Ecology and Environment Management

UNIT 2

POPULATION DYNAMICS

Dr. Dharam Vir
Department of Zoology,
Kirori Mal College
University of Delhi ,
Delhi – 110 007

Date of Submission: 09.07.2006

Contents:

POPULATION DYNAMICS

In the web of life, the organisms not only live in different environment but themselves form a part of the environment for other organisms. There exists a great complexity in nature in the relationship amongst organisms. **Intraspecific interaction** occurs in the individuals of a single species population. It results in the formation of social groups, helps in spacing of the individuals and reduces stress in the members of the population as they compete for food, space and mate. **Interspecific interaction** occurs among members of different species population in the community. These relationships can be lifelong and vital or causal and temporary; and influence the structure, growth, survival and evolutionary trends in population and communities.

The effects of these relationships on population growth can be positive, negative or neutral. Generally negative interactions are more frequent in the early development stages or in disturbed conditions. In the development and evolution of ecosystem, negative interactions are minimized in favour of positive interactions. The negative interaction can increase natural selection resulting in new adaptations. They help in population regulation as they may prevent overpopulation and extinction of the species. Therefore, negative interactions cannot be called harmful for the population. Neutral interactions have no effect on the interacting populations while positive interactions benefit both the populations. Table 2.1 summarizes the different types of interactions in nature.

Table 2.1 - Population Interaction (Two species System) in nature.

S. No.	Type of interaction	Species-1	Species-2	Nature of interaction
1	Neutralism	0	0	Neither population affects the other.
2	Competition	-	-	Inhibition of one species by the other.
3	Amensalism	-	0	Population 1 inhibited, 2 not affected.
4	Parasitism	+	-	Population 1, the parasite generally smaller than the host and benefited.
5	Predation	+	-	Population 1, the predator generally larger than 2, the prey and benefited.
6	Commensalism	+	0	Population 1, the commensal benefits while 2, the host is not affected.
7	Protocooperation	+	+	Interaction beneficial to both but not obligatory.
8	Mutualism	+	+	Interaction beneficial to both but obligatory.

INTERSPECIFIC NEGATIVE INTERACTIONS

COMPETITION: It is a negative type of interaction that adversely affects the growth and survival of the interacting populations. Some interacting species secrete a chemical substance called **allelochemic** and it provides a competitive advantage to one species against the other species. The term **allelopathy** is used for such type of interaction. Interspecific competition is of two types:

Resource, scramble or exploitative competition occurs when a number of organisms of the same or different species utilize common resources that are in short supply. The winner is dependent on the efficiency of utilization of the resource by the competitors. Usually it results in reduced growth of the competitors.

Interference or contest competition occurs when the organisms seeking a common resource harm one another in the process. The animals exhibit more aggressive behaviour in this competition.

Competition is always for the resources and a number of resources may become the center of competitive interaction. Usually, the competition is for food, space, mate and water etc. Competition for space may be of different types like for birds it may be for nesting sites or wintering site or a site that is protective against predators.

Lotka-Volterra Model

Lotka (1925) and Volterra (1926) have given mathematical models independently to explain as to what happens when two species living together share the same resource i.e. food, space or mate etc. The mathematical models are based on the logistic curve and are called Lotka-Volterra equations. But for Lotka – Volterra model to be applicable to populations certain conditions must be met with. These conditions are:

- The environment should be stable without any fluctuations.
- Migration need not be an important factor.
- The effect of competition is instantaneous.
- Coexistence is possible only with a stable equilibrium point. Competition is an important biological interaction.

The logistic equation when applied to the two species competing for a resource (food or space) can be written as

$$dN_1/dt = r_1N_1\frac{(K_1 - N_1)}{K_1} \qquad \text{for species 1.}$$

and

$$dN_2/dt = r_2N_2\frac{(K_2 - N_2)}{K_2} \qquad \text{for species 2}$$

In these equations,

N_1 and N_2 refer to population size of species 1 and 2.

t = time

r_1 and r_2 = per capita rate of increase of species 1 and 2

K_1 and K_2 =carrying capacity/asymptotic density for species 1 and 2 respectively.

When these two species interact, they affect the population growth of each other; therefore, a constant to account for the interference of one species on the population growth of the other must be added to the growth equation. This constant, infact converts the members of one species into an equalent number of members of the other species. When there is competitive interaction for a resource, we can define

$$\mathbf{N_1 = \alpha N_2}$$

Where α is the conversion factor for expressing species 2 individuals in units of species 1. The competition equation for species 1 can be written as:

$$\frac{dN_1}{dt} = r_1N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1}\right)$$ population growth of species 1 in competition

Fig. 2.1a shows it graphically for the equilibrium position when $dN_1/dt= 0$. In the graph the ordinate will represent the population size of species 1 and the abscissa the population size of species 2. As shown in the graph, all the space for species 1 is used when there are K_1 individuals of species 1 or when there are K_1/α individuals of species 2 shown at the ends of the diagonal line. Population size of species 1 will increase until it reaches the diagonal line, which represents all points of equilibrium. It is called isocline. The population increase is shown by green dots. The point of equilibrium along the diagonal line will be somewhere at or between the points $N_1 = K_1$ and $N_1 = 0$

Similarly, incase of species 2 population in competition with species 1, we must covert N_1 into an equalent numbers of species N_2 and this can be written as

$$N_2 = \beta N_1$$

Where β is the conversion factor for expressing species 1 individual in units of species 2. The competition equation for species 2 can be written as:

$$\frac{dN_2}{dt} = r_2N_2 \left(\frac{K_2 - N_2 - \beta N_1}{K_2}\right)$$ population growth of species 2 in competition

Fig. 2.1b shows it graphically for the equilibrium position when $dN_2/dt = 0$. The red dots show the population increase. The point of equilibrium will lie anywhere along the diagonal line between $N_2 = K_2 =0$

When these two species interact with each other, three outcomes are possible:

1.Only species1 exists

2. Only species 2 exists

3. Both the species coexist.

Infact, the outcome of competition will depend on as to which species has more depressing effects on the other. If the species 1 has more depressing effect on species 2, it will survive and species 2 will become extinct; if species 2 has more depressing effects on species 1, it will become extinct and species 2 will survive. But in a situation where neither species has a strong depressing effect on the other, both the species may coexist. At equilibrium the simultaneous equation for the two populations is written as follows:

$$dN_1/dt = 0 = dN_2/dt$$

When the fig. 2.1a and 2.1b are superimposed and the vectors shown by arrows, four possible geometric configurations result. The outcome can be traced by following the pattern of overlap of the graphs. Species 1 will increase in green dotted areas and species 2 will increase in areas of red dots. The important thing to note is that there will be no equilibrium of the two species unless the diagonal lines cross each other. In Fig. 2.2a and 2.2b there is no equilibrium and only one species survives. As shown in the graph one species increases in an area where the other must decrease leading to its extinction. However, if the diagonal lines cross, the equilibrium point represented by their crossing may be stable if the vectors about the point are directed towards the point and unstable if the vectors are directed away from it. In fig. 2.2c, the point where the two lines cross is unstable and either of the two species can win. If due to some favourable conditions the populations move downwards in the area of green dots, N_1will increase and the population will come to an equilibrium point at K_1. Similarly, if the conditions favour N_2 species, population will increase in the area of red dots and it will come to an equilibrium point at K_2. However, the two species may coexist as shown in Fig. 2.2d. Each species regulates its population through intraspecific and inter specific interaction. Neither species reaches a higher density to out compete the other. And as long as each species is limited by a different resource, the two species will continue to coexist.

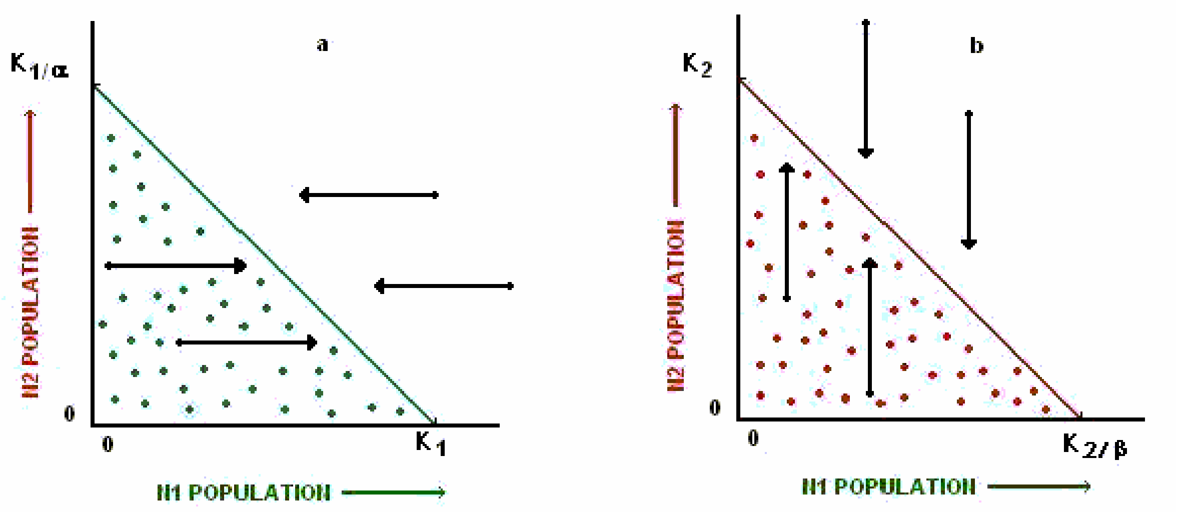

Fig. 2.1 (a & b) - Population growth of species N1 and N2 when competing with the other species

Gause's principle, 1934: It states that two species with identical ecological requirements cannot occupy the same environment. Joseph Grinnell (1904) originally gave the concept while studying the food habits of organisms. Gause's principle is also known as **"competitive exclusion principle".**

Competitive interaction may involve space, food and light etc and result in equilibrium adjustment by two species or one species replacing the other or forcing it to occupy another space or to use another food. So the closely related organisms either do not occur in the same place or use different food or are active at different times or occupy somewhat different niches. Thus there is one species to a niche. Infact, Hardin (1960) wrote: "Complete competitors cannot coexist".

For complete competitive exclusion to take place, certain conditions must be fulfilled. These conditions are:

Competitors must maintain their genetical identity for a long time.

Immigrants from different conditions should not be allowed into the population of loosing species.

Environment should remain uniform.

Species should compete for sufficiently long time to allow them to reach an equilibrium point.

Examples of laboratory studies on competition:

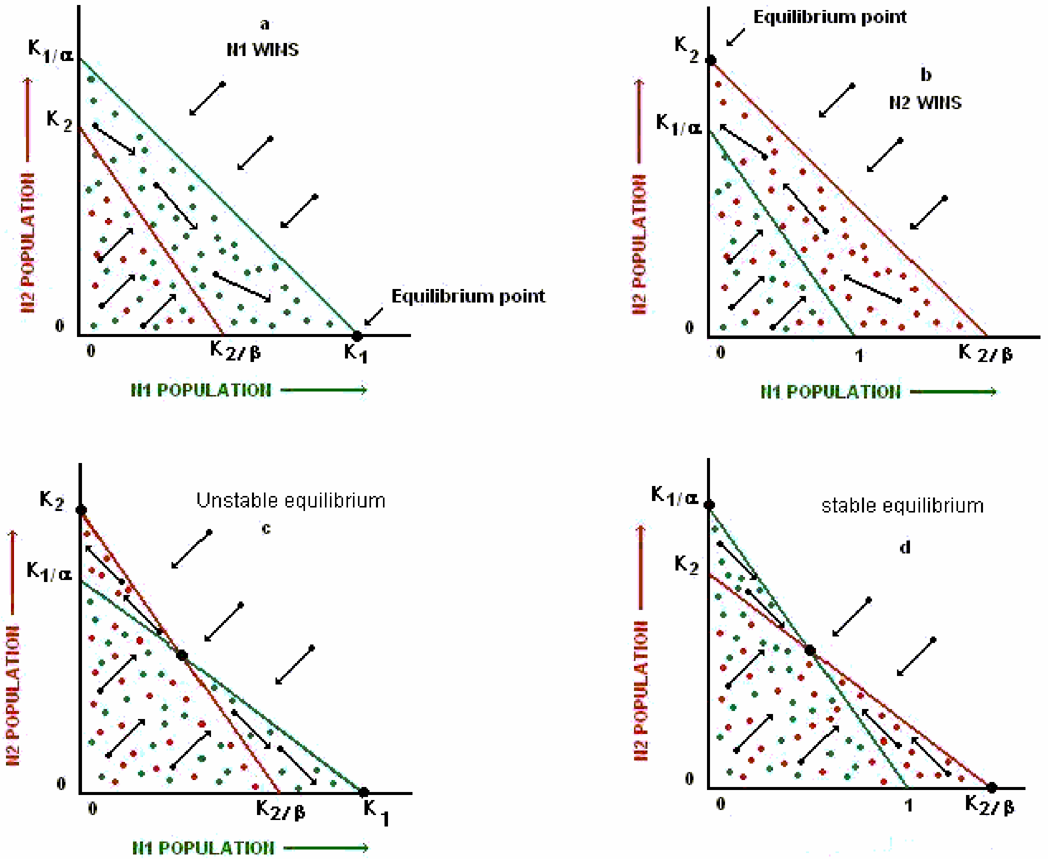

Fig. 2.2 - Possible outcomes of interspecific competition between N1 & N2 populations when their isoclines are superimposed

a Population N1 wins

b Population N2 wins

c No population wins and the situation is unstable

d N1 and N2 populations co-exist

Gause's 1934 original experiment on two closely related ciliates is a classic example of **"competitive exclusion principle."** He used two species of *Paramecium*, *P. aurelia* and *P. caudatum*. In separate cultures (Fig. 2.3a) both the species exhibited typical sigmoid growth curves but *P.aurelia* had a higher rate of increase than *P. caudatum*. When both the ciliates were placed in the same culture with a fixed amount of bacterial food, *P. aurelia* alone survived after 24days, *P. aurelia* had a more rapid growth rate and out-competed *P. caudatum* for the limited amount of food under the existing conditions (Fig. 2.3b). In another experiment Gause used P. *caudatum* and *P. bursaria*. Both the species were able to survive and reach a stable equilibrium in the same culture medium (Fig. 2.3c). Though both the ciliates used the same food but *P. bursaria* confined its feeding to bacteria on the bottom of the culture, where as *P. caudatum* fed on bacteria suspended in solution. Although they used the same food supply, they occupied different parts of the culture exhibiting difference in spatial niche. Thus habitat diversification allowed the two species to coexist.

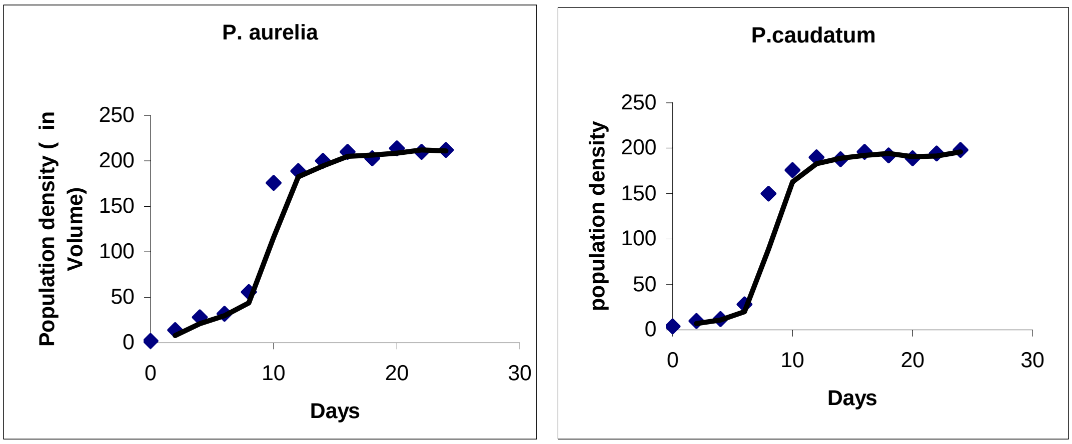

Fig. 2.3a - Population growth of *P. aurelia* and *P. caudatum* in controlled cultures with constant food supply.

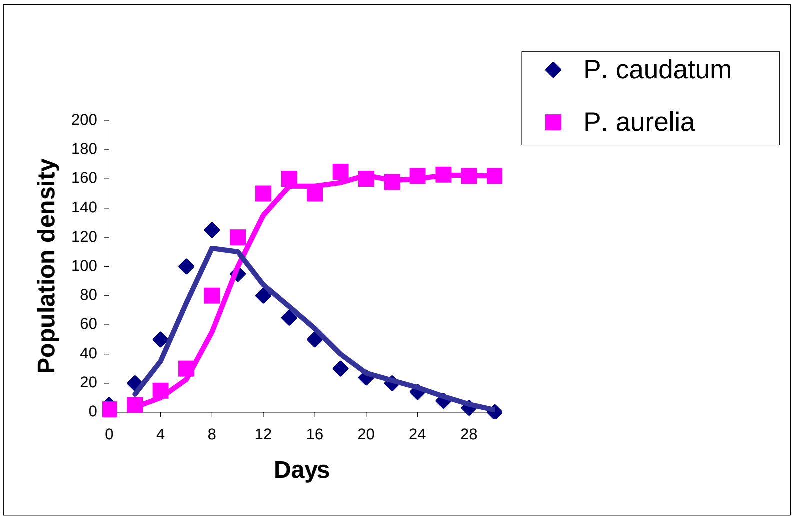

Fig. 2.3b - Interspecific Competition of *P. aurelia* and *P. caudatum* under
controlled conditions in the same culture. *P. Aurelia* is eliminated

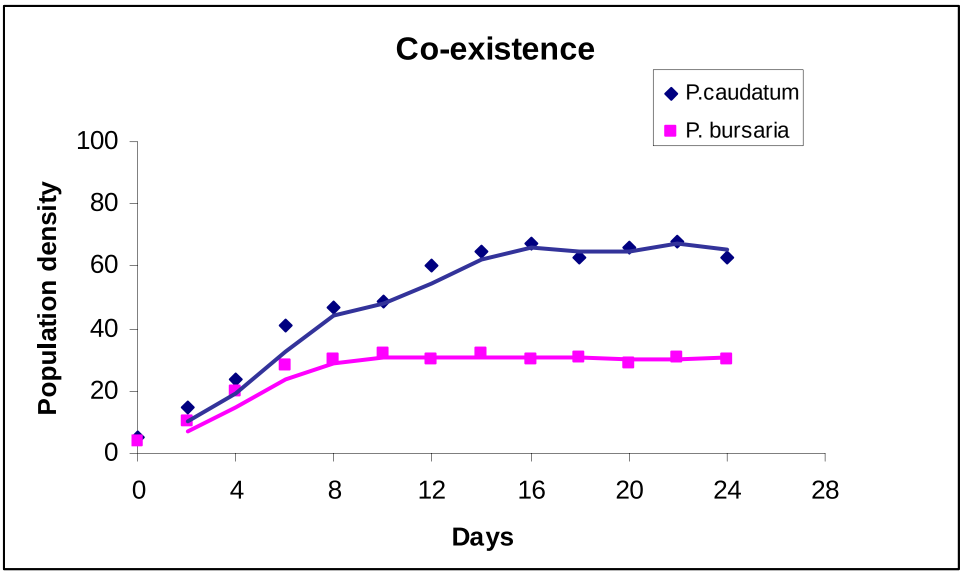

Fig. 2.3c - Interspecific competition in *P. caudatum* and *P. bursaria* showing co-existence. Food is same for the two species but *P. caudatum* is a surface feeder while *P. bursaria* is a bottom feeder.

Crombie (1947) described as to how habitat diversification in flour beetles can reduce competition to allow co-existence instead of exclusion of the interacting species. He found that *Tribolium* eliminates *Oryzaephilus* when both live together in flour because *Tribolium* is more active in destroying the immature stages of the other species (Fig. 2.4a). However, if glass tubes are placed for the escape of the immature stages of the *Oryzaephilus*, both the populations survive (Fig. 2.4b). Thus when one niche environment is converted to two-niche environment, competition is reduced for the support of two species. This is an example of direct interference type of competition.

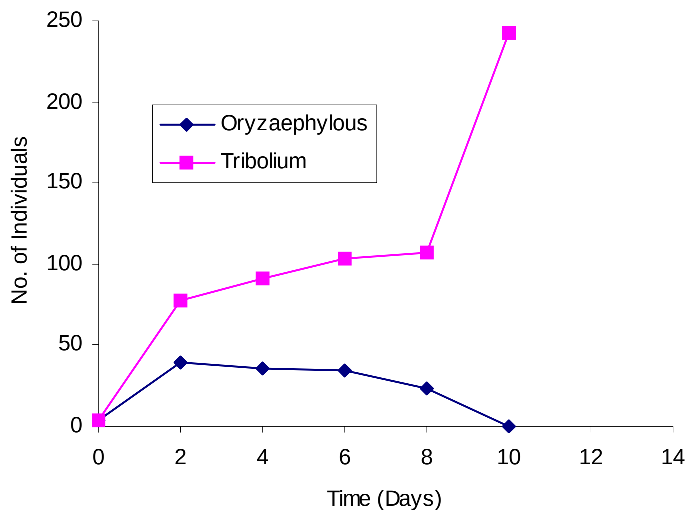

Fig. 2.4a - Growth of closely related beetles, *Tribolium* and *Oryzaephylous* in plain flour medium. *Oryzaephylous* is always eliminated.

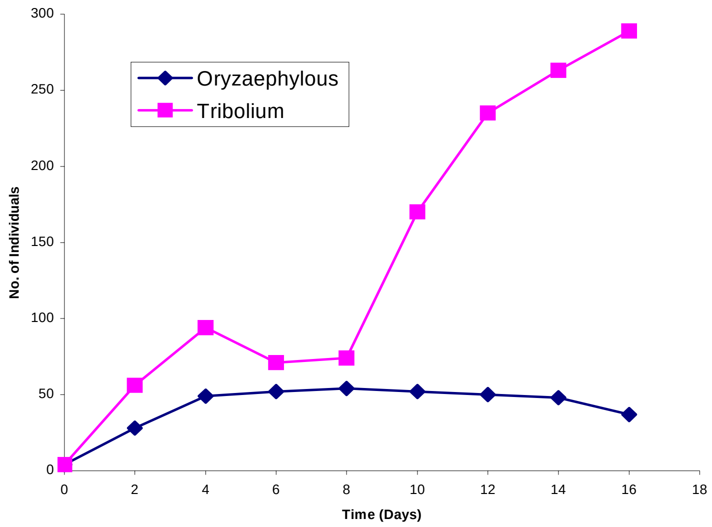

Fig. 2.4b - Growth of closely related beetles *Tribolium* and *Oryzaephylous* in plain flour medium with glass tubes. Both the populations surviv

The outcome of competition between two closely related species can be altered by change in one component of the environment. Birch (1953) raised the grain beetles (*Calandra oryzae)* and (*Rhizopertha dominica)* at several different temperatures and observed that *Calandra* eliminated *Rhizopertha* at 29^{0}C (Fig..2.5a) but at 32^{0}C *Rhizopertha* would always eliminate *Calandra*. (Fig. 2.5b) He attributed these results to the innate capacity for increase of the beetles, which varied with change in temperature. At 29^{0}C the r_m value for *Calandra* is 0.77 and for *Rhizopertha* 0.58 but when the temperature is increased to 32^{o}C, *Rhizopertha* has r_m 0.69 and *Calandra* 0.50 (Fig. 2.5).

Competition plays an important role in determining the distribution of species but in nature it is very difficult to test Gause's rule, as there are many variables in the environment, which may affect the extinction or survival of the organisms. Conell (1961) demonstrated to some extent the degree of competitive exclusion between two species of barnacles on the Scottish coast. As shown in the Fig. 2.6, larvae of *Chthamalus stellatus* can grow on the rocks down to the mean tide level but in the presence of another barnacle *Balanus balanoides,* they are able to grow up to the level of mean high neap tide and during neap tide the range between low and high water mark is the least. Conell observed that *Balanus* that has a higher growth rate actually removed *Chthamalus* larvae of the rocks or simply grew over them. Thus *Balanus* competes for the available space directly in an aggressive manner. When *Balanus* was removed from the area, *Chthamalus* inhabited the intertidal zone to the mean tide level. In the absence of *Chthmalus, Balanus* was found to be unsuccessful in maintaining population above the mean high neap tide. The density of barnacles in this region is regulated by weather. If the weather is adverse i.e. warm and calm, *Balanus* suffer high mortality especially in the first year of life. Below the mean high neap tide, *Balanus* population is regulated by itself and by predation. Self-regulation by intraspecific competition is the most significant in the first year of life. Individuals older than six months are preyed upon by *Thais lapillus*. Thus zonation of barnacles in the upper part of the inter tidal zone is regulated by weather and it has greater affect on *Balanus* than *Chthamalus*. Biological factors are important in the lower part of the intertidal zone. Interspecific competition results in the exclusion of *Chthamalus* by *Balanus* and intraspecific competition and predation on *Balanus* by *Thais* regulate the population of *Balanus* in this zone.

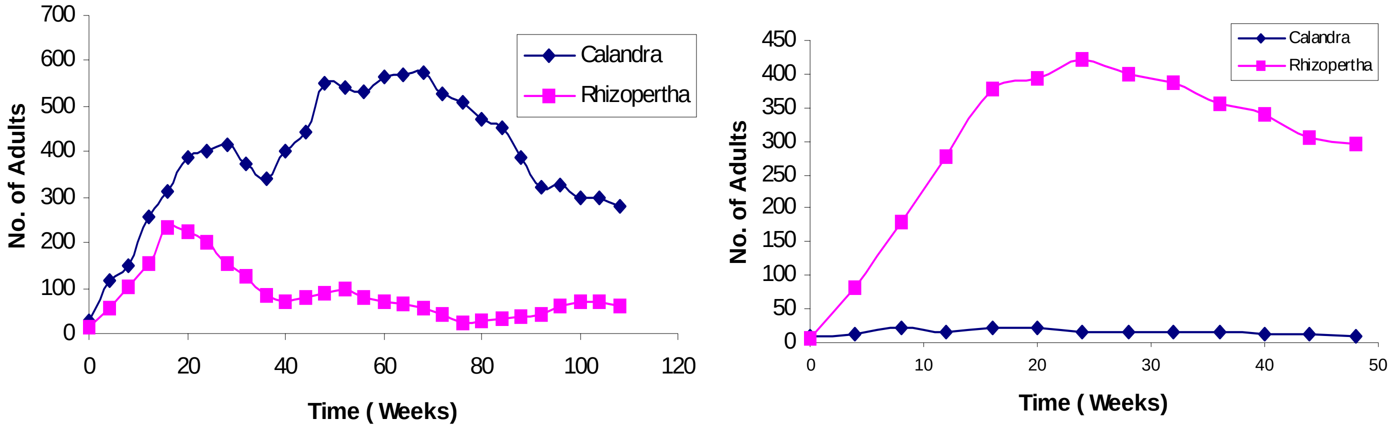

Fig. 2.5 - Interspecific competition between *Calandra oryzae and Rhizopertha dominica* co-existing in wheat at *a) 14% moisture and 29.1° C, and* *b) 14% moisture and 32°C.*

When competition is between closely related or ecologically similar species, the range is restricted to the optimum. When interspecific competition is less severe, intraspecific competition allows wider habitat selection. Lack (1945) studied the feeding habits of two similar fish eating birds, the cormorant (*Phalacrocorax carbo*) and the shag (*P. aristotelis*), which feed in same waters. But on close observation, he found that the shag feed in surface waters on free-swimming fish and eels while the cormorants are bottom feeders of flat fishes and shrimps. Both the birds may share the same spatial niche but trophic niche is different allowing them to coexist in the same habitat.

Sometimes in nature two species may live in different environment due to different requirements or preferences and not because of competition as studied by Teal (1958) in fiddler crabs (*Uca sp.*) One species *Uca pugilator* inhabits open muddy flats while the other *Uca pugnax* is found in muddy areas covered with marsh grasses. It seems one species will not invade other's habitat even in its absence and dig burrows only in the preferred habitats bringing about their ecological separation.

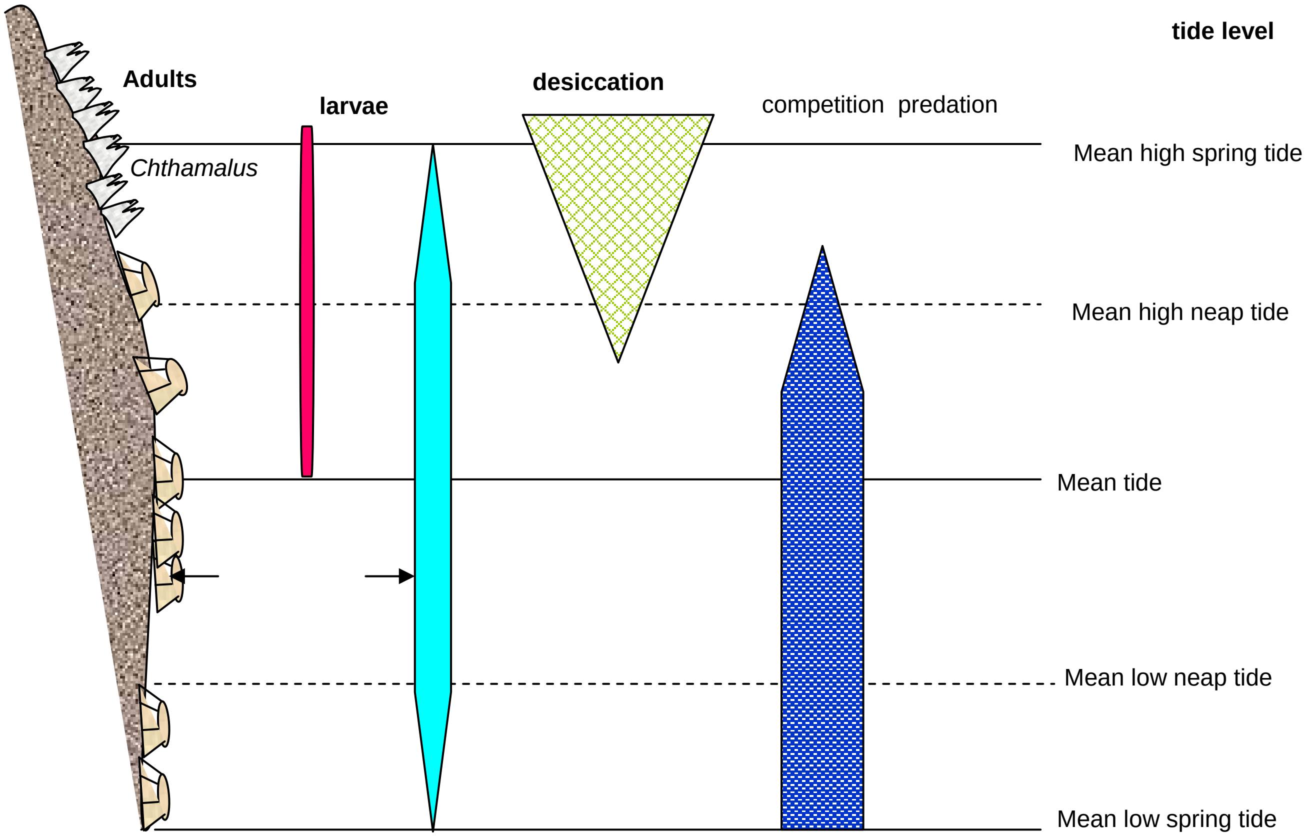

Fig. 2.6 - The effects of competition, predation and weather on the distribution of barnacles in the

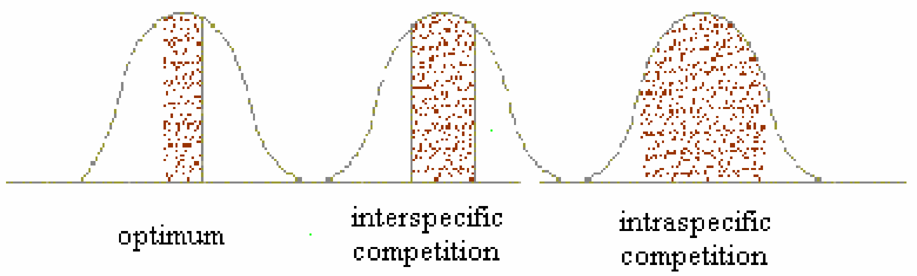

Fig. 2.7- Interspecific and intrascpecific competition for habitat occupancy in organsims

THE NICHE CONCEPT

It is closely associated with interspecific competition**.** Many ecologists have defined the term niche.

Joseph Grinnell (1917) was the first to use the term niche and defined it as the ultimate distributional unit within which each species is held by its structural and functional limitations. He viewed it as a part of the habitat while describing the niche of the species.

Charles Elton (1927) described it as the functional role of the organisms in the community. He stressed the occupational status of the organisms in the community.

Pianka (1978) describe niche as the sum of factors, which favour an individual, population or species to live in the environment.

G.E. Hutchinson (1957) defined niche in terms of many needs of the organism. He observed that many environmental factors affect the distribution of species and each factor can be counted as a point in a multidimensional space and he called it **hypervolume niche.**

For describing the niche of a species, we can take two variables like temperature and humidity and determine for the species the range of values, which allow it to survive and multiply (Fig. 2.8a). When we plot temperature against humidity, it defines a two-dimensional area within which the organisms can survive. If a third gradient/factor like pH is added, the living space can be plotted in three dimensions as a volume (Fig. 2.8b). Although there are no more dimensions that can be drawn on a page yet there are many more gradients that will determine where a species can live. Since there are many gradients, Hutchinson described his views of niche as an **n- dimensional hypervolume** (n is the number of relevant gradients both biotic as well as abiotic). Whenever an individual or a species occupies the full hypervolume or the range of variables to which it is adapted without interference from another species or individuals it is designated as the fundamental niche of the species.

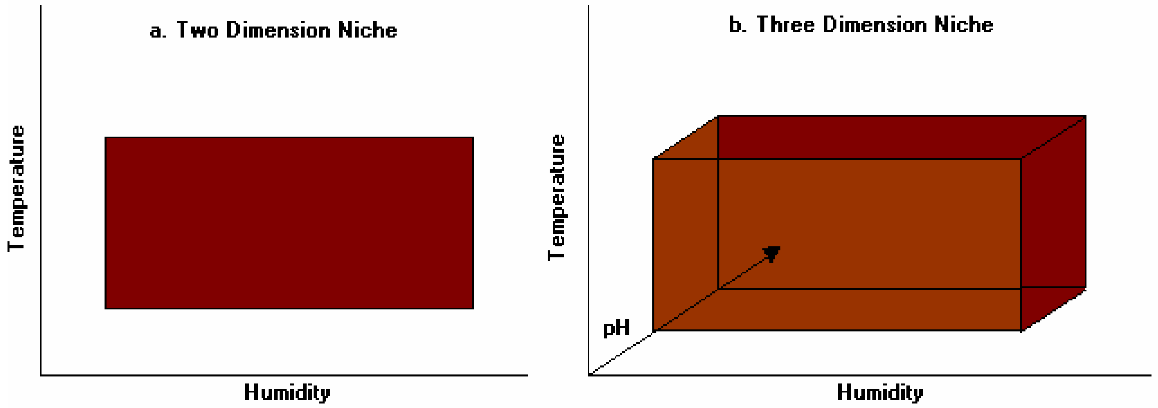

Fig. 2.8 - Ecological Niche Models for a hypothetical animal

The **fundamental niche** of the species assumes that there is no competitor (Fig. 2.9a). But actually the organisms seldom fill their entire fundamental niche as it is reduced by competition from other species. Where the fundamental niches of two species overlap, only one species can survive. In a two dimensional representation of the niche, if competing species B and C are introduced into the area, they affect the area of the niche where the species A has absolute advantage and now it is constrained to occupy a much smaller range of the environmental gradients. The area that is actually occupied in the presence of a competition by species B and C is its **realized niche** (Fig. 2.9b). The realized niche is thus a more realistic definition of where a species will actually be found than is the fundamental niche.

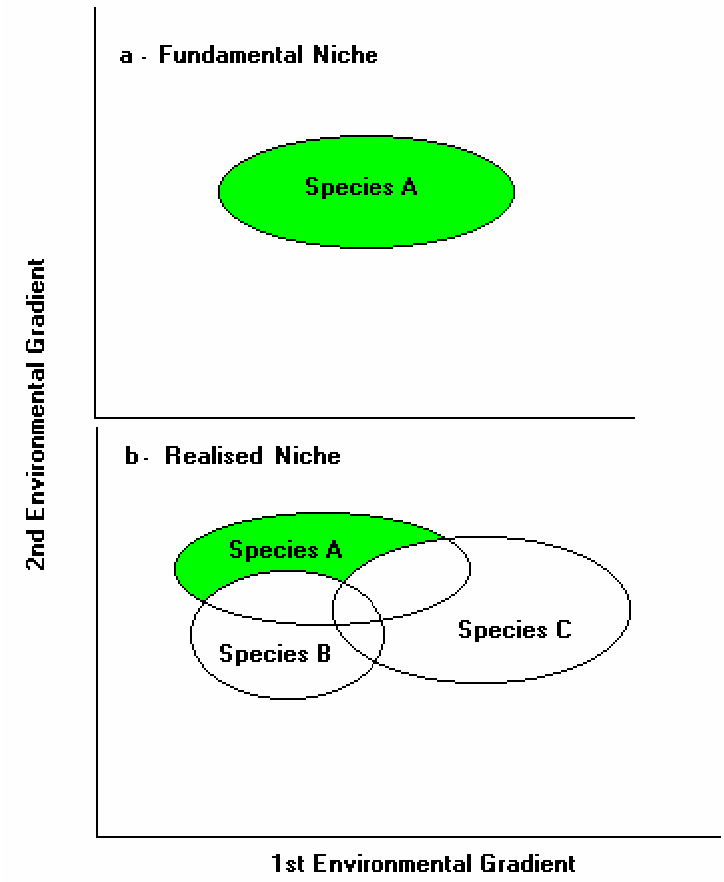

Fig. 2.9 a and b - Fundamental and realized niches of an organism

In nature, the fundamental niches overlap and during this overlap some space is shared and some is exclusively utilized by the species. This allows co-existence of the species. If the overlap is more, it does not necessarily mean that the competition between the species is severe. Usually, competition occurs when the resource is in short supply, but when extensive overlap of the niches is there, it indicates abundance of resources and almost no competition between the species. Therefore, overlap may or may not indicate competitive interaction.

However, the fundamental niche has some drawbacks.

It has an infinite number of dimensions and we cannot completely determine the niche of an organism, as it is not possible to measure all the dimensions at the same time.

We assume that all environmental variables can be linearly ordered and measured but it is not possible to measure the impact of biotic components.

The model refers to a particular instant at a particular time but competition is a dynamic process.

According to MacArthur (1968) the solution to the problem lies in restricting our analysis at a time to differences between niches in one or two dimensions only such as feeding or breeding niches.

The range of resources used by an organism suggests its **niche width**. Niche width is also called **niche breadth** and **niche size** and it represents the range of hypervolume occupied by the realized niche. The niche width is described as narrow in case of specialized species or broad in case of generalized species. Most of the species have generalized niches and as competitors they are more successful than the specialized species even when the resources are sometimes undependable. The specialists utilize a particular set of resources but as competitors they are superior to generalists if the resources are dependable and renewable.

Competition sometimes results in **niche compression**, which is the contraction of the habitat rather than a change in the type of food or resources utilized by the organisms. Niche compression occurs in nature when a community made up of broad niches is invaded by competitors and the severe competition forces the occupants to restrict or compress their utilization of space and confine feeding and other activities to those areas of the habitat which provide the optimum resources.

However, if interspecific competition is reduced, the species may expand its niche, utilizing space, which was not available to it earlier. Thus in the absence of competition, the organism may expand its niche and it is called **ecological release**. It occurs when a species invades a new area like an island or a habitat that is never occupied and increases its density utilizing the available resources.

Sometimes two or more competing populations reduce interspecific competition by changing their feeding and behavioral patterns and this is called **niche shift** in the species. The niche shift involves changes in the morphological characters and behaviour and it may be in the form of temporary or permanent adaptations and lead to some evolutionary changes in the population to reduce interspecific competition enhancing coexistence of the interacting species.

PREDATION

It is a type of interaction between two populations that result in negative effects on the growth and survival of one population and a beneficial effect on the other. The members of one species eat those of the other species and generally but not always, it involves the killing of the prey. Predation is of four types:

Herbivory is a type of predation in which the predator is a primary consumer (animal) and the prey is a primary producer (plant). Generally the plants eaten are not killed but damaged.

Cannibalism is a form of predation in which the predator and the prey are of the same species. Cats and dogs are known to eat their little ones. Especially at the time of delivery of young ones, the females eat the kittens and pups if no food is provided to them.

Parasitoidism or insect parasitism where the insect parasite lays eggs on or near the host insect, which is subsequently killed and eaten. Surprisingly it is an example of weak organisms attacking the strong ones.

Typical predation occurs when the carnivores prey on herbivores or other carnivores. In a broader sense, predation can be defined as one organism feeding on another living organism or **biophagy.**

Predation can be an important factor in the maintenance of biodiversity as it may prevent competitive exclusion. Predators must be large enough to overpower their prey with ease as they avoid struggle at all cost. A predator controls prey population or it can be otherwise also, when prey population regulates predator population. When the predator restricts the size of prey population, the system is called as **top down control** because it is the number of predators that will determine the number of prey but when the system is regulated by factors at the base of the food chain, it is called as **bottom up control**. Snowshoe hare and lynx 10-year cycle is an example of top down control as lynx regulates the hare population.

Predation models

Interaction between predator and prey in nature results in reciprocal oscillations in their populations, with some time delay in the predator's response (Fig. 2.10a). Theoretically, these oscillations should continue indefinitely if not affected by external factors.

Lotka (1925) and Volterra (1926) independently presented predator – prey interaction model. They did not use the logistic equation to explain the predator – prey interaction and based their assumptions on the random encounters between the predator and the prey in the environment. The intensity of interaction between the two was supposed to be in proportion to their population.

They based their model on two equations, one for the prey population and the other for the predator population. The prey equation can be written as follows:

$dN/dt = aN – bNP$

The prey growth equation has two components i.e. aN, where a is the per capita rate of change of prey population and N is the density of the prey; and bNP, where b is the rate of change in prey population due to interaction of predator and prey population and P is the density of the predator.

Similarly for the predator population, the equation can be written as follows:

$$dP/dt = cNP – dP$$

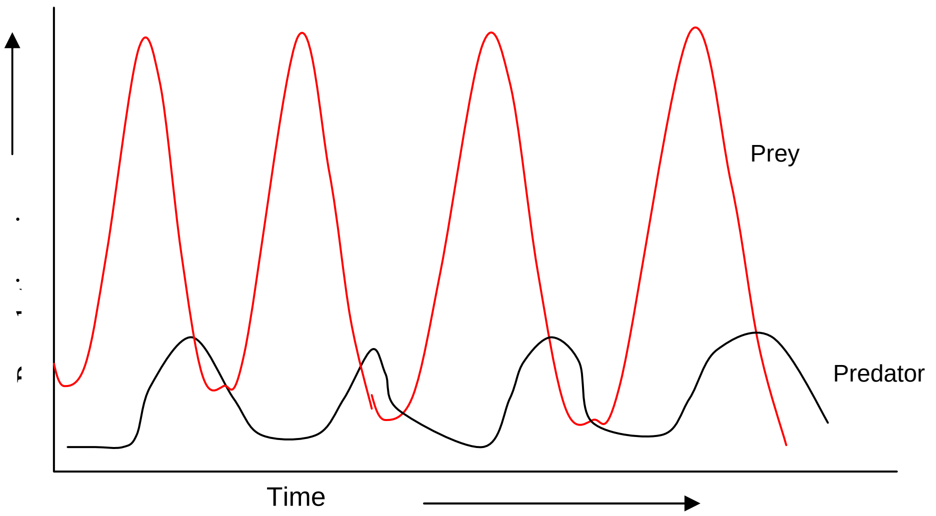

Fig. 2.10 a - Classical oscillations in Predator- prey system

The predator growth equation also has two components i.e. cNP, where c is the rate of change in predator population due to interaction of predator and prey population; and dP, where d is the per capita rate of change in the predator population.

The Lotka – Volterra model is shown graphically in (fig. 2.10b). The number of predators is shown along the ordinate and the number of prey is shown along the abscissa. The isocline or the zero growth curve for the prey is horizontal where as for the predator the isocline is vertical. As shown in the graph, predators increase on the right side of the vertical line and decrease on the left side. The prey increase in the area below the horizontal line and decrease in the area above the horizontal line. The circle of arrows in the center shows the interaction of the predator and the prey. An arrow on the left of the vertical line in the model means the prey population is not large enough to support the predators and the predator population declines. When the arrow is on the upper left side, it means both the populations are declining. As the predator population is declining it allows the prey population to increase as shown in the lower left side of the vertical line. Due to increase in the prey population, the predators also increase as shown on the lower right side of the vertical line. Under the pressure of increasing predator population, the prey population again decreases as shown on the right upper side of the vertical line.

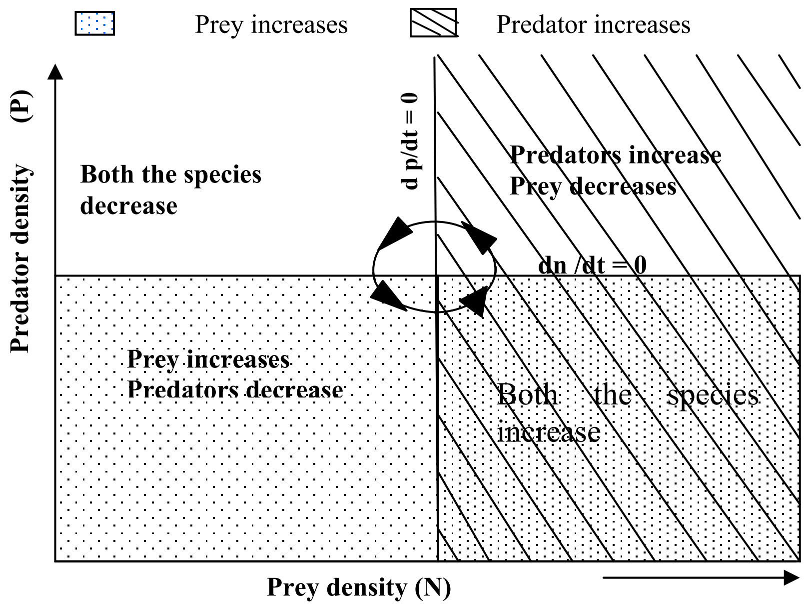

Fig. 2.10 b – Lotka-Volterra model for Predator-Prey interaction

The Lotka-volterra model is based on certain assumptions like:

There is random movement of the predators and prey in the environment.

The encounters resulting in the capture and consumption of the prey are constant at all predator and prey densities.

The number of prey taken increases in direct proportion to the number of predators.

All responses are instantaneous with no time lag for handling and ingesting the prey.

The Lotka - Volterra model takes into consideration the influence of predators on prey population, while other factors like stress, aggression, hiding places and emigration also influence the predator-prey interaction in nature. The oscillations or fluctuations in predation model observed by Lotka – Volterra are not likely to occur in nature.

Rosenzweig and MacArthur (1963) suggested another model of predator-prey interaction. The prey and predator **isoclines** (dN/dt=0 and dP/dt=0) respectively are represented graphically in Fig. 2.11a and 2.11b .The prey isocline is shown in the form of a convex curve, implying that overcrowding as well as undercrowding is harmful to the prey population and there is an optimum intermediate range at which it can support maximum number of predators. The prey population increases in the area below the isocline and decreases above the isocline. The predator isocline is shown in the form of vertical line, which levels off at the high prey density. As shown in Fig. 2.11b, below a particular threshold prey density (X), predators decrease on the left of this line, as they do not get enough resource to replace themselves. The predators increase on the right side if they are below the carrying capacity K_2.

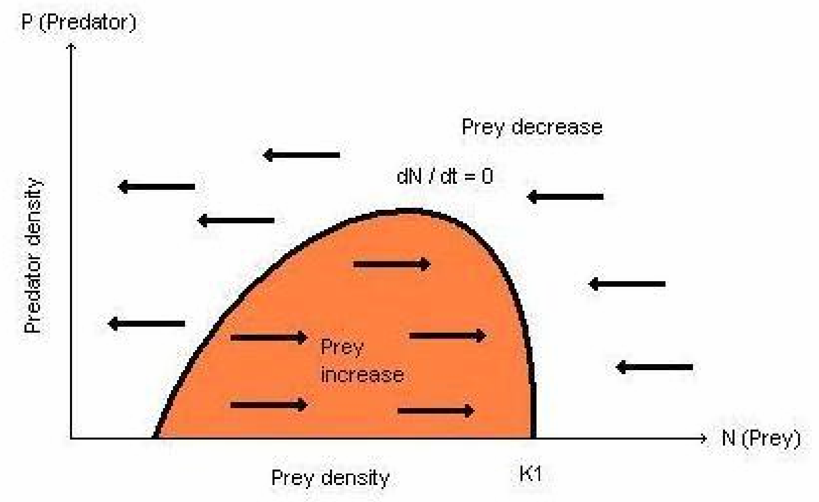

Fig. 2.11a-Hypothetical Prey isocline. The prey curve is convex, showing density dependent growth.

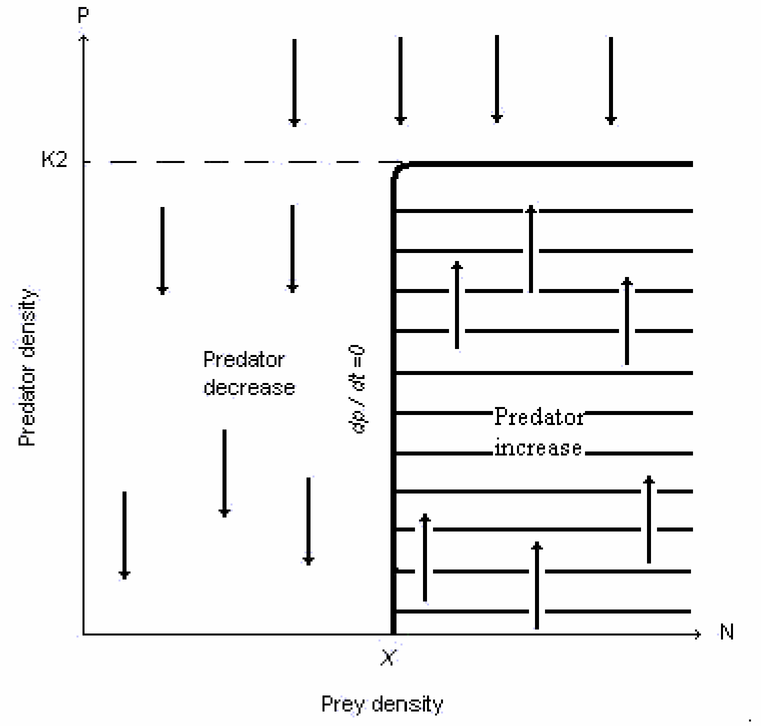

Fig. 2.11b- Hypothetical predator isocline, shown as straight line

When the predator and prey isoclines are superimposed to show their interaction, the growth curves intersect and form four quadrants, A, B, C and D (Fig. 2.11 c). The predator and prey populations increase on the right side of the vertical line in the region of the convex curve (A) and decrease outside the convex curve (C) on the left side of the vertical line. The prey population increases in the convex curve region on the left side of the vertical line (D) and the predator population increase on the right side of the vertical line outside the convex curve (B). The point if intersection of prey isocline by the predator isocline will determine the nature and intensity of interaction between the two populations.

When the predator isocline cuts the prey curve at right angle, the predator exploit the prey at some intermediate density and the vectors form a closed circle. The populations of predator and prey oscillate in time with neutral stability (Fig. 2.11c).

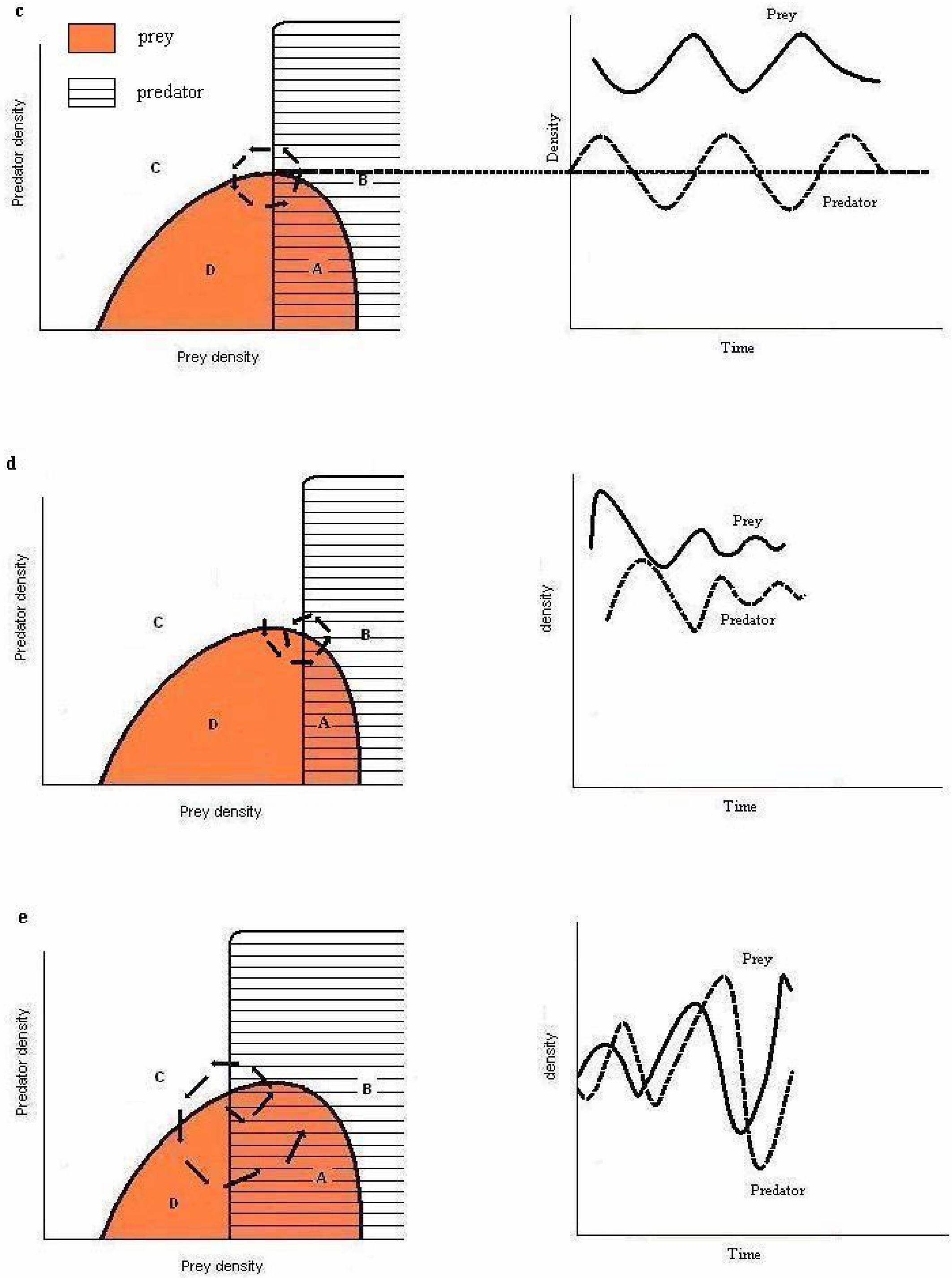

Fig. 2.11 c,d,e Predator - prey isoclines superimposed to show the nature of interaction and stablity in their relationship.

c: The isoclines interact at right angles, the isolations are stable
d: The predator isocline interact the descending part of the isocline. Oscillations are damped
e: The predator isocline intersect the ascending part of the isocline. the oscillations inclrease in amplitude and lead to unstable state

When the predator isocline is moved to the right, it intersects the descending part of the prey isocline. It shows that the predator is inefficient and is not able to exploit the prey population until it reaches the carrying capacity level. The vectors spiral inwards and damped oscillations are produced (Fig. 2.11d) .The damped oscillations, however reach an equilibrium level if the predator and prey densities do not show any change.

When the predator isocline intersects the ascending part of the prey isocline, the predator is extremely efficient at exploiting the prey population even at very low density. The vectors spiral outwards with increasing amplitude of population oscillations (Fig. 2.11e). However, these oscillations are unstable and lead to the extinction of either the predator or both the populations. Such oscillations are not observed in nature.

It is evident from the above model that an increase in prey population does not increase the equilibrium density of the prey population. The predator utilizes all the gain in prey density and it can be observed by moving the vertical predator isocline to the left or right side on the convex prey curve. The Rosenzweig and MacArthur suggest that prey equilibrium is independent of prey density and stability of the prey population depends on the nature of predators.

Laboratory studies: Gause (1934) was the first to test the oscillations in Lotka-Volterra model of predation- prey interaction. He reared *Paramecium caudatum* (prey) and *Didinium nasutum* (predator) together in an oat medium. In initial experiments, it was observed that *Didinium* always exterminated *Paramecium* and then died of starvation (Fig. 2.12a). Instead of the expected classic oscillations, he got divergent oscillations and extinction. He concluded that the *Paramecium-Didinium* system did not show the oscillations as predicted by Lotka-Volterra for predation models. He attributed it to the biological peculiarity of *Didinium* which was able to multiply rapidly even when the prey were scarce with the individuals becoming smaller and smaller in the process.

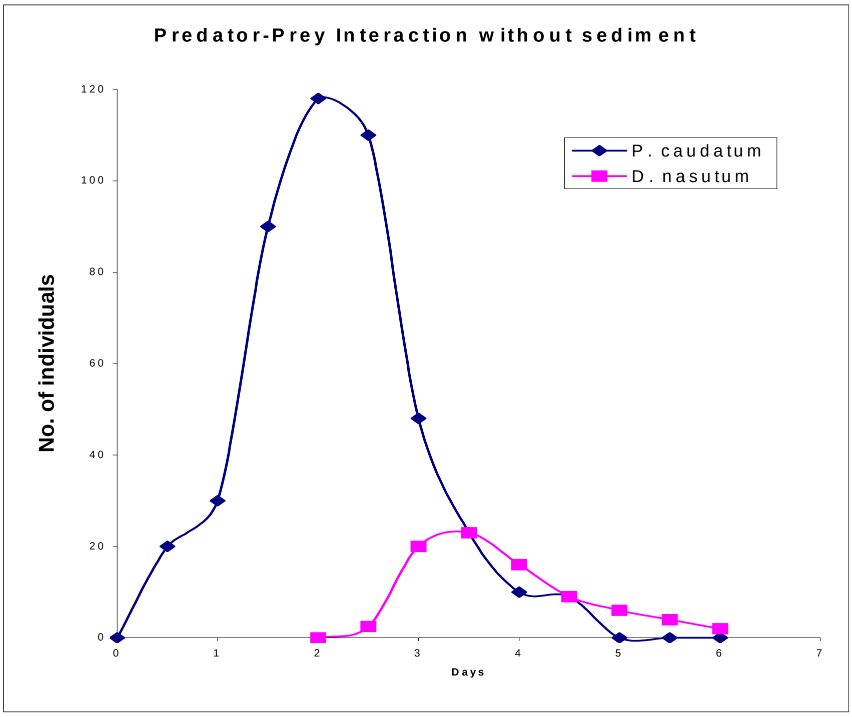

Fig. 2.12a - Predator-Prey interaction between *P. caudatum* and *D. nasutum* in oat medium without sediment

He then used oat medium with sediments. *Paramecium* in the sediment were safe from *Didinium,* thus adding a refuge to the system. Here also *Didinium* again eliminated *Paramecium* but only from the clear fluid medium. *Didinium* then starved to death and *Paramecium* hiding in the sediment emerged to increase in numbers. The experiment ended with many prey but no predators (Fig. 2.12b). He again failed to get the classical oscillations on the pattern of the mathematical model of Lotka and Volterra.

In yet another experiment, he introduced immigrations into the experimental setup. Every third day he added one *Paramecium* and one *Didinium* to the culture medium and got the oscillations as expected (Fig. 2.12c). Gause concluded that in *Paramecium-Didinium* system, the periodic oscillations in the numbers of predators and prey are not entirely due to interaction of the predator and prey but were the result of constant interference from outside the system. Gause experiment thus does not support the conclusions made buy Lotka-Volterra on the predator –prey system.

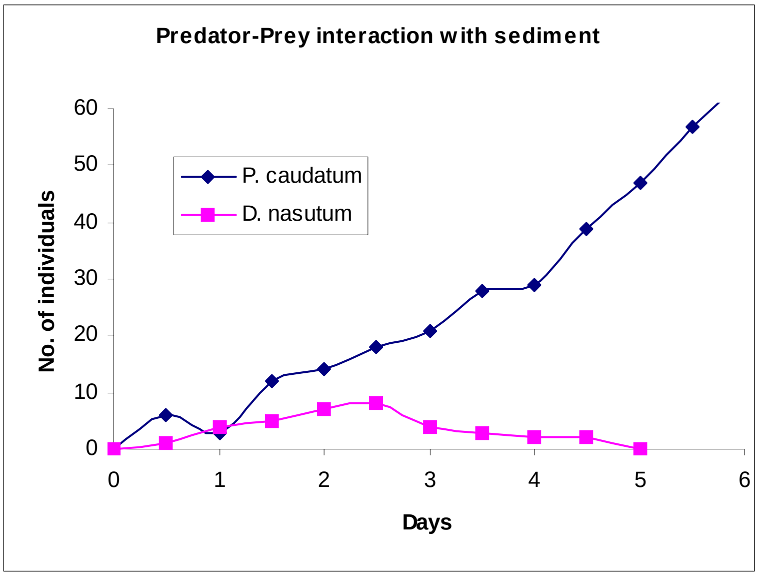

Fig. 2.12b - Predator-Prey interaction between *P. caudatum* and *D. nasutum* in oat medium with sediment

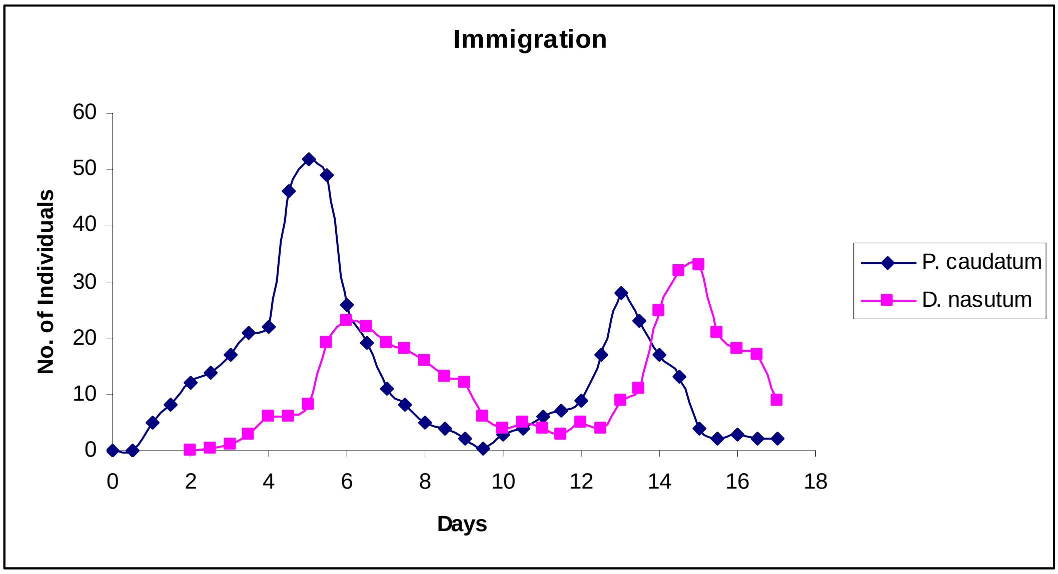

Fig. 2.12c - Predator-Prey interaction between *P. caudatum* and *D. nasutum* in oat medium without sediment but with immigration

Huffaker (1958) was not satisfied with the conclusions of Gause and believed that he used a very simple experimental system to study oscillations of predator-prey system. He experimented with a phytophagus mite (*Eotetranychus sexmaculatus*) as a prey that infests oranges and a predatory mite (*Typhlodromus occidentalis*). He performed a series of experiments by introducing more and more spatial heterogeneity in his experimental systems and ultimately he was successful in getting oscillations in a 252-orange universe with a complex series of petroleum-jelly barriers. In this experimental system, he observed that the prey were able to colonize oranges in a hop skip and jump manner and keep one step ahead of the predator, and eliminated each colony of the prey it found. The predators died out after 70 weeks and the experiment was terminated. Huffaker proved that heterogeneity was the key to oscillations in the predator-prey interactions; however, there is no mention of it in Lotka-Volterra Model. The conclusions derived from Huffaker's studies were:

Predators cannot survive when the prey population is low for a long period.

Predator-prey relationship cannot be maintained without immigration of the prey.

Predator response: The predators respond to changes in prey density in two ways:

Functional response in which the consumption of the prey by the individual predator changes. The functional response of many predators increase with increase in prey density but the upper limit is fixed by the handling time i.e. the time a predator takes to catch, kill and eat the prey organism. This is also influenced by the searching capacity of the organisms.

Numerical response in which the density of the predator increases through reproduction by the predators or because of movements or aggregations of predators in areas of high prey density. Predators are mobile and do not search at random but they concentrate in areas of high prey density.

Holling (1959) demonstrated the functional and numerical responses in small mammals, *Blarina, Peromyscus and Sorex.* These mammals prey on the cocoons of European pine sawfly (*Neodiprion sertifer*). He measured the functional response of the predators in terms of number of cocoons opened per day per individual predator. Each predator has a characteristic numerical and functional response. There need not be direct relationship between the numerical and functional responses of the predators. If the predator is limited by the abundance of the prey, the numerical response will be closely tied to the functional response but if a predator's abundance is determined by other factors, it may show a functional response with no numerical response. The functional response is affected by the quality of alternative food available, prey vulnerability, palatability, food preferences and sensory abilities of the predators.

Holling described three types of functional responses (Fig. 2.13) for predators:

Type-1. The number of prey consumed by an individual predator increases in a linear fashion to a maximum as prey density increases. This response is seen in simple predation models and can be best demonstrated in the experimental studies in the laboratory.

Type-2. The number of prey eaten increases at a decreasing rate towards a maximum value. Generally but not exclusively this type of response is demonstrated by invertebrate predators. However type-2 response does not help in the stabilization of the predator-prey population.

Type-3. The number of prey taken is low at first and then it increases in a logistics manner and has an upper asymptote. Vertebrates dominantly exhibit type-3 response. Prey consumption is density dependent and acts as a stabilizing factor for the population.

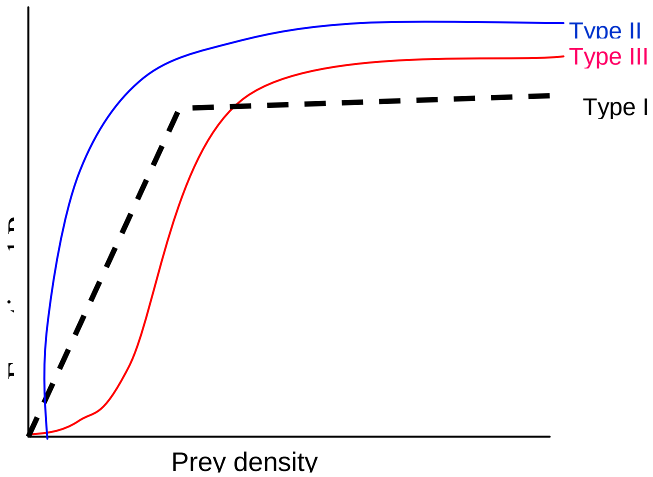

Fig. 2.13 - Functional Response Curves of predator

Numerical response: It is dependent on increased migration and reproduction of the predators. Migration of the predators is in response to prey density. Fecundity is dependent on the factors like food, space and mate and always a time lag is there in the maturing of the individuals, development and birth of young ones and their maturation to reproducing individuals. Numerical response affects the predators in the three basic ways (Fig. 2.14):

Number of predators increase with increase in prey density (Direct response).

Predator population does not show any change in density (No response).

Predator population may decrease in relation to prey population (Inverse response).

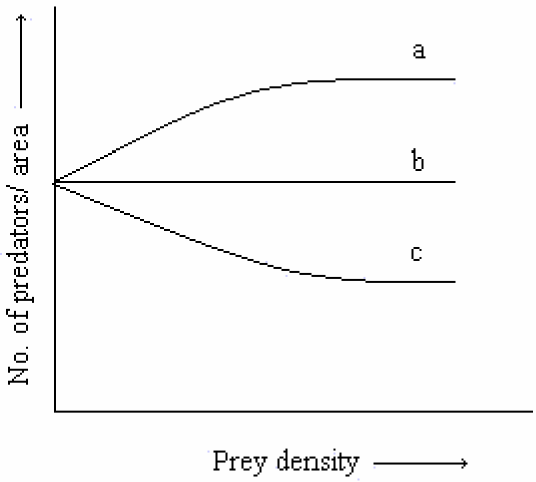

Fig. 2.14- Numerical response of a predator
a. Direct response b. No response
c. Inverse response

HERBIVORY: It is a special kind of predation dealing with the specific relationship of herbivores with the plants. Since most of the plants cannot move, escape from herbivores can be achieved only through some clever adaptations. Also the herbivores may be selective in their choice of plants and the **evolutionary interplay** between them results in a co-evolutionary game with plants and animals trying to surpass each other in the evolutionary time.

The herbivores predate upon different plant parts like the leaves, fruits, seeds, flowers, roots and bark etc. Some predators like the aphids suck plant juices without killing the plants while others may eat tissues directly. Thus the herbivores damage the plants and affect their survival, reducing the vigor, competitive ability and their **reproductive fitness**. However, some predators kill the plants completely.

Defense mechanisms in plants: Plants have developed certain modes of defense to counteract the herbivores. Some of the mechanisms are described below.

Structural defenses: To avoid damage from the herbivores, some plants have developed tough leaves, spines or hairs on the epidermis. Many plants produce seed with hard coats as protection against seed eating animals. These structural defenses may not be completely effective but they help in reducing grazing and make eating plants a time consuming process for the herbivores.

Mimicry: To confuse the predators, some plants change their appearance by modification in the leaves or other plant parts and look like a plant, which is inedible. For example, passionflower butterfly (*Heliconius*) feeds on the passionflower (*Passiflora*). The plants confuse the butterfly by converging the leaf shape with those of the associated plants. Also some species of *Passiflora* like *P. cyanea* have developed glandular outgrowths on the stipules near the bases of the leaves, which mimic the size, shape and golden colour of *Heliconius* eggs. Since the butterfly does not feed on shoots carrying the eggs and the young of other females, the plant achieves some protection by mimicking the eggs.

Reproduction strategy: Some plants try to compensate for the loss due to predators by producing seeds in large numbers so that a large number of offspring is produced. The great abundance of the prey satiates the predators and some of them will be still available for the propagation of the race. To ensure the continuity of the race, these plants have evolved certain strategies like:

Seeds are dispersed over wider areas so that all the seeds are not available to seed predators.

Restriction in the time of seed availability so that predators are not able to use the entire lot in the short period and some seeds are still available for germination in the next season.

Seed production should not be a frequent affair; rather seeds should be produced annually or even longer period so that dependency of predators on seeds is reduced.

Seed production by a plant should be synchronized with other plants to reduce seed predatory on a particular plant.

Chemical defenses*:* Generally, chemical defense in plants is by secondary plant substances and these are by-products of primary metabolic pathways ranging from **alkaloids** to terpenes, phenolics, cyanogenic, glycosides, steroids and resins. They may be stored within the cells and released when the cells are broken or may be stored in epidermal gland cells and function as contact poison or inhibitor. Juglone is an acetogenin produced by walnut trees. The spices cinnamon and cloves contain phenyl propane and terpenes are present in peppermint oil. Morphine, caffeine and nicotine are alkaloids found in different plants.

There are different opinions regarding the functioning of these substances. Some consider them to be the waste product of plant metabolism and plants have developed different ways of eliminating these substances by volatilization or leaching or converting them into harmless substances within the plant body. These substances may then be released into the immediate surroundings to suppress the competitors with an allelopathic effect or store them in stem and leaves to make the plant unpalatable or harmful.

Others feel that secondary plant substances are produced by the plants at their metabolic cost and are specifically evolved to drive away the herbivores and thus they keep the plants at a selective advantage. Defense in plants depend on the vulnerability of the plant tissues. Young shoots and leaves are more needed by the plants than mature ones and so plants invest more in the defense of these parts. The chemicals therefore are concentrated in these parts of the plants to increase their effectiveness e.g. a milkweed *Asclepias curassavica* contains a secondary plant substance called cardiac glycosides which affects the vertebrate heart beat, is poisonous to birds and mammals and is not eaten by the cattle inspite of its rich growth.

Plants exhibit qualitative defenses when substances like cardiac glycosides prove highly toxic even in small amounts and quantitative defenses when the defense of the chemical depends on the amount of substance ingested by the herbivores, as the chemicals produced by the plants may be bitter in taste or upset the stomach so that food becomes indigestible. Tannins reduce the digestibility of plant materials consumed and slowdown the growth rate.

Chemical defenses also result in **mutulasitic** relationship between plants and fungi. The mycelium of a fungus (*Acremonium ceonophialum)* grows in the intercellular spaces of the leaves of the grass (*Festuca arundinacea*). It derives nutrition from the intercellular fluids and protects the plants against drought and herbivores by its strong toxic effects on cattle and horses. The cattle suffer from poor weight gain, intolerance to heat and reproductive failures.

Some non-toxic plants coexist with toxic plants and produce similar chemical attractants to confuse the host specific herbivores. Some insects may lay their eggs on a closely associated plants and it results in the death of their larvae.

Man makes use of the defense chemicals produced by the plants in making different types of drugs and different body parts of a single species of plant can provide different potentially useful chemicals.

Herbivore interactions: The plants use different mechanisms to repel the predators (herbivores) but the herbivores are dependent on plants for their survival. The herbivores try to counteract the defense mechanisms of the plants either by evolving enzymes to detoxify plant chemicals or time their life cycles in such a way that they can avoid the noxious chemicals of the plants and thus the coevolution of plants and animals occur. There are two basic types of herbivore-plant systems:

Interactive herbivore system in which the herbivores influence the rate of growth and subsequent history of the vegetation. The ungulates of the Serengeti Plains of East Africa are an excellent example of interactive grazing system. The Serengeti Plains cover wide area and have luxurious growth of grasses.

The dominant grazers of the Serengeti Plains are migratory and respond to the growth of grasses in a fixed sequence and the grazers do not feed on different grasses but on different parts of the plants. The Zebras eat grass stems and sheaths and they are the first to enter the plains. Wild beasts migrating in large herds follow Zebras. They eat more of the sheaths and leaves and trample the grasses to short heights. Thomson's gazelles enter next and feed on grass sheaths and herbs. The grass stems are low in protein and high in lignin while grass leaves are high in protein and low in lignin and provide more energy. Herbs contain more protein and energy then grass leaves. Zebras thus seem to have the worst diet and Thomson's gazelle the best. Zebras survive by processing large volume of plant material and they need much less energy and protein per unit weight then the smaller species. This enables the larger animals to tolerate low food quality better then smaller animals.

Competition for food does not occur between wildbeast and Thomson's gazelle, even though they eat same parts of the grass. Grazing by wildbeast infact increased the production of grasses for Thomson's gazelle. Wildbeasts have a devastating effect on the grassland as they pass through in migration. However, the grazed areas recovered after the wildbeast migration and produced a dense growth of grass. When gazelle entered the area during the dry season, they concentrated their feeding only in those areas where wildbeast had grazed previously. The example proves that feeding activity of one herbivore species improves the food supply available to second species. The interactive feeding will suffer if any of the links in the sequence is removed.

Many insect populations show irruptions depending on the availability of their food plants. The spruce budworms feed on the buds, flowers and needles of conifer trees and their populations irrupt every 30-40 years along with the flowering of the trees. Kimmins (1971) attributed irruption in budworm population to high amount of amino acids in the young leaves of the trees. White (1974) observed that any plant material deficient in nitrogen is not suitable for insects. Therefore, any increased availability of amino acids sets the stage for insect outbreak as larval forms survive much better when more of amino acids are available.

2. Non-interactive herbivore system: There is no relationship between herbivore population and the subsequent condition of the vegetation. The best example is of European finches, which feed on the seeds of trees and herbs. The finches depend upon plants for their food but in no way contribute towards the production of their food plants and the interaction operates in only one direction i.e.

Production of plants →Herbivore density.

Population stability in finches is determined by fluctuations in seed production from year to year. Herbs in the temperate zone produce almost the same amount of seeds every year but trees require more than one year to accumulate reserves necessary to produce fruits.

Finches that depend on tree seeds undergo irruption in population density and survive only by being opportunistic. They cover large areas looking for areas of high seed production. The finches breed in northern areas and periodically move south in large numbers. Southward movement helps finches tide over the food shortage and breeding. Moving south is advantageous for the birds that stay behind. Also the migrants have the chance of colonizing new areas in the south and leave new descendents. But they are more likely to move north once the food crisis is over.

Significance of predation: Predators help in maintaining the balance of animal populations. The best example of this can be observed in our national parks and sanctuaries where the attempt is made to make the wild populations self regulatory and it has the predators as well as the prey species.

One of the first examples of population regulation by predation is of mule deer in the Kaibab National Forest in 1920s. Intensive predator control from 1906 to 1930 resulted in large-scale killing of wolves, coyotes and lynx and the mule deer population erupted from a herd of 4000 to 100,000 by 1924. The deer population exhausted the resources and 60,000 deer died in the winter of 1924. The crash was perhaps due to range deterioration and food shortage. It took several decades for the recovery of the forest vegetation and the deer population in the forest.

Predators are known to remove young, old, diseased and injured individuals from the prey populations. Schaller's studies on deer and tiger in India (1967) and wildbeast and lion in Africa (1969) have supported the above statement. According to Murie (1944), predation was the primary limiting factor on the numbers of Dall sheep in The Mount McKinley region of Alaska. The Dall Mountain sheep data for 608 skulls suggest that that the wolves kill the very young, very old and avoid confronting a very strong fit sheep. It is rare for the predators even when working as a group to kill a large animal in its prime. Thus, predation acts as a natural method of quality control. The adult, healthy and well-adapted animals are less likely to fall victim to the predator.

Ecologists have promoted predation as a method of biological control of pest animals particularly insects and rodents and in the control of desirable animals like deer in national parks and sanctuaries to prevent them from becoming pest. According to Schaller (1967), tiger population is the main controlling factor on the population of chital, sambhar and swamp deer in Central India. He estimated that an adult tiger requires 6300 to 7800 pounds of prey animals per year in its diet, which involves 30 to 60 prey animals per year with an average weight of 50 to 100 kg per animal and thus it represents a major controlling factor for the prey population.

Predation has been used in the biological control of insect pests:

Predatory mice control a dipterans insect, knapweed gallfly (*Urophora jaceana*) that feeds on its pupae.

Tsetse flies (*Glossina* species) in Africa are controlled in distribution and abundance by the predatory spiders.

The cottony cushion scale (a pest of citrus crops) is controlled by ladybird beetle.

Capsid bugs have controlled the sugarcane leafhoppers in Hawaii.

Vector of yellow fever, *Aedis aegypti* is controlled by the predator mosquito (*Toxorhynchites)*

But sometimes, predators may not have a significant controlling influence on the prey populations as in the case of snowshoe hare and lynx populations, food supply and intrinsic factors seem to have major controlling influence. Generally, it is observed that predators take primarily surplus individuals. They may be physically inferior, might be in sub-marginal habitat or behaviourally vulnerable to predation, disease, starvation or any one of the several mortality factors. Errington (1967) wrote about predation as "Predation belongs in the equation of life."

Predation also leads to the development of a great variety of adaptations in the interacting populations. Protective colouration, warning colouration and mimicry fall in this category. Apart from this, predation results in the development of morphological and behavioural responses of flight, speed, armor and freezing to reduce mortality through predation. For example, the bats locate the moths by emitting ultrasonic pulses and detecting the reflecting echoes from flying moths. The moths have evolved the ability to detect these ultrasonic pulses of bats and on sensing the approach of a feeding bat; the moths undergo a complicated flight spiral to avoid the bat. This interaction becomes a sort of aerial dogfight between the bat and the moth, with the moth trying to avoid the bat. Similarly the flying fox (*Pteropus vampirus*), a fruit bat with a wingspan of one metre is known to be fond of bananas. They live during the day on treetops and at dusk, they visit banana plantations. However, the nocturnal habit is a strategy to avoid the predators like hawks and eagles, which are diurnal hunters. If these predators are absent, then the bats forage more during the daylight. This ability and behaviour has evolved in selective response to predation and this advantageous mutation has been selected and propagated.

Evolution of predator-prey system: Lotka-volterra developed predation-prey models to show that their interaction results in oscillations or fluctuations in their number in simple laboratory animals. But these oscillations are not common in the real world. Perhaps, continued interdependency of the predator and prey has brought about changes in their characteristic and natural selection has resulted in the stability of both the population leading to the coevolutionary process.

The predators are brave, is actually a myth, as natural selection favours them to be cowards; the braves disappear early. In predation, the killing is not glorified, rather it is just an ordinary process. The predator kills only those animals that it can overpower with ease.

According to the **optimal foraging theory**, predators evolve to hunt in a way that saves energy as well as keep it physically fit. Hunting is seen as a cost control exercise and the cost includes energy spent in searching the prey and in handling the prey when it is caught. Generally, the predators hunt for smaller animals though it may yield lower energy. The predators also change their prey items if one type of prey becomes scarce e.g. bluegill sunfish feed on the largest *Daphnia* species and smaller *Daphnia* were ignored. When the prey population decreased, the bluegills were forced to feed on all the potential prey items, they encountered

If a predator is better than the other at catching the prey, it will leave more descendents to subsequent generations. So the predator is continually selected to become more efficient at catching the prey. But by becoming too efficient, the predator will destroy the prey and then suffer starvation. Therefore, a predator should harvest with a constraint against over harvesting. Slobodlin (1961) called them **"Prudent predators"**. Generally, two constraints operate in a habitat with several species of predators and prey. The existence of several species of predators feeding on several species of prey constrain a predator's efficiency e.g. a prey species may escape by hiding under a rock, the other may run very fast and the predator is constrained by conflicting pressure, either to be very good at running or at turning rocks. Thus, we can say that the prey population is being selected for escape responses. Since there are several predators with different hunting strategies, prey will not be able to evolve specific escape behaviour suitable to all species of predators.

A prudent predator would not eat prey individuals in their peak reproductive ages as this type of mortality would reduce the productivity of the prey population, so they eat only the oldest and the youngest individuals in the prey population which otherwise contribute little towards prey productivity. Also, the old individuals may be post-reproductive while the young ones suffer high mortality due to other factors.

The co-evolution of predator-prey system occurs most tightly when the predators regulate the abundance of the prey. But in some predator-prey systems, the predator does not determine the abundance of the prey; hence the evolutionary pressure is considerably reduced. The prey species has refuges where the predator does not occur or the prey may have certain size classes, which are not vulnerable to predation. Sometimes, the predators develop territorial behaviour especially during the breeding season and restrict their own density and do not respond easily to increased prey population.

Most of the stability in the predator-prey system is the result of continued coevolution. Predators which do not have prudence forced on them by their prey may exist only for a short time in the evolutionary record. Therefore, what we have today is perhaps a residue of highly selected of predator-prey system.

COEVOLUTION: Erlich and Raven (1964) first gave the term **coevolution.** It is defined as the evolutionary relationship between two or more non-interbreeding species, which are closely associated ecologically. The evolution of one species in the relationship is linked to the evolution of the other species. The interaction can be predation, competition and mutualism. The interacting species adapt and counter adapt to each other's selection strategy. Coevolution may be:

Pair wise and

Diffuse type.

In **diffuse type** of coevolution, more than two species evolve together and it is seen in the evolution of communities, where the species are affected by their interaction with other species and the environmental factors. Ungulate populations of Serengeti Plains of Africa cooperate with each other in feeding and maintaining the growth of the vegetation and are an ideal example of diffuse type of coevolution.

In the **pair wise** also called **one to one coevolution**, the characteristics of one species evolve in response to the characteristics of the other species, setting a sort of evolutionary race, where each species try to surpass the other. It may be mutualistic or antagonistic type in nature.

Mutualistic coevolution has been demonstrated in the relationship of ants and swollen thorn acacias in New World tropics by Janzen (1966). The ants depend on the acacia tree for food and get a place to live, while the acacia depend on the ants for protection from the herbivores and neighbouring plants. The ants live in the hollow thorns and feed on the beltian bodies, leaflets and the nectaries. The beltian bodies are rich in oils and proteins while nectaries are a rich source of sugars. The acacia maintain round the year production of the leaflets to feed the ants. If ants are removed from the swollen thorn acacias, the herbivores and other plants growing in the neighbourhood quickly destroy the trees.

The ants move regularly on the leaves and branches of the tree and quickly remove any herbivore that tries to eat acacia leaves. They also remove any vegetation growing in the area surrounding the acacias. The ant-acacia model represents an ideal example of coevolution of two species for mutual benefit The acacia provides the place for living as well as food to the ants while the acacias in turn get protection from the herbivores and other vegetation in its surroundings. However, either one or both the species are incapable of survival without the other.

Since plants cannot move, they use animals for seed dispersal and for pollination. The herbivore-plant interaction is beneficial for both the interacting species. A high degree of specificity has developed in some cases and animals that pollinate a particular plant are called as pollinating vectors. The pollinators help in the dispersal of pollen and seeds to far off places and in return get nutrient rich food consisting amino acids and carbohydrates. Thus a sort of obligatory relationship exists between the plants and their pollinators. However, some plants cheat by mimicking female insects or rotting meat. For example, the flowers of the orchid Ophrys are shaped like a bee and even they smell like a bee. They attract only male bees, which land on the flowers and appear to be mating with it. The male bees come in contact with the pollen masses, which get attached to the lower side of the body. When the insect visits another flower, the pollen is rubbed against the stigma to complete the process of pollination in coevolution.

In **antagonistic coevolution** like herbivore-plant, predator-prey and parasite-host, one species harm the other and to avoid the herbivore, predator or parasite, the species develop counter mechanisms. The plant-herbivore relationship involves the production of poisonous chemical substances or changes in the physical structures of the plants to escape herbivory. The animals also develop physiological mechanisms to detoxify the chemical substances of the plants or develop some adaptations so that they can feed on these plants. Some herbivores even use plant poisons to make themselves poisonous and unpalatable to avoid the predators and exploit the defense mechanism of the plants. For example, the monarch butterflies feed on the milkweed plants (*Asclepias curassavica*) without any harmful effects. The milkweed plant contains cardiac glycosides, which affects heartbeats in birds and mammals and is poisonous to them. The monarch butterflies have developed a mechanism to feed on milkweeds containing cardiac glycosides and then storing the poison in their tissues to get protection from its predatory birds. The monarch butterflies are distasteful to insect eating birds and so they avoid eating these butterflies. However, the edible monarch butterflies escape predation as they look exactly like the toxic monarch butterflies.

Inedible animals like bees, wasps and butterflies have bright colours sending signals to the predators not to touch them and the animals to their advantage have used bright colouration. Coevolution results in the development of **mimicry**, where one species tries to mimic in colour and form another totally unrelated species, which is harmful or distasteful to the predator. Mimicry is of different types. In **Mullerian mimicry**, the model and the mimic are unpalatable or harmful to the predator and have the same colour and pattern. The butterflies (*Heliconius erato*) and (*H. melpomene*) living in the same geographical area of Amazon basin have similar wing pattern and both are poisonous. The birds identify them by their colour and pattern; and through learning behaviour know that they are harmful and therefore, do not prey on them. It gives the prey species a survival advantage as the predators do not prey on them and they associate that colour with distastefulness.

In **Batesian mimicry,** a palatable mimic imitates a harmful or distasteful species to avoid predation. The monarch butterfly (*Danaus*) is brightly coloured but distasteful to the birds and not preferred by them as food. The viceroy butterfly is edible but it is mistaken for the monarchs butterfly by the birds and do not prey on it.

Lotka-Volterra assumed a constant and unchanging prey species and a predator species but evolutionary changes in the predator–prey system have been observed by Pimental *et. al.* (1963) in housefly (*Musca domestica*) and a wasp parasite (*Nasonia vitripennis*), experimental set up maintained for 20 generations. The evolutionary changes occurred both in the housefly and the parasitic wasp. The host became more resistant to the parasite, and the parasite became less virulent to the host and thus natural selection produced evolutionary changes in a short time to reduce the intensity of interaction between the host and the parasite so that they can coexist in a much more stable equilibrium.

Some scientists believe that there is no proof in favour of coevolution on one to one basis. It is suggested that the so-called coevolutionary forms must have evolved in different environments under different selection pressures and when they happened to invade the new habitats, they adjusted with the local species. The characteristic of these species fitted with the environment and the two interacted in a manner as if they have a long coevolutionary relationship between them. Thus it is not essential that the coevolved forms have undergone evolutionary changes only after interacting with each other. But the relationship can be further selected for coevolutionary interaction.

The interacting species grow up together over evolutionary time and for the survival of the system, the negative interactions tend to be minimized in favour of positive interactions culminating in mutualistic association.

PARASITISM: A **parasite** is an organism living in or on the body of another organism and derives nutrition from it. It is an interspecific population relationship, which may be balanced or unbalanced in its effects on the host. A seriously unbalanced relationship in which the host dies is of course selectively disadvantageous to the parasite as well .The parasite has certain features like:

It is physiologically dependent on its host.

It has higher reproductive potential then its host

The parasites have the ability to kill highly infected host.

The infection results in wide distribution of the parasite within the host population.

The parasite has a much shorter generation time than the host

A parasite may be temporary such as a wood tick or a more permanent resident such as tapeworm. It may weaken, debilitate or eventually kill the host or it may cause relatively little harm. Parasitism is universal in plants and animals. In vertebrates, the parasites are found with in many organ systems, most commonly in the digestive, urinary, respiratory and urinogenital systems and they are called **endoparasites** e.g. viruses, bacteria, protozoans, nematodes and tapeworms. They are often called disease agents or **pathogens**. **Ectoparasites** occur on or within the skin and its appendages such as hairs and scales e.g. ticks and mites. It is not only human diseases that are caused by parasite; a huge sum is spent every year to control fungal infections of crops and parasitism among livestock.

Parasites like fleas, lice and intestinal worms are **biotrophic** parasites as they survive till the host is alive, if the host dies, they have to leave it and find a new host. The blowfly is an example of **necrotrophic** parasite. It lays its eggs on a live sheep. The maggots burrow in to the sheep and if there is large number of them, they may kill it. Even after the death of the sheep, the larvae continue to feed and mature inside the corpse.

Parasites that always kill their host are called **parasitoids**. Most of the parasitoids are fleas and wasps and they lay their eggs on the larvae of other insects e.g. parasitoid wasp injects its eggs beneath the skin of a larval butterfly. The eggs hatch and the parasitoid larvae eat the host from inside. The host suffering from the disease continues to survive and may grow also, providing nourishment to the parasitoids. When the parasitoid larvae are mature, they emerge through the skin of the host and pupate, and this emergence through the skin of the host kills the host.

Parasites can also be classified as **microparasite** like viruses, bacteria and protozoan and they have a short generation time. They develop and multiply rapidly within the host. The duration of the infection is short and transmission from host to host is direct and **macroparasites** like ticks, mites, roundworms and flatworms and they have a comparatively long generation time. They persists in the hosts by continued reinfection and spread by direct transmission from host to host or indirect through intermediate hosts and vectors.

However, there is no sharp demarcation between obligatory commensalisms and parasitism. Theoretically, *Entamoeba histolytica* feeding on the tissues of the host is a parasite where as the flagellate *Trichomonas hominis* feeding on digested foods before incorporation into host tissues is not a parasite. Also *Entamoeba coli* feeding on undigested particles of food and intestinal bacteria is not considered a parasite.

Many parasitic organisms may be pathogenic in one individual and non pathogenic in another. For example, *Entamoeba histolytica* in the digestive tract of most of the individuals do not cause amoebic dysentery but it may cause severe disease and even death in other organisms.

There is no sharp line of distinction between a parasite and a predator as well apart from differing in size. We take predator as killing their prey in a short time. But in some cases, the distinction is arbitrary e.g. the lamprey may kill the fish in a few days or in a few weeks depending upon its size in relation to the fish and may be considered either a predator or a parasite.

Host Response to Parasitism

The host responds to the invasion of parasite by different methods. It may defend itself by producing immunity to infections. The lymphocytes in the blood produce **antibodies** to neutralize the invading **antigen**. But sometimes due to protein deficiency and poor diet, normal antibody production is inhibited and the immune system becomes weak. It allows the virus and the parasite to become pathogenic. The ultimate breakdown of immune system occurs in humans infected with the human immunodeficiency virus (HIV), which causes AIDS. The virus attacks the immune system of the host causing a number of deadly diseases.

Sometimes, the parasite lives safely in the host body without any attack from the host's immune system. It results due to **molecular mimicry** in which the anntigenic determinants of the parasitic origin resemble the antigenic determinants of their hosts and the host does not produce antibodies. *Trypanosoma* is known to sheds its coat and antigens every time it is under attack from the host's immune system to confuse the host. The tapeworm protects itself in the intestine from the host's antibodies by covering with a mucous layer formed of sugar and protein called **glycocalyx.**

Sometimes, there can be inflammation due to death or damage to the host's tissues.There is increased secretion of histamine and more blood to the site bringing in phagocytes, lymphocytes and leucocytes. In some cases the parasite forms a calcareous cyst in the host's body to protect itself from the host's defense system. The round worm (*Trichinella spiralis*) that causes trichinosis in human, forms cysts in the muscles of pigs and bears.

Abnormal growth occurs in vertebrates due to infection by the parasite e.g. infection by malarial parasite causes enlargement of spleen due to increased production of red blood cells and antibodies in human beings and larvae of botfly (*Cuterebra emasculator*) produce swellings or warbles on the skin of mammals before they emerge through the skin. It is believed that pearl formation in oysters is mainly in response to parasitic infection.

Effects on the host population

There are numerous examples where the parasitic infection is harmful and debilitating to the host e.g. malaria still remains a major health problem throughout the tropical world and causes a great amount of illness and human misery. **Schistosomiasis** is the most debilitating disease caused by the blood fluke (*Schistosoma*). It is water borne infection, which has spread throughout the world with the expansion of irrigated agriculture. In animal populations, parasites weaken the infected individuals and may cause death also. For example, in dogs and wolves heartworms reduce animal's vitality and hunting success. Lungworm infection in the big horn sheep of Idaho, **myxomatosis** in rabbits of England and Europe in 1950 and **coccidiosis** in gray squirrels of Baltimore were responsible for heavy mortality in these animals.

Parasitic infection is reported to affect the reproductive ability in some animals like fungus eating *Drosophila* flies, which are parasitized by an intestinal nematode (*Howardula aoronymphium*). The female nematodes living in mushrooms infect the larvae and grow in it. They produce the eggs and release larval nematode in the haemocoel of the flies. The nematodes leave the body when drosophila flies visit the mushrooms. It causes sterility in females but in no way interfere with the mating success of the males.

Abnormal behaviour has been reported in rabbits infected with a bacterial (*Pasteurella tularensis*) disease **tularemia** transmitted by the rabbit tick (*Haemaphysalis leporis-*

paulstris). The rabbits become sluggish and are not aware of the presence of predators. Heavily infected with ectoparasite, the birds and mammals respond by **grooming.** Birds can be seen scratching their plumage with beak or leg to get rid of the ectoparasites in their plumage.

A heavy load of ectoparasite may affect the colouration and brightness of the plumage or fineness of any other derivative of the skin. The selection of mate seems to be affected by the parasitic burden of the host as the females select healthy males with bright plumage.

The most important aspect of parasitism ecologically is its effect on the host population. Like the predator-prey interaction, the parasites and the hosts are also involved in an antagonistic evolutionary interaction but with time negative interactions tend to be minimized in favour of positive interaction as natural selection favours evolution of reduced parasitic virulence. Thus the oldest and the best-adapted parasites have little or no pathogenic effects on the host. Pinworm infection in children is relatively harmless, though it may cause minor irritation around the anus. In West Bengal, hookworm infection due to *Necator* sp. and *Ancylostoma* sp.is very common but has no pathological effects on the people. The infectious burden seems to be small and insignificant. Most of the wild animals have parasites and are able to maintain excellent health e.g. Zebras in Kenya are heavily infected with many internal and external parasites but still maintain robust health.

Transmission of the parasite: The parasite needs a host not only for nutrition but also for a place to live. To move from one host to another, the parasites have evolved different ways in their life cycle. But irrespective of the mechanism of transfer from one to the other host, the parasites can escape only during the transmission stage when the contact between the host and the infective stage of the parasite is a must. Parasites are transferred from one host to another by:

Active locomotion of the parasite itself.

By ingestion as one animal sucks the blood of, or eats another.

By ingestion as one animal takes in eggs, spores or encysted stage of a parasite along with its food or drinking water,

As a result of bodily contact between the hosts and

By transportation from one host to another by way of vectors.

In the life cycle of a parasite, there are two types of hosts. The definitive or the primary host in which the parasite becomes an adult and reaches maturity and the intermediate host in which some developmental stages of the parasite occur. The number of intermediate hosts varies in the life cycles of different parasites.

Transmission of parasite from one host to another may be direct or indirect. During direct transmission of the parasite, there is no involvement of intermediate host and transmission is either through contact or carrier or vector. Lice, ticks and botfly larvae spread by direct contact and they lay their eggs directly on the host. In macroparasites like *Ascaris,* which lives in the digestive tract of mammals, infection is direct from infected to uninfected host. The female *Ascaris* lay eggs in the intestine, which are expelled out of the body along with the faecal waste. When swallowed by a host, the eggs hatch in to larval form in the intestine of the host. The larva then takes a ten-day tour through the body of the host before finally settling in the intestine.

During indirect transmission, the parasites require primary, secondary and in some cases even tertiary hosts for different stages of their life cycles. *Plasmodium falciparum* has parts of its life cycle, the sexual phase of reproduction in the mosquito and asexual phase of reproduction within the human host. *Schistosoma* infect man or other vertebrates as the primary host for sexual reproduction and inhabit aquatic snails for asexual reproduction. The sheep liver fluke (*Fasciola hepatica*)) passes the sexual phase in the sheep, the definitive host and the asexual phase in the snail, the secondary host. The Chinese liver fluke (*Clonorchis sinensis*) infests man as the primary host, aquatic snails as the secondary host and fresh water fish as the tertiary host. Despite this complexity, it is very successful and wide spread parasite infecting millions of people throughout the oriental region.

Evolution of parasitism: The ancestors of ectoparasites were most probably free-living forms. These free-living forms either in water or on vegetation could have settled accidentally on the outside of a larger species and found the conditions favourable for survival. The niche would be of selective advantage, if the organisms find a good source of food. The biting lice probably evolved from psocid insects that live below the bark of the trees. From this niche, they may have moved to bird's nest and then to the birds themselves.

Most of the ectoparasites probably are derivatives of carnivores, saprovores or suckers of plant juices. Endoparasites may in some cases have evolved directly from free living ancestors or commensals e.g. free living nematodes and scavenger beetles both feed on decaying organic matter and it is possible that beetles could have accidentally consumed some nematodes. Many organisms like protozoan and flat worms, which are now parasitic could have had first entrance into the alimentary canal of the prospective host via drinking water and then invaded other organs of the body. The invaders would have found in their host abundant food resources but they needed some preadaptations such as:

To live at low oxygen level characteristic of digestive system.

To resist being consumed by the digestive juices of the host and

To resist being carried out along with the faecal waste.

As succeeding generations of parasite became increasingly adapted to live either in or on their hosts, many organisms lost the capacity of free-living existence. Specialization to internal parasitism required certain characteristics such as

i. Loss of organs of locomotion.

ii. Loss of sensory organs

iii. Loss of digestive system.

Also, it resulted in the development of certain adaptive features in the parasite such as

Organs of attachment in the host's body.

Increased reproductive capacity and in many cases existence of polyembryony.

Presence of intermediate hosts and complicated life cycles.

Many parasitic species are more highly evolved than others. Some parasites live their entire existence in one host; others require one, two or three intermediate hosts. It is of ecological significance that both the primary and intermediate hosts of a parasite occur in the same habitat or community. Even then the hazards to successful passage from one host to another are so great and mortality so high that large quantity of offspring are produced to ensure that at least a few individuals will complete the life cycle.

SOCIAL PARASITISM: It is a parasitic relationship in which one organism is parasitically dependent on the social organization of the other. Social parasitism is of two types.

Brood parasitism

Kleptoparasitism.

Brood parasitism: It is foisting incubation of the eggs or care of the young onto surrogate mothers. It may be temporary or permanent, facultative or obligatory. On the basis of relationship between the parasite and the host, brood parasitism is further of three types.

Temporary facultative

Temporary obligatory and

Permanent obligatory.

Temporary facultative brood parasitism is exhibited by ants, wasps and some birds like ducks. For example, a newly mated ant queen (*Lasius reginae*) enters the nest of host species *L alienus* and kills its queen. The *L. alienus* workers look after the queen and her brood, but over a period of time *L. alienus* workers die because of their replacements by workers produced from the new queen and, therefore, the colony has only *L. reginae* and its workers. Newly mated queen in the wasp (*Polistes*) attack established colonies of her own species and remove the resident egg-carrying queen. Similarly, some species of ducks like the red head duck (*Aythya americana*) lay their eggs in nests of other species.

Temporary obligatory brood parasitism occurs in ants and birds like old world cuckoos and the cowbirds. They are obligatory parasites and pass on their duties of nest building, incubating the eggs and looking after the young to the host by laying eggs in their nest. The host birds react differently to the situation either by pushing the eggs from the nest or may incubate the eggs and rear the young at the expanse of their own eggs. At times, their eggs are either pushed from the nest or their young die because of availability of a limited supply of food due to aggressive nature and larger size of the young of the parasitic birds in the nest. Thus cowbirds and cuckoo ensure the survival of their race at the expanse of other birds.

Permanent obligatory brood parasitism is very common in ants and wasps. The parasitic form spends its entire life cycle in the nest of the host. The queen enters the nest of the host and either dominates it or kills it and takes over the colony. Most of these forms are workers and queens that are not able to build their own nests.

Generally, brood parasitism results in reduction in the fitness of the host as some of its energy is diverted towards rearing the young of the others. But it may lead to increase in the reproductive success of the host, as the improved survival of the host's own young may compensate for reduced clutch size due to incubating the eggs and care of the young of the social parasite.

Brood parasitism occurs in birds and insects due to unfavourable situations like lack of suitable nesting sites or reproductive failures of the organisms. The reproductive failure occurs in females when their nests are damaged before incubation and then they may drop their eggs in the nests of others. Sometimes, the individuals leave their own nests unguarded and parasitize some other's nest. They lay eggs in different nests and sometimes a species behaves like a parasite and a nester (host) to ensure survival of some offspring and improve their reproductive fitness.

Kleptoparasitism: It is the forcible theft of the prey by the parasite from the host. For example, a bald eagle may force an osprey to drop the fish caught by it and then eats itself. It is very common in birds like eagles, falcons, gulls and waders. Kleptoparasites depend on other species to locate and obtain prey that can be stolen. They invade the social structure of the host and take advantage of the situation when the hosts assemble into breeding or feeding groups and offer little defense to the kleptoparasite.

Black-headed gull (*Larus ridibundus*) parasitizes feeding groups of golden plovers (*Pulvialis apricaria*) and lapwings (*Vanellus vanellus*) and exploits their social structure to get food. The gulls disperse themselves amongst golden plovers and lapwings and chase and harass the birds to get the worms picked by them from the fields.

The hosts develop different strategy to avoid the kleptoparasites.

They may maintain certain distance amongst themselves and the kleptoparasite.

They may shift to some other areas.

They may devise some evasive tactics or

They may take more food to compensate for the loss due to kleptoparasite.

INTERSPECIFIC POSITIVE INTERACTIONS

The negative interactions discussed already play an important role in regulating the population size and maintaining its stability. The positive interactions are also equally important and beneficial for the populations and ecosystem. **Symbiosis** means living together and in broader term refer to a relationship of any type between two or more living organisms. It may be beneficial or detrimental to the interacting population and should include parasitism and amensalism apart from commensalisms, protocooperation and mutualism. But usually we use the term symbiosis for relationships, which are beneficial or stimulating to one or more of the interacting population. Hence symbiotic relationships include neutralism, commensalism, protocooperation and mutualism. True neutralism is rare in nature and deserves no description. A brief account of other symbiotic relationships follows.

Commensalism: It is a relationship in which two populations interact in a way, which is beneficial to one and neutral to the other.

An example of commensalisms is the remora-shark relationship where the remora fish (*Echeneis*) attaches to the skin of a shark by means of a strong sucker disc and is transported widely and rapidly by shark's motive power. It also consumes food remnants cast off from the jaws of the shark. So it benefits in two ways while shark is relatively unaffected, though it's speed may be impeded slightly.

Whales provide attachment sites for barnacles, algae and other sessile marine forms. These plants and animals are not parasitic and only utilize the habitat provided by the host.

Sometimes, various species of plants and animals use burrows or nests constructed by other organisms. Termite nests provide ecological niches to animals like ants, aphids, beetles, millipedes and isopod crustaceans. Tube dwelling annelids like *Chaetopterus* inhabiting the tidal zone of the seashore provide habitat for small crabs like *Polyonyx* that are benefited by the protection of the tube and does no harm to the annelid worm.

Most of the animals including man contain intestinal commensals. Several types of bacteria inhabit the human digestive system as *Escherichia coli,* which merely resides in the alimentary canal. The man is unaffected but the bacteria get a place to live. Our hair follicles and sweat ducts have many microscopic mites, causing no harm but get a living from the oil on our skin. Though it is essential for the mite's well being but is of no concern to us.

Cattle egrets and cattle provide another example of commensalisms. It is a rather unusual association in which the egrets follow the grazing cattle in the fields and prey on beetles, grasshoppers, flies, crickets and frogs, which come out of the grass as it is trampled or grazed by the cattle.

Protocooperation: It is a type of positive interaction in which both the interacting populations are benefited by their association but it is not obligatory. Some examples of protocooperation are as follows:

Small tickbirds accompany rhinos and other ungulates picking off ticks and other ectoparasites from the skin. The association benefits both as the animals are freed of the ticks and the birds get their food but can live without each other as well. Some birds depend on the food particles stuck between the teeth of crocodiles. The birds get the food and the crocodiles get the teeth cleaned. The wrasses or cleaning fishes, which feed on surface debris and ectoparasites of larger fishes is another example, where both the fishes are benefited by the association..

In the association of the hermit crab and sea anemone, the hermit crab provides an attachment site and transportation for the sea anemone on a discarded mollusk shell that the hermit crab has occupied. The sea anemone provides camouflage and defense for the hermit crab.

Some ants like (*Cremastogaster lineolata*) exploit the aphids (*Aphis caliginosa*) for the latter's honeydew. The ants maintain the aphids in specially constructed nests and feed upon a nutrient liquid called honeydew secreted by the aphids. The aphids are sometimes called cows as they release the secretion when stroked by the antenna of the ants. Thus the ants receive the food from the aphids and the aphids receive protection, harborage and care from the ants.

An African bird, honey guide forms an association with the honey badger (a mammal). The honey guide locates the beehive and leads the honey badger to it. The honey badger tears the hive and eats the honey and the bee larvae while the honey guide eats the beeswax and larvae. The honey guide can find the hive but it is unable to open it where as it is difficult for the honey badger to trace the beehive. Thus cooperation between the two species increases their efficiency.

In the baboon-impala relationship, the superior vision of the baboon (*Papio anubis)* provides visual sentry and alarm for the impala (*Aepyceros melampus),* while the superior sense of impala provides olfactory warning for the baboons.

Mutualism: It is an association where both the interacting population benefit and neither can survive without the other and therefore it is obligatory for both the organisms. Some examples of mutualism are as follows:

The association of algae and fungi to form lichens is a classical example of mutualism. Fungi provide the framework, moisture and attachment sites in which the algal cells grow and the algae provide food by photosynthetic activity for themselves and fungi.

Another example involving plant's roots and fungi is the mycorrhizal roots, where the plant supplies energy to the fungi and the fungi absorb the required nutrients from the soil and supply them to the roots of the plants. **Mycorrhizae** is important to the plants as they help in the decomposition of litter and increase the nutrient absorbing capacity of the roots specially in nutrient poor soils. They obstruct the movement of pathogens in the roots and cause the production of chemical inhibitory substances while the host plant provide support and a constant supply of nutrient rich food.

The wood eating termite and the flagellate protozoan *Trichonympha* cannot live without each other. The protozoan lives only in the digestive tract of the termites and digests cellulose. The termites provide the essential habitat, a constant environment and the basic food material for the protozoan. The protozoan provides a vital digestive process for the termites.

Pollination represents an ideal example of mutualism. The flowers attract to themselves different creatures like bees, butterflies, moths and birds, because of their colour, shape or scent. The nectar provides energy in the form of sugars for these visitors and when the animal gets into the flower to get the nectar, its body touches against the pollen bearing stamens. The pollen attached to the body of the animal is then rubbed against the female portion of the second flower, ensuring pollination. Thus pollination helps the plants in fertilization and the pollinators get the food supply.

INTRASPECIFIC INTERACTION

It occurs between the members of a species population. The nature of interaction varies depending upon the population density and the availability of resources. A number of factors such as food, space and mate can act as resource for intraspecific interaction. The interaction brings about adequate spacing of individuals in an area and may help in population regulation.

However, in the absence of intraspecific interaction, the population density increase and may have harmful effects on the population. So, when the individuals are crowded and therefore under stress, it may alter the functioning of the endocrine system of the individuals. Secretion of growth and sex hormones may also be affected. The following trends may be observed:

Changes in the behaviour, growth, reproduction and production of the young.

The immune system of the organisms is affected making them susceptible to diseases and infection.

The population may show increase in mortality and decrease in fertility.

Some of the factors that help in the efficient utilization of resources and fair spacing of the individuals in an area are dispersal, territoriality and social dominance.

Dispersal: It refers to the movement of individuals into or out of the population.

Dispersal can take the form of emigration, immigration or migration. It helps in reducing competition by spacing out individuals so that efficient utilization of resources can take place. Depending on the circumstances, dispersal can take place either at or below the carrying capacity level. The number of young and females may be more in dispersing population, if the dispersal is below the saturation level.

Territoriality: Elliot Howard (1920) first used the term “Territory” in his book

“Territory in bird life”. It is an area, which contains a resource of sufficient value to the animal and is actively defended against other members of the same species. A **territory** has more or less fixed boundaries and is occupied by an individual or a group exercising control over it. The process of occupying a defended boundary is known as territoriality. It is very common and widespread in mammals, birds, reptiles, amphibians, fishes, insects and crustaceans.

A territory may be occupied and defended by an individual as in male stickleback fish (*Gasterosteus aculaetus*), by a pair as in many birds or a social group as in gibbons (*Hylobates lar*). The nature of territory varies according to the needs of the animals. Basically, the territories are defended either for food source or for breeding sites. The breeding site contains the mating as well as the nesting site as in birds. The nature of territories maintained varies in different groups as exemplified below:

The general territory fulfills all the needs of the animals from breeding, mating, nesting to rearing of the young ones. It is observed in muskrats and songbirds e.g. green warbler (*Sylvia borin*) and blackcap (*Sylvia atricapilla*) of England.

Some solitary animals may hold food territory e.g. tiger hunts over a large territory. Humming birds and some squirrels also defend a feeding territory.

Hawks maintain a mating and nesting territory with feeding done elsewhere.

Some birds are known to defend roosting territories, when roosting sites are not very common. Swallows and colonial birds defend only a nesting territory.

Animals, which have a **lek** i.e. an area where the males gather and display to attract females, have minute territories. The European ruff (*Philomachus pugnax*) and the American sage grouse (*Centrocercus europhrasianus*) have leks. In lek, the best males control small areas at the center of display areas; less good males have larger territories around the edges of the lek.

Thus territorialism is a highly variable and complex phenomenon and it covers a wide spectrum of behaviour patterns. They are defended for the resource like food, reduction in the risk of predation, attraction of a mate resulting in increased survival and reproductive fitness. Once established, territories are maintained by different behavioural patterns and displays.

It may involve aggressive behaviour and fighting as in jungle fowl *(Gallus gallus*), elephant seals (*Mirounga angustirostris*) and wild antelopes. It may result in injuries and even deaths or the defeated animals leave the territory.

The fishes spread their fins and brighten their colours as a mark of their presence.

Birds, frogs and insects defend their claim by singing from some prominent posts. They send the signals that the territory is already occupied and trespassing will not be tolerated. The male birds claim their territory by puffing out their chest and yelling at the top of their lungs from song posts. Some birds indicate their presence and territory occupancy by raising the crest, fluffing the body feathers and spreading the wings and tails.

Mammals use postural, auditory and olfactory signals as communicative displays for the maintenance of the territory. Many carnivores like wolf, lion and tiger have territorial calls, which can be heard for miles. The carnivores also mark their territories with scent glands and urine. Even a domestic cat maintains its territory and at times rubs its face against your legs to mark you with scent glands located at the corners of mouth and eyes, they make you a part of their territory.

The size of the territory is flexible and highly variable. If the resource such as food is in abundance, the territory may be small and if scarce, it may be larger. Huxley (1945) compared flexibility in territory to an elastic disc compressible to a certain size. But with increase in the size of the territories, the cost of territorial defense also increases. In many animals, the boundaries of territories are withdrawn to make the area more manageable, however this increases the density in the area but beyond a certain limit, the residents resists further decrease in the area and do not allow other organisms to settle. Some spiders have fixed territories irrespective of the resource availability or spider density. This trait is inheritable in spiders and the fixed territory may also be transferred from one owner to the other.

Quality rather than the size of the territory is important for some birds. Some male birds are known to occupy the best of the territories. American grassland finches select a territory having more of litter and high vegetation density. Humming birds and honeycreepers are known to defend areas with the richest nectar supplies. The quality of territory maintained by the males, distinguish them from other males and the successful males are always able to obtain a mate and the less successful males are either on the sub-optimal territory or may even fail to get a territory.

Many species do not maintain territories while some closely related species might be territorial in one case and non-territorial in the other. Indian swamp deer (*Cervus duvacelli*) is non-territorial but the Indian black buck (*Antelope cervicapra)* is territorial. Many ungulates are territorial during mating or rut season and non-territorial at other times of the year. In some cases, territoriality is related to population density and/or environmental circumstances. Wild house mice (*Mus musculus*) show territorialism at low population densities and mass group behaviour at higher densities but in langur (*Presbytis entellus*), territory is maintained at higher densities while at lower densities, they are non-territorial.

Territoriality may also help in population regulation in some wild animals under certain conditions by spacing individuals, avoiding conflicts during mating and ensuring better food An area normally inhabited by an animal is its **home range**. Usually, it is larger than the territory and has no fixed boundaries. Home range may be continuous or discontinuous but connected by certain routes. Usually, the resources are not evenly distributed in the home range; therefore the animals will be concentrated most of the time in those areas, where the resources are in adequate quantity. The home range is not actively defended and there may or may not be overlap of home range. The area of the home range is in proportion to the body size of the animals, therefore larger herbivores and carnivores have wider home ranges as compared to the smaller organisms. For example, tigers have bigger home ranges as compared to songbirds, which have very small home range. Usually the males and adults have larger home ranges than females and sub adults. The home range is useful for the animals as it fulfills their requirements of feeding, mating, shelter and protection from enemies or predators.

Social Dominance: Many animals are social and live in groups with other members of the species. Living in groups has certain advantages for the organisms. For example, the animals have less risk of being harmed by other animals and also they can defend themselves better from the enemies. Getting food is also easier while living in groups as has been observed in tiger, lion and wild dogs.

However, living in groups has its disadvantages as well. For example, the animals of a group may not get equal opportunity of sharing the available resources e.g. food, mate and space etc. In herbivores like rabbits, which have fixed feeding areas around their homes, feeding competition is intense. Similarly in carnivores, the presence of other carnivores on the kill reduces the amount of food available to each individual

It is commonly observed that in a group, it is easier for a few males to monopolise opportunities like feeding and breeding. When the competition is amongst adult males, it results in dominance hierarchy and individual at the top gets most of the advantages as it allots resources on an individual’s priority basis. The individuals at lower order may face starvation, feed on the left out part of the resource or disperse,

Social dominance is defined as the physical dominance of an individual over another, maintained by some manifestation of aggressive behaviour. Dominance is generally manifested between animals by simple physical displacement of one individual by another at a particular site. Each individual in a group occupies a position based on its dominance or submissiveness. Social dominance was first described by Schjelderup-Ebb (1922) for the domestic chickens. In domestic chickens, an alpha individual is dominant over the rest of the group while beta is dominant over all but not the alpha individual and so on. The dominance forms a straight line or linear peck order, where birds peck at others of lower order as shown below.

$$\text{Alpha} \longrightarrow \text{Beta} \longrightarrow \text{Gamma}$$

But complexities may exist within a peck order and it may be triangular hierarchy, where the first individual is dominant over the second, which in turn is dominant over the third. The third individual is dominant over the first. In this case, an individual at the lower order is able to peck an individual of higher rank as shown below.

$$\begin{tikzcd} \text{Alpha} \arrow[rr] & & \text{Beta} \arrow[dl] \\ & \text{Gamma} \arrow[ul] & \end{tikzcd}$$

Once the **hierarchy** is established, it is maintained by some sort of display by the animals or memory. For example, once a rhesus monkey has established high rank, it need not display it in the social group, as it becomes an accepted social norm in the group. In songbirds, peck order is replaced by peck dominance and the individual that pecks the most becomes the dominant.

The level of male hormones, their strength, size and maturity as well as close associates and environmental conditions influence the position of the individual in the social hierarchy. Rise in hierarchy is based on the increase in sexual activity and hormones of the sub dominant individuals and their aggressiveness in the group. If there is an intruder in the group, it is very difficult for it to rise in ranks and they are accepted only on the lower side of the social order. Social dominance may also help in population regulation by affecting reproduction and survival of the organisms.

References

1. Bush.M.B. “Ecology of a changing planet.”2000. Prentice-Hall of India Private Limited.
2. Chapman, J.L. & Reiss, M. J. “Ecology, principles and applications”, 1995. Cambridge University Press.
3. Cunningham, W.P. and Cunningham, M.A. “Principles of Environmental Science”. 2004.TATA McGraw- Hill Publishing Company Limited.
4. Krebs.C.J. “Ecology. The experimental analysis of distribution and abundance”, 1985. Harper Collins Publishers.
5. Miller, Jr. G.T. “Environmental Science, Working with the earth”2004.Thomson Asia Pte Ltd., Singapore.
6. Odum, E.P. “Basic Ecology”, 1983.Saunders College Publishing, Holt-Saunders Japan.
7. Pianka. E.R. “Evolutionary Ecology”. 1983. Harper and Row Publishers, New York.
8. Ricklefs. R.E. 2000. G.L. Miller, W.H. Freeman and Company.
9. Smith. R.L.”Ecology and Field Biology, 1996. Harper Collins Publishers”.
10. Southwick, C.H. “Ecology and the quality of our environment.”1976. D. Van Nostrand Company.