UNIT 13 SPECIATION

Structure

1 31 INTRODUCTION

In Unit 11 and 12 of the course on Evolution we explained to you that adaptations arise by gradual changes in genotypes, monitored by natural selection. We also pointed out that natural selection promotes different types of adaptations in different environmental conditions. Since environmental conditions tend to change from time to time, and from place to place, it is obvious that changes in genome also occur so that resulting phenotype is best adapted to the changed environment. Essentially the diversity of organisms and their characters are a result of natural processes. In this unit we extend this concept further and explain the origin of species. Also we shall ask the question 'What is species?' Species, as we shall show later are important that they represent a significant level of integration in living nature. We shall define the concept of biological species and then look into the process of speciation. Speciation is important in evolution because it adds to the diversity in nature, and in certain occcasions leads to progressive evolution.

Ernst Mayr, for whom, species and species problem have been the main concern of research, points out that speciation, the multiplication of species, that is division of one parent species into several daughter species is one process responsible for the evolutionary diversity of organic world. Darwin no where in his book ***Origin of*** Species defined the word species precisely although he interpreted speciation in terms of reproductive isolation (Darwin again did not use the term reproductive isolation in his book.) Darwin did emphasise that occupation of an unique ecological niche by each species could be a major characteristic of speciation. In this unit we shall briefly analyse the species concept laying emphasis on biological species and discuss in detail different types of mechanisms of speciation. Further we shall briefly look into how isolation brings about genetic repatterning and proceed to discuss the mechanisms of isolation with well chosen examples. As an illustration of how isolating mechanisms develop gradually, we shall explain the concept of ring species — the evolution of distinct new species. Finally there will also be a discussion on a phenomenon called genetic drift which however has no causal connection with speciation process but explains that in peripheral isolates gene frequencies drift due to smapling error.

Objectives

This unit should enable you to:

- comprehend the species concept and define species,
- describe the major types of speciation,
- explain the formation of ring species by the gradual development of isolating mechanism,
- explain the concept of-genetic repatterning during isolation process,
- classify different types of isolating mechanisms, and
- discuss large scale change in gene frequencies in small populations — the genetic drift phenomenon.

13.2 CONCEPT OF SPECIES

We discussed in Unit 11 of Block **3** the universality of variations among organisms. In Unit **3** of Block **1,** in taxonomical studies you have studied about the division of living organisms into different kingdoms. Also each kingdom is further divided into phylum, class and so on. Such classifications are made taking advantage of variations among different groups of organisms, although as we go down the ladder, that is at lower levels we require more refined methods to establish variations. Starting from microorganisms to man, although one could see an increasing complexity in organisation, such a complexity is not a continuous one. The discontinuities in organisation are illustrative of extinction of certain intermediates. And considering the fact that amount of extinction is so immense and the fossil record is so incomplete that it would never be possible to arrange all the organisms that live in this world into a single assemblage. At the same time we should remember that a classification of organisms is possible because discontinuities do exist between varying groups of organisms. There might be some differences of opinion as to the inclusion of a particular organism(s) into one group or another, but there is an overall agreemenl on the entire classification system. One may split an order into several families and the other may group these families into an order. But there is indeed an agreement on what should be split and what should be grouped. But such a taxonomic classification of organisms into specific groups is arbitrary rather than natural and is based on certain.convenience. If this is so, then what is a species?

Many definitions of species have been offered, but none of them proved to be satisfactory. The definitions did not categorically provide the basis to decide whether two similar groups are distinct species or only sub-species. Again what is the criterion to decide the distinctness of a species? Some tried to specify the degree of difference that would distinguish a species from another. Apart from the difficulty in quantifying such differences, there are also other problems. Certain forms which show very little morphological differences proved to be very distinct species. In other cases, such as ***Homo sapiens,*** undoubtedly a single species, different races have pronounced differences. The discontinuity between groups, it appears, depends less on the degree of differences and more on the constancy of differences.

Another approach to define species was to distinguish related organisms on their inability to breed. Many definitions of species have relied upon such interspecific sterility and sterility of offsprings, that is hybrid sterility. This proposition also has certain inherent problems. It is not easy to identify cases in which organisms do not interbreed, and those which can breed, but do not do so for certain reasons. At these times, sterility cannot be deemed to be an appiopriatc criterion for defining species. Nevertheless, reproductive isolation or inability to breed has been the common element in the definition of species provided by many evolutionary biologists, be it Dobzhansky, Goldschmidt or Ernst Mayr. Reproductive isolation, the discussion of which follows later in this unit, has been the basis for defining the species and speciation.' Such an isolating mechanism becomes a barrier for the flow of genes between related populations and the concept of biological species centres around this phenomenon.

More specifically, three types of species concept have been proposed so far. (1) The typological species concept (2) The nominalistic species concept and **(3)** The biological species concept. Let us briefly look into each one of them and find out why the biological species concept is more appealing for the definition of species than the other concepts.

1. The Typological **Species Concept**

The typological species concept was suggested by Plato more than 2000 years ago. According to this concept, the immense variety in nature can be reduced to a few "types". Individuals may vary but they belong to a single type. In practice this is just a morphological species concept. Most modern evolutionists find the typological species inadequate as it is a static concept. It fails to capture the dynamism of speciation as a significant evolutionary process. .

2. The Nominalistic **Species** Concept

The nominalists deny the existence of Plato's "types". For them only individuals exist. Species are man-made artificial abstractions.

But naturalists, the biologists who have actually studied plants and animals in their **natural conditions** and have observed them closely for many years, claim that the nominalistic species concept is simply not true.

3. The Biological Species Concept

The **biological** species concept claims that species consist of natural populations and that species are real and objective. They are not man-made subjective abstraction. According to this concept, the members of a species are a reproductive community. The species is also an ecological unit. It interacts as a unit with other species with which it shares the resources of the environment. The species is also a gene pool. These aspects of the biological species concept are made clear in the famous definition of the Harvard evolutionist **Ernst** Mayr. According to Mayr, "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups". The biological species is not only a distinct unit at any given time, but it also has the evolutionary capacity to change continuously over long periods of time, measured in millions of years.

SAQ 1

State whether the following statements are **true** or false.

i) The discontinuity between groups of organisms depends less on the degree of difference and more on the constancy of differences. (True/False)

ii) Reproductive isolating mechanism has been the basis for defining the species and speciation. (True/False)

iii) The typological species concept is most sound and dynamic concept of speciation. (True/False)

iv) Species are groups of interbreeding natural propulations that are reproductively isolated from other such groups. (True/False)

13.3 MECHANISMS OF SPECIATION

In the previous section we discussed the concept of species in detail and concluded that the concept of biological species and **Mayr's** definition of species have a wide acceptance among biologists. In this section we shall proceed to discuss the mechanisms of speciation or the mode of formation of a species. Mayr's definition of species amply makes it clear that to qualify for the title of the species, the individuals must be reproductively isolated from other groups. This naturally raises a question whether a new species **could** arise from populations occupying the same territory. In other words, should the populations of parent species live in quite separate territories in the formation of new species? In our earlier discussions.on natural selection, you have learnt that **origin of** adaptations is a gradual process, This is much more true of speciation. Biologists **recognise** three different kinds of speciation.

- **Sympatric** speciation,,+
- **Peripatric** speciation
- **Allopatric** speciation..

As we shall see later, peripatric and allopatric speciation can be grouped into a single type, namely ***geographic speciation.*** We shall now discuss the different types of speciation.

13.3.1 Sympatric Speciation

Sympatric speciation can be regarded as speciation where parent species gives rise to a daughter species without the individuals of a species being separated by space or territory. Both instantaneous and gradual models of sympatric speciation have been proposed. Barring one mode of instantaneous speciation by a mechanism known as polyploidy, other modes of sympatric speciation have remained quite controversial.

Polyploidy is quite common among plants. (For a detailed discussion on polyploidy refer to Unit 10 of Block 2 of LSE-03 of Genetics course). A cross between two diploid plants could result in a tetraploid hybrid. The hybrid would remain largely reproductively isolated from its diploid parents. The reason for such isolation is that due to back-crossing if a triploid individual were to be formed, it will produce a high proportion of nonviable gametes. There is also a possibility that interbreeding between deploid and tetraploid forms or between different tetraploids may give rise to other polyploids.

Polyploidy is rare or virtually non-existent in sexually reproducing organisms which include almost all animals. In sexually reproducing organisms, if a single mutational event or chromosomal change such as polyploidy results in reproductive isolation, the organism will not successfully reproduce unless there is close inbreeding. Among animals, close inbreeding is quite uncommon. But in a group of hymenopterous parasites chalcidoidea, there is mating between brothers and sisters that emerge from a single host. Such matings have facilitated a high species diversity in this group. But instances of instantaneous speciation in animals is a very rare phenomenon. Speciation in general is a gradual process and whether or not such speciation can occur within the confines of a single interbreeding population is a debatable point. Nevertheless, the possibility of such a speciation is not totally ruled out, as we would see from the following discussion.

It has been pointed out that sympatric speciation may occur whenever disruptive or diversifying selection is active (For a detailed discussion on disruptive selection refer to Unit 11 of Block 3 of Evolution). For example, take a population of individuals with genotypes AA and A'A', each of which is adapted to live specifically on plant species 1 and 2 respectively. The heterozygote AA' is not well adapted to either species of plants. Essentially it means that each homozygote would have a higher fitness if it mated assortatively or non-randomly. By assortative or non-random mating it is meant that males and females of similar phenotypes (hence genotypes) tend to mate with each other. Such an assortative mating would very much minimise the production of unfit heterozygous progeny. Also the selection process would tend to establish two different populations, each composed of a distinct genotype. You may recall from your studies on Unit 11 that this is precisely the role of disruptive or diversifying selection. Another locus B may be conferrring the assortative mating trait on the two genotypes. This locus may influence the mating behaviour or impel the organism to choose a specific host species, to find a mate and lay eggs. Genotypes BB and Bb may mate and lay egg on host 1 and bb mates and lays eggs on host 2. You may observe here that difference in the selection of specific host species isolates the two genotypes from one another and a reproductive isolation sets in. In many groups of phytophygous insects such as treehoppers, it is observed that closely related species are confined to different host plants for feeding and breeding.

13.3.2 Geographic Speciation

In almost all animal groups, the mode of speciation is geographic speciation. It is essential that a population which is a prospective new species is geographically isolated from the parental species. Geographical isolation, according to Ernst Mayr, is almost invariably necessary for speciation to occur. Geographic speciation, as we pointed out earlier, in turn can be typed into two categories:

i) 'Allopatric Speciation

Speciation by populations of parent species which occupy quite separate territories is the most common mode of species formation among animals. Allopatric speciation occurs in large continental areas, and perhaps, also in the vast continental slopes and ocean floors. A once continuous series of population may be divided into two parts by a new barrier. The barrier may be a newly formed desert or river or mountain range. The population on other side of new barrier becomes geographically isolated. The separation may be gradual as shown in Fig. 13.1. This model of allopatric speciation is known as dumb-bell model.

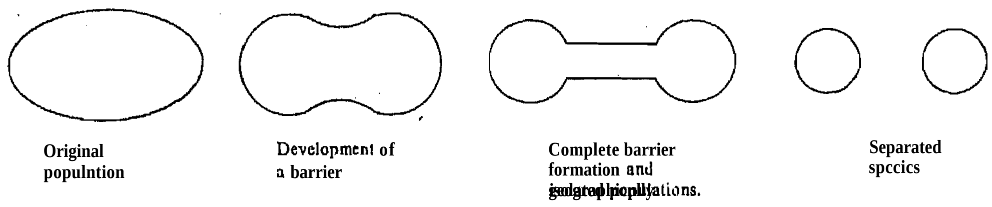

Fig. 13.1 : Illustration of allopatric speciation.

Essentially in allopatric system, speciation occurs by the more or less equal subdivision of a large population. It is believed that allopatric speciation is characteristic of K strategists (see marginal remarks on K strategy) which are highly mobile, long lived and high in competitive ability.

K strategy : Populations living in nearly saturated environments are said to be K selected. In such populations selection favours the fine tuning of adaptations. The reproductive rate of the population may not be high and the emphasis is on developing better adaptations. Individuals on which K selection is active are known as K strategists.

ii) Peripatric Speciation

Speciation by small populations isolated on the periphery of the distribution of the parent population can be described as peripatric speciation. Small, peripheral populations occupy ecological niches not occupied by parental population and these founder populations can carry only a small part of the genetic variability of the parent population. Origin of species by peripatric speciation can be explained as follows:

Initially species consists of uniformly distributed individuals (Fig. 13.2a). The individuals are grouped as populations between which there is a limited gene flow. This gene flow keeps the populations as an integrated species. As long as there is a free flow of genes, even if it were to be limited, a new species cannot be formed.

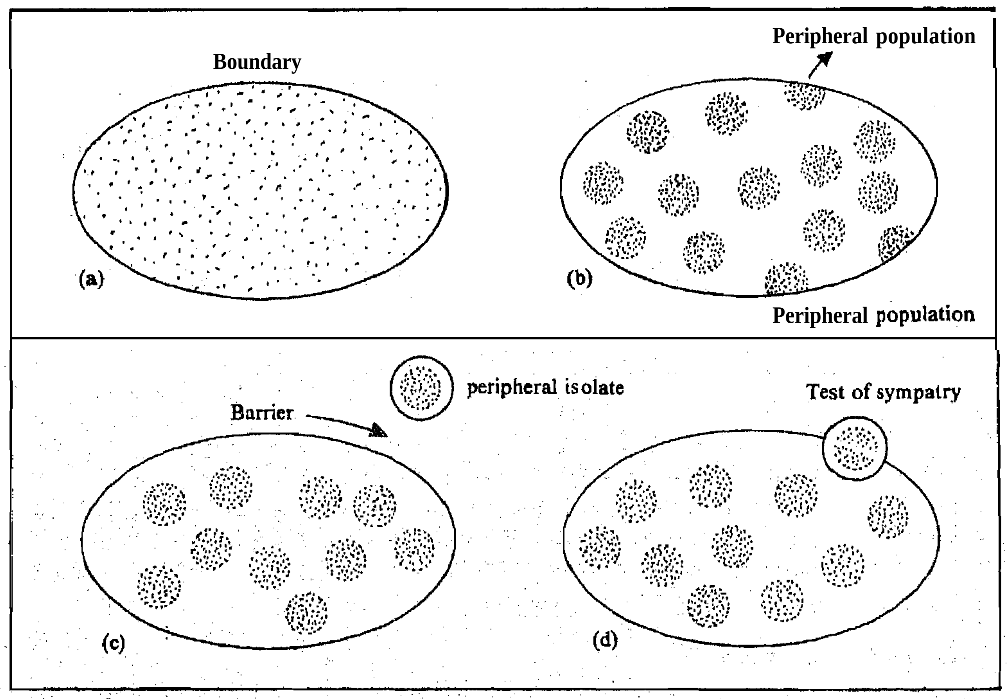

Fig. 13.2 : Illustration of peripatric speciation

Peripheral populations (13:2b) (individuals living in the periphery of a population) may experience less gene flow than central populations. But still they will form an integral part of the species. Only when the population is a peripheral isolate (13.2c) and not just a peripheral population, that it has the possibility of becoming a new species (13.2d).

A peripheral isolate can be formed in different environments. For instance it may be formed on an island off the coast of a large subcontinent. The finches that Darwin observed during his voyage on the ship H.M.S. Beagle were evolved from peripheral isolates on the Galapagos island, off the west coast of South America.

Before we start discussing in detail the various mechanisms of isolation that in turn were instrumental for the formation of a new species, we shall look into two concepts: (1) The concept of ring species — an example which shows beautifully how isolation of population develops gradually resulting in distinct new species, and (2) the concept of genetic repatterning during isolation. And prior to that, attempt the following SAQs.

SAQ 2

Fill in the blanks with suitable words from the text.

i) To qualify for the title of species the individual must be .... from other groups.

ii) .... refers to the speciation process where the individuals of a species are not separated by space or territory.

iii) .... is a common mechanism of speciation in plants.

iv) Sympatric speciation may occur wherever .... is active.

v) It is essential that a population which is a prospective new species is .... from the parental species.

vi) .... speciation refers to speciation by populations of parent species which occupy quite separate territories.

vii) Speciation by small populations isolated on the periphery of the distribution of parent population is ....

13.4 RASSENKREIS AND SPECIATION

According to the current concept of speciation, a widely distributed species should break up into partially isolated rule species. The different subspecies become differentiated further due to the action of selection and other factors. This would result in a circle or group of races or Rassenkreis. And the terminal members of such a circle will be sufficiently different from others, so that a sterility barrier sets in. We shall try to explain the concept with an example of an amphibian species.

In the west coast of USA there are two high mountain ranges, the Coastal Range and the Sierra Nevada. At their northern ends, near the Canadian border they are united (Fig. 13.3). Proceeding south, they are separated by a hot and arid desert, Further south, close to the Mexican border, these high mountains meet again. There is an amphibian species ***Ensatina eschscholtzii*** at the place marked as A in Fig. 13.3, It is supposed that this original species split into two populations, B and G, which then moved down the two respective mountain ranges. On one range the populations can be seen to change gradually from B to C to D to E and on to F. On the other mountain range the population G, like B derived from A, gradually moved south changing into H, I, J and K. While these changes were taking place the two series were isolated from each other by the desert, and isolating mechanisms were gradually developing. Since this amphibian ***Ensatina*** has poor locomotor powers, it must have taken hundreds of thousands of years for them to proceed from the Canadian border to the Mexican border. It stands to reason that populations B and G will have the least amount of isolating mechanisms. The isolating mechanisms will be more between D and I. They will be greater between E and J. Remember, both the series, BCDE and GHIJ, are derived from a single species, ***Ensatina eschscholtzii***, designated in Fig. 13.3 as A. But when they reach the Mexican border, the two populations F and K are able to overlap, as seen in the cross-hatched area, without mating. **They** have passed the test of sympatry. F and K are now two distinct species. Similar ring species have been shown to occur in sea-gulls forming a circumpolar ring around the world.

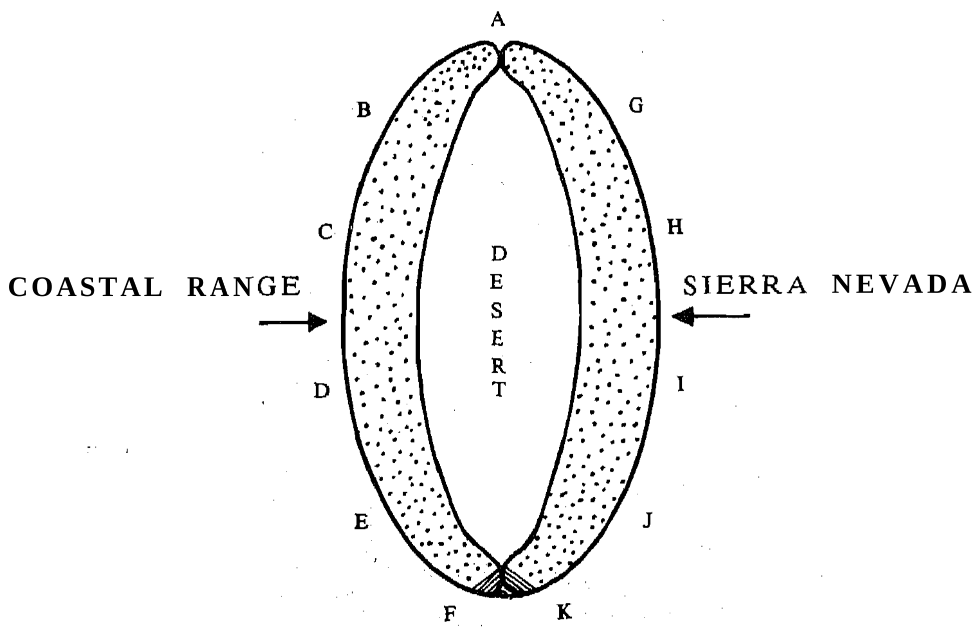

Fig. 13.3 : Formation of ring species.

13.5 GENETIC REPATTERNING DURING ISOLATION

An island may be colonised by just a few individuals, or just a pair:, or even a single gravid female. When a new population develops from these early colonisers of the island, they undergo drastic genetic repatterning. This is sometimes described as a genetic revolution. The founder being small in number, the first major change in the colonisers is a drastic reduction in the variability (Fig. 13.4 A to B).. Inbreeding further reduces variability (Fig. 13.4 C). Inbreeding eliminates recessives as homozygotes and the genetic load is reduced. The decisive change is from **a** large open population to a small closed population. In the closed population, overdominance, that is the superior fitness of the heterozygote (say, Aa) over the other two homozygotes (AA and aa), increases. Non-allelic epistatic interactions of genes greatly alter the functioning of the gene complexes. As a result the genetic cohesiveness is broken and the founder population becomes plastic and pliable enough to be moulded into a newer one with better adaptations. This, in essence, is the genetic repatterning or the genetic revolution.

The founder population, the peripheral isolate, usually becomes extinct due to the greatly reduced variability (Fig. 13.4 C) However, if it survives the genetic revolution, the population builds up to greater variability and better adaptedness (Fig, 13.4D). It may even acquire greater variability than the original parental population and stabilise at a higher level of genetic cohesion as a new species" **(Fig.** 13.4E). This status of a new species, distinct from the parental species is made possible by the development of isolating mechanisms during the genetic revolution

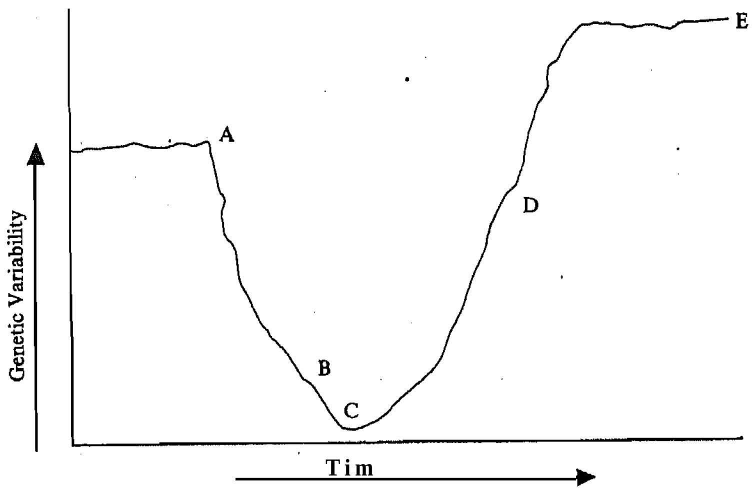

Fig. 13.4 : Genetic revolution.

SAQ 3

Answer in about 50 words each.

i) Explain briefly the term ring species.

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ii) Explain the concept of genetic repatterning during isolation.

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13.6 ISOLATING MECHANISMS

In this section we are to discuss the means by which populations get separated or isolated from each other, first gain the status of sub-species and finally evolve mechanisms which prevent them from mating with local populations to be called as a distinct species. In short, we are to discuss the mechanisms that are responsible for keeping populations from the access of each other that in turn leads to origin of new species. You are aware that local populations generally interbreed among themselves with only rare cases of outbreeding. Therefore, the genotypes of different populations of a single species may show differences in some or many loci. The resulting phenotypes could be classified into sub-species based on the differences in parts. These subspecies because of their proximity to other populations tend to meet the other members with the result that a single generally intermediate and variable population is formed. This would result in the loss of the status of subspecies for the population. However, if a sub-species is isolated over a long period of time and the breeding with its relations is prevented, then by continuing to accumulate the genetic differences it may lose its ability to interbreed with the parental species. Under such circumstances, the sub-species gets elevated to the status of a species, satisfying Mayr's definition of a species. When two groups are geographically separated from each other, it is often difficult to determine whether they do not interbreed any more. In other words, could they be referred to as allopatric species? Once they move into the same territory, fail to interbreed and form intermediates, they may said to have passed the test of sympatry or they could be regarded as sympatric species. In many cases it has been noticed that once the species status has been established, selection tends to promote those characters which act as a deterrent for the formation of hybrids, since usually hybrid progeny have a reduced fitness.

George Romanes, an American neurologist who evinced a very keen interest in evolutionary problems once wrote, "without isolation or the prevention of interbreeding, organic evolution is in no case possible". Many recent studies on origin of new species have proved that Romanes was largely true in his assessment of the problem. Let us now look into the details of mechanisms of isolation.

Ernst Mayr classified isolating mechanisms into two major types. The ***pre-mating isolating mechanisms*** and ***the post-mating ones.*** The difference between the two types of mechanisms is as follows. Pre-mating isolating mechanisms prevent the occurrence of mating and the post-mating ones ensure failure of such matings once they occur. In the discussion on pre-mating isolating mechanisms, besides the biological barriers evolved by the organisms which prevent effectively mating between the individuals, isolation by space will also be included. We shall also examine how the ecology, seasons and even the behaviour of individuals could be instrumental in bringing about the isolation of populations leading to species formation. We shall also look into the details of post-mating isolating mechanisms which prevent the formation of successful hybrids, thereby ensuring the distinctness and identity of a species.

13.7 PRE-MATING ISOLATING MECHANISMS

We mentioned earlier that pre-mating mechanisms are concerned with the prevention of occurrence of interspecific crosses. In such cases,

a) the potential mates do not meet in which case the isolation is due to either geographical, seasonal or habitat reasons.

b) the potential mates do meet but fail to mate in which case the isolation is due to ethological reasons.

c) the potential mates meet and mate but no transfer of sperm takes place in which case the isolation is due to mechanical reasons.

Let us have each one of these mechanisms examined in detail.

13.7.1 Geographical Isolation

Many species of organisms are restricted in their distribution even as they may be found over a vast geographical regions. Studies using distribution maps of organisms have shown that although species may be continuously found over vast areas, a close scrutiny would reveal that the distribution is rather restricted to those regions with suitable ecological features. For instance, the American plane tree, ***Platanus occidentalis*** although distributed over more than half the United States, the natural groves of the plants are confined to bottom lands and stream banks. This is true of several species of organisms whose populations are separated by barriers of territory which they cannot use for ecological reasons. For instance, take the case of amphibians. A small body of salt water could be a barrier for their dispersal. Oceanic islands are not inhabited by amphibians except as in the case of Hawaii where they are introduced by man. Salt water is also a barrier for fresh water fishes. Pacificocean receives many parallel streams of fresh water each of which had its own sub-species or species of fishes. Only the flooding during the rainy season join the streams and the fishes may be found together.

Similarly populations of land birds are separated by large bodies of water. Normally species and sub-species of birds living on opposite banks of rivers are different. Mayr observed that different sub-species of birds occupy different tropical islands despite that distances between these islands are not very far. Darwin reported that 21 of the 26 species of land birds and only 2 of the 11 species of marine birds are endemic to Galapagos islands. This is a significant finding in that the land birds could not migrate to either direction because of the water barrier and were confined to their territories. More than the birds, it is the mammals which are often stopped by water barriers. Rodents living in opposite banks of rivers usually belong to different sub-species.

Mountains often separate organisms occupying low lands. Studies on the distribution of different species of rabbits showed their restricted distribution to specific geographical regions. *Sylvilagus floridanus* confines itself to planes while its cousin the jack rabbit *Lepus americanus* is found only in mountains in United States. Similarly the white footed mouse *Peromyscus leucopus* is found in priaries and its close relative *P. maniculatus* has invaded the mountains. Thus every natural feature could be a barrier to either a plant or an animal paving the way for sub-speciation and ultimately the speciation process.

13.7.2 Ecological Isolation

Ecological isolation is based on the fact that population shows preference to one habitat over the other. This extensive forests become barriers to the dispersal of organims living in grasslands. The reverse that priaries being barriers to forest organisms is also true. The red tree *mousephenocomys longicaudus* lives on fir needle trees and feeds on fir needle. It is understandable that for these mice not only priaries but the non-fir forests will also be a barrier for dispersal.

You may recall that in unit 11 of this block we discussed extensively MacArthur's study of five species of warbler birds living in spruce trees. The five species of *Dendroica* are effectively isolated by ecological factors although they have a similar distribution. As a matter of fact, the ecological and food preference of the different species of warblers are very similar. Under such circumstances one would have expected a severe competition among them. But each species has carved a well defined niche and forages at a particular level in the trees. Differences in breeding dates and occupation of different habitats outside the breeding season are the contributing factors for the minimum competition and niche overlap among the species. There are other instances where potential mates keep away from each other because of their habitat preferences. In these cases there might even be a broad niche overlap and the individuals may exist in the same general area, but the distinctness of sub-species and species is maintained. Dice cited an example from United States where the two sub-species of mice *Peromyscus maniculatus* have overlapping niches and do not interbreed in nature, although there is interbreeding in the laboratory. Similarly another study showed that the fresh water and salt water races of the water snake *Natrix sipedon* may come close together but may not interbreed because of their habitat preferences.

An interesting study was reported by A. Pictet in Swiss moths *Nemeophila plantaginis.* Two races of the moth are known, one living at an altitude of above 2700 meters and the other below 1700 meters, The two races differ by a single gene. Midway at an altitude of 2200 meters a hybrid population of the two races is found and all the moths living here are heterozygous. When the two races are brought to the laboratory and bred, the offsprings exhibit typical Mendelian inheritance, namely that the F_2 consisted of both homozygotes and the heterozygote. The fact that at 2200 meters only heterozygous genotypes are found showed that there is a severe selection pressure against the homozygotes at this altitude and they are all eliminated. You may. observe here that differences in habitat requirements act as barriers to random mating.

Breeding between populations or races or sub-species may be effectively prevented if the seasons in which they breed are to be different. This phenomenon appears to be quite common among plants. **A** good example comes from the study of five species of cypress trees belonging to the genes *Cupressus*. The five species of trees have distributed themselves as ten groups each one of which could be called a sub-species. Each group has a limited distribution and may be represented by a few trees. Very rarely hybrids are formed between any two groups despite'the closeness of their existence. The reason appears to be that the groups shed their pollen at different times or seasons preventing the occurrence of cross pollination. The rare occurrence of hybrids is explained by the fact that some trees shed their pollen earlier than or later than the usual time.

Seasonal isolation is very effective among the animal groups which have **a** highly restricted breeding seasons. This is true of all poikilothermic vertebrates and invertebrates. A revealing example comes from the study of three species of frogs living and breeding in the same pond in north eastern United States. The three species R. *clamitans,* R. ***pipiens*** and *R. sylvatica* have staggered breeding seasons. R. *sylvatica* completes breeding before others arrive at the pond and R. *clamitans* begins breeding only when all others have completed. The breeding time of each species appears to be determined by the temperature of the waters of the pond which they occupy. The following table gives you temperature of the water at which the frogs begin their breeding.

Species of frog	*Water temperature at which breeding commences*
Rana sylvatica	44°F
R. pipiens	55°F
R. clamitans	>60°F

Further each species has developed specific and elaborate mating call and this again prevents breeding between syrnpatric forms. Finally even if mating takes place between species, the development fails beyond the embryonic stage. Thus the seasonal isolation has led to sterility barrier and the three species have no chance of forming.hybrids.

13.7.3 Ethological Isolation

Members belonging to different species refrain from mating because of the behavioural differences between them. Such behavioural differences usually centre around specific courtship patterns which the species have evolved. The behaviour patterns are more conspicuous in animals rather than in plants. And among animals, once again, the courtship behaviour is more pronounced among terrestrial and fresh water organisms than in marine forms. Mayr points out that in those forms where there is an elaborate courtship behaviour the interspecific hybrids are rare. Closely related species that do not have pair-binding courtship rituals do commonly give rise to hybrids. Mayr is of the opinion that in species where there is a courtship behaviour pattern, the "engagement" may be broken if the pairs do not belong to the same species,

A detailed study of the courtship behaviour of six species of Drosophila showed that courtship and mating could be divided into six phases. If there is incompatibility at any one of these six phases, the potential mates break off and the courtship is discontinued. Under laboratory conditions, the interspecific crosses have not been successful and the courtship was terminated even in the first stage. What is more interesting here is that even to a trained observer differences in courtship behaviour exhibited by different species may appear to be trivial and insignificant. But the species **recognise** the specific signals and respond suitably. In certain other forms differences in courtship behaviour between species could be very pronounced, The courtship dances of **the** different species of Uca (shore crab) could be recognised from a distance. This is also true of mating dances of salamanders, turtles and birds.

Earlier it appeared that *Rana* ***pipiens*** consisted of a single species. This assumption was based on morphological considerations. But today researches have shown that there are a number of species and the frogs have no difficulty in recognising their own species. Both the frogs and researchers could distinguish the characteristic mating song of each species. Some species of birds which show only minor morphological differences can be easily differentiated by their songs.

Apart from the species specific dances and songs evolved by organisms to attract their mates, specific scents are produced by certain organisms for purposes of species recognition. These scents, otherwise known as pheromones have been proved to elicit selective response from males when left with females of two closely related species in the same area. A study by B. Patterson in Scandinavian valley has shown that nearly thirty seven species of moths belonging to a single genus live together without any interbreeding among them. The author has concluded that despite all minor morphological differences among the species, conspecific matings are assured because of the specific scent produced by each species. Essentially the above account tells you that specific behaviour patterns play a vital role in species recognition and serve as a powerful isolating mechanism.

13.7.4 Mechanical Isolation

In certain instances differences in the morphology of genitalia between species make it impossible for normal mating to occur, and sympatric species tend to remain isolated. When there is no correspondence between the male and female external genitalia for copulation to occur, the members belonging to different species are reproductively isolated. When interspecific crosses occur between individuals having no exact correspondence in their genitalia, it resulted in the death of copulating pairs. Insects and snails are usually quoted as examples of such fatal rnatings which occur "due to mechanical differences in their genitalia. It must alao be stated that differences in copulatory organs, in many instances, have not proved to be a barrier for ihterbreeding. Breeding between dogs belonging to different races is an often cited example.

Mechanical isolation appears to play a more important role in the speciation of plants. Since many plants are aided by insects and birds in cross pollination, a morphological compatibility is required between the plants and the pollinating agents. You may recall the example that has been cited in unit 11 in which the flowers of different species of **Pedicularis** plant are pollinated differently by bumble bees. Further, queen bees with their long mouth parts pollinate the nector producing species of **Pedicularis** and the other species of the plants are pollinated sternotribically or nototribically.

13.8 POST-MATING ISOLATING MECHANISMS

The second category of isolating mechanism that may permit interspecific mating but ensures reduced viability is called post-mating isolating mechanism. This category could be subdivided into two types.

- **Interspecific steiility :** Organisms belonging to different species may mate, but may not produce any offspring.
- **Hybrid sterility :** Here the interspecific cross may result in an F_1 offspring but the offspring is invariably sterile.

We shall now briefly look into each one of these sterility mechanisms with plant and animal examples.

13.8.1 Interspecific Sterility

In interspecific sterility, the failure in mating occurs because of inability of the sperm to reach the egg in animals and the pollen to reach ovules in plants. In plants interspecific crosses usually result in the non-growing of the pollen tubes or the slowing down of the growth. If pollen from another species is transferred to a plant along with the pollen from conspecific individuals, the growth of the pollen tube of the latter is much faster than the former and all the fertilisation is conspecific.

In certain cases of interspecific crosses the pollen tube begins to grow but then bursts ensuring that no fertilisation occurs. Such an event occurs when the chromosome number of the male parent is higher than female parent. For instance, three specie: of tobacco plants are known to occur: ***Nicotiana tabacum, N. sylvestris*** and ***N. tomentosa.*** N, *tabacum* has ***48*** chromosomes and the other two species have 24 each. Probably N. ***tabacum*** is a tetraploid produced by a cross between the other two species. A cross between either of the two species and N. ***tabacum*** is successful only if the latter is used as a female parent. In such a cross the style tissues have 48 chromosomes and the pollen tube has only 12 chromosome, giving a ratio of 4:1. When the cross is between N. *sylvestris* and ***N. tomentosa,*** the style tissue of both the species has 24 chromosomes and the pollen tube has 12 chromosomes giving a 2:1 ratio. But if ***N. tabacum*** were to be a male parent, and the either of the other two species a female, then the style tissue has 24 chromosomes and the pollen tube has 24 chromosomes giving 1:1 ratio. It is only under these circumstances, that is when the ratio is close to 1:1 the bursting of pollen tube occurs. It is assumed that a high osmotic pressure in the pollen tube causes it to burst and that this trait is controlled by a gene. Essentially a genetically coupled physiological mechanism prevents interspecific crosses in the tobacco plant.

There are other instances where a zygote may be formed but its further development may not occur beyond a stage. Thus in interspecific crosses of jimson weed plant, the embryo dies around the eight cell stage. In the case of hybrid plants, it is believed that there is an inadequate nutritional relationship between the developing embryos and the endosperm resulting in the death of the embryos.

The genetic basis of interspecific sterility is not clearly understood in many cases. Yet, one good example comes from studies on the tropical fish of the genus ***Xiphophorus.*** X. *maculatus* (moon fish) carries a dominant gene (Sd) responsible for a dark spot on its dorsal fin. The gene produces macromelanophores which are potential tumors. In a closely related species X.***helleri*** (swordtail), the gene occurs in recesive form (sd). A cross between the two species produced fertile F_1 offspring. The hybrid offspring has the heterozygous genotype Sdsd and in such a condition the fins are more heavily pigmented than the homozygous (SdSd) genotype. The Sdsd progeny always have lethal tumors. A backcross of Sdsd fish with the recessive genotype (sdsd) have shown that half the progeny have lethal genotype (Sdsd). Thus in ***Xiphophorus*** interspecific sterility manifests in the form of production of offsprings with lethal genes in them.

13.8.2 Hybrid Sterility

Hybrid sterility can be regarded as yet another form of interspecific sterility. The offspring of the interspecific crosses are mainly sterile. Geological studies have shown that the chromosomes of the hybrid individuals fail to synapse at the time of meiosis and thus result in either non-production of gametes or defective gametes. Unless the chromosomes of parents are accurately separated which might result in viable gametes,, in most cases the gametes are not produced and if produced they may not be fertile. The commonly cited example is the mule, a sterile animal the product of a cross between a donkey and a horse. Further, the hybrid species in general are found to have grossly abnormal reproductive system. If normal reproductive system is present, then meiosis is abnormal and non-viable gametes are produced.

Thus various types of reproductive isolating mechanisms are at work in different groups of organisms to maintain the distinctness and uniqueness of species.

SAQ 4

1) Match the following:

Column1	Column II
a) Non-meeting of the potential mates	i) Ethological isolation
b) Potential mates do meet but fail to mate	ii) Mechanical isolation
c) Potential mates meet and mate but no transfer of sperms	iii) Geographical, seasonal or habitat isolation

2) Answer in about 50 words each.

a) Explain the concept of geographical isolation with suitable examples.

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b) How does habitat preference of organisms promote speciation process?

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c) Cite an example to show that highly restricted breeding seasons of populations contribute to isolation process.

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d) Discuss the role played by courtship behaviour and scents in the isolation process.

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e) Distinguish the terms interspecific sterility and hybrid sterility.

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13.9 GENETIC DRIFT

In this section we shall be discussing a phenomenon associated with small populations. You may recall from your studies in Genetics (LSE-03, Block 4, Unit 2) that in large populations the frequencies of alleles lend to remain constant generation after generation provided the populations do not experience any mutation, genetic recombination, gene migration and selection. You may further recall that this phenomenon is known as Hardy-Weinburg equilibrium. But evolution essentially depends on changing gene frequencies. In the unit on 'Behaviour of Genes in Populations' in Block 4 of LSE-03 Course, you may find illustrations of how gene frequencies are altered in natural populations by factors such as mutations and natural selection. Such factors although they affect gene frequencies, do it in a small way. But genetic drift is a phenomenon that causes a large change or a drift in the frequencies of genes in small populations. The phenomenon was first investigated by the American population geneticist Sewall Wright and therefore is also known as Sewall Wright effect.

It is generally believed that genetic drift occurs as a result of sampling error. As we said earlier it occurs in small populations such as peripheral isolates. We may demonstrate genetic drift by a small experiment. Take beads of same size but different colours, say blue, red, green and yellow. Take a thousand of each colour and mix them well in a bag or mug. The 4000 beads now constitute a population. Now put your hand in without looking, pick up just four beads with your finger tips. Let us say that you get two blues, one red and one green. This will mean that the blues have increased from 25% to 50% but the yellows are reduced to zero. You could see that the random drifting or large scale changes in the frequencies of coloured beads is a result of sampling error. Just as the frequencies of coloured beads drift randomly in the experiment, in small populations or peripheral isolates gene frequencies may drift due to sampling error. Hence the phenomenon is known as genetic drift.

Can such drift be observed in natural populations? The answer appears to be yes. Let us take a small population of mice living in the rice barn of a farmer as four or five extended families. The farmer tries a variety of methods like setting up of traps, use of a shot gun, surprise visits, cats etc. to eradicate them. Such acts of the farmer exert a severe selection pressure on the mice. Under such circumstances the trails that would be selected are the swiftness, short tail, hearing acuity, cautiousness etc. Naturally the frequencies of the alleles that control thcsc traits would tend to be high in the population as only those mice which possess such traits can survive in an hostile environment. After a couple of months, let us say there is an environmental change and a severe winter sets in. The farmer confines himself to a fire place and as a result the selection pressure on those traits we mentioned earlier is now lifted. And in order to survive in a changed environment, the mice need to possess totally a different set of traits and essentially mice with such traits would be selected for. Thus swiftness and visual acuity are no more the trails that would be selected for, but the mice with a thick fur on them and similar such traits which would protect them from the severity of the winter would be selected. The net result is that the frequencies of the alleles that controlled the traits in the earlier environment undergo a drift — (i.e.) their frequencies become significantly low in the new environment. It should be emphasised that such a drift is characteristic of only small populations.

Sewall Wright suggested that genetic drift may have important consequences for evolution. At one time he even seemed to have suggested that, in special circumstances, genetic drift may override Darwinian natural selection. This view'was criticised by the Oxford biologists R.A. Fisher and E.B. Ford who showed that natural selection is the chief agent of evolutionary change not only in large and medium populations, but also in very small populations. E.B. Ford demonstrated the occurrence of wingspot polymorphism in small populations of Meadow Brown butterflies in the lsles of Scylly, at the South Western tip of England. For, where the polymorphism occurs, it is the surest indication that natural selection is operating at its highest potential. Sewall Wright also found such arguments to be true and has now modified his genetic drift theory into a more acceptable shifting balance theory.

SAQ 5

Fill in the blanks with appropriate words.

i) In large populations the factors which tend to alter the gene frequencies are ...., ..., ... and ...., ...

ii) .... that causes a large change in gene frequencies is characteristic of small populations.

iii) In small populations or peripheral isolates the genetic drift usually occurs because of ....

iv) The genetic drift is also come to be known as .... effect.

v) Sewell Wright has modified his genetic drift theory into .... theory.

13.10 SUMMARY

In this unit you have learnt:

- The concept of species and the definition that the species are a group of interbreeding natural populations that are reproductively isolated from other such groups. The biological species concept is more realistic than the typological or nominalistic species concept. It explains species as a distinct unit of time, with a capacity to change continuously over long periods of time. In short, species has an evolutionary capacity.
- The different modes of speciation. (a) The sympatric speciation refers to speciation among populations living together. (b) Allopatric speciation refers to speciation in populations separated by space and (c) Peripatric speciation refers to speciation of individuals isolated as a peripheral population.
- Concept of ring species in which a population becomes isolated, changes gradually, passes the test of sympatry and becomes a distinct species.
- The concept of genetic repatterning in which a new population develops from the early colonisers of the island by a process of genetic revolution. Reduction in variability, elimination of homozygote recessives by inbreeding process, overdominance resulting in heterozygote superiority and non-allelic epistatic interactions are sorne of the genetic events that break the genetic cohesiveness of populations. Such events render the founder population more plastic and pliable arid move it into a new species with better adaptations.
- The different types of isolating mechanisms—the geographical, ecological, mechanical, ethological and reproductive (both pre-mating and post-mating) all of which promote the formation and distinctness of species.
- That genetic drift is a process that may operate in small populations bringing about large scale changes in gene frequencies. Also known as Sewall Wright effect, in small populations the drift is due to sampling error.

13.1 TERMINAL QUESTIONS

1 Briefly comment on the three types of species concept.

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2) Distinguish the terms sympatric, peripatric and allopatric speciation.

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3) What do you understand by the term ring species? Illustrate your answer with suitable example.

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4) To what type of isolation the following barriers contribute to?
   a) Oceanic islands inhabited by amphibians ....
   b) Salt water as a barrier for fresh water organisms ....
   c) Large bodies of water as barrier for land birds ....
   d) Priaries as barrier for forest organisins ....
   e) Mountains as barriers for low land organisms ....
   f) Restricted breeding seasons ....
   g) Courtship patterns ....
   h) Specific mating calls ....
   i) Specific scents ....
   j) Distinct morphology of genitalia ....
   k) Hybrid sterility ....
   l) Higher chromosome number of male parent ....

5) In small populations the gene frequencies often tend to drift. Justify the logic of the statement with a suitable example.

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13.12 ANSWERS

Self-assessment Questions

1) i) T, iii) T, iii) F, iv) T.

2) **i)** Reproductively isolated
   ii) Sympatric speciation

iii) Polyploidy
iv) Disruptive selection
v) Geographically isolated
vi) Allopatric
vii) Peripatric speciation.

3) i) It is quite possible that the action of selection could differentiate the different sub-species further resulting in a circle or group of races. The terminal members of such a ring or circle sufficiently different from others evolve into a species — the ring species.

ii) When a new population develops from early colonisers of the islands they undergo a variety of genetic changes by way of reduced variability, elimination of recessive homozygotes, reduction in genetic load, superior fitness of heterozygotes and non-allelic epistatic interactions, all of which result in a genetic revolution or more precisely the genetic repattering.

4) i) a) iii), b) i), c) ii)

ii) a) The concept of geographical isolation refers to the restriction of organisms to certain specific geographical regions with suitable ecological features. For instance oceanic islands are not inhabited by amphibians. Pacific ocean receives many parallel streams of fresh water each of which has its own species or sub-species of fishes which live isolated.

b) Habitat preference do promote speciation process. In Swiss moth ***Nemeophila plantagenis*** the habitat preference of the two races appears to con'tribute to the speciation process. One race of the moth lives at an altitude of about 2700 meters and the other race below 1700 meters. Although the two races breed in the laboratory the hybrid population is confined at an altitude of 2200 meters.

c) The five species of cypress trees of the genus ***Cupressus*** are divided into 10 groups. Each one of these could be called as sub-species. Very rarely hybrids are formed between two groups although the groups live close enough. The reason appears to be that the groups shed their pollens at different times or season, preventing the occurrence of cross pollination.

d) Courtship behaviour patterns which are very specific for each species act as a deterrent for the members belonging to different species. Mayr opines that where there is courtship behaviour pattern the engagement may be broken if the pairs do not belong to the same species. Similarly specific scents produced by certain organisms to attract their mates help in the process of species recognition.

e) Interspecific sterility: Organisms belonging to two different species may mate but may not produce any offspring.

Hybrid sterility : The interspecific cross may result in a sterile F_1 offspring.

5) i) Selection, mutation, genetic recombination and gene migration.
ii) Genetic drift
iii) Sampling error
iv) Sewall wright
v) Shifting balance.

Terminal Questions

1) Three types of species concept have been proposed.

a) The typological species concent, as suggested by Plato, reduces the immense variety of organisms in nature to a few "types". It proposed that individuals might vary but belonged to a single type.

b) The nominalistic species concept regarded species as man-made abstraction.

c) The biological species concept, a more realistic and objective approach to the problem of species conceived species as members'belonging to a reproductive community and as an ecological unit. It also regarded species as a genetic unit where individuals are held as a large, strongly united gene pool.

2) Sympatric speciation refers to speciation where parent species give rise to a daughter species without the individuals of the species being separated,

Speciation by populations of parent species which occupy quite separate territories is the allopatric speciation and the most common mode of species formation. Speciation by small populations isolated on the periphery of the distribution of the parent population can be described as peripatric speciation.

3) Ring species refers to a concept of speciation in which a widely distributed species breaks up into partially isolated species and then acted by selection and other factors results in a circle or group of races or Rassenkreise. For the example refer to section **13.4.**

4) a) Geographic isolation
   b) Geographic isolation
   c) Geographic isolation
   d) Ecological isolation
   e) Ecological isolation
   f) Ecological isolation
   g) Ethological isolation
   h) Ethological isolation
   i) Ethological isolation
   j) Mechanical isolation
   k) Reproductive isolation
   l) Reproductive isolation

5) In small populations genetic drift occurs due to sampling error. It refers to accidental but pronounced fluctuations in the frequency of a particular allele. In a population consisting of 100 individuals, assuming an allele is present only in one individual, the chances are that either the allele is irrevocably eliminated from the population in one or two generations or the frequency of allele may increase by 10%. In other words, due to genetic drift, the genes may be consequently lost or completely fixed in small populations. For an example refer to section **14.3.**