4

Population : Structure, Growth and Regulation

UNITARY AND MODULAR POPULATIONS

Although there are fundamental similarities between attributes of animals and plant populations, generalisations are difficult to be drawn. Most of the population studies are made with animals. Why population ecologists preferred animals for studies on population attributes and population dynamics ? Plants do not move from place to place, are easy to count, whereas animals move and need to be trapped, chased or shot for counts. We face problems in counting the plants, as in most cases it is difficult to identify an individual, and therefore, to ascertain the **unit** of population.

Populations may consist of either **unitary** or **modular organisms**. In populations of **unitary** organisms, each individual is produced directly from a zygote and the form and development of individuals is highly predictable. An individual developing from a zygote is called a **genet**. Mammals, birds, amphibians and insects are all examples of unitary organisms. In contrast, in populations consisting of **modular** organisms (Fig. 4.1) the zygote develops into a unit of construction, or **module**, which then gives rise to further modules to form a branching structure. Each genet thus gives rise to numerous individual units, each of which can give rise to new individual. These individual units are called **ramets**, which may be flowers, tillers of grass, vegetative parts as buds, branches etc. The form and timing of development are not predictable. Most plants, sponges, hydroids and corals are modular.

Higher plants grow by accumulating modules that usually consist of one leaf, a bud and a piece of stem. Flowers are a type of module. Some modular organisms such as trees and sea fans concentrate on vertical growth, while rhizomatous grasses and encrusting sponges spread laterally over a substrate.

Connections between the parts of spreading modular organisms may die and rot away leaving individuals that are separated but genetically identical and derived from a single zygote; these are known as **ramets** (Fig. 4.1A). Floating aquatic plants such as duckweed literally fall apart into ramets as they grow. In some cases a single **clone**

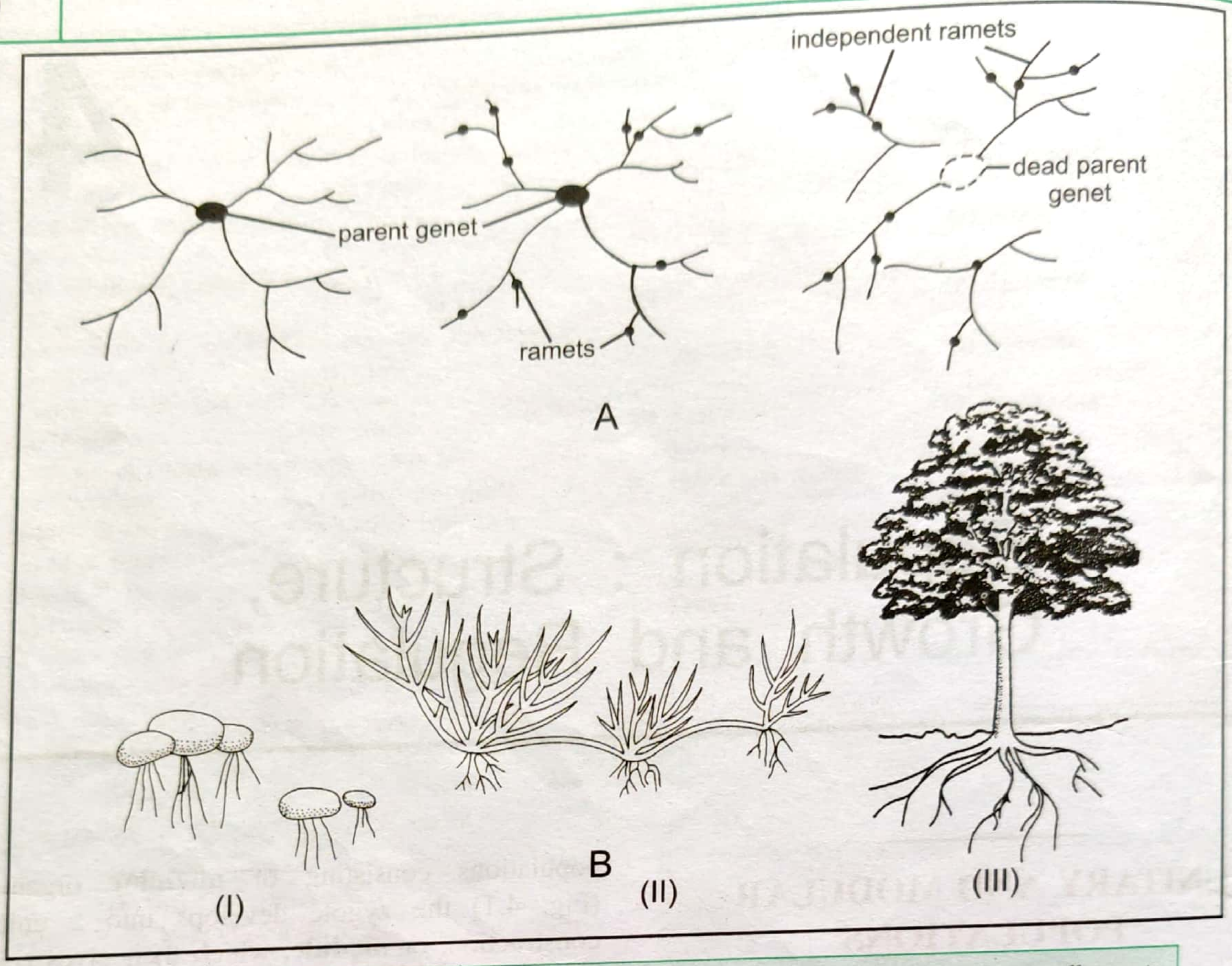


Fig. 4.1. (A). Lateral modular growth, showing the original genet and its ramets. Because all ramets are genetically identical, the ramets collectively make up the genet. **(B)**. Examples of modular organisms; (i) duckweed, which separates into individual ramets as it grows; (ii) grasses, ramets attached by stolons or rhizomes; and (iii) trees, which grow by accumulating persistent modules.

(or **genet**) may extend over large areas, as has been recorded in bracken fern (*Pteridium aquilinum*) in Finland where one clone, comprising many thousands of ramets, covers nearly 14 hectares and is estimated to be 1400 years old.

Most animals are unitary, except a few such as sponges, hydroids and corals. An elephant will always have four legs whether it is undernourished or over-nourished, whereas an individual plant will show wider changes in number of its part under varying environmental conditions. It may attain more height and produce more seeds when properly nourished, but may produce few seeds under stress. Unlike plants, most animals do not lose their parts in the lifetime. In plants, leaves, branches, twigs may have different life cycles. In plants, unlike most animals, there are two levels of population structure, genets and ramets, that make populations modular rather than unitary. So also in protists and fungi, where both these two levels of populations are present. Asexual reproduction is very common in these microorganisms. It is thus difficult to ascertain units of population in plants and such microorganisms. This is the chief reason why most population studies are made with animals.

UNIQUE (GROUP) ATTRIBUTES OF POPULATION

A **population** is a group of the same species occupying a given space (area) at the same (specific) time. Let us first explain in some detail the operating word **group** in the above sentence, defining a population. An essential and etc. in their feathers and helminthes in the intestines. **Human** are examples of carriers of rats, cockroaches, houseflies and grain feeding insects during their travel. **Pets** (dogs, cats, rabbits, sheep, goat) travel with men world over.

There may be three **patterns of dispersal :** exponential, normally distributed, and uniform pattern. Dispersal supplements natality and mortality that results into change in density leading to change in growth form of population.

Age Structure (Age Ratio)

In most populations, individuals are of different ages. The proportions of individuals in each age group is called **age structure** of that population. For instance an understory palm tree population (*Astrocayum mexicanum*) in an evergreen forest of Mexico, had 50% individuals as seedlings (less than 2-year-old), 19% as saplings (8-year-old), 5% as 30-year-old-adults and so until 70-year old trees made up less than 2% of the population.

Age distribution is important, as it influences both, natality and mortality of the population. The ratio of the various age groups in a population determines the current reproductive status of the population, thus anticipating its future. From an ecological view point there are three major ecological ages (age groups) in any population. These are, **prereproductive**, **reproductive** and **postreproductive**. The relative duration of these age groups in proportion to the life span varies greatly with different organisms. In man, the three 'ages' are relatively equal in length, about a third of his life falling in each class. Many plants and animals have a very long prereproductive period. Some animals, particularly insects, have extremely long prereproductive periods, a very short reproductive period and no post-reproductive period.

The model representing geometrically the proportions of different age groups in the population of any organism is called **age pyramid**. The **three** hypothetical pyramid types are shown in Figure 4.5 which are as follows :

1. A pyramid with broad base

It indicates a high percentage of young individuals. In rapidly growing young populations birth rate is high and population growth may be exponential as in yeast, house-fly, paramecium etc. Under such conditions, each successive generation will be more numerous than the preceding one, and thus a pyramid-with broad base would result (Fig. 4.5 A).

2. A bell-shaped polygon

It indicates a moderate proportion of young to old. As the rate of growth becomes slow and stable, *i.e.,,* the prereproductive and reproductive age groups become more or less equal in size, post-reproductive group remaining as the smallest, there results a bell-shaped structure (Fig. 4.5 B).

3. An urn-shaped figure

It indicates a low percentage of young individuals. If the birth rate is drastically reduced the prereproductive group dwindles in proportion to the other two groups and it results in an

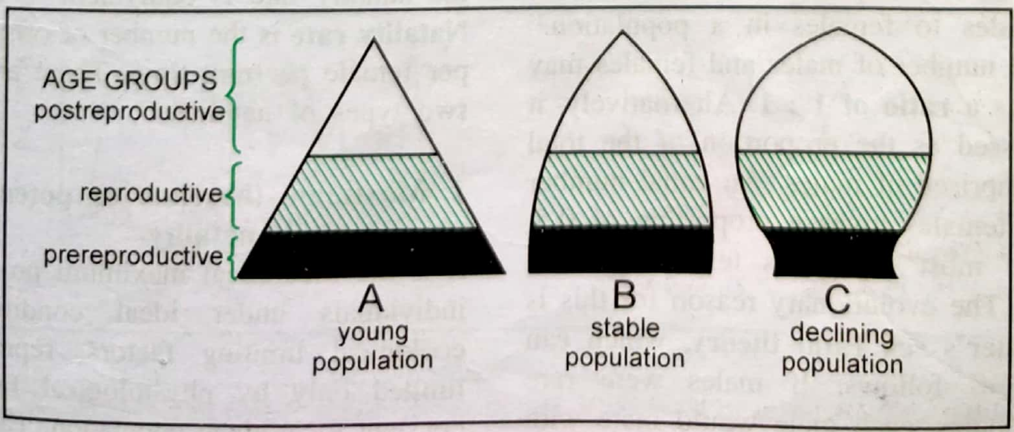


Fig. 4.5. Different types of age pyramids.

urn-shaped figure (Fig. 4.5 C), which indicates that population is dying off.

While density reveals little about differences between populations in developed and developing countries, age structure highlights some of the causes of rapid population growth in the latter. Developing countries have a much greater preponderance of young people, and the side of pyramids become concave. Such a shape means high population growth, not only at present but also likely in future.

The age structure describes the number of individuals in each (ecological age) class as a ratio of one class to another. Age classes can be specific categories, such as years or months, or life history stages, such as eggs, larvae, pupae and instars.

The body of a plant, as a modular organism, also has an age structure and is composed of young and developing, actively functioning and senescent parts. Moreover, leaves, shoots and roots change in activity as they age. For an ecologist to treat all leaves as equal would be to ignore the fact that other organisms such as herbivores will discriminate between them. In the sand sedge, *Carex arenaria,* the age structure of shoots is changed dramatically by the application of fertilizer even though the total number of shoots is unaltered. The population becomes dominated by young shoots and older shoots die.

Sex Ratio

Sex ratio is usually expressed as "the relative number of males to females in a population." Thus, an equal number of males and females may be expressed as a **ratio of 1 : 1**. Alternatively, it may be expressed as the proportion of the total population comprised of males. An equal number of males and females gives a proportion of 0.5. Populations of most organisms tend towards a 1: 1 sex ratio. The evolutionary reason for this is known as **Fisher's sex ratio theory,** which can be illustrated as follows. If males were rare relatives to females, each male would mate with many females and produce many offspring. The male fitness would thus be higher than the female fitness. If the opposite situation occurred, and females were rare, then female fitness would exceed male fitness. Thus we would expect any sex bias to be corrected by evolution as a mother's fitness would be higher if she biased production of offspring to the rare sex. This is an example of **rare type advantage.** Fisher's sex ratio theory suggests that there should be **equal investment** in either sex as a result of rare type advantage.

However, there are a variety of exceptions to equal sex ratios. These are **unequal costs** of two sexes (as in solitary bee, *Anthophora abrupta,* where females are 58% heavier than males; another examples is general bias in mammals in the sex ratio at birth towards males); **crowding with local resource competition,** and; **mate competition.** These all can bias the sex ratio, which can be male-biased (more males than females) or female-biased (more females than males).

Sex ratio varies according to the age profile of the population, which could be primary, secondary, tertiary or quaternary sex ratio. Different factors can influence sex ratio. These are density-independent mortality, intraspecific competition, breeding pattern, and crowding.

Natality (Birth Rate)

It is simply a broader term covering the production of new individuals of any organism. These new individuals are born, hatched, germinated, arise by division etc. In human population, however, the natality rate is equivalent to the 'birth rate'. **Natality rate** is the number of offsprings produced per female per unit time. There are distinguished **two** types of natality.

1. Maximum (absolute or potential or physiological) natality

It is the theoretical maximum production of new individuals under ideal conditions (*i.e.,* no ecological limiting factors, reproduction being limited only by physiological factors). It is a constant for a given population. This is also called fecundity rate.

2. Ecological or realised natality

It is also known simply as **natality**, which refers to population increase under an actual, existing specific condition. Thus it takes into account all possible existing environmental conditions. This is also designated as **fertility rate**.

Natality is expressed as

$\Delta N_n/\Delta t$ = the absolute natality rate (B)

$\Delta N_n/N\Delta t$ = the specific natality rate (b) (natality rate per unit of population)

Where N = initial number of organisms

n = new individuals in the population

t = time

Three population characteristics determine the rate at which females produce offspring:

- **Clutch size** or the number of young produced on each occasion.
- the time between one reproductive event and the next, and
- the age of first reproduction.

Natality rate usually increases during the period of maturity and then falls again as the organism gets older (Fig. 4.6). Some trees seem to continue to increase fruit production as they get older, but this at present can not be explained due to lack of information we have at present

Natality patterns differ in tropical and temperate populations. **Breeding time** and **clutch size** are two important criteria. In tropical areas with dry periods, breeding is at least as seasonal as in temperate areas. In continually tropical humid areas breeding may occur throughout the year, with some population showing a seasonal peak. Clutch size in tropical environment is smaller than in temperate zone. Many birds, some plants, some insects and some small mammals exhibit this trend.

Mortality (Death Rate)

It refers to death of individuals in the population. It may be minimum and ecological mortality :

Minimum mortality

Also called **specific** or **potential** mortality, it represents the theoretical minimum loss under ideal or non-limiting conditions. It is a constant for a population. Thus, even under the best conditions, individuals would die of 'old age' determined by their **physiological** longevity.

Ecological or realised mortality

It is the actual loss of individuals under a given environmental condition. It is, like ecological natality, not a constant and varies with population and environmental conditions.

Like natality, mortality may be expressed as the number of individuals dying in a given period (deaths per time), or as specific rate in terms of units of the total population or any part thereof.

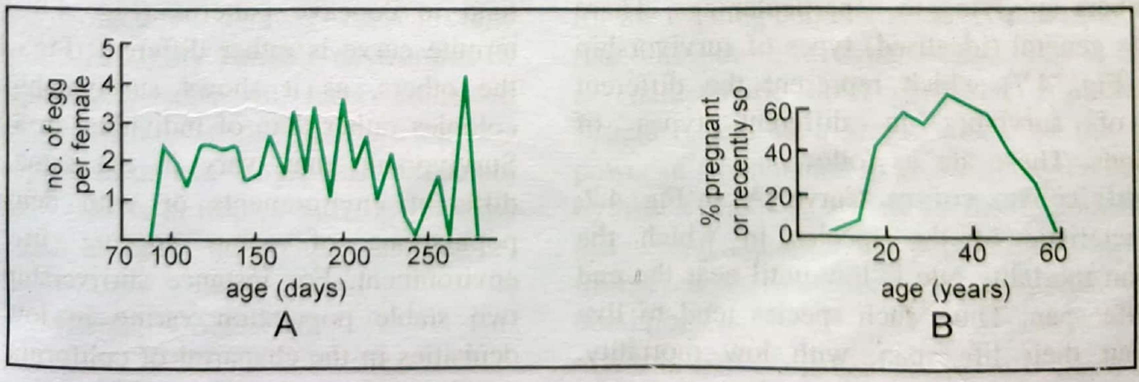


Fig. 4.6. Fecundity of female animals is usually low at the onset of sexual maturity, then reaches a lengthy plateau, followed by a decline in old age. **(A).** Milkweed bug *(Oncopeltus unifosciatellus)* cultured in laboratory. **(B).** African elephants *(Loxodonta africans)* in a National Park, Uganda.

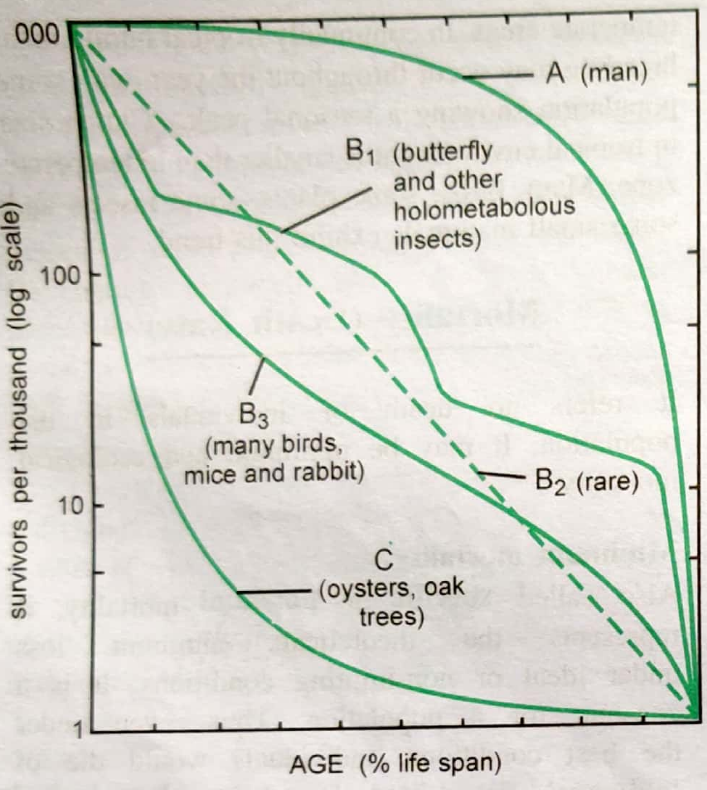


Fig. 4.7. Different types of generalised/idealised survivorship curves plotted on the basis of survivors and age.

A birth-death ratio $\left(100\times\frac{\text{births}}{\text{deaths}}\right)$ is called **vital index**. For a population, the important thing is not which members die but which members survive. Thus **survival rates** are of much interest than the death rates. Survival rates are generally expressed by **survivorship curves**.

The pattern of mortality with age is best illustrated by **survivorship curves** which plot the numbers surviving to a particular age. There are **three** general (idealised) types of survivorship curves (Fig. 4.7) which represent the different nature of survivors in different types of populations. These are as follows :

Highly convex curves. Curve 'A' in Fig. 4.7, is characteristic of the species in which the population mortality rate is low until near the end of the life span. Thus, such species tend to live throughout their life span, with low mortality. Many species of large animals as deer, mountain sheep and man etc. show such curves.

Highly concave curve. This curve ('C' in Fig. 4.7) is characteristic of such species where mortality rate is high during the young stages. Oysters, or other shell fish, oak trees etc. show this type of survivorship.

Diagonal curves. If age-specific survival is more nearly constant, the curve approaches a diagonal straight line (curve B_2 in Fig. 4.7). It thus shows a constant proportion of organisms dying per unit time. **Probably, no population in the real world has a constant age-specific survival rate throughout the whole life span.** Thus a slightly concave or sigmoid curve (B_3 in Fig. 4.7) is characteristic of many birds, mice and rabbits and black tail deer. In these cases, the mortality rate is high in the young but lower and more nearly constant in the adult (1 year or older). Still, in some halometabolous insects (insects with complete metamorphosis), such as butterflies, there is expected generally a 'stair steptype of curve (B_1 in Fig. 4.7). In such cases survival differs greatly in successive life history stages. The shape of survivorship curve may vary with the density of the population. In plants, studies on survival rates were begun by Harper (1969). Details on survivorship curves in plants may be found in Sarukhan and Harper (1973).

Survivorship of a variety of tropical populations shows that few match exactly the idealised curves. A convex pattern is shown by some large mammals, particularly primates and humans (Fig. 4.8 A). Approximately diagonal curves are found in some rodents and birds (Fig. 4.8 B, C) while many plants and insects tend to concave patterns (Fig. 4.8 D, E). The termite curve is rather different (Fig. 4.8 D) than the others, as it shows survivorship of whole colonies rather than of individual in a population. Survivorship may vary in the same species in different environments or with density of the populations of some specing in the same environment. For instance surriveship curves of two stable population varing in low and high denisities in the chaparral of colifornia U.S.A. **Do patterns of survivorship differ in tropical and temperate populations ?** Convex curves are more

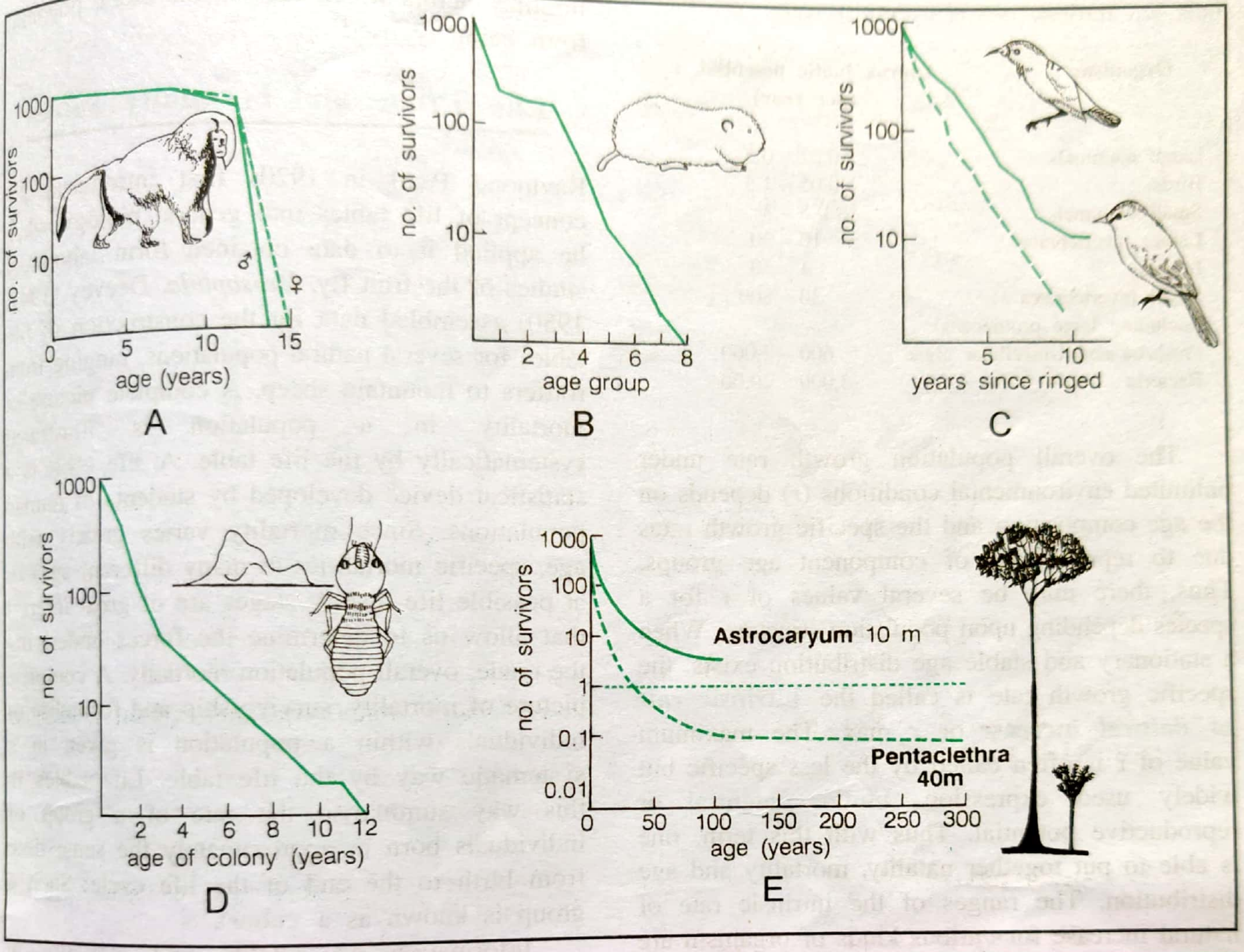


Fig. 4.8. Survivorship curves of real populations rarely fit the hypothetical types of Figure 6 precisely. (A). convex curve in gelada baboons, montane Ethiopia),. (B). and (C). approx. diagonal curves, B-mole rat (Nairobi, Kenya), C-Brown-throated sunbird (forests of south east Asia. D and E concave curves. (D). whole termite colonies (Nigerian savanna), (E). two rainforest trees (.from neotropics). Solid line is for understory palm in Mexico; broken line for a canopy tree in Costa Rica.

probable in fairly constant climates as found in moist tropics. Sometimes convex curves come from populations in highly variable environments. Tropical populations seem to have enhanced survivorship compared with their temperate relatives. Tropical birds live longer than temperate ones. Cottontail rabbits in tropics show lower rates of survival than those in the temperate zone.

Biotic Potential

Each population has the inherent power to grow. When the environment is unlimited (space, food, other organisms not exerting a limiting effect), the specific growth rate (*i.e.*, the population growth rate per individual) becomes constant and maximum for the existing conditions. The value of the growth rate under these favourable conditions is maximal, is characteristic of a particular population age structure, and is a single index of the inherent power of a population to grow. It may be designated by the symbol *r*, which is the exponent in the differential equation for population growth in an **unlimited environment** under specific physical conditions.

The index *r* is actually the difference between the instantaneous specific natality rate (*i.e.*, rate per time per individual) and the instantaneous specific death rate and may thus be expressed as:

$$r = b - d$$

Table 4.1. **Intrinsic rate of natural increase.**

Organisms	**Approx biotic potential, r (per year)**
Large mammals	0.02 – 0.5
Birds	0.05 – 1.5
Small mammals	0.3 – 8
Larger invertebrates	10 – 30
Insects	4 – 50
Small invertebrates (including large protozoans)	30 – 800
Protozoa and Unicellular algae	600 – 2,000
Bacteria	3,000 – 20,00

The overall population growth rate under unlimited environmental conditions (*r*) depends on the age composition and the specific growth rates due to reproduction of component age groups. Thus, there may be several values of r for a species depending upon population structure. When a stationary and stable age distribution exists, the specific growth rate is called the **intrinsic rate of natural increase** or *r* max. The maximum value of r is often called by the less specific but widely used expression **biotic potential** or reproductive potential. Thus with this term, one is able to put together natality, mortality and age distribution. The ranges of the intrinsic rate of natural increase for various kinds of organism are shown in Table 4.1. Chapman (1928) proposed the term **biotic potential** to designate maximum reproductive power. He defined it as "the inherent property of an organism to reproduce, to survive, *i.e.*, to increase in numbers. It is sort of the algebraic sum of the number of young produced at each reproduction, the number of reproduction in a given period of time, the sex ratio and their general ability to survive under given physical conditions." For details, reader may refer to Graham (1952). But under natural conditions, this is a rare phenomenon, since environmental conditions do not permit unlimited growth of any population. Its size is kept under natural check. The difference between the maximum *r* **(biotic potential)** and the rate of increase which occurs in an actual laboratory or field condition is often taken as a measure of the **environmental resistance**, which is the sum total of environmental limiting factors which prevent the biotic potential from being realised.

Life Tables and Fecundity Tables

Raymond Pearl in 1920s first introduced the concept of life tables into general biology when he applied it to data obtained form laboratory studies of the fruit fly, *Drosophila*. Deevey (1947, 1950) assembled data for the construction of life tables for several natural populations, ranging from rotifers to mountain sheep. A complete picture of mortality in a population is illustrated systematically by the life table. A **life table** is a statistical device developed by students of human populations. Since mortality varies greatly with age, specific mortalities at many different ages or at possible life history stages are of great interest that allow us to determine the forces underlying the crude, overall population mortality. A complete picture of mortality, survivorship and fecundity of individuals within a population is given in a systematic way by the life table. Life tables in this way summarise the fate of a group of individuals born at approximately the same time from birth to the end of the life cycle. Such a group is known as a **cohort**.

Information on natality and mortality in different ages and sexes can be combined in the form **of life tables**. From these it is possible to estimate the growth or decline of a population. As with survivorship curves, life tables are standardised to follow the progress of a cohort. In each table there are columns for age of individuals; number surviving to each age; the number dying in each age group; the proportion dying from the previous age category; fertility rate; and the number of young born by each age groups. The information obtained from these figures provides the **net reproductive rate** of the population *i.e.*, offspring left by each individual. Similarly from life table, mortality in a logarithmic form is also obtained. These are then used to calculate the rate of population growth.

Life tables summarise the fate of a group of individuals born at approximately the same time from birth to the end of the life cycle. Such a

Table 4.2. A cohort life table for the common field grasshopper, *Chorthippus brunneus* (after Richards and Waloff, 1954).

Stage (x)	Number observed at start of each stage (n_x)	Proportion of original cohort surviving to start of each stage (l_x)	Proportion of original cohort dying during each stage (d_x)	Mortality rate (q_x)	$\log_{10}n_x$	$\log_{10}l_x$	$\log_{10}n_x$-$\log_{10}n_{x+1}$ $=k_x$	Eggs produced in each stage (F_x)	Eggs produced per surviving individual in each stage (m_x)	Eggs produced per original individual in each stage (l_xm_x)
Eggs (0)	44000	1.000	0.920	0.92	4.64	0.00	1.09	–	–	–
Instar I (1)	3513	0.080	0.022	0.28	3.55	–1.09	0.15	–	–	–
Instar II (2)	2529	0.058	0.014	0.24	3.40	–1.24	0.12	–	–	–
Instar III(3)	1922	0.044	0.011	0.25	3.28	–1.36	0.12	–	–	–
Instar IV (4)	1461	0.033	0.003	0.11	3.16	–1.48	0.05	–	–	–
Adults (5)	1300	0.030	–	–	3.11	–1.53	–	22617	17	0.51

$$R_0 = \Sigma l_x m_x = \frac{\Sigma F_x}{a_0} = 0.51$$

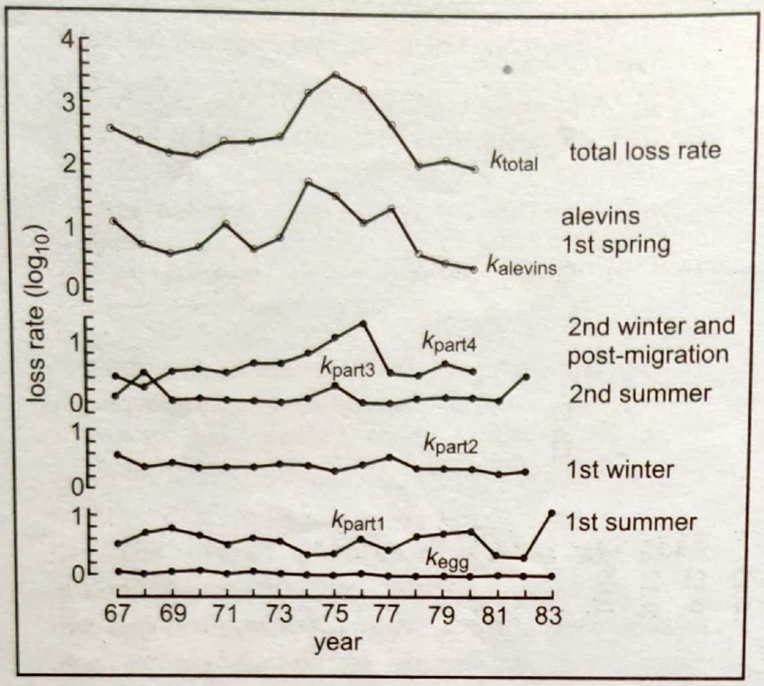


Fig. 4.9. k-values for the brown trout life cycle.

group is known as a **cohort** and the investigation of this time is termed **cohort analysis**.

Table 4.2 shows the life table for the grasshopper *Chorthippus brunneus*. Eggs hatch into first instar nymphs and progress through a number of instars, shedding the larval skin and replacing it with a new, larger one each time. By mid-summer the fourth instars will have moulted into adults and by mid-November all the adults will have died, leaving their eggs in the soil. n_x is the number present at the start of each of the six identified stages.

The proportion surviving to the start of the next stage (l_x) is the **age-specific survival rate**. This has been standardized as a proportion, such that l_x for the first stage is 1 (no mortality has occurred yet) and subsequent values give the proportion of the original number of eggs surviving to that stage. This allows studies conducted at different times with different numbers of individuals to be compared.

The next column is the proportion of the original eggs dying during the stage (d_x). This is the difference between l_x at one stage and the next. These values do not allow comparison of the importance of mortality at different stages because d_x depends on how many individuals there are at each stage. The more individuals there are, the more there are available to die and the d_x value will be larger.

The proportion dying at each stage gives the **age-specific mortality rate** (q_x). This is d_x as a fraction of l_x. This is also the chance of an individual dying. The q_x values give an excellent indication of the intensity of mortality at each stage, but because they act multiplicatively, they cannot be summed down the table to give total nymphal mortality. *k*-values get around this problem. *k*-values are simply the logarithm of the numbers in one stage minus the logarithm of the number in the next stage. Because adding two logarithms is the same as multiplying the unlogged numbers together, by converting the number of survivors to logs and calculating *k*-values we are able to add these together to find the total effect of mortality (k_{total}) and how it was distributed among life stages. The *k*-value of a life stage is referred to as its **killing power.** Thus, the killing power of the nymphal stages is 0.15 + 0.12+ 0.12 + 0.05 = 0.44 compared with 1.09 for the egg stage (*i.e.*, the egg stage is the major contributor to total mortality).

k-factor Analysis

With a series of life tables for cohorts born in successive years, we can see at which stage mortality has the greatest influence on population size. That is, we can see which **key factor** makes the largest contribution to k_{total}. This technique is known as *k*-factor analysis. It allows the identification of key factors contributing to mortality. Stage-specific *k*-values obtained over successive years are compared to the values for total mortality (k_{total}). *k*-factor analysis highlights those stages suffering the greatest mortality which are responsible for fluctuations in loss rate hence population size.

Figure 4.9 is derived from the first three years of life for brown trout, *Salmo trutta*, in the Lake District, England. Life tables were compiled each year for 17 years with mortality identified at each of six stages. Eggs hatch and emerge as alevins which survive for several weeks on their yolk sacs before developing into immature fish or parr. The figure shows a close relationship between the killing factor of the alevin stage (k_{alevin}) and total mortality (k_{total}). Therefore, it can be concluded that variations in alevin mortality are behind fluctuations in the total loss rate and hence population size.

The Fecundity Schedule

An example of a fecundity schedule is given in the last three columus of Table 4.2. The first coloum gives the number of offspring (eggs) produced during each life stage. Only adults produce eggs so there is only one entry, F_x. The next column gives the individual **fecundity,** or birth rate, which is the mean number of eggs produced per surviving individual. The fecundity schedule allows an important term, the **basic reproductive rate Ro** to be calculated. This is the number of offspring (eggs) produced per original individual by the end of the cohort and can be calculated by dividing the number of eggs produced by the number of individuals present at the start.

$$R_0 = \frac{\Sigma f_x}{n_0}$$

This is the same as summing the number of eggs produced per original individual for each of the life stages, or $R_0 = \Sigma l_x m_x$. R_0 is the average number of offspring produced by an individual in its lifetime. In an annual species (without overlapping generations) R_0 indicates the extent to which the population has increased or decreased over the duration of the table. The value of 0.51 for the common field grasshopper (Table 1) indicates that the population has declined. If this were to continue the grasshopper population would rapidly shrink. However, values of R_0 alter from year to year and data for one year only do not allow long-term patterns to be predicted.

Population Growth Regulation

The logistic model of population growth and its derivatives assume that a population will level off at its carrying capacity *i.e.,* there is an upper limit to population density set by the environment and that the population growth is regulated at or around that level. The significance of **regulation in** population has been the subject of controversy among ecologists for last more than 50 years or so. What regulates population growth ?

Population density can only be increased by natality or immigration and decreased by mortality or emigration. These factors may be density dependent or density independent in their effects. **Density-dependent factors** increase in their proportional effect as a population increases. Density-dependent factors include competition and predation. For example, rate of population growth is increasingly depressed by intraspecific competition as density is increased. **Inverse density dependence** also occurs if the intensity of the factor decreases proportionately as density increases. **Density independent factors** do not vary systematically in their effects as density changes. Abiotic environmental factors are often density independent but not always so Floods or fires may damage all populations regardless of their densities. Cold weather in tropics is also a factor of this type. Both density-dependent and density-independent factors may interact in most populations to determine observed densities. For example in tsetse flies (*Glossimia morsiotans*), both types are involved. These factors play important role in population dynamics also.

Density-Dependent Factors

Any factor, whether limiting or favourable (negative or positive) to a population, is **density-independent** if its effect (change in numbers) is independent of the size of the population; or **density-dependent** if its effect on the population is a function of population density. Density-dependent response is usually **direct** because it intensifies as the upper limit (carrying capacity) is approached. It may, however, also be inverse (decrease in intensity as density increases). Direct density-dependent factors act like governors on an engine (hence can be termed **density governing**) and, for the reason, are considered one of the chief agents in preventing overpopulation competition. **Climatic factors** often, but by no means always, act in a density-independent manner, whereas **biotic factors** (as competition, pathogens, pests) often, but not always, act in a density-dependent manner.

Let us recall the theoretical equation of population growth. In density-independent population growth, where extrinsic factors operate, a population reproduce over a protracted period and has overlapping generations, that is individuals of different ages are present in the population at any one time. The population that is increasing at its intrinsic rate will undergo a geometric increase in population number and will follow the characteristic geometric **J-shaped growth curve**. This theoretical situation is best described by a continuous population model and expressed in terms of the rate of change in population numbers at the time t :

Rate of change of population size at time t

$$\text{i.e.,} \quad \frac{dN}{dt} = \text{Intrinsic rate of increase} \times \text{Population size}$$

$$\text{i.e.,} \quad r \times N = rN$$

In density-dependent growth, the growth of a simple population in a confined space, where resources are not unlimited is simply described by the so-called **sigmoid graph** *i.e.*, **S-shaped graph**. The population increases geometrically until an upper limit is approached. This upper limit (saturation value) is constant for a particular set of conditions in a particular habitat and is called the **carrying capacity (k).** The population growth rate declines to zero as the population becomes more crowded and the population size stabilises at the maximum that the environment can support, reaching an **equilibrium density**. Competition among individuals of the same species has a limiting effect on population growth.

Density dependence has set in, resulting in a decline in r with increasing density. This is in contrast with density-independent case (theoretical continuous model, indicated earlier) where r remains constant. The sigmoid (real situation) curve can be explained and described by **miltiplying the equation for density-independent growth by a density-dependent factor** to give the **logistic equation :**

Rate of change of population size at time t = Intrinsic rate of increase × Population size × **Density-dependent factor** *i.e.*,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

What are these density-dependent (intrinsic) factors that actually regulate the population growth under natural conditions and tend to maintain a population in a stable pulsing state or to hasten the return to such a level. These factors are as follows :

1. Competition

It is one of the most important factors in regulating the population growth, operating in availability of shelter, food, space and other resources required for the growth and reproduction of the species. All these factors influence the population density.

2. Reproductivity

The birth and death rates play key role in regulation of population growth. However, fecundity alone may not necessarily be a density stabilizing factor. The important factor is as how many individuals developing from the eggs or youngs produced are able to reach sexual maturity or able to survive and reproduce.

3. Predation

There is enough evidence that variation in population levels of predators often coincide or closely follow variations in the prey populations. However, it is difficult to understand whether the predator number depends on the abundance of their food source (prey) or predators regulate the prey populations through feeding on them. Their relationship seems to be quite complex and not yet much clearly understood. There is some experimental evidence that predators affect their prey population levels through feeding on them. Predation exerts a selective force so that individuals with less fitness are likely to be eliminated at higher rates than those which are fit.

4. Dispersal

Dispersal (nondirectional movement) supplements natality and mortality in determining the density and population growth. Organisms can respond to high levels of intraspecific competition by dispersing from the area of high population density. Dispersal is undertaken very often by the younger members. Intraspecific competition is responsible for dispersal and territoriality.

Emigration, immigration and migration (periodic departure and return) greatly influence the size of a population. Emigration occurs under overcrowding conditions.

5. Diseases

Pathogens and pests results into mortality of animals. However, diseases become important as a regulatory factor in their population only when there is an outbreak (epidemic) of the diseases. Epidemics cause death of the animals over large geographic areas of animals distribution.

Density-Independent Factors

Density-independent environmental (extrinsic) factors have a greater role in physically stressed ecosystems; density-dependent natality and mortality become more important in benign environments where extrinsic stress is reduced. Basically all such factors are physical in nature. They all together contribute to environmental resistance. It includes variations in space or cover, favourable weather and food which all are independent of population density. These may cause abrupt drastic changes in population size.

1. Space or cover

Differences among species in their relative demands for space, water availability, food and shelter affect the population levels. Animals of small size require less space than large-sized animals. A drought may dry up a marsh making it unfit for aquatic animals like muskrats and waterfowl.

2. Weather and climate

The limits of tolerance to various climatic factors beyond which they cannot survive vary with the species. A severe winter freeze may kill all but a few hardy individuals, regardless of the size of original population. Climatic conditions also affect growth and reproduction, and populations subjected to intolerable weather conditions commonly fluctuate violently and erratically.

3. Food

The available food/nutrients sets an upper limit to the size of the population when other conditions are favourable. The availability of food varies from place to place with nature of substratum, vegetation type, soil fertility, climate and other factors. The lack of enough food to maximise reproductive potential may be the most important factors in regulation of size of the population.

4. Natural disasters

Disasters like fires, floods, hurricanes, earthquakes, volcanic eruptions, and meteor impacts affect the population size. However, these events do not regulate the population in a stable way like other physical factors. A natural disaster may wipe out many species in its vicinity. As a result new species may establish in the area by immigration. Due to establishment of new species the population of original species may take some time to re-invade these sites again.

The concept of population regulation was introduced by P.F. Verhulst (1838) and the term **density-dependence** was coined by H. S. Smith (1935). Under natural conditions population growth is sooner or later checked and it never continues to increase for indefinite period of time. As a result of check (by prevailing environmental conditions) the population size usually oscillates around the **carrying capacity** of the environment/ resources. Thus population growth enventnally attains a form of stability/equilibrium with its environment/resources (Fig. 4.10). If the controlling action/effect on population growth is

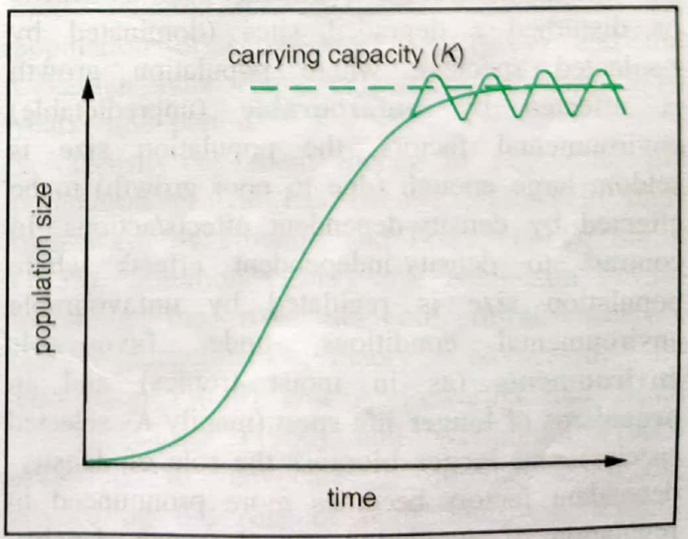


Fig. 4.10. The population size usually oscillates around the carrying capacity (dotted curve).

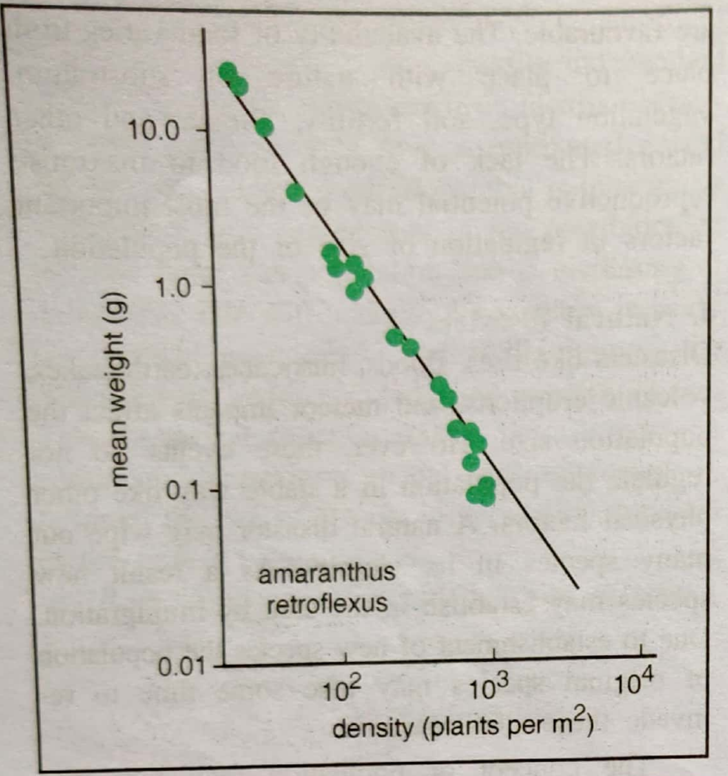


Fig. 4.11. The relationship between plant density and plant weight showing self-thinning in *Amaranathus retroflexus*.

independent of the size (density) of population, the effect/action is called **density-independent**, and when the effect is a function of density of population it is called **density-dependent**. For instance, a sudden decline in population growth by a sudden fall in temperature, or in response to severe storms, is largely independent of the size of the population. Such cases are examples of density-independent effects on population growth.

Under stressful environments, such as deserts or disturbed / degraded sites (dominated by *r*-selected species), where population growth is affected by **unfarourable** (unpredictable) environmental factors, the population size is seldom large enough (due to poor growth) to be affected by density-dependent effects/actions. In contrast to density-independent effects where population size is regulated by unfavourable environmental conditions, under **favourable environments** (as in moist tropics) and in **organisms of longer life span** (manily *K*- selected species) **and larger biomass** the role of density-dependent factors becomes more pronounced in regulation of population growth. Such density-dependent factors include **interspecific checks** such as competition, parasitism and predation as well as **intraspecific competition.** As the population attains a certain density, some density-dependent factors reduce its growth rate by decreasing birth rate and by increasing death rate. In plants, response to density results in a decrease in the mean density of individuals and an increase in mean weight of individuals, the relationship is called Yoda's –3/2 Law or self-thinning or –3/2 power law. Relationship between plant **density** and its **biomass** is called the **self-thinning curve** which typically has a slope of –3/2 on a log-log plot (Fig. 4.11).

The abovesaid principles of regulation of population growth can be better explained by an example of population dynamics of the Australian psyllid insect *Cardiaspina albitextura,* which feeds on eucalyptus leaves, described by L.R. Clark (1964). Several factors, both density-independent and density-dependent related to weather, predation, parasitism etc. effect the population dynamics of the insect. These are shown in Fig. 4.12. Normally, the population size remains stable at a low level (Level 1), well below the level that can be reached if all available resources are optimally utilised. During this phase the population is too small to exploit all the food and space resources. At this level population size is regulated by prevailing weather, density-independent predation and parasitism on nymphal stages, and density-dependent predation by birds on adults. However, occasionally this natural control fails to operate due to unusually low temperatures. The decline in temperature reduces parasitism of insect individuals, resulting into rapid eruption of population growth. The parasitism on nymphs is also reduced due to rapid increase in hyperparasites, and the bird predators can not increase as rapidly as the insect. But this increasing population of the insect is finally checked by the decreasing supply of its food resource, the eucalyptus leaves, The abruptly rising population of the insect then crashes/halts at level 2, due to defoliation of the eucalyptus tree and also due to increase in parasitifm and predation.

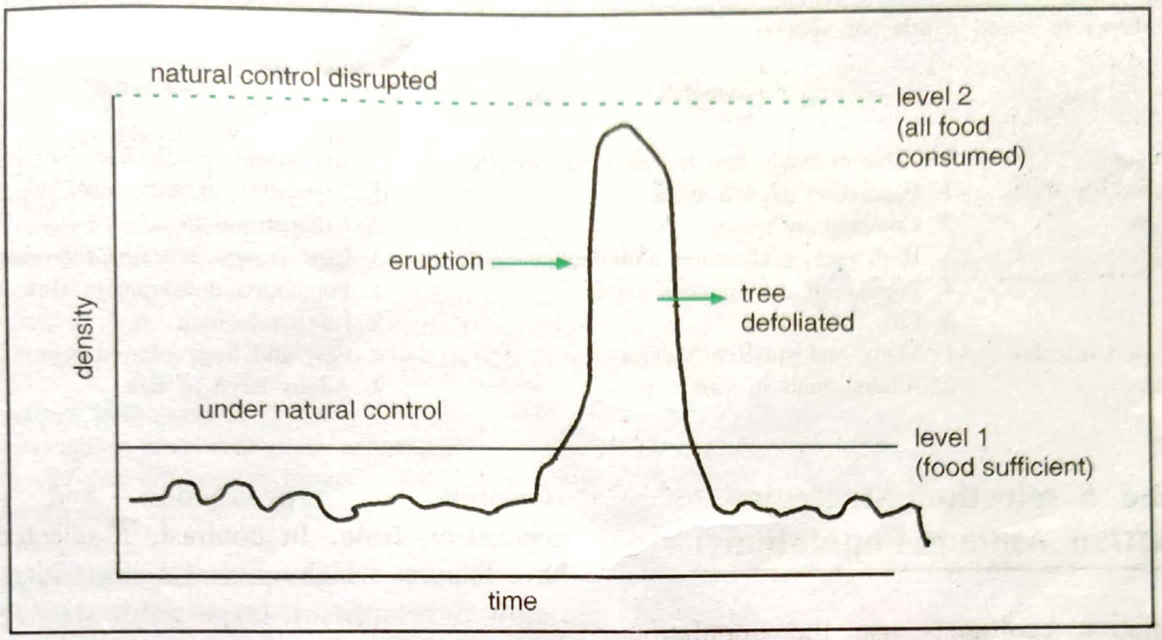


Fig. 4.12. Ecology of a population eruption, illustrated by population dynamics of a psyllid feeding on eucalyptus leaves.

At level 2, again the population is controlled by a combination of density-independent and density-dependent factors.

These seems to be a consensus among population ecologiets that a combination of both, density-independent and density-dependent factors plays role in controlling/regulation of population growth.

Among animals, territoriality is generally a form of intraspecific competition and social behavioural mechanism for spacing the individuals among its population. Selection pressure can also result into interspecific territoniality. Home range and territoriality exert internal environmental resistance on population by restricting food supply and mating between partners. Birds, mammals, lizards, fishes and many social insects often defend space by aggressive signals. In cases of some social animals and colonial plants, the growth rate is greater above a minimum density. According to Allee's Principle, under-as well as over crowdings may be limiting to population.

From the above account it can be concluded that density-dependent factors regulate population size at or near carrying capacity of the environment by regulating the availability of abiotic and biotic environment/resources, whereas the density-independent factors often reduce the population size below the carrying capacity or may cause population to fluctuate about their equilibrium level/size.

Besides above, in nature some populations overshoot or surpass the carrying capacity of the environment resulting into repeated cycles of population growth and decline. These cycles may be very regular if they depend on a few simple factors (seasonal variation in light and temperature-dependent algal bloom in lakes) or complex if depend on complex environmental and biotic relationships, as cyclic variations in the population of snow-shoe hare (prey) and the Canadian lynx (predator), occurring over 9-10 years time period.

Density-dependent theory in regulating the population growth has been explained in their own ways by Howard and Fiske (1911), Smith (1935), Solomon (1949) and Nicholson (1954) including the role of competition, whereas density-independent theory advocated by Thompson (1939) and Andrewartha and Birch (1954). Chitty (1960) and Wellington (1960) preferred to advocate a middle approach, advocating the role of both, density-dependent and density-independent factors.

Table 4.3. **Features of *r*-and *K*-selected species.**

	r-selected	*K*-selected
Environment	Unstable or stable near the carrying capacity	Nearly stable, predictable
Population and life style characteristics	1. Population growth high 2. Competition low 3. High energy allocated reproduction 4. Population development rapid 5. Life cycle short	1. Population growth slow 2. Competition high 3. Low energy allocated reproduction 4. Population development slow 5. Life cycle long
Offsprings (Individuals) characteristics	1. Many and small offsprings 2. Adults small in size	1. Few and large offsprings 2. Adults large in size

r-and *K*-selection Strategies (Evolution Among Populations)

Most population ecologists use the population parameters to draw conclusions about evolution of species. The important synthesis was done by MacArthur and Wilson (1967) after critical studies on logistic equation of population growth. According to them populations are the outcome of *r*-or *K*-selection strategies. Two distinct life history strategies are described by *r*-and *K*-selection theory, which states that *r*-selected species are **adapted** to maximise the rate of increase of the population size, whilst *K*-selected species are **adapted** to be competitive. ***r*-selected** populations have a higher intrinsic rate of growth (*r*) and tend to "boom" when environmental conditions are favourable and "best" when those conditions deteriorate. As a result they exhibit large fluctuations in density, and incidentally have the potential for large genetic change through the founder effect. ***K*-selected** populations have relatively constant density at or near the carrying capacity (*K*) of the environment.

The concept of *r*-and *K*-selection theory, suggests that **r-selected species** have evolved in **unstable environments** and thus **maximize population growth** (the *r* of the logistic equation), or evolved in **stable habitats** near the **carrying capacity** (*K* of the logistic equation) and are thus adaptive to low competition. Thus, *r*-selected species have all the characters which **maximize population growth : rapid development, small adults, many** and **small offspring, a high energy allocation to reproduction** and a **short generation time**. In contrast, *K*-selected species have features which **maximise competitive ability : slow development, large adult size, few, large offspring, a low energy allocation to reproduction** and **long generation times.** The features associated with each of these types of populations are listed in Table 4.3.

Some examples illustrate these two general patterns. Woodland trees and large mammals have many *K*-selected characters, whilst annual plants and insects have some *r*-selected characters, although close analysis suggests the fit is less than perfect. More robust evidence supporting the *r*/*k* dichotomy is provided by two species of the plant seed mace (*Typha* sp) from Texas and North Dakota respectively. The North Dakota species, *T. angustifolia* experiences high winter mortality and low competition compared to Texas *T. domigensis.* As predicted by *r*/*K* scheme, *T. Angustifolia* matures earlier, reaches a lower height and produces more fruits than *T. domigensis.*

However, there are many cases which do not fit the *r*/*K* dichotomy, and one study found only 50% of examples agreed with the predictions. For example, aphids have among the highest population growth rates of all animals of comparable size (suggesting they are *r*-selected) and give birth to relatively large offspring (a K-selected trait). The *r*/K theory is now not generally regarded as wrong, but rather of being a **special case.** Although some species fit this theoretical dichotomy, many do not, and this theory is now out-dated as better models have wider predictive powers.

5

Population Interactions

INTERACTIONS CLASSIFIED

Insteractions between individuals of the two species (interspecific) and between those of the same species (intraspecific) can be classified on the basis of the **mechanism** and **effect** of the interaction. The key **interspecific interactions** are **competition, predation, parasitism,** and **mutualism,** whereas the main **intraspecific interactions** are **competition, cannibalism** and **altruism** (Table 5.1). **Parasitoidism** is a type of parasitism, also known as **hyperparasitism,** which occurs in some insect species (mainly wasps and flies), in which parasitoid lays eggs in or on the body of the host, and usually results in death of the host.

Occasionally, interactions between species (interspecific) occur where one species exhibits no effect, while the other either benefits (**commensalism**) or is adversely affected (**amensalism**). Hermit crabs often carry hydroids on the mollusc shell they occupy, which benefits the hydroid by transporting it to feeding sites, but bears no obvious cost to the crab — an apparent example of commensalism. According to some the hydroid in return provides protection to crab, and they include the association under protocooperation – non-obligatory mutual beneficial interaction. Examples of amensalism are the species producing toxins (as antibiotics by soil fungi), or other inhibitory chemical principles (allomones) implicated in allelopathy and similar mechanisms.

It may be convenient to classify population interactions on the basis of the **effect.** The effects of interactions may be positive (+), negative (–), or neutral (0) (Table 5.2).

Various types of population interactions are briefly explained in the following section :

Mutualism

Mutually beneficial interspecific interactions are more common in the tropics than elsewhere. Here both the species derive benefit. In such association, there occurs a close and often permanent and obligatory contact more or less essential for survival of each. The two populations enter into some sort of physiological exchange. The following are some common examples of mutualism :

Table 5.1. **Possible combinations of (0), (+) and (–) to give different kinds of interactions** (Burkholder, 1952)

Combinations	Detailed effect(s)	Interaction type
0 0	Neither population affects the other	**Neutralism**
– –	Direct-inhibition of each species by the other.	**Competition** (Direct interference type)
– –	Indirect inhibition where common resources is in short supply.	**Competition** (Resource use type)
– 0	Population 1 inhibited, 2 not affected.	**Amensalism**
+ –	Population 1, the parasite, generally smaller then 2, the host.	**Parasitism**
+ –	Population 1, the predator, generally larger then 2, the prey.	**Predation**
+ 0	Population 1, the commensal, benefits while 2, the host, is not affected.	**Commensalism**
+ +	Interaction favourable to both but not obligatory.	**Protocooperation**
+ +	Interaction favourable to both and obligatory.	**Mutualism**

Pollination by animals

Bees, moths, butterflies etc., derive food from the nectar, or other plant product, and in return bring about pollination (Fig. 5.1 I).

Dispersal of fruits and seeds

Seeds and fruits are commonly transported by animals. The fruits are eaten by birds, mammals etc., and seeds contained in them are dropped in the excrement at various places.

Lichens

These are examples of mutualism where contact is close and permanent as well as obligatory. Their body is made up of a matrix formed by a fungus, within the cells of which an alga is embedded (Fig. 5.1 II). The fungus makes moisture as well as minerals available, whereas alga manufactures food. Neither of the two can grow alone independently in nature. Lichens grow abundantly on bare rock surfaces.

Symbiotic nitrogen fixers

This is a well known example of mutualism, where the bacterium *Rhizobium* forms nodules in the roots of leguminous plants, and lives symbiotically with the host (Fig. 5.1 III A, B). Bacteria obtain food from the higher plant and in turn fix gaseous nitrogen, making it available to plant. Similarly, root nodules of *Alnus, Alopecurus, Casuarina,* Cycadacease, *Myrica, Podocarpus* etc., and leaves of about 400 species of non-legumes are examples of such associations.

Mycorrhizae

This is also an example of similar nutrition in fungi that form mycorrhizal structures either inside the roots, or on outside surfaces of plants (Fig. 5.1 IV A, B). Ectotrophic mycorrhizae are very common in nature on pines, oaks, hickories and beech, and endotrophic ones occur in red maple and are common in roots and other tissues of many orchids and members of Ericaceae. In ectotrophic mycorrhizae, the fungal hyphae are the natural substitutes of root hairs absorbing water and nutrients from the soil. In some cases, the plants are restricted in their distribution to acidic soils which suit to the fungus partner. In endotrophic mycorrhizae, fungi occur internal to the root tissue.

Zoochlorellae and zooxanthellae

Some unicellular plants, especially algae, known as *Zoochlorellae,* live symbolically in the outer tissues of certain sponges, coelenterates, molluscs and worms (Fig. 5.1 V A, B). Some brown or yellow cells, probably flagellates (*Zooxanthellae*) are also present. Algae are photosynthetic and produce nitrogenous compounds beneficial to hosts and in exchange, they obtain materials released

Table 5.2. A classification of interactions between individuals of two species (interspecific) and between those of the same species (intraspecific) based on the nature of mechanisms operating therein. Note that by these definitions, herbivores may be either predators (e.g., wildebeest, horse, camel, etc.) or parasites (e.g., aphids).

Mechanism	Interspecific	Inraspecific
1. Direct inhibition of each species by the other.	Competition (direct interference type)	
2. Use of the same limiting resource, with resulting fitness loss.	Competition (resource use type)	Competition (resource use type)
3. Consumption of all or part of another individual.	Predation	Cannibalism
4. Individuals live in close association with mutual or one-way benefit.	Mutualism, (obligatory), Protocooperation (non-obligatory), Commensalism (one-way)	Altruism or mutualism
5. Individuals live in close association, to cost of host	Parasitism and hyperparasitism (Parasitoidism)	*Parasitism
6. Individuals live together with no mechanism of effect.	Neutralism	Neutralism
7. Inhibition of one through secretion of inhibitory principle (allochemicals or allomones) by the other.	Amensalism (Allelopathy)	Amensalism (Allelopathy)

* Intraspecific parasitism is relatively rare, and may be difficult to distinguish from mutualsim, especially if individuals are related.

by metabolism of hosts animals. The unicellular green alga, *Chlorella vulgaris* lives within the gastrodermal cells of *Hydra*. Alga, through photosynthesis provides food and oxygen to *Hydra*, which in turn provides shelter, nitrogen wastes and CO_2 to *Chlorella*. Similar relationship exists between the alga, *Zoochlorella* and aplanarian, *Convoluta roscoffensis*.

There are associations between animals themselves. For example, termites which feed on wood and the protozoans (species of *Trichonympha*) present in their guts. Termites can not digest cellulose of wood. The protozoans digest cellulose for termites and in return obtain food and shelter from the termite.

Mathematical models of mutualism received much less attention than those of competition and predation. The simplest Lotka-Volterra model produces unrealistic predictions, with both populations increasing indefinitely.

Commensalism

In this association between members of different species only one is benefited and neither is harmed (cf. mutualism). Here two or more populations live together without entering into any kind of physiological exchange. One is benefited without any effect on the other. Some common examples are as follows :

Lianas

These are vascular plants rooted in the ground and maintain erectness of their stems by making use of other objects for support. Thus, with much economy of mechanical tissues they are able to get better light. Lianas are common in dense forests of moist tropical climates. They maintain no direct nutritional relationship with the trees upon which they grow. On the basis of the type of device used for climbing their supports, lianas may be leaners, thorn lianas, twiners or tendril lianas. Common lianas are species of *Bauhinia*, *Ficus* and *Tinospora*.

Epiphytes and epizoans

Epiphytes are plants growing perched on other plants (Fig. 5.1 VIA). They use other plants only as support and not for water or food supply. They differ from lianas in that they are not rooted into the soil. Epiphytes may grow on trees, shrubs, Or larger submerged plants. They grow either on the trunks or leaves. Epiphytes are most common in tropical rain forests. Many orchids, bromeliads, hanging 'mosses', *Usnea* and *Alectoria* are well known epiphytes. Some of them show intermediate gradations between epiphytes and parasites, as well as between epiphytes and lianas. For example, a fern *Nephrolepis,* in the beginning remains rooted in the soil, later on spreading its rhizome over tree trunk, sooner or later becoming completely separated from the soil, thus becoming an epiphyte. In *Tsuga heterophylla,* seeds germinate on tree surfaces, where their seedlings in the beginning live as epiphytes till they develop their own roots, by which ultimately maintain relation with soil and thus become independent. In epiphytes, there is a special layer - velamen over the root surface (Fig. 5.1 VI B). The cells, of the velamen are whitish which can take up abundant water rapidly from the atmosphere.

Some plants grow on the surfaces of animals. For example, green algae grow on the long, grooved hairs of the sloth. Similarly, *Basicladia* (Cladophoraceae) grows on the backs of freshwater turtles.

A variety of microorganisms, saprophytic bacteria and fungi, and protozoans live within tissues or cavities of higher plants and animals. Some microbes are found in lower intestines of animals. *Escherchia coli* is found in human colon. Some invertebrates grow as fixed commensals attached to plant or other animals. *Ostrea frons* grows on the roots of the red mangrove and certain barnacles found on the backs of whales. Several species of molluscs, barnacles and tube worms are found attached to the shells of horseshoe crab, *Limulus polyphemus.*

There are several commensals that make temporary contact with other organisms. For example, squirrels, monkeys, tree frogs, snakes, birds, insects etc., use trees and other plants for substratum, shelter or breeding sites. Certain beetles are found in nests of meadow mice. A small tropical fish, *Fierasfer* finds shelter within the cloacal cavity of a sea cucumber. Sponges generally harbour a rich fauna within their spongocoel.

Some commensals as oyster crab, *Pinnothers ostreum* is found in the mantle cavity of the oyster. In addition to shelter, it also gets food from the host mollusc, oyster, without causing any harm. In oceans there are many commensals. For example, in the burrow of the echiuroid worm, *Urechis caupo*, three commensls, namely small goby, scale worm and pea crab are found, which get shelter in the burrow (Fig. 5.1 VII). Hydroids and vorticellians use fish for transport. Some as *Treponema macrodentium* living in mouth of man and *Entamoeba coli* in the intestine of man are harmless commensals.

Besides above cited various associations, there exist in nature some similar situations where we find such associations between a variety of microorganisms and higher plants. For instance, the zone of soil around the roots of higher plants characterised by intense microbial activity, known as the **rhizosphere**; the surface proper of the roots growing in soil - the **rhizoplane**; the boundary layer of air over the green leaves with active microbes - **phyllosphere**; and the leaf surface-**phylloplane**, constitute important ecological niches, where we find rich populations of microorganisms, mainly fungi, actinomycetes and bacteria, that remain all the time active there. It is now well established that, from the living root as well as leaves of higher plants, there is a continuous diffusion of their metabolic products, mainly sugars and amino acids. These are the sources of nutrition for microorganisms present therein. Thus, these are nice examples of commensalism. Moreover, it is also known that these microorganisms in turn provide protection to roots and leaves against the attack by pathogens directly by inhibiting the growth of the pathogens. It has also been shown very recently that some microorganisms present in soil as well as in air produce some metabolic products which have been identified as the auxins. If it happens so indeed, then these microbes may perhaps play an important role in regulating the growth and development of the higher plants, and under such situations the associations approach towards

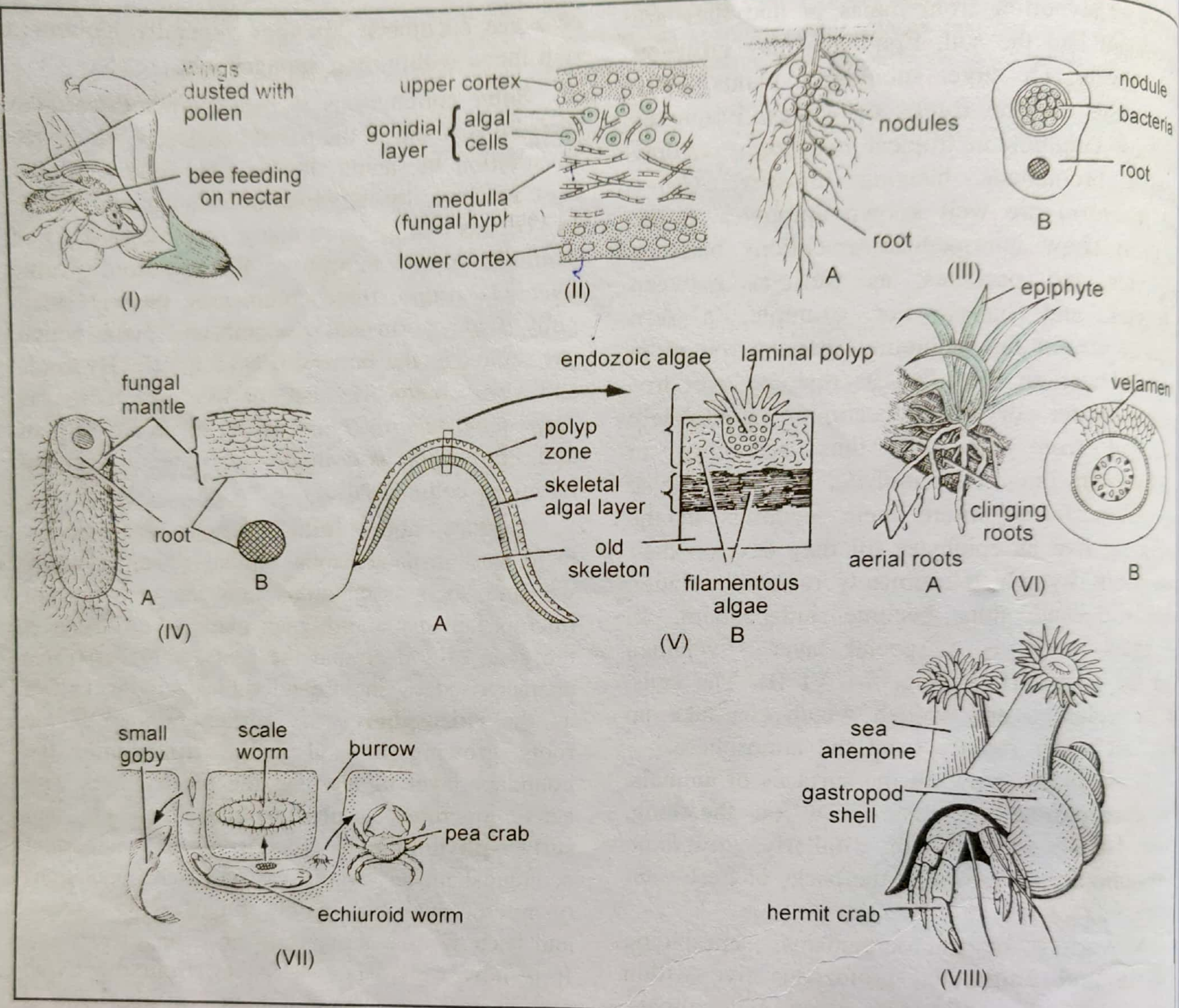


Fig. 5.1. Positive interactions **(I).** A bee feeding on nectar of flower and also becoming dusted with pollen (mutualism) **(II).** A part of T.s. of lichen thallus showing algal and fungal partners (mutualism) **(III).** Association between a legume's root system and root-nodule bacteria (mutualism). **(A).** Root system of a legume showing nodules. **(B).** T.s. (diagrammatic) through the root and a nodule. **(IV).** Association between root of higher plant and fungal hyphae (mutualism) **(A).** Root tip of a mycorrhizal root covered by fungal hyphae **(B).** A part of T.s. (diagrammatic) of mycorrhizal root showing fungal mantle. **(V).** Reclationship. between the polyp (animal) and several algae (mutualism). **(A).** Cross section (diagrammatic) of a coral colony or "head" showing intimate relationship between the coral animal (polyp) and algae. **(B).** A part of "head" magnified (diagrammatic). **(VI).** Association between an epiphyte and higher plant (commensalism). **A.** An epiphyte orchid growing perched on the branch of another plant. **(B).** T.s. (diagrammatic) of aerial root of orchid showing velamen. **(VII).** Diagrammatic sketch showing three commensals, the small goby, scale worm and pea crab, living in the burrow of the echiurid work (commensalism). **(VIII).** Diagrammatic sketch to show association between sea anemone and hermit crab (protocooperation).

mutualism. Thus, the situations mentioned here may belong to commensalism, mutualism or even gradation between two, depending upon the conditions present at that particular type of association.

Protocooperation

However, in some cases the association is ahead of commensalism, where both the populations are benefited. But the association, although benefited to both, is not obligatory *i.e.*,, not essential for the survival of either population (cf mutualism, where survival depends mostly on each other). Such associations are referred to as **protocooperation or non-obligatory mutualism.** One good example is of a coelenterate, sea anemone —*Adamsia palliata* attached to the shells of hermit crab - *Eupagurus prideauxi* (Fig. 5.1 VIII). Sea anemone is carried by the crab to fresh feeding sites and crab in turn is said to be protected from its enemies by sea anemone. Some ecologists prefer to include this association under commensalism.

Predation

In contrast with a parasite which derives nourishment from its host without killing, a predator is free living which catches and kills another species for food. Most of the predatory organisms are animals, but there are some plants (carnivores) also, especially fungi, which feed upon other animals. In some animals only the adults are predatory whereas the young are parasitic. In other animals, such as insects, most of the eating is done by larvae. Predators feed upon the adults, or larvae or even eggs of their prey. A number of fungi, such as species of *Dactylella, Dactylaria, Arthrobotrys, Zoophagus* capture insects, nematodes and other worm-like animals. Such fungi use specialised structures, the traps or snares, formed on their mycelia to capture the nematodes. The following are some of the common examples of predation:

Browsing and grazing

Herbivores kill the plants and use unharvested herbs, shrubs or even trees as their food and sometimes pose much problems of management of natural and artificial vegetations. Different plants receive varying degrees of harmness as a result of browsing and grazing. Many insects and ruminants browse lightly over the vegetation. Cattle, camels, goats etc. frequently browse the tender shoots of shrubs and trees and sheep graze the grasses. Generally annuals suffer more due to grazing than the perennials, shrubs are damaged less than herbs. Grazing and browsing may bring about marked changes in vegetation. Grazing in shrubby vegetation generally increases the number and sizes of the shrubs by removing the competitive grasses.

Seeds and seedling destruction

Animals such as insects, squirrels, mice, rodents etc. consume much quantities of seeds as food. Moreover, they browse seedlings of shrubs and trees, and damage most of them by trampling.

Plants as food

Aquatic plants are frequently eaten by animals like ducks, fish, muskats etc. and they really create problems of management of these water bodies. Aquatic filter feeders destroy the diatoms, flagellates and other algae.

Carnivorous plants

A number of plants as *Nepenthes, Darlingtonia, Sarracenia, Drosera, Utricularia, Dionaea* consume insects and other small animals for their food. They are also known as insectivorous plants. They are adapted in remarkable ways to attract, catch and digest their victims. Their leaves or foliar appendages produce proteolytic enzymes for digestion of the insects. The carnivorous habit in plants is said to be an incidental feature of their nutrition, since none of them is dependent upon its animal prey for nitrogenous compounds.

To a population ecologist predation is an important interspecific interaction which many determine the population growth. Laboratory studies have been made to derive Lotka-Volterra equations, though less informative. Behavioural aspects of predation as **functional response** have been studied. Such response is affected by **rate of encounter** and **handling time.**

Parasitism

A parasite is the organism living on or in the body of another organism and deriving its food more or less permanently from its tissues. Whereas a predator derives its food by killing its prey, a parasite does so **without killing** its host. Parasites

Table 5.3. **A selection of microparasitic diseases**

Microparasite	Human host	Plant hosts
Viruses	Measles HIV (the cause of AIDS) Influenza	Barley dwarf yellows virus Cauliflower mosaic virus
Bacteria	Typhoid Scarlet fever Streptococcus	Fireblight Willow watermark disease
Fungi	Ringworm	Cabbage clubroot Rusts Potato blight
Protozoan	Trypanosomes (sleeping sickness) Plasmodium (malaria)	

live in close association with their hosts. Unlike predator, parasite does not consume all parts of its host.

Parasites can be classified into two broad groups : (i) **microparasites,** which multiply within, or on the surface of, the host, and (ii) **macroparasites,** which grow in or on the host but do not multiply. The main microparasites are **viruses, bacteria, fungi** and **protozoans.** A selection of human and plant examples is given in Table 5.3. Macroparasites of plants and animals are dominated by invertebrates. In animals, **helminth worms** are particularly important (Table 5.4), whilst **insects** are the main macroparasites of plants (particularly butterfly and moth larvae and beetles), though other plants (e.g., mistletoes) may be important. Note that the size of the parasite is not always the determinant of whether it behaves as a microparasite or a macroparasite. Thus, aphids are microparasites of plants (reproducing on the surface of the plant) whilst fungi may be macroparasites of insects and plants, not reproducing until the host is killed.

Parasitoids (also known as hyperparasites) comprise a large group of insect macroparasites (mainly wasps and flies) which lay eggs in or on the body of their insect host and usually cause the death of the host.

Most parasites are **biotrophs**, only surviving on living tissue, but some (such as the sheep blowfly, *Lucilia cuprina,* and the plant fungal disease *Pythium,* which causes 'damping-off') continue to live on the host after causing its death. These are **necrotrophs**.

Parasite transmission can be either **horizontal** (among members of a population) or, less commonly, **vertical** (passed from mother to offspring). Horizontal transmission may either be **direct** or **indirect,** mediated by a vector (e.g., a mosquito) or an alternate host. Occasionally the major route of transmission is 'accidental' acquisition via another species. Some examples

Table 5.4. **A selection of animal macroparasites**

Class	Order	
Helminth worms	Tapeworms	e.g., ox tapeworm in humans
	Schistosomes	e.g., bilharzia in humans
	Flukes	e.g., liver fluke in cattle
	Monogeneans	fish gill parasites
	Nematodes	e.g., elephantiasis in humans
Insects	Fleas	e.g., cat flea
	Lice	e.g., swift louse
	Fly and wasp parasitoids	macroparasites on parasitic insect hosts
Arachnids	Ticks	

Table 5.5. **Modes of transmission in selected human parasites.**

Modes of transmission	Examples in humans
Vertical	HIV, rubella
Horizontal	
Direct	
close contact	Measles, common cold
sexual	HIV, syphilis
water contamination	Poliovirus, cholera
Indirect	Malaria (mosquito), sleeping sickness (tsetse fly)
Other species	Rabies, plague

of human parasites using alternative modes of transmission are given in Table 5.5.

Many parasite species **obligately switch** between two or even three host species in the source of their life cycle (Fig. 5.2, Table 5.6). Often, there are a suite of different morphs associated with the different hosts. In most cases, sex only occurs on the primary host, and if reproduction occurs on the other host(s), it is asexual.

Why do parasites commonly have such complex life cycles ? Three different explanations have been advanced.

(1) Some alternate hosts were initially used simply as **vector's** which have subsequently been attacked by the parasite to increase its reproductive output. However, this cannot apply to cases where the alternate hosts are sessile.

(2) Complex life cycles are a result of **optimal habitat use.** Thus, it has been suggested that host-alternating aphids use the hosts on which phloem sap quality (on which aphids feed) is highest when plants are growing most rapidly, which is in trees in the spring and herbaceous plants in the summer.

(3) Alternatively, complex life cycles may be due to an **evolutionary constraint** as parasites become highly adapted to one host for the sexual part of their life cycle and are unable to leave the primary host even though the rewards are higher elsewhere. This explanation may account for a few cases, but it seems unlikely that the general widespread patterns is explained by such maladaptation.

Social parasites do not feed on the tissues of their hosts like true parasites, but gain benefit from their animal hosts by coercing them to provide food or other benefits. One such example is **brood parasitism** in birds. **Intraspecific brood parasitism** is found in a number of species, and is particularly common in ducks, including the goldeneye (*Bucephala clangula*). After the parasitic female has laid some eggs in foreign nest, the host female typically responds by reducing the number of eggs she subsequently lays. **Interspecific brood parasites** include the cockoo (*Cuculus canorus*) in Europe and the brown cowbird (*Molothrus ater*) in North America, which lay eggs in the nests of other bird species. The cuckoo lays an egg in the nest of its host and

Table 5.6. **Examples of complex life cycles in parasites. Two examples of single host use are provided for comparison.**

		Host		
Parasite	One host	Primary	Secondary	Tertiary
Measles	Human			
Apple sawfly	Apple			
Biharzia		Human	Freshwater snail	
Ox tapeworm		Human	Cattle	
Black stem rust		Barberry	Wheat	
Trypanosoma brucel (sleeping sickness)		Man	Tsetse fly	
Peach-potato aphid		Peach tree	Potato	
Potato leaf roll virus		Potato	Peach-potato aphid	
Tapeworm (*Diphyllobothrium latum*)		Human	Copepod	Fish

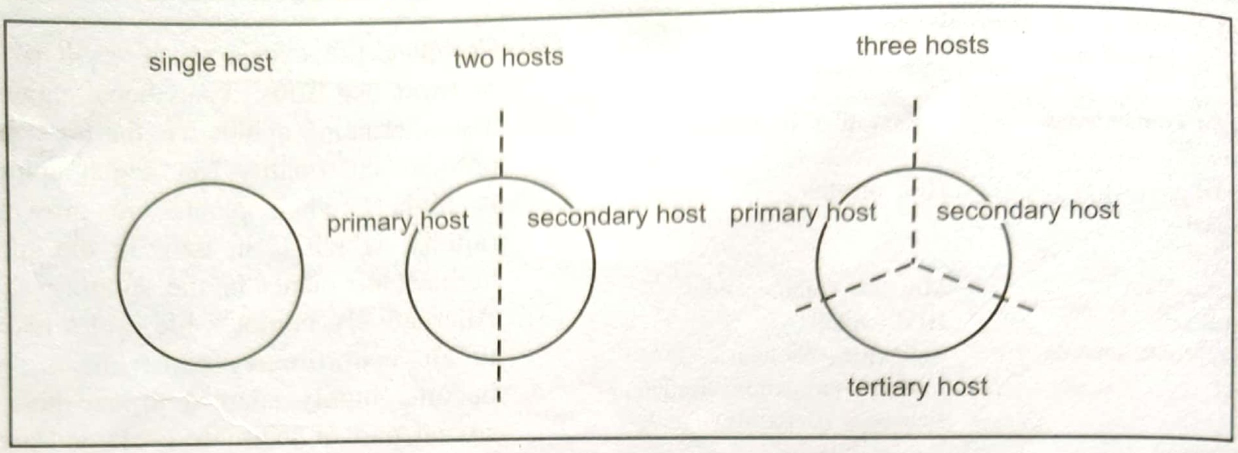


Fig. 5.2. Complex life cycles in parasites.

removes one of the original clutch, thus conserving the clutch size. Social parasitism is also prevalent among **ant and wasp** species. Some species, such as the ant *Lasius regina,* have a worker caste and are able to rear their own broods but may coerce other species to undertake this task, whilst other, obligate parasites, are workerless and depend entirely on other species to rear their young. In either case, colony takeover usually occurs by the parasite queen invading the nest and killing or dominating the resident queen. The resident workers continue to supply food and services to the brood, to which the parasite queen adds her own eggs.

Parasitoidism (Hyperparasitism)

Examples of parasitoids are some insect species (Diptera and Hymenoptera, mainly wasps and flies). The parasitoid lays its eggs in or on the body of its parasitic insect host. This eventually results in the death of the host. The parasitoid deposits its eggs in the immature stages of parasitic insect host; the larvae of parasitoid on hatching feed on the host until they are fully grown. A moth, *Samia cecropia* suffers the destruction of its cocoons by the parasite, *Spilociyptus extrematis* which deposits its eggs on the inside of cocoon or on the surface of larvae of *S. cecropia.* The host larva dies in a few hours. *S. extrematis* becomes infested by the parasitoid, *Aenoptex smithii.*

Amensalism

It is a negative type of interaction in which one population is inhibited by another population through the secretion of inhibiting principle. The mechanism is referred to as **antibiosis**. Antibiotics are good examples, which are secreted by a microbe, inhibiting the growth of another microorganism. Such chemicals have also been reported in some algae like *Chlorella vulgaris,* and diatoms. Such inhibitory substances produced by one species are also called **allelochemicals**, which on the basis of nature of their action are also classified as **allomones**, **kairomones** and **depressants**. In plants, phenomenon of inhibition of one plant species by the production of inhibiting chemicals by another species is referred to as **allelopathy**.

Neutralism

This is a type of interaction between two species in which they do not affect each other. It appears merely theoretical under natural conditions. Since there operate complex interactions among natural ecosystems, it is hard to believe that there exist no interactions between their biotic components. Neutralism appears to be nonexistent in nature, interactions may be negligible or insignificant. It is practically difficult to prove that there are no any type of interactions between species under natural conditions.

Cannibalism

It is an **intraspecific** interaction where the larger individuals eat up the smaller ones of their own species. The individual that eats is called **cannibal**, and the one eaten as **prey.** Cannibalism is common in the insects such as cockroach, ant and termite, and also observed in frog, cobra and scorpion. Female spider eats up the male after mating. Some animals regulate their population through cannibalism. Flour beetles and guppy fish eat up their own eggs.

Altruism

It is a type of **intraspecific** interaction in which an individual causes an increase in the fitness of another individual of the same species at a cost to its own survival or offspring production. Altruistic behaviour, whereby an individual appears to sacrifice its own fitness to benefit another, seems paradoxical on first impression. However, if the altruist is related to the beneficiary, this strategy may result in more of the altruist's genes passing to the next generation. An example is the sterile worker in the eusocial ant society, which sacrifices its opportunity of reproducing and instead supports its mother's reproduction. Another examples are aphids and wasps who produce **soldier** larvae to defend the colony but do not develop into adults. The solution lies in the idea of **inclusive fitness**. An individual's fitness is high if it passes many copies of its genes on to future generations. An example is also a herd of spotted deer attacked by a predator. The stag with best antlers is surrounded by other individuals to save its life. In doing so, many defenders may be killed or injured by the predator. Sterile female workers in colony of honey bees working tirelessly for the queen is also example of altruism.

Home Range and Territoriality

Home range is an area in which an animal normally lives, regardless of whether or not the area is defended as a territory. A **territory** is an area in which the resident enjoys priority of access to limited resources that the animal (he/she) does not enjoy in other areas. Territories in contrast to home range are defended and used exclusively by an individual, a pair, or a family or a small inbred group of individuals. Within their own territories animals typically acquire a heightened position of dominance in relation to other members of the same species. Examples of territorial defense are wide variety of insects, fish, amphibians, reptiles, birds and mammals.

Some **other examples of instraspecific interactions are, dominance, leadership co-operation** and **communication. Dominance** is "a priority of access to an approach situation or of leaving an avoidane situation that one individual has over other". **Leadership** is "a cooperative interaction among the individuals of a group in which one behaves as a leader". The leader does not enjoy any special social benefit and there is no mutual dependence of the leader and other members of the group. Leadership behaviour is common in mammals but also observed in lizards, birds, fish and arthropodous. **Cooperation** is a commonly observed phenomenon among animal species where "individuals (of the same species) act for the mutual benefit (non-obligatory) of each other". Cooperation is often temporary or transitory, as in the example of offspring care, but may be permanent, lasting the life span of the individual (e.g., an ant colony, or a pair or mute swans). The commonest general kind of cooperation involves the provision of nutrition and defense of the young. Cooperation (protocooperation) is a type of interspecific interaction, wherein two species benefit mutually, but association is non-obligatory. In **communication**, there is "transmission and exchange of information among the members of a species". Most animals send, receive and interpret signals (chemical, tactile, visual, auditory or electrical). For example, **pheromones** are the "chemicals released by an animal into the environment to evoke a certain behaviour in other members of the same species". They are involved in sexual acts between animals, where these attract individuals of the same species.

Competition

Competition is an interaction among individuals utilising a limited resource (food, space etc.) resulting in reduced fitness in the competing individuals. Competition occurs both, between species utilising a shared resource – **interspecific competition,** as well as among members of a species – **intraspecific competition**. The **niche** of an individual or species (the conditions under which it is found, the resources it utilises and the time it occurs there) is critical in determining the degree of competition with other species or individuals. The greater the degree of niche overlap, generally the more intense the degree of competition.

1. Interspecific Competition

It occurs between two species using the same limited resource. Very few species can escape from the effects of other species competing for the same resource. There are several examples of interspecific competition, which have been studied in detail. These include protozoans (*Paramecium* spp), diatoms (*Asterionella* sp. and *Synedra* sp), Darwin's finches, barnacles and several invasive weeds.

This type of competition can operate in the following **two** ways :

[I] Exploitation competition

It occurs solely via the depletion of the limiting resource whereby individuals only interact indirectly. One species either reduces or more efficiently uses a resource and therefore depletes its availability for the other species. An example is tadpoles of *Rana tigrina.*

[II] Interference competition

It occurs by direct interaction between competing individuals fighting over limited resource. The most obvious instances of such type of competition are animals which fight over territories or food items. Lions may arrive at the kill of a small carnivore and displace it. Interference may occur via the use of toxins by competitors. A braconid wasp parasitic on aphids produces a toxin as it hatches from the egg, which kills all other parasitized eggs. In plants, the process of competing via toxin production is termed **allelopathy**. There are many examples of allelopathy. The black walnut kills many plants by this mechanism. *Salvia leucophylla* and *Typha latifolia* also are examples of allelopathy.

2. Intraspecific Competition

It occurs between members of the same species. It is likely to be intense because individuals will tend to share requirements for the same resource. Although there may be age differences in resource requirements (as some young fish feed on small zooplankton, whereas adults on large benthic invertebrates) or sex differences (as the male of most birds of prey is much smaller than the female, the preferred prey size differs between the sexes), the general degree of overlap in resource use means that intraspecific competition is a major force in ecology. By depressing the fitness of individuals in crowded populations, it both influences fecundity and mortality, and hence regulates population size, and leads to behavioural adaptations to overcome or cope with competition, such as **dispersal** and **territoriality**.

Intraspecific competition basically operates in the following **two** ways :

[I] Scramble competition

Where the resource is divided into many small parts to which all have access. Individuals scramble for the resource which results in shortage. Each individual ultimately obtains such a small amount of the resource that it is unable to survive.

[II] Contest competition

Where each successful individual claims a part of the resource and the unsuccessful denied any access to it. This results into territoriality, social dominance and hierarchy, migration and psychological stress. Altruism, dominance, leadership, home range and territoriality, communication, and cannibalism are examples of intraspecific competition.

Lotka-Voltera Equation for Competition

The Lotka-Voltera mathematical model was developed to explain the influence of **interspecific competition** on population growth. This model is a development of the logistic equation of population growth. Let us recall the logistic equation :

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$; where N is the population density, K the carrying capacity and r the intrinsic rate of a species. As there are two species, we have two sets of these variables : N_1, N_2, K_1, K_2, r_1, r_2. Accordingly, for growth of species 1, the logistic equation is :

$$\frac{dN_1}{dt} = r_1N_1\left(\frac{K_1 - N_1}{K_1}\right)$$

and, for growth of species 2, the logistic equation is :

$$\frac{dN_2}{dt} = r_2N_2\left(\frac{K_2 - N_2}{K_2}\right)$$

When the two species grow together, the equations assume the forms as follows :

For species 1 :

$$\frac{dN_1}{dt} = r_1N_1\left(\frac{K_1 - N_1 - \alpha_{12}N_2}{K_1}\right)$$

where α_{12} is the competition coefficient *i.e.*, inhibitory (competitive) effect of species 2 on species 1

For species 2 :

$$\frac{dN_2}{dt} = r_2N_2\left(\frac{K_2 - N_2 - \alpha_{21}N_1}{K_2}\right)$$

where α_{21} is the competition co-efficient, *i.e.*, inhibitory (competitive) effect of species 1 on species 2.

The Lotka-Voltera equations are based on the assumption that it works under the homogeneous environment, where migration is negligible and competition effect is instantaneous and is the **only** important biological interaction. These equations have been used for modelling competition (including predator-prey and parasite–host interactions), mostly for controlled laboratory conditions or in the environments having very negligible input and output.

To apply this model to two competing species, it is necessary to be able to translate the number of individuals of one species that are competitively equivalent to the one member of the other species. This is the **competitive coefficient**, and is denoted α. There are two competitive coefficients : (i) the perceived competitive equivalence of species 2 on a member of species 1 (α_{12}), and (ii) the perceived competitive equivalence of species 1 on a member of species 2 (α_{21}).

If each member of species 2 exerts five times the competitive effect of a member of species 1 on species 1 (which may occur if say, species 2 are bigger and hence consume more resources), then α_{12} will be 5.0. Thus, we can translate the number of individuals of species 2 into species 1 equivalents by multiplying N_2 by α_{12}. The maximum number of individuals of species 1 the environment can support is of course the carrying capacity K_1. But as more and more members of species 2 are present, this maximum will fall, until when there are K_1/α_{12} members of species 2 present, the environment will be saturated. Thus, it is possible to represent the numbers of species 1 the environment can support for all values of the numbers of both species – this is the **zero net growth isoçline** for species 1, shown graphically in Fig. 5.3 A. A reciprocal effect of the number of individuals of species 1 on species 2 occurs, as shown in Fig. 5.3 B.

By adding together both of the zero net growth isoclines defined in Fig. 5.3 we can find the different outcomes of the model (Fig. 5.4). Four different outcomes arise from this simple model, based on the relative values of the species carrying capacities K_1 and K_2 and their competitive equivalents K_1/α_{12} and K_2/α_{21}. In the simplest cases, as shown in Fig. 5.4 A and B, one species will win if it is a superior competitor

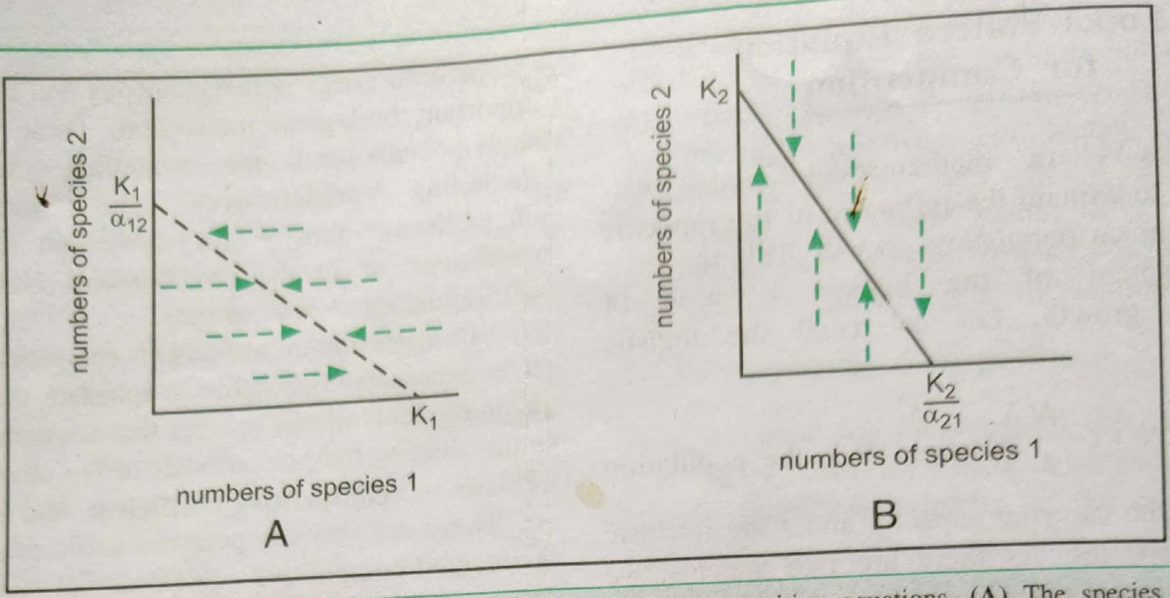


Fig. 5.3. The zero growth isoclines from the Lotka-Voltera competition equations, **(A)** The species 1 zero growth isocline. Species 1 increases to the left of the line (the environment is not saturated) and decreases to the right of the line (the environment is over-saturated). **(B)** The species 2 zero growth isocline. Species 2 increases below the line (the environment is not saturated) and decreases above it (the environment is over-saturated). The arrows indicate the change in population size for a range of different values of N_1 and N_2.

at all values on N_1 and N_2. In these cases, the weaker competitor is eliminated. This occurs when intraspecific competition within the dominant species exceeds the interspecific effects of the competitor and the interspecific competitive impact on the inferior species exceeds the intraspecific effects of that species on itself. If both species exert more intense intraspecific than interspecific competition, then stable coexistence occurs, as shown in Fig. 5.4 C. This may happen if competitors have only partial niche overlap. In the final case, where both species have more intense interspecific than intraspecific competition (which may occur in cooperative animals which may act aggressively towards competitive species), the outcome is more complex. There are two alternative stable states, in which the species numerically dominant will exclude the other (Fig. 5.4 D). If equivalent densities balance, an unstable coexistence may temporarily occur, but in real populations this will not persist and one or other species will be excluded.

It becomes clear from Lotka-Voltera equations that if two species compete in a **stable** environment, there are **two** possible outcomes : (i) one species is **excluded,** or (ii) both species **co-exist.** The **competitive exclusion principle** states that co-existence can occur only in a stable environment if the **species niches are differentiated.** How much niche differentiation is needed for species to co-exist ? This critical threshold of differentiation in resource utilisation in termed the **limiting similarity**.

The two outcomes (competitive exclusion and competitive co-existence) of two species competing with each other in a stable environment are explained in some detail as follows :

Competitive Exclusion

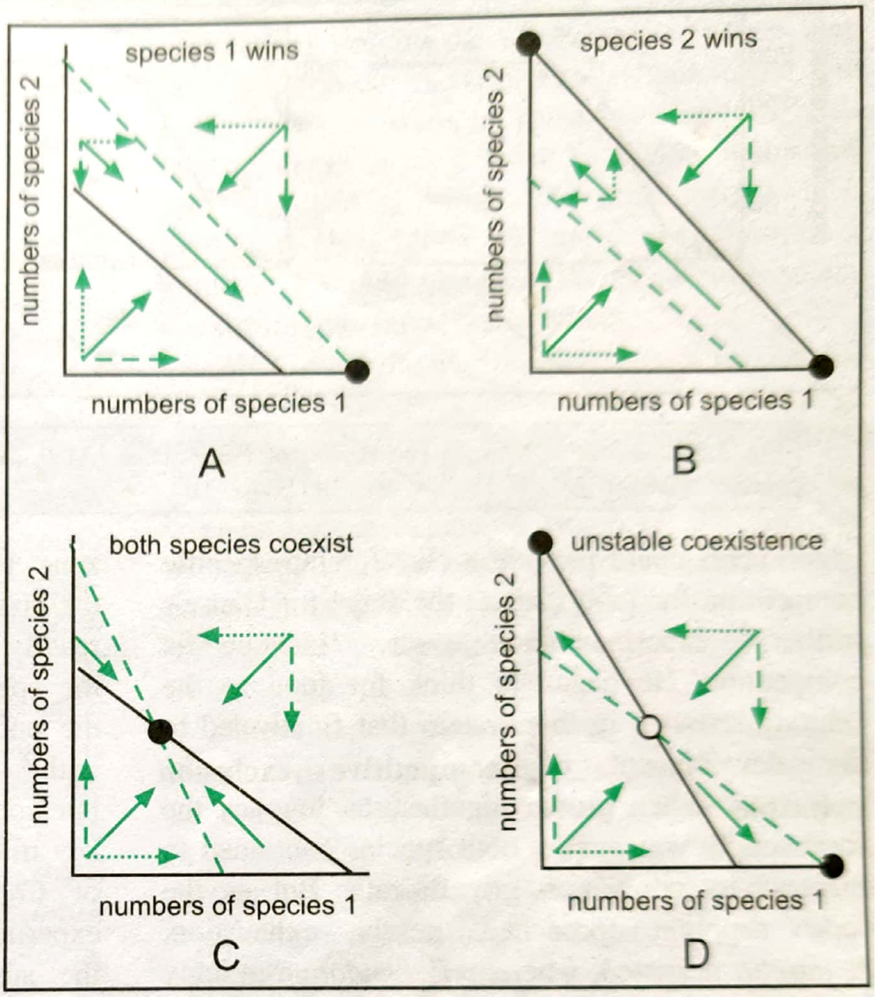
As indicated in Lotka-Voltera model, when two species compete in a stable, homogeneous environment, either one species will win and the other be excluded, or both species will manage to co-exist. The **competitive exclusion** principle states that co-existence can only occur in a stable, homogeneous environment if the species niches are differentiated, because if two species had **identical requirements** one would dominate and out compete the other. Precisely, the competitive exclusion principle states that **complete competitors (for same resources) cannot coexist.** This concept of competitive exclusion was developed by Gause (1934).

Gause's Principle and His Laboratory Experiments

Based on his experiments designed in the **laboratory**, G. F. Gause (1934) developed the concept that more closely the two species related (for a given resource), the more severe the competition between them. The species with similar requirement (say food/nutrition) cannot occupy the same environment.

If the similarity of requirement is too much, this would result in competitive exclusion of population of one species by another. (This principle states that two species cannot coexist on a single limiting factor for a long time, and finally one of these is excluded.) In laboratory Gause performed experiments with two species of *Paramecium*, *P. aurelia* and *P. caudatum*. Both species were grown on yeast medium as well as in aquaria having the bacterium, *Bacillus* sp. as its food. When cultured separately in the yeast medium, *P. aurelia* had a faster growth rate than *P. caudatum*. When grown together in the mixed culture in same culture vessel, *P. aurelia* dominated the mixture and eventually *P. caudatum* died out (Fig. 5.5)

Similarly when grown separately in aquaria providing bacterial food, each showed a sigmoid growth curve, with both full-and half-strength concentrations of food supply. The carrying capacity of each species, when grown separately, was reduced almost to half, when grown and half- strength food supply. These initial



Summary

	Outcome
one species is not limited by its competitor and exerts strong **interspecific** competition	(a), (b) One species wins
Both species have intense **intraspecific** competition (possibly due to niche differentiation)	(c) Coexistence
Both species have intense **interspecific** competition (possibly due to co-operation within a species)	(d) One species wins, but the outcome depends on the starting densities (unstable coexistence may temporarily occur).

Fig. 5.4. The four alternate outcomes of the Lotka-Voltera model. The dotted arrowed lines represent the trajectories of species 1, the dashed arrowed lines represent the trajectories of species 2 and the solid arrowed lines the joint trajectory.

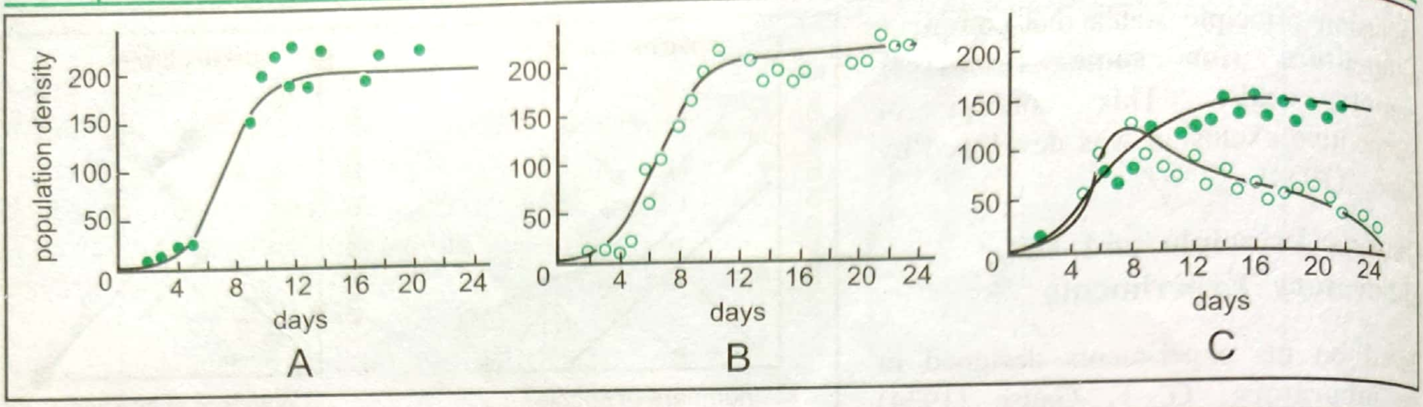


Fig. 5.5. Competition between two species of *Paramecium* (A) *P. aurelia* alone; (B) *P. caudatum* alone; (C) both species together.

experiments could provide a clue for intraspecific competition for food that set the stage for Gause's further experimentation on interspecific competition. He began to think for food as the limiting resource in this system that finally led to the development of **competitive exclusion principle.** When grown together, as long as the food supply was ample, both species continued to increase its population growth rate. But as the food supply approached nearly exhaustion, *P. aurelia* persisted, whereas *P. caudatum* quickly declined till it finally disappeared (excluded). The results could show that *P. aurelia* was capable of faster population growth and more resistant to accumulating waste products in the medium than *P. caudatum*. Similar results on competitive exclusion were also obtained with other studies made on other protozoans as well as on flour beetles and fruit flies.

Field Examples of Gause's Principle

The results of laboratory experiments designed by Gause were also confirmed by studies made under field conditions by other authors on different animal species. For instance competition studies were made on the barnacles, *Balanus balanoides* and *Chthamalus stellatus* by Joseph H. Connell (1961) and on blackbirds by Orians and Collier, (1963). The adult *Chthamalus* are restricted to the **upper** intertidal zone, whereas the adult *Balanus* in the middle and lower intertidal zones along the Scottish coast. *Balanus* cannot withstand its longer exposure to air in the upper intertidal zone. However, such factors only partially explain the distribution of *Chthamalus*. Larval *Chthamalus* readily settle in the intertidal zone below where the species perists as adults but these colonists die out within a relatively short period. Connell with field experiments could show that interspecific competition with *Balanus* played a key role in determining the lower population limit of *Chthamalus* within the intertidal zone. He experimented during March-April, 1954, prepared the area maps of the populations of the two barnacles by re-mapping the sites periodically. It was found that in the middle zone *Chthamalus* was able to survive at higher rates than *Balanus*. In the upper zone, removal of *Balanus* had no effect on survivorship of *Chthamalus*, because the population density of *Balanus* was too low to compete effectively with *Chthamalus*. These results could show that *Chthamalus* is excluded from the middle intertidal zone by interspecific competition with *Balanus*.

Competitive exclusion was also observed in the results of field observation on distribution of two species of blackbirds in California. Red-winged blackbirds fully occupied marshy areas during February-March and then suddenly a colony of tri-coloured blackbirds invaded the area. Only a few intact nesting territories of red-winged ones could be seen along the margin. This was found to be due to competitive exclusion achieved more quickly and efficiently through **interference.** This is very common evolutionary trend among birds, used to defend their territories.

Character Displacement

When realised niches contract under the influence of interspecific competition, morphological changes in the competing species may follow as adaptations to the new resource spectrum. Such an occasional niche contraction due to competition results in morphological character change, known as **character displacement**. It should be noted that behavioural and physiological changes also occur as a result of niche shifts. An example is the harvester ant, *Veromassor pergandei,* where the variability in mandible size is inversely correlated with the number of competing seed-eating ants. This suggests that as the competition from other ant species increases, *V. pergandei* becomes more specialised and concentrates on a smaller range of seed sizes. Another example is the Darwin's finches. On the Galapagos, when the two, *Geospiza fortis* and *G. fuliginosa* occur on islands alone, they have similar beak sizes, whereas when occurring together, *G. fuliginosa* invariably has a markedly narrower beak than *G. fortis*.

Competitive Co-existence

One of the conclusions derived from Lotka-Voltera equations is that when interspecific competitions are weak two species are able to co-exist. In Fig. 5.4C, there occurs a **stable co-existence,** as neither species wins, and species are able to co-exist sharing the resources between them. Neither species can contain the other, but both inhibit their own population growth (through more intense intraspecific competition) more than that of the other species (*i.e.* interspecific competition). This type of co-existence if favoured by **differential resource partitioning** in fluctuating environments and differing life history traits. According to resource partitioning, no two species utilise the resource in exactly the same way, resource may be partitioned (differentiated) spatially and temporally. For example, some insectivorous birds feed in upper canopy, some in middle and some on the ground in forests. The time during which they feed also differs. In this way, inspite of a common resource (insects), different bird species coexist in the same environment.

How much niche differentiation is needed for species to coexist ? This critical threshold in resource utilization is termed **limiting similarity.** The limit in the similarity of competing species is caused by a balance between (i) the intensity of intraspecific competition (which a narrow niche width intensifies), and (ii) the intensity of interspecific competition (which a broad niche width intensifies (Fig. 5.6).

However, theory is currently unable to predict where this balance might lie in real world examples. **Evolution** may act to reduce the degree of competition between species — thus current patterns of resource utilisation are a result of competition over time, even though little or no competitive interactions are currently observed. This phenomenon is known as **the ghost of competition past.**

In the final case (Fig. 5.4 D), where both species have **more intense interspecific than intraspecific competition,** the outcome is more complex. There are two alternative stable states. Here the coexistences is **unstable** (cf. 5.4 C *i.e.,* stable co-existence). Either species of the two wins depending upon ecological conditions at that instant of time. Each species is able to contain the other; each inhibits the other's population growth more than its own (as the intraspecific competition is less). One alternative is that the species numerically dominant will exclude the other. Otherwise if equivalent densities balance, an unstable co-existence may occur temporarily, but in real populations this will not persist and one or the other species will be excluded.

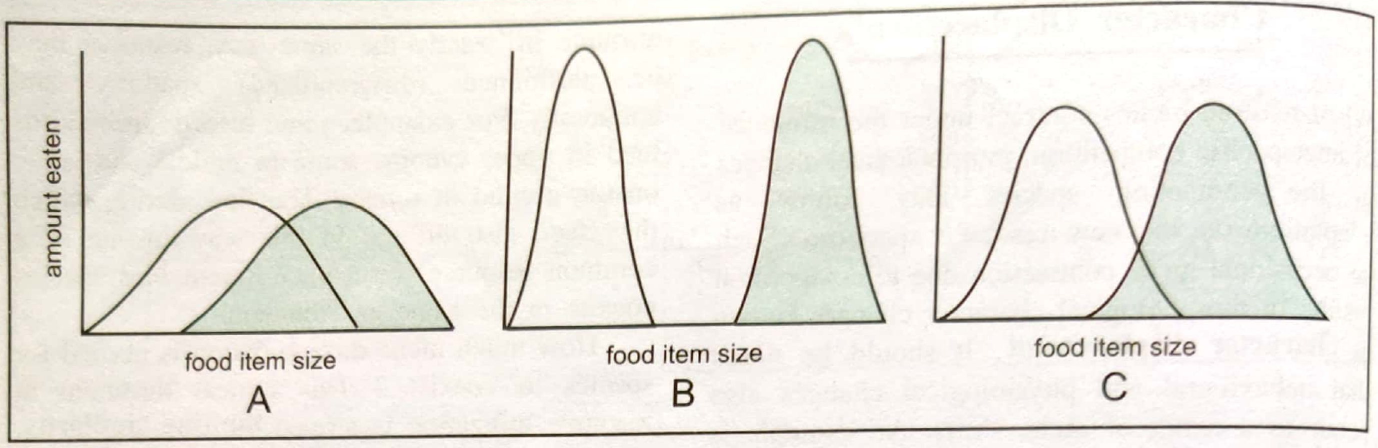


Fig. 5.6. Resource utilization curves for two species, where species vary in the range of size of food items they can utilize. In **(A)** there is strong interspecific competition and weak intraspecific competition; in **(B)** there is strong intraspecific competition and no interspecific competition; and in **(C)** the curves overlap only slightly, so interspecific competition is relatively weak, yet the range of resource utilized by each species is quite wide, so intraspecific competition is also relatively weak.

Lotka-Voltera Equation for Predator-Prey Dynamics

A variety of mathematical models have been developed to explore predator-prey dynamics. The **Alfred Lotka (1925) and Vito Voltera (1926) predator-prey model** is a simple yet valuable example for understanding predator-prey relationship. Lotka was inspired for studies on moth and butterfly larvae, whereas Voltera on marine fish populations. Their predation equations were as follows :

$$\frac{dN_1}{dt} = r_1N_1 - p_1N_1N_2$$

$$\frac{dN_2}{dt} = p_2N_1N_2 - d_2N_2$$

where

N_1 – prey population density
N_2 – predator population density
r_1 – instantaneous rate of increase of the prey population
d_2 – death rate predator population
p_1 and p_2 – predation constants
p_1N_1 – functional response (consumption response of individual predators to changes in prey density, a constant)
p_2N_1 – numerical response (the way in which preys converted into new predator individuals)

The equations are solved by setting *dN/dt* equal to zero, factoring out the appropriate *N* to get the actual rate of increase, and setting this *r* equal to zero. These manipulations show that (i) the prey reaches an equilibrium population density when the predator's density is r_1/p_1, and (ii) similarly, the predator is at equilibrium when the prey's density is d_2/p_2.

The Lotka-Voltera model makes **three** simplifying assumptions : (i) there is only one predator and one prey species involved in the interaction, (ii) prey numbers increase if the number of predators falls below a threshold and decrease if there are more predators, and (iii) predator numbers increase if the number of prey rises above a threshold and decrease if there are fewer prey. As shown in Fig. 5.7, the two assumptions, (ii) and (iii) give rise to a very interesting prediction; the **predator and prey populations cycle in abundance.** Figure 5.7 A shows the prey zero growth isocline, the critical predator density above which the prey population falls as death from predation exceeds the birth rate. In Fig. 5.7 B, the predator zero growth isocline is shown. This is the critical prey density below which the predator population falls due to starvation. Combining these two isoclines combines the change in prey numbers and predator numbers to give the joint instantaneous change in predators and prey (Fig. 5.7 C). A cyclical pattern will be followed, almost regardless of the starting numbers

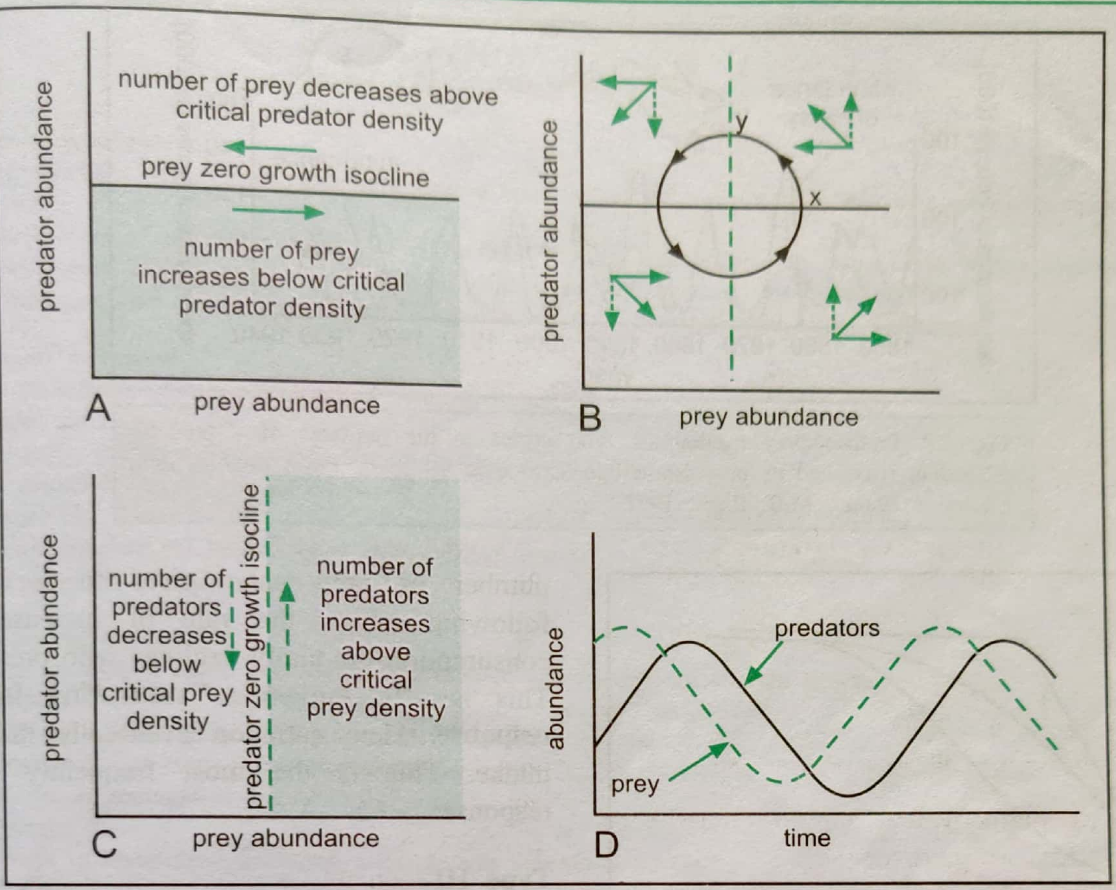


Fig. 5.7. The Lotka-Volterra predator-prey model, **(A)** The prey zero growth isocline; **(B)** the predator zero growth isocline; **(C)** both isoclines are combined to give the joint instantaneous change in predators and prey (solid arrows, change in prey numbers; dashed arrows, change in predator numbers). Note that the peak prey abundance occurs at x whilst the peak predator abundance occurs at y; **(D)** the coupled cycles of the abundances of predator and prey in **(C)** plotted against time.

of predators and prey (providing both are above zero), as rising numbers of prey are followed by a rise in predator numbers, which in turn reduces the number of prey leading to a fall in predator numbers. Prey numbers are then able to rise and the cycle begins again. (The cyclical pattern illustrated in Fig. 5.7 represents a single possible outcome-different starting numbers would result in cycles of different magnitudes). Despite the simplicity of this model, the pattern shows clear similarities to the delayed density dependent cycles observed in the classic example of predator-prey cycle, illustratd by Canadian lynx (*Lynx canadensis*) and the snowshoe hare (*Lepus americanus*) (Fig. 5.8). In this case, high lynx numbers depress the snowshoe hare population. This in turn causes a reduction in the number of lynx in subsequent years, allowing the hare population to rise again, resulting in a roughly 10-year cycle. However, as with the larch bud moth, the plants the hares eat also influence this cycle. As the hare numbers increase, the food quality of the plant leaf tissue decreases, which decreases the hare's reproductive potential. Thus, snowshoe hare-lynx population cycling is best thought of as the result of three interacting components : plants, hares and lynx.

Functional and Numerical Responses

In Lotka-Voltera model, the **two variables, predator and prey densities** affect predation. It was observed that as the prey population increased in density, predator density also increased up to a maximum possible rate, consuming more and more of prey. This was designated as **functional response,** (Holling, 1959), wherein the following

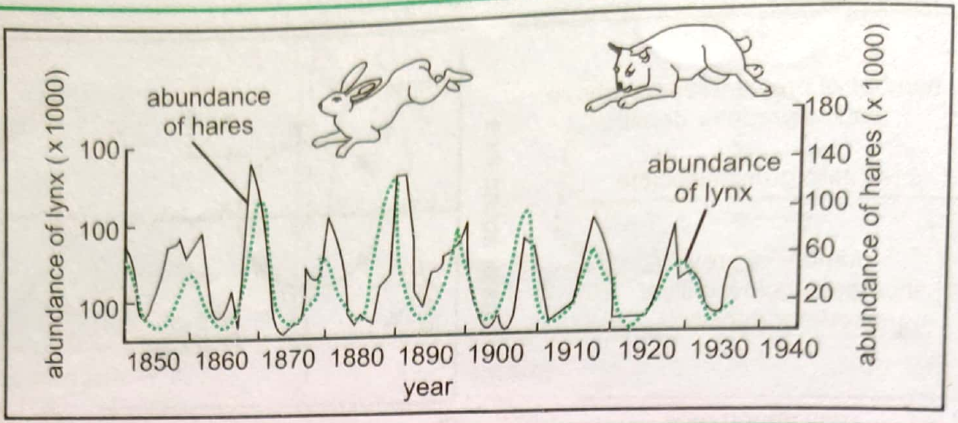


Fig. 5.8. Predator-prey oscillations. The cycles in the numbers of a predator (Canadian lynx) and its prey (snowshoe hare) over 90 years. From *Ecology of a Changing Planet*, M.B. Bush, 1997.

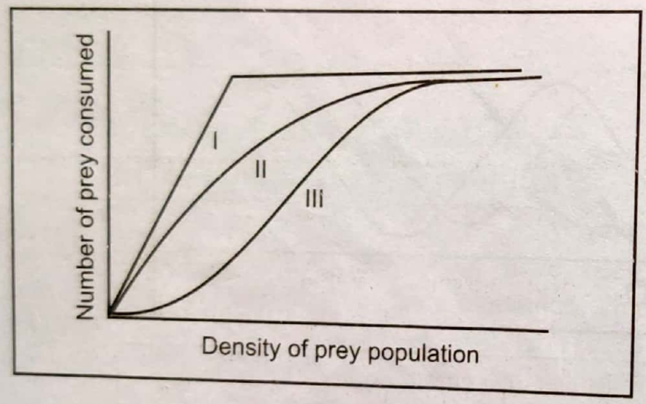


Fig. 5.9. The function responses of predators to increasing prey density. Functional responses of Types I, II and III are shown.

three types of functional response were observed in the predator-prey dynamics (Fig. 5.9).

Type I

The prey is consumed in direct proportion to their abundance to a maximum and when the predator's processing ability is saturated the consumption rate levels off. Neither saturation (satiation) nor the processing time of predator has any role. This response seems valid for the lower range of prey densities for some species. There is direct linear relationship with predator consumption increasing at a constant rate as prey density increases, until the predator's ability is saturated and the consumption rate plateaus.

Type II

The predator's processing ability gradually becomes satiated as it consumes prey. As a result, number of prey eaten rises to a maximum following which the rate of increase in the consumption gradually declines with prey density. This is also known as **saturating functional response.** Here satiation eventually limits food intake. This is the most frequently observed response.

Type III

This is also known as **sigmoid functional response.** The number of prey eaten is low at low prey density due to low hunting ability or other factors, increases rapidly at intermediate prey densities and levels off at high prey density.

Numerical response means that predators become more abundant as prey density increases. This may happen due to the following two reasons :

(1) Increased rate of reproduction in predator when preys are abundant (numerical response per se)

(2) Attraction of predators to prey aggregations (aggregation response).

Numerical response is a slow process, where **time internal** by which the predator density lags behind that of the prey, plays important role. This is due to relatively later appearance of the predator than the prey. Both, functional and numerical responses of the predator are affected by a number of other factors. Such as characteristics of the prey and predator.