Male to male encounter and (2) male to female encounter. In most of the cases, **the forelegs, wings, mouthparts of the male serve as signalling structures.** The female signals are more limited as compared to those of the male and are produced by the **wings, legs, genitalia and movement of the abdomen.** Females perform these signals into two phases : rejection phase and acceptance phase. During courtship, the orientation movement can be described as follows.

The male initially moves to face the prospective mate and turns toward abdomen of the mate and usually taps the abdomen of the mate. Copulation occurs only if the female responds by displaying acceptance signals. The male positions to the genitalia of the female when she shows readiness for copulation. The male mounts and copulates by curling the tip of the abdomen underwards, simultaneously lunging upwards, and forward pushing his head under or between the female's wings (Fig. 1). Near the end of copulatory phase, the female kicks vigorously backward with her hind legs against the face and thorax of the male. The male withdraws and detached away from the female, falls inertly to the substratum and remains inactive for a short period.

Male courtship elements : Tapping, wing flicking, wing fluttering, wing scissoring, wing vibration, leg vibration and licking.



A
Orientation

B
Tapping and Following

C
Wing Vibration

D
Licking

E
Attempted Copulation

F
Copulation

Fig .1. Different Stages of courtship behaviour in *Drosophila*.

Female acceptance signals : Opening and spreading of genitalia, wing spreading and extension of ovipositor.

Female rejection signals : Abdomen elevation, abdomen depression, decamping, flickering, fluttering, kicking etc.

Stimuli involved in courtship and mating :

The role of various stimuli, such as visual, chemical, auditory and tactile have been identified during courtship. The male communicates the female with such stimuli and in response the female may agree or reject the male in copulation.

(1) **Auditory stimuli** : During courtship, *Drosophila* males produce wing vibration which results courtship song. These songs consists of two elements, the **sine song and pulse song.** In different species of the *Drosophila* this song types are of different characteristics. Thus, for species recognition such type of auditory stimulus is essential. Both males and females are capable of receiving auditory courtship signals by their antennae.

(2) **Olfactory stimuli** : The role of olfactory stimuli of the pheromone in mating behaviour *of Drosophila* has also noted. The main olfactory receptors of both sexes are located on the third antennal segment.

(3) **Tactile stimuli** : Through the forelegs and mouthparts the tactile or mechanostimuli and chemostimuli are effective.

(4) **Visual stimuli** : Visual stimuli play a role in *Drosophila* mating behaviour. Majority of the species *of Drosophila* court at day time and some also "court in darkness.

- **Courtship behaviour of scorpions :**

In scorpions, courtship takes place in the form of a dance known as **"Promenada a deux".** On finding a suitable mate, the male and female stand face to face with their telsion upraised and interwined. The male seizes the pedipalp of the female, and both go on moving round and round for a considerable time period. When the pair reaches a suitable surface which the male detects with his pectens, he deposits a **spermatophore** on the ground forcibly jerks his partner over it and the spermatophore is subsequently sucked by the female through her genital aperture.

- **Courtship behaviour of spider :**

Spiders are always offensive. They are invertebrate cannibals; even they eat their conspecific member. Therefore, mating is difficult and dangerous for male.

In such situation, the male courtship behaviour not only stimulates the female sexually but also inhibits the trophic nonsexual behaviour. Among web making spiders, the male vibrates the female's web with some specific signals indicating that he is a potential mate instead of prey items. In some cases, male spider presents the female with a nuptial gift containing a prey item wrapped with cob-web. The mating procedure is quite interesting. Male makes a pad of silk on which a drop of sperm is deposited and is sucked by modified pedipalps. In due course of time, this is inserted into the genital chamber of the female.

- **Birds :**

In birds, the display of courtship behaviour is varied and complex. In some birds, a song is often an important feature to attract and stimulate the female in copulation. Lek behaviour and territorial aggressiveness is the common feature of some birds.

The great crested grebe *Podiceps crestatus* shows elaborate type of courtship (Fig. 2). The courtship ceremony consists of series of behavioural patterns, such as

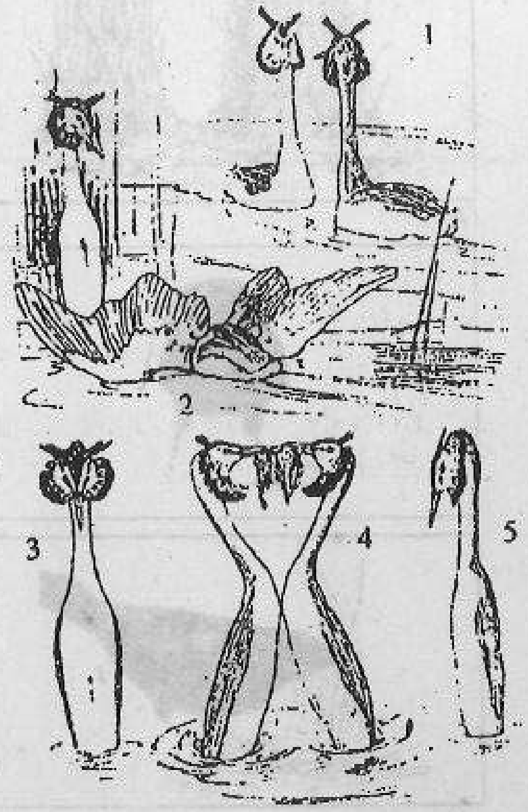


Fig. 2. : Incidents in the courtship of the great crested grebe. 1. Mutual head shaking. 2. The female is displaying before the male who has dived and shoots out of the water in front of her. 3. and 4. Further views of the male rising from the water. 5. Both birds have dived and brought up weeds..

head shaking ceremony; dive; cat display; mutual gretting and penguin dances. The courting birds go through a head shaking ceremony in which they raise their conspicuous head crest, face each other and shake their heads emphatically from side to side. Sometimes when a pair come together, one bird dives when other waits in a cat attitude. The diver then emerges with its back to the waiting bird and closes to it. This often follows penguin dances in which both the birds dive and reappear with bunches of weeds held in their bills. They swim to wards one another, and then spring upright like penguin and move together shaking their heads in a typical pattern.

Fig. 3. : *Ptilonorhynchus* sp. constructs a bower with arched twigs.

The male stain bower birds *(Ptilonorhynchus* sp.) of East Australia (Fig. 3) constructs a bower with arched twigs. One side of it is a display arena in which things like blue parrot feathers, mollusc shells, papers, wasp nests, broken glass etc. as display materials. The male stands on his territory making a whirring round, display his tail in a fan like manner and stiffens his wings. The prospective courting female rounds a few guttural sounds. In the mean time, the female may arrange the disordered twigs of the bower. The male then snatches up one of the display objects and hops arounds.

The Indian peacock, while courting, it spreads its beautiful tail feathers at the approach of a peahen, as she comes near him, he takes an about turn, showing her his rear part. This courtship display may be repeated several times before mating.

9.6 Mechanisms of sperm competition

Sperm competition does not involve individual sperm actually fighting it out to gain access to eggs, rather it involves a selection pressure after mating that has led to two opposing types of adaptation in males. **First, that reduces the chances that the second mate's sperms will be used for fertilization (first-mate advantage). Secondly, that reduces the chances that the previous mate's sperms will be used (second mate advantage).** On the other hand polyandrous female may select among the sperms of different males after copulation, a device called **cryptic female choice.**

- **First-mate devices :**

First-mate devices include, **mate-guarding behaviour** and deposition of **copulatory plug,** both of which reduces the chances of sperm displacement by a second male. In mate-guarding device the male mate prevents his female mate from copulating with other male mate. More commonly, male remains near or physical contact with his female mate ready to react aggressively to the arrival of other male mate. Among mammals, **copulatory plugs** occur in rodents and some primates. In these species males control further insemination of their mated females by other males by sealing the female's genital opening with various secretions. Such sealing of genital opening is called **copulatory plug.** Such plug formation is found in guineapig *(Cavia porcellus}* and deer mice *(Peromyscus maniculatus).*

In fruit flies *(Drosophila melanogaster),* first male mate may also transfer to mated females **antiaphrodisiac** substances that inhibit courtship by other males.

- **Second-mate devices :**

The second mate devices may include **'sperm scooping'** of previous mate and 'dilution of sperms' of the previous mate by frequent ejaculation of large amount of sperm from a second male. Sperm scooping is most evident in damselflies and dragonflies. The male first grasps the front of the female's thorax with specialized claspers at the tip of his abdomen. A receptive female swings her abdomen under the male's body and places her genitalia over the male's penis equivalent, which occupies a place on the underside of his abdomen adjacent to thorax.

The male then rhythmically pumps his abdomen up and down; during this time his penis acts as a scrub brush, sweeping and drawing out any sperm already stored in the female's sperm storage organ or **spermatheca.** In the dunnock *(Prundla modularis),* a small European sparrow like bird,'when a male's mate is likely to have mated with another male previously, the present male repeatedly pecks at the cloaca of his mate until she reverts it, sometimes ejecting a sperm bundle. He then reinseminates her (Fig. 4).

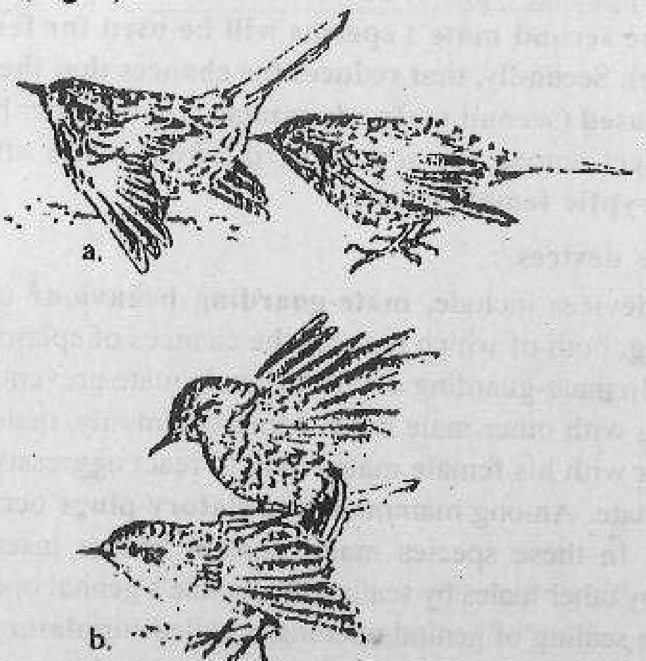


Fig. 4. : Cloaca-pecking in dunnocks. (a) Prior to copulating with a female, the male repeatedly pecks her cloaca, sometimes causing her to eject sperm from a previous copulation, (b) During the very brief copulation, the male appears to jump over the female, and cloacal contact lasts, for a fraction of a second.

In mammals, adaptation of second male is probably restricted to dilution of the first male's sperm by frequent ejaculation of large amounts of sperm from a second male. Females of the rocky moutain bighorn sheep *(Ovis canadensis)* usually mate with more than one male during estrous. Dominant rams guard estrous females from forced copulations by subordinate males. If a subordinate male copulates a already mated female, the dominant male immediately copulates with that female, probably reducing chances that the subordinate male's sperm will fertilize the eggs.

- **Cryptic female choice device :**

In most animals, especially in insects, the male does not place his sperm directly on the eggs, instead places them in some sort of sperm storage organ of the male, usually known as **spermatheca**. In such species, sperm transport and storage is under the control of the female, and when the female mates with more than one male, she has the potential to control which male's sperm fertilizes her eggs. In many species of insects, the male continues to perform courtship displays during and after copulation. These displays function to improve the chances that the female will use the sperm fim horn rather than some other males.

9.7 Sexual selection

The success of potent individual is measured by the number of offsprings it produces. In this respect, the success of male depends on whether he will be allowed or selected by the female/females to fertilize her/their eggs. On the other hand, success of female depends on the selection of good mates with good traits ensuring survival of the offsprings. Darwin (1871) introduced the concept **of sexual selection** traits (in the form of morphological and behavioural traits) that affect an individual's ability to acquire mates. Darwin was not able to explain why it was usually males that competed for access to females in order to mate with them, while females usually seemed to be choosing among males as mates. The explanation was given by Bateman (1948) and Trivers (1972). **Bateman argued that the fertility of the female is limited by the production of developmentally active eggs (fertilized eggs in case of diploid organism and unfertilized egg in case of haploid organism). While in males, fertility is limited more often by the number of female-mates.**

Trivers (1972) generalized Bateman's concept and argued that the **mating systems** and adult **sex ratio** that controls **sexual selection** are function of a single variable-Parental **investment.** Trivers (1972) defined parental investment as **"any investment by the parent in an individual offspring the increases the offsprings chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offsprings" (expected future offsprings).**

The female's general parental investment may be enumerated as **nutritive egg production; selection of good egg-fertilizing mate; energy and time and other costs for raising offsprings in the form of parental care.**

On the other hand the general parental investments of male are fertilization of eggs of a single female (in case of monogamous strategy) different females (incase of polygynous strategy) and additional investments in case of monogamy are nest building, protection and feeding of offspring etc. From the aforesaid discussion it is apparent that, generally the female's parental investment is most cost effective from both sides of male and female. Since, the fertility fitness of both sexes depends on the development of eggs to viable offsprings. Hence, the females have to play most important role, and to pay more costs for parental investment than male. It is also apparent from the afore-made discussion that the **sexual selection** by the females to have good fertilizing genes in order to produce quality offsprings is a parameter of **parental investment.**

The supply of fertilizing -sperms having good genes may be done by the sexual selection either at the level of **intersexual selection** (among the opposite sex) or at the level of **intrasexual selection** (among the members of the same sex).

- **Intersexual selection :**

Darwin proposed that, in animal kingdom males as sexual partner compete among themselves displaying some characters to attract the females for copulation and females choose selectively someone as her breeding partner. Therefore, intersexual " selection is synonymous to **'choice of female'.** Most naturalists after Darwin discounted the importance of mate choice in evolution, but in the last two decades it has become widely accepted as an important evolutionary force. Subsequently various views have been put forward to explain the phenomenon. These are discussed as follows :

- **Runaway selection hypothesis :**

Fisher (1958) proposed a model for sexual selection of male's **epigamic traits**

The character of an animal which is concerned in sexual reproduction other than the gonads and their associated systems which convey the gametes, e.g. bird song, antlers of deer, plumages of bird by females using birds as an example. Suppose a plumage characteristic in males, such as a longer tail, is attractive, for some reason (for e.g. owner is better parental investor) to female. Second condition is that, tail length is heritable in males and preference for the tail length of male sex is also heritable in females. Hence, the development of tail-length trait will proceed in males as will the preference for the female, resulting in a self-reinforcing, **runaway selection process** (Fig. 5). An extreme result of this process is seen in peacock.

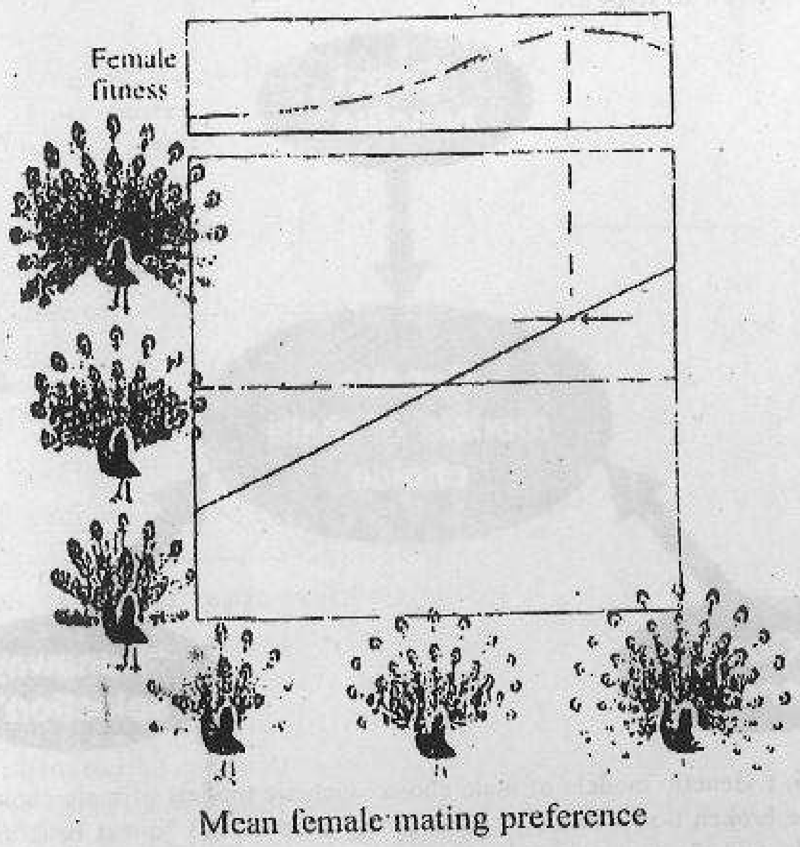


Fig. 5. : A graphical representation of the direct benefits model of female mate choice. Here males provide a direct benefit (food, safety, and so on), and females choose males based on how the benefit affects their fitness.

- **Selection for 'Good genes' hypothesis :**

  Selection for 'Good genes' assumes that the eigamic trait favoured by females, in some way indicates male's fitness. The phenomenon is explained by Zahavi (1975) by his **handicap hypothesis.** Some traits preferred by females in males are detrimental to survival and both costly to produce. For example, the conspicuous and costly to produce tail feathers of some birds, or a stag that can afford to spend energy on a huge bony growth of antlers, are equally detrimental to their survival value because such handicaps could make them easy victims of predators. In spite of these **handicaps,** if they are able to survive and breed, these **handicaps** must be linked to their **over all genetic fitness.** The important notion of this hypothesis is that **"truth in advertising"** and the apparently handicapped traits are reliable index of the male's over all fitness.

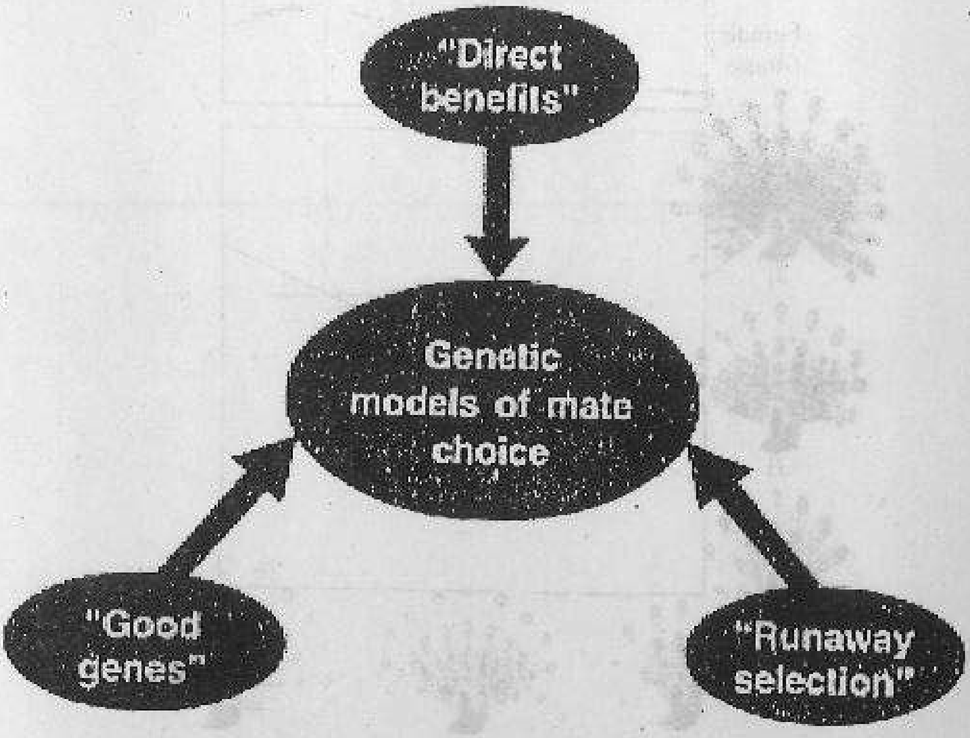


Fig. 6. : Genetic models of mate choice. Genetic models of mate choice can be broken down into (t) "good genes" models, (2) "direct benefits" models, and (3) "runaway selection" models.

- **Intrasexual selections :**

It is the direct competition between the males. It is an event of male rivalry. Rivalry among females is rare in animal kingdom. In red deer *Cervus elaphus* stags grow antlers each year during breeding season. They fight each other for the winning of females which usually do not have antlers. The winner takes possession of all the females of a herd. Now the females have no choice in selection of mates. In this case, the female's mate selection is done by the intrasexual selection by males indirectly.

In is to be noted that, since stags do not have antlers during non-breeding reason and since females do not have antler at all, it is unlikely that antlers are protective arms against predators, rather it is an organ necessary for the intrasexual selection among stags.

Although Darwin, Fisher, Zahavi thought that sexual selection is a process distinct from natural selection, some biologists argue that both are inseparable.

9.8 Parental care

Parental care is a component of **parental investment. In iteroparous** animals, parental care is cost an effective phenomenon, since the parents invest energy and time at the cost of future offsprings. Since, parents increase **direct fitness** through the protection of self-offsprings it seems to be a **selfish behaviour** rather than **altruistic approach.** Some authors (Metcalf *et al)* define parental care as an altruistic behaviour from the gene-centric point of view. Since, parents are loosing the perpituation of some genes as they render parental care to their present offsprings at the cost of some future offsprings. Indeed, from the gene-centric point of view both the parental care and altruistic behaviour through kin-selection is out and out selfish in nature as the main objective of both strategy is to perpetuate the genes of the self.

The phenomenon of direct parental care is not a universal strategy in animal kingdom. The act of parental care depends on mating systems, mode of fertilization and ecological factors.

- **Ecological factors :**

Ecologists have attempted to relate environmental conditions to parental care. These can be categorised as **k-selected strategy** and **r-selected strategy.**

k-selected strategy : Species adapted to stable environments have a tendency toward larger body size, slower developmental rate, longer life span and having youngs at intervals **(iteroparity)** rather than all at once **(semelparity)**; such stable conditions favour production of small number of youngs that receive extensive parental care and thus have a low mortality. Such species are said to be k-selected, in reference to the fact that populations are usually at or near 'k'—the carrying capacity of the environment. Example—Mammals.

r-selected strategy : The species, that are adapted to fluctuating environments have high reproductive rates, rapid development, small body size - and need little parental care. Such populations are controlled by physical factors, and mortality rate is high. This is said to be **r-selected,** where 'r' refers to the reproductive rate of the populations. Example—insects and some fishes like salmons.

- **Mating systems and parental care :**

The relation of parental care to mating systems, if present, can be tabulated as follows :

Mating systems	Participant of Parental Care
Monogamy	Both the parents
Polygyny	Only female
Polyandry	Only male

- **Mode of fertilization and parental care :**

The relationship between mode of fertilization and parental care can be discussed by the following hypotheses :

(1) The "Low reliability of paternity" hypothesis :

Mart Gross and Richard Shine proposed this hypothesis based on the fact, that females are more likely to be the parent of an offspring when internal fertilization occurs in a polygynous mating system. In this case, when a female lays a fertilized egg or gives birth to an offspring, this progeny will definitely have 50 percent of her genes. In **polygynous** system, a male has no such assurance, especially if his partner practices **internal fertilization.** Therefore, the male runs the risk of caring for progeny other than his own; his potential gain from parental care is uncertain. At the same time the maternal care will be assured fully.

(2) The "order of gamete release" hypothesis :

According to this hypothesis **internal fertilization** should be linked with **exclusive maternal care,** because after a male inseminates a female, he can departs at once in polygynous system.

In this case, the female would be forced to provide maternal care at the absence of her mate. In contrast, when fertilization is external, females often deposit their eggs before males shed their sperms. Thus, female will flee, leaving the males to face the responsibility of parental care. Data on the relationship between mode of fertilization and parental care in fishes and amphibians are consistant with the **'order of gamete release' hypothesis.**

- **Cost of parental care for male and female :**

Male typically pay a mating cost for parental care; losing fitness when caring for youngs interferes with matings of new mates. In contrast, for female, parenting may involve an unmitigated fertility cost in terms of loss of future egg production. When a female gives parental care to one brood she cannot eat as much as she could by foraging freely and so cannot grow as rapidly as she might otherwise. This loss of growth sometimes damages the fecundity power of the female, since it increases exponentially with increasing body size. In other words, for each unit of growth loss a female pays an especially heavy price in loss of eggs produced in the future.

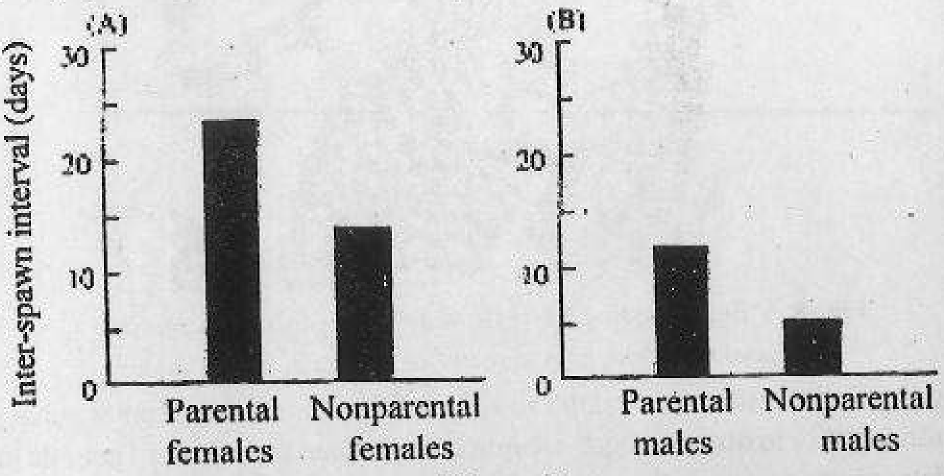


Figure 7. :

The cost of parental behaviour for males and females can be observed in a mouth-brooding Cichlid St. Peter's fish, in which either male or female may care for their youngs by orally incubating the fertilized eggs. In this case, both sexes lose body weight when mouth brooding, since they cannot feed. Furthermore, the interval between two spawnings increases for both parental male and female, compared with male and female whose clutches are experimentally removed from their mouths (Fig. 7). The mean nonreproductive interval is greater for brooding females than for brooding males. Moreover, parental females produce fewer young in their next clutch than non parental females. Whereas parental males are able to fertilize same number of eggs in their next spawning as nonparental males could do. Thus, although both sexes pay a price for parental behaviour, the costs of brood care to females seem especially high.

- **The back-brooding in waterbugs :**

Among the exceptional parental insects are water bugs. In some cases, the male guard and moisten clutches of eggs *(Lethocerus sp.)* that females glue onto the stems of aquatic vegetation above the waterline. Males in some other genera of water bugs (e.g. *Abedus, Belostoma)* permit their mates to lay eggs directly on their backs, after which the males take the responsibility for the welfare of the eggs. A brooding male *Abedus,* spends hours perched near the water surface, diving up and down of water surface repeatedly and to keep well-aerated and moistening the eggs by turns.

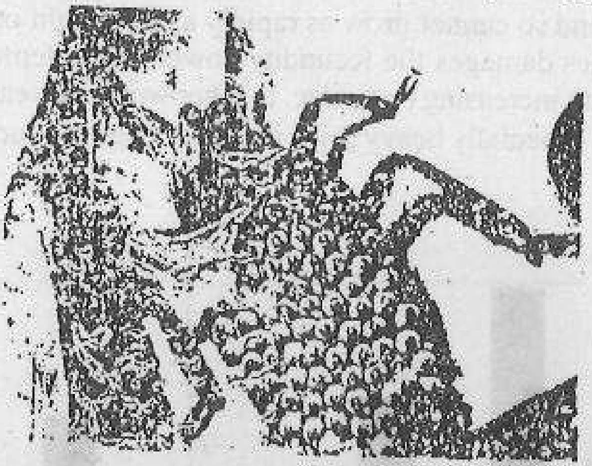


Fig. 8. : Egg brooding by male water bug *(Abedus herberti)*. The female lays the eggs directly on the back of the male.

Bob Smith has studied the adaptive value of these unusual parental behaviour. Smith notes that belostomatid eggs are much larger than the standard aquatic insect eggs. Water bugs are among the world's largest insects, and this huge size is achieved only by five to six molts rather than several molts. It is also noted that about 50 percent of the growth is done only after hatching from egg, which is invariably larger in size. To reach the 50 percent initial growth, the metabolic rate should be high in embryonic development. But the relatively low surface to volume ratio of a large aquatic egg leads to an oxygen deficit in metabolism under water. Since, oxygen diffused through air much more easily than through water, laying eggs out of water on vegetation can solve the problem. But this solution creates another problem, the risk of desiccation. Thus, the solution is done by moistening and aerating the eggs alternately by the male's repeated diving out and in the water. It is probable that back brooding by female itself is not possible, hence the mating males have to do this peculiar and important job of parental care. (Fig. 8)

Unit 10 ❒ Biological Rhythms or Chonobiology

Structure

10.0 Introduction

Biological rhythms occur when animal activities and behaviour patterns can be directly related to distinct environmental features, that occur with regular frequencies. So, biological rhythms are the external manifestations of **biological clock** and are regulated by them. Biological clocks are internal timing mechanisms, that involve both self sustaining physiological **pacemakers** and environmental cyclic synchronizers **(Zeitgebers).**

In this chapter we first describe the properties/characteristics of biological rhythms. Next, look at pacemaker and its physiology, circadian and circannual rhythms. We then ask questions about the functional significance of biological rhythms. Finally, we cover the significance of biological clocks with particular emphasis on migration of some animals like fishes, turtles and birds.

10.1 Structure and characteristics of biological rhythms

Each biological rhythm is composed of repeating units called **cycles.** The length of time required to complete an entire cycle is the biological rhythm's **period** (24 hrs is the period of circadian rhythm). The magnitude of the change in activity rate during a cycle (the difference between peaks and troughs) is called **amplitude.** Any specified part of a cycle is called **phase** (active phase, passive phase etc.) (Fig.1)

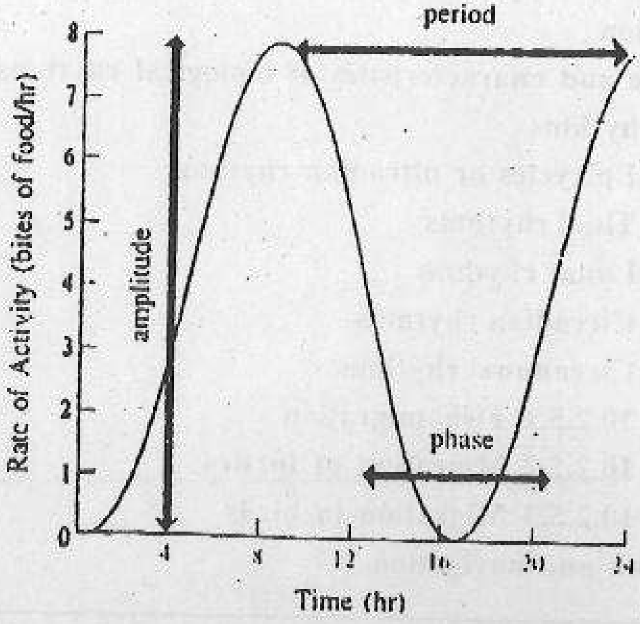


Fig. 1. Biological rhythm : The characteristics of a biological rhythm include period, phase, and amplitude. Phase refers here to the quiet period in terms of activity. Each of these characteristics can vary over time for the same animal, between animals of the same species, or between animals of different species.

The biological rhythms may be characterised by the following properties :

- **Temperature-compensated** : Biological rhythms are relatively insensitive to change in temperature of the environment, especially in endothermous animals. This fact is significant, for if biological rhythms are sped up or slowed down by ambient temperature changes, they would not help the organism keep accurate time.
- **Biological clocks are generally unaffected by metabolic inhibitors** : Biological clocks are generally unaffected by metabolic poisions or inhibitors that block biochemical pathways.
- Biological rhythms occur with approximately the same frequency as one or more environmental features.
- Biological rhythms are self sustaining, maintaining approximately their normal cyclicity even in the absence of environmental cues.

- Biological rhythms can be entrained by environmental cues. The self sustaining, internal pacemaker mechanism may be set and readjusted according to the input from the external environment. The **entrainment** is the process by which a biological clock is set or reset by synchronizing with the period of some external environmental stimulers (e.g. length of photo period etc.).

10.2 Types of rhythms

10.2.1. Epicycles or ultradian rhythms

Some of the organisms exhibit a variety of biological activities with varying frequencies and periods. Some of these cycles are of short duration and are termed **epicycles or ultradian rhythms.** Small mammals like meadow voles *(Microtus pennsylvanicus)* that are active primarily during daylight hours show short cycle of activities followed by a period of rest that vary from 12 minutes to 12 hours.

10.2.2. Tidal rhythms

A unique feature of the seashore is the **ebb and flow of the tides.** Tidal rhythms affect activity periods in many organisms of the seashore. Usually tide is the result of the unequal gravitational forces of the sun and moon, about 12.4 hour period from one low tide to the next low tide (some variation in time period may exists from one location to another). Many species of small crabs *(Uca minax; Uca crenulata* etc.) of the seashore adjust their activity cycle with tides so that they feed on the sandy shore when the tide are out, but return to burrows when the tide flow returns.

10.2.3. Lunar rhythms

The lunar rhythms are based on 29.4 day cycle of the moon. Lunar rhythms are clearly related to tidal rhythms. Some marine insects, like the midge *(Clunio marinus),* coordinate eclosion, mating, and egg-laying activities with the lunar cycle. They lay their eggs at very low tide, thus ensuring that the larvae will hatch in the proper marine environment. .

10.2.4. Circadian rhythms

Circadian means **'about (=circa) a day (=dian)'**. Thus the circadian rhythm means the activities of an organism during the whole light and dark phases consisting about **24 hours day cycle.** This is governed by self-sustaining internal **pacemakers.** In their daily cycle, some animals exhibit peak activity during the day-light hours, called **diurnal;** some are active primarily at night, called **nocturnal;** and others may exhibit peak activity around—**dusk or dawn,** called **crepuscular.**

- **Endogenous pacemaker :**

One of the important characteristics of biological rhythms is the existence of an internal self sustaining **pacemaker** or **internal chronometer.** The following information speaks in support of the existence of internal pacemaker :

1. **Free-running period :**

First, let us consider the case of an animal in constant environmental conditions; for example, in constant darkness. In this constant condition the animal shows normal daily activity pattern, with a period different from that of any known cyclic environmental condition (i.e., normal dark-phase and light phase consisting a daily cycle). This is called **free-running rhythms.** This provides indirect evidence for an endogenous pacemaker. The free running period follows **Aschoff s Rule** (Aschoff, 1960, 1979). When animals are kept in constant darkness, their activity rhythm continues with a period of nearly 24 hour period, but it drifts slightly, becoming shorter or somewhat longer each day. **Aschoff's rule states that the direction and rate of this drift away from 24-hour period are a function of light intensity and of whether the animal is diurnal or nocturnal.** For nocturnal animals, housing under constant dark conditions results in a free-running rhythm period shorter than 24-hours; the activity starts slightly earlier each day. On the otherhand, for a diurnal animal housed under constant darkness, the free-running period is slightly longer each day, and the activity begins slightly later each day.

2. **Isolation :**

Hoffman (1959) maintained lizard eggs under one of three conditions :

(a) 18-hour days consisting of 9 light hours and 9 dark hours, (b) 24-hour days, with 12 light hours and 12 dark hours; and (c) 36 hour days with 18 light hours and 18 dark hours. Lizards hatched from all three groups maintained under constant, conditions, showed free-running activity period of 23.4 to 23.9 hours. Therefore, one could conclude that the component of biological clock mechanism in these lizards is inherited, and is thus endogenous.

3. **Genetics :**

Another evidence for an endogenous pacemaker comes from the study of mutations in the genes that regulate the basic program of biological clocks in various invertebrates.

Recent studies have explored several species of *Drosophila* to understand the genetics of biological clock. *Drosophila* have a diurnal activity phase that is entrained (i.e., seting and reseting of biological clock) by photoperiod. Two types of behaviour rhythms have been studied, **locomotor activity and eclosion** (the process when the adult fly emerges from the pupa). A gene, called **period** (per) mutation can lengthen or shorted, or even abolish circadian rhythm of locomotion or eclosion. The **per** locus is active in the photoreceptor cells of the compound eye, in glial cells of the brain, and in two groups of brain neurons, one in the dorsal cortex and the other near the optic lobes. Recently, a second mutation has been discovered called **timeless (tim)**, flies with this mutation do not exhibit circadian rhythm.

Glossup *et al.* (1999) demonstrated that for the circadian rhythm in *Drosophila* there are two interlocked negative feedback loops involving gene expression (Fig. 2).

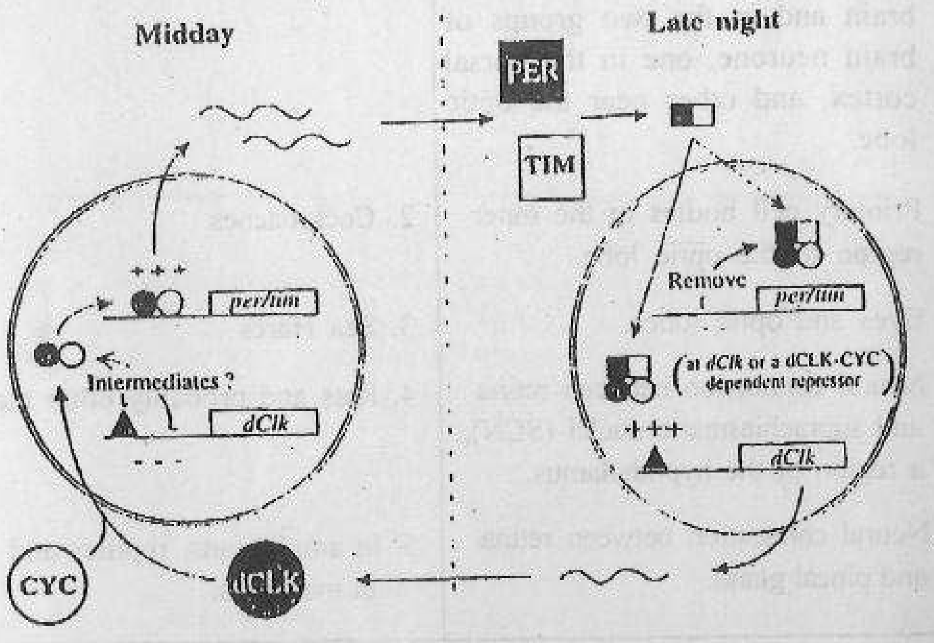


Fig. 2. Model for gene regulation within the *Drosophila* circadian oscillator. During the late evening (right side of diagram), PER-TIM dimers (closed and open squares, respectively) enter the nucleus and bind dCLK-CYC dimers (closed and open circles, respectively), thereby repressing *per-tim* activation. Concurrently, the binding of PER-TIM dimers to dCLK-CYC releases dCLK-CYC-dependent repression ofd*CLK*, thus enabling the *dCLK* transcription via a separate activator or activator complex (triangle). By midday (left side of diagram), high levels of dCLK-CYC (in the absence of PER-TIM) serve to activate per-*tim* transcription and repres . *dCLK* transcription (either directly or through intermediate factors). As the circadian cycle progresses, PER-TIM dimers accumulate and enter the nucleus during the late evening to start the next cycle. Dashes denote maximal repression; plus signs denote maximal activation; wavy lines denote mRNA. Dimers are combinations of two molecules.

The two negative feedback loops involve gene pairs with activation or repression of a particular locus by the presence or absence of proteins that are produced from the other member of the gene pair.

The different endogenous self-sustaining pacemakers in different animals are given below :

Pacemakers	Animals
1. Active **per** locus mutation in the photoreceptor cells of the compound eye, the glial cells in the brain and in the two groups of brain neurone, one in the dorsal cortex, and other near the optic lobe.	1. *Drosophila* spp.
2. Primary cell bodies in the inner region of the optic lobe.	2. Cockroaches
3. Eyes and optic lobes.	3. Sea Hares
4. Neural connection between retina and suprachiasmatic nuclei (SCN), a region of the hypothalamus.	4. Rats and probably other mammals
5. Neural connection between retina and pineal gland.	5. In amphibians, reptiles and partly in mammals.

- **Zeitgebers :**

From the previous discussion it appears that under constant environmental condition the biological rhythm generally does not match the normal environmental cycle; it is somewhat longer or shorter. Therefore, endogenous rhythm must be synchronized with the changing external stimulus. The process is called **entrainment.** The environmental stimuli by which biological clocks are reset in variable conditions, called **Zeitgebers ("time givers") Zeitgebers are cyclic environmental cues that can entrain or adjust free-running endogenous pacemaker to their environmental periodicity.**

The different major types of **Zeitgebers** in different animals have been tabulated below :

Zeitgebers	Animal groups
1. Photoperiod	1. For most endothermic vertebrates
2. Temperature	2. For most ectotherms
3. Ebb and flow of the tide	3. Tidal sheashore animals

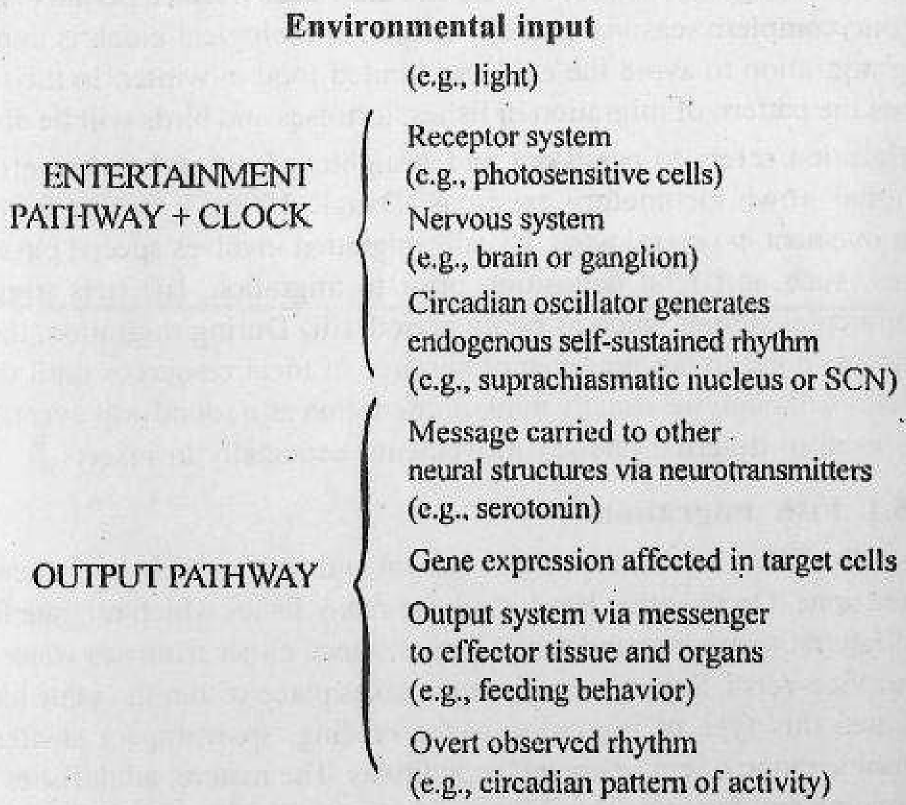


Fig. 3. Model of a mammalian pacemaker system portraying the various component parts and how they may function together, resulting in the overt behavioural and physiological rhythms that can be observed.

- **A model of biological clock mechanism :**

We can construct a model system depicting mechanism of the operation of biological clock. The major elements important for biological time keeping are : (1) an endgenous self-sustaining pacemaker and (2) a system for entrainment to environmental **Zeitgebers.** In this example, we note that some form of environmental input (e.g., light) is sensed from the environment by the appropriate receptor system and transmitted to the circadian oscillator (e.g., suprachiasmatic nucleus in the brain of mammals). From here a message, which may be neural, hormonal, or both is sent to various tissues and organs and results in behavioural rhythmic output. Thus, producing the rhythm we observe.

10.2.5. Circannual rhythms

Circannual rhythms are behavioural and physiological patterns that are governed by self-sustaining internal pacemakers and that occur within a period of about one year (one complete seasonal cycle). An annual biological clock is important in timing migration to avoid the cold and limited food in winter. In the following sections the pattern of migration in fishes, tortoises and birds will be discussed.

Migration refers to persistant and straightened out movement effected by the animal's own locomotory exertions (Dangle 1996). It differs from routine daily movement in several ways. Usually migration involves special physiological changes, such as (i) fat deposition prior to migration, (ii) It is triggered by environmental signals, such as photo period, (iii) During migration, the animal does not respond to the presence or absence of local resources until the trip is complete. Although we usually think of migration as a round-trip event, the term is also used to describe oneway movements, especially in insects.

10.2.5.1 Fish migration

Usually, fishes live in a constant habitat and restrict their movement within a limited zone. On the other hand, there are many fishes which migrate from one type of habitat to another and travel long distance either from sea water to fresh water or vice-versa. Sometimes migration takes place within the same habitat. In most cases this type of migration is for feeding, spawning or shelter within comfortable range of environmental conditions. The mature, adult fishes migrate for spawning and feeding. The following types of migrations in fishes have been observed.

Heape (1931) defined migration as **"a class of movement which impels migrants to return to the region from which they have migrated."**

Fish migration can be typed as follow :

(1) **Alimental migration :** For the need of adequate food.

(2) **Spawning or gametic migration :** For the reproduction and development.

(3) **Climatic migration** : For securing suitable climatic condition.

(4) **Osmoregulatory migration** : For better aquatic condition to have a better osmoregulation.

The migratory fishes can be categorized as follow : -

(1) **Anadromous (away from sea)** : Those fishes which have spend a major part of their lives in the sea but migrate to fresh water during breeding season for **spawning**. Salmon and Hilsa have been found to travel several thousand miles in the sea and then several hundred miles in rivers to reach the spawning ground.

(2) **Catadromous (towards sea)** : Those fishes which spend a major part of their lives in freshwater but migrate to the sea for breeding purposes. *Anguilla*, a freshwater eel, travels several thousand miles from river to the target **spawning ground** of the sea.

(3) **Amphidromous** : Those fishes which migrate from freshwater to the sea, and **vice-versa,** not for breeding but regularly at some other stage of life cycle. Aforesaid three types are collectively called **Diadromous fishes,** e.g., "Asiatic milk fish *(Chanos)*. .,

(4) **Potamodromous** : Truely migratory fishes whose migration is confined within freshwater only e.g., Carps and Trout.

(5) **Oceanodromous** : Truely migratory fishes which live and migrate in the sea, e.g., *Clupea, Scomber.*

- **Migration patterns :**

The migratory movements of the fishes are done by the following mechanisms :

1. **Drifting** : By this method, fishes are carried passively along with the water current. This may result in 'directional movement' if the overall water current is at one direction. The migration of spawns and eggs are done by drifting.
2. **Swimming** : The fishes swim in a particular direction either towards or away from the source of stimulation or at some angle to an imaginary line between them and point of stimulation. Migration by swimming along the direction of water current is called **denatant migration,** and swimming against the water current is called **contranatant migration.**

- **Factors regulating fish migration :**

The factors influencing fish migration may be physical, chemical or biological which are as follows :

1. **Physical factors** : These include water temperature, photoperiod, wate current etc. Rise in water temperature in summer of freshwater rivers triggers a stimulus for upstream movement of fishes for spawning Lampreys and sturgeons migrate during the night hours and herring migrates during full moon. The water current considerably influences the direction of the migration.
2. **Chemical factors** : Chemical factors affecting fish migration are salinity pH etc. Salinity of water influences fish migration. Most of the freshwate fishes are **stenohaline** (can tolerate a very short range of salinity). Usually they restrict their movement to freshwater only and do not cover large scale migration with a drastic change of salinity. A few species like *Salmon, Hilsa, Anguilla* are **euryhaline** (tolarent to drastic salinity changes), and used to travel long distance from ocean to freshwater rive and **vice-versa.**
3. **Biological factors** : In most of the migratory fishes, the internal pacemaker, is an integrated function of gonadal activity and endocrine glands related to reproduction.

10.2.5.2 Migration of turtles

Among the turtles, the most well known migratory turtle is the green turtl *(Chelonia mydas)*. This sea turtle is found throughout the warmer oceans of the world. Adult green turtles are herbivorous. They feed on the so called **turtle grass** that grows abundantly in tropical shallow seas. Green turtles nest only in places where the average temperature of the surface water during the coldest months of the year is above 68°F. In the Atlantic, the northern limit of their nesting range seems to be **Bermuda;** early voyagers to the New World destroyed the colony there. The most Northernly nesting site known in the Pacific is French Frigate Shoal, an outlier of the Hawaiian Islands. These sea-turtles travel thousands of kilometers (about 2000 kms) from their feeding ground of Brazilian sheashore up to the **Ascension Island** in order to complete their breeding. Satellite transmitters have been attached to turtles so that they can be followed day and night. This reveals that they do not need to track the sun's position in order to navigate their journey. Therefore, turtles must make use of some other navigational cues. Probably, the earth's magnetic field can be used in this navigational pattern. To test this hypothesis, Lohmann and associates captured some young turtles, brought them back to the main land, tied them with a rope and reared them into an artificial plastic pool of sea water. The pool was surrounded by a computer driven magnetic coil system that the researchers used to alter the magnetic field around the pool. This simulates the condition that a magnetic field detector animal would experience hundreds of kilometers to the north or south. If the turtles were capable of sensing the earth's magnetic field and using it as a map, then an individual that experienced magnetic field conditions associated with an area 340 kilometers to the north of Melbourne Beach should swim steadily south, rowing along its rope. If the magnetic field was one that the turtle once experienced 340 kilometers to the south of the testing place, then the same turtle should orient in such a way as to head north and continues swimming. In the experimental condition by computerised alterable magnetic field, the turtles did what was expected. Thus, it is evident that **green sea turtle are indeed geomagnetic map navigators.** (Figs..4 & 5).

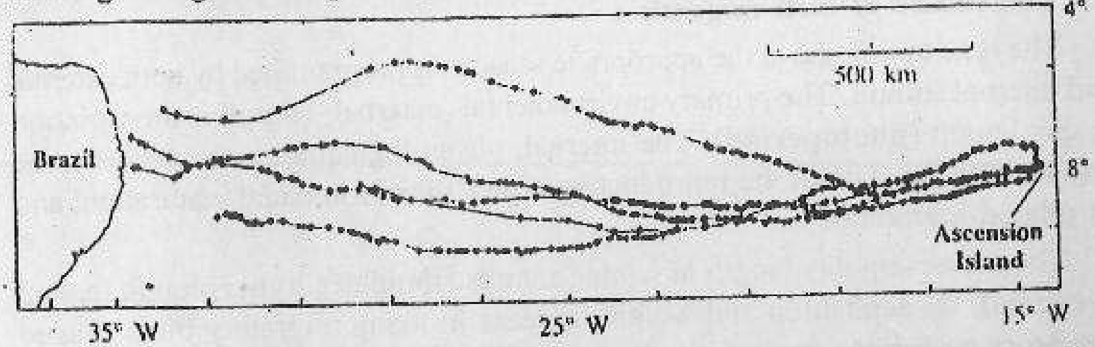


Fig. 4. Migratory routes taken by five green sea turtles that nested on Ascension Island and then returned over 2000 kilometers to feeding areas in the South Atlantic Ocean near Brazil. After Luschi et al. [753]: photograph by Ursula Keuper-Bennett and Peter Bennett.

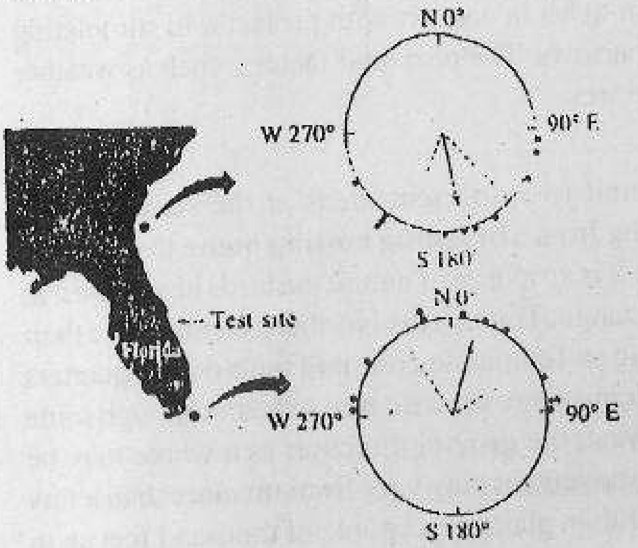


Fig. 5. Experimental manipulation of the magnetic field affects the orientation of green sea turtles. Individuals that experience the magnetic field associated with an area to the north of their actual location swim south; turtles that sense the magnetic field of an area to the south of their actual location swim north. After Lohmann et al.

10.2.5.3 Migration in birds

The subject of migration is one of the most qutralling branches of bird study. The pattern of movements and the regularity and orderness of their occurrence are unique in nature. The entire phenomenon is so reliable that the Red Indians of the Fur countries actually named their traditional calender months after the arrival of the migrant birds.

Landsborough Thomson, an eminent authority, describes bird migration as "changes of habitat periodically recurring and alternating in direction, which tend to secure optimum environmental conditions at all times." Thus the **back and forth** movement is the crucial feature of the bird migration.

- **The causes of bird migration :**

The urge to migrate at the appropriate seasons is programmed by both external and internal stimuli. The primary environmental (external) stimuli is the variation in day length **(photoperiod).** The internal, physiological stimulus seems to be provided by the state of the reproductive organ, mainly gonadal maturation; and its related hormones.

The increasing day length in winter months stimulates **hyperphagia** (eating to excess), fat deposition and weight increase in many migratory birds. Caged migratory passerines predictively become restless just before the times at which they could migrate in the wild. The phenomenon — called **migratory restless or Zugunruhe.** Non migratory birds do not show **Zugunruhe** behaviour. Adrenocortical hormones are known to act in concert with prolactin in stimulating this behaviour in- white-crowned sparrows. The proximal factors, such as weather and food, trigger day to day departures.

- **Types of migration :**

Migration enables birds to inhibit two different areas at the seasons most favourable in each. It involves a swing from a **breeding nesting home** to a **feeding or resting place** in its winter quarter. It is an axiom of nature the birds always nest in the colder portion of their migratory range. Thus, in the Northern Hemisphere their breeding grounds lie nearer the Arctic or Temperate zone and their winter quarters nearer the Equator. In the Southern Hemisphere the case is reversed. Although some migration takes place from east to west, the general direction as a whole may be considered as North and South. The movement may vary from no more than a few kilometers—such as from the north Indian plains to a couple of thousand feet up in

Himalayan foothills—to several thousand kilometers either way as is the case with many'wild-fowl. The longest known migratory journey is performed by the Arctic Tern *(Sterna paradisaea)* which from the Arctic winter travels south acrossing the globe to the Antarctic summer and back again—a distance of about 17,000 km each way (Fig. 6).

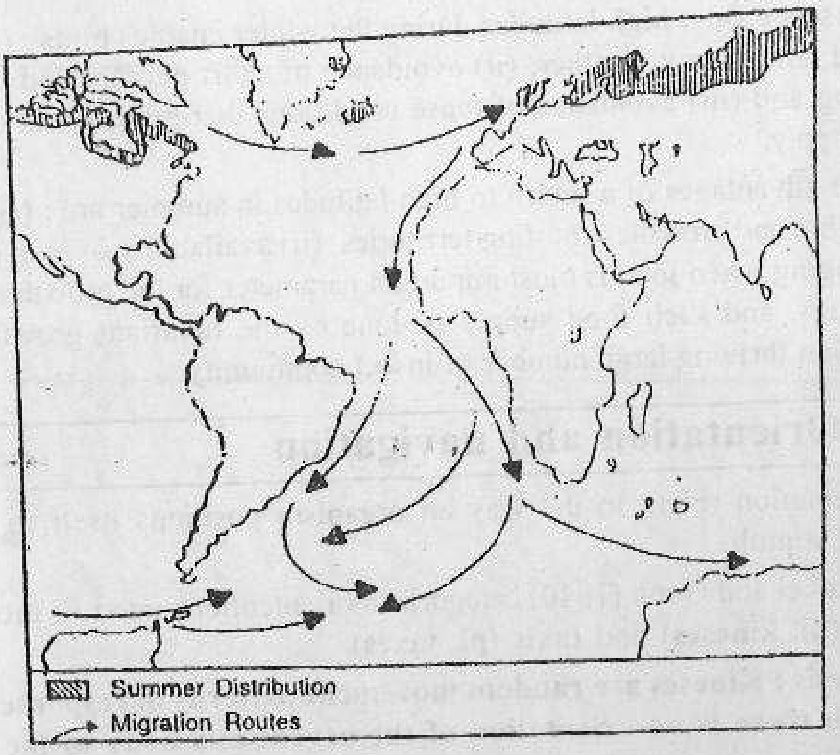


Fig. 6. Figure showing migratory routes of Arctic Terns that breed in Northern Canada.

In the spring, the adult males are the first to arrive on their breeding grounds. They are followed by the adult females, while immature birds that will not breed till the following year follow next. In autumn, the order of departure is reversed; the southward journey is performed more leisurely with many stopovers on the way.

- **Navigation :**

The long distance regular periodicity of bird migration requires precise navigation between breeding territories and wintering stations. Bird ringing method of study proves that individual birds return to a particular tree in Canada after wintering in South America or migrate annually between particular sites in Europe and Africa.

The choice and maintenance of compass direction is the part of accurate navigation is such a hemispheric scale. Ayian navigation system have interactive compass senses including **landmarks, the position of the sun by day and the stars by night, the topology of the Earth's magnetic fields, as well as the position of the setting sun and its bands of polarized light in the evening.**

- **Advantages of bird migration :**

Absence from high latitudes during the winter enables birds : (i) avoidance of cold and stormy weather; (ii) avoidance of short photoperiod available for foraging and (iii) avoidance of those conditions that bring about a scarcity of food supply.

The advantages of a return to high latitudes in summer are : (i) availability of suitable and crowdless nesting territories; (ii) availability of long photoperiod for foraging when food is most important parameter for the growth and survival of youngs, and such food supply is done by the luxuriant growth of spring vegetation thriving large number of insect community.

10.3 Orientation and navigation

Orientation refers to the way an organism positions itself in relation to external stimuli.

Fraenkel and Gunn (1940) categorized oriententions into two broad classes. **kinesis (pi. kineses)** and **taxis (pi. taxes).**

- **Kinesis : Kineses are random movement patterns in response to stimuli in which there is no orientation of the organism's body to the source of stimulation.** The rate of movement increases with the intensity of the stimuli. Although a kinesis is not directed toward or away from the stimulus, it causes to settle organisms in a suitable location. Wood lice *(Porcellio* sp) are commonly found aggregated with least activity under shelters having humid conditions. They cluster in moist areas, because they will die if they are exposed to dry air for a long time due to excessive desication. Under experimental condition, it is proved that more than 70% of the animals were motionless at 90% humidity, but an average of only 20% were motionless at 30% humidity (Gunn 1937). Thus, the rate of movement and clustering increases with the intensity of the stimuli.
- **Taxis** : The simplest directed orientation mechanism is **taxis.** In which generally animals move toward or away from the stimulus. Thus, taxis is based on

the determination of the direction of the stimulus gradient. A taxis can be viewed in different ways. Some categorized taxes according to the response of the animals to the different stimuli. Thus, phototaxis to light; geotaxis to gravity; chemotaxis to chemicals; rheotaxis to a current, or phonotaxis to sound etc. Some describes taxis whether an animal moves toward or away from the stimulus. Thus, an animal that moves toward light and away from gravity is positively phototactic and negatively geotactic respectively.

Different types of animals use different methods to determine the direction of stimulations by moving the receptors appropriately. The maggot of house fly *(Musca domestica)* moves to a dark place at the time of pupation, just orienting head from side to side and sampling the light intensity. If the intensity of light is brighter in one side, moves to the less illuminated side (Fig. 7).

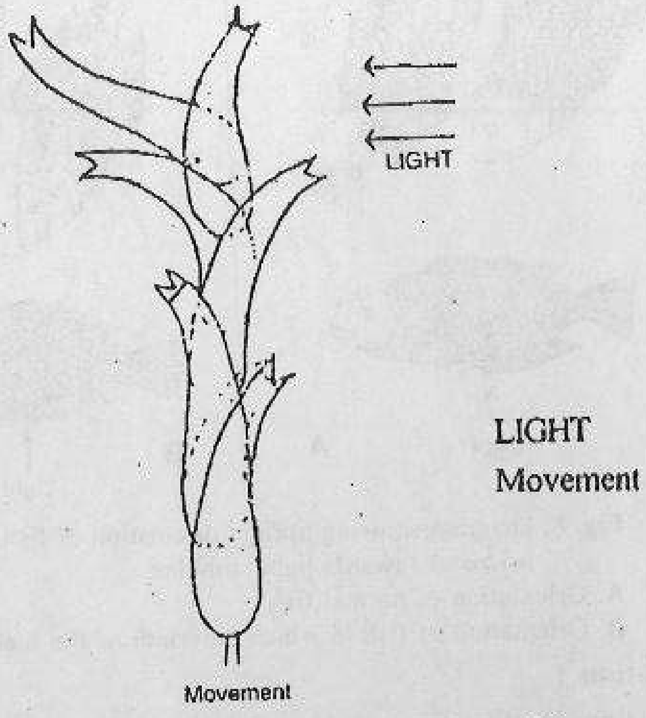


Fig. 7. Diagram to show klino-taxis in the maggot of flies.

Some animals with two receptors senses the intensity of the stimulus on each side and then orient itself so that the receptors are stimulated equally. If such animal displays a positive phototaxis and is blinded in one eye, it will continuously circle to the side of the good eye.

Many aquatic animals orient to light in a manner that helps them swim horizontally. Some fishes may show a dorsal light reaction, one in which the dorsal side is kept toward the light. Others, such as the brine shrimp *Artemia,* show a ventral light reaction in which the ventral side is directed toward the light (Fig. 8).

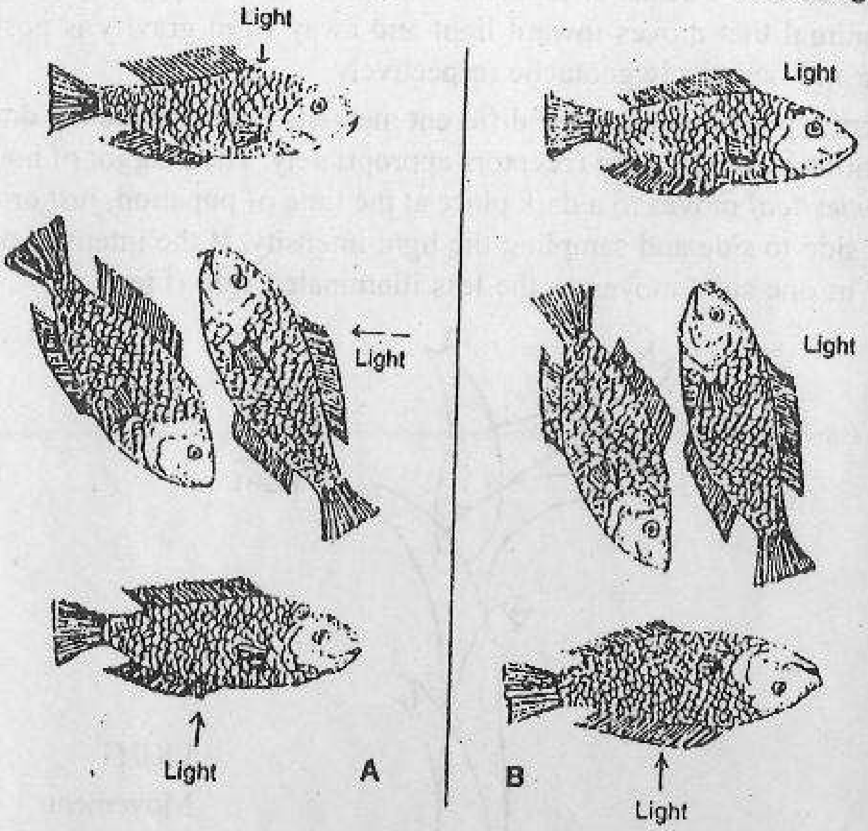


Fig. 8. Diagram showing upright orientation of fish, *Crenilabrus rostratus* towards light stimulus.
A. Orientation of normal fish.
B. Orientation of fish in which labyrinth of the inner ear is destroyed.

- **Navigation :**

Navigation is the process by which an animal uses various cues to determine its position in reference to a known goal (nest, breeding or resting place etc.) as it migrates or homes.

Most mechanisms for navigation involve allocentric, or geocentric cues that require an external frame of reference. These can be placed into three categories : (i) **Piloting**—which refers to the ability to use fixed and familiar reference points or landmarks to orient. (ii) **Compass orientation**—in which the animals uses external cues such as the sun to maintain a heading, (iii) **True navigation**—in which the animals move to a goal in unfamiliar territory in the absence of any sensory contact with that goal. **True navigation requires both a compass and a map.**

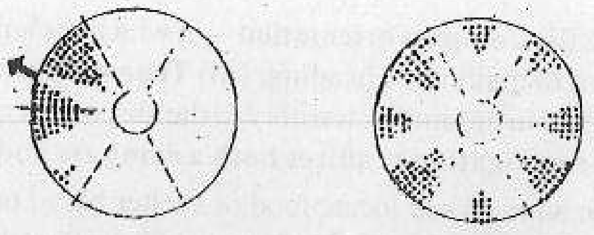
- **Piloting** : Some animals can locate food or shelter based on their relationship to distant, known fixed cues, a mechanism usually referred to as **piloting.** A female digger wasp makes a nest in the ground, then she leaves to capture prey to feed the future young. But before doing so, she circles the hest site several times. When returning with food, she flies straight to the nest. Niko Tinbergen (1951) hypothesized that the returning female uses local land-marks to identify the exact location of the nest. To test this idea, he moved the objects nearest the nest holes a short distance away when female was out for foraging. Upon returning, they invariably searched for their nest hole by the displaced objects. Since, Tinbergen's early work, the use of landmarks has been demonstrated in many species including honey bees, in both field and laboratory.

- **Compass orientation :**

One way to maintain direction in unfamiliar terrain is to use some celestial cues, such as sun, moon, stars etc.

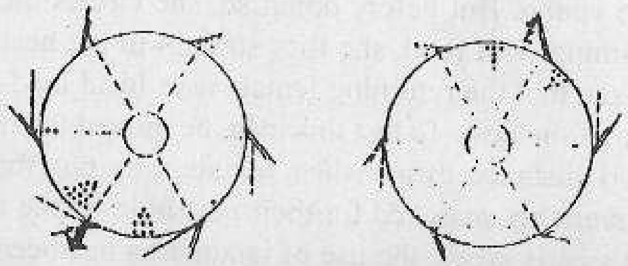
- **Sun :** Sun is not fixed in the sky, the relative movement of the sun across the sky is about 15 degrees per hour. So, some sort of internal clock that help to compensate the movement of the sun is needed. In a classic experiment with the ant *Lasins niger,* Santschi (1911) used a mirror to trick the ants with an altered source of sun light. In this way, the direction of the ant's journey could be changed in relation to "new" position of the sun made by the mirror reflextion for travelling long distances.

Kramer (1950, 1951) showed that European starlings *(Sturnus vulgaris)* placed in an outdoor cage exhibited migratory restlessness in the appropriate direction in the spring and fall (Fig. 9). When mirror was used to alter the apparent position of the sun, the pattern of the starling's migratory restlessness shifted direction in a predictable manner. After the initial discovery of sun compass orientation in birds, theories were put to explain how birds use the sun cue. Some investigators thought that birds use the sun only to gain a compass bearing to head in a particular direction. Others theorized that they use true navigation—the ability to orient toward a goal regardless of its direction and without the use of familiar landmarks.



a. Clear skies

b. Overcast skies



c. Sun's image deflected 90° counterclock wise by mirrors

d. Sun's image deflected 90° clockwise by mirrors

Fig. 9. Use of the sun as a compass by European Starlings.

Bees and other insects, including ants, can receive and interpret information about polarized light. The plane of polarization can provide an axis for orientation for these animals.

- **Moon** : The moon is not as useful as sun in navigation for several reasons. It is visible on an average only half of the night. The moon moves more slowly than the sun (24.83 versus 24 hours/cycle) so that an animal that uses both the moon anc sun have to use two different internal clocks. However, the moon is a prominent feature of the night sky. So, variety of nocturnal animals have a moon compass.
- **Stars** : Most long distance migrants fly at night. When nocturnally migrating birds such as blackcaps *(Sylvia atricapilla)* and lesser whitethroats *(Sylvia curruca* were placed in a outdoor cages with a view of the clear night sky, they exhibited migratory restlessness in a direction appropriate to the seasonal migration (Kramer 1950, Sauer, 1957). Sauer exposed birds to planetorium sky, which permitted him manipulate star patterns experimentally. When he shifted the planatorium's star patterns 180 degrees the direction of the birds activity also shifted. Sauer's experiment

were confirmed both in field and laboratory by Emlen (1967) in Indigo buntings *(Passerina cyanea)*.

Emlen rotated the night sky in a planetorium. He conducted an experiment with three groups of young indigo buntings. The birds in group ' 1' were raised in a windowless room, only with diffuse light. Birds of the group '2' were allowed to the normal night sky in the planetorium with a normal rotation of the night stars around the **North star** once every other day. Birds with group '3' were raised in the same way as those in group '2' except that the night stars were rotated around **Betelgeuse, a star in the Constellation Orion.** Later, their migratory orientations were recorded :Two major conclusions can be drawn from this experiment. First, exposure to stellar sky patterns is necessary for normal southward migratory orientation in young buntings. Birds in group '1' exhibited random patterns of orientation when placed under the normal night sky. Second, birds in group '3' oriented 180 degree away from Betelgeuse — as if headed south, using that star to define the southerly direction. Thus, early experience plays a critical role in determining the migratory orientation in buntings, and they may use the sky pattern, they learnt at this stage throughout life. Finally, it should be noted that whether birds are using the stars merely as a compass or whether they are capable of true navigation using stellar configurations is a matter of debate.

- **Magnetic Field :**

The geomatric fields of the earth provide a map of horizontal space, just as gravity and barometric pressures give information about vertical space. The intensity and angle of the magnetic field change with latitude in ways that provide reliable, omnipresent information about geographical orientation and position.

Many migrating bird species navigate by using the Earth's magnetic field. William Keeton (1971, 1972) showed that free-flying homing pegion fitted with bar magnet often did not orient properly on cloudy day, where as control pegion wearing brass bar usually did (Fig. 10). Finally Charles Walcott and Robert Green (1974) fitted homing pigeon with electric cap (containing Helmholtz coils) that produced a magnetic field through **the bird's head.** Such magnetic field can help the bird to find the direction even in the overcast, cloudy sky. The reversal of electric current which reversed the magnetic field, caused the pigeon to reverse its orientation direction on overcast days (Fig. 11).

In birds, one system is a direction-finding magnetic compass based on **photo-pigments in the** eye. This magnetic compass responds to the -poleward' or'

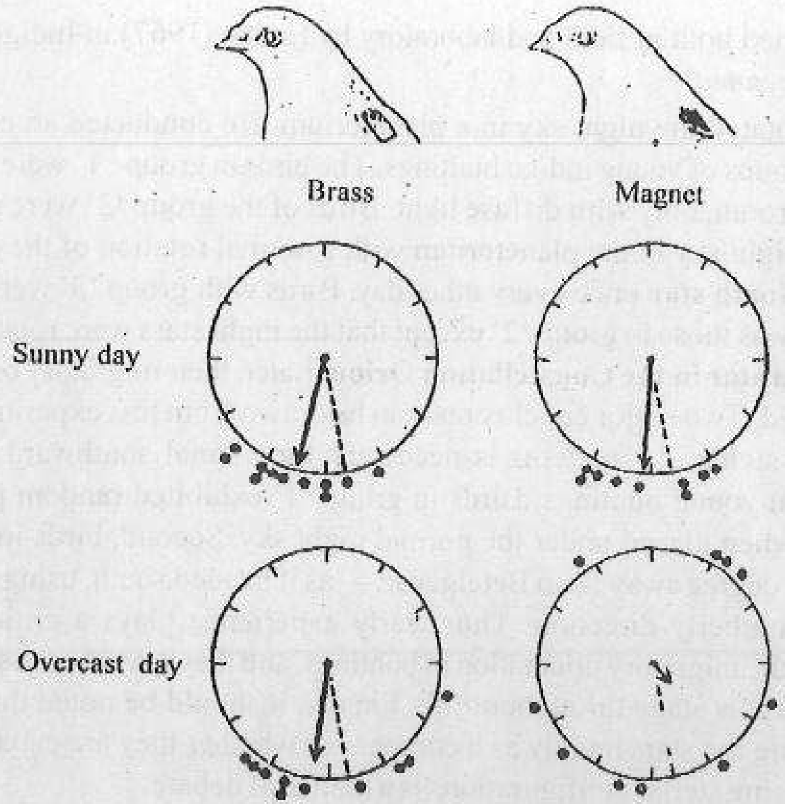


Fig. 10. A bar magnet interferes with a homing pigeon's ability to return to its loft on overcast days. On sunny days, pigeons wearing magnets and control pigeons wearing brass bars both adopt accurate home bearings at unfamiliar release sites. On overcast days when they cannot orient by the sun (their preferred cue), the pigeons wearing magnets become disoriented. The control group, however, orients by means of the Earth's magnetic information. Vectors (arrows) show mean direction and consistency of orientation among individual birds ; long vectors show consistent orientation, and the short vector shows variable orientation. Dots represent bearings recorded for each pigeon tested. The dashed line represents the correct orientation. *[From Keeton 1974]*

'equatorward' angles of inclination of a magnetic field; but not to its "north-south" polarity. The other system, a map location system, is based on **magnetite (Iron oxide) receptors in the ophthalmic branch of the trigeminal nerve.** The magnetite based system enables a bird to determine its location relative to a goal. Such magnetic receptors are sensetive to very small changes in the intensity or topography of the Earth's magnetic fields.

Other than bird, the impact of geomagnetic field in navigation has been proved in whales and turtles.

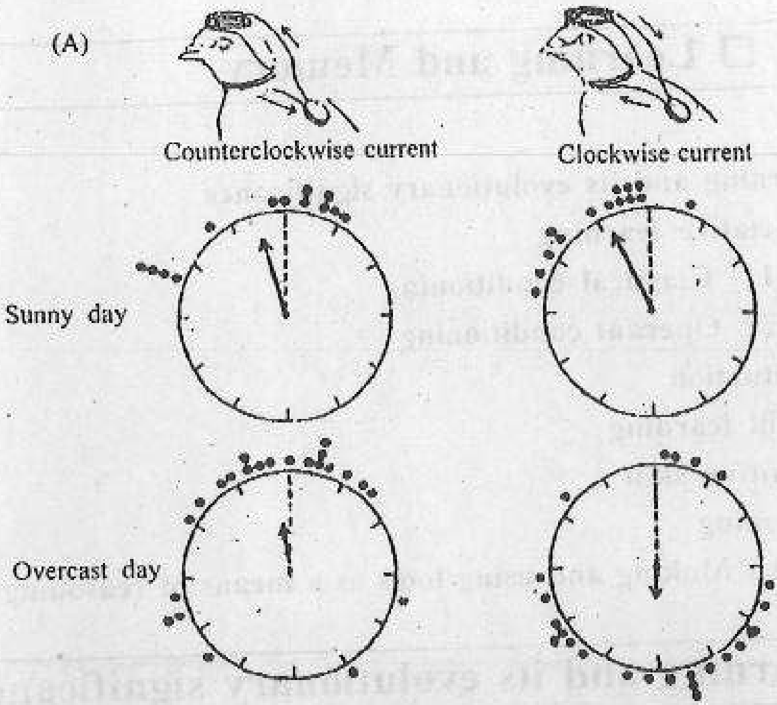


Fig. 11. (A) By attching Helmholtz coils to the heads of homing pigeons, Charles Walcott and Robert Green generated artificial magnetic fields by allowing an electric current to flow through the coils. The reversal of electric current, which reversed the magnetic field, caused the pigeons to reverse their orientation direction on overcast days. Vectors are portrayed as in Figure 10. A homing pigeon equipped with Helmholtz coils. *[(A) After Walcott and Green 1974 and Keeton 1974]*

- **Olfactory and other cues :**

Pacific female salmon migrate from ocean to fresh-water streams for spawning. After hatching the fry develop in the stream during summer and then migrate to the ocean, where they mature. Some *3-5* years later most of the surviving adults return to spawn and die in the stream where they spawn.

The results of numerous experiments conducted over many years (Hasler 1960, 1966, 1978) indicate that young salmon fry are imprinted with the odor of the water of natal stream. When ready to spawn, they apparently respond to minute differences in the odor structure as they move from the ocean into their natal river mouth.

Other cues for navigation may include meteorological parameters and sounds.

Unit 11 ☐ Learning and Memory

Structure

11.1 Learning and its evolutionary significance

When we observe the behavioural patterns of an animal in nature, we find that its behaviour ensures its chances of reproduction and thereby its survival value. Natural selection, as a whole, acts as a mechanism for producing behaviour adapted to environmental conditions. Some biologists consider the concept of **adaptation** only to those behaviours which are shaped by the natural selection. **However, others define adaptation more broadly, including all behavioural traits that increase the inclusive fitness. Adaptation may thus include not only traits with known genetic causes but also the inherited potential for learning.** Learning is a process in which the animal benefits from experience so that its behaviour is better suited to environmental conditions. So, learning should be viewed here as an **adaptive trait.**

Therefore, we can enumerate the properties of learning as follows :

- The ability of learning affecting behaviour is inheritable.
- The ability of learning is a product of natural selection.
- Learning is adaptive when it ensures the survival of the organism concerned.
- The behavioural change that results from learning is not always expressed immediately. For example, a person may memorize some experience for a particular fact and not demonstrate the result of learning until it may require the same.

Learning is often grouped into different categories, but they may overlap and the distinction between them may not be clear-cut. Nonetheless, categorizing types of **learning is somewhat** useful. The following types of learning may be discussed :

11.2 Associative Learning

Associative learning, sometimes called **conditioning,** is a type of learning in which an association is made **between a stimulus and a response.**

11.2.1 Classical Conditioning

The principle of classical conditioning was first stated by Ivan Pavlov (1927), a Russian physiologist. Pavlov's work began with the common observation that a dog salivates **at the** anticipation of food. He thought that the animal had learned to associate the sight or smell of food and the salivation was due to such, learning. Such inborn response to a certain stimulus is called the **unconditioned (or unconditional) stimulus (US),** because the animal did not have to learn the response to it. On the other hand. Pavlov experimentally proved that in anticipation of food, the dog would begin to salivate to a new stimulus, such as sound, that signaled the arrival of food through the process of learning. A **connection had formed between an inborn response and a learned, new stimulus.** This new stimulus is now called the **conditioned stimulus (CS),** because the animal's response has become conditional upon its presentation. The whole phenomenon is called a **conditioned reflex.** The second, new stimulus is repeatedly presented immediately before the US. After

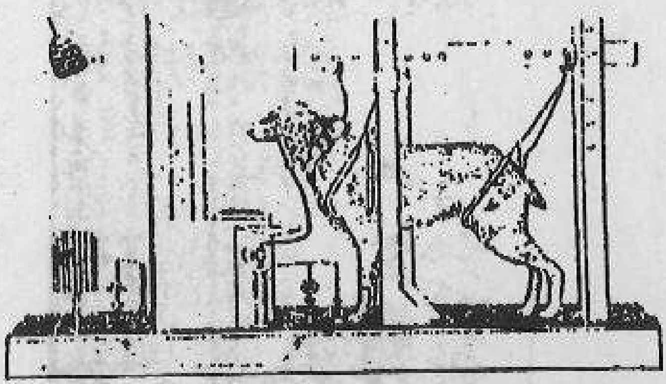


Fig. 1. : Conditioning test apparatus.
Ivan Pavlov discovered classical conditioning through his work on the salivary reflex in dogs using an apparatus similar to this. The dog in the restraining apparatus is ready to be tested using the classical conditioning paradigm.

several pairing, the second stimulus is able to create the response of salivatio through the process of learning only. The order of presentation of the US and C is important. The CS must precede the US. The CS serves as a signal, that th US will appear. Also, the two stimuli must occur fairly close together. If the C is presented frequently without being followed by the US, the association betwee the stimuli is gradually lost. The loss of the classically conditioned response i called **extinction.** (Fig. 1).

11.2.2 Operant Conditioning

Operant conditioning is sometimes called **instrumental learning.** In suc learning, the animal learns to associate its behaviour with the result of th behaviour. When a behaviour has favourable consequences, the probability tha the act will be repeated. This relationship may develop because the animal learn to perform the behaviour in order to be rewarded. This type of learning has bee named **operant conditioning.**

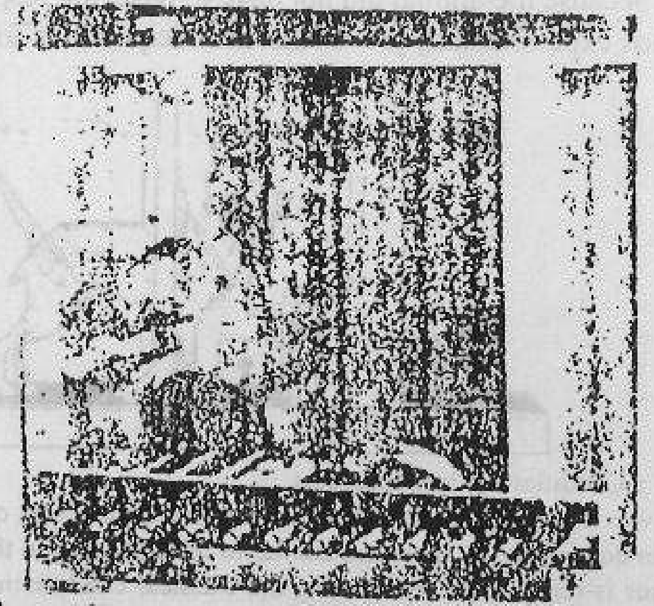


Fig. 2. : Skinner box.

The interior of "the box contains a lever, a light, a food bin. and a grid floor. Additional apparatus for automation and for monitoring the rat's behavior is housed behind the back panel and on the left side of the cage.

B. F. Skinner (1930) devised an apparatus that is still used to study operant conditioning in the laboratory. When a hungry animal is placed into a Skinner box it will move about randomly, investigating each nook and corner. Eventually, it will put its weight on a lever provided in the box accidentally (Fig. 2). When the lever is pressed, a bit of food drops into a tray. The animal will usually press the lever again within a few minutes. In other words, the animal first presses the lever as a random act, and when it is rewarded with food, the probability of repeation of pressing the lever will be increased. A stimulus (e.g. food for hungry animal) that alters the probability that a behaviour will be repeated is called **reinforcer. Positive reinforcers** are those that increase the probability of an act to be repeated against a reward. Examples include food offered to hungry animal or drink to thirsty one. **Negative reinforcers** are those that increase the probability of an act to avoid unpleasant or painful stimulus. For example, an animal will learn to push a panel to stop an electric shock or push a bar to turn off a bright electric light. So, **reinforcement** is best defined operationally to alter the probability of an act. When reinforcement is withheld, the response rate will gradually decline, just as the strength of the conditioned reflex decreases when the CS is presented many times without the US. This process is called **extinction.**

11.3 Habituation

The habituation often considered as the simplest form of learning. The animal learns not to show a characteristic response to a particular stimulus because, during repeated encounters, the same stimulus was proved to be non-effective. **Habituation has been defined more precisely as a "relatively permanent wanning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement. It is specific to the stimulus (Hnide, 1970)".** "Permanent" here means that the effects of habituation are rather long lasting, once they are acquired.

The marine polychaete *(Nereis)* lives in underwater burrows. *Nereis* partially emerges from the tube while feeding. However, certain sudden stimuli, such as shadow may cause it to withdraw quickly in anticipatory approach of predator. They habituate to specific non-harmful stimuli in their environment but retain escape reactions to harmful stimuli.

The benefit of habituation learning is clear : without habituation animals would spend too much time responding to meaningless stimuli rather than foraging or engaging in some other useful behaviour.

11.4 Insight learning

Insight learning is one kind of **Problem-solving abilities.** In insight learning, the animals find new relationships among events. Such relationships were not specifically learned in the past, and they are able to consider the problem as a whole, not just the stimulus response association between certain elements of the problem. The animals here, form a mental representation of the problem and then mentally apply trial-and-error patterns to it. An animal could be thinking through the possible responses and evaluating the possibility of success of each trial based on its past experience. The problem-solving ability might seem sudden to observers because they do not have access to the animals mental processes.

A femous example of insight learning comes from the Wolfgang Kohler's (1927) chimpanzee, named as Sultan. In one experiment, Sultan first learned to use a stick as a tool to get a banana on the ground outside his cage. He mastered this trick to get the banana from the outside of the cage with the help of the supplied stick. In the next experiment the same stick was halved into two equal pieces and supplied to the Sultan to collect the banana, but since the sticks were not joined, he could not collect the banana with the stick from outside of the cage. For over an hour, he persistantly tried, and failed to get the banana. Finally, he gave up and began to play with the sticks. Later an intellectual flash struck Sultan. As the chimpanzee was playing with the sticks (Figs. 3, 4) he realized that the end of one stick could be fitted into the other, thus lengthening the stick enough to reach the banana.'Immediately, he ran to the bars of his cage and began to rake the banana. The chimpanzee understood that fitting two sticks together was an effective way to increase the length of the stick enough to obtain the fruit. Kohler believed that Chimpanzee developed insight learning behaviour in a way that he was able to apply the information gained from the experience of playing with the sticks to solve a problem, getting the bananas.

It is to be noted that the concept of insight learning is controversial. Some workers believe that insight learning shows that the animal is thinking, and an animal that thinks about objects or events can be said to experience a simple level of consciousness (Griffin, 1991). An animal that thinks must also form mental representation of objects or events. Therefore, insight has been used as evidence of animal awareness in a chimpanzee.

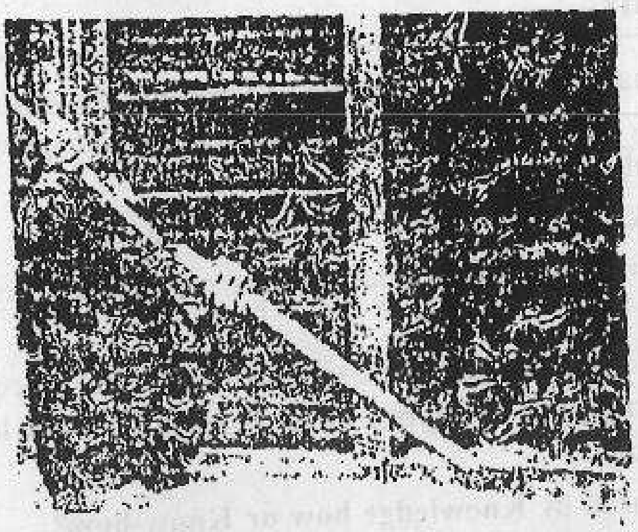


Fig. 3. : Sultan playing with sticks. After playing with sticks, Sultan gained insight into how to obtain the banana placed beyond his reach. The sticks could be fitted together end to end to increase his effective reach.

Fig. 4. : A chimpanzee using a stick to obtain an apple.

11.5 Cognitive skill

We have seen that animal can learn to associate two events—the association of **stimulus and response.** There are two basic alternatives about knowledge acquiring process of animals. These are :

(1) The animal can make association between different stimuli.

(2) Animals can acquire knowledge about various relationships in their environment.

Another aspect, which is more important to understand the process of congnitive aspect, is to distinguish two types of knowledge : **"Knowledge-how" and "Knowledge-that".**

What do we normally mean by **Knowledge how or Know-how?**

We mean knowing as a matter of knowing how to do something, such as how to swim, how to ride a bicycle. This type of knowledge cannot be transferred from one task to another, and cannot be articulated. Thus, knowing how to ride a bicycle involves a type of knowledge that cannot be used for anything except riding a bicycle. Riding a bicycle involves a procedure that is implicit. This type of knowledge is generally called **"procedural knowledge".**

What do we normally mean by **"knowledge that"?** We mean knowing about an object, a person, a place etc. In studies of humans, this has usually been called **"declarative knowledge".** The people can declare such type of knowledge by language to another people. Therefore declarative knowledge need a basic communication system in the form of language. Anhnals do not have language abilities, and so cannot have declarative knowledge system. However, some animals (e.g. Honey bees) linguistic equivalent of declarative knowledge. The animals that do not have linguistic-equivalent would only have procedural knowledge. The declarative knowledge is a variety of **explicit knowledge which involves representions of facts that are accessible to many processes.**

An animal that do have explicit representations that it could manipulate to apply its explicit knowledge to a variety of tasks would be capable of some form of **cognition.** Therefore, **cognition,** may be defined as the manipulation of representations of the **explicit knowledge system.**

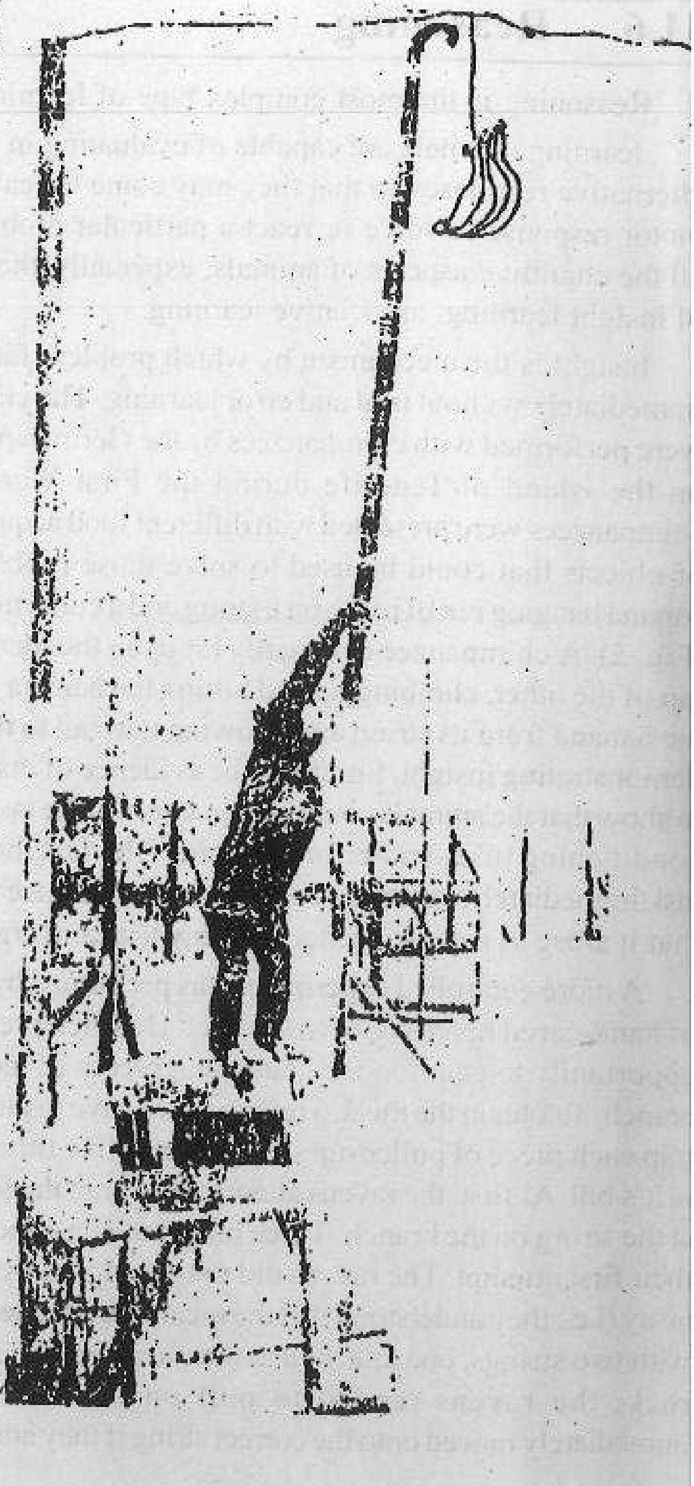
11.6 Reasoning

Reasoning is the most complex type of learning in animals. In this type of learning, animals are capable of evaluating in a comparative manner all the alternative responses so that they may come to realise which would be the right motor response to solve or react a particular problem or event. It may involve all the cognitive aspects of animals, expecially, the problem-solving parameters of insight learning, associative learning.

Insight is the mechanism by which problem faced by the first time is solved immediately without trial and error learning. The classic studies on animal insight were performed with chimpanzees by the German psychologist Wolfgang Kohler on the island of Tenerife during the First World War (Kohler 1925). The chimpanzees were presented with different food acquisition problems, and a number of objects that could be used to solve those problems. A famous example is a banana hanging out of reach on a string and a collection of boxes located underneath (Fig. 5). A chimpanzee eventually hit upon the idea of stocking the boxes one on top of the other, climbing up and hitting the banana with a stick, thereby knocking the banana from its string and allowing it to fall to the ground to be retrieved, thus demonstrating insight. For this to be evidence of insight, however, we would need to show that the animals could not have solved the task by conventional instrumental conditioning (trial-and-error learning). The fact that the chimps did not solve the task immediately, but required extensive experience with sticks and boxes, suggests that it arose as a consequence of many trial and error responses.

A more controlled experiment was performed by Heinrich (1996), with a group of hand-cared ravens *(Corvus corax)*. Heinrich presented his ravens with a novel opportunity to gain food, by attaching pieces of meat to string suspended from a branch. To obtain the meat, a raven would have to pull the string up with its feet, and trap each piece of pulled-up string at least five times before it could grab the meat in it's bill. At first, the ravens attempted to grab the food from underneath or pecked at the string on the branch. Three birds pulled up the string and grabbed the meat at their first attempt. The ravens did not attempt to fly off with the food when chased away (i.e., they understood that the meat was attached to the string). When presented with two strings, one attached to the meat and a second attached to a similar-sized rock, the ravens tended to pull on the string attached to the meat (or immediately moved onto the correct string if they attempted to pull up the string with

Fig. 5. : One of Kohler's chimps standing on stacked boxes to obtain food suspended from above.



the rock attached. When the birds were presented with a novel string (dark-green shoelaces rather twine), the birds almost exclusively pulled on the shoelaces attached to the food. This suggests that the birds did not just form an association between particular string and food, but had generalized to all string like substances to food. This is perhaps a more convincing example of insight than Kohlers chimpanzees as the ravens were hand-reared and therefore Heinrich could be certain that the birds were experiencing the problems and the materials for the first time.

11.6.1 Making and using tools as a means of reasoning :

The propensity to manufacture, transport and use tools was previously thought to be exclusive to humans, but in the 1960s Jane Goodall reported the use of tools by chimpanzees at Gombe, Tanzania. Chimpanzees strip the leaves off tree stems and poke them into termite mounds, thereby extracting termites. The last 30 years have provided numerous examples of tool use in primates in the wild and the laboratory, with different pupulations of chimpanzees using different tools for different uses, e.g., σ wooden anvil and stone hammer to crack open palm nuts, or chewing leaves into a sponge so that it can be used to collect liquids. It has been claimed by some, that these variations in tool use are cultural. However, neither the occurence of social learning nor the mechanisms underlying it can be inferred from observation alone. With field studies one never knows precisely what previous experiences the individuals have had, and whether they have learned by trial and error. The common assumption is that if a particular behaviour must have depended upon the social learning. This is not necessarily the case.

Tool use has not been demonstrated in monkeys and apes to some degree in the laboratory. Visalberghi and colleagues presented Capuchin Monkeys *(Cebus paella)* with a problem that required knowledge of the relationship between objects and tools. The monkeys were given a "trap-tube" problem in which a clear tube contained a hole and well in the middle (Visalberghi & Limongelli 1994). A piece of food was placed next to the well and the monkey was provided with a stick of the correct length to push the food out of the tube. The monkey should have pushed from the side furthest away from the food to avoid pushing the food into the well (Fig. 6a). Infact, only one of the four Capuchins succeeded in the majority of the trials. When the trap was inverted (so that it was no longer a barrier to gaining the food), the monkey that was originally successful used the same technique as previously. This suggests, that this particular monkey was using the rule "always push from the side

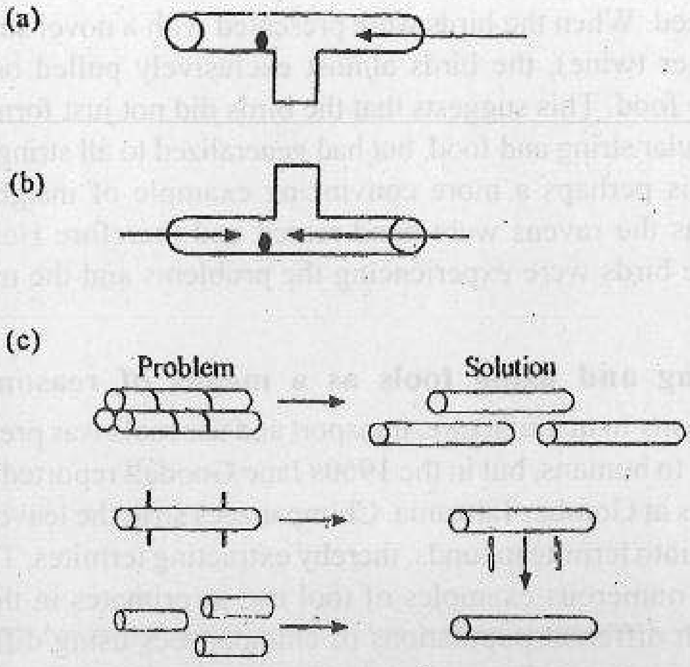


Fig. 6. : (a) "Trap-tube" problem used in capuchin monkeys (Visalberghi & Limongelli 1994), chimpanzees, and more recently New Caledonian crows. The plastic tube is transparent so that the food (black ellipse) can be seen by the subject, and an enclosed trap is located in the center of the tube. To successfully remove the food, the subject must push a stick in the direction of the arrow, i.e., over the trap, (b) In the control condition, the trap is inverted so that it is no longer functional, i.e., it no longer makes a difference from which side the stick is pushed. The subjects are said to not understand the function of the trap if they persistently push the stick from the previously successful side, (c) Additional problems based on changing the physical properties of the sticks : a bundle of sticks tied together (problem) that need to be separated (solution); a stick with small sticks pushed through the center (problem) that need to be removed (solution) : and three small sticks too small to be functional (problem) that need to be stuck together (solution).

furthest from the food" rather than possessing a conceptualization of how the problem should be solved. Finally, the monkeys were provided with a series of problems associated with the functionality of the sticks were pushed through them, or the monkeys were presented with a series of smaller sticks (Fig. 6c). The capuchins readily learned to solve these additional problems! When the "trap tube" experiment was repeated with chimpanzees, only two of the five performed correctly, thereby suggesting that there are few appreciable differences between capuchins and. chimpanzees in their understanding of tool use in this task.

Tool use in animals is not restricted to primates. For example, Asian elephants *(Elephas maximus)* and African elephants *(Loxodonta africana)* manufacture tools to swat away flies, and the Galapagos woodpecker finch *(Camarhynchus pallidus)* uses sticks to probe for insects in ordinary inaccessible holes in trees. Perhaps the most spectacular use and manufacture of tools is demonstrated by the New Caledonian crow *(Corvus moneduloides).* Hunt observed, four crows manufacture two types of tools and 68 crows carry or use tools in three forests in New Caledonia in order to catch insects in trees or under detritus leaves. Hunt categorized the tools into two main types : hooked-twing and stepped-cut tools. The hooked-twing tools were made from living secondary twings that were stripped of there leaves and bark, with a hook at their wider end. The stepped-cut tools, in contrast were fashioned from pandanus leaves by tapering the ends into points. Different techniques were employed in using to tools depending on the location of the prey. If the prey was located under detritus, the tool was used with rapid back-and-forth movements, whereas if the prey was located at the base of the holes and leaves, slow deliberate movements were used. New Caledonian crows studied by Kacelnik and colleagues were presented with a tube containing food and a "tool box" containing twings of deffering lengths; the crows consistently chose the appropriate length of twing to push the food out the rather end of the tube. A single crow also fashioned a straight piece of wire into a hook so that it could pull up a small bucket containing food (Weir *ei al.* 2002). This may demonstrate a case of insight as the crows had previous experience of wire that was bent into hooks but not of straight pieces of wire.

Unit 12 ☐ Concepts of evolution and theories of organic evolution with an emphasis on Darwinism

structure

12.1 Introduction

"Nothing in Biology makes sense except in the light of evolution" — Theodosius Dobzhansky.

Evolution in its simplest understanding means change- change between generations. In seventeenth century, the term "evolution" has an embryological origin defined as the "unfolding" of parts and organs in attaining a preformed body plan. It was only in the nineteenth century that people came to use evolution to mean the transformation of species. The evolution also termed as "organic evolution' deals with changes undergone by living things. The form and behavior of organism between generations can be modified from those of their ancestors. The doctrine of evolution assumes that the present day complex animals and plants have been developed in the course of long ages by a process of gradual change in the earlier simpler forms of life. However, not all kinds of biological change can be addressed as evolution; Developmental change within the life of an organism should not be considered as evolution in strict sense and the definition refers to "descent with modifications". In other word, it means change between generations within a population of a species. The evolution of various organisms on this universe is an intricate and elaborative process. The concept of evolution should not include the idea that evolution is always progressive leading invariably from simpler to more complex forms of life. When the members of a population reproduce and new generation is formed, a lineage of population made up of a series of population through time might be formed. Each population is giving rise to the descendant population in the next generation.

Evolutionary modification in living thing possesses some other distinctive properties. It depends on external environmental change and on random genetic innovation. Thus, the form of future change cannot be predictable.

12.2 Thories of orginic evolution with special emphasis on Darwinism

The concepts of evolution though reckoned with Darwin in respect to publication of his very famous book 'On the origin of species". Long before Darwin, attempts were made to explain the obvious diversity of living organisms. People noticed the basic structural and functional similarities, which exist between organisms. As knowledge has advanced, different concepts have 'evolved' further and at present time also, scientists are arguing for every single details of a particular theory and they are proposing still another theory.

Ideas of evolution developed from the observations of the constant change in the plants and animals of the world.

Empedocles [495 - 443 BC] first stated that evolution in living world occurred step by step. Empedocles is considered as the **father of this concept of evolution.**

Other scientists like **Anaximander [611 - 547 BC], Xenophane** [480 -376 BC], **Aristotle** [384 - 322 BC] worked with the development of egg in chick.

In the Middle Age, **Bacon** [1561 - 1626], **Bonnet** [1720- 1793], **Kent** [1724 - 1780], **Oken** [1776 - 1801] *et al* also worked in this line. Among the other scientists of eighteenth century, **Linnaeus** [1707 - 1778], **Bufon** [1707

- 1780] & **Erasmas Darwin** [1731 - 1802] tried to establish a real picture o Organic Evolution.

Jean Baptiste De Lamark [1744 - 1829] published a book named *'Philosophic Zoologique'* in 1809 in which he described the theory **"Inheritance of Acquired Character"**. According to this theory - the Plants & Animals undergo physical changes to co-opt with the environment. And these changes are inherited to their future generations, such as -

1. The long neck of giraffe was a result of constant stretching of their neck muscles through generation after generation to collect leaves from high branches.
2. The muscles of left arm of Blacksmith developed due to constant use.
3. Limbs of snakes - Degenerated or disappeared through generations due to lack of use.
4. Degeneration of Eye (visual organ) in animals due to absence of light in caves.

The offspring acquire these developed characters & inherited to their offspring. In this way new species appear after many generations.

Lamarck's ideas had little impact during his lifetime. The contemporary respected zoologists criticized him very much. Lamarck's ideas of how evolution works were wrong but he was the first who proposed a coherent theory of evolution and for that he deserves proper honour.

12.2.1 Charles Darwin [1809 - 1882]

Charles Robert Darwin was the son of an English physician. He studied medicine for a brief period of time and then turned to studying for a career in the clergy at Cambridge University. He was passionately interested in natural history. In 1831 Charles Darwin joined a sea voyage which continued for 5 years in a ship named 'H.M.S. Beagle' and visited every island along the coastal region of South America in the Atlantic Ocean & South Pacific Ocean.

During this voyage, he collected large number of specimens of Plants & Animals & Fossils. Mainly in Galapagos Island he observed a large number of variations in living & fossil Animals & Plants. Especially he observed the finch birds of the island are different from those of the mainland. The variation of beaks & colours of the finches are quite different.

While analyzing the data of his collection he came in contact with R. Malthus in respect to his publication of the article "The Principle of Populations". In his article Melthus expressed the principle for struggle for existence and on the basis of which Darwin wrote the theory of Natural Selection. Almost simultaneously **Alfred Russell Wallace [1823-1913]** published the article "The Tendencies of Varieties to depart from the Original Type". Like Darwin he also visited Malayan Archipelago and observed local flora & fauna. Darwin highly appreciated his theory & they together wrote two articles (i) On the tendency of species to form varieties & (ii) On the perpetuation of varieties by Natural Selection. These two articles were published in the "Journal of Proceedings of Linnean Society" in 1859.

In the same year Darwin published his famous book 'On the origin of species by means of Natural Selection or Preservation of favoured races in the struggle for life'.

12.2.2 Detail account of Darwinism

The idea of Natural selection is simple but its operation is highly complex & extremely subtle. Darwinism is based on three facts of nature from which deduction have been made:

I) Prodigality or fecundity: According to Darwin, all the living organisms have the tendency to increase their numbers rapidly. For example, one female toad may lay as many as 12,000 eggs. It has been calculated that one pair of house flies may have 191,010,000,000,000,000 offspring if all eggs are hatched. We do not see such conditions in reality because of the following limiting factors:

i) Limited food supply

ii) Predatory animals

iii) Disease

iv) Shortage of space

v) Climatic conditions

II) 'Struggle for existence': Each species attempt to produce many more individuals that can live up to maturity under the prevailing conditions. The result is an intense competition among the offspring for food, shelter, mates etc. In this struggle, those will succeed who have favourable inheritable variations.

III) Variations in nature: No two organisms are exactly alike no matter how closely related they are. This is a common observation in nature. Such differences are called variations and are prerequisite for evolution. Without variations no change can occur and evolution cannot occur.

IV) Survival of the fittest: Best fitted organism in a changed environment can survive the change and will propagate successfully in the future. Nature selects the best adapted individuals and select out the less adapted ones.

V) Origin of species: The triumph of nature is the emergence of new species from the older ones. This is achieved by natural selection. So by natural selection evolution works.

VI) Mutations as raw material for natural selection: Mutation is one of the ways by which variations can emerge and thus it acts as raw material for natural selection.

12.3 Suggested questions

a) Give an idea of Lamark's theory on 'Inheritance of aquired character'?

b) How do you interprete 'struggle for existance' in the origin of species?

c) 'Mutations as raw material for natural selection'— Justify.

Unit 12 ☐ Neo-Darwinism

tructure

13.0 Introduction

The theory of evolution as proposed by Darwin has been modified in the ight of evidences from genetics, molecular biology, palaeontology, ecology and behavioural biology and is known as neo—Darwinism [neo, new]. This theory states that the organic evolution occurs by the Natural selection of inherited characteristics.

Following are the prerequisites to accept neo-Darwinism:

a) **Past evolution** : establishment of the fact that change or evolution has taken place in the past

b) **Natural selection of genes:** demonstration of a mechanism which results in evolution

c) **Evolution in action:** observation of the fact that evolution is happening today

Evidences for the past evolution come from fossil records and by estimating the order of the rock formation.

Evidences for the mechanism of genes in action and natural selection of genes come from Mendel's works of genetics.

Finally, evidences for the action of evolution at present time come from the study of speciation in herring gull and also the results of artificial selection and genetic engineering, as in the case of cultivation of wheat etc.

13.1 Hardy-Weinberg law of genetic equilibrium

Darwin believed that there was a blending of characters of parents among their offspring and he considered the variation as continuous variation. On 1871, Galton opposed this notion and proposed the Concept of discontinuous variation. After the rediscovery of Mendel's work in 1900, it became evident that there is no mixture of any parental characters when they produce their offspring and the characters maintain their identity throughout the generations. This is known as the particulate inheritance.

Another shortfall of Darwinism is that it cannot explain the reasons for emergence of variations. The **Germ-plasm theory of Weismann and the Mutation theory of De Vries** were the two cornerstones of the development of neo-Darwinian era and' the proposition of synthetic theory later on. The Germ plasm theory stated that the continuity of germplasm was the main criterion for inheritance of characters. This was in contrast to the pangenesis theory proposed by Darwin. While Darwin believed in the continuity of variations, it was Hugo de Vries who proposed that the discontinuous variations were more important than the continuous one and this saltatory variations or mutations were the ultimate source of new and different genetic material appearing in a population. Mutations arise spontaneously and are not directed by the environment. Environmental influences can affect the mutation rate but they cannot induce a mutation to take place. Mutation is the source of variations on which natural selection may act upon.

The modern synthetic theory of evolution is the result of the works of a number of population geneticists, namely. T. Dobzhansky, R. A Fisher, J. B. S. Haldane, Sewll wright, Ernt Mayr and G. L. Stebbins. They opined that mutations and natural selection both are important for organic evolution. They gave emphasis on the study of population for understanding the flow of any particular gene. The population can be defined as a group of organisms belonging to the same species inhabiting a certain area. Population expresses most direct hereditary and reproductive relationships among individuals and it distinguishes a sort of evolutionary unit.

Hardy and Weinberg independently formulated the founding theorem o population genetics. This law states that the process of heredity does not change either gene frequencies or genotypic frequencies at a particular gene locus in case of a random mating population unless acted upon by external forces such as mutations, genetic drift etc.

Before entering into the detailed account of the Hardy Weinberg Equilibrium, we should start with the definition of the important terminologies:

Gene pool; A gene pool is the total variety of genes and alleles present in a sexually reproducing population.

Allele frequency: The alternative or several forms of a particular gene is known as allele. The number of organisms in a population carrying a particular allele determines the allele frequency.

Genotype frequency: The number of individuals of particular genotypes in a population determines the genotype frequency and it is used in predicting possible outcomes of particular mating or crosses.

An English mathematician G.H. Hardy and a German physician W. Weinberg developed the mathematical relationship between the frequencies of alleles and genotypes in populations independently in 1908. The relationship, known as the Hardy-Weinberg equilibrium is based upon a principle that states that '**the frequency of dominant and recessive alleles in a population will remain constant from generation to generation provided certain conditions exist.**'

These conditions are:

i) the population is large;

ii) mating is random;

iii) no mutations occur;

iv) all genotypes are equally fertile, so that no selection occurs;

v) generations do not overlap;

vi) there is no emigration or immigration from or into the population, that is there is no gene flow between populations.

Any changes in allele or genotype frequencies must therefore result from the introduction of one or more of the conditions stated above. Thus the factors or forces that destabilize the equilibrium are

a) Natural selection, b) Mutation, c) Genetic drift, d) Migration, e) Meiotic drive.

Hardy-Weinberg equation provides a simple mathematical model of how genetic equilibrium can be maintained in a gene pool and also helps to calculate the allele and genotype frequencies of a population i.e. the two basic aspects population genetics deals with.

Now, first of all consider a large population of sexually reproducing diploids and suppose that at some autosomal locus there are two possible alleles, A and a. There will be three possible genotypes, AA, Aa and aa. Let us imagine that we count a large sample size, N, of the population having these above genotypes with the following distributions of individuals:

Genotypes	**AA**	**Aa**	**aa**	**Total**
Number	**n1**	**n2**	**n3**	**N**
Frequency	**P= n1/N**	**Q= n2/N**	**R=n3/N**	

From the numbers, we can calculate the genotype frequencies, P. Q, and R. P+Q+R = 1.

Now we can define the frequency of the allele A as the number of A genes in the population, divided by the'total number of genes. Thus, if p is the frequency of A gene of a diploid organism, the frequency of other allele, a will q where $q = 1-p$ or. $p + q = 1$.

Therefore, $p = 2n_1+n_2/2N$

$q = n_2 + 2n_3/2N$ 1

or, equivalently,

$p = P + \frac{1}{2} Q \; ; \; q = \frac{1}{2} Q + R$ and 2

obviously, $p + q = P+Q+R = 1$ 3

This definition can easily be extended to any number of alleles at a locus.

Example: In a population of 10,000 individuals, one person is albino that is. the frequency of albino genotype frequency is 1 in 10,000. Since we know the albino condition is recessive, the albino person is homozygous recessive for albino allele, i.e., aa. If the frequency of.that recessive allele is q, the aa individual has genotype frequency q^2 (as two a alleles are present in that individual). Thus

$$q^2 = 1/10{,}000$$

$$= 0.0001$$

$$\text{so,} \quad q = \sqrt{0.0001}$$

$$= 0.01$$

Then p, the frequency of the dominant pigmented allele in the population will be

$$p = 1 - q \text{ ,[since } p + q = 1]$$

$$\text{so,} \quad p = 1 - 0.01$$

$$= 0.99$$

So, the frequency of the dominant allele in the population is 0.99 or 99%.

Since,

$$p = 0.99$$

$$p^2 = (0.99)2$$

$$= 0.9801$$

the frequency of the homozygous dominant genotype in the population i 0.9801, or approximately 98%

Since,

$$p = 0.99 \text{ and } q = 0.01$$

$$2pq = 2 \text{ x } (0.99) \text{ x } (0.01)$$

$$= 0.0.198$$

the frequency of the heterozygous genotype is 0.0198 or, approximately 2% o the population carry the albino allele either as heterqozygotes or albino homozygotes.

13.2 A detailed account of destabilizing forces

The Hardy Weinberg principle states that in a given condition the allele frequencies remain constant from generation to generation. Under these conditions, a population will be in genetic equilibrium and there will be no evolutionary change. However, the Hardy-Weinberg principle is purely theoretical. Following are the factors that can change or destabilize the equilibrium of a population:

(i) Natural selection, (ii) Mutation, (iii) Genetic drift, (iv) Migration, v) Meiotic drive.

13.2.1 Natural selection

Natural Selection is the mechanism by which new species arise from a preexisting species. This hypothesis/ theory was proposed by Darwin & Wallace and was based on three observations and two deductions:

1) Individual within a population produced on average more offspring than are needed to replace themselves.

2) The numbers of individuals in a population remain approximately constant.

3) Variation exists within all population.

The deductions are

1) Many individuals fail to survive or reproduce. There is a 'struggle for existence' within a population.

2) In the 'struggle for existence' those individuals showing variations best adapted to their environment have a 'reproductive advantage' and produce more offspring than less adapted one.

The second deduction offers a hypothesis called 'natural selection' which provides a mechanism accounts for evolution.

13.2.2 Mutation

Mutation is a particularly important process in evolution because it is the original source of genetic variation in a population. It is a multilevel process & may involve change in a single nucleotide, several nucleotides. part of a gene. part of a chromosome, a whole chromosome or sets of chromosomes. The immediate cause of a mutation may be a mistake in DNA.replication, an insertion of a transposable element, a physical breakage of the chromosome or a failure in disjunction of meiosis. Mutagens are the agents. chemicals or radiation that induce & cause mutation. For example, the chemical ethylmethanesulfonate (EMS) causes the replacement of a cytosine with a thymine; UV radiation causes the formation thymine dimmers & the subsequent insertion of the wrong nucleotides during replication. These are the agents that cause the artificial mutations. Spontaneous mutations are the mutations for which the immediate causes are not known. Mutation is a very slow process that changes the genetic constitution of population at a very low rate. If mutation be the *only* process of genetic modification, evolution would occur at an impossibly low rate. Mutation will change the gene frequencies and will destabilize the Hardy-Weinberg equilibrium.

13.2.3 Genetic drift

Variation in gene frequencies can occur within the population by chan This is known as random genetic drift or Sewall Wright effect (named after t American geneticist who realized its importance in evolution) may be an mporta mechanism in evolutionary change in small or isolated populations. In a sm population all the alleles that are representative of that particular species m not be present. Chance events would result in the elimination of particular alle from the population when the size of that population is not large. Similarly, it equally possible for an allele to drift to a higher frequency. Random genetic dr in a small population may lead to the extinction of population or result in t population becoming better adapted to the environment. It may help the populati to become divergent from the parental population. In due time, this may lead the origin of new species by natural selection. Genetic drift is thought to ha been an important factor in the origin of new species on islands and in oth reproductively isolated populations.

Associated with this, there is another phenomenon called **Founder's effe** This refers to the fact that when a small population becomes split off from t parent population, it may not be true representative of the parent population terms of alleles. Some alleles may be absent and others may be disproportional represented. Continuous breeding within the pioneer population would produ a gene pool with allele frequencies different from that of the original populatio Continual mating within a small population decreases the proportion c heterozygote and increases the number of homozygote.

While genetic drift may lead to a reduction in variation within a populatio can increase variation within the species as a whole. If the small isolate populations have a selective advantage when environment changes, they may b selected in by natural selection & develop into a new species.

13.4 Migration

Migration or gene flow occurs when individuals move from one populatio another and interbred with the latter. Migration does not change allele frequencie for the whole species but may change them locally when the allele squencies i the migrants are different from those in resident.

Let us assume that individuals from surrounding populations migrate certain rate into a local population and they interbreed with the residents. The proportion of migrant is *m*, so that in the next generation (1-m) of the genes are descendants of residents and *m* are descendants of migrants. Also assume that in the surrounding population a certain allele X_1 has an average frequency P, while in the local population it has the frequency p_0. In the next generation. the frequency of X_1, in the local population will be

$$p_1 = (1 - m)p_0 + mP$$

$$= P_0 - m\,(P_0 - P)$$

i.e. the new allele frequency will be the original allele frequency p_0 multiplied by the proportion of reproducing individuals that are residents (1 - *m*), plus the proportion of reproducing migrant individuals *(m)* multiplied by their gene frequency P.

13.2.5 Meiotic drive

There are several well-known genetic systems in animals in which heterozygous individuals do not produce equal proportions of their two different alleles in gametes, as predicted by Mendelian segregation. This phenomenon is generally called meiotic drive or segregation distortion.

It is an example of ultra-selfish genes that interfere with the function of other genes and there by increase their own frequency. In heterozygotes, the selfish chromosome interacts with the normal chromosome to either destroy their gametes or make them non-functional. The well-known examples are the t allele in the house mouse, SD allele in *Drosophila melanogaster* etc. The distortion from normal segregation proportion takes place only in males and in general such meiotic deviations take place in one sex.

To understand the effect of meiotic drive on allele frequencies, assume that the male heterozygote produces a proportion k of the driven allele A_2 and 1 - k of wild type allele A_1. Therefore the allele frequency of A_2 after one generation, assuming half of the alleles come from females with normal segregation and half from males with meiotic drive, is

$$\begin{aligned} q_1 &= \tfrac{1}{2}(p_0 q_0 + q^2_0) + \tfrac{1}{2}(2kp_0 q_0 + q^2_0) \\ &= q_0\,[p_0\,(k + \tfrac{1}{2}) + q_0] \end{aligned}$$

The change in allele frequency is

$$\begin{aligned} Aq &= q_1 - q_0 \\ &= pqk^* \end{aligned}$$

where $k^* = k - {}^1/2$ the deviation from normal segregation.

13.3 Suggested questions

a) Define gene Pool, allele frequency and genotype frequency?

b) Give a detailed account of destabilizing forces of neo-Darwinism?

c) What is meiotic drive?

d) Discuss the Hardy-Weinberg Law of genetic equilibrium?

Unit 14 ❐ Quantifying genetic variability

Structure

14.0 Introduction

There are two different ways in which a population may respond genetically to a changed environment. One, suggested by the examples of melanism insecticide resistance, is as follows. When the new conditions first arise, required mutations are either absent or very rare. There is an inevitable deb in the response of the population while the required mutations occur and increase from their initial low frequencies. Even for a fully dominant gene, takes three times as long for a frequency to increase from, say, 1 in 100,001 to 1 in 100 as it does from 1 in 100 to 1 in 10: the subsequent increase fror 1 in 10 will be rapid. During the first period, little observable change in the population would occur.

There are two main sources of information about genetic variability in natural populations.

1. Response to artificial selection
2. Study of protein variability

If a sample of sexually reproducing species is brought into the laboratory, will be found to respond to artificial selection for almost any trait.

The most widespread measure of genetic variability in a population is th amount of heterozygosity. Individuals in diploid species are either heterozygou or homozygous at a given locus and thus this measure represents a biologicall useful quantity.

The expected Hardy-Weinberg heterozygosity of a population for a particula locus with n alleles can be calculated as

$$H_E = 1 - \sum_{i=1}^{n} p_i^2$$

which is one minus the Hardy-Weinberg homozygosity.

14.1 Genetic structure of natural populations

In most species, populations are often subdivided into small units because o geographical, ecological or behavioural factors. For example, the populations o fish in pools are subdivided because suitable habitats for these species are no continuous . Behavioural aspects are also responsible for the subdivision of population such as in troops of primates.

A population may have substructure depending on the differences in genetic variation among its constituent parts. For example, a population may have localized subpopulations in which there is genetic drift. Exchange of individuals may not have equal probabilities in a population or selection may have different effects in different part of the population. There are several models studying the effect of population structure on the pattern and amount of genetic variation, the simplest of which is the continent - island model. Other model is the general model of population structure. Such models may not precisely fit a particular biological example, but they give close simulation to many incidences and allow an evaluation of the effect of limited gene flow.

14.2 Phenotypic variations

The basis of Natural selection is the performance of different phenotypes in a particular environment. Phenotypic variability may be caused by genotypic variability, but even a single genotype can produce different phenotypes in different environments. This is known as **phenotypic plasticity.** The reaction to a particular environment may reflect the developmental and physiological program expressed by the genotype to produce a specific phenotype during ontogeny. It is called **developmental reaction norm.** The reaction norm is the property of the genotype and may be subject to natural selection. For example. in a rapidly fluctuating environment it may be advantageous to buffer the metabolism and show an integrated response, while in a slowly changing environment it may be better to closely follow the environmental change. Thus, an organism's reaction norm should be related to fitness.

The predictability of a habitat is also an important ecological factor. If the environment changes in a predictable fashion (e.g. in an annual cycle), genotypes can be well adapted to this pattern. By reacting phenoypically to environmental changes, organisms can be optimally adapted to various environments in contrast to a generalist genotype that would be sub optimally adapted under all conditions. Adaptive phenotypic plasticity has been demonstrated frequently in freshwater organisms.

14.3 Models explaining changes in genetic structure of populations

As stated earlier, there are two distinct models to elucidate the effect of population structure on the pattern and amount of genetic variation: The Continent-Island model and General model.

14.3.1 The Continent - Island model

There are many examples of unidirectional gene flow such as occurs from a continent to an island population. Such examples include species with population on land island and nearby large land masses i.e. continents, aquatic species in ponds with a lake as the source of gene flow and peripheral populations of any species that are continuously replenished by the main part of the species range.

To formulate a model for this situation, let us assume that an island population receives migrants from a large source (continental) population as shown in Figure 1.

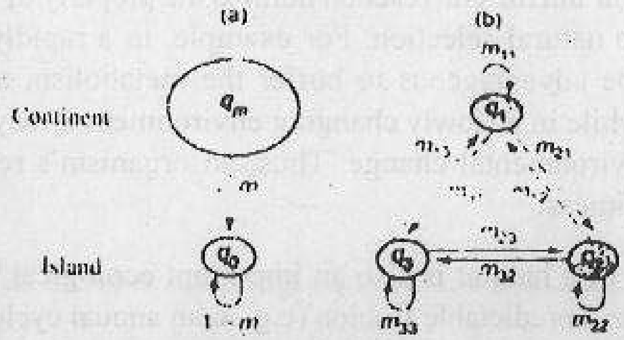


Fig. 1 Illustration of (a) the continent —island model and (b) population structure with three sub-populations.

Here we neglect the reciprocal gene flow though it may occur. We also assume that the island population is large enough that the effect of genetic drift is small relative to that of gene flow. Let the proportion of migrants moving into the island population each generation be m and the proportion of nonimmigrant (residents) be 1-m. If the frequency of A_2 in the migrants (the continents) is q_m and the frequency of A_2 on the island before gene flow is q_0, the allele frequency after gene flow is

$$\begin{aligned} q_1 &= (1 - m)q_0 + mq_m \\ &= q_0 - m(q_0 - q_m) \end{aligned}$$

14.3.2 General model

The continent - island model examines the allele frequency change only in the island population and assumes that only gene flow to the island is important. A more general model, assumes that gene flow can occur among all. parts of a population with many substructures.

Assume that a population consists of k subpopulations and that the proportion of individual migrating from subpopulation *j* to subpopulation *i* every generation is m_{ij}. As a result, there is a matrix of gene flow parameters. called the backward **migration matrix** by Bodmer and Cavalli-Sforza. This describes the gene flow pattern among subpopulations. The proportion of nonmi grants or residents for subpopulation I is given by m_{ii}. Each row of this matrix sums to unity because it describes the proportion coming from even other possible subpopulation to that particular subpopulation or

$$\sum_{j=1}^{k} p_{ij} = 1.0$$

14.4 Suggested questions

a) What is Hardy-Weinberg homozygosity?

b) What do you mean by phenotypic plasticity?

c) Discuss "the Continent-Island model" in the light of genetic structure of population?

Unit 15 ❒ Molecular population genetics

Structure

15.0 Introduction

A thorough understanding of population genetics is a must to comprehend the evolutionary process. Population genetics is a field that has had periods of great interest and growth and other periods in which there was less innovation and fewer contributions.

This area of study attracted such scientific geniuses as Ronald A. Fisher, J. B. S. Haldane, and Sewall Wright. They provided the theoretical basis to population genetics and formed much of the paradigm still used today. Population genetics includes facets of several different disciplines and various approaches to scientific knowledge. The advent of enzyme electrophoresis and molecular biological techniques enabled the scientists to get the first population molecular data and to interpret these fundamental data in the light of molecular population genetics and evolutionary biology. Understanding the evolutionary significance of the data of DNA variations that exist both within and between species is the new challenge for a population geneticist. Furthermore, the role of this molecular variation in adaptive differences in morphology, behaviour, and physiology and nonadaptive variation in complex genetic diseases is a topic to which population genetics can make fundamental contributions.

There are ihree different approaches that can be used to investigate phenomena in population genetics:

a) Empirical, b) Experimental and c) Theoretical

Empirical approaches are traditional extensive observations of genetic variation of a gene or genes of interest.

Experimental tests can provide necessary support for hypotheses developed from empirical data about the effect of particular factors on levels and patterns of genetic variation.

Using the information gathered either from empirical or experimental studies; one can construct a general theoretical model. This model may also provide a general framework as well as allows scientists to make predictions. However, caution is necessary to extrapolate the prediction to the reality.

15.1 Patterns of change in nucleotide and amino acid sequences

With the spectacular development of biochemical and molecular biological techniques, nucleotide and amino acid sequences of individuals within populations have become available for a number of genes. Understanding the basis for the patterns of this variation within populations, between populations, and between species is basis of study molecular population genetics.

The simplest way to measure the amount of nucleotide variation is to determine the number of nucleotide sites that are variable in the sample of sites examined. If a sample of DNA sequences are examined and let the number of nucleotide sites that are segregating be S and the total number of sites compared be N then the proportion of nucleotide sites that differ in the population is

$$ps = S/N$$

$$V(ps) = p(1 - p)/N$$

This value is called p distance for nucleotide sequences.

One of the first estimation of nucleotide diversity was for the Adh gene in *Drosophila melanogaster.*

Similarly the proportion of aminoacid sites that are different or segregating in the population can be estimated by

$$ps_{aa} = S/N$$

Where S indicates the number of amino acid sites that differ among sequences and N is the number of codons compared.

15.2 Ecological significance of molecular variations

From 1960s onward, biological realism was advocated in population genetics. The hope was that a broader discipline of population biology would be created through the application of population ecology in the field of population genetics and vice versa. The idea implies that relative fitness value does not depend only on a particular genotype but also on the environment in which the genotype exists. For example, in one environment, relative fitness of a given genotype may be high, whereas in another environment, it may be low. Environmental factors that potentially influence relative fitness are physical factors such as temperature, moisture, and soil type; biotic factors such as inter specific competitors, predators or prey, and hosts or parasites. In order to assess the ecological significance of variation, first we have to assume that the selective values are environmentally dependent and that the environment may vary over time or in space. Such an analysis is particularly appropriate in case of the effect of physical factors of the environment. Secondly, we consider the selective effects of different genotype frequencies within a population. The effects of population numbers of the same species can be examined by using an extension of the logistic equation from population ecology that allows density-dependent selection.

A number of approaches have shown apparent associations between genetic variation and environmental factors. One of the most thoroughly investigated polymorphisms is that of colour and banding patterns in the shell of the snail *Cepaea nemoralis.*

There are differences between the effects of spatial and temporal variation in the environment on genetic variation. If the environment varies over time– for example, one year is wet & the next is dry - then every individual must endure every different environment whether they are genetically adapted to it or not. However, if the environment varies over space for example, one area is wet & another is dry - then only part of the population encounters a partial'. —' environment at a given time. In fact most of the substantive cases of genetic - environmental associations are related to spatial environmental heterogeneity rather than two temporal variations in the environment.

15.3Emergence of Non-Darwinism—Neutral hypothesis

With the spectacular development of enzyme purification, protein separation. and molecular biology in 1960s, it became possible to study evolution all molecular level. The amino acid sequences of the same protein in a number of different species were becoming available and the size of difference in the sequence suggested the presence of 'molecular clock'. It means the proteins evolve at a constant rate. The rates are different between proteins. Some proteins evolve faster than others-but the rate for any one protein appears to be almost constant.

Protein electrophoresis, a sensitive process by which variation of protein structure can be assessed faithfully, made it possible to study the variation exists in a natural population. It was observed that many more variants exist for each protein than had been assumed. Lewontin was one of the first to apply gel electrophoresis in this way. The important consequence of these early observations that they led Japanese theoretician, Moto Kimura, to propose a radical hypothesis about the force driving molecular evolution. In 1968. Kimura opined that molecular evolution was mainly driven not by natural selection but by random drift among equally well-adapted sequence variants. This famous theory is known as Neutral theory of evolution. According to this theory, the great majority of evolutionary mutant substitutions at the molecular level are caused by random fixation, through sampling drift, of selectively neutral mutants under continued mutation pressure. This view is in sharp contrast to the traditional neo - Darwinism theory of evolution.

According to Kimura, when one compares the genomes existing species, the vast majority of molecular differences are selectively "neutral." That is, these differences do not influence the fitness of either the species or the individuals who make up the species. As a result, the theory regards these genome features as neither subject to, nor explicable by, natural selection. This view is based in part on the genetic code according to which sequences of three nucleotides (codons) may differ and yet encode the same amino acid *GCC* and *GCA* both encode alanine for example). Consequently, many potential single-nucleotide changes are in effect "silent" or "unexpressed". Such changes are presumed to have little or no biological effect. However, it should be noted that the original theory was based on the consistency in rates of amino acid changes, and hypothesized that the majority of those changes too were neutral.

A second assertion or hypothesis of the neutral theory is that most evolutionary change is the result of genetic drift acting on neutral alleles. A new allele arises typically through the spontaneous mutation of a single nucleotide within the sequence of a gene. In single-celled organisms, such an event immediately contributes a new allele to the population, and this allele is subject to drift. In sexually reproducing multicellular organisms, the nucleotide substitution must arise within one of the many sex cells that an individual carries. Then only if that sex cell participates in the genesis of an embryo and offspring does the mutation contribute a new allele to the population. Neutral substitutions create new neutral alleles.

Through drift, these new alleles may become more common within the population. They may subsequently decline and disappear, or in rare cases they may become "fixed"—meaning that the substitution they carry becomes a universal feature of the population or species. When an allele carrying one of these new substitutions becomes fixed, the effect is to add a substitution to the sequence of the previously fixed allele. In this way, neutral substitutions tend to accumulate, and genomes tend to evolve.

According to the mathematics of drift, when looking between two species or two isolated populations, most of their single-nucleotide differences can be assumed to have accumulated at the same rate as individuals with mutations are born. This latter rate, it has been argued, is predictable from the error rate of the enzymes that carry out DNA replication - enzymes that have been well studied and are highly conserved across all species. Thus, the neutral theory is the foundation of the molecular clock technique, which evolutionary molecular biologists use to measure how much time has passed since species diverged from a common ancestor. While the mutation rate is no longer considered a constant, diverse and more sophisticated clock techniques have emerged.

Many molecular biologists and population geneticists besides Kimura, contributed to the development of the neutral theory, which may be viewed as an offshoot of the modern evolutionary synthesis.

15.4 Suggested questions

a) What are the approaches that can be used to investigate phenomena in population genetics?

b) What are the patterns of change in nucleotide in the population genetics?

c) Discuss the neutral hypothesis in the emergence of Non-Darwinism?

Unit 16 ☐ Genetics of Speciation

Structure

16.1 Phylogenetic and / biological concept of species

What is a Species?

Small almost imperceptible changes in an existing species lead to the shifts that at length are manifested in the appearance of new species. The species provides a common ground where micro- and macroevolution meet. In this role, the species is the critical unit in evolution. New species must come from old if there is to be evolution. To a considerable extent two new species arising from one original parent species would constitute the first step in evolutionary change.

Species/Subspecies

Earlier definition of species is: a species is a community, or a number of related communities, where distinctive morphological characters are in the opinion of a competent systematise sufficiently definite to entitle it, or them, to a specific name.

Later. Mayr as defines it: Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups. Given reproductive isolation, distinctive morphological characters usually will arise in due course.

Subspecies are geographical races of a species and stands one step forward of an existing species. They are genetically open populations.

Evolutionary Significance of Subspecies

Several contrasts exist between species and subspecies?

1. Members of different species do not ordinarily interbreed when they come into contact; members of different subspecies within one species ordinary do so.
2. Different species frequently occupy separate territories, but the territories may overlap, in which case intermediate separate territories that do not overlap, and if the territories come into contact intermediate or transitional forms are frequently found.
3. Structural differences between species are usually greater than those between a subspecies.

However, isolating mechanisms are primary need towards the establishment of subpopulations, which later will develop into subspecies or species.

Biological Species Concept

Species have independent reality and are typified by the statistics of populations of individuals. It differs from both by stressing the populational nature and genetic cohesion of the species and by pointing out that the species receives its reality from the historically evolved shared information in its gene pool.

As a result, the members of a species form a *reproductive community*. The individuals of a species of animals recognize each other as potential of devices ensure intraspecific reproduction in all organisms. The species is also an *ecological unit* consisting of a large, in temporary vessel holding a small portion of the contents of the gene pool for a short period of time. These 3 properties show that species are biological populations. The biological species definition, which result from this theoretic species concept is as follows: *A species is a group of interbreeding natural populations that is reproductively isolated from other such groups.*

The development of the biological concept of the species was one of the earliest manifestations of the emancipation of biology from an inappropriate philosophy based on the phenomena of inanimate nature. This species concept is called biological not because it deals with biological taxa but because the definition is biological. It utilizes criteria that are meaningless in the inanimate world.

A species is a protected gene pool; it is a Mendelian population shielded by ts own devices *(isolating mechanisms)* against unsettling gene flow other gene pools. Genes of the same gene pool form harmonious combinations because hey have become coadapted by natural selection. Mixing the genes of two different species usually leads to a high frequency of disharmonious gene combinations; mechanisms that prevent this are therefore favored by selection.

This makes it quite clear that *the word* species *in biology is a relational term:* A is a species in relation to B and C, because it is reproductively isolated "from them. This concept has its primary significance with respect to sympatric md synchronic populations (nondimensional species), and these are precisely he situations where the application of the concept poses the fewest difficulties. The more distant two populations are in space and time, the more difficult it becomes to test their species status in relation to each other but the more biologically irrelevant this status becomes.

The biological species concept (BSC) also solves the paradox caused by he conflict thai made Linnaeous deny evolution and Darwin denies the reality of species (Mayr 1957). The biological species combines the discreteness of the local species at a given time with an evolutionary potential for continuing change. The importance of the biological species concept lies in the fact that it is the concept employed in the largest number of biological disciplines, particularly ecology. physiology and behavioral biology.

All species mat conform to the biological species concept are evolutionary species. but not au evolutionary species need conform to the biological species concept (Eodkr 1989; Templeton 1989).

Biological species are real, but not in same sense that "hydrogen" is real. A nolecule of hydrogen found anywhere, and formed at any time, in the universe would be a member of the class hydrogen. By contrast, an organism that looks ike a tiger another planet unless the two organisms shared a common ancestor, viewed in this way, we can see that classes are defined by convergences, whereas individuals are defined by homology. So the typological view and the purely populational view of species are nonevolutionary, because they are based on homoplasy and evolutionary descent involves homology (common ancestry: Wiley 1989).

Under this "species as individuals" view, the most important characteristic of a species is that its members are bound together by unique common ancestry, and not that its members are reproductively isolated from members of other species. The evolution of a single species is analogous to the development of a single organism; just as an organism changes its appearance without losing its identity during development, so a species can change its appearance without loosing its identity during evolution. Over time, distinct historical trajectories emerge from the speciation process, each differing to some degree from its ancestor and closest relatives, but retaining some of its ancestry in the form of synapomorphies. We take advantage of this historical mosaic nature of the attributes of organisms that comprise species when we use synapomorphies to reconstruct phylogenetic trees (fig. 16.1).

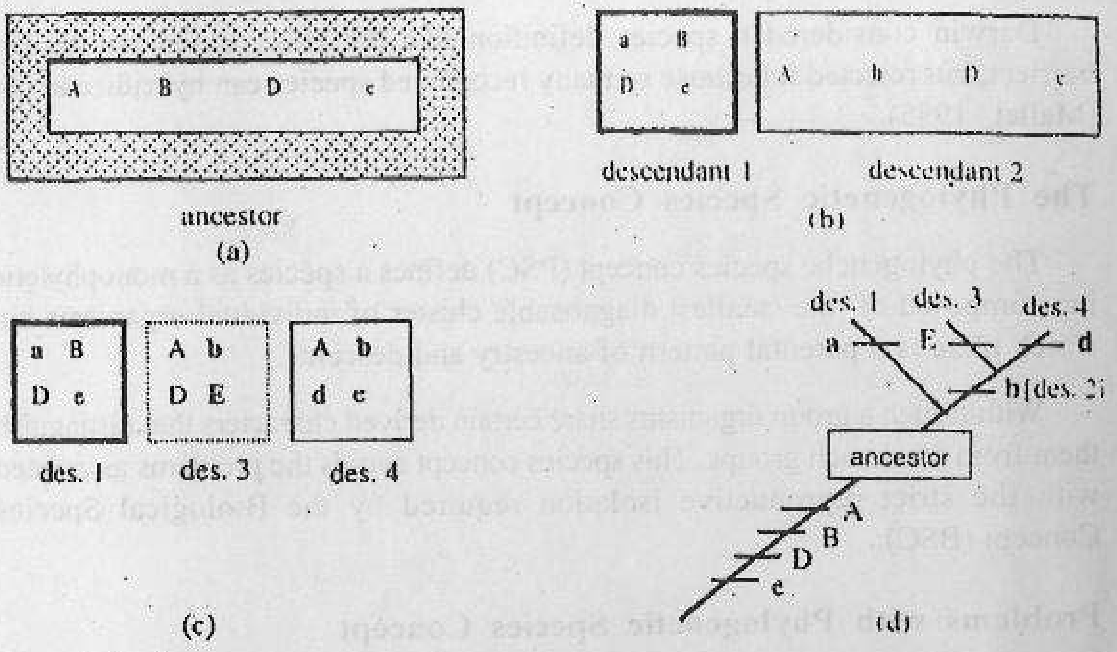


Fig: 16.1. Species are a mosaic of ancestral and derived traits, but only synapomorphies distinguish phylogenetic relationships. *Bold letters* = derived traits, (a) Ancestral species, (b) Ancestral species divided, descendant species 1 and 2 produced, (c) Descendant species 2 divided, specie; 3 and 4 produced, (d) Phylogenetic tree depicting the relationships between the ancestor anc all its descendants. Notice that descendants 1 and 2 are sister species (possession of charade: c); descendants 3 and 4 are sister species (possession of character b). Autapomorphies (a, d, E) distinguish individual species, but not phylogenetic relationships.

Problems with the biological species concept (BSC)

Not all organisms occur in groups within which there is sexual interbreeding and between which gene flow is prevented.

1. *Asexual organisms:* Absence of sexual recombination is rare but does occur in some groups of organisms. Because the BSC refers by definition to sexual reproduction, asexually reproducing organisms (agamous species) cannot be considered for BSC.
2. *Interspecific hybridization:* The BSC is also problematic when species are sexual, but barriers to interspecies breeding are not strong. Interspecies mating producing fertile hybrids are not common among related animal species, but they are frequent in plants and fungi.

Darwin considered a species definition like the BSC, based on sterility barriers, but rejected it because so many recognized species can hybridize in tire (Mallet, 1995).

The Phylogenetic Species Concept

The phylogenebc species concept (PSC) defines a species as a monophyletic iup composed of 'the smallest diagnosable cluster of individual organisms hin which there is a parental pattern of ancestry and descent'.

Within such a group organisms share certain derived characters that distinguish them from other such groups. This species concept avoids the problems associated with the strict reproductive isolation required by the Biological Species Concept (BSC).

Problems with Phylogenetic Species Concept

First, it is not clear how many shared derived characters a monophyletic aup of organisms should have to be classified as a separate species. If one searched hard enough with high-resolution molecular methods, an established species could be split up into many very small groups of individuals that each shared a common derived character. Clearly, giving species status to all such small groups is not meaningful, for in this way any newly derived trait would produce a new species and the number of species would explode. Recently the phylogenetic species concept has started to be modified to avoid extreme division of species, which may well lead to an attractive or addition to the biological species concept.

Evolutionary Species Concept

Some authors, particularly paleontologists, are not satisfied with the biological species concept because of its strict applicability only to the nondimensional situation. Simpson (1961) therefore proposed the following definition: "An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies."

The principal weakness of the so-called evolutionary species definition is that it ignores the core of the species problem - the causation and maintenance of discontinuities between contemporary species - and concentrates instead on trying to delimit species taxa in the time dimension.

Neither Simpson, Wiley, nor Hennig has solved the problem of how to deal with the relationship of descendant populations in a single lineage. Hennig (1966) arbitrarily terminated every evolutionary species when a daughter species branched off the parental lineage, ignoring the fact that a peripatric speciation event usually leaves the parental species unchanged.

16.2 Patterns and mechanism of reproductive isolation

Production of divergence

Three basic phenomena play important roles with regard to the production of divergence.

1. Random incidence of mutations: The origin of diversity in living organisms is due to mutations. But most of the inherited diversity actually seen in different populations is due not so much to the appearance of one mutation here and another there, as to the continual shuffling and recombination by true sexual reproductions, of different mutations.

II. Genetic drift: A second process leading to divergence under certain conditions, is known as genetic drift. It may be described very briefly as the cumulative effect of random sampling errors. In large populations genetic drift can not take place and selection is the principal agent producing changes. But in a large population, subdivided into numerous partially isolated groups, both adaptive and non- adaptive differentiation are to be expected and such conditions are most favourable for evolution.

III. Natural selection: Evidence of the roles played by natural selection in producing geographical variation and divergence is very considerable in importance. There are four main lines of evidence, stable clines, the enological rules, the study of overlaps and direct investigations of selection.

Stable clines are smooth character gradients that are subjected to the approval of natural selection.

Many different species show the same sort of variation under the same ecological conditions and such regularities of variation are explicable only by the action of natural selection. Some ecological rules provide evidences.

Two closely related species come to overlap for part of their ranges, or when part of a species escapes from its coexisting relatives by colonizing a distant district.

It is possible to estimate the selection coefficients involved for effectiveness of natural selection. Since no two localities on the earth are identical in every feature, and even slight differences between localities can produce considerable selective differences between populations inhabiting them the production of geographical diversity in populations by local selection is only to be expected.

Mechanism of Reproductive Isolation

1. If two populations are ecologically isolated for a long enough time, differential mutation, drift, and selection will ultimately lead to gene combuations producing reproductive isolation.
2. If two formerly ecologically isolated populations become sympatric, selection will operate against any hybrids produced by accidental interbreeding and favor and reinforce all reproductive isolating mechanism.

3. If the genetic controls of hybrid sterility are correlated with genetic features with a positive selection value, then genetic incompatibility will result from any crosses.

4. If sterility - producing genes are neutral or even nonadaptive, they may become fixed by genetic drift in small populations.

Table 16.1 Summary of the most important isolating mechanisms, which separate species of organisms.

A. Prezygotic mechanisms : Prevent fertilization and zygote formation.

1. **Habitat**: The populations live in the same regions, but occupy different habitats.
2. **Seasonal or temporal** : The populations exist in the same regions but are sexually mature at different times.
3. **Ethological (only in animals)** : The populations are isolated different and incompatible behavior before mating.
4. **Mechanical.**: Cross-pollination is prevented or restrict differences in structure of reproductive structures (genitalia in animals flowers in plants).

B. Postzygotic mechanisms : Fertilization takes place and hybrid zygotes formed, but these are inviable, or give rise to weak or sterile hybrids.

1. **Hybrid inviability or weakness.**
2. **Developmental hybrid sterility :** Hybrids are sterile because gonads develop abnormally, or meiosis breaks down before it is completed.
3. **Segregational hybrid sterility :** Hybrids are sterile because of abnormal segregation to the gametes of whole chromosomes, chromosome segments, or combinations of genes.
4. **F_2 Breakdown** : F_1 hybrids are normal, vigorous, and fertile , but F_2 contains many weak or sterile individuals.

16.3 Models of speciation (Allopatric, Parapatric, Sympatric)

14.3.1 Allopatric Speciation

"Allopatric" speciation is a generic term for models that invoke the comp geographical separation of two or more populations of an ancestral specie initiate speciation.

Allopatric speciation mode I

Usually called **vicariance**, or geographic speciation, allopatric speciaation mode I combines gene flow among populations prior to separation with a passivate role for range changes in the ancestral species. It occurs when an ancestral species is geographically separated into two or more relatively large and isolated populations, with subsequent lineage divergence by the isolated descendant populations. The speciation rate will depend on the degree of variation in the ancestral species prior to isolation and the rate of origin of evolutionary novelties in the subdivided populations.

Three predictions from this model are of interest to students of speciation :

(1) The phylogenetic tree for the group will be predominantly dichotomous because the fragmentation of the ancestral species and concomitant interruption of gene flow among the isolated populations make is unlikely that either of the descendant species will be identical to the ancestor or to each other. In this case, the ancestor experiences "extinction through total speciation."

(2) The points of geographical disjunction between sister species will correspond to the historical boundaries established'by the geological changes. Based on this, the ancestral range may be estimated by combining the distributions of the descendant species, assum substantial range expansion or contraction following speciatioin (Fig. 5.2).

(3) A multitude of ancestral species, fragmented in the same way by the same geological event, could all theoretically speciate subsequent to

the event, because the mechanism initiating speciation is independent of any particular biological system.

Hence, we would expect to find the same biogeographical distribution pattern shared by a number of different clades. The research program called "vicariance biogeography" relies on this mode of allopatric speciation to detect episodes of parallel biological and geological evolution.

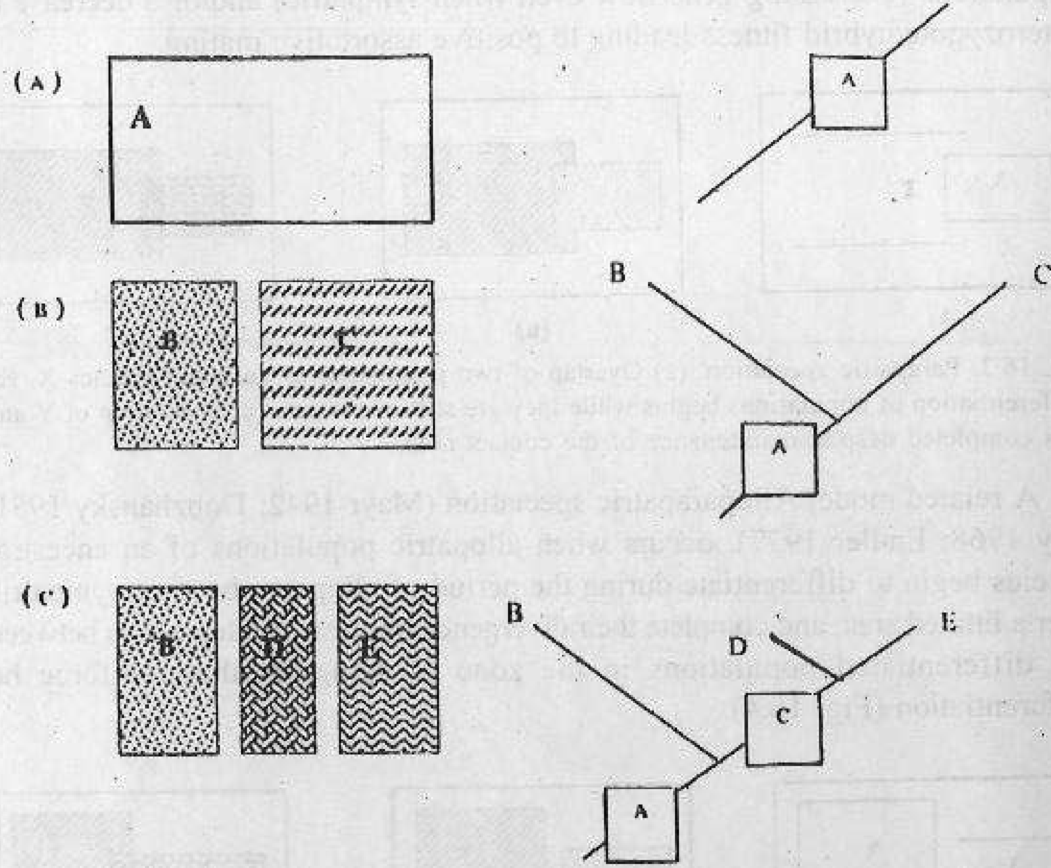
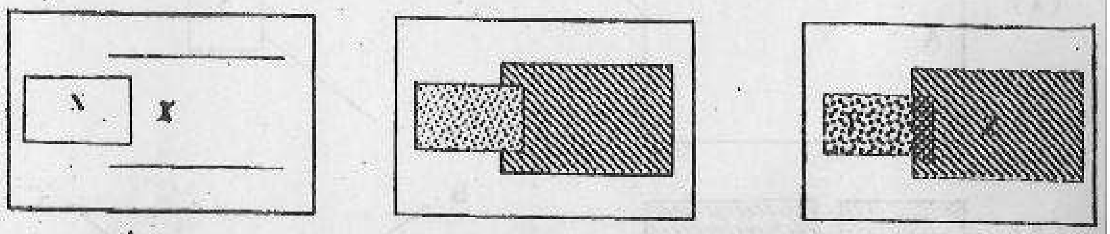


Fig. 16.2. Allopatric speciation mode I. (a) Species A extends throughout a geographical area.(b) The species is divided by the appearance of some geographical barrier preventing gene flow; the two populations continue to evolve independently of one another, producing new species B and C. (c) Species C undergoes another geographical upheaval, gene flow is eliminated, and changes continue in isolation, leading to the eventual production of new species D and E. The outcome of this division of space through time is the production of three extant species (B, D, and E) and the extinction through total speciation of two ancestors (A and C).

16.3.2 Parapatric Speciation

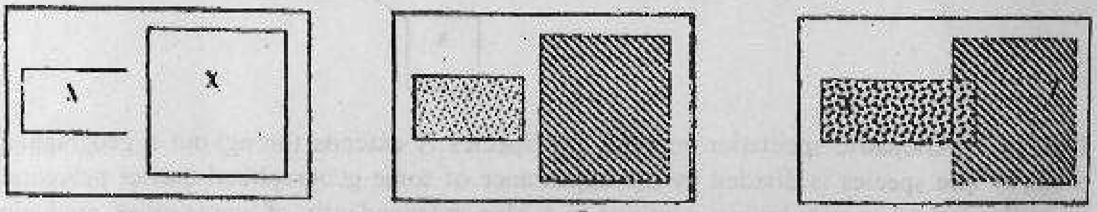
Parapatric speciation occurs when two populations of an ancestral species differentiate into descendant species despite the maintenance of some gene flow and geographical overlap during the process (Fig. 16.3). Stochastic events (e.g., drift) and/or adaptive responses to local selection pressures initiate the differentiation, which is then promoted by low vagility among members of the populations (decreasing gene flow even when sympatric) and/or a decrease in heterozygote/hybrid fitness leading to positive assortative mating.



(A) (B) (C)

Fig. 16.3. Parapatric speciation. (a) Overlap of two population of ancestral species X. (b) Differentiation of populations begins while they are still in contact, (c) Speciation of Y and Z is completed despite maintenance of the contact area.

A related mode. Alloparapatric speciation (Mayr 1942; Dobzhansky 1951; Key 1968: Endler 1977). occurs when allopatric populations of an ancestral species begin to differentiate during the period of allopatry, become sympatric over a limited area, and complete their divergence because of interactions between the differentiated populations in the zone of sympatry that reinforce he differentiation (Fig. 16.4).

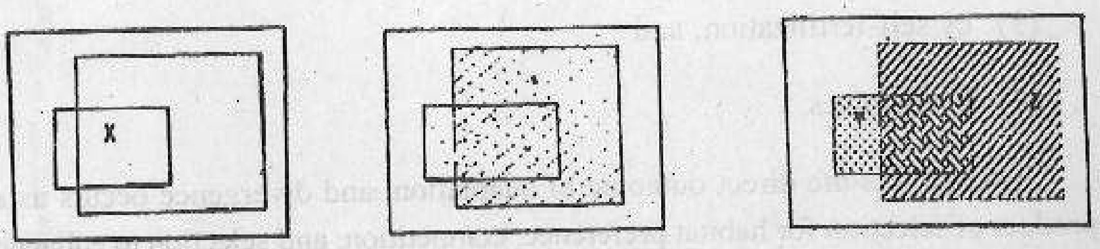


(A) (B) (C)

Fig. 16.4. Alloparapalric speciation. (a) Two populations of ancestral species X are separated geographically, (b) Differentiation of populations begins while they are allopatric. (c) Speciation of Y and Z is completed when contact is established between the diverging populations.

16.3.3 Sympatric Speciation

Sympatric speciation (Maynard Smith 1966; Dickinson and Antonovics 1973; Felsenstein 1981; Gittenberger 1988) occurs when one or more new species arise without geographical segregation of population (Fig. 16.5). Unlike the allopatric models, which postulate that gene flow between populations is initially served by factors extrinsic to the biological system, sympatric speciation requires the involvement of biological processes intrinsic to the system, for example hybridization, ecological partitioning, the evolution of asexual or parthenogenetic. populations, or a change in mate recognition. Additionally, differentiation must occur "within the dispersal area of the offspring of a single deme [the cruising range]" (Mayr 1963:257).



(a) (b) (c)

Fig. 16.5. Sympatric speciation. (a) Extensive overlap of two populations of ancestral species X. (b) Differentiation of populations begins while they are still in contact, (c) Speciation of Y and Z is completed despite maintenance of the contact area.

Although this was the mode originally preferred by Darwin (1859), support for sympatric speciation wavered when population geneticists demonstrated that the effects of gene flow among populations would tend to swamp out or homogenize any novel traits arising within a population. If gene flow were restricted or interrupted, as in the allopatric or parapatric speciation models, the novel trait would have a better chance of becoming fixed within a deme, and the whole process would operate much more smoothly. The work of the population geneticists was coupled with the earlier recognition that most "related" species (this usually meant members of the same genus) exhibited allopatric distributions, and this combination provided a strong foundation for the hypothesis that most speciation was allopatric. However, in recent years there has been a revival of interest in the possibility of sympatric speciation modes, as researchers have intensified investigations of mechanisms of phenotypic plasticity, disruptive selection, and chromosomal divergence. One of the most eloquent supporters of this and other nonallopatric models has been Guy Bush, who suggested that it is unnecessary to postulate a link between speciation and adaptation in allopatric speciation models, while in nonallopatric models (Bush 1982).

Sympatric speciation may occur, at least among higher plants, in four principal ways:

(1) by polyploidy;

(2) by hybridization between distinct species;

(3) by self-fertilization; and

(4) byapomixes.

Speciation is the direct outcome of adaptation, and divergence occurs as a product of selection for habitat preference, competition, and selection to enhance reproductive isolation.

Sympatric speciation requires observations of the sympatric distribution of sister species that differ in some special ecological or genetic characteristics that could, in themselves, produce independent species. Phylogenetic trees reflecting incidents of sympatric speciation may be either dichotomous or polytomous, depending on whether or not the ancestor persists. Biogeographically, this mode requires that sister species be broadly sympatric today and *at the time of speciation.* Observing that the two species are sympatric today is not sufficient evidence of either sympatry in the past or a sister-group relationship.

The elementary processes in microevolution are genetic changes-first mutations, then changes in gene frequencies driven by selection, migration, and drift. Phenorypes with better reproductive success get more copies of the genes

Relationship between allopatric and sympatric speciation

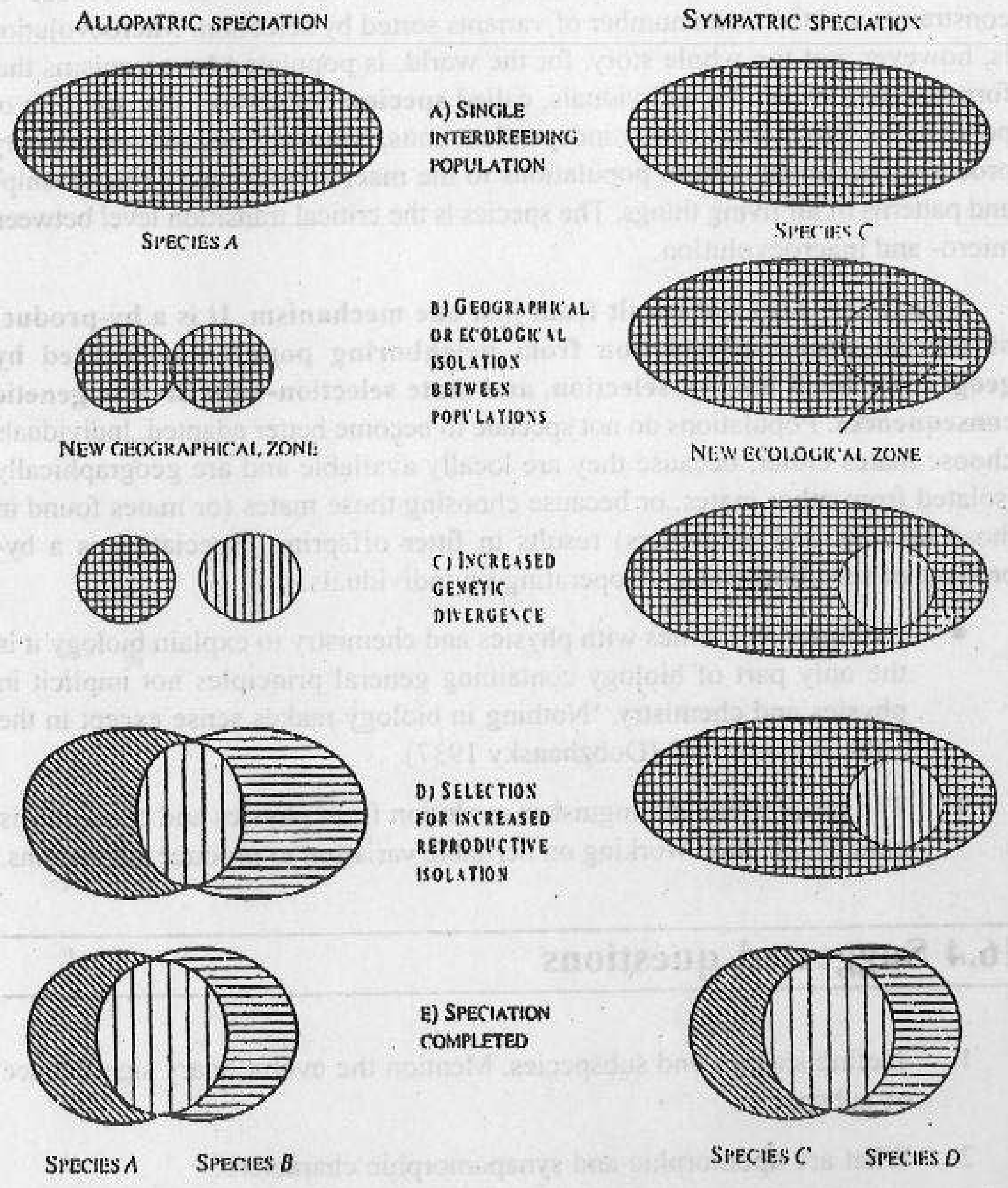


Fig : 16.6. Simplified diagram of allopatric and sympatric speciatiion, showing, different modes of divergence.

they carry into future generations, leading to inherited changes in the design o phenotypes. Adaptation-occurs but perfection does not result because o constraints and the finite number of variants sorted by selection. Microevolutio is, however, not the whole story, for the world, is populated by organisms tha form clusters of similar individuals, called **species.** Speciation, the splitting o populations into evolutionarily independent units, connects the microevolutioar processes occurring within populations to the macroevolutionary relationship and patterns of all living things. The species is the critical transition level betwee micro- and macroevolution.

Speciation does not result from just one mechanism. It is a by-produc of several processes-isolation from neighboring populations caused b geography, local habitat selection, and mate selection-with diverse geneti consequences. Populations do not speciate to become better adapted. Individual choose mates either, because they are locally available and are geographicall isolated from other mates, or because choosing those mates (or mates found i those habitats and not others) results in fitter offspring. Speciation is a by-product of selection and drift operating on individuals.

- Evolution combines with physics and chemistry to explain biology it i the only part of biology containing general principles not implicit i physics and chemistry. 'Nothing in biology makes sense except in th light of evolution' (Dobzhansky 1937).
- The process that distinguishes evolution from physics and chemistry i natural selection working on heritable variation to produce adaptations.

16.4 Suggested questions

1. Define species and subspecies. Mention the evolutionary significanc of subspecies.
2. What are apomorphic and synapomorphic characters?
3. Explain briefly Biological Species Concept. Mention the limitation o this concept.

4. 'Species are a mosaic of ancestral and derived traits' - explain.

5. Define Phylogenetic Species Concept. Why this concept is not applicable to all kinds of species?

6 What are the sources of divergence in a population? Briefly categorize the mechanism of reproductive isolation.

7. Tabulate the important isolating mechanisms that separate species.

8. What is vicariance? Explain a model of Allopatric speciation.

9. Characterize parapatric speciation. Describe the process of sympatric speciation with the help of diagram.

10. Describe with the help of a flow chart the relationship between allopatric and sympatric speciation.

11. Compare the processes of allopatric and parapatric speciation.

12. What do you mean by evolutionary species concept?

Unit 17 ☐ Origin of higher categories

Structure

17.1 Phylogenetic gradualism and punctuated equilibrium

Evolution of different characters at different rates within a lineage is called **mosaic evolution.** It is one of the most important principles of evolution, for it says that an organism (species) evolves not as a whole, but piecemeal: many of its features evolve quasi-independently. (There are important exceptions; for example, features that function together may evolve in concert.) This independence is seen not only in comparisons among distantly related taxa, but even within a species: characteristics usually vary independently among different geographic populations of a species. These observations largely justify the theory of evolutionary mechanisms, in which we analyze evolution not in terms of whole organisms, but in terms of changes in individual features or even individual genes underlying such features.

Because of mosaic evolution, it is inaccurate or even wrong to consider one living species more "primitive" or "advanced" than another. Although it is in - accurate to describe a living taxon as more primitive than another, it is often useful to speak of a BASAL lineage, one that branches off a phylogenetic tree below others with which it is compared.

Evolution is gradual

One of the most difficult issues in evolutionary biology, still a matter of contention is whether or not Darwin was right in arguing that evolution proceeds by small" successive changes (GRADUALISM) rather than by large "leaps (SALTATIONS).

Innumerable observations on both living and fossil organisms indicate that gradual evolution is common, and is likely to be the pattern in many cases in which evidence is lacking. Cases of mosaic evolution show that the various features of a higher taxon evolve piecemeal, not all at once. Cases of GRADUATION of individual characters among species imply that characters usually evolve by sma steps, not by large, discrete jumps.

The limits of higher taxa are often arbitrary points along a continuum. Many higher taxa can be defined only because gaps do exist, at least among living species.

Another line of evidence in favor of gradualism is that the same discrete characters that clearly define certain higher taxa frequently vary within or among closely related species in another taxon.

There is nothing intrinsic to a particular character that makes it diagnostic of higher taxa rather than species. Hence, it is reasonable to assume that features that now distinguish higher taxa (such as cotyledon number) arose as variations at the species level. Features that distinguish closely related species also vary within species. Thus, at every level of comparison of adjacent taxonomic levels-within vs. among species, species vs. genus, genus vs. family, etc.- many instances of gradation and of mosaic change are known. This pattern implies CONTINUITY of evolutionary change, from slight to great differences.

Arguments for Gradualism

Darwin was well aware of "sports"-what we now call mutations with large, discontinuous effects on one or more features-but held that most evolution is based on the slight individual differences that we observe within populations (which we now recognize as polygenic variation). This gradualist position was reaffirmed by neo-Darwinians such as Ronald Fisher (1930), and has been the majority opinion ever since (reviewed by Maynard Smith 1983). The *chief* *arguments of contemporary- gradualist* are based on (1) intermediates among both living and extinct species; (2) functional considerations; (3) fitness effects of mutations; and (4) the genetics of species differences.

Punctuated Equilibrium

The highly controversial idea of **punctuated equilibrium,** introduced by Eldredge and Gould (1972) and elaborated both by them (e.g., Gould and Eldredge 1977, 1993) and by Steven Stanley (1979), consists of both a *claim about the pattern of change* in the fossil record and a *hypothesis about evolutionary processes.* Many or most phenotypic characters change little over extended spans of geological time (equilibrium, or stasis), but when they do evolve, they change relatively rapidly from one static state to another (that is, the stasis is punctuated by change). The *hypothesis* that Eldredge and Gould introduced is that characters evolve primarily in concert with true speciation. Moreover, if, as Mayr hypothesized new species (reproductively isolated entities) evolves rapidly in small, isolated populations, the transitional stages in the divergence of these populations will seldom be preserved in the fossil record. Eldredge and Gould, suggested that the widespread ancestral form does not change very much because of genetic "constraints" that prevent features from changing, even if natural selection would favor new features. If a newly arisen species becomes widespread and abundant, its new features likewise become stabilized, and little further evolution occurs unless it in turn buds off new "daughter" species.

Eldredge and Gould contrasted their model with what they look to be the traditional view in paleontology - which features evolve slowly, steadily, gradually, without any particular association with speciation. They called this the "phyletic gradualism" model. Another possibility, which Malmgren *et al.* (1983) called "punctuated gradualism," is that character evolution may not necessarily be associated with speciation, but may nevertheless slow rapid transitions between long-stable states (Fig. 17.1).

Gould and Eldredge (1993) have concluded that punctuation and stasis is the most common pattern in the fossil record, but some other researchers (Levinton, 1988) disagree.

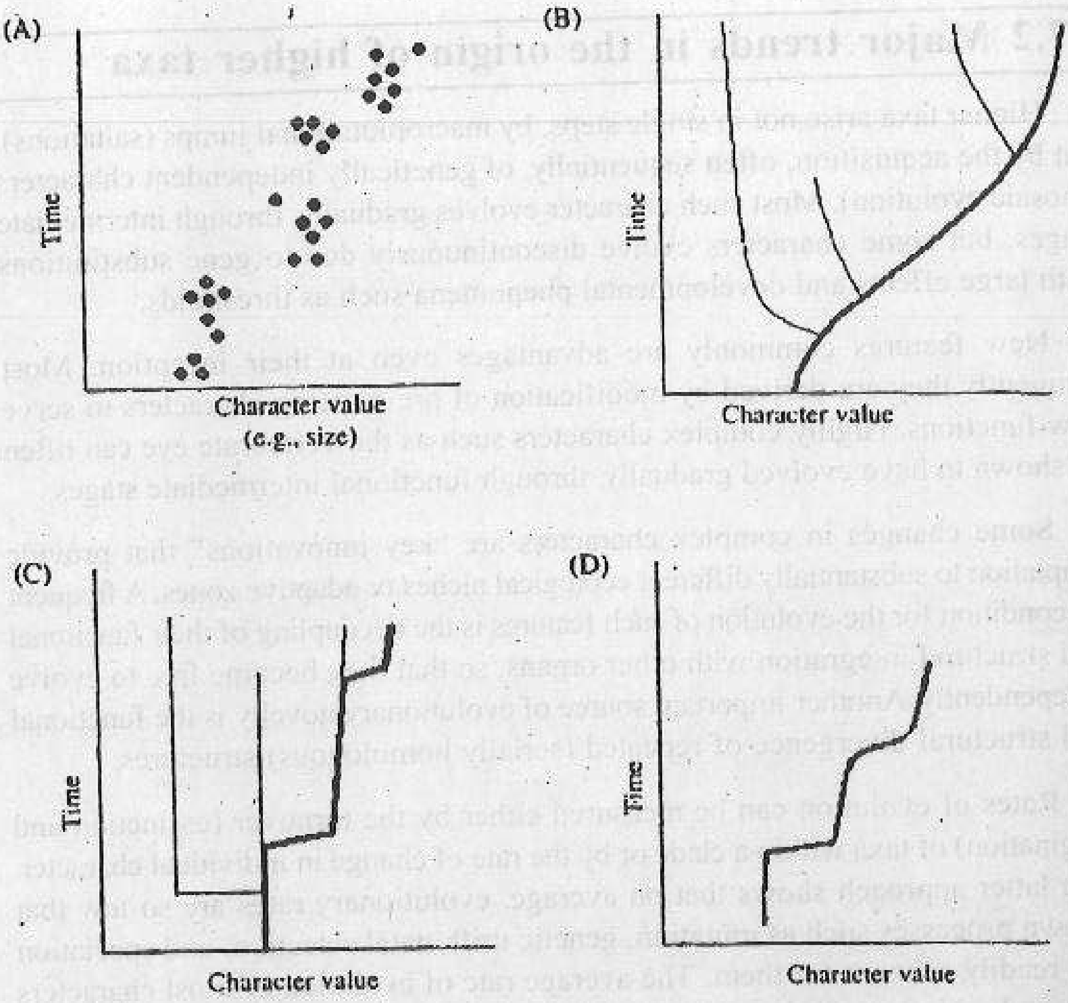


Fig. 17.1. Three models of evolution, as applied to a hypothetical set of fossils (A). (B) The "phyletic gradualism" model, said by Eldredge and Gould to be the traditional paleontologicalj model. The data in panel A might correspond to the boldly darkened line. Evolutionary change is not associated with speciation. (C) The "punctuated equilibrium" model of Eldredge and Gould, in which morphological change occurs in new species, while the parent species remain' unchanged. Morphological evolution, although rapid, is still gradual, as shown in the inset, which illustrates the shift in the mea of the variable character. (D) The "punctuated gradualism" model of Malmgren *et al.* (1983), in which a lineage rapidly evolves from one equilibrium to another, but speciation need not occur. The absence of intermediates between successive morphologies is attributed to the imperfection of the fossil record.

17.2 Major trends in the origin of higher taxa

Higher taxa arise not in single steps, by macromutational jumps (saltations), but by the acquisition, often sequentially, of genetically independent characters (mosaic evolution). Most such character evolves gradually, through intermediate stages, but some characters evolve discontinuously due to gene substitutions with large effects and developmental phenomena such as thresholds.

New features commonly are advantages even at their inception. Most frequently they are derived by modification of pre-existing characters to serve new functions. Highly complex characters such as the vertebrate eye can often be shown to have evolved gradually, through functional intermediate stages.

Some changes in complex characters are "key innovations" that provide adaptation to substantially different ecological niches or adaptive zones. A frequent precondition for the evolution of such features is the decoupling of their functional and structural integration with other organs, so that they become free to evolve independently. Another important source of evolutionary novelty is the functional and structural divergence of repeated (serially homologous) structures.

Rates of evolution can be measured either by the turnover (extinction and origination) of taxa within a clade or by the rate of change in individual character. The latter approach shows that on average, evolutionary rates are so low that known processes such as mutation, genetic drift, natal selection, and speciation can readily account for them. The average rate of evolution of most characters is very low because long periods of little change ("stasis") are averaged with short periods of rapid evolution; but known processes such as natural selection can readily explain even the rapid shifts.

Origin of higher categories

The term "higher categories" refer to the units of classification called genus, family, order, class and phylum. Families, and even more strikingly orders, consist of groups of animals that have a characteristic similarity in their manner of life and occupy certain envirormental (ecological) "niches'. A comparable figure of speech for the broader limits of adaptation characterizing families and orders is ADAPTIVE ZONE (Simpson 1953). The processes of speciation will lead to the formation of families (and orders) if a species is fortunate enough to find a broad adaptive zone open to it. For most species this opportunity will not be present; for them the processes of speciation lead to adaptation to narrower environment niches. Such niches may continue to exist for a long time, or they may disappear as the environment changes. If they disappear, occupants of the niche usual become extinct, though a small minority may be able to shift to another niche another way of life. But occasionally a species is offered a larger opportunity.

A higher category is higher because it *became* distinctive, varied, or both to a higher degree and not directly because of characteristics it had when it was arising. Modern members of genus *Equus* and their prehistoric relatives ancestors are included in the family Equidae. How do such families arise evolution? In effect, there was no family Equidae when eohippus *(Hyracotherim)* lived. The family and all its distinctive characters developed gradually as time went on. There is no particular time at which the Equidae became a family rail . than a genus or a species; the whole process is gradual and we assign the categorical rank after the result is before us (Simpson 1953).

Broad adaptive zones are frequently divided into subzones, and so at am given time a taxonomic family is likely to contain subdivisions adapted to these subzones. So in the early Pliocene we find three-toes browsers in the forest and three-toed grazers on the plains. In other words, adaptive radiations occur. *Miohippus*, for example, in addition to giving rise to *Parahippus* was ancestral to *Anchitherium andArcheohippus*, two "horses" we have not mentioned previously. They became extinct; only *Parahippus* gave rise to a higher type of horse: *Merychippus*, a three-toed grazer. *Merychippus*, in turn, was ancestral to at least six lines of descendants, most of them three-toed grazers; but one of them, *Pliohippus*, was the first one-toed grazer.

When we turn our attention from families to orders we find that adaptive zones are still broader. Most orders of mammals, for example, consist of assemblage of families that have some striking characteristic in common-some adaptive trait that characterizes them all. The multitudinous members of the order Rodentia, for example, all have gnawing incisor teeth. Members of the order Catacea, whales and porpoises, have their well-known adaptations for aquatic life. The order Proboscidea, elephants, mastodons and their ancestors, we have already discussed. Bats, of the order Chiroptera, have wings. Members of the order Carnivora - e.g.. cats of all kinds, wolves, bears, weasels, and skunks-have teeth adapted for flesh eating. And so it goes. Of the orders we mentioned especially Perissodactyla, the odd-toed hoofed mammals, and Artiodactyla, the even-toed hoofed mammals. Both orders are herbivorous and have developed long legs for running away from enemies.

Both perissodactyls and artiodactyls are believed to have arisen from Paleocene condylarths. The fundamental difference between the two lines was in the manner in which the weight of the body was distributed in the limbs. In perissodactyls the weight-bearing axis runs through the third digit. In artiodactyls the weight is borne equally by the third and fourth digits. Presumably this difference in the manner of body support arose among the condylarths. Condylarths starting the trend toward prominence of the third digit gave rise eventually to rhinoceroses, tapirs, horses and so on. Condylarths starting the trend toward equal prominence of the third and fourth digits gave rise eventually to antelopes, deer, cattle, pigs, buffalo, camels and their numerous relatives-a much larger assemblage than that of the perissodactyls.

In the above example we have assumed that all perissodactyls had one common ancestor and that ariodactyls had one common ancestor. In the case of orders, and especially of classes, there is always the possibility that not all the organisms placed in one order or class did in fact inherit the distinctive trait from a single ancestral group. We must never forget the possibility of parallel evolution. In the case of the class Mammalia itself we noted that several lines of therapsid reptiles became essentially mammalian. The question of whether a given taxonomic group is *manophyletic* (composed of organisms all inheriting form a common ancestor) or *polyphyletic* (composed of organisms of diverse ancestries) is much debated.

The evolution of vertebrate novelties

Structural novelties (or "key innovations") are associated with adaptive radiations into new ecological territories. The movement of vertebrates onto land is tied to the evolution of the tetrapod limb; the escape of insects into their adaptive range required the evolution of wings. The distinctive molar tooth shape has evolved indecently several times in association with herbivory. Other novelties such as feathers and butterfly scales permit the display of colors and color patterns used for communication or predator avoidance' (Carroll *et al.* 2005).

New structures require the evolution of new developmental programme "novelty" is defined as a structure or pattern element, or even an entire body plan that has a new adaptive function.

Quantitative morphological variation, even when extreme, is not consider novel unless it encompasses a fundamental functional shift. Thus me homologous body parts are not considered novelties, even when the range of a vertebrate forelimb, for example, extends from the gigantic size of a whale flipper to the tiny arm of a tree shrew.

The success and ecological dominance of the vertebrates can be attribute to several unique traits that arose during the evolution of vertebrate lineage include the following:

- The notochord
- Populations of cranial placodes and neural crest cells
- Jaws
- Paired pectoral and pelvic limbs

By comparing the morphology, ontogeny developmental genetics and fossil history of vertebrates and other chordates (such as the cephalochordate amphioxi and urochordate ascidians), it is possible to trace the evolutionary origins of these structures. Conserved regulatory genes control the pattern of these new developmental fields and tissues, revealing once again that new developmental programs have evolved through the co-option of existing regulatory genes and circuits and the expansion of ancestral patterning roles.

Evolution of the notochord - an example of origin of higher taxa

The evolution of the notochord involved the co-option of an ancestral regulatory gene, *Brachyury (T),* a member of the T-box class of transcription factor (Fig. 6.2). In vertebrates, 7 is expressed in developing notochord cells and other mesodermal derivatives and is required for notochord differentiation. Similarly, the urochordate (ascidian and larvacean) *T* genes are expressed in cells that form the notochord and are sufficient to confer notochord fate. In larvaceans as well as hemichordates and invertebrates that lack a notochord, homologs of the *T* gene are expressed in posterior gut tissues. This expression may reflect the ancestral function of *T* before the evolution of the notochord. This gene began to play a new role in notochord development after the chordate and hemichordate /echinoderm lineages became separated, as the hemichordate *T* gene is not expressed in the stomochord (a possible precursor of the notochord).

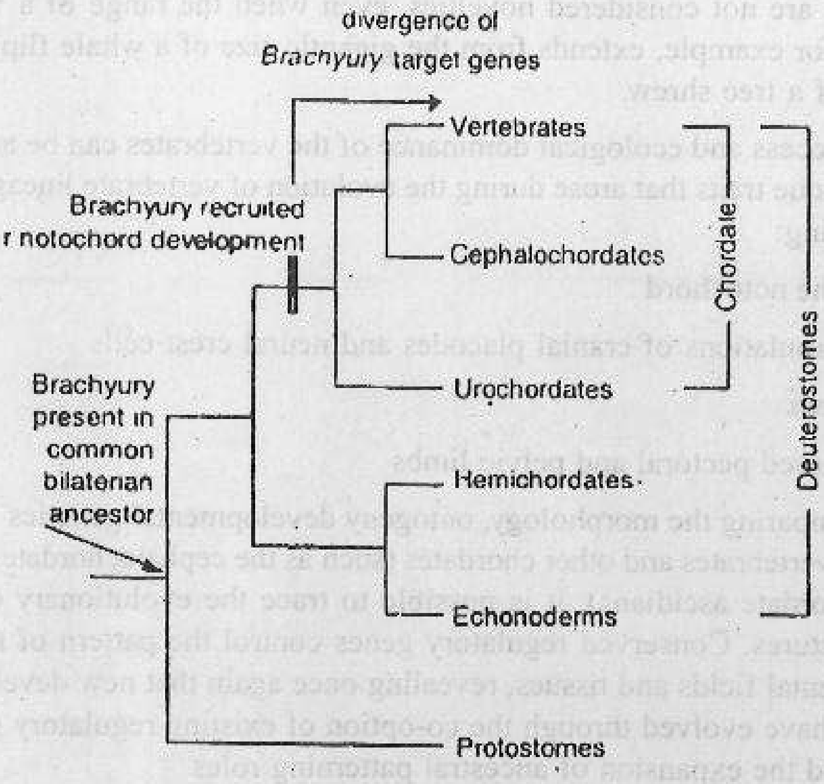


Figure 17.2. Recruitment of the *Brachyury* gene during evolution of the notochord

The *Brachyury (T)* gene predates the origin of the chordate notochord. During the early evolution of the chordates, expression of the *T* gene was recruited to pattern the notochord. Targets of the *T* gene have evolved as the chordate lineages have diverged (after Carroll *et al.* 2005).

17.3 Micro and Macroevolution

One of the most important tenets of the theory forge during the Evolutionary Synthesis of the 1930s and 1940s was that "macroevolutionary" differences among organisms - those that distinguish higher taxa - arise from the accumulation of the same kinds of genetic differences that are found within species. Opponents of this point of view believed that "macroevolution" within species, and are based on a totally different kind of genetic and developmental repatterning. The iconoclastic geneticist Richard Goldschmidt (1940), who held this opinion, believed that the evolution of species marks the break between "microevolution" and "macroevolution"- that there is a "bridgeless gap" between species that cannot be understood in terms of the genetic variation within species. Genetic studies of species differences have decisively disproved Goldschmidt's claim. *Differences between species* in morphology, behavior, and the processes that underlie reproductive isolation all *have the same genetic properties as variation within species;* they occupy consistent chromosomal positions, they may be polygenic or based on few genes, they may display additive, dominant, or epistatic effects, and they can in some instances be traced to specifiable differences in proteins or DNA nucleotide differences. *The degree of reproductive isolation between populations,* whether prezygotic or postzygotic, *varies from little or none to complete.* Thus, *reproductive isolation, like the divergence of any other character, evolves in most cases by the gradual substitution of alleles in populations.*

The causes of evolution within populations and species may be considerable over the course of sufficient time; they are often referred to as *Microevolution.* The principles of *Macroevolution* deal with the origin and diversification of higher taxa. Many biologists consider the study of species and speciation to constitute the bridge between microevolution and macroevolution. Macroevolution can be defined as the pattern at above the species level, including most of fossil history and much of systematics. On the other hand, microevolution is the process of evolution within populations, including adaptive and neutral evolution.

Population and quantitative geneticists think about microevolution, which occurs within populations over relatively short period of time; about the effects of changing the frequency of the different forms that one gene can take (its alleles) or holding these frequencies at a stable intermediate level. The main aspect is to understand what maintains genetic variation. Microevolution describes how populations change in the relative abundance of genes or phenotypes. Two concepts and a link between them explain microevolution. The two concepts are heritable variation in traits and variation in reproductive success among individuals within a population. The link is the correlation between the two types of variation. These three elements explain both adaptive and neutral evolution. When the correlation between reproductive success and a trait is positive or negative, natural selection is operating on that trait, for natural selection consists precisely of variation in reproductive success correlated with variation in a trait. When that correlation is zero, natural selection disappears, even though variation in reproductive success may remain, and is termed as neutral evolution.

Macroevolution describes patterns perceived in the comparisons of species and larger groups - families, orders, and phyla. How microevolution connects to macroevolution is an important question that has not yet been answered satisfactorily. A promising approach suggests that the microevolution of developmental mechanisms produces constraints on the further evolution of the organisms containing those mechanisms. Different lineages evolve different developmental mechanisms. All the species sharing developmental mechanisms may therefore also share similar body plans and evolve under similar constraints. This is probably why we can recognize major groups of organisms by their body plans, what Darwin called Unity of Type.

Evolutionary change: adaptive and neutral

Microevolution describes how populations change in the relative abundance of genes or of phenotypes. Two concepts and a link between them explain microevolution. The two concepts are heritable variation in traits and variation in reproductive success among individuals within a population. The link is the correlation between the two types of variation. These three elements explain both adaptive and neutral evolution. When the correlation between reproductive success and a trait is positive or negative, natural selection is operative on that trait, for natural selection consists precisely of variation in reproductive success correlated with variation in a trait. When that correlation is zero, natural selection disappears, even though variation in reproductive success may remain, and what is left is neutral evolution.

The production of surviving offspring is achieved through the number of offspring born, their survival, the survival of the parents to reproduce again, the number of offspring they have in their second and subsequent breeding attempts, the survival of those offspring, and so forth. Variation in reproductive success is made up out of variation in all these components.

On the one hand, if there were no variation in reproductive success, neither the distribution of genes nor the distribution of phenotypes would change. (This statement excludes mutations, which affect the variation in reproductive success of molecules). Note that there is always some variation in reproductive success in natural populations. For example, in Newton's (1988) study of sparrow hawks in southern Scotland, 72% of the females that fledged died before they could breed, 4.5% tried to breed but produced no young, and the remaining 23.5% produced between 1 and 23 young apiece.

On the other hand, if there is no heritable variation in a trait, there will also be no evolutionary change-even if there is variation in reproductive success-for the differences in performance exhibited by the parents will not be reflected in the offspring. Only if there is some variation both in the trait and in reproductive success can there be a correlation between the two producing natural selection. Both conditions are necessary for adaptive change. Both are also necessary for neutral change, in which case the correlation between the two must be near zero.

When there is both heritable variation and variation in reproductive success, it is the correlation between them that determines the type of evolutionary change that occurs. If there is little or no correlation between heritable and reproductive variation, then the things that are inherited and that do vary, whether genes or traits, will fluctuate randomly in the population within the limits of the available variation. This is **neutral evolution.** If the correlation between reproductive success and heritable variation is strong, then evolutionary change in the gene or trait will not be random but will move in the direction of increasing adaptation. This is **adaptive evolution.** The engine of adaptive evolution, **natural selection,** consists of two of the three parts of the evolutionary mechanism: variation in reproductive success and the correlation between reproductive success and the trait under consideration. It does not include the heritable variation that enables a response to selection.

17.4 Suggested questions

1. What do you mean by mosaic evolution? What is basal lineage?
2. Explain the concept of phylogenetic gradualism.
3. Enumerate 'punctuated equilibrium' concept introduced by Eldredge and Gould and compared it with model proposed by Malmgren and coworkers.
4. What is 'macromutational jumps'? Define stasis. Why 'key innovations' are important in evolution?
5. Explain with a suitable example how higher taxa originates.
6. What are 'evolutionary novelties' ? Mention some important examples.
7. Write a short note on evolutionary novelties.
8. What do you mean by evolutionary turnover?
9. Distinguish between macro- and microevolution. What phenomenon can be considered as bridge between them?
10. How you can distinguish between neutral evolution and adaptive evolution?
11. Describe the process of microevolution.
12. Analyze the process of macroevolution.

Unit 18 ☐ Molecular Phylogenetics

Structure

18.1 How to construct phylogenetic trees

Systematics estimates the relationships among taxa to get working hypotheses in the form of phylogenetic trees. A phylogenetic tree records the history of a group.

To construct a phylogenetic tree, one first determines which characters are homologous, measures them on all the taxa being analyzed then codes the measurements for analysis. Different coding can produce different results.

Trees are built from data using methods that can produce different trees. If all methods yield the same branch of a tree in a large and reliable data set, then that branch can be regarded with confidence. If the data are equally consistent with several branching patterns, judgment about relationships should be suspected.

Phylogenetic analyses are becoming increasingly reliable. They are producing surprises about both relationships and character evolution.

Molecular systematics is not only used to build trees of relating species; it is also used to construct the history of single genes. The trees constructed from different genes in the same organisms often have different structures because each gene has had a different evolutionary history. For events occurring within a species, the recovery of a reliable gene genealogy must be done in sequences with little or no recombination, such as the mitochondrial genome, because recombination produces nets, not branches. A gene genealogy can differ from a species phylogeny because mutations do not occur simultaneously and are not constrained to occur during speciation (Fig. 7.1). One gene may have diverged prior to a speciation event; another gene may have diverged after that speciation event. Thus genes have different genealogies, and only some genealogies have the same structure as the phylogeny of the species in which the genes occur.

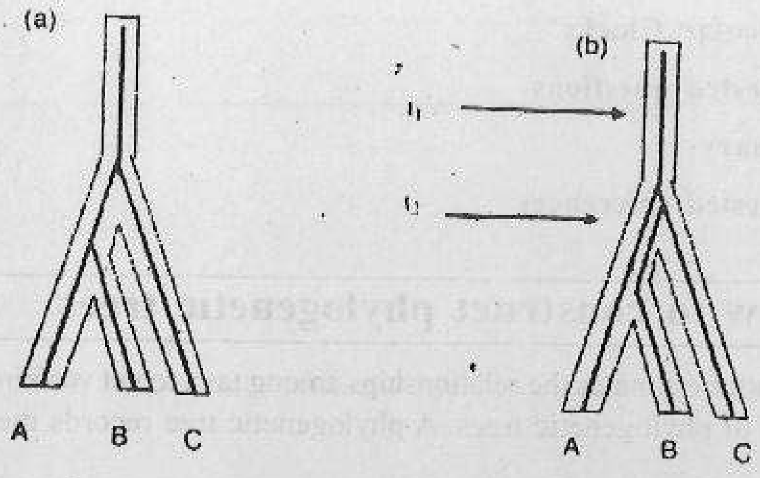


Fig. 18.1. Phylogenies of species and genealogies of genes. The species tree is described by the large outer figure and is the same in both cases. The lines contained within the tree describe the gene genealogy. Whenever more than one line is present, the gene is polymorphic. In both cases there is a mutation at rime t_1, prior to the speciation event, (a) The gene tree and the species tree have the same branching pattern, i.e. the second mutation occurs between the first and the second speciation event, (b) The genes and species have different branching patterns. The second mutation event occurs shortly after the first mutation event at time t_2, and the genealogical spilt predates species divergences (Avise 1994).

A Hypothetical ***Example:***

Unrelated person AAGCTTCATAGGAGCAACCATTCTAATAAT

Suspect A	AAGCTTCACCGGCGCAGTTATCCTCATAAT
Suspect B	GTGCTTCACCGACGCAGTTGTCCTTATAAT
Rape victim	GTGCTTCACCGACGCAGTTGCCCTCATGAT

Using a computer program, one can prepare a phylogenetic tree based on these four sequences. The program examines all the possible trees and delivers the one that implies fewer mutations in nucleotides than any other (Fig. 7.2).

This tree clearly suggests that the Suspect B infected the rape victim. The conclusion is supported by four changes in sequence that are shared by the Suspect B and the victim at position 1, A®G; at position 2, A®T; mat position 12, G®A; and at position 20, A®G. since the rape occurred the virus has continued to evolve in both suspect and victim. In the Suspect there has been a change at position 25,C®T; and in the victim there have been two changes, at position 21,T®C and at position 28, A®G.

This example is artificial but shows how to construct a genealogical tree.

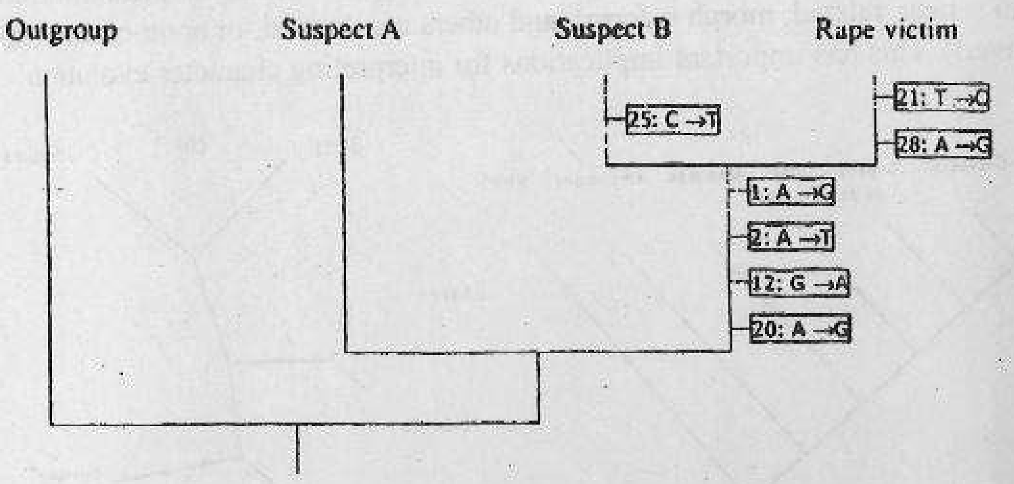


Fig. 18.2. The phylogenetic tree based on the nucleotide sequences in the text that implies the fewest changes overall. The tree is rooted using the unrelated person, and it clearly identifies the Suspect B as the probable rapist. The character changes that support each branch unambiguously are listed (Prepared by C. Baroni-Urbani).

What is phylogeny?

A phylogeny is a hypothesis about relationships expressed as a tree diagram. All parts of a tree are inferred except for the tips of the branches, which are the observed and described species, living or fossil. The usual phylogenetic methods assume that there is no hybridization or horizontal gene transfer through microbial vectors once speciation is complete (this is certainly not the case for many bacteria). Fossils, which help to test, support, and calibrate phylogenetic trees, are usually interpreted as tips of dead branches, not as direct ancestors of living species.

Types of phylogenetic trees

Phylogenetic trees may be rooted or unrooted (Fig 18.3). To root a tree, one uses an outgroup that is clearly not in the group being analyzed; a sister group is best if it can be identified reliably. Thus the outgroup for a phylogeny of the tetrapods should be a fish, probably a lungfish, not an echinoderm. The connection to the outgroup defines the root of the tree. If the tree is unrooted, then one cannot identify the outgroup or-as in the tree of life-there is no outgroup because cellular life is thought to have originated only once. Rooting a tree is an important step, for rooting introduces the notion that some character states are ancestral, or plesiomorphic (plesio = near, related; morph = form), and others are derived, or apomorphic (apo = derived). This has important implications for interpreting character evolution.

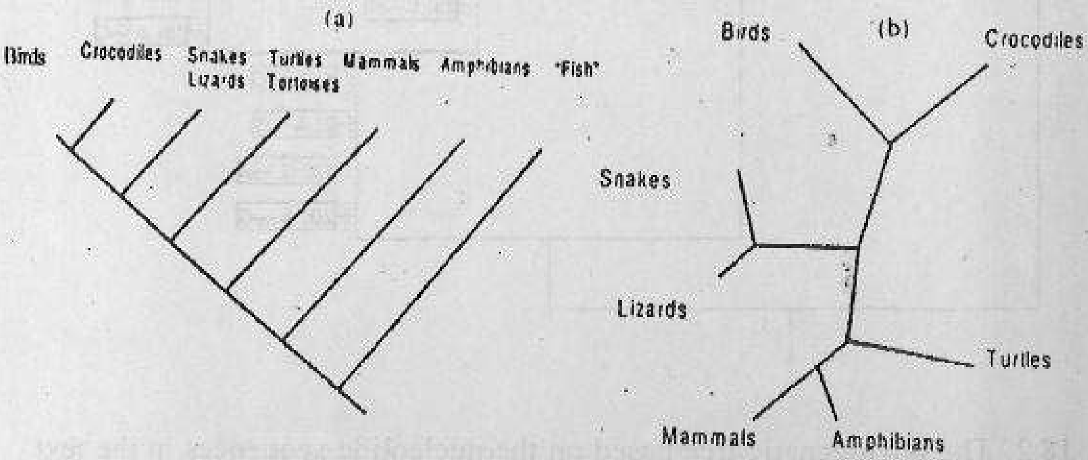


Fig. 18.3 (a) A rooted tree of the living tetrapods. The evolutionary sequence is clear, and the outgroup ('fish') is specified, (b) An unrooted tree. There is no outgroup, and the evolutionary sequence is obscure.

Hennig introduced several important Greek terms that are now commonly used in systematics:

PLESIOMORPHY (adjective, plesiomorphic): An ancestral (primitive character state (with reference to another, derivied, state).

SYMPLESIOMORPHY: An ancestral character state shared by two or more taxa.

APOMORPHY: A derived ("advanced") character state (with reference to another, ancestral, state).

SYNAPOMORPHY: A derived character state shared by two or more taxa.

AUTO POMORPHY: A derived character state possessed by only one of the taxa under consideration.

COMMON ANCESTOR: A species that at some past time split into two (or more) species, each of which gave rise to one of the clades under discussion. Because all organisms are believed to have descended from one remote common ancestor, any two taxa have had a common ancestor at some time in the past. (For example, even though no amniote vaguely resembling either a human or a snake existed 300 million years ago, this is the minimal estimate of the time since these lineages diverged; the synapsid reptiles, from which mammals evolved, were by this time distinct from the diapsid lineage that much later gave rise to snakes.)

NODE: A branch point in a phylogenetic tree. It represents a common ancestor at the time of divergence into two or more lineages.

TERMINAL TAXA: Taxa at the tips of a phylogenetic tree, such as whale and human. The term *operational taxonomic unit* (OUT) is approximately synonymous.

SISTER GROUPS (or SISTER TAXA): Two groups with the same immediate common ancestor. (Either group may contain one or more than one species.)

STEM GROUP and CROWN GROUP (used especially in discussing taxa with a fossil record): A stem group is an ancestral group, with relatively primitive characteristics, from which a crown group with relatively "advanced" characteristics has evolved. Often the crown group is extant and the stem group is extinct.

GROUND PLAN: The set of character states typical of relatively unmodified members of a clade. For example. the ground plan of mammals includes teeth differentiated into incisors, canines, premolars, and molars. Some mammals, such as anteaters and whales, have evolved away from this ground plan, having homogeneous teeth or none.

18.2 Phylogenetic inference-Distance methods, Parsimony methods, minimum likelihood method

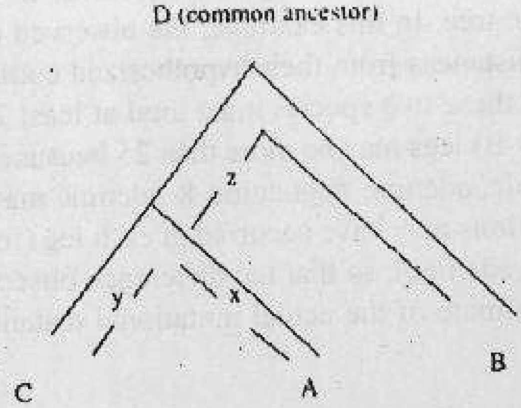
There are three commonly used methods for building trees; parsimony, distance, and maximum likelihood. Parsimony methods apply the logic of cladistics to molecular data, morphological data, or both together. Distance and maximum likelihood methods are usually applied to DNA sequence data where homoplasy is common.

Parsimony methods

This family of methods is based on cladistics; simpler hypotheses are preferred to more complicate ones, and shared derived similarity is decisive. As much similarity among taxa as possible is explained by common ancestry. In most data sets, some characters will conflict with this explanation, making necessary assumptions of homoplasy (convergence, parallelism, or reversal). When parsimony is applied to sequence data, evolutionary rates must be small or nearly equal in different lineages if the method is to yield trees that approach the true tree with increasing amounts of data. Otherwise, the information needed will be washed away by repeated mutations to one of the only four possible nucleotide states (this effect is also called saturation).

The Parsimony Principle, also known as "Occam's razor." Parsimony has the advantage that a true hypothesis generally involves fewer assumptions than a false hypothesis; for example, we can better explain a phenylalanine codon (UUU) as deriving from a single nucleotide substitution in a serine codon (UCU ® UUU) than as deriving from a triple nucleotide substitution in a glutamic acid codor (GAA®UUU). Note that "unparsimonius" explanations are not necessarily false, but, *in the absence of further information,* choices are made on the bases of parsimony.

Given parsimoniously determined evolutionary distances between species, resolving their phylogenetic relationships can follow. For example, if the minimum or most parsimonius mutational distance for a particular protein comparison between species A and B is 25, between A and C is 20, and between B and C is 30, then the two most closely related species are obviously A and C. If we assign legs *x*, *y* and z to represent the numbers of mutations responsible for their divergence, we can portray the phylogenetic relationship among the three species as follows:

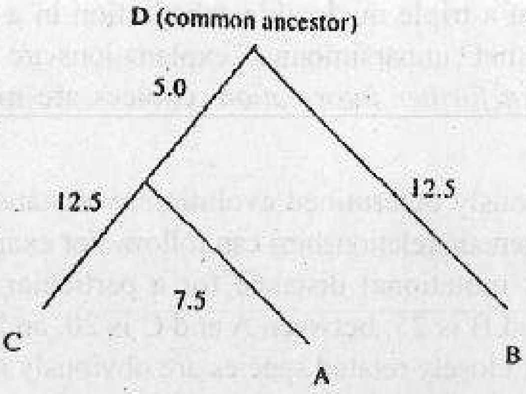


We can determine the lengths of these legs by noting that the A-B distance (25) is less than the C-B distance (30), hence the leg x must be 5 mutations less than y. since $x + y = 20$ and $y - x = 5$, we can subtract one equation from the other and solve for x :

$$x + y = 20 - (- x + v = 5) \quad 2x = 15 \quad x = 7.5,\ y = 12.5$$

The leg z must therefore equal the A-B distance minus x (or the C-B distance minus y); that is, $z = 25 - 7.5$ (or $30 - 12.5$) $= 17.5$.

These mutational distances therefore yield.



It is to be noted that an important condition of the parsimony method is the observed mutational distance between two species must be less than or equal to the sum of the distances from their common ancestor to each species in the projected phylogenetic tree. In this example, the observed distance between A and B is 25, and the distances from their hypothesized common ancestor at the triangular apex (Di to these two species must total at least 25, if not more. The sum of the (D-A) + (D-B) legs may be more than 25 because undiscovered **back mutations** (for example, adenine ® guanine ® adenine may exist in these two legs, or **parallel mutations** may have occurred in each leg (for example, cytosine ® adenine; guanine ® adenine). so that the difference observed between A and B is really an underestimate of the actual mutational distance.

Distance methods

A distance is the number of differences in character states between two taxa. All distance methods start by calculating the distances between all pairs of species. Common methods include cluster analysis, neighbor-joining, and optimality methods.

Cluster analysis

Cluster analysis is simple and fast but flawed. It assumes that changes occur at the same rate along all branches of the tree, whichi9s questionable, and that grouping on the basis of total similarity is logically valid, which ignores the cladistic distinction between informative synapomorphies and uninformative plesiomorphies.

Neighbor joining

Neighbor joining is the most important of the methods that yield additive trees, trees in which it is assumed that the lengths of the branches between any pair of taxa can be summed to yield the amount of evolutionary change that has occurred between them. It proceeds by linking the closest pair of nodes, which converts the new common ancestor into a terminal node on a smaller tree; then continuing. This method can deal with trees in which changes are occurring at different rates in different branches.

Optimally methods

There are several definitions of optimality and ways to find the best tree. Optimally methods produce estimates of the uncertainty with which we can view - the various parts of trees.

Maximum likelihood methods

Maximum likelihood methods find the most likely tree given the data. That tree is found be considering a large set of hypothetical, candidate trees-all possible trees or a representative sample of them. For each candidate tree the probability is calculated that a given initial state will yield a given final state at the end of a defined interval of time. The probabilities for all changes in the tree are then multiplied to yield the total likelihood of the tree. In making those calculations, branch lengths play an important role. The best tree is then the one with the maximum likelihood (Felsenstein 1988). The method is logically appealing and computationally expensive. Its range of application is increasing as computers improve.

18.3 Immunological Techniques

Comparative molecular methods use immunological techniques in which antibodies produced in a particular host (usually a rabbit) against proteins (antigens) of one-species are measured for their activity against proteins of other species. For example, if antibodies against species A precipitate much of the protein in species C but little of the protein in species B, then researchers presume the A and C proteins have more similar molecular configurations (antigenic components) and are more evolutionary alike (smaller **antigenic distance**) than those of A and B.

Using a variety of antibodies, one can analyze immunological data by various mathematical rules (algorithms) to construct a phylogenetic tree that best correlates the antigenic distance between species with the length of time since they shared a common ancestor. If species A and C are aritigenically closer to each other than to species B, we can presume species B broke off earlier from the common stem that all three originally shared. Successive comparisons are then made between all possible combinations of species until the entire phylogenetic tree is obtained.

Other immunological techniques, such as the **microcomplement fixation** (Sarich and Wilson 1966). involve measuring antibodies produced against specific proteins found in blood serum (albumin and transferrins) or enzymes such as lysozyme. Antigenic distances, which can be detect by measuring the amount of antigen-antibody reactions provide data that generally support the phylogenies we can obtain by other taxonomic methods, although some differences occur. In microcomplement fixation, rabbits immunized with a protein antigen from one species produce antiserum that gives a strong reaction against that antigen (homologous antigen) but not against the same protein from another species (heterologous antigen). The degree of antigenic difference is then measure between the two species by the concentration to which the antiserum must increase for the heterologous antigen to react like the homologous antigen.

18.4 Amino acid sequence and Phylogeny

Amino acid sequences

One of the first molecular phylogenetic analyses (Fitch and Margoliash, 1970) used the amino acid sequence of cytochrome *c* to describe the phylogeny of numerous vertebrates and other taxa. The characters used are either the amino acid sequences themselves or the nucleotide sequences of the encoding genes, inferred from the genetic code.

Popular, approach to molecular phylogeny is sequencing the amino acids in proteins by biochemical methods and comparing such sequences for the same protein in different species. Among the first proteins to yield its amino acid sequence was **hemoglobin,** and it probably still remains one of the most investigated of all proteins. The basic unit of hemoglobin consists of an iron-containing porphyrin (heme) that reversibly can bind oxygen attached to a globin. polypeptide chain that is usually no less than 140 amino acids long. The demonstration that hemoglobin-like molecules appear in a wide range of organisms, from invertebrates to vertebrates, and even in plants, fungi and bacteria (Hardison) indicates their origin far back in the history of life. In vertebrates, hemoglobins are usually the primary protein of red blood cells, making them relatively easy to isolate and purify in large amounts.

Red blood cell hemoglobin of normal human adults is a four-chain molecule or tetramer, consisting of two pairs of polypeptide chains, one pair bearing the a sequence and the other pair mostly bearing the b sequence (a_2b_2). Some adult hemoglobin uses d chains instead of b's (a_2d_2), and a common form of embryonic hemoglobin has two a's and two g's (a_2g_2). Other types of hemoglobin chains also occur (for example, e), and hemoglobin-like molecules such as **myoglobin** appear in other tissues. All these chains are distinguished by their somewhat different properties and different amino acid sequence.

That a species can possess different kinds of globin molecules and each such molecule can differ among different species, points to two major kinds of globin evolution:

- Different kinds of globin chains arose during evolutions, producing the variety carried by a particular vertebrate (a differs from b, which differs from g, and so on).
- Each particular globin chain followed its own evolutionary path, leading to changes in its amino acid sequence in different species (a chains are different in different species, as are b chains, and so on).

The figure given below portrays the genetic phylogeny of the five globins in terms of the numbers of nucleotides necessary to account for the amino acid differences, along with the chronological periods in which evolutionists presume each duplication occurred (Fig. 18.4). We can see that duplication events led to the early coexistence of myoglobin with an a-like chain, the former probably assuming (or maintaining) an intracellular function and the latter probably assuming a circulator function.

When a duplication of the a-like gene further evolved into a b-like gene, the advantage of having two pairs of different chains in a tetramer hemoglobin molecule must have been sufficiently great to account for preserving tetramer organization in the circulating blood of most vertebrates. After the b-like gene formed, a translocation separated it from a and transferred it to a different chromosome. Duplications then occurred in the b-like gene, eventually yielding the modern b. g. and d genes.

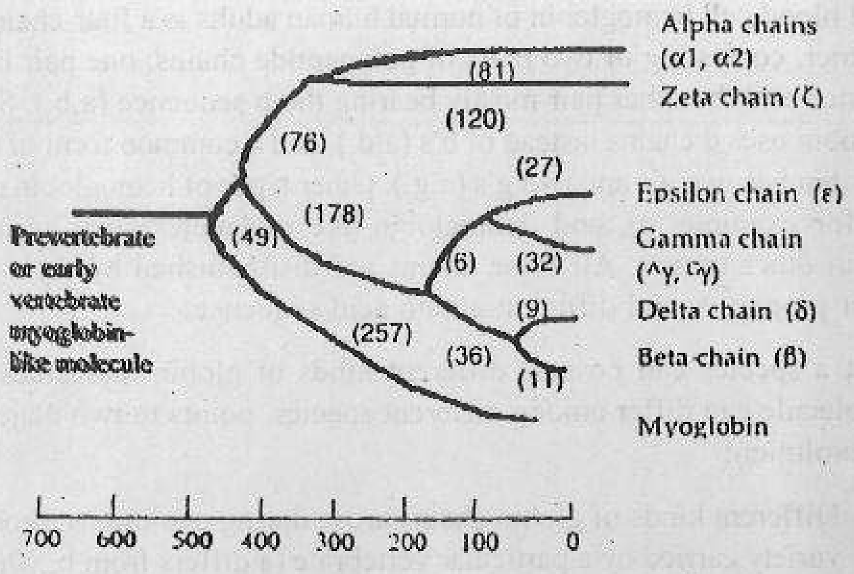


Fig. 18.4. Phylogenetic relationships between globin type proteins found in humans, showing the estimated times at which they originally diverged from each other. The estimated number of nucleotide replacements necessary to cause the observed amino acid changed in each branch of the lineage is given in parentheses.

18.5 Nucleic acid phylogeny

DNA-DNA hybridizaton : The thermal stability of heteroduplexes formed by complementary strands of DNA from two species is taken as a measure of the overall similarity of their DNA. The similarity is measured by a *single number* quantifying similarity or its complement, "distance". Many cladists object to the use of "distance value" for inferring phylogeny, partly because one does not have information on the state of each individual character (i.e., each base pair), so one cannot determine how much of the overall similarity is due to synapomorphies, and how much to simple-siomorphies. Advocates of the technique respond that averaged over millions of nucleotide sites, differential rates of evolution are likely to cancel each other out, so that overall similarity should accurately reflect recency of common ancestry. Two groups of investigators have independently used this method to assess relationships among humans and apes (Sibley and Ahlquist, 1987); Caccone and Powell, 1989). and both arrived at the same phylogeny that has been derived from DNA sequence data.

The two strands of the DNA double helix become separated (denatured) at high temperature, and reestablish their structure (reanneal) when the temperature is lowered. The heat required to denature a DNA sequence depends on the degree of complementarity of the two strands: the more bases of one strand are mismatched with those of the other (i.e.. the greater the number of departures from A-T and G-C pairing), the less heat is required.

A genome that has been fragmented by restriction enzymes can be heated to produce single strands. These DNA fragments are then bound to a filter, and the filter is exposed to another, similarly treated but radioactively labeled, preparation of DNA fragments. The filter bound DNA might be from one species and the radioactively labeled DNA from another. As the temperature is lowered, the free fragments "hybridize" with the filter-bound fragments to which they are complementary, forming double-stranded (duplex) DNA. The *rapidity* of such "hybridization" depends on how likely a fragment is to "find" a complement; this is more likely for a highly repetitive DNA sequence, so the dynamics of reannealing can measure the proportion of the genome that consists of highly or moderately repetitive sequences. The *stability* of the hybridizes duplexes, measured by how much heat is required to separate them again, is a measure of how complementary their base pair sequences are overall. This technique may be used, for instance, to measure the overall sequence similarity of the DNA of two different species.

- **Restriction enzyme sites.** A certain DNA sequence (e.g., mitochondrial DNA) may show either presence or absence of a specific restriction site (i.e., a four- or six-base sequence that is cleaved by a specific enzyme). Each restriction site is treated as a character with two states, and the data can be analyzed by a standard cladistic method.

A number of enzymes have been isolated, mostly from bacteria, that recognize specific, short (e.g., four or six base pairs) DNA sequences ("restriction sites") and cut the DNA within these regions. These restriction enzymes can be used to cut into fragments either a whole (nuclear, mitochondrial, or chloroplast) genome or a specific DNA fragment isolated from such a genome. The resulting DNA fragments can be separated by size by placing the preparation on a gel (e.g., of agarose) and applying an electrical current (electrophoresis). The fragments can be "visualized" by several methods, including AUTORADIOOGRAPHY: radioactively labeling the DNA, and then exposing the gel to a radiation-sensitive film. The size of each fragment (in number of base pairs) is measured by its mobility relative to known standards, and the sum of the fragment sizes equals the size of the sequence that has been cut. By comparing the fragments produced by combinations of different restriction enzymes with those produced by each enzyme singly, it is possible (although rather complicated) to map the different restriction sites, i.e., to specify their order and the number of base pairs between them. These restriction sites can then be used as genetic markers for relatively short sequences of DNA, just as mutant alleles are used as genetic markers in traditional genetics.

- **DNA sequences.** A sequence of DNA from minute samples of tissues, sometimes from long-preserved museum specimens or even certain fossils, can be amplified by the polymerase chain reaction (PCR) and then sequenced. The most difficult step is extracting the particular gene one wishes to sequence, but once this has been done in one species, copies of the sequence (primers) can be used to extract the sequence from closely, or sometimes distantly, related species. This has become the most popular molecular method in systematics.
- **Nucleotide sequence comparisons and homologies.** A more precise method of phylogenetic determination is to compare known nucleotide

sequences from different organisms rather than to infer relationships from hybridization studies for restriction enzyme maps. This procedure offers advantages in comparing changes between protein-coding and noncoding DNA sequences and in determining the extent of synonymous and non-synonymous nucleotide substitutions in the amino acid coding regions.

A large amount of information on nucleotide sequences (on some 2.5 million DNA sequences) has recently been accumulated from a. number of organisms ranging from viruses to eukaryotes. Among the nine sequenced prokaryotic genomes, a number of interesting evolutionary features have appeared which shows:

- Extensive horizontal gene transfer between genomes
- Considerable amounts of gene duplication - as high as 25 percent in the *Bacillus subtilis* genome
- Greater similarity of archaebacterial protein sequences to eubacterial proteins rather than to eukaryotic proteins
- Proteins used in replication, transcription, and translation show a reverse relationship: greater similarity between archaebacteria and eukaryotes
- As much a 50 percent or more of genes in some genomes are "orphans" with no known function
- Based on the 480 genes in *Mycoplasma genitaliurn,* that number or even smaller may represent the minimal set of genes necessary for cellular life.

18.6 Molecular Clocks

The rate of evolution of DNA sequences can be shown in some cases to be fairly constant ("molecular clock"), such that sequences in different lineages diverge at a roughly constant rate. In such cases, degrees of similarity can indicate phylogenetic relationships. The absolute rate of sequences evolution ca sometimes be calibrated if fossils of some lineages are known.

All molecular methods indicate that non-interbreeding evolutionary lineag (species and higher taxa) become steadily more different with time. The theor of population genetics predicts that if natural selection does not favor on molecular variant over others, DNA or protein sequences should diverge, *o average,* at a constant rate. Early in the history of molecular phylogenetic studie the data suggested that macromolecules might indeed evolve and diverge at constant rate. This concept has been dubbed the **molecular clock** (Zuckerkand and Pauling 1965). If it were true, it would have two important implications f the study of evolutionary history.

First, if the rate of overall divergence is constant, phylogeny can be inferre directly from the *overall similarity* of species (or, conversely, "distance", whic includes the autapomorphies that cladists consider anathma). One could the legitimately use phenetic methods to infer phylogeny from "distance measures such as those yielded by DNA-DNA hybridization, when information is lackin on the ancestral and derived states of individual characters (such as base pairs

Second, if one could calibrate the clock-if one could discover how fast it "ticking"-one could *estimate the absolute time* since different taxa diverge The clock might be calibrated by, say, information from the fossil record on th absolute time of divergence of certain taxa, and it could then be used to estimat the divergence times of other taxa that have not left a good fossil record. Be in mind that the phylogenetic trees we have considered so far portray *relativ* times of divergence (the branching *sequences)* of taxa, not absolute times.

Initially, we need to calculate the number of differences (e.g., in base pair that have accrued among pairs of species since their common ancestor. This ca be estimated by plotting on our estimated phylogeny where each change too place. For example, figure 18.5 shows 76 autapomorphic changes between *Hom* and its common ancestor with *Pan* (e.g., site 6374), 14 synapomorphic change between that common ancestor and the *Gorilla* branch (e.g., site 5365), and 9 autapomorphies along the *Gorilla* branch (e.g., site 6374). Since the commo ancestor of all three species, there have been 94 changes leading to *Gorilla,* 7 + 14 = 90 changes leading to *Homo,* and 92 + 14 = 106 leading to *Pan.* From th more remote common ancestor of these species and *Pongo*, there have been 160 changes to *Homo*, 176 to *Pan*, 178 to *Gorilla*, and 199 to *Pongo*.

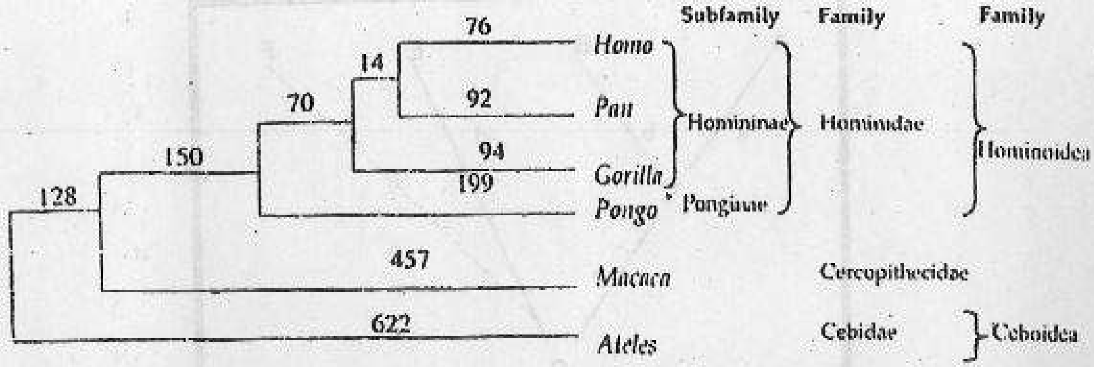


Fig. 18.5. Evidence for phylogenetic relationships among primates, based on the yh-globin region (Goodman et al. 1989). The most parsimonious (shortest) phylogeny based on yh-globin sequence, using *Ateles* as an outgroup. The minimal number of changes is indicated along each branch. A tree that split up the *Homo-Pan-Gorilla* clade would be 65 steps longer, and one that split *Homo* and *Pan* would be 8 steps longer. Note that from the common ancestor of apes and Old World monkeys *(Macaca)*, the number of changes along the branches leading to Human (310) or any ape is less than that in the branch leading to *Macaca* (457). The figure also includes the classification proposed by Goodman et. al. 1989.

The *average rate of base pair substitution* in any lineage can be calculated if we have an estimate of the absolute time of divergence. For example, the oldest fossils of cercopithecid monkeys are dated at 25 million years ago (My). Thus the divergence between *Macaca* and the hominoids is at least this old. This is a *minimal* estimate of divergence time, because it is possible that older cercopithecids (and hominoids) exist that has not yet been found in the fossil record. If, however, we take this date as the age of the cercopithecid / hominoid divergence, we can calculate the average rate of sequence evolution. The number of substitutions per base pair per million years for the cercopithecid lineage *(Macaca)* is 457/10,000 base pairs sequenced / 25 My = 0.0457 substitutions per base pair / 25 My = 1.83′ 10^{-3} per My, or 1.83′ 10^{-9} per year. From the common ancestor to *Homo*, the average rate has been 310 / 10,000 / 25 = 1.24′ 10^{-3}per

My, or 1.24´ 10^{-9}per year. Figure 7.6 explains relative rate test for constancy the rate of molecular divergence in a hypothetical model.

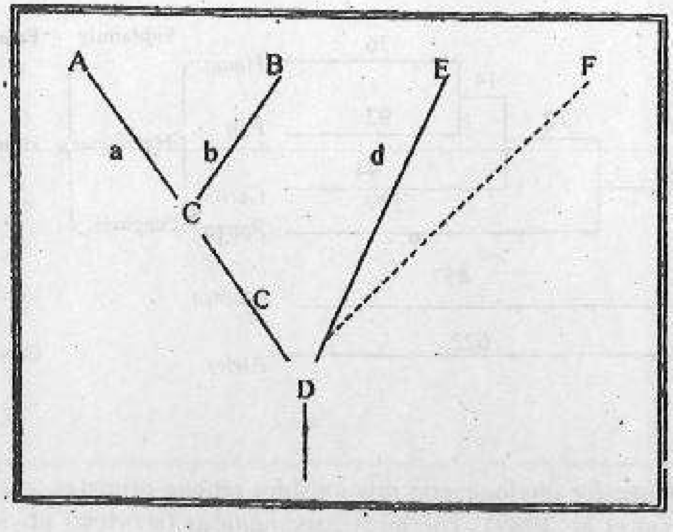


Fig. 18.6. The relative rate test for constancy of the rate of molecular divergence. Sequence are obtained for living species A and B and for outgroup species E (perhaps also F). C an D represent common ancestors. The genetic distance (e.g., in terms of nucleotide differences between A and E is D_{AE} = a + c + d. that between B and E is D_{BE} = b + c + d. If th rate of nucleotide substitution is constant, a = b, so $D_{AE} = D_{BE}$. If rate constancy hold throughout the tree, the distance between any pair of species that have D as a commo ancestor will equal that between any other such pair of species (e.g., $D_{AE} = D_{BF}$).

18.7 Suggested questions

1. What is molecular systematics and phylogeny?
2. Explain how a phylogenetic tree is constructed (use a hypothetica example).
3. What are plesiomorphy and symplesiomorphy?
4. Define terminal taxa, sister taxa, stem group, common ancestor anc ground plan.

5. Explain 'rooted' and 'unrooted' phylogenetic tree.

6: Define Parsimony method for detection of phylogenetic distance. Explain how mutational distances are derived in this method.

7. Write notes on Distance methods and Maximum likelihood methods for construction of phylogenetic tree.

8. What are antigenic distance and micro complement fixation?

9. Why molecular phylogeny is important in studying evolution. Cite an example where amino acid sequences is used in phylogenetic analysis.

10. Elucidate with example that DNA-DNA hybridization can explain nucleic acid phylogeny.

11. What do you mean by Restriction enzyme sites? How this can help in constructing molecular phylogeny?

12. How the average rate of base pair substitution is calculated (use any example).

13. Define molecular clocks. Elucidate the significance of molecular clocks in molecular phylogenetic analysis.

18.8 Glossary

Adaptation: A state that evolved because it improved reproductive performance, to which survival contributes. Also the process that produces that state.

Adaptive evolution : The process of change in a population driven by variation in reproductive success that is correlated with heritable variation in a trait.

Antagonistic pleiotropy : One gene has positive effects on fitness through its impact in one trait but negative effects on fitness through its impact on another trait.

Apomixis : A form of clonal propagation in which progeny genetically identical to the mother are formed without genetic recombination.

Bootstrapping : A statistical method to estimate our confidence in a pattern.

One takes random samples of the original data (with replacement to get a data set of the same size) and repeats the calculations with the new, artificial data sets many times. The patterns that do not change, or only rarely change, receive our confidence.

Canalization : The limitation of phenotypic variation by development mechanisms. It can be demonstrated by disturbing developmental control to reveal the underlying genetic variability that had been canalized.

Clade : A branch of the evolutionary tree containing all the species descended from a single common ancestor.

Cladogenetic : Evolutionary change occurring during speciation events. Usually applied to fossils.

Cline : A spatial gradient in train values or gene frequencies.

Coevolution : Evolutionary changes in one thing-genes, sexes, species-induce evolutionary changes in another, which in turn induce further evolutionary changes in the first, and so forth.

Comparative trend analysis : The relations of two or more traits among higher taxa are analyzed with proper control for phylogeny and covariates such as body weight.

Conserved function : A property of paralogous genes with high DNA sequence homology that code for proteins with similar function in distantly related organisms.

Convergence : Two species resemble each other not because they shared common ancestors but because evolution has adapted them to similar ecological conditions.

Cyclical parthenogenesis : A life cycle typical of aphids, rotifers, cladocerans, and some beetles, in which a series of asexual generations is interrupted by a sexual generation are often adapted to resist extreme conditions and to disperse.

Density-dependent selection : Selection that favors different things at different population densities.

Density-independent selection : Selection that favors the same things at all population densities, or that has always occurred at the same population density so that density effects did not occur.

Derived : Defined relative to ancestral: originating later in evolution than the ancestral state.

Directional selection: Selection that always acts in a given direction; for example, always to increase the value of a trait, or always to decrease it.

Disruptive selection: Selection that favors the extremes and eliminates the middle of a frequency distribution of trait values; for example, increasing the frequency of small and large individuals and reducing the frequency of medium-sized individuals.

Divergence : Related species no longer resemble each other because evolution has adapted them to different ecological conditions.

Downstream gene : A gene under the control of a regulatory gene; the genes downstream from a regulatory gene constitute a regulatory pathway.

Drift: The random walk of gene frequencies that occurs in both large and small populations when variation in genes is not correlated with variation in reproductive success.

Effective population size : The size N_e of an ideal population consisting of individuals with equal reproductive output that would experience the same amount of genetic drift as a real population of size N'. This defines effective population size for drift; there are other definitions for unequal family sizes, subdivided populations, differences in male versus female reproductive success, and variable population sizes.

Epigenetic inheritance : Somatic inheritance of the differentiated state of the cell through cycles of cell division.

Exon : The part of a eucaryotic gene whose DNA sequence is preserved in post - transcriptional splicing and is represented in the spliced mRNA and in the resulting amino acid sequence of the protein product. Exons occur in eucaryotes but not in prokaryotes.

Founder effect: Major changes in gene frequencies that occur in a population founded with a small sample of a larger population.

Frequency-dependent selection : A mode of natural selection in which either rare types (negative frequency-dependent selection) or common types (positive frequency-dependent selection) are favored.

Genealogy : A tree describing the history of a single gene, as opposed to a phylogeny, which uses information from many genes or traits to reconstruct the history of a set of species.

Gene flow: Genes flow from one place to another when organisms born in one olace have offspring in another place that survive to reproduce there.

Gene frequency : The frequency of an allele in a population. If there are 100 individuals in a population of diploid individuals, and we consider one locus (one gene) that is present in tow forms (two alleles), *A* and *a*, then if 20 of the individuals carry two copies of A (they are *AA* homozygotes), 60 of the individuals are *Aa* heterozygotes, and the remaining 20 individuals are *aa* homozygotes, then the gene frequencies are calculated as the number of each allele divided by the total number, in this case. (40 + 60)/200 = 0.50 for both alleles.

Gene substitution : The process by which a new mutation becomes fixed in a population.

Genetic bottleneck : A reduction in population size to a low-enough level for long enough that many alleles are lost and other are fixed.

Genetic diversity: The probability that two homologous alleles chosen at random from a population differ.

Genetic drift: Random change in allele frequencies due to chance factors.

Genetic imprinting : Genes marked by DNA methylation in the germ line of parents; some are marked in mothers, others in father. Methylated genes are not expressed in the early development of the offspring.

Genomic conflict : Occurs when genes affecting the- same trait experience different selection pressures because they obey different transmission rules.

Genochorism : Having separate sexes; individuals are either males or females, not both; used for animals.

Heterogametic : The sex having tow different sex chromosomes; for organisms with chromosomal sex determination; mates are XY in humans.

Heterozygosity : The proportion of a population that is heterozygous at a locus; also the average proportion of loci heterozygous per individual.

Hitch-hiking : Changes in the frequencies of neutral traits that are pleiotropically lined to other traits that are under selection; or changes in the frequencies of neutral genes that are linked on chromosomes to changes in other genes that are under selection.

Homeobox : A 180 base-pair sequence in important regulatory genes that codes for a protein segment that binds to DNA as a key part of a transcription factor.

Homogametic : The sex having two similar sex chromosomes; for organisms with chromosomal sex determination; females are XX in humans.

Homology : Identity of one trait in two or more species by descent form a common ancestor.

Homoplasy : Similarity for any reason other than common ancestry. The commonest cause of homoplasy in morphological trait s is probably convergence; in DNA sequences, simple mutation.

Inbreeding depression: The reduction in the survival or reproduction of offspring of related parents caused by the expression as hemozygotes of deleterious recessive genes that were present in the parents as heterozygotes.

Infinite-allele model: A model in the neutral theory of molecular evolution that assumes that every mutation is unique in the sense that it does not already exist in the population; plausible for long DNA sequences.

Intron : A sequence within a gene that is removed after transcription and before translation by gene splicing; its DNA sequence is not represented in the RNA sequence of the spliced mRNA or the amino acid sequence of the resulting protein; introns occur in eucaryotes but not procarytes.

Kin selection : Adaptive evolution of genes caused by relatedness; an allele causing an individual to act to benefit its relatives will increase infrequency if that allele is also founding the relatives and if the benefit to the relatives more than compensates the cost to the individual.

Lek : A traditional display site where males gather to defend mating territories and females come to mate; Swedish for sports field or display.

Lineage-specific developmental mechanisms : Developmental mechanisms found within all organisms of one lineage but not I other lineages, responsible for the morphology that characterizes the lineage. They limit the genetic variation that can be expressed in the lineage.

Macroevolution : The pattern of evolution at and above the species level, including most of fossil history and much of systematics..

Meiotic drive : Distortion of the fairness of meiosis by nuclear genes to increase their representation in the gametes at the expense of other alleles.

Mendelian lottery : A particular allele will or will not be represented in the offspring because of the segregation of alleles at meiosis and the random chance that any particular gamete will form a zygote. Most easily seen with small family sizes. Think about single children.

Microevolution : The process of evolution within populations, including adaptive and neutral evolution.

Molecular clock : The approximately constant rate of nucleotide substitution for particular genes and classes of genes within particular lineages. The constancy of the rate depends on the randomness with which particular neucleotide mutate and then drift to fixation.

Monophyletic : All species in a monophyletic group are descended from a common ancestor, and all species descended from that ancestor are in that group.

Multigene family: Sets of multiple copies of genes derived by duplication from a common ancestor gene and retaining the same function.

Multilevel evolution : Adaptive evolution occurring simultaneously at several levels of a biological hierarchy, e.g. nuclear and cytoplasmic genes.

Narrow-sense heritability : The fraction of total phenotypic variance in a trait that is accounted for by additive genetic variance; measures the potential response to selection.

Neutral evolution : The change and occasional fixation of alleles caused by the drift of alleles not correlated with reproductive success.

Paralogy : DNA sequence homology plus conserved functions.

Paraphyly : A group does not contain all species descended form the most recent common ancestor of its members.

Parsimony : A criterion used in cladistic tree-building: the best tree has the fewest changes in character states and the least homoplasy.

Phenotypic differentiation : The differentiation of phenotypes in separated gene pools during and after speciation.

Phenotypic plasticity : Sensitivity of the phenotype to differences in the environment. Less precise than reaction norm.

Phylogeneit ctrait analysis : A comparative method in which one constructs a phylogenetic tree, plots character states (traits) on the tree, and infers transitions in character states from their position on the tree. Geographical locations of taxa can be plotted onto the tree to infer the location of ancestors.

Phylogeny : The history of a group of taxa described as an evolutionary tree with a common ancestor as the base and descendent taxa as branch tips.

Pleiotropy : One gene has effects on two or more traits.

Pleisomorphic : Ancestral, relative to a derived, or apomorphic, state.
Polyphenism : A form of induced response in which the phenotypes are discrete.

Polyphyly : A group is polyphyletic if its species are descended from several ancestors that are also the ancestors of species classified into other groups.

Population genetics: The discipline that studies changes in frequencies of alleles in populations; issues include mutation, selection, inbreeding, assortative mating, gene flow, and drift; suitable when genetic differences at one locus can be detected as phenotypic differences.

Punctuated equilibrium : A pattern seen in many but not all lineages in the fossil record, in which a long period of stasis is broken by a short period of rapid change. In some cases the rapid change is associated with speciation.

Quantitative genetics : Studies changes in traits in populations when genetic differences at one locus are too small to detect in phenotypes and when many genes affect one trait; common themes are heritability, genetic covariance, response to selection.

Regulatory gene : A gene that turns another gene, or group of genes, on or off. Small changes in regulatory genes cause large changes in phenotypes.

Replicator: The organism in its role as information copier, the mechanism that copes the DNA sequence of the parent and passes it to the offspring.

Reproductive success : A measure of fitness defined as the number of offspring produced per lifetime. I, can be extended through several generations; for example, one could define it as the number of grandchildren tha, survive to reproduce.

Reproductive value : The expected contribution of orgamsms in that stage of life to lifetime reproductive success.

Residual reproductive value : The remaining contribution to lifetime reproductive successes after the current activity has made its contribution.

Segregation distortion : Deviation from the Mendelian ratios that give equal chances to homologous alleles in meiosis; unfair ratios can be caused by nuclear genes that intertere with meiosis or with the products of meiosis to improve their own chances at the expense of their homologs.

Sexual selection : The component of natural selection that is associated with success in mating.

Sibling species : Species that are reproductively isolated but cannot be distinguished, or can be distinguished only with difficulty and by experts, using morphological criteria.

Species : Either a set of organisms that could share grandchildren (the biological species concept), or the smallest diagnosable cluster of individual organisms within which there is a parental pattern on ancestry and descent (the phologenetic species concept).

Stabilizing Selection : Selection that eliminates the extremes of a distribution and favors the center.

Stasis : A long period without evolutionary change.

Strict consensus tree : A phylogenetic tree derived form a set of equally parsimonius trees and constructed by only including the groups that are supported in all the equally parsimonious trees.

Synapomorphy : A shared, derived character state indicating that two species belong to the same group.

Synergism : A non additive interaction between two or more factor.

Synonymous mutation : A point mutation (change in a single nucleotide) does not change the amino acid for which the DNA triplet codes.

Terrane : A piece of continental crust that did not originally belong to the continent on which it is found but moved there from elsewhere.

Trade-off : A change in one trait that increases fitness causes a change in the other trait that decreases fitness.

Transcription factor : A gene product that binds to DNA at a specific site and regulates the expression of genes downstream from that site.

Transduction : A vims that infects bacteria picks up some bacterial DNA from one host and transfer it to the next host, which may incorporate the DNA if it scurvies the infection.

Wild type : A term used in classical genetics to designate the standard genotype in the population form which mutations formed rare deviations. Modern molecular data have destroys the concept by revealing so much variation that the concept has become meaningless.

18.9 Suggested references

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