NETAJI SUBHAS OPEN UNIVERSITY

STUDY MATERIAL

POST GRADUATE ZOOLOGY

Paper : 2
Group : B
Units : 1-18

Ethology & Evolution

PREFACE

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

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

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

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

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

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Ethology & Evolution

Unit 1 ❑ Introduction to Ethology

Structure

1.0 Introduction
1.1 Ethology as a branch of biology
1.2 Animal psychology—classification of behavioral patterns, analysis of behaviour (ethogram)

1.0 Introduction

Ethology literally means 'character study' .It developed from the works of A. Vesalius (1543) and Darwin and Wallaces' theory of evolution. From their studies it is evident that neurobiology, physiology and psychology are very much involved with the study of ethology. In seventeenth century, the word 'Ethology'' was used in human ethics and by middle of nineteenth century this term was used inrespect of living organisms in the ecological sense rather than in behavioural sense (Grier, 1984). In 1940's the term ethology was widely used in the study of animal behaviour. Ethology deals with the study of species specific patterns of animal behaviour under natural conditions with little emphasis on learning. On the other hand, comparative psychologists paid much attention to the principles of associated learning under laboratory conditions using certain experimental designs and biostatistical methods. They concentrated more on the learning behaviour of man and other vertebrates like pigeons, dogs, rats and other rodents etc. Parallel to this neurobiologists provided understanding of the functional units of behaviour by making observations on proximate mechanism of nervous system. The causes of behaviour were explained by physiological psychologists, Maier and Schmeirla (1935) in their book 'Principles of Animal Psychology and Ethology'. Following confrontations, ethologists and psychologists are now very close to each other concerning the thought and results because behaviour may be defined as the observable act of animals (Grier, 1984) which is dependent on ecology and sociobiology on the one hand and neurobiology on the other.

However, whatever be the controversy ethology was brought into the fore-front in 1972 when ethologists Konard Lorenz, Niko Tinbergen and Karal von Frisch (Fig. 1.1) were honored by award of Nobel Prize.

Fig 1.1 : Ethology's three Nobel prize winners : (a) Konrad Lorenz (photograph by H. Kacher, (b) Niko Tinbergen (photograph by B. Tschanz) and (c) Karl von Frisch (photograph by M. von Frisch).

1.1 Ethology as a branch of biology

Ethology is defined as the biology of behaviour. It helps us to understand why an animal exhibits certain behaviour patterns under certain circumstances. Since biology involves with the study of life processes of an organism or group, behaviour of an animal, like its structure, is the result of natural selection. Perhaps more often than not, structure and behaviour evolved together, structure influencing behaviour evolved together, structure influencing behaviour, and behaviour in turn influencing the development of the structure. To respond to the environmental changes, physical and social, the animal must first receive a stimulus from the environments through its sensory system—sight, taste, smell, touch and hearing. From here the stimulus is transmitted to the motor organs, the muscular system, and the type and development of motor organs determine the manner in which the animal is able to respond to its environment. Thus how an animal perceives and reacts to the world is limited by what its eyes are built to see, its ears designed to hear, and its organs to taste, hear, and smell are designed to respond to respective environmental stimuli. Because of this, the world appears different to other animals than it appears to man. What'is visible and important to other animals may be unperceivable to man. Thus, it appears that the functions of an organ is dependent on the structure of the same. Therefore, structural peculiarities of an organism play significant role in assuring the targeted function. Since the structural components of an organism are determined by the biology of the individual concerned then the behaviours exhibited by the said organism by using these structures are very much dependent on the same. That is, ethology is the functional aspect of biology. In other words, ethology is a branch of biology.

1.2 Animal psychology—classification of behavioural patterns, analysis of behaviour (ethogram)

How behaviour does develop is a vital question to all ethologists. It is argued that the behaviour is initiated by psychology of the animals concerned. Edward Thorndike (1874—1949) used the puzzle box to perform a series of task-learning experiments, using cats as test subjects. A cat was placed in the box, which was fastened shut; by manupulating a shuttle-lever, the cat could open the door and obtain a reward placed outside the box. From these experiments Thorndike concluded that much of the animal learning takes place by trial and error and that rewards are critical component of learning processes.

During 1930—1960 comparative psychology was dominated primarily by theories of learning and secondarily by work on development. Thereafter truly broad-based comparative work came into the sight. Dewsbury (1984) characterizes the subject matter of current comparative psychology as involving the study of either behaviour patterns that are closely tied to work on learning, motivation, or physiological psychology, on species other than those commonly used for such studies, or both. For comparative psychologists, the primary emphasis has been on 'how' questions about the mechanisms that underlie observed behaviour patterns occur. One way to begin research in comparative psychology is by identifying and characterizing the classes of behaviour patterns in two or more species. A second way to begin is by selecting a species that is the most appropriate for investigation of a particular problem. However, too much emphasis on a single species limits the generality of the conclusions we may draw (Beach 1950, Hoods and Campbell 1969; Lockard 1971; Dewsbury 1984).

Both the ethological and psychological perspectives have a great deal to contribute to the investigation and understanding of animal behaviour. Because, both 'how' and 'why' questions must be tested, an integrated approach that combines the methods of each discipline provides the best total analysis of behaviour. During the last decade there has been a great deal of sneurgism between scientists approaching proximate (how) and ultimate (why) questions (Drickamer 1998; Dewsbury 1999). The integrated discipline that is emerging involves combining laboratory and field approaches to study simultaneously internal mechanisms of behaviour, their ecological significance, and their evolutionary origin.

The systematic study of the function and evolution of behaviour, called *ethology*, is now a little over a century old. One of its most important principles is that behavioural traits, like anatomical and physiological traits, can be studied from the evolutionary viewpoint. For example, C.O. Whitman (1842--1910) made extensive observations of display patterns, which he termed instants, in various species of pigeons. Whitman found that he could use displays (patterns of behaviour exhibited by animals that function as communications signals) to classify animals according to similarities and differences in behaviour. The ethogram, an inventory of a species, has been a starting point for many ethological studies. After making observations of an organism's behaviour, ethologists then formulate specific questions about the adaptativeness and function of particular behavioural patterns. A student of Whitman, Wallace Craig (1876 —1954), defined two key categories of behaviour patterns from his work with doves and pigeons. The first category includes the variable actions of an animal, such as its searching behaviour to find food, a nest site, or a mate; these are called *appetitive behaviour.* The second category includes stereotypical actions that are repeated without variation, such as the act of mating or the killing of prey; these are called *consummatory behaviour.* Ethologists of 1940's and 1960's have broken down any behaviour in nine patterns like (i) eating (ii) shelter-seeking, (iii) agonistic; (iv) reproductive, (v) epimeletic, (vi) et-epimeletic, (vii) eliminative, (viii) mutual-mimicking, and (ix) investigative behaviour. Modern ethologists tend to retain of some the categories, to modify some and to discard others. Thus, now-a-days, behaviour is categorised as (i) communication and releasers, (ii) motivation and drive, (iii) biorhythms, (iv) instinct and learning, (v) genetic and evolutionary, (i) evolutionary, (vi) agonistic, (vii) reproductive and parental and (viii) social behaviour.

After making observations of an organism's behaviour ethologists then formulate specific questions about the adaptativeness and functions of particular behavioural patterns. The ethogram, an inventory of the behaviour of a species, have been a starting point for many ethological studies.

Unit 2 ☐ Innate behaviour

Structure

2.0 Introduction to innate behaviour

- Early research in the field of animal behaviour—notably by Nobel Prize winners Karl von Frisch, Konard Lorenz, and Niko Tinbergen—focused on behavioural patterns that appeared to be instructive or innate.
- Because behaviour is often *stereotyped* (appearing in the same way in different individuals of a species), these early researchers argued that it must be based on preset paths in the nervous system. In their view, these paths are structured from genetic blue prints and cause animals to show essentially the same behaviour from the first time it is produced throughout their lives.
- These researchers based their opinions on behaviour such as egg retrieval by geese. Gesse incubate their eggs in a nest.
- If a goose notices that an egg has-been knocked out of the nest, it will extend its neck toward the egg, get up and roll the egg back into the nest with a side-to-side motion of its neck while the egg is tucked beneath its bill.
- Even if the egg is removed during retrieval, the goose completes the

behaviour, as if driven by a programme released by the initial sight of the egg outside the nest.

- According to ethologists, egg retrieval behaviour is triggered by a *sign stimulus* (also called a *key stimulus),* is the appearance of an egg out of the nest; a component of the goose's nervous system, the *innate releasing mechanism* provides the neural instructions for the motor program, *or fixed action pattern.*
- More generally, the sign stimulus is a 'signal' in the environment that triggers a behaviour. The innate releasing mechanism is the sensory mechanism that detects the signal, and the fixed action pattern is the stereotyped act.
- One interesting aspect of sign stimuli is that they are often not very specific; in some situations, a wide variety of objects will trigger a fixed action pattern. For example, goose will attempt to roll baseballs and even beer cans back into their nests. Moreover, once the objects are in the nest, the goose recognizes that they are not eggs and removes them!
- A similar example is provided by a male stickleback fish. During the breeding season, males develop bright red coloration on their undersides. Territorial males react aggressively to the approach of other males, performing an aggressive display and even attack. Niko Tinbergen observed a male stickleback in a laboratory aquarium displaying aggressive posture when a red fire truck passed by the window. He realized that the red coloration was the sign stimulus. Subsequent experiments revealed that males would respond to many unfaithful models as long as the models had a red stripe.
- This phenomenon is taken one step further by what are termed *supernormal stimuli.* Given a choice between two sign stimuli, one of normal size and the other much larger, many animals will respond to the larger of the two. Thus, geese given a choice of a normal goose egg and one the size of a volleyball will choose to roll the bigger one back to the nest. Why supernormal stimuli exist is not always clear. One aspect to keep in mind, however, is that in many cases, supernormal stimuli do not occur in nature. Thus, geese may prefer eggs the size of volleyballs, but they never encounter eggs of that size. It may be that geese have evolved to respond to the larger

object so that they will attend to eggs, rather than smaller, circular rocks. As a result, natural selection may have found the evolution of a preference for larger objects. This general response may lead to unexpected outcome in experiments but probably doesn't often lend to maladaptive behaviour.

There are many striking examples of behaviour appearing apparently normally in animals whose experience is distinctly abnormal. A case in point was shown by experiments carried out by Janet Kear on ducklings which she had reared by hand from the egg. Most duck species nest on the ground, but some of them, such as the wood-duck, do so in holes far up in trees from which the fledglings have to leap to the ground beneath. Fortunately they are light and fluffy when they do so and as a result, they bounce and run off rather than suffer multiple fractures. Kear tested chicks of various species on a visual cliff. In the apparatus the animal is placed in the centre and can move either to one side where there is a drop looking like a cliff beneath the glass or to the other where the floor is immediately under the glass so that it looks shallow. The behaviour of the ducklings was appropriate to their normal nesting place. Tree-nesters did not avoid the deep side of the cliff but, if they moved that way, they would leap as if casting themselves into space. On the other hand, the ground-nesters tended to move to the shallow side rather than the deep one, suggesting that they avoided heights. Interestingly, if they did move to the deep side their behaviour was quite different: they pushed off with both feet as they would when moving out from the edge of a pond!

Being hand-reared, these young birds had no opportunity to learn the actions they showed form others or from earlier experience with ponds or with cliffs. Many ethologists would therefore have used this evidence the argue that the behaviour must be innate because it develops despite deprivation of opportunities for learning, and the main motivation for carrying out such experiments has often been to discover whether behaviour is 'innate' or 'learnt'. Sometimes, as with the duckling, behaviour develops normally even though the animal is reared in a very *impoverished environment.*

Another good example here is the hoarding behaviour of squirrels whereby, even in captivity, they will bury nuts underground to form stores which they eat later when food is scarce. If such an animal is raised on a liquid diet, so that it never experiences nuts, with masses of this food available the whole time, so that it never needs to hoard, and on a bare floor so that digging is impossible, the first time it encounters nuts and earth it still digs a hole and buries them.

By contrast with these experiments, others have shown behaviour patterns to be radically altered unless particular experiences are available. If a young dog is reared in total isolation from all others, in a chamber in which it can be fed and cared for without contact with even its human caretakers, it turns into a strange animal, apparently careless of its own welfare. It will put its paw in a fire and singe it and it will repeatedly approach an object that gives it an electric shock. This is quite unlike a normal puppy of the same age, which hastily withdraws from such painful experiences. Furthermore, the normal puppy will yelp when hurt, whereas the one that had been isolated behaves as if it did not even feel pain. Clearly its deprivation has led to a drastic alteration in the way its behaviour developed. In another example, to which we will return later, a young male chaffinch reared out of earshot of all birds of its species has been found to develop a very simple and unstructured song quite unlike that of a normal adult. If he is defended as well, so that he can not even hear his own efforts at singing, the song he produces is even worse, being little more than a screech.

These Kaspar Hauser experiments vary enormously in what they actually deny the animals. The isolated chaffinch cannot copy song from other birds, but he can practice singing, if deafened he can still practice, but cannot hear the outcome. The hoarding squirrel has had experience of neither nuts nor earth so its deprivation is more extreme; it can not copy from others, it cannot learn for itself, not can it practice digging in earth, though it can carry out the movements concerned on the bare cage floor. In many cases it has proved very difficult to deny animals all the experiences one might think likely to be relevant. Finches with no hay that they can use for nest building will carry seed, latency, faeces and feathers to their nest site. Some bizarre behaviour results when the feathers used are still attached to themselves or to their mates. A bird may have to walk rather than fly to its nest site because it is holding its own wing in its beak as nest material; after carefully placing the wing in a corner of the nest it will then fly down, pick the wing up again and struggle back to the nest with it!

2.1 A false dichotomy

To ethologists such as Konrad Lorenz, deprivation experiments were the main evidence used in deciding whether or not particular aspects of behaviour were innate. But the examples mentioned above point to a problem in interpreting these experiments : it is almost impossible to tell exactly of what one has deprived the animal. This difficulty was one of those pointed out forcefully by a leading critic of Lorenz's theories, the American psychologist Danny Lehrman. The points he raised deserve discussion here because they were very influential in leading to current views of behaviour development. They fall under three main headings.

2.2 Criticism of the deprivation experiment

Lehrman argued that deprivation could show where experience was important but not where it was not. Thus the chaffinch which sings abnormally after being isolated shows that hearing the song of others is essential for normal song development. But the bird that builds a normal nest the first time it encounters hay may have had many experiences, form grooming its own feathers to husking seeds which could have contributed to its nest building capability. Sometimes the strangest and most unexpected experiences turn out to be important. Thus baby rats will not urinate for the first time unless thin genital area is stimulated, normally this occurs because their mothers lick them soon after they are born, but if they are isolated before this occurs they will swell up until their bladders burst. Given the existence of such unlikely influences, it is rash to assume that a simple deprivation experiment has removed all the experience that may be relevant.

2.3 Criticism of viewing learning as the only environmental influence

The environment has many influence on animal development to which it would not be appropriate to apply the word learning. The example of the baby rats can also be used to illustrate this point. Though the young rat is stimulated to start urinating, no one would suggest that it has learned to do so.

2.4 Criticism of viewing behaviour

The discovery that many unexpected factors can influence behaviour has led ethologists to examine the development of behaviour much more carefully and to avoid making sweeping statements about how this or that behaviour pattern is innate' or 'inherited'. These words suggest that the behaviour is absolutely fixed and that it would develop in exactly the same way no matter what environment the animal found itself in.

Unit 3 ☐ Perception of the environment

Structure

3.0 Introduction

Broadly speaking perception of the environment by an animal is reflected through their communication system. In a communication system one is the sender and other is the receiver. The following methods are adopted by the animals for chief communication purposes: (i) mechanical; (ii) electrical; (iii) chemical; (iv) olfactory; (v) auditory and (vi) visual.

3.1 Mechanical

A number of points of information are transmitted by tactile communication which is more developed in social interactions of many invertebrates like that seen in the blind workers of some termite colonies. The tactile communication is highly developed in monkeys where one monkey grooms another by touching and passing some information. Cockroaches and lobsters have long 'feelers' which help them to know each other in their sex act. Few animals have machine receptors by which they know some mechanical disturbances in air or water around them. Pond-skaters ascertain the sex of other adults by producing ripples on the water surface. The blind fishes know the presence of other fishes in the group by creating mechanical disturbances in the water through their lateral line organs. The tactile communication is highly developed in monkeys where one monkey grooms by touching and passing some information.

3.2 Electrical

Electric sense is a kind of 'sixth sense'. It is seen in many animals who live dim light and are poor in vision. Many lower animals are able to orient themselves in artificial electric fields, but little is known about the sensory basis of this behaviour. A number of species of fish make use of electrical sensitivity in their normal orientation and communication, and scientists know a considerable amount about their electrosensory systems. Sensitivity to magnetic fields has also been domesticated in a number of animals. Certain bacteria, for example, orient toward magnetic North and will respond to a magnet in the laboratory. Examination by electron microscope reveals that these bacteria have chain-like structure containing crystals of magnetite, which have also been found in the abdomen of honey-bees and in the pigeon retina. The bacteria in the northern hemisphere follow the declination of the earth's magnetic field and this steers them down into the anaerobic mud, their normal habitat. Those in the southern hemisphere have the polarity reversed. Magnetically directed behaviour has been studied also in bees and pigeon and some researchers have claimed that humans are sensitive to magnetic fields.

Fishes use electricity in three principal ways :

(a) The so-called 'strongly electrode fish' such as the electric ray *(Torpedo* sp.) and electric eel *(Electrophorus electricus)* produce electric shocks capable of stunning prey but may not possess an electric sense.

(b) Electrosensitive fish such as the dogfish *(Scyliorhinus)* and sharks do not produce electricity. Dogfish are capable of detecting prey, even when buried in sand, by the local distortion of the earth's electric field. The sense organs responsible are the ampullae Lorenzini, which are distributed widely over the body surface, especially near the head.

(c) The so-called 'weakly electric' fish (Gymnotidae and Mormyridae) generate their own electric fields and are sensitive to electrical changes in the environment.

These fish are usually nocturnal and live in turbid water where vision is not practicable. They have two types of electrosensitive receptor : *ampulla* receptors, which respond to slowly changing electric fields; and *tuberous* receptors, which only respond to rapidly changing fields. Some species possess only one type of receptors; others have both. They generate weak electric fields by means of electric organs, which are modified muscles or neuronal axons. The electrical discharges typically are pulsed at up to 300 pulses per second. Some fish can vary the pulse rate as a means of communication with other fish or as a part of a jamming avoidance response designed to reduce interference from the fields generated by other members of the species. In other words when one fish is subject to electrical interference from another fish it can change its pulse rate to reduce the interference. The electo-receptors are also used to locate objects in the surrounding water by the distortions they cause in the electric field. Some fish, like *Gymnarchus,* can discriminate (Fig. 3.1) between good and poor electrical conductors such as a metal rod and a plastic rod.

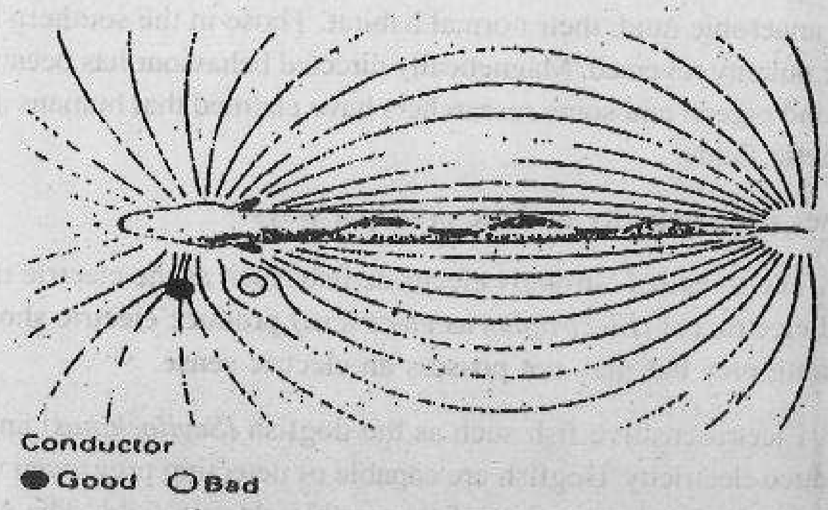

Fig 3.1 : The electric field of *Gymnarchus.* The field on the animal's right is undistorted. The field on the left is distorted by a good conductor (black) and by a poor conductor (white). The animal can detect the presence of these two objects by sensing the effects they have on the electric field.

33 Chemical

Orientation with respect to the source of some chemical diffusing in air or water, called *Chemotaxis*, is almost universal. Chemotaxis makes possible some behavioural performances that seem amazing to 'non-olfactory, creatures like ourselves. For example, *Paramecium* back-and-turn if they happen to swim into a region containing a noxious chemical. Chemoreception is the capability of identifying chemical substances and detecting their concentrations. It exists even among very primitive forms of life. In a technical sense, virtually every nerve cell is a chemoreceptor in that it reacts specifically to substances released by other nerve cells. The mechanisms of chemoreception involve the recognition of specific molecules by receptor sites on cell membranes. Exteroceptors detect the presence of chemicals in the external environment while interoceptors detect substances circulating in the body fluids, such as carbon dioxide, nutrients and hormones. Chemical substances when come in contact with the taste organ only ihen it is possible to feel the taste of the substance concerned. In many animals there is a neurological distinction in that some nerves are concerned with olfaction, or the detection of low concentrations, while others convey *gustatory* messages from different receptors specialized for detecting high counteractions of chemicals. In blowfly, chemoreceptors on antennae detect small quantities of airborne substances, and chemoreceptors on the tarsi (feet) are capable of detecting salt, sugar and pure water.

3.4 Olfactory

Olfactory signals or pheromones as they are usually called might seem to have very few advantages. Smells diffuse only through the environment, their speed and direction of travel being highly wind dependent and they can carry very little information, for after one smell is released time must elapse for it to disperse before another signal can be employed. However, these are situations where pheromones are ideal. A small animal such as moth could not be seen or heard from more than 100 meters or so away, no matter how brightly coloured or noisy it was. Yet the male of some moth species can detect the pheromone produced by the female several kilometers away. The chemical involved is a small molecule so that it diffuses rapidly, yet large enough that its structure can be species-specific; the male need only sense a few molecules to start moving upwind to where to ; female waits for him. Moths (also in many other insects) have various types of olfactory sensilla (Fig. 3.2). Thus usually have numerous minute pores in the surface, which terminate fluid-filled tubules. Dendrites of the receptor cells extend ; into the sensilla and the receptor exons travel directly to the brain. Airborne, pheromone molecules enter the pores of the sensillum and pass through the pores into the fluid-filled interior, where they come into contact with the receptor

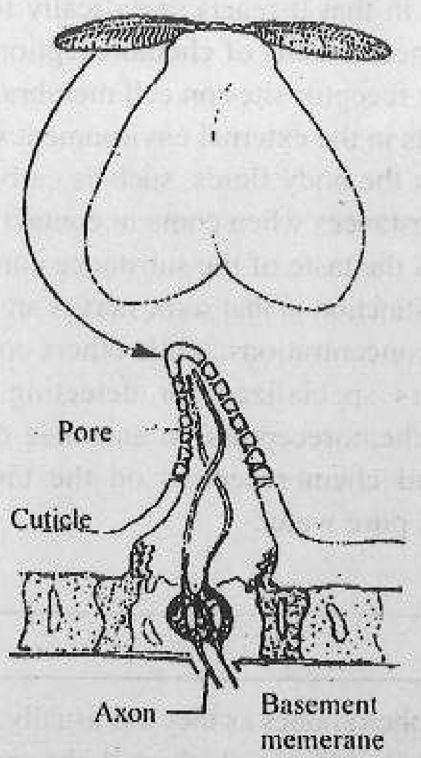

Fig 3.2 : Schematic diagram of the olfactor sensillum of a moth.

membranae. In vertebrates the olfactory receptors are primary sensory neuron with dendrites that extend as cilia into a mucous layer (Fig. 3.3). The axons of these neurons go to the olfactory bulb where they synapse with secondary neurons| whose axons form the olfactory tract that enters the forebrain.

Pheromones continue to signal even when the animal is not there. Man) mammals have different scent glands which they use for various purposes.)

Territorial species often mark the boundaries of their range as a signal to others that the area is occupied. They may do this with special gland, or with scents in their urine or faeces, and a wealth of information can be contained in such signals. The potential intruder may glean, for example, not only where the territorial boundary is, but which individual is occupying it, what reproductive state he is in and even, by sensing how fresh the mark is, how long ago it was that the owner of the territory last went by. Thus, though olfaction might seem to us the poor sister of the senses as far as communication is concerned, its very persistence and slowness of dissipation make it adapted for uses of its own for which the other sense would be of battle use.

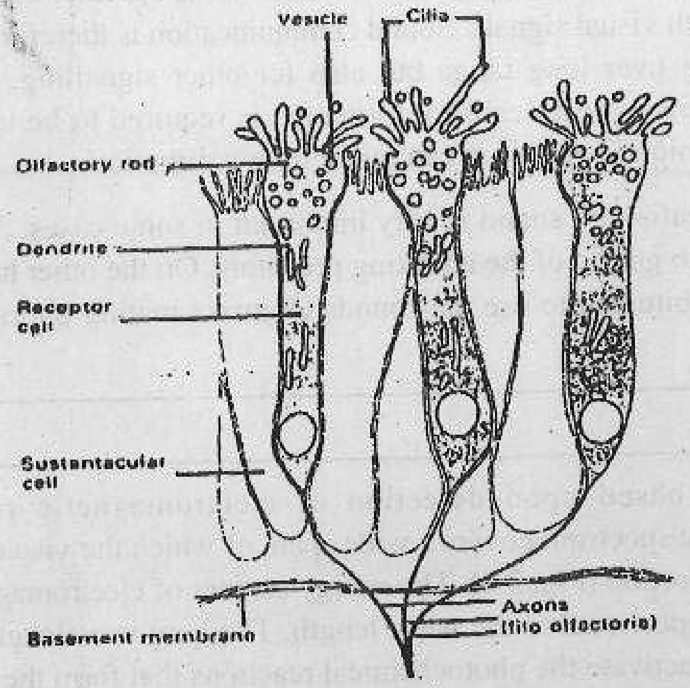

Fig 3.3 : Schematic representation of the olfactory mucosa of a rabbit. Three receptor cells are surrounded by supporting cells.

3.5 Auditory

Sound results from minute changes in pressure that originate from a vibrating source within a medium such as air or water. The receptors that detect sound are basically mechanoreceptors that show rapid adaptation and that are thus sensitive to vibration. The auditory systems of animals, though diverse, have certain features in common. There is peripheral device for convenient sound pressure to vibratory motion. Sensory receptors convert this motion into nerve impulses that can be decoded by the central nervous system. There are many properties of sound to which an animal might respond. The extent or amplitude of the waves determines the intensity or loudness of the pierced sound. In air, sound travels at about 340 meters per second. Sound communication has the merit that a great deal of information can be transmitted very rapidly. The pattern of frequency in time which codes this information can be changed with great speed so that one signal can allow quickly on the heels of another to a much greater extent than would be possible with visual signals. Sound communication is therefore ideal not only for advertising over long range but also for other signalling, such as in our language, where a great deal of information is required to be transmitted very rapidly. It is unique because it can move in any direction.

Communication by sound is very important in some cases. An alarm call is very effective to get rid of the attacking predators. On the other hand advertising animals are habituated to use the sounds to attract mating partners.

3.6 Visual

Vision is based upon detection of electromagnetic radiation. The electromagnetic spectrum covers a wide span, of which the visual spectrum is a very small proportion (Fig. 3.4). The energy content of electromagnetic radiation is inversely proportional to the wave length. The long wavelengths contain too little energy to activate the photochemical reactions that form the basis of photo reception. The short wave lengths contain so much energy that they damage living tissue most of the short-wave radiation from the sun is absorbed in the ozone layer of the atmosphere and it is doubtful that life could have evolved on earth if this had not been the case. All photobiological responses are confined to a narrow band of the spectrum between two extremes.

The pigment present in the photoreceptor cells is bleached by the action of light. The bleaching involves changes in the shape of the pigment molecules. The bleaching process leads to electrical changes in the receptor membrane that

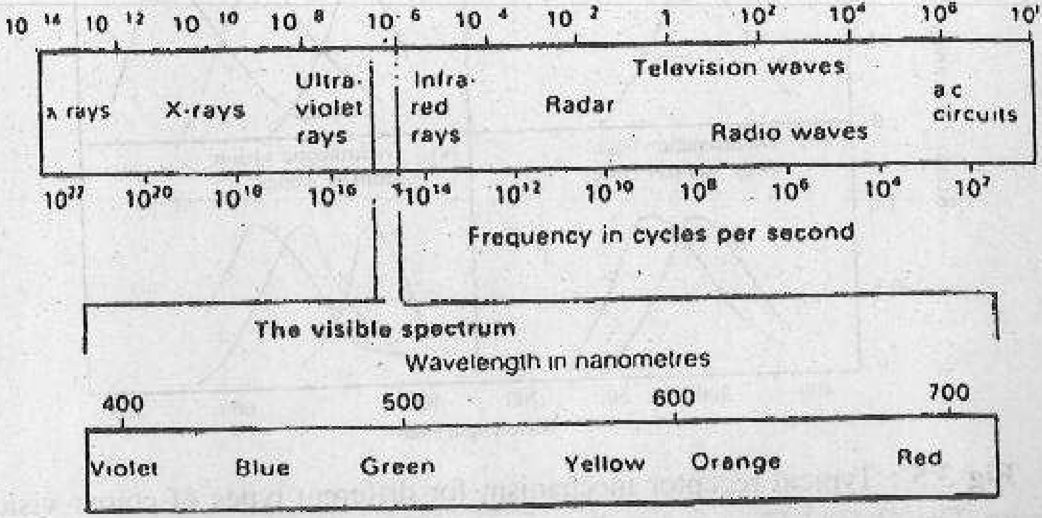

Fig 3.4 : The electromagnetic spectrum (above) wavelengths in metres, with the visible portion enlarged (below).

are not fully understood. The photoreceptors are of two types, called rods and cones. The rods are more elongated than the cones.They are very sensitive to low levels of illumination and have only one type of photopigment, called rhodopsin. Rod vision is therefore colourless. Many rod cells are connected to the single ganglion cell. Consequently, single fibre in the optic nerve receives information from many rods, an arrangement that increases sensitivity at the expense of acuity. Rods are predominant in nocturnal species where sensitivity is at a premium. Cones provide sharp vision. Cones may be of more than one type, the photopigments absorbing in different parts of the spectrum.Cones thus provide the basis for colour vision. Cones are most sensitive to the wave lengths that are most strongly absorbed by their photopigments. Vision is monochromatic when there is only one active photopigments. This is the case with twilight vision in humans when only the rods are operating (Fig. 3.5). Vision may be dichromatic when two photopigments are active as in grey squirrel. In the visual systems where three receptors are involved trichromatic vision is developed. This sort of vision is found in many spices including humans.

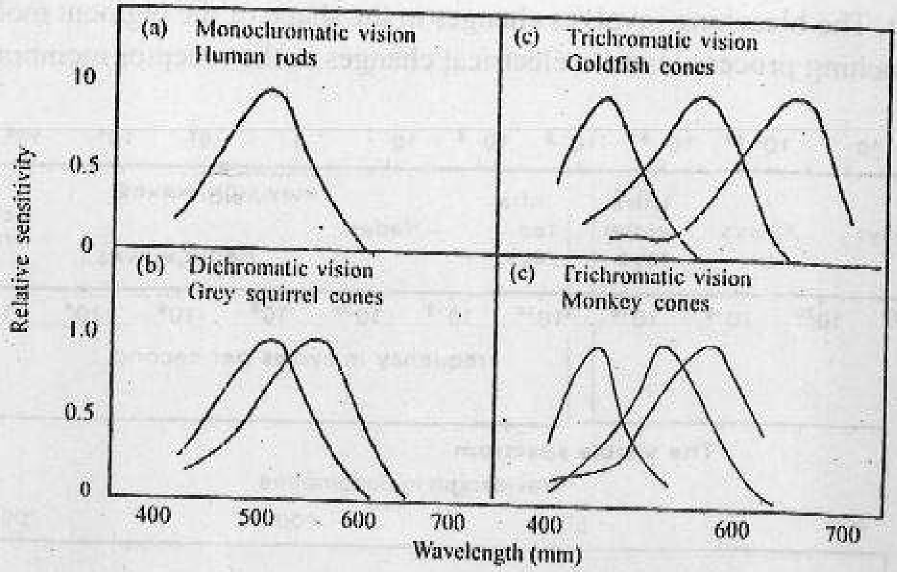

Fig 3.5 : Typical receptor mechanism for different types of colour vision (From *The Oxford Companion to Animal Behaviour*, 1981).

Changes in posture and colour are the main ways that animals communicate through the visual channel. Vision is the most important sense and by predators that hunt by day, for it is the best for location and homing in on, prey. So, this is not an ideal sense for animals that use it in advertising for mates. Also, in dense forest it is not that much effective. Moreover, small animals could not be seen from a distant place. However, this signal is very much helpful in short range communication i.e., between mates or between rivals in territorial boundary.

Unit 4 ☐ Behaviour and Neural Mechanisms

Structure

4.1 Introduction

The survival of all animals depends on their ability to solve all the problems encountered by them. The problems like food foraging, antipredator defence, mate selection etc. are solved by different patterns of behavioural activities. The aim of this section is to link between nervous system and such behaviour. The job of nervous system can be divided into three components: (i) The reception of sensory information from the environment, (ii) the processing of this information and making of decision, and (iii) the motor response to that information. The general plan of functioning of nervous system is same in all nervous system intensive animals. Through natural selection nervous systems have been shaped by the demands of constrains imposed to different animals differently. A toal can recognize which one is food and which one is non-food. A little skate can differentiate the electric field produced by its own breathing movement and electric field produced by the movement of its prey. These are just few examples we will discuss in this section taking nervous system as proximate factor. Although, we will focus on mechanism, we will also consider the ultimate cause or euolutionary significance or adaptive value of such nervous system oriented behaviours.

4.2 Nervous system and development of instinctive and learning behaviours

The ethologists labeled an instinctive behaviour a *fixed action pattern* or FAP The key component that activates FAP is called *sign stimulus or a releaser* (if the sign stimulus is a signal from one individual to anthor). The hypothetical neural mechanism that receives sensory input from sign stimulus and activates the FAP is labeled as *innate releasing mechanism.* Learning behaviour also needs a specific pattern of nervous system. All kinds of learning needs a well organised sensory receptor systems as well as an effective motor system for the manifestation of the same. The interrelationship between nervous system and instinctive and learning behaviour may be illustrated as follows.

Instincts	**Learning**
All individual of a species	An individual of a species
↓	↓
Genome + environment	Genome + environment
↓	↓
Developmental system	Developmental system
↓	↓
Neural networks relating to innate releasing mechanism	Neural networks relating to learning mechanisms
↓	↓
Fixed action pattern of behaviour (instinctive behaviour)	Learned changes in behaviour (learning behaviour)

The following examples of male and female behaviour in rat can help us to understand the whole process.

The male and female behaviour arises from an interaction between rat's genetic makeup and its environment. The basic pattern is laid out by sex-chromosomes leading to the production of testis in embryonic males and ovaries in females. The embryonic testis of male secretes testosterone, while the female's ovarian cells donot. The hormonal differences activate a developmental mechanism that provides male a masculinized brain capable of male-behaviour, and feminized brain with female behaviour. The hypothesis that testosterone is an internal signal that changes the developmental pattern modifying receptors in nervous system. There are experimental evidences that if a small amount of testosterone is injected into a new born female rat, it will attempt to copulate with other females after adulthood. Her nervous system (brain) became masculinized as a result of exposure to testosterone early in life. Conversely, if one removes the testosterone producing gonads from new-born male rat, it will develop female-like brain and may produce female like behaviour in adulthood if it receives proper amount of estrogen in adulthood. After the development of such instinctive behavioural pattern the same may be modified by learning. The process of learning is directly associated with the advancement of nervous networks. The mammals having most advance type of nervous system possess the faculty of learning uniuely.

4.3 Nervous system as the proximate causes of some behaviour

The role of nervous system as the proximate causes of some behaviour can be understood in the study of the following examples :

4.3.1 Aplysia learning behaviour and synaptic changes

The sea hare *Aplysia* moves across the oceanic battom in order to forage on seaweeds. During such foraging its siphon is extended and gills are spread out on the dorsal side. The gills are partly covered by mantle sheet, which terminates in siphon. Such siphon is a fleshy tube through which *Aplysia* can expel out excess seawater and wartes when siphon is disturbed the mantle sheet with gills are withdrawn into the mantle cavity. It is a defence response, called the gill-withdrawal reflex.

The gill-withdrawal response can be modified by experience, that is, through learning. The forms of learning have been studied here are *habituation* and *sensitization.*

Habituation : The habituation occurs when an animal learns not to respond to a repeated stimulus that proves to be harmless. The habituation form of learning is adaptive because it saves energy ignoring irrelevant, harmless stimulus. The demonstration of habituation may be done disturbing the siphon by touch or a brief jet of seawater. After 15 such stimuli at 10 minutes apart, the reflex response becomes half of their initial value. A diagram of the neural circuitry for gill-withdrawal reflex is as follows :

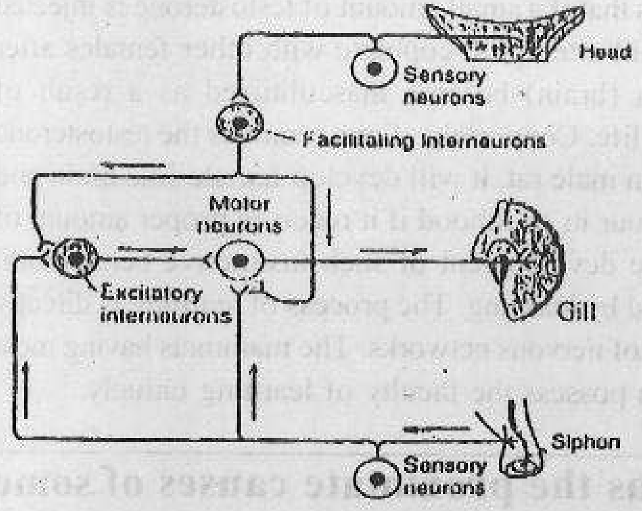

Fig 4.1 : Neural circuitry for habituation and sensitization of the gill-withdrawal reflex in *Aplysia.*

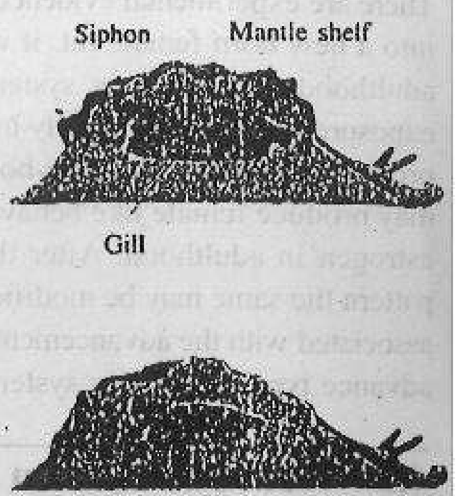

Fig 4.2 : The gill-withdrawal reflex in the sea hare, *Aplysia.* The gills, mantle shelf, and siphon are drawn here as if the animal were transparent. Normally, the gills are spread out and are only partially protected by the mantle shelf. The siphon, through which water is drawn in over the gills and excess water is expelled, is extended so just the tip is visible when the animal is seen from the side (a). It the siphon is touched, the gills, mantle shelf, and siphon are withdrawn into the mantle cavity (b). The gill-withdrawal reflex can be modified by learning.

The habituation occurs because the sensory neuron releases less neurotransmitter as a result of repeated harmless stimuli. This, in turn, results in fewer action potentials in motor neuron for gill withdrawal. The reason is that calcium channels become less effective because of repeated harmless stimuli. So, they allow less Ca^{++} into axon terminal. Calcium ions are needed for the synaptic vesicles to fuse with the presynaptic membrane. The changes in synaptic functioning during habituation is as follows :

Habituation of gill withdrawal response :

Repeated stimulation of sensory neuron from siphon of ***Aplysia***

↓

Less effective calcium channels in axon terminals of sensory neuron

↓

Decreased Ca^{++}inflow

↓

Decreased neurotransmitter release by sensory neuron

↓

Decreased firing rate of gill motor neuron

Sensitization : In second form of learning in ***Aplysia*** regarding gill-withdrawal response is *sensitization.* The gill-withdrawal reflex becomes stronger when a stimulus that causes gill-withdrawal is preceded by a strong, noxious stimulus, such as an electric shock anywhere on *Aplysia's body.* Sensitization also involves changes in the functioning of synapses. In this case the rate of release of neurotransmitter from axon terminal of sensory neuron is increased. Thus, it increases the rate of firing of motor neuron. Sensitization requires a facilitating interneuron. These interneurons release *serotonin* onto the axon terminal of sensory neuron. Serotonin increases intracellular concentration of second messenger, in this case, cyclic adenosine monophosphate (CAMP). CAMP causes the closing of certain types of k^+ channels of neuronal cell membrane. This keep k^+ inside the cell and causes sensory neuron depolarized allowing additional Ca^{++} to enter the cell. The raised Ca^{++} levels cause more neurotransmitter to be released. The entire event may be depicted as follows:

Strong, noxious stimulation to skin stimulates sensory neuron from skin.

↓

Stimulates facilitating interneuron that synapses on the axon terminal of sensory neuron from skin.

↓

Release of serotonin from facilitating interneuron.

↓

Increased CAMP level at axon terminal of sensory neuron from skin.

↓

CAMP causes closing of certain type of k^+ channel and k^+ increases in cell, prolonging depolarization of sensory neuron.

↓

More Ca^{++} enter than normaly entering the axon terminal.

↓

Increased release of neurotransmitter by sensory neuron.

↓

Increased firing rate of gill motor neuron.

4.3.2 Neuromodulators and Leech feeding behaviour

The European leach *(Hirudo medicinalis)* feeds on blood of animals, mammals in particular. A hungry leech usually rests at the water's edge: It senses a prey, it begins to swim in an undulating fashion in the direction of the target. Once the leech reaches the target, it tries to search out warm region of the animal body. When a warm region is reached, the leech bites with its three jaws. It flows blood from the wound, ingestion begins. Rhythmic contractions of the muscular pharynx pump blood into the crop for next half hour or so. Then the leech enormously distended and detaches from its host.

Charles Lent ***et al*** (1989) demonstrated that **serotonin** modulates the physiology and pattern of behaviour associated with feeding in leeches. Bathing leeches in serotonin (a method that does not cause injury to leech, therefore, preferable to the method of injecting serotonin) produces profound effect on feeding behaviour. A serotonin bath reduces the time of swimming toward potential prey, increases the frequency of biting by 40%, and pharyngeal contraction by 25%, and increases the volume of ingested blood. It needs to be noted that though the action of serotonin in feeding behaviour is activational, it inhibits the leech's sexual behaviour. The modulatory effects of serotonin in leech are summarized below .

Effect of serotonin in leech

Activational effect on :

(i) biting
(ii) pharyngeal pumping of blood
(iii) salivation
(iv) mucus secretion
(v) swimming pattern
(vi) cardiac pattern

Inhibitory effect on :

genital organs

Functionally, neuromodulators appear to be intermediate to classic neurotransmitters and hormones. Whereas neurotransmitters are released at specific synapse and hormones are broadcast throughout the body via blood stream, neuromodulars are released in the general vicinity of the traget tissue. It is difficult to establish the specific point at which a neurotransmitter becomes a neuromodulator, and a neuromodulator a hormone. For examples, dopamine acts as neurotransmitter at some synapses, and as modulators at others.

4.4 Specialization for perception of biologically relevant stimuli : sensory processing

Animals encounter wide variety of stimuli from its environment. The job of an animal's sensory system is not to transmit all available information, but rather to be selective and prodive only information that is vital to the animal's survival and reproductive success. How does an animal's nervous system enable it to select important stimuli and to ignore irrelevant ones? Here we will discuss the selective filtering action of nervous system in the little skate and common toad.

4.4.1 Stimulus filtering in the little skate

The little skate ***(Raja erinacea)*** has specialized receptors and brain structure that are capable of detecting and analyzing different types of electric fields. This specialized sensory ability of skate is called **electroreception.** There are two general categories of electroreception, **active and passive.** The electric fish of Africa **(Mormyriformes)** and south America **(Gymnoriformes)** have electric organ to generate electric field around their body water—this is called **active electroreception.** Electric fish has two types of electroreceptors, called ampullary

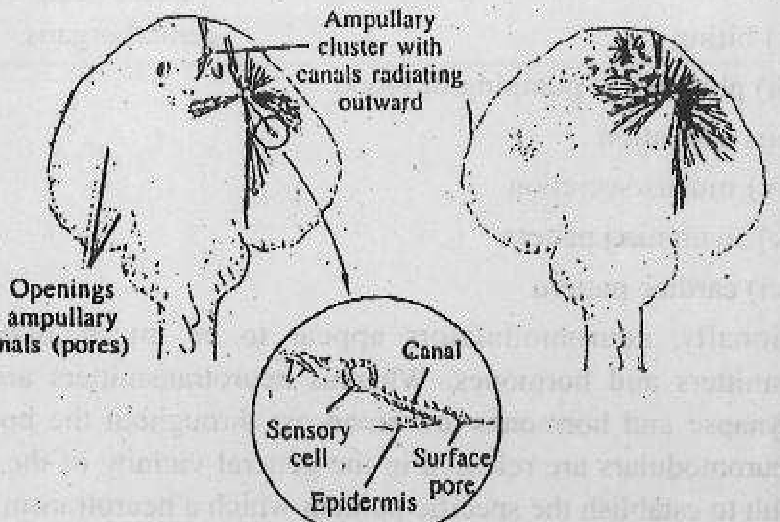

Fig 4.3 : Distribution of canals and ampullary clusters in the thornback ray, a relative of the little skate, (a) Dorsal surface, (b) Ventral surface, (c) A single ampullary organ. Elasmobranch fish such as skates and rays use electroeception to locate prey—note the concentration of receptors on the ventral surface, especially around the mouth, (a and b : Redrawn from Montgomery 1984.)

and tuberous receptors. Little skates do not have their own electrical field generated by their own electrical organ. Instead skates respond to electrical field in their environment such as those field produced by preys or the earth's magnetic field. Such type of electroreception is called **passive electroreception.** Animals with this system have only one type of receptor, called ampullary organ. In case of elasmobranchs. ampullary organ is called **ampullae of Lorenzini.** The ampullae of Lorenzini of the little skate are distributed in clusters over the head and pectoral fins (Fig 4.3). Eighty percent of the receptors are distributed on the ventral surface of the body and are densely in the snout area. One problem faced by skates, as well as by other same animals having electrosensory systems, is how to deal with self-generated 'noise'. The skate's respiratory movement can generate weak electrical field. This self-generated electrical field can interfere with the detection of extrinsic electrical signal produced by prey.

The filtering of irrelevant electrical information (generated by respiratory movements) is done in the following ways.

First, all receptors distributed on both sides of the body respond equally. Second, as a result of peculiar type of synaptic connections with the central nervous system, the signal from one side of body is excitatory, whereas that from other side is inhibitory. As a result of this arrangement, the equal and opposite signals essentially cancel each other out. Thus the neural mechanism allows the skate to focus on biologically relevant electrical stimuli associated with prey animals only.

4.5 Hormonal control of behaviour

Hormones affect behaviour in two fundamental ways; **organizational and activational** effects.

In organizational effects of hormome, hermones act as proximate factor during an organism's development. It produces relatively permanent changes in the organism's nervous system and other tissues. For example, the sex differentiation and pattern of growth for body tissues. In **activational effects,** hormones act as triggering influences on the expression and performance of behaviour patterns in adulthood.

4.5.1 Examples of organizational effect of hormones on behaviour

Studies of quail, zebra finches, rats, guineapigs, mice and rhesrus monkey have provided clear evidence that certain hormones have impact on sex differentiation during early development. Now, let's consider some examples ol hormonal impacts on organization effects on behaviour and related processes.

4.5.2 Sexual behaviour of rat

If a male neo-natal rat is castrated within the first four or five days of his birth, he will not show normal sexual behaviour as an adult. It a neonatally casteratec male rat is given the normal doses of estrogen and progesterone of adult female he will exhibit female sexual behaviour, such as, the **lordosis posture.** By lordosis postures, a receptive female permits a male to mount and intromit. It is characterisec by shifting the tail to one side, raising hindquarters, lowering the abdomen (Fig 4.4). If we select an adult castrated male rat to give estrogen and progesterone, h will not show female sexual behaviour. Neonatal female rats if treated with androger within first four or five days after birth it exhibits male like sexual behaviour Similar studies have been made on guineapig and rhesus monkey.

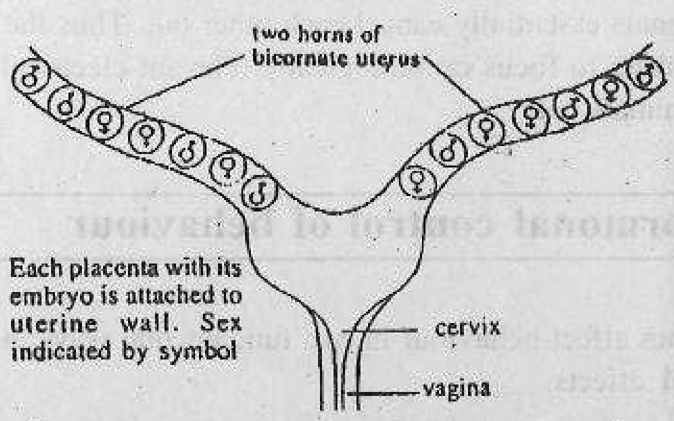

Fig 4.4 : Rat uterus. Both rats and mice have bicornate uteri. The often numerous fetuse of a pregnancy are arranged sequentially in each of the two horns of the uterus as show here for the rat. Pups of one sex may by positioned between two pups of their own se between two of the oposite sex, or between fetuses of opposite sexes. The location of female next to a male fetus results in masculinization of the genetic female.

The intrauterine position of a female fetus in rats and mice can influence he genital morphology and sexual behaviour. Both species have bicornate uteri fetuses are arranged sereially in each arm.of the uterus (Fig. 4.4). Thus, feture of one sex can be positioned between two other fetuses of the same sex, between two of the oppositve sex, or between two fetuses of opposite sexes. In rat and mice testicular androgens are released late in gestation. The female fetus in utero could be masculinized by exposure to testosterone from adjacent male fetuses if present. It is evident that **anogenital distance** (measurement of distance between the anal opening and the genital opening) is a reliable measure of androgen exposure. For rats and mice, anogenital distance for female fetus positioned between male fetuses are larger than females positioned between two female fetuses in utero. The rat females that have been masculinized due to in-utero position show more malelike mounting behaviour.

4.5.3 Examples of activational effects of hormones on behaviour

In adulthood, steroid hormones produce activational effects on sexual behaviour in male and female rats. Female rats with high blood levels of estrogen and progesterone display feminine sexual behaviour in the presence of a sexually active male. This type of behaviour rarely occurs when the levels of these ovarian hormones are low in blood stream. In fact, an adult female with removed ovary will not copulate unless she receives injections of estrogen and progesterone. Similarly, removal of testes in adult male eventually eliminates copulatory behaviour, unless he is given injection of testosterone. Results from researches indicate that the presence or absence of testosterone influenced aggressive behaviour in birds, mammals, if ring doves, roosters, mice rats, cats. Intact male birds and mammals show more aggression behaviour like fighting than castrated animals of the same species.

4.5.4 Influence of hormones on reproductive behavioural sequence in Ring doves

- A male ring dove bagins courtship display shortly after being placed with a receptive female. The failure of castrated male to court female indicates the importance of continuous supply of androgens for the initiation of the reproductive cycle.

- Male courtship stimulates release of FSH from pituitary in the female dove. FSH, in turn, stimulates follicle development in the ovaries. The follicles secrete estrogen, which affects uterine growth and development.

- Within a day or two, the birds begin nest construction, during this phase they capulate and continually add nesting materials to their nest.
- The presence of a nest stimulates the production and secretion of progesterone in femles. Progesterone promotes inculation behaviour after eggs are laid. Egg laying is activated partially by secretion of LH by the females pituitary.
- Under the influence of the presence of eggs in the nest and as a result of stimulation from incubation behaviour, both the sexes secrete prolactin. Prolactin acts to inhibit FSH and LH sécretion, and all sexual behaviour ceases.
- Prolactin stimulates crop development and production of **crop milk** (a nutrient rich fluid in the crop). The parents feed hatchlings with crop milk.
- During next ten to twelve days the prolactin level gradually drops down, as well as feeding behaviour gradually ceases.
- As prolactin decreases, the pituitary secretes FSH and LH, the same pair of doves again starts courtship, and the whole sequence repeats again.

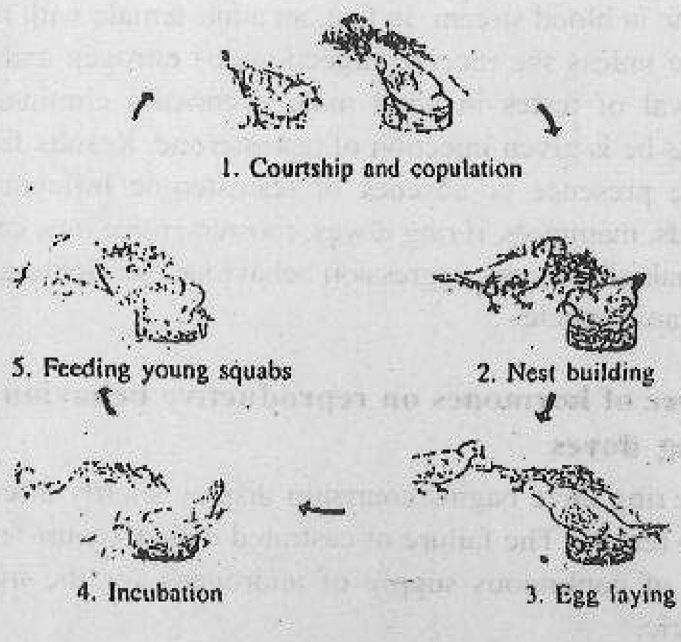

Fig 4.5 : Reproductive behavior cycle of the ring dove. This cycle provides an example of indirect environmental determinants of behavior. The sequence involves (1) courtship and copulation, (2) nest building, (3) egg laying, (4) incubation, and (5) feeding crop milk to the young squabs after they hatch. The cycle then repeats.

Unit 5 ❐ Genetic and Environmental Components in the Development of Behaviour

In humans, identical twins are genetically identical. It is obvious that most sets of identical twins are raised in the same environment. Therefore, it is not possible to determine whether similarities in behaviour result from their genetic similarity or from experiences shared as they grew up. Experimental studies on the twins separated at birth revealed many similarities in personality, temperament, and even leisure-time activities, even though the twins had often been raised in very different environments. These similarities indicate that genetics plays a role in determining behaviour in humans.

Young birds of some species begin to follow their mother within a few hours after hatching, and their following response results in a bond between mother and young. However, the young birds' initial experience determines how the imprint is established. Konrad Lorenz showed that birds will follow the first object they see after hatching and direct their social behaviour toward that object. Lorenz raised geese from eggs, and when he offered himself as a model for imprinting the goslings treated him as if he were their parent, following him dutifully.

Grohmann, in a classic experiment, reared a group of pigeons in tubes so that they could not move their wings. Another group of the same age was allowed to develop without restraint. When the unrestrainted pigeons had reached the stage at which they could fly satisfactorily, those that had been restrained were freed.Grohmann discovered that they also were able to fly immediately upon being released.

Thus, it appears that the geese and pigeons responded in respect to the conditions in which they were exposed. Therefore, the impact of environment on the development of these behaviours could not be ruled out.

From these examples it is clear that both genetical and environmental components are prerequisite for the development of behaviour. Because, if any one factor of the two would have been enough to provide the expected result then the behaviour manifested by the human twins maintained under diffrent environmental conditions would not have been different. Likewise the geese would have been failed to follow the first object they saw when they hatched if the imprinting was not influenced by the hereditary factor. Similarly, the restrained pigeons find no problem to fly at the same time along with the unrestrained individuals.

'The question whether the nature or the nurture, the genotype or the environment, is more important in shaping man's physique and his personality is simply fallacious and misleading. The genotype and the environment are equally important, because both are indispensable. The question about the roles of the genotype and environment in human development be posed thus : to what extent are the differences observed among people conditioned by the differences of their genotypes and by the difference between the environments in which people were born, grew and were brought up?' (Dobzhansky, 1964). These statements are very much applicable to most of the animals too. It is said that the behaviour patterns in organisms are 'blueprinted in the genes'. An important point to appreciate here is that natural selection has only determined how development should take place in the normal environment of each species. Thus a behaviour pattern may appear extremely fixed and constant in all individuals of a species because their genes interact with that environment to ensure that this is the case. However, moved to another environment, different from any the species has encountered before, the result may be quite different. Natural selection can not ensure that the genes will interact with any environment to give the same result; it can only give the right outcome in environment in which it has had a chance to work.

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Unit 6 ❐ Communication

Structure

6.0 Introduction

Wilson (1975) defined biological communication as an ‘action on the par of one organism (or cell) that alters the probability pattern of behaviour ir another organism (or cell) in a fashion adaptive to either one or both the participants’. The word **adaptive** means the signal or response is to some extent genetically controlled and under the influence of natural selection.

Smith (1984) defined communication as ‘any sharing of information’. The sociobiological view of communication considers that natural selection acts primarily at the level of the individual. Thus, communication is a means by which the sender manipulates others for his or her own benefit. The receiver may benefit or may be harmed.

6.1 Signals and its role in communication

A **signal** is the physical form in which a message is coded for transmission through the environment. Some signals are **discrete** (digital) but others are **graded** (analog). For example, zebras communicate hostile behaviour by flattering their ears and communicate friendliness by raising their ears (discrete signals). The intensity of aforesaid emotions are indicated by the degree to which the mouth opens (graded signal) (Fig. 6.1).

Two or more signals can be combined to form a **composite signal** with a new meaning. In zebras the meaning of the open mouth depends on whether the ears are forward (friendly) or backward (hostile). Animals can convey additional information with a limited number of displays by changing the **syntax,** or sequence of displays.'For example, the two signals A and B would have different meanings depending on whether A or B came first. The same signal may have different meanings depending on the **context.** For example the lion's roar can convey as a spacing device for neighbouring prides, as an aggressive display in fights between males; or as a means of maintaining contact among pride members. The communication about communication is called **metacommunication.** We can see good examples in play behaviour.

canids such as, dogs and wolves precede play with the play bow. Monkeys communicat play behaviour through a relaxed, open mouthed face.

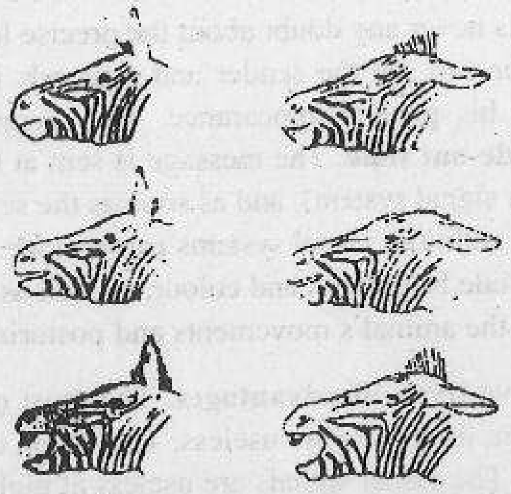


Fig 6.1 : Composite facial signals in zebras. Ears convey a discrete signal. They are either laid back as a threat or pointed upward as a greeting. The mouth conveys a graded signal and opens variably to indicate the degree of hostility or friendliness.

6.2 Channels of communication

The sensory channels are the physical forms used to transmit signals from sender to receiver. Communication can involve any of a variety of sensory channels—vision, audition, chemical, touch, and electrical fields. The characteristics of different sensory channels are as follows :

Table 6.1 : Characteristics of different sensory channels for communication

	Type of Signal				
Feature	**Visual**	**Auditory**	**Chemical**	**Tactile**	**Electrical**
Effective distance	Medium	Long	Long	Short	Short
Localization	High	Medium	Variable	High	High
Ability to go around obstacles	Poor	Good	Good	Good	Good
Rapid exchange	Fast	Fast	Slow	Fast	Fast
Complexity	High	High	Low	Medium	Low
Durability	Variable	Low	High	Low	Low

6.2.1 Vision

There are two important properties of visual signals. First is visibility of localization of sender and receiver. For example, when a male is displaying to attract a mate, there is never any doubt about the precise location of sender and receiver. The receiver can see the sender and responds in terms of his exact location, as well as his general appearance. The second property is **rapid transmission** and **fade-out time.** The message is sent at the speed of light (as it is a light dependent signal system), and as soon as the sender stops displaying the signal is gone. In addition, visual systems can provide a enormous varieties of signals. These include brightness and colour, as well as spatial and temporal pattern (produced by the animal's movements and posturing).

Visual signals have some **disadvantages.** The most obvious is that if the sender can not be seen, its signals are useless. The vision can be blocked by all sorts of obstructions. The visual signals are useless at night or less illuminated places (including the depth of the sea), except for light producing species. Furthermore, visuals power is confined within the visual range of a particular species, beyond this range of vision all kinds of singnals are useless. So, distance is an important factor.

6.2.2 Audition

Sound signals have number of advantages. They can be transmitted over long distance. Although sound signals are transmitted at a slower speed then light, it is still a rapid means of sending a message. After the message has been sent, the signal disappears without a trance. Sound signals have an additional advantage as it can convey message in limited vigibility, such as at night, in water, or in dense vegetation.

6.2.3 Chemical Communication

The chemical senses, smell and taste information may be transmitted by chemicals over long distance, especially when assisted by currents of air or water. The rate of transmission and fade-out time are slower than the visual and auditory signals. Demanding on the nature of function, this may be an advantage. For example, the demarkation of territorial boundaries, a durable, odoriferous signal is more efficient, because, if remains after the signaler has gone. Furthermore, chemical signals can be used in situations where visibility is limited. The detection of chemical signal depends on the quantity of chemicals emitted. It is difficult to locate a chemical signaler than one using visual or auditory-signals.

Chemical signals can be varied to serve different functions. For example, odoriferous pheromones are involved in mate identifications attraction, spacing mechanism, or alarm devices. Bronson (1971) suggested that pheromones in mice can be classified by function.

Priming pheromones : • Estrus inducer • Estrus inhibitor • Adrenocortical activator.

Signaling pheromones : • Fear substance • Male sex attractant • Female sex attractant • Aggression inducer • Aggression inhibitor.

Many of the substances produced by mammals function as a means of staking out territories or home ranges.

6.2.4 Touch

Short ranged communication in the form of physical contact is used by many animals. In some arthropods antennae covered with sensory receptors are used in such communication system. Antennae are used in such commuonication system. Antennae are used by sub social insects, such as cockroaches and by social insects, such as bees.

Perhaps, the most wide spread use of tactile stimuli occurs during copulation. In many rodents, stimulation of back end of an estrous female produces typical posture of lordosis. In some mammals vaginal stimulation induces ovulation.

6.2.5 Electric field

Two groups of tropical fresh water fish produce electrical signals used in both orientation (electrolocation) and communication. These groups are the knife fish (gymnotid) of south America and elephant nose fish (mormyrid) of Africa. The electrical signals are generated by electric organs that are derived from muscle in most species, but in one family of gymnotids they are derived from nerve.

Now let us consider the characteristics of electrical signals. When an electric organ discharges an electrical field is created in the water. It also disappears when the discharge stops. As a result, electrical signals are ideally suited for transmitting information that fluctuates quickly, such as aggressive tendencies.

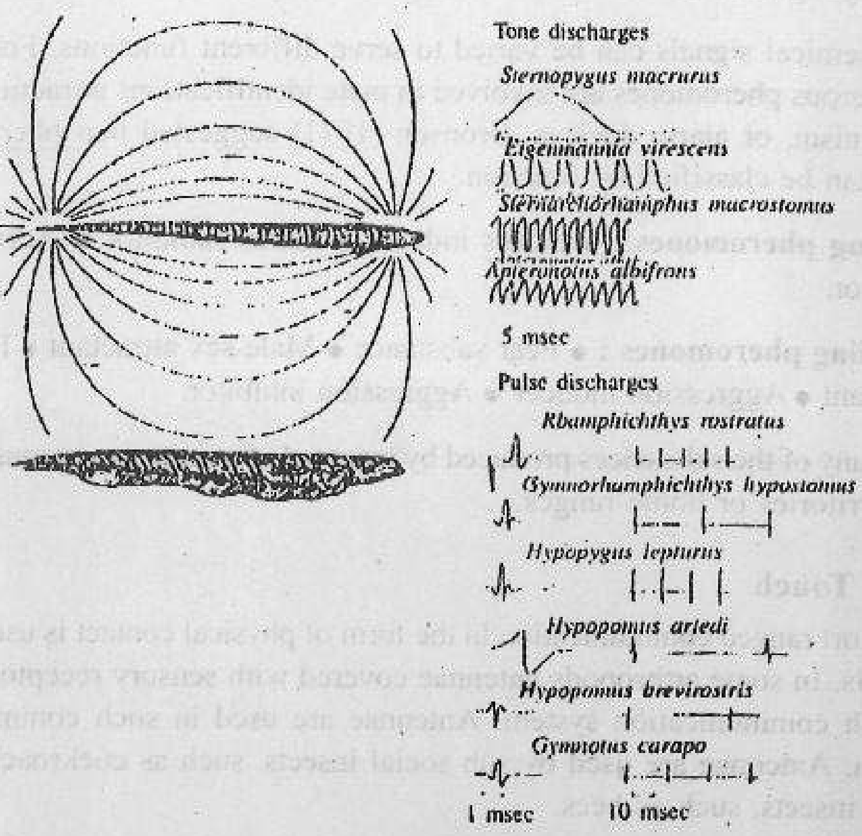


Fig 6.2 : (a) Discharges from an electric organ create an-electrical field around a weakly electric fish that is used as a communication signal. The signal can be varied by altering the shape of the electrical field, the waveform of the electrical discharge, the discharge frequency, and the timing patterns between signals from the sender and receiver, as well as by stopping the electrical discharge, (b) Some species of weakly electric fish produce electrical signals with a delay between each pulse, and others produce a continuous "buzz" of signals. (From Hopkins 1974.)

An electrical signal does not propagate away from the sender, but exists as an electrical field around the sender. Since, the electrical signal is not propagated, its wave form is not distorted during transmission. As a result the wave form of electrical field may be taken as a reliable indicator of the sender's identity.

Discharge from an electric organ create an electric field around a electric fish that its used as a communication signal. The signal can be varied by altering the shape of the electrical field, the wave form of the electrical discharge, the discharge frequency, and the timing patterns between signals from the sender and receiver, as well as by stopping the electrical discharge. Some species of weakly electric fish produce electrical signals with a delay between each pulse, and others produce a continuous "buzz" of signals (Fig. 6.2)

6.3 Species specificity of songs

Communication is an **important** adaptive behaviour for the survival of the species. Intraspecific communication helps in sexual reproduction, prarenting offsprings, alarming dangers and other such actions. The relationship between sexual behaviour and the maintenance of species identity is obvious among animals. The insects, like ***Drosophila*** sp. and mammals like humpback whale ***(Megaptera novaezangliae)*** and some birds have some specific **song pattern** by means of which they can announce their territory or convey message to their potential mates. Such song patterns are highly species specific. Some song patterns are discussed below,

6.3.1 Song and group cohesion across long distance

Payne and McVay 1971 analyzed songs of humpbacked whale ***(Megaptera novaeangilae)***, which are varied, occur in sequences of seven to thirty minutes'

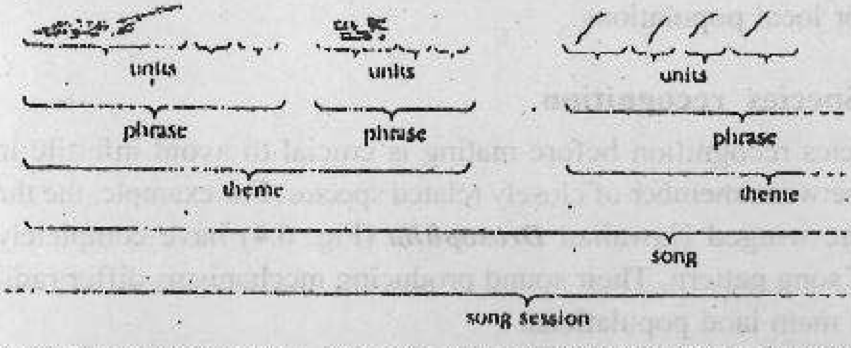


Fig 6.3 : Song of humpback whale. The song of a humpback whale can be broken up into units, phrases, themes songs, and song sessions. Each whale sings its own variation of the song, which may last up to a half hour.

duration with repeated manner. The songs have a great deal of individuality.' Researchers have not yet ascribed a clear function to these sounds. They may-serve to maintain group cohesion across thousands of miles. (Fig. 6.3)

6.3.2 Individual recognition and song

Indigo buntings ***(Passerina cyanea)*** produce a complex song that is quite variable. Most of the phrases are paired (sweet-sweet, chew-chew ....). Emlen (1972) analyzed the song pattern, and discovered the significance of the song. Past of the song sequence was species-specific, communicating the message, "I am an indigo bunting", and another part was variable from individual to individual. Therefore, such type of song pattern is useful to identify both the species and individual performing the song.

6.3.3 Neighbour recognition and song

Falls and Brooks (1975) studied that white-throated sparrow male can recognize neighbours individually or as a class.

6.3.4 Deme (local population) recognition and song

Local dialects in bird song have been demonstrated for a number of geographically separated populations of white crowned sparrows. Females from one population perform compilation-solicitation displays when they hear songs of males from their own population, but rarely do so when they hear songs from another population. This tends to lead to mating with members of locally adapted dames or local populations.

6.3.5 Species recognition

Species recognition before mating is crucial to avoid infertile mating and energy between member of closely related species. For example, the three species of picture winged Hawaiian ***Drosophila*** (Fig. 6.4) have completely different types of song pattern. Their sound producing mechanisms differ radically from those of main land populations.

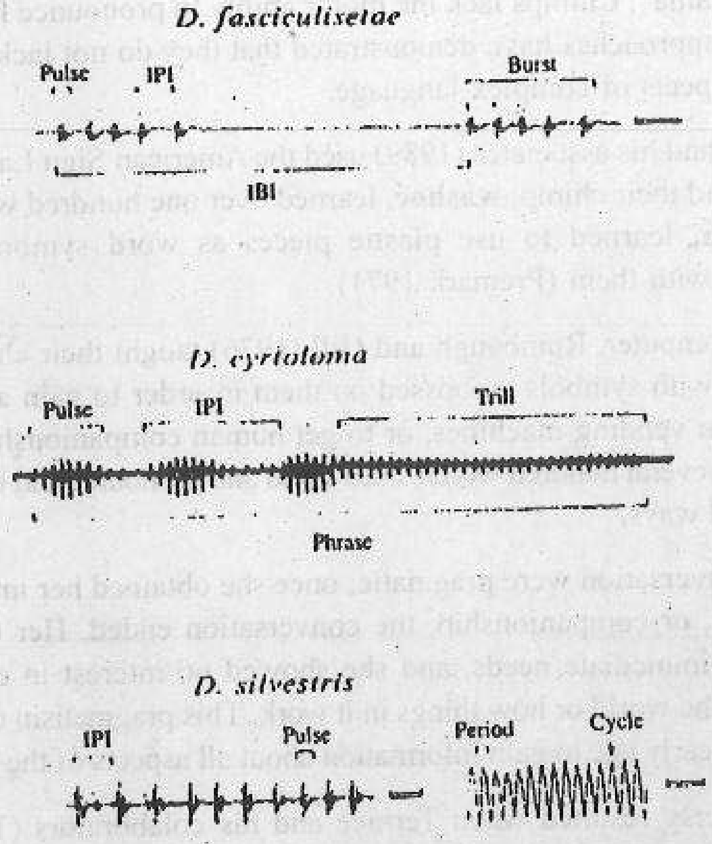


Fig. 6.4 : Song of Drosphila.

6.4 Language acquisition

Communication using unique language pattern has provided a clear-cut separation of humans from other animals. **True language means both the use of symbols for abstract ideas and the understanding of syntax, so that symbols convey different messages depending on their relative position.**

6.4.1 Language acquisition in Chimpanzees

Some researches indicate that there is a potential of chimpanzees *(Pan troglodytes)* to learn language. Hayes (1951) demonstrated that chimp can use human language. Its vocabulary consisted of only a few simple words, such as "cup" and "mama". Chimps lack the motor ability to pronounce human sounds, but different approaches have demonstrated that they do not lack the ability, to learn other aspects of complex language.

Gardener and his associates (1989) used the American Sign Language (ASL) for the deaf and their chimp, **washoe**, learned over one hundred words. Another chimp, **Sarah,** learned to use plastic pieces as word symbols and could communicate with them (Premark 1971).

Using a computer, Rumbaugh and Gill (1976) taught their chimp, Lana, to press buttons with symbols embossed on them in order to gain access to food and drink from vending machines, or to get human companionship. She had a vocabulary of several hundred words, used verbs and pronouns, and could anemble words in novel ways.

Lana's conversation were pragmatic; once she obtained her immediate goal of food, drink, or companionship, the conversation ended. Her curiosity was related to her immediate needs, and she showed no interest in extending her knowledge of the world or how things in it work. This pragmatism contrasts with language at an early age to.gain information about all aspects of the environment.

A controversy resulted when Terrace and his colaborators (Terrace et al. 1979) asserted that chimps could not really create sentences. They worked with their own chimp, Neam Chimpsky (Nim for short, named after the famous linguist Noam Chomsky), and also reanaglyzd the videotapes and films made by other investigators. Nim mastered a respectable vocabulary of sign language words and, like other chimps, used them to convey information to another individual. Nim did use two-sign combinations that were syntactically consistent; he signed the correct "eat banana", for example, more often than "banana eat." But he was apparently initiating his teachers' previous uttarances or responding to other cues, rather than creating sentences of his own. The Gardners sain in response that Nim was trained in an environment unlikely to produce spontaneous behavior and that the film segments of Washoe that Terrace analyzed were too short to demonstrate the complexity of communication (Marx, 1980).

The Rumbanghs questioned whether Lana and her successors, Austin and Sherman, were using symbolic representation in the same way that humans do

Savage-Rumbaugh et. at. 1980). Symbolyzation means the use of arbitrary symbols to refer to objects and events that are removed in time and space. Although chimps may learn to string words together in social interaction routines to attain goals, this accomplishment is not proof that they can do more than associate a word with an object — that is, their language learning does not demonstrate a referential relationship. However in another paradigm, Sherman and Austin learned how to request tools from one another in order to obtain food that they then shared (Savage-Rumbaugh 1986). Thus, if Sherman was shown a container of food that required a wrench to open, he would punch the appropriate symbol on his keyboard. Austin than knew a wrench was needed rather than some other tool, and would hand it to Sherman, who could then obtain the food. This example appears to be a case of symbolic communication between two nonhumans.

Unit 7 ❑ Ecological Aspects of Behaviour

Structure

7.0 Introduction

In recent years scientists tried to relate ecology with the behaviour of organisms. Accordingly a new branch of behavioural science known as ecoethology or behavioural ecology which is particularly concerned with the behaviour of an organism and its relationship and with the living and non living components of its environment. The major aspects of ecoethology now deal with different attribute like habitat selection, food optimization, aggression, territory defenses, dispersal, host-parasite interactions etc. A comprehensive account of all these aspects is given below.

7.1 Habitat selection

A habitat is defined as any part of the biosphere where a particular species can live, either temporarily or parrnanently (Krebs, 2001). The planet earth possesses a mosaic or patchwork of such habitats having a non-random or uniform distribution of organisms. This is because some organisms do not occupy all their available potential habitats even though they could have physically able to dispers into the unoccupied areas.

Habitat selection is a specialized behaviour of an organism and refers to the choice of a place to live. In a particular environment habitat selection is quite a discernible event. But some species can not adapt quickly when habitat changes. Thus they inhabit only a portion of their potential range. This particular behavioural aspect is regarded as one of the most poorly understood eological processes because of the following attributes :

(i) What are the reasons for the presence or absence of a species in a particular habitat (distribution pattern)?

(ii) What are the exact reasons for choice of a particular breeding sites and why so many animals disperse from their brith place.

(iii) How dispersal ability, interactions of other organisms and physico-chemical factors restrict hapitat use?

(iv) Whether the fundamental niche is really often much larger than the realized niche?

[a fundamental niche is a multidimensional space occupied by a species in an ideal condition without having any competition while the realized niche in the space occupied by species under real world conditions involving competitions, predations and diseases].

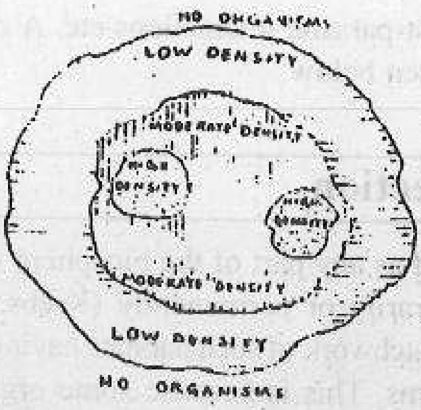


Fig 1: A typical relationship between the spatial distribution and density of a species. High density areas have optimal habitats and are surrounded by saboptimal habitats with lower densities, source : Drickmar, L.C. et.al. 2002.

7.1.1 Different aspects of habitat selection

Two broad aspects of habitat selection have been suggested by Krebs (2001). These two approaches.

(a) **The proximal approach** : This suggests habitat choice as a consequence of behavioural mechanism and

(b) **The ultimate or evolutionary approach** : It suggests the adaptive reasons for habitat choice and also the evolutionary significance of the associated behaviour.

Remark: Animals in most cases use their behavioural mechanisms to select their habitats and consequently individual movements become an essential component of the resulting habitat selection. But an opposite situation is found in case of plants owing to their apparent inability to move from one habitat to another, seeds or spores reach in different habitats through dispersals whether they will either survive and grow or will just die.

7.1.2 Factors associated with habitat selection

The following determinant factors govern habitat selection.

1. Inherited experience and leaning : Several experiments suggest that the genetic manipulation to respond to certain stimuli can be altered by habitat imprinting or early experience. This phenomenon is normally noticed in migratory vertebrates. The migratory birds usually return back to their birth place for nest building and breeding and this produce young at particular intervals. This condition is known as interoparity. However, some organisms produce offsprings only once in their life time—and the condition is known as semelparity. Haser *et al* (1978) demonstrated that salmon hype of fishes, after feeding in the open ocean for serveral years, normally return to the same upstream spawning bed where they were hatched. The olfactory system of these fishes is programmed to respond to **unique odours of the home stream** during their early life (Drickamer, 2002).

2. **Heredity :** Hereditary basis of habitat selection is quiter common among several groups of invertebrates like arthropods (crustaceans and insects), molluscs etc. Some examples include background matching by moths and butterflies in their specific host plants before egg laying, differential habitat preference by ***Drosophila*** larvae etc.

3 **Tradition :** This important behaviour is also common among certain vertebrates and normally passes from one generation to the next through the process of learning. Many species of waterfowl have specific transitory staying places within their migration route. These areas are, used year-after year for resting and feeding during migration from breeding grounds to winter grounds.

7.2 Factors restricting habitat selection

When a species occupies an area and evntually reproduces there, the required conditions will be definitely in its favour. This favourable conditions will help it to compete with other speeies successfully. Behavioural scientists have suggested a useful way to identify the factors affecting the distribution of species and the best way to do that is to determine why it is absent from a place. Krebs (1985) in his earlier work has suggested a methodological approach for studying the geographical distribution of a species. He considered four basic interacting factors with the involvement of behaviour in each category.

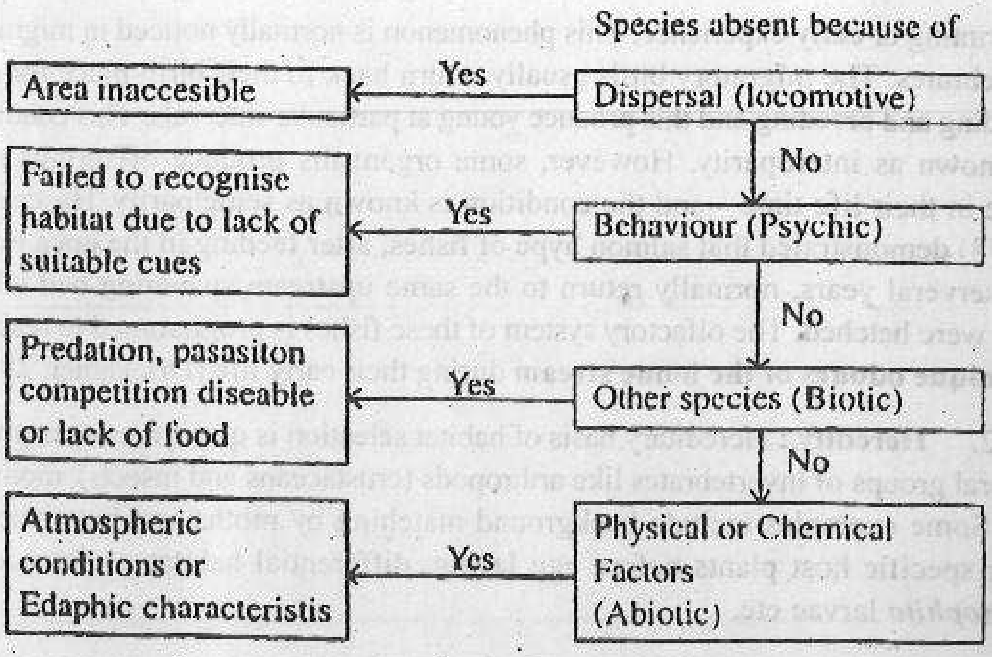


Table 7.1 : Krebs' Species distribution analysis.

7.2.1 Theory of habitat selection

According to Rosenzweig (1985) no single general theory of habitat selection is currently accepted. However, two earlier theories, explainng habitat selection may be mentioned here.

1. Optimal foraging theory : Mac Arthur and Pianka (1966) proposed this theory. This theory predicts that which habitat patch an animal should select and when to leave that patch for another suitable habitat in order to obtain maximum benifit at a minimum cost. One of the major factors for this type of habitat selection is food (energy) although nesting site or mate selections are also equally important factors. .

2. Ideal free distribution : This second approach, proposed by Fretwill and Lucas (1970), predicts about the conditions by which organisms distribute themselves in such a manner so that they can have the highest possible fitness. And for this purpose the animals must have the following :

(i) Complete and accurate knowledge about the distribution of resources ideal).

(ii) They would be passive toward one another.

and (iii) Can more to the best possible site (free).

When the organisms settle in their habitats they get the best resources and consequently their density increases. Gradually they will occupy the less desirable areas and all have the same fitness due to the absence of intraspecific competition.

Anti-predator defenses : In any stable ecosystem, harbivore-carnivore systems involve interactions between the second and third trophic levels. These interactions influence the fitness of both predators and prey. The various species in this system have developed different anti-predator defense strategies.

Defense strategies : Different 'prey' animals have evolved different defensive strategies ranging from chemical defenses to simply overwhelming the predators. The sole aim of all these strategies is affect the 'diet-eath' of the predators and also to minimize the predators ability to secure prey. Various methods are:

(i) Chemical defense :

Several groups of arthropods, fishes, amphibians and snakes produce chemical substances repel predators. The active components in the defensive secretions of many arthropods include saponins, glossypol etc.

(ii) Warning colouration and mimicry :

Some animals also possess warning colouration that send warning signals to would be predators. The black and white stripes of the skunk, bright orange colour of the monarch butterfly, yellow and black colour of many bees and wasp's send danger signals to their predators.

Besides warning colouration, some animals evolved a mimetic or false warning colouration similar to their habitats. Two very popular types of mimicry are —

(a) ***Batesian mimicry*** : Proposed by H.W. Bates (1896). He described that some edible (palatable) species develop resemblances (mimic) to an inedible one (model). Once the predator has learnt to avoid the models, it avoids the mimic also.

(b) ***Mullerian mimicry*** : Described by Fritz Muller (1879). This is a less common type of mimicry where one unpalatable or venomous species mimics another. Such mimicry is advantageons to both.

(iii) Cryptic colouration :

Another important anti-predator defense that makes locating prey more difficult certain colour patterns and behaviours euolved by prey enable them to hide from the predators. Such cryptic colourations involve patterns, shapes, postures, movements and behaviours that make the prey less visible. Cryptic colouration is common among fishes, reptiles and many ground nesting birds.

(iv) Flashing colouration :

This is another type of anti-predator strategy often associated with cryptic colouration. Certain butterflies, grass hoppers, birds and ungulates especially white tailed deer display flashing colour in the form of extremely visible patches when disturbed. This flashing colour distracts and disorient the predators. When the animals having flashing colouration come to rest, the bright or white colours vanish and the animals blend perfectly into their surrounding.

(v) Armor and weapons :

One of the most effective means of defense developed by animals like molluscs, armadillos, turtles and certain beetles. All have such hard armor coats or shells. Porcupines, hedge hogs and echidanas have quills (modified hairs) which effectively drive away predators.

(vi) Behavioural defense :

An important behavioural defense is the alarm calls produced by the prey animals during the sighting of a potential predator. However, it is not clearly known whether the alarm call is altruistic or selfish type. Another type is group living. This behaviour reduces the chances of possible predator activity'and is also known as attack—abatement effect.

(vii) Predator satiation :

This is another unique defense mechanism by means of which the timing of reproduction is manipulated in such a way so that most of the offsprings are produced in a very short period of time. The major advantage is the synchronization of births to reduce predation on the new born. Reduction of predatory activites occurs in three ways.

(a) breeding aduths collectively defends the yong .

(b) interference with the predators ability to pickout a prey individual; and

(c) maintaining a high production rate so that the predators can take only a fraction of them.

Conclusion :

Habitat selection have an impact above the level of the individual affecting population structure and even the formation of new species. However, such mechanism has yet to be established and needs further, probes.

7.2.2 Aggression

Moyer (1976) defined aggression as a complex behaviour that appears to be intended to inflict noxious stimulation or destruction on another organism and is not a unitary concept. However, the act of aggression is precisely described as agonistic behaviour and includes all aspects of conflict like threats, submission, chases and physical combat excluding predatory aggression. Moyer (1976) listed the following different forms of aggressive behaviours —

i) Teritorial — Exclusion of others from the same physical space.

ii) Dominance — Control of the behaviour among conspecific groups due to previous encounters.

iii) Sexual — Use of threats and physical punishment, usually by males for obtaining and retaining males.

iv) Parental — In the presence of newborn, usually by the females.

v) Parent-offspring — Disciplinary action by parents against offsprings.

vi) Predatory—Act of predation and cannibalism.

vii) Anti-Predatory—Defensive attack by prey or predators.

7.2.3 Homing

Several species of animals, either migratory or simply foraging within the home range, usually return to their nest site or den. This process is called homing. Several groups of molluscs especially *Chitons* use the most direct method of homing with the help of a chemical trail. Any disruption to this trail often lead to confusion. It has been observed that they vigorously search the area of disruption during return journey. This kind of coordinated actions, however, are not so well pronounced in other groups.

7.2.4 Territoriality

Territory is an area exclusively occupied by an organism or group and is avidly defended by them. Its allied form is home range—the area used habitually by an animal or group, in which the animal spends most of its time. The area of heaviest use within the home range is the core area. In all these areas, the organisms normally maintain a minimum distance between the members of the same species. This phenomenon is called individual distance. The behavioural mechanism of animals associated with the maintenence of a territory or home range is called territoriality.

Territorial mechanisms are quite common among animals who spend much time petrolling the boundaries of their space and show specific behaviours like singing, visiting scent posts or making other displays. The most common display is the tendency to respond less aggressively to neighbours than the total strangers. This behaviour is called 'dear enemy' phenomenon.

The reason behind the establishment of a territory by an organism is not very clear. Brown (1964), however, suggested a probable reason known as economic defendability. It probably accurs when costs of living (energy expenditure) are overwighted by the benefits (access to resource).

7.2.5 Dispersals

It may be defined as a more or less permanant movement of an individual from an area like the movement of a juvenile away from its place of birth. But it becomes somewhat a problemetic issue since animals have to decide about whether to remain or return at the natal site (emigration) or to disperse to other breeding site (immigration).

In most species of birds and nammals, members of one sex tend to disperse, while members of other sex are **'philopatric'** i.e. breed near the place where they were born. Male mammals usually disperse while the female perching birds who are mostly monogomous normally disperse (Greenwood, 1980).

Causes of dispersals

It can be explained at the following levels

i) ***At the proximate level:*** Individual may be forced out by the parents or other residents or it may respond involuntarily to increase in testosteron levels associated with sexual maturation.

ii) ***At the ultimate level:*** It suggests the long term evolutionary causes of dispusal. When an individual fails to disperse, it will have a lower reproductive success because its offsprings will be compelled to inbreed and therefore will be less viable. Natural selection would then favour the dispersers.

7.3 Host-parasite relation

Hosts are homes (habitats) for parasites and parasites exploit every conceivable habitat on and within them—showing extreme specialization for resource exploitation. Thus parasitism is a situation in which two organisms live together, but one derives its nutrition at the expense of the other. Parasites exhibit a tremendous diversity in the ways they exploit their hosts. They may parasitize plants or animals or both.

Parasites may be ectoparasites living outside the body of the host or endoparasite living within the body of the host. On the basis of size parasites may be microparasites like viruses, bacteria and protozoans or macroparasites like worms, the platyhelminthes, acanthocephalans, roundwarms, flukes, lice, fleas, mites and fungi.

All parasites reach a stage in their life cycle within the host's body when they can not develop further. On this basis a host may be classified into—

a) ***Definitive host:*** an organism in which the parasite becomes an adult and reaches maturity.

b) ***Intermediate host*** : the organism which harbours only some developmental phase of the parasite.

7.3.1 Parasitic transmission

Most successful parasitic transmission occurs when the population of potential hosts is dense, particularly if the parasites depend upon direct contacts among hosts. In animal population (other than humans) rapid spread of parasitic diseases especially in dense population is called **epizootics.** In human the same phenomenon is called **epidemics.**

7.3.2 Host—parasite relations

The relationship between hosts and parasites is best understood by mathematical models. These models suggest the intricate mechanism of prey—predator interrelationships involving the following parameters :

(i) parasite density within the host
(ii) density of the host
(iii) proportion of parasites in the transmissive stage
(iv) rate of production of eggs and subsequent life stages, and
(v) influence of the parasites on the host survival.

7.3.3 Special type of parasitism

At least two specialized typical parasitism also occur in nature. These are (i) Brood parasitism and (ii) Klepto parasitism.

(i) **Brood parasitism**

Here one organism depends upon the social structure of another to rear its young. This brood parasitism may be temporary or permanent, facultative or abligatory, inter or intraspecific. Brood parasitism frequently occurs among ants, wasps and birds.

(ii) Klepto parasitism

It involves the piracy of food by one individual from another. It is most conmon among organism where potential hosts are aggregated in large breeding colonies and feeding groups Birds like hawks, gulls, skurs waders are good examples.

From the eco-ethologcal stand-point, kleptoparasitism is energetically profitable for the parasites but adversely affects the foraging behaviour and enngy budgets of the hosts.

Unit 8 ☐ Social Behaviour

Structure

8.0 Introduction

We can define a **society** as a group of individuals of the same species that is organised in a cooperative manner extending beyond sexual and parental behaviour and well call their behaviour **social behaviour.** The study of social behaviour involves aggregations or group diving cooperative behaviours and eusocial organization of animal societies. In this chapter we will discuss the nature of aggregations cooperative behaviours like altruism, group selection and organization of insect and primate societies.

8.1 Aggregations

The animals live at least part of their life in a group, but the details of their behaviour vary tremendously. Some species barely tolerate conspecifics, and get together only briefly for mating, others live in groups but show no cooperations. Others spend every moment of their lives in cooperative interations with conspecific. The term **group or aggregation** does not imply any particular form of special behaviour or cooperation: the type of cooperation involves pairwise, is called **dyadic interactions.** In these dyadic interactions, two individuals interact in such a way that,the fitness of each is affected by both its own action and the action of the partner. Cooperation can also occur in **polyadic interactions,** that is, interactions that involve more two individuals. One example of polyadic interactions involving cooperation is **coalition behaviour,** which is typically defined as a cooperative action taken by at least two other individuals or groups against another individual or group. When coalition exist for long period of time, they are often referred to as **alliances.** The pattern of aggregations, or groups are called differently in different animals. For example, schooling or shoaling in fishes, flocking in birds and herding in mammals.

8.1.1 Schooling in fishes

Shoaling—sometimes referred to as schooling is a measure of group cohesiveness **motion.** It can be accounted as an **antipredator defence behaviour** in fishes in addition to the potential **hydrodynamic and foraging benefits.**

When a predator is sighted, schooling fish often increase "effective group size" and adopt following antipredator tactics.

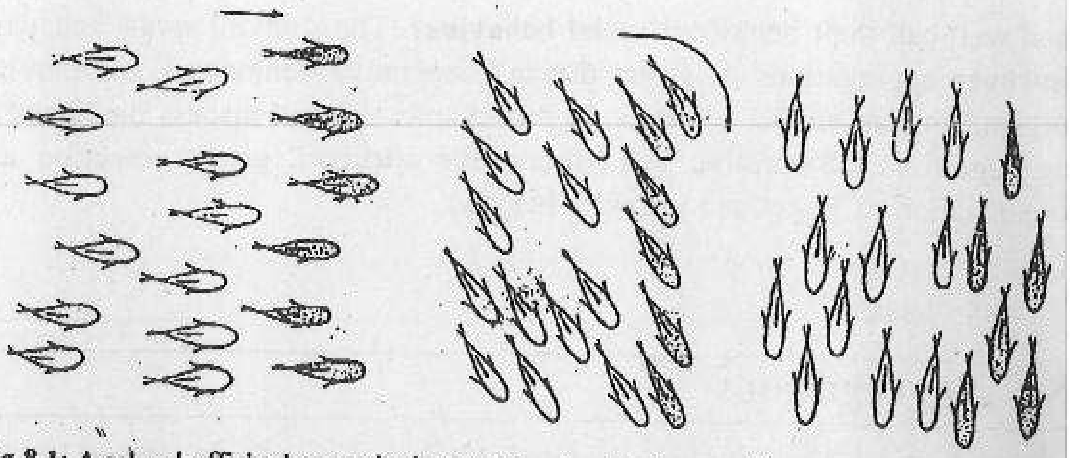


Fig 8.1: A school offish changes its leadership when it changes direction. The leaders at th left (stippled) are shifted to the flank when the school makes a 90° turn, as shown i sequence in the center and at the right (Modified from Show, 1962).

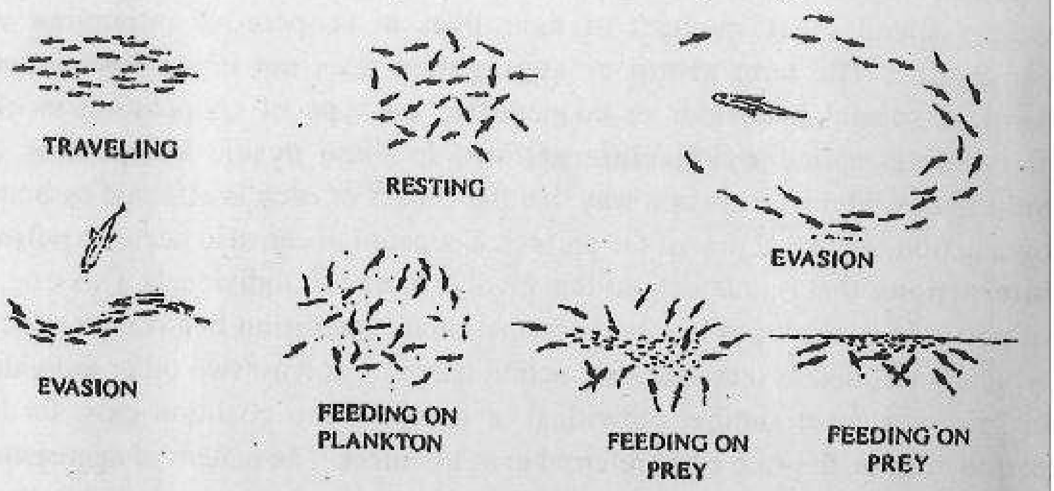


Fig 8.2 : In open water members of fish schools change their alignments according to conditions in the environment. In general, organization declines and behavior is individualized when the fish rest or feed (Modified from Radakov, 1973).

- **Fountain Effect** : Schools, maximize their speed, split around a predator, and then reasemble behind the predator.
- **Trafalgar Effect**: In tight groups, the information about a predator spreads from individual to individual more quickly than in loose school. Trehene and Foster (1981) coined the term "Trafalgar Effect" because it resembled the quick transfer of information through the use of battle signals followed by Lord Nelson at the battle of Trafalgar.

- **Flash expansion :** Tightly packed schools of fish "explode" with fish quickly swimming off in all directions. This can temporarily confuse a predator and allow for escape.

- **Confusion effect :** Schooling fishes often confuse predator by moving around in a erratic patterns within group making it difficult to home in on a single target by the predator. This effect differs from flash expansions in that the school remains in a single group.

- **Predator inspection :** Here, a few individuals break away from a school, approach a predator to gain information, and then return to school, where this information may be spread across individuals.

Evolution of schooling in fishes : ***a cash at study***—The American icthyologist C. P. Haskins (1957*1* conducted a unique study on the effect of predator and schooling in guppy *(Poecilia reticulata)*. Generally speaking guppies from high predation sites school more tightly and in greater number than guppies from low-predation sites. Further **more,** fish from high predation sites inspect a predator less closely than their low-predation counterparts.

At high predation site swimming in large groups provide more protection than swimming in small groups. In the early 1990s, Anne Magurran and her colleagues fortunately observed some natural incidents on the evolution of antipredator behaviour in guppies. This study was the follow-up of the study conducted in 1957 by C. P. Haskins. Haskins transferred 200 guppies from a fish predation site (in the Arima River) to a low predation site (in the Turure River). Magurran realized that after 33 years it was a golden opportunity to examine natural selection on antipredator behaviour on schooling of guppies. If natural selection, via predation pressure, shapes schooling behaviour as an antipredator response, then the lack of predation pressure in the Turure should have led to selection for weakened schooling behaviaur in guppy descendants studied in the 1990s. Magurran and her associates sampled numerous sites in the Turure and examined both the behaviour and genetic composition of fish of these sites. Genetic analysis suggests that the fish transferred from Arima River back in 1957 had spread all arounds the site in the Turure River. Because of strong natural selection pressures, the descendents of Arima River fish evolved schooling in

Turure River more similar-to guppies at low predation sites than their ancestral site of Arima River with strong predation pressure.

8.1.2 Flocking in birds

Studies reveal that two environmental influences on group size or flocks are **food and predators.**

8.1.2.1 Avoiding predation

Living in group might help an individual to avoid becoming a meal of a predator. This could happen in the following ways :—

(a) Increased vigilance: The goshawks are potential predator of pigeons. The hawks are less successful in attacks on large flocks of pigeons mainly because the birds in a large flock take to the air when the hawk is still some distance away. If each pigeon in the flock occasionally looks up to scans for a hawk, the

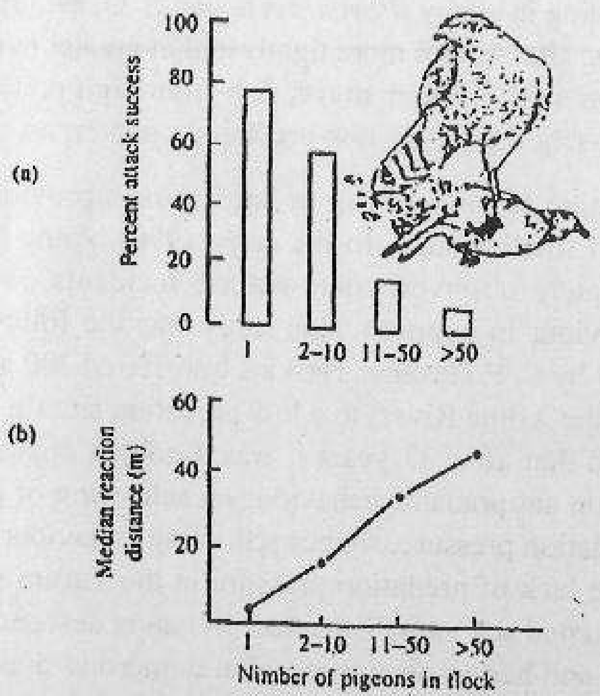


Fig 8.3 : (a) Goshawks *(Accipiter gentilis)* are less successful when they attack larger flocks of wood pigeons *(Columber polumbus)*. (b) This is largely because bigger flocks take flight at greater distances from the hawk. The experiments involved releasing a trained hawk from a standard distance. From Kenward (1978).

bigger the flock the larger the chances to be alert when the hawk looms over the horizon (Fig. 8.3 a, b). The way in which vigilance changes with flock size depends on how individuals in the group spend their time. In ostrich flocks, it is found that each individual spends a smaller portion of its time scanning in group than when lives alone. Therefore, each bird in the flock has more time to feed and enjoy greater protection from approaching lions (a potential predator of ostrich).

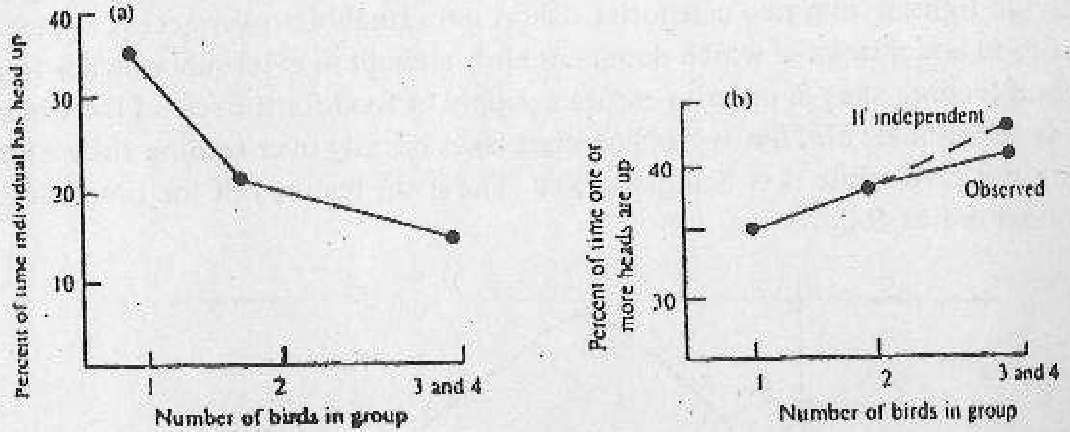


Fig 8.4 : Vigilance in groups : - (a) An ostrich *(Strmhio camelus)* spends a smaller proportion of its time scanning for predators when it is in a group. (b) The overall vigilance of the group increases slightly with group size (solid line), as predicated if each individual looks up independently of the others (broken line). (From Bertram; 1980).

(b) Dilution an cover : By living in large group each individual dilutes the impact of successful attack by a predator because there is a good chance that another member will be the victim. Although there is only a slight increase in vigilance with increasing group size in ostriches, the chances that any one individual will be eaten during an attack by lions decreases rapidly with group size, because the lions can kill only one ostrich per successful attack.

8.1.2.2 Time budget and the optimal flock size / group size : ***A case study of yellow-eyed Junco:*** Ron Pulliam (1976) and Tom Caraco (1979) have used time as a currency and developed a model of optimal group size based on the time budget. The model is used to illustrate the factors influencing winter flocks of small birds. The survival of birds in flock is considered to be dependent on two main risks, **starvation and predation.** The time budget is divided into three types of behaviour associated with these risks : scanning for predators, feeding and infighting for food. The three activities in the time budget are assumed to be mutually exclusive, that is a bird can not, for example, scan and feed at the same time. In order to scan it has to point its head upwards, while picking involves facing forwards the ground. The scanning for predators takes precedence over feeding, since failing to see an approaching predator is more dangerous than failing to eat a seed. Dominant birds give higher priority to satisfying their daily energy requirement than to eviction of subordinates. **Pulliam and Carago** divide fighting into two categories : short term stuabbles over access to pieces of food and attacks in which dominant birds attempt to evict subordinates from good feeding sites in order to ensure a supply of food for the rest of the winter. For subordinate bird the aggression must takes priority over feeding since a bird can not feed while it is being attacked. The main features of the time budget model are as follows :

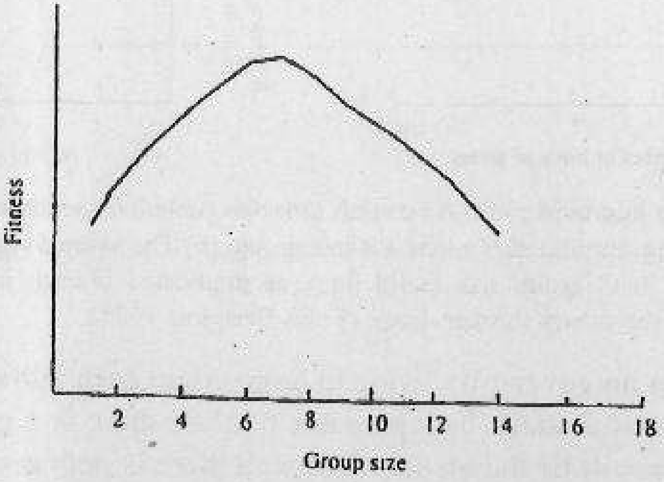


Fig 8.5 : Sibly's model of optimal and stable group size. Each individual join the group that maximizes its fitness, so that the optimal size of seven is not necessarily stable—it will be joined by solitary individuals for example. Alo Sibly (1983).

(1) The proportion of time spent of scanning by an individual is assumed to decrease with increasing group size. The basis for this assumption to that a given level of vigilance can be maintained with less scanning time per individual as group size increases.

(2) As group size increases, and encounters between birds become more frequent the proportion of time spent in aggression increases.

(3) The time spent in feeding is, therefore, maximum in flocks of intermediate size. Using this time budget model the optimum flock size can be measured in different conditions as follows :—

(i) If the only benefit of flock living is to increase the time available for feeding while maintaining a certain level of vigilance, the optimal flock size is the one indicated in the Fig. 8.6a.

(ii) If the benefits of flocking such as dilution and increased vigilance for predators, the optimal flock size may be larger than the one shown in Fig. 8.6b. However, the picture is probably more complicated than Fig. 8.6c, because the optimal flock size may be different for dominant and subordinate birds. Dominant birds obtain a long-term benefit from evicting subordinates, so they should prefer to be in smaller groups.

In order to test whether time budgets influence flock size in the way suggested by the model. Caraco *et. al.* predicted the effect of various environmental changes on flock size. The predictions are as follows :

1. As average daily temperature increases, the dominant bird should have more time to evict subordinates because they can satisfy their energy requirements more rapidly. Flock size should therefore decrease. This prediction was supported by observation on winter flocks of yellow eyed juncos in Arizona by **Caraco** *et al*(1980).

Evolution of group living or flocking in weaver birds : John Crook (1964) studied about 90 species of weaver birds in order to a certain the evolution of flocking in birds. Crook's approach was to search for correlations between the social organization and the species' ecology. The ecological variables he considered.were the type of food, its distribution and abundance, predators and nest sites. His analysis shows that weaver birds fell into three broad categories :

(1) Species living in the forest tended to be insectivorous, solitary feeders, defend large territories and build cryptic solitary nest. They are monogamous, and males and females have similar plumage.

(2) Species living in the savannah tended to eat seeds, feed in flocks and nest in tight colony' in bulky conspicuous nests. They are polygamous

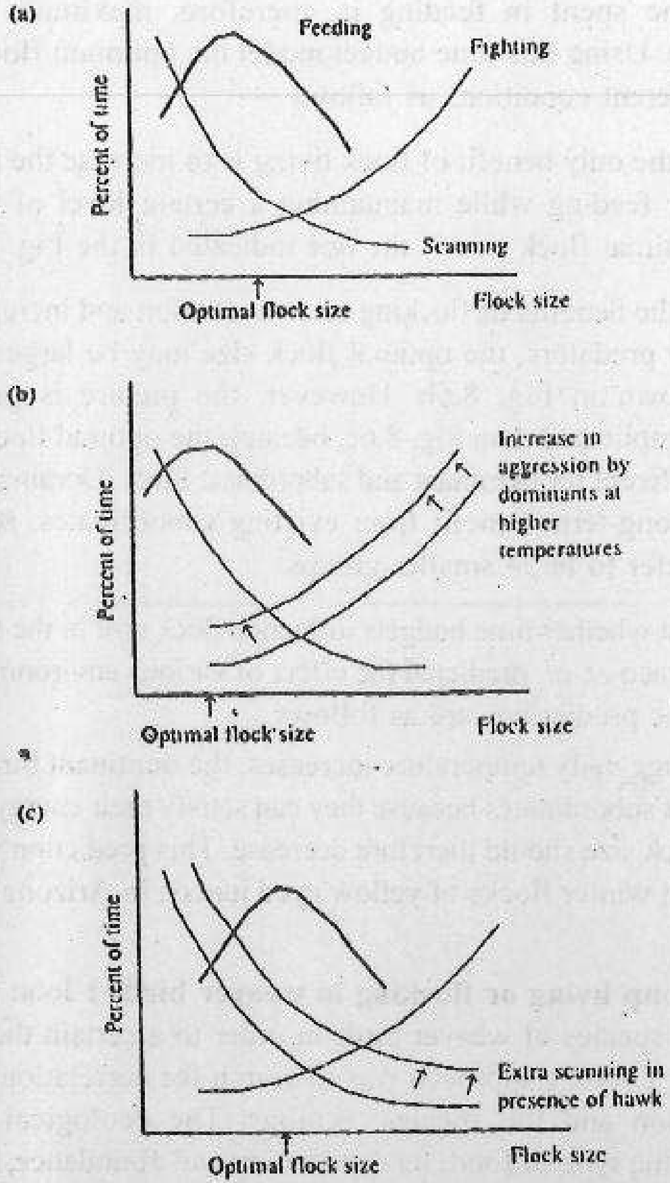


Fig 8.6 : A model of optimal flock size (a) As flock size increases birds spend more time fighting and less time scanning. An intermediate flock size gives the maximum proportion of time feeding, (b) At higher temperatures (or when food is more plentiful dominant birds can afford to spend more time attacking subordinates. The optimal flock size the average bird therefore decreases, (c) When predation risk is increased by flying a hawk over the flock, the scanning level should go up and the optimal flock size is increased. Harval and Pulliam (1976) and Caraco et.at. (1980).

and there are sexual dimorphism in plumage, the males being brightly coloured and the females rather dull.

(3) The species with intermediate ecology have an intermediate social organization, nesting in loose colonies and feeding in flocks.

Crook invoked **predation and food** as the main selective pressures that have influenced the evolution of social organization. His argument was as follows:

1. In the forest insect food is dispersed. Therefore, it is best for birds to feed solitarily and defends their scattered food sources as a territory. Because the food is difficult to find, both parents have to feed their young and therefore stay together as a pair throughout the breeding season. Both must have to be dull coloured to avoid attracting predators. Cryptic nests decrease their vulnerability to predation.
2. In the savannah seeds are patchy in distribution and locally super abundant. It is easy to find patches of seed .being in a group, because groups are able to cover a wider area in their search. Furthermore the patches contain so much food that there is little competition within the flock for food.

In open country the birds can not hide their nests and so they seek safety in protected sites, such as spiny' acacia and date trees. Nests are bulky to provide thermal insulation against the heat of the sun. Many birds nest in the same tree. Within a colony, males compete for nest sites and those defend the best sites attract several females while males in poorer parts of the colony fail to breed. Because of abundant food supply the female can feed the young by herself and so the male is emancipated from parental care and can spend most of his time by attracting more females. This has favoured evolution of polygamy.

(3) Supporting evidences for this inter pretation comes from species with intermediate ecology. The grass land seed-eaters have patchy food supplies so group living is favoured in efficient food finding. However, in grassland the nests are vulnerable, so predation favours spacing out. The result is compromises, these species have an intermediate social organization, nesting in loose colonies and feeding in flocks.

These results show how food and predation may be important in determining flocking pattern in weaver birds.

8.1.3 Herding in mammals

The herding in mammals generally centers around the following factors : (I) Reproductive behaviour, (II) Antipredator defence, (III) Social grooming etc.

(I) **Reproductive behaviour and herding :**—*A case study in lions :* Reproductive behaviour influencing herding in lions includes mate aquisition, raising young etc. Lions live in a **pride** consisting of between 3 and 12 adult females, 1 to 6 adult males and several cubs. The group defends a territory in which it hunts for prey. Within a pride all the females are related, they are sisters, mothers and daughter, cousins and so on. All were bran and reared in the pride and all stay there to breed. For males, life is very different. When they are three years old, young related males (sometimes brothers) leave their natal pride. After a couple of years as monads they attempt to take over another pride from old and weak males. After a successful take over they stay in the pride for breeding for 2 to 3 years before they, in turn, are driven out by new males. The lions pride, thus consists of a permanent group of closely related females and a smaller group of separately unrelated males present for a shorter time.

Within a pride all the adult females tend to come into oestrus in about the same time. The mechanism or causal explanation may be the influence of an individual's pheromones on the oestrus cycle of other females in pride. The function of oestrus synchrony in lions is that different mother breed at the same time, and cubs born synchronously survive better. This is because there is a communal suckling. In addition, with synchronous births there is a greater chance that a young male will have more brothers when it leaves the pride lead a all-male group-life. This will increase the chance of successful pride take over by them.

(II) **Herding in Indian elephants** : Indian elephants live in matriarchal society where the oldest female is the leader. Males leave their-natal families after attaining puberty and then lead more or less solitary lives. They forms transient associations with other males or herds of females they may take over.

Elephant populations are composed of several **clans** and solitary males. Clans are group of elephants, mainly adult females and their offsprings, which may be related to each other. Different clans or members of different clans, however, do not associate with each other. Though associations between clans has been recorded in African elephants.

Clans basically represent large extended families. It should be pointed out that within the clan all members do not associate with each other equally. Some develop special affinities with each other more frequently than with other members of the clan. It is defined as **bond groups** that are actually made up of several family units with special bond between them. These family units comprising adult females and their dependent offsprings are seldom seen apart from each other. The birth of sibling is momentous occasion to the female calf. She adjust to the weaning quickly and play a role of an allomother. This behaviour helps the young females to develop the trait required to be successful mother in later life. At times. Adult females who do not have calves of their own and act as allomother, but this not common. By and large sub adult females play the role of allomother. Females calves continue to live and grow in their natal bond group till they become adults and have family units of their own. They may in fact spend their entire lives in such a group. Ecological stress may sometimes lead to competition for resources between the adult virgin females and their mother or with other bond group members and this could force her to leave the bondgroup.

Unlike females, male calves look upon the arrival of a sibling as competitior. They do not take to weaning and often the mother has to use force to weaning them away. Once weaned males take absolutely no interest in their sibling and contribute nothing to the family. Males reaching the age of nine or ten they are already two big to defend any predator like tigers. Around now they are able to free themselves of the dependency of group bond or clans. Nevertheless, not all contact with the clan was broken as young males continue to return to their natal clan of ten. By the age of 15 male association with the natal clan is irregular at best. Without a doubt, the matriarchal society is the key to the survival of elephants.

(III) Herding in African Ungulates: Jarman (1974) considered 74 species of ungulates. The species were grouped into five ecological categories (Table—8.1). The major correlate of diet and social organization of body size. Small species have higher metabolic requirement per unit weight and need high quality patches of food. These trend occur in the forest and are scattered in distribution, so the small speeds are forces to live a solitary life. At the other extreme, the largest species eat poor quality food in bulk and graze less selectively. It is not economical to defend such food supplies and these species wander in herds. In these herds there is potential for the strongest males to monopolize several females by defending a **harem.** When predator came along these species cannot hide on the open plains and so either flee or rely on safety in members of the herd.[1] Ungulates of intermediate size show aspects of ecology and social organization in between these two extremes.

Table 8.1: Table showing body weight, diet and herd size of different grade of species

Grade	Body weight (kg)	Diet	Herd size
I	3—60	Selective browsing, fruit, buds	1 or2
II	20—80	Selective browsing or grazing	2 to 12
III	20—250	Graze or browse	2 to 100
IV	90—270	Graze	150 to 1000
V	300—900	Graze unselectively	1000 or more

8.2 Group Selection

The change in allele frequency in a panmictic population disrupting Hardy-Weinberg eqilibrium is the usual measure of evolutionary change of microlevel. One of the important parameters introducing such change of allele frequency is **natural selection.** What does selection act upon—single gene and its alleles, individuals, groups or whole species? Natural selection sees the individual organism and its phenotype. It is the organism as a whole that survives and reproduces. Because of this, Charles Robert Darwin and many people consider the individual as the unit of selection. Another view is that the gene and its alleles are best considered as the unit of selection. Groups may also be considered to be selective units. **According to E.O. Wilson (1980) selection can be said to operate at the group level, and deserves to be called group selection.** Just above the level of the individual we can delimit various group : a set of sibs, parents and their offsprings, a close-knit family, an entire breeding population and so on. If the selection affects the frequency shared by common descent in relatives (related by atleast the degree of third cousin) ; the process is referred to as **Kin Selection.** At higher level an entire breeding population may be the unit, so the populations (demes) possessing different genotypes are extinguished differentially, or disseminate different numbers of colonists, such type of selection may be called **interdemic (or overpopulation) selection.** The theory of kin-selection will be discussed later on. let us consider the process **of interdemic (interpopulation) selection.**

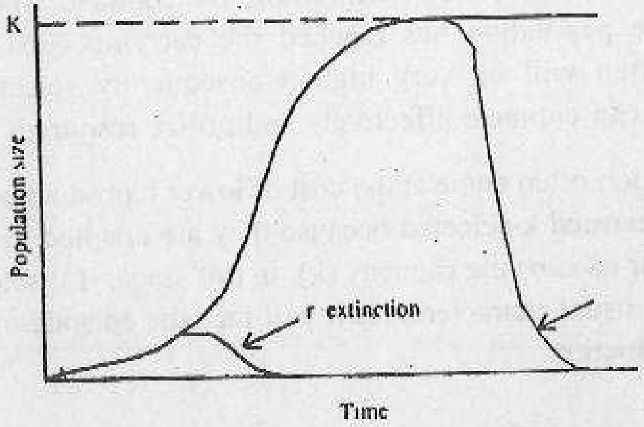


Fig 8.7 : Extinction of a population probably most commonly occurs at an early stage of its growth, particularly when the first colonists are trying to establish a foothold (*r* extinction), or after the capacity of the environment has been reached or exceeded and a crash occurs (*k* extinction). The consequences in evolution are potentially radically different. (From Wilson, 1973).

8.2.1 Interdemic (interpopulation) selection

Species often exists as a network of distinct populations that interact with each other by exchanging individuals. Such network of populations is termed **metapopulations.** Such papulation usually occur in areas in which suitable habitat is patchily distributed and separated by intervening stretches of unsuitable habitat. At any moment of time a given patch may contain a population or not; empty patches are occasionally colonized by immigrants that form new populations, while old papulations occasionally become extinct leaving an empty patch. In considering interdemic selection, it is important to distinguish the timing of the extinction event in the history of population (Fig. 8.7). There are two moments at which extinction is most likely at the very beginning, when the colonists are struggling to establish a hold on the site, and soon after the population has reached the carrying capacity of the site, and is in most danger of crashing from starvation or destruction of habitat. The former event can be called **r-extinct** L and the latter **K-extinction.** At the initial stage of colonization in an empty patch, the population is far below the carrying capacity, resources are abundant, cost of reproduction is low. Selection here favours individuals with the highest reproductive rates (r), such populations are termed **r-selected.** In this stage the extinction of colony is called **r-extinction.** By contrast, when resources are limited, and the papulation has reached the carrying capacity, the cost of reproduction often will be very high. Consequently selection will favour individuals that can compete effectively and utilize resources efficiently.

Such adaptation often come at the cost of lower reproduction rates, and such populations are termed k-selected because they are adapted to thrive when the population is near its carrying capacity (k). In this stage, if k-selected population deviates from its usual characteristics it will face the episode of extinction, and it is called k-extinction.

8.3 Theory of inclusive fitness

Darwinian fitness can be achieved through personal reproduction and care (parental care), and **Kin selection.** The term **Kin selection** was originally defined by John Maynard Smith to account the effects of both parental aid given to **descendant Kin (offspring)** and altruism directed to **non-descendant kinds (relatives other than offsprings).** The term **Kin selection** is, however, currently used very widely by biologists as a synonym for altruism directed to close relatives other than offsprings.

Altruism is a self-sacrificing behaviour. When an animal increases fitness of its close relatives at the expense of its own fitness, it can be said to have performed an act of **altruism.** The self-sacrifice for the well being of own offsprings through parental investment is **altruism** in the conventional sense, but not in the strict genetic sense, because individual fitness is measured by the number of surviving offsprings.

The components of selection and fitness have been shown in the following figure.

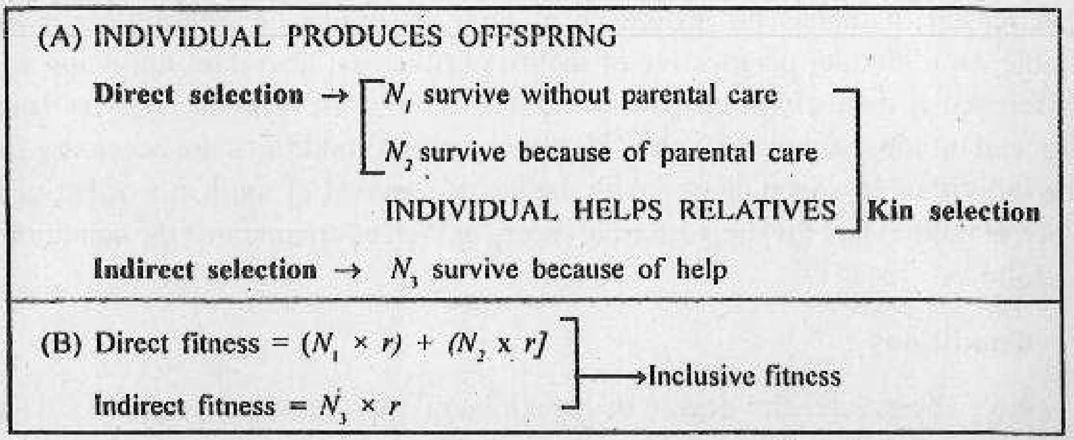


Fig 8.8 : The components of selection and fitness. (A) Direct slection acts on variation in individual reproductive success. Indirect selection acts on variation in the effects individuals have on their relatives' reproductive success, (B) Direct fitness is measured in terms of personal reproductive output, indirect fitness is measured in terms of genetic gains derived by helping relatives reproduce. Inclusive fitness can be considered the sum of the two measures and represents the total genetic contribution of an individual to the next generation (After Brown).

The **direct selection** acts on variation in personal reproductive success. **Indirect selection** acts on variation in the effects individual have on their close relative's reproductive success. **Direct fitness** is measured in terms of personal reproductive output, and **indirect fitness** is measured in terms of genetic gains derived by helping relatives reproduce. **Inclusive fitness** can be considered the sum of the two measures (both direct fitness and indirect fitness), and represents the total genetic contribution of an individual to the next generation through the production **of reproductives** (able offsprings to reproduce).

8.3.1 Kin relection and Hamilton's rules on the evolution of altruism

Usually, alleles of the genes remain in the gene pool of a species. By common ancestry the genes are not found exclusively in the genome of an individual itself, but also in the genomes of their close relatives or kinds with a greater probability. In the case of sexual diploid organisms, half of the genetic traits of the offspring comes from the random meiotic shuffle of the genome of each parent before fertilization. For this reason, each allele possesses an average probability of being found simultaneously in two siblings, which coincides with the probability of being found simultaneously between a parent and each one of its offspring. For this reason, it makes no difference of own offsprings or siblings are made viable. In a broader perspective of inclusive fitness, it also does not make any difference if own offsprings (descendant kins) or offsprings of relatives (non descendant kins) are made viable. However, certain conditions are necessary for the individual to spend energy with the act of survival of the Kin's offsprings. W.D. Hamilton had given us a formal theory as well as enumerated the conditions as follows :

Conditions :

- The greater the degree of genetic similarity between two individuals, the greater the probability that an allele may be shared by two individuals.

- The greater the increase in fitness for the benefited per unit of cost for the performer of the altruist act, the greater the possibility that the gene codifying for this altruistic act will be popagated.

Hamilton's Rule :

Hamilton's rule states that **an altruistic trait can evolve through Kin Selection, if the number of offsprings gained by the recipient of altruistic act, multiplied by the altruist's genetic relatedness to those gained, is greater than the number of offspring lost by the donor of altruist act (which can be achieved by personal reproduction), multiplied by the altruist's relatedness to those lost.**

The entire scheme has been depicted in the following —

- Benefit (b) = $n_1 \times r_1$

  n_1 = number of offsprings of the relative reared by the altruist.

  r_1 = genetic relatedness to the offsprings of the relative.

- Cost (C) = $n_0 r_0$

  n_0 = probable number of offsprings would have been produced by the altruist, if not engaged in the altruistic act.

r_0 = genetic relatedness of the altruist to its own offsprings, if produced.

Rule I

$$\frac{b}{c} > \frac{1}{r}$$

b = benefit to the recipient, C = cost to the donor, r - genetic relatedness between donor and recipient of altruistic act.

This rule is useful to predict when an individual will be selected to sacrifice its own reproductive life to help its relatives.

Rule II

$$n_1 r_1 > n_0 r_0$$

n_1 = number of relatives reared,

r_1 = genetic relatedness to relatives.

n_0 = number of offspring reared.

r_0 = relatedness to offsprings.

This rule is useful to predict when a sterile individual who rears relatives will be selected over a fertile individual who rears its own offsprings.

8.3.2 Calculation of the coefficient of relatedness (r)

r is the probability that a gene in one individual is an identical copy, by descent, of a gene in another individual.

Calculation of 'r' in diploid system :

General method

Draw a diagram with the individuals concerned and their common ancestors, indicating the generation links by arrows. At each generation link there is a meiosis and so a 0.5 probability that a copy of a particular gene will get passed on. For L generation links the probability is $(0.5)^L$. To calculate r, sum this value for all possible pathways between the two individuals.

$r = \Sigma\ (0.5)^L$.

Specific examples

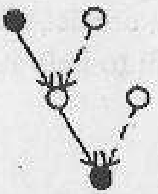
These diagrams show calculations of *r* between two individuals represented by solid circles, other relatives are indicated by open circles. The solid lines are the generation links used in the calculations; the dotted lines are the other links in the pedigrees :

(a) Parent and offspring

$r = 1(0.5)^1$

$= 0.5$

(b) Grandparent and grandchild



$r = 1\ (0.5)^2$

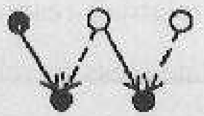
$= 0.25$

(c) Full sibs (brother, sister)

$r = 2\ (0.5)^2$

$= 0.5$

(d) Half-sibs



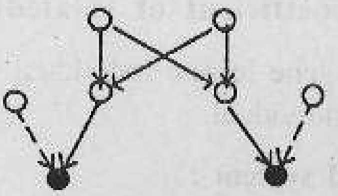
$r = 1\ (0.5)^2$

$= 0.25$

(Identical genes by descent can be inherited by two pathways, either mother or father)

(Identical genes by descent can only be inherited from one parent)

(e) Cousins



$r = 2(0.5)^4 = 0.125$

Table : Coefficients of relatedness (r) for descendant and non-descendant kin in diploid system.

r	**Descendant kin**	**Non-descendant kin**
0.5	Offspring	Full siblings
0.25	Grandchildren	Half-siblings Nephews and nieces
0.125	Great-grandchildren	Cousins

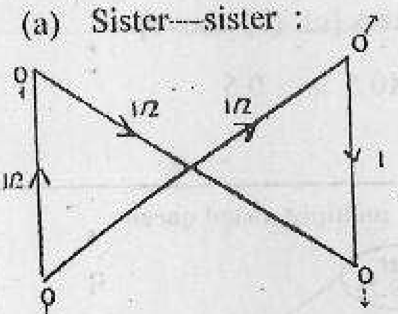
- *Calculating coefficients of relatedness, r, in haplodiploid system.*

General point : Males develop from unfertilized eggs and so are haploid, ll of a male's sperm are genetically identical so the probability of sharing a copy of gene via the father is 1. Females develop from fertilized eggs and so diploid; the probability of sharing a copy of a gene via the mother is 0.5, because of meiosis.

Method : Draw out a pedigree, linking the two individuals through their recent common ancestors. To determine the coefficient of relatedness between individual A and individual B, draw arrows along the pathways, pointing from A to B. Indicate on each link in the pathway the probability that a copy of a gene will be shared.

Examples :

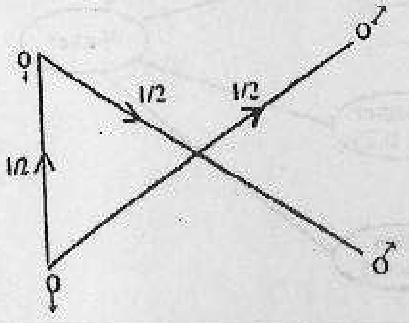
(a) Sister—sister :



Half of a female's genes come from the father; the probability that a copy of one of these is shared with the sister is 1. The other half come from the mother; the probability that a copy of one of these is shared is 0.5.

Via mother = (0.5 x 0.5) + Via father = (0.5 x l)r = 0.75

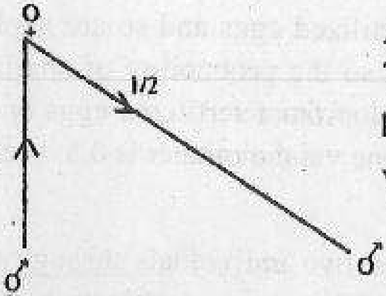
(b) Sister—brother :



A female is linked to her brother only via her mother, as her brother develops from an unfertilized egg. Half of her genes come from her mother; the probability that a copy of one of these is shared is 0.5. The other half come from her father; the probability that a copy of one of these is shared is zero.

Via mother (0.5 x 0,5) + Via father (0.5 x 0)r = 0.25

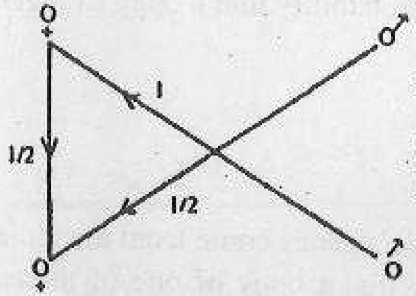
(c) *Brother—brother*



All of male's genes come from his mothe
There is a 0.5 chance of sharing a copy of
particular gene with his brother.

Via mother (1 x 0.5) r = 0.5

(d) *Brother—sister :*



All of a male's genes come form his mothe
There is a 0.5 chance of sharing a copy of
particular gene with his sister.

Note the asymmetry in relatedness betwee
brothers and sisters [cf. (b) above].

Via mother (1 X0.5)r = 0.5

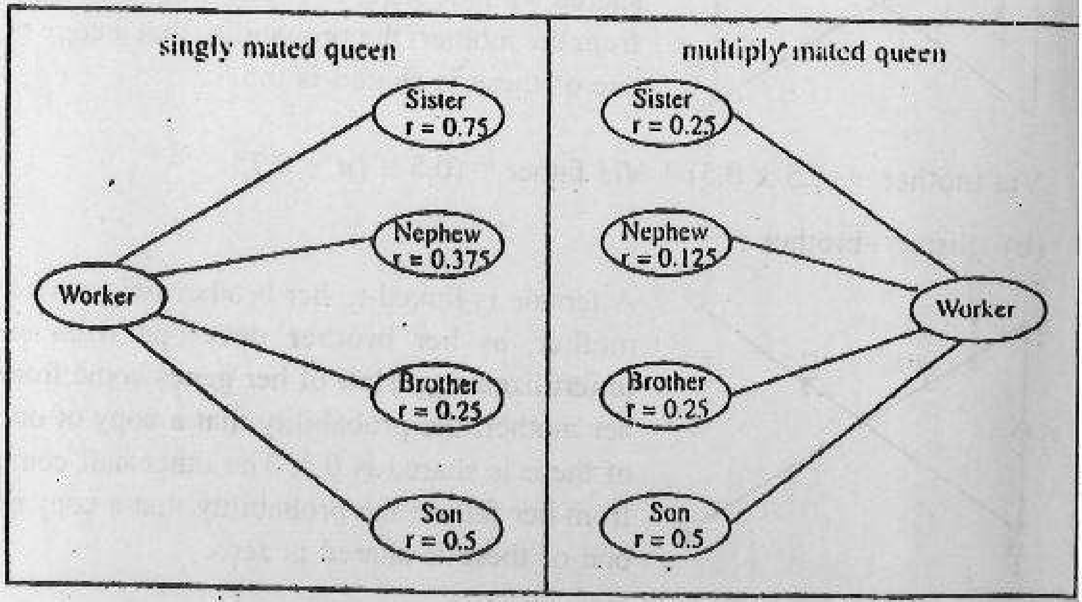


Fig 8.9 : Different classes of relatives and their relatedness levels available to worker hone bees under single mating and multiple mating by the qûeen bee (based on Ratnieks, 1988)

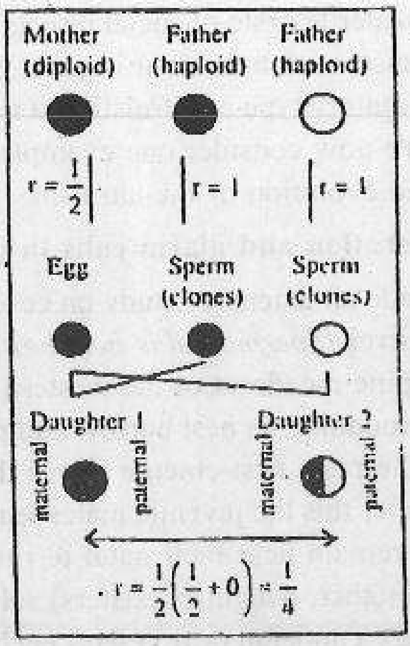


Fig 8.10 : Genetic relatedness under haplodiploidy with multiple matching. Notice that the genetic relatedness between half sisters is 0.25.

Table : Degrees of relatedness between close relatives in a haplodiploid species [(1) in single mating system, (2) multiple mating system]

(1)		Mother	Father	Full-sister	Brother	Son	Daughter	Niece or nephew (via sister)	Half-sisters
	Female	0.5	0.5	0.75	0.25	0.5	0.5	0.375	—
	Male	1	0	0.5	0.5	0	1	0.25	—
(2)	Female	0.5	0.5	—	0.25	0.5	0.5	0.375	0.25
	Male	1	0	—	0.5	0	1	0.25	0.25

8.3.3 Examples of altruism between close relatives

The functions of sterile castes in social insects provide good examples of extreme altruism. The sterile workers are altruistic in another way because they rarely reproduce themselves, but instead help others in the nest (mainly few fertile males and single queen) to produce offsprings.

The act of altruism in sterile caste of social insects is an example of extrem altruistic behaviour, because, such behaviour is genetically and developmentall predetermined. Such obligatory type of altruistic act may or may not follow th rules of kin selection. We now consider one example where kin selection ha been a major force in the evolution of the altruism.

■ Example : Cooperation and alarm calls in ground squirrels

Paul Sherman has made an extensive study on co-operation and alarm call of Belding's ground squirrel *(Spermophilus beldingi), a* diurnal social roden which inhabits the subalpine meadows of the western United States. A femal establishes a territory surrounding its nest burrow and produces a single litter o 3 to 6 young per year. The pups first emerge above the ground at the time o weaning, and then soon after this the juvenile males leave the territory while th juvenile females tend to remain near their natal territory. Sherman found tha closely related females (mother, daughters, sisters) seldom fought for burrow and territories. Indeed they cooperated to defend each other's youngs agains infanticidal members of the same species. Eight percent of all young born wer dragged from their burrows and killed by other non-related ground squirrels Such altruism in form of co-operation among close relatives, in contrast t conflict among unrelated individuals, could be well explained by the theory o kin selection.

The young females who had yet to produce their own young gave alarm call to warn their mother and sisters of the approach of a predator. The alarm caller may suffer a cost for giving the alarm, because they are more likely to b attacked by the predator. Others, however, benefited from the early warning an are more likely to escape.

■ The haplodiploidy hypothesis : the evolution of sterile forms an their altruistic behaviour in social insects

Darwin introduced the idea of natural selection operating at the level of th family rather than of the single organism. If some of the individuals of th family are sterile and yet important to the welfare of fertile relatives, as in th case of honey bees and wasps colonies, selection at the family level is inevitable Here the entire family serving as the unit of selection, and the production o sterile but altruistic offsprings has been adaptive by natural selection.

W. D. Hamilton was the first to fully appreciate the significance of special genetic make up of hymenoptera to form sterile castes. The special feature is haplodiploidy : males develop from unfertilized eggs and are haploid, while females develop from normally fertilized eggs and are therefore diploid. A haploid male forms genetically identical sperms, this means that each of his daughters receives an identical sets of genes to make up half of her total diploid genome. With a diploid father, a daughter would have a 50 percent chance of sharing any particular one of his genes with her sisters, but with a haploid father she is certain to share all of them. The other half of genes come from her diploid mother, so she has a 50 per cent chance of sharing one of her mother's genes with a sister. Now the total degree of genetic relatedness between sisters is 0.5 + (0.5 x 0.5) = 0.75. In other wards, because of haplodiploidy in singly mated system full sisters are more closely related to one another than her parents and offerprings in a normal diploid species. .

Hymenopteran queens are diploid and are therefore related to their sons and daughters by the genetic relatedness value (*r*) of 0.5 only. A female worker can therefore make a greater genetic profit by rearing a reproductive sister (queen), instead of producing her own offsprings becoming fertile. By contrast, in the termites in which both males and females are equally related to their siblings, both sexes may become sterile workers. The cautionary note is that the simple calculations of relatedness hold true only if the colony is formed by a single queen who has mated once. If two workers do not share the same father (half-sisters), they are related by only 0.25. In honey bees, the queen may mate up to 20 times with different males, but the workers are able to discriminate between sister (in real sense, half sisters) that are only related with '*r*' value of 0.25 oly and rear them faithfully.

8.4 Reciprocal altruism

Reciprocal altruism is an altruistic interation between genetically unrelated animals. In this behavioural pattern both participants will gain, if the benefit of an altruistic act to the recipient is greater than the cost of the actor subject to the condition that the altruistic act will be reciprocated at some later date. For example.

A helps B today and then B helps A tomorrow. The problem for its evolution in animals is the possibility of cheating. We will explore the conditions under which reciprocity can be evolutionarily stable by using a simple model called the **Prisoner's Dilemma.**

The **Prisoner's Dilemma Model** : This is an elegant model to illustrate the problems of achieving co-operation in animal societies. Imagine two players in a game who have the choice of cooperating or defeating (being selfish). The payoff matrix is given in the following table with some imaginary numerical values. The values represent the gain in fitness from the interactions.

Imagine a scenario in which two criminals are caught and jailed. The police have good evidence that the men committed a crimes, but they are suspected of a more serious crime. They are questioned separately in different places. Each prisoner has the choice to either cooperate with the other by denying the major crime, or they may defect and accuse the other of the major crime. If both prisoner cooperate (neither acauses the other), the each get a reward R, and pay the penalty only for the minor crime. If both defect (accuse on each other), they each get a punishment, 'P', and have to pay for major crime. If one cooperates and one defects, the defector is set free and gets the best possible reward, T' (the temptation to defect). The prisoner that cooperates when the other defects the sucker's pay off of 'S', because he pays the price for both crimes. The exact values of the pay offs don't matter as long asT > R > P > S, as illustrated in the pay off matrix.

What should a prisoner do? Let us examine it through the analysis of pay off matrix. In a single round of game, player A's best strategy is to defect regardless of what player B does. If player B cooperates, T > R, and if player B defects, P > S. The same logic applies to player B.

Fig 8.11 : The pay off matrix for player A and B in the prisoner's dilemma

	Player B	
Player A	Cooperation	Defection
Cooperation	R = 10	S = 0
Defection	T= 12	P = 2

The imaginary numbers shown are the years saved off of a maximum prison sentence of 12 years (2 years for the minor crime and 10 years for the major crime). The exact values are not important, as long as $T > R > P > S$.

However, both the players will do worse if they both defect rather than if they both cooperate ($R > P$). Hence the dilemma. Therefore, players are predicted to defect when they play a single round game even though pay offs are lower than if the cooperated. What happens when individuals play multiple rounds of the game with they same opponents. After conducting an international computer tournament on the problem the best strategy has been ascertained as **"tit-for-tat"**. In this strategies one player cooperates on the first move and than does whatever the other player did on the preceding moves. Axelrod and Hamilton argue that this strategy is evolutionarily stable and that it shows how cooperation based on reciprocity could get started in an asocial group.

Reciprocal altruism is most likely to evolve if—

(i) Doner must be able to recognize cheats, and refuse to feed previous recipients who fail to reciprocate.

(ii) Sufficient repeated pairwise interactions so that there are interchanges of role and therefore net benefits to all donors.

(iii) The benefit of receiving aid must outweigh the cost of donating it.

❑ Example of reciprocal altruism: regurgitation of blood by vampire bats

Wilkinson (1984) studied a population of individually marked vampire bats *(Desmodus rotimdus),* in Costa Rica. Bats quite often failed to obtain a blood meal during the night and they then begged for blood meal from other roost mates in the day time. In an experiment, it was found that 5 out of 8 bats captured in the evening before feeding and released into the roosts at dawn were subsequently given blood by a well-fed individual in the roost. By contrast, none of 6 bats captured and released after feeding successfully were given a blood meal.

Wilkinson discovered that regurgitation occurred only between close relatives or between unrelated individuals who were perennial roost mates. Such reciprocity has got a evolutionarily stable status as it fulfills all the aforesaid conditions for evolution of reciprocal altruism.

8.5 Social organization in insects

The truly social insects or eusocial insects include all of the ants, termites, and more highly organized bees and waspes. These eusocial insects must include the following traits :

(1) Individuals of the same species cooperate in caring for the young (broods).

(2) There is a reproductive division of labour, with more or less sterile individuals working on behalf of fecund nestmates.

(3) There is an overlap of at least two generations in life stages capable of contributing to colony labour, so that offsprings assist parents during some periods of their life.

These are the qualities by which we can define **eusociality.** The social evolution has been shown in the following table. In the **parasocial** sequence, adults belonging to the same generation assist one another to varying degrees. At the lowest level, they may be called **communal,** which means that they cooperate in constructing a nest but rear their brood separately.

Table : The degrees of sociality in the insects, showing intermediate parasocial and subsocial states that can lead to the highest (eusocial) form of organization.

	Qualities of sociality		
Degrees of sociality	**Cooperative brood care**	**Reproductive castes**	**Overlap between generations**
Parasocial sequence			
Solitary	—	—	—
Communal	—	—	—
Quasisocial	+	—	—
Semisocial	+	+	—
Eusocial	+	+	+
Subsocial sequence			
Solitary	—	—	—
Primitively subsocial	—	—	—
Intermediate subsocial I	—	—	+
Intermediate subsocial II	+	—	+
Eusocial	+	+	+

The next level is quasisociai. in which brood are attended cooperatively, but each female still lays eggs at some time of her life. In the **semisocial state,** quasisocial cooperation is enhanced by the addition of a true worker caste, in other words, some members of the colony never attempt to reproduce. Finally, when semisocial colonies persist long enough for members of two or more generations to overlap and to cooperate, the three basic qualities are complete, and such species are referred as eusocial species (or colony). Once a species has crossed the threshold of eusociality, there are two complementary means by which it can advance in colonial organization : through the increase in numbers and degree of specialization of the worker castes, and through the improvement of communication system by which colony members coordinate their activities.

■ Why is eusociality so prevalent in the hymenoptera?

Hamilton proposed a hypothesis known as haplodiploidy hypothesis in favour of the Explanation of eusociality in hymenopteran insects.

The Haplodiploidy hypothesis :

William Hamilton noted that hymenoptera have an unusual genetic system called haplodiploidy and argued that this predisposes them to eusociality.

Background on haplodiploidy :

- Males are haploid (one X chromosome) and develop from unfertilized eggs.
- Females are diploid (two X chromosomes) and develop from fertilized eggs.

→ As a result of haplodiploidy, females are more closely related to their sisters (full-sibs) than they are to their own offspring.

■

Summary of relatedness under haplodiploidy	**Female**	→	**Sister**	$r = 3/4$
	Female	→	**Daughter**	$r = 1/2$
	Female	→	**Son**	$r = 1/2$
	Female	→	**Brother**	$r = 1/4$

The Haplodiploidy Hypothesis States :

Females will maximize their inclusive fitness by giving up their direct fitness (production of their own offspring) in favor of investments in indirect fitness (production of sisters).

- In other words, in haplodiploid organisms a female's alleles will increase faster in the population when she invests in the production of sisters rather than her own offspring!

■ **Testing the haplodiploidy hypothesis :**

Sundstrom and co-workers determined the sex ratio of reproductive offspring in the wood ant, *Formica exsecta.*

- They found that queens laid a roughly equal number of male and female eggs but that sex ratios were heavily female-biased at hatching.
- They hypothesized that workers (all female) are able to determine the sex of eggs and that they selectively destroy male offspring.

→ In general, female'-biased sex allocation is widespread in eusocial Hymenoptera, indicating that haplodiploidy has a strong effect on how workers behave.

Question : Is haplodiploidy the reason why so many hymenopterans are eusocial?

■ **The haplodiploidy hypothesis and Sex Ratio evolution :**

- Queens are equally related to their sons and daughters, $r = 1/2$, and should invest equally in both.

  —Predict queens to favor 1 : 1 sex ratio of reproductive offspring,
- Female siblings (full-sibs) are related to sisters at $r = 3/4$ and to brothers at $r = 1/4$.

  —Predict female workers to favor a 3 : 1 female biased sex ratio of reproductive offspring.

→ The fitness interest of queens and workers are not the same!

Question : Do queens or workers control the sex ratio of reproductive offspring?

Does the hapiodipioidy hypothesis explain eusociality?

- Researchers used to believe that the answer was yes.
- Now most researchers conclude that the answer is no.
  - → We will consider three reasons why not...

Why haplodipioidy doesn't explain eusociality

1. The prediction that workers favor the production of sisters over their own offspring assumes relatedness between sisters, $r = 3/4$, is greater than between mother and offspring, $r - 1/2$.

- These relatedness values assume that all workers in a colony have the same father and so are full-sibs.

In many species, however, this is apparently not true—

- For example, in the honey bee a queen mates an average of 17.25 times before founding a colony.
- With so many fathers, relatedness among workers is often $r = 1/3$, less than $r = 1/2$ for mothers / offspring.

Why haplodiploidy doesn't explain eusociality

2. In many species, there is more than one queen per nest.

- For example, in invasive populations of the red fire ant, *Solenopsisinvicta*, colonies typically have multiple queens.
- Why haplodiploidy doesn't explain eusociality

3a. Many eusocial species are not haplodiploid, example termite, naked mole rats.

3b. Many haplodiploid hymenoptera are not eusocial, example, Pompilidae, mutilidae.

Table : Primitive (or at least relatively simple) social traits in *Bombus* compared with the more advanced traits found in the highest social bees, the honey bees of the genus *Apis* and the stingless bees of the tribe meliponini. (From Wilson, 1971).

Bombus	***Apis and Meliponini***
1. Queens and workers differ morphologically to a slight degree, and intermediates are common.	1. Queens and workers are morphologically very different from each other, and intercastes are normally absent.
2. The life cycle is annual, at least among the majority of species; new colonies are founded by single queens, and the mature colony size is small.	2. The life cycle is perennial, new colonies are started by swarming, and colony size is moderate to very large.
3. The queen maintains reproductive dominance by aggressive behavior, and the workers tend to behave toward one another in the same way. Workers. Occasionally steal eggs from one another and the queen.	3. The queen maintains reproductive dominance by pheromones, at least in *Apis*, and aggressive behavior is muted or absent. Egg stealing is unknown except as a ritual form of eating by the meliponine queens.
4. The larvae are often reared in groups and must compete with other larvae for food placed indiscriminately in their vicinity.	4. The larvae are reared in separate cells on the brood comb, which greatly increases the chances for individual attention on the part of the nurses and control of caste determination.
5. The larvae are fed with raw pollen and regurgitated mixtures of pollen and honey.	5. In *Apis*, larvae are fed at least in part with special food manufactured by the mandibular and pharyngeal glands.
6. The adults rarely regurgitate food directly to other adults or try to groom them.	6. Both grooming and direct transfer of food by regurgitation are very frequent and, in the case of *Apis* at least, known to play an important role in communication and regulation.
7. The queen regulates colony growth by building all of the egg cells herself and laying in them, following the same behavior patterns by which she initiates the colony.	7. The queen plays no direct role in colony growth or in the construction of the brood combs. The workers determine these matters and are subject to much more feedback from the environment outside the nest.
8. Temporal division of labor is weakly developed.	8. A temporal division of labor is strongly developed, in which the young adult worker first engages in brood care (or nest work), then nest work (or brood care), and finally in foraging in *Apis*, at least, this progression is associated with orderly changes in the exocrine glands.
9. Chemical alarm communication is lacking.	9. Chemical alarm communication is well developed and involves pheromones apparently especially evolved for the purpose.
10. Recruitment among workers is lacking.	10. Recruitment is well developed and mediated by special assembling or trail pheromones, in Apis there is also a symbolic waggle dance.

Table : Basic similarities and differences in social biology between termites and higher social hymenoptera (wasps, ants, bees), Similarities are due to evolutionary convergence. (From Wilson, 1971).

Similarities	Differences	
	Termites	Eusocial Hymenoptera
1. The castes are similar in number and kind, especially between termites and ants.	1. Caste determination in the lower termites is based primarily on pheromones, in some of the higher termites it involves sex, but the other factors remain unidentified.	1. Caste determination is based primarily on nutrition, although pheromones play a role in some cases.
2. Trophallaxis occurs and is an important mechanism in social regulation.	2. The worker castes consist of both females and males.	2. The worker castes consist of females only.
3. Chemical trails are used in recruitment as in the ants, and the behavior of trail laying and following is closely similar.	3. Larvae and nymphs contribute to colony labor, at least in later instars.	3. The immature stages (larvae and pupae) are helpless and almost never contribute to colony labor.
4. Inhibitory caste pheromones are similary in action to those found in honeybees and ants.	4. There are no dominance hierarchies among individuals in the same colonies.	4. Dominance hierarchies are commonplace, but not universal.
5. Grooming between indiduals occurs frequently and functions at least partially in the transmission of pheromones.	5. Social parasitism between species is almost wholly absent.	5. Social parasitism between species is common and Widespread.
6. Nest odor and territoriality are of general occurrence.	6. Exchange of liquid anal food occurs universally in the lower termites, and trophic eggs are unknown.	6. Anal trophallaxis is rare, but trophic eggs are exchanged in many species of bees and ants.
7. Nest structure is of comparable complexity and, in a few members of the Termitidae (e.g., *Apicotermes, Macrotermes),* of considerably greater complexity. Regulation of temperature and humidity within the nest operates at about the same level of precision.	7. The primary reproductive male (the "king") stays with the queen after the nuptial flight, helps her construct the first nest, and fertilizes her intermittently as the colony develops; fertilization does not occur during the nuptial	7. The male fertilizes the queen during the nuptial flight and dies soon afterward without
8. Cannibalism is widespread in both groups (.but not universal,		

8.6 Primate social organizations

In 1932 Solly Zuckerman proposed in "The Social Life of Monkeys and Apes" that the binding force of primates society is sexual attraction. He believed that the uninterrupted sexual life of monkeys, apes and man is the prime force of social organization in primates. Zuckerman's theory is proved wrong. It was disproved by the field studies of primate biology that began to flourish in the late 1950's. The primates have been found to possess distinct breeding seasons. Many of the fine details of social interaction have proved not associated with the reproductive behaviour. The nonsexual phenomena associated with the social organization of primates are (i) presence or absence of territory, (ii) the strategy of defense against predators, (iii) level of intelligence due to large size of brain etc. The scheme presented in the Figure 8.12 postulates certain basic primate qualities to be evolutionary prime mover of social organization.

The basic systems of mammalian reproduction and heredity are ultraconservative. Consequently the reproductive and genetic systems are inertial in their effects.

There is a tendency for males to be polygynous and aggressive toward one another, although pair bonding and pacific associations are permissible. Where long term sexual alliances are not the rule, the strongest and most enduring bonds are between the mother and her offerprings, to an extent that the **matrilinies** can be said to be the heart of the society. Mothers are the principal socializing force in early life. Their influence may even extend to later generations. The second class of ultimate determinants of primate social behaviour consists of the basic **postadaptive traits.** The vast majority of arboreal animals (insects to squirrels) are small and have no difficulty moving through the canopies of trees. However, most primates are unusual in being large arboreal animals. The physiological consequence of this adaptive trait are supportive toward social organization. Being large size arboreal and diurnal they possess the following adaptive features :

(1) Increased manipulative skill and improved vision have increased the level of intelligence.

(2) Greater reliance on visual and auditory communication and reduction of chemical communication are contributory toward increased repertory and composited form of graded signals.

The aforesaid adaptive features consequently result into :

(1) Prolonged socialization and increased in complexity.

(2) Behavioural flexibility, and more variable social organization.

(3) Conducive alliances and complex social strategies.

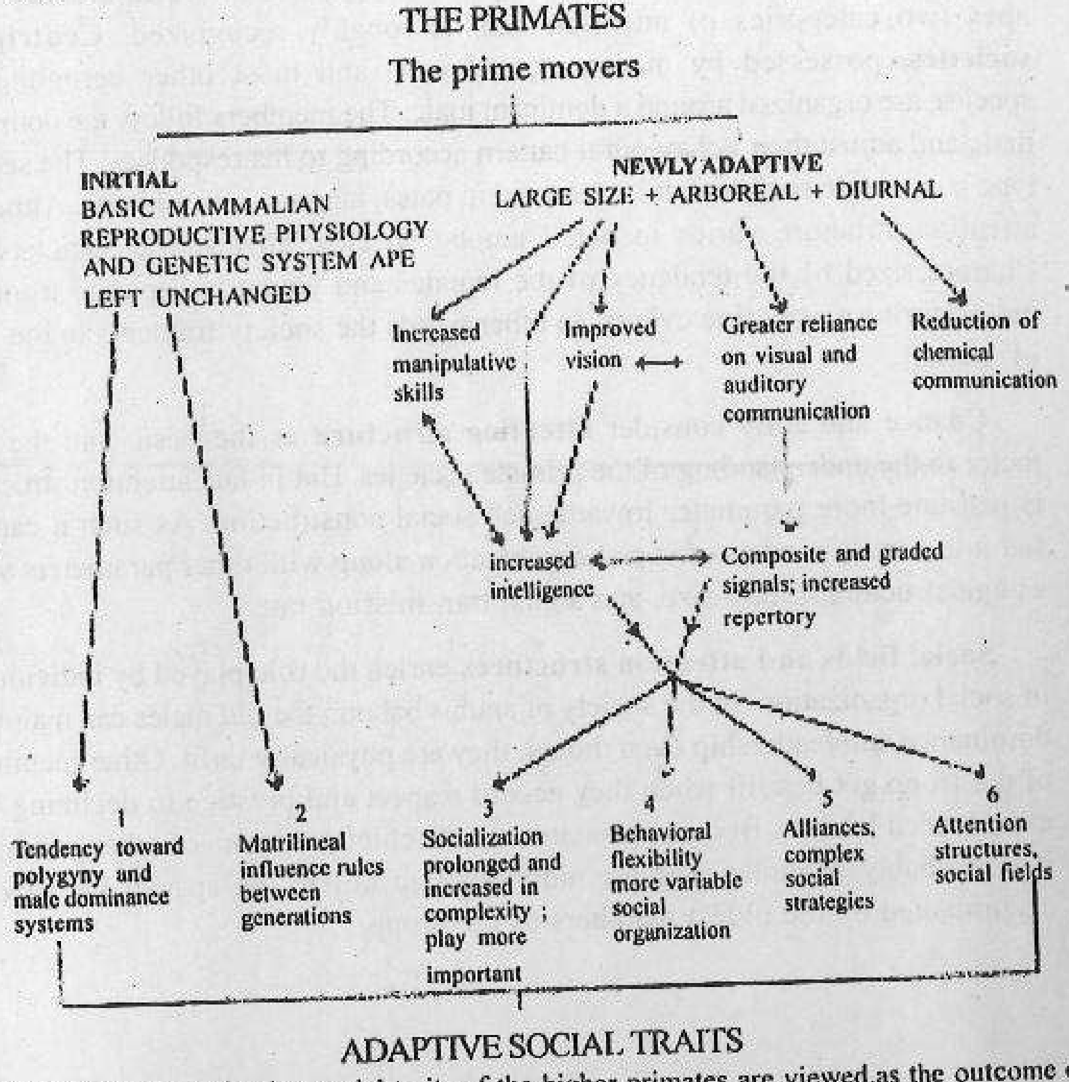


Fig 8.12 : The distinctive social traits of the higher primates are viewed as the outcome of conservative mammalian qualities ("inertial" forces) and adaptation to arboreal life. Even phyletic lines that are now terrestrial have retained the evolutionary advances made by their arboreal ancestors.

In addition to the aforesaid adaptive features of social organization, the primates can evaluate the behaviour of many individuals within the society simultaneously. The animal lives in a **social field** in which it responds to multiple individuals simultaneously. Chance (1967) and Chance and Jolly (1970) have conceptualized the organization of individual social field in terms of the **attention structures** of whole societies. Among the species of Old World monkeys and apes two categories of attention can be roughly recognized. **Centripetal societies,** possessed by macaques, baboons, and most other ceropithecoid species, are organized around a dominant male. The members follow the dominant male and adjust their behavioural pattern according to his responses. The second type is **acentric societies,** it is observed in pates, langurs, and gibbons. Although attention structure varies in detail among species, all acentric societies are Characterized by the tendency of the females and young to separate from the males during aggressive events. In other words the society framents in the face of crisis.

Chance and Jolly consider **attention structure** as the basic and the key factor to the understanding of the primate societies. But in fact attention structure is just one more parameter toward such social construction. As such it can be fed into certain models of social organization along with other parameters such as age structure, group size, and signal transmission rate.

Social fields and attention structures enrich the role played by individuals in social organization. In the society of anubis baboon the old males can maintain dominance and leadership even though they are physically unfit. Other members of the troop get benefit when they accord respect and prestige to declining but experienced leaders. Because primates are the chief predators of other primates, it is probably advantageous for individuals to utilize the special knowledge accumulated by the oldest members of the group.

Unit 9 ❐ Reproductive Behaviour

Structure

- 9.0 Introduction
- 9.1 Definition and types of sexual reproduction
- 9.2 Evolution of sex
- 9.3 Evolution of differences in sex roles
- 9.4 Mating systems
- 9.5 Courtship mating behaviour
- 9.6 Mechanisms of sperm competition
- 9.7 Sexual selection
- 9.8 Parental care

9.0 Introduction

Reproduction and its related behavioural traits create a environment of social interactions. Especially, the mode of sexual reproduction results conflict and competition among individuals of a particular species. In this chapter the important components of sex and reproductive strategies will be discussed along with their related functions like sexual selection, courtship, parental care etc.

9.1 Definition and types of sexual reproduction

Sexual reproduction always involves free haploid gametes, on the contrary asexual reproduction is always agametic phenomenon. Sexual reproduction, in turn can be classified as biparental panmixis reproducing diploid type of organism by means of fertilization or fusion of male and female gametes, and uniparental parthenogenesis-producing haploid organism by means of a single female gamete. In the most micro-organisms, fungi and algae the sexes are anatomically similar and the gametes are all of the same size called **isogamy.** I higher sexual organisms one sex produces few large, sessile, less energeticall and developmentally active gamete, called female gamete or ovum. On the contrar other sex produces many relatively small, motile, energetically cheap gamete— called male gamete or sperm. This difference in gamete size, called **anisogamy** Both the male and female gamete producing organs or gonads may be present i the same organism, called **monoecious or hermaphrodite,** or with separat male and female individuals, called **diecious or gonochoris.** Hermaphrodit animals (e.g. snails) may develop both the male and female gonads anatomicall simultaneously but functionally either maleness or femaleness at a time, sinc they perform cross fertilization. On the other hand some hermaphroditism i sequential in which case first one sexual function appears then the other. Whe male sex is followed by the female sex in the same individual, it is calle **protoandrous** (e.g. some echinoderms), and when female sex is followed b male sex sequentially in the same individual, it is called **protogynous** (e.g. some fishes—coral reef fish *Anthias squamipinnis).* Parthenogenesis is a specia type of sexual reproduction, in which organism develops with a definite se from an unfertilized female gamete. When haploid males are developed b parthenogenesis, it is called **arrhenotoky** (e.g. gamasid mites, honey bee). On the contrary, when haploid females are formed, it is called **thelytoky** (e.g. oribatid mites).

9.2 Evolution of sex

Every thing evolving in the biological world must have a good adaptive value in time and space, otherwise it will be simply washed out in due course of time. The adaptive value of a strategy is determined by estimating its costs and benefits in terms of **Darwinian fitness or reproductive fitness.** Now, let us discuss— why is sexual reproductive strategy so wide spread? The cost of sexual reproductive strategy should be compared with the asexual reproductive strategy. Comparison is given as follow:

Cost

Asexual reproductive strategy	Sexual reproductive strategy
(1) One organism maximizes its genetic contribution to offsprings by creating cloning of itself.	(1) Genotypes are broken up at meiosis and the genes combined with those of the another individual during fertilization. This results 50% reduction in transmission of genes to the next generation, which is known as **cost of meiosis.**
(2) One offspring is sufficient to pass the same number of genes to the next generation.	(2) A female would have to produce two sexual offsprings to pass the same number of genes to the next generation.
(3) The cost of courtship and mating is nil.	(3) The cost of courtship and mating is high-energy consuming.
(4) The cost of producing male is absent.	(4) The cost of producing male is high. Since, most of the sperms are useless, and some of the males never even fertilize single egg, from this point of view males waste resources.

Benefits of sexual reproductive strategy :

Going through the aforesaid comparison one might expect that asexual species will replace the sexually reproducing organisms, instead of, the real picture is reverse. So, let us. discuss the possible benefits of sexual strategies over asexual strategies in favour of evaluation of sexually reproducing organisms.

Benefits of sexually reproducing organisms :

(1) **Faster evolution** : Fisher (1958) first pointed out that sexually reproducing organisms can evolve faster in heterogenous changing habitat. Since the rate of evolution is the function of the degree of genetic variations through genetic recombination and mutations in sexually reproducing organisms such variations are produced.

(2) **Muller's ratchet** : A second advantage was noted by Muller (1964) and

known as **Muller's ratchet.** In asexually reproducing organisms if there is deleterious mutation, it will be transmitted to all its offsprings. Only this type of mutation can be edited out by means of **reverse mutation,** which is an unlikeh event. Thus the ratchet turns on notch each time a deleterious mutation occurs, and such mutations accumulate in the population. On the contrary, in sexual organisms recombinations between two individual with different mutations could produce offsprings with neither mutation. In this way the harmful mutation can be edited out of the population. It is evident from the aforesaid discussion that the **faster evolution and elimination of mutation** from the **gene pool** of a population are the main advantages of sexual reproduction.

9.3 Evolution of differences in sex roles

The differences in sex and sex role are the major characteristic features of sexually reproducing organisms. The sexual dimorphism in the form of male and, female sexes and their corresponding features can be tabulated as follow :

Male	**Female**
(1) Males are those individuals that produce the smaller, motile male gametes,, usually no more than a set of genes in a package. Just large enough to contain the energy needed to drive the male's DNA to an egg.	(1) Females are the sex that produces larger gametes. The eggs are non-motile in nature.
(2) Male gametes are good at fertilizing female gametes, having good fertilizing devices.	(2) Gametes developed better after being fertilized having good developmental devices.
(3) In general, males make less **parental** investment than famale.	(3) Usually, females make larger parental investment than male.

The difference between the sexes in respect to size and function of the gametes each donates to an offspring can be expressed as a difference in **parental investment.** Robert L. Trivers invented this term to emphasize the trade-offs for parents that make contributions to offspring. **Parental investment includes time, energy and risks**

that a parent invests in one or a **clutch of offsprings that reduces the chances that the parent will have more offsprings in the future.** On the plus side, parental investment may increase the probability that an existing offspring will survive to reproduce. But this fitness benefit may come at the cost of the parent's ability to generate prospective additional offsprings in the future.

This is to be noted, that this **theory of parental investment** is applicable solely to **iteroparous organisms,** (Those that have their young at intervals throughout the breeding life. Such as birds, mammals etc.). On the other hand this theory can not be applied to **semelparous breeders,** those that have their offsprings all at once in the whole life. Such as semelparous insects (Butterfly, Moths), fishes like salmon.

Primary sex ratio : The sex ratio at the time of fertilization of female gametes is called **primary sex ratio.**

Secondary sex ratio : The sex ratio at the time of birth or hatching is referred to as **secondary sex ratio. The primary and secondary sex ratio always approximizes 1:1.**

Operational sex ratio : The sex ratio available at the time of mating is referred to as **operational sex ratio.** The operational sex ratio may deviate from **primary and secondary sex ratio.**

This deviation from 1 : 1 ratio can have large impact on the mating system, since members of the abundant sex will compete for access to the scarcer sex.

Reasons for shift in operational sex ratio :

The probable causes for change of sex ratio from primary equal ratio (1 : 1) to an uequal operational sex ratio, may be as follows.

- **Physiological cause** : Owing to differential immune system in sexes, one sex may be proned to some sex specific microbial diseases than other. This type of immunological aspect may result into the change of sex ratio. In mammals, sometimes it may cause such shift of sex ratio.

- **Behavioural cause** : Sex biased infanticide, siblicide are more important behavioural cause of sex ratio change. In primates and carnivorous mammals' (Lion, Cat) male infanticide by intruder males affect the sex ratio. In honey bee male siblicide also responsible for such change.

Manipulation by parent :

In bees and wasps, especially in honey bee, the queen can manipulate the se ratio by manipulating the fertilization of female gametes. The queen mates with several male and reserves sperms in its 'sperm pocket' or **spermatheca.** At the tim of egg laying in brood cells it can release sperm and fertilize some eggs producing diploid females and haploid males parthenogenetically.

Temperature and sex ratio : In some species, sex determination is temperatun dependent. In reptiles, ambient temperature influences the sex ratio. The red eared slider turtle *Trachemys scripta* eggs when incubated at 20°C-29°C, they produce maximum males.

Dispersal and sex ratio : The dispersion of one sex-group from its **natal place** may affect the sex ratio locally. Among birds, usually females are the main dispersers and males are **philopartic** i.e., remain confined to their natal place.

On contrary, males are the main dispersers in mammals (e.g. all male herd of lions and elephants). So, due to sex biased dispersion the sex ratio of local population may be male dominated or female dominated.

- **Local mate competition and sex ratio :**

The parasitoid wasp *Nasonia vitripennis,* lays eggs in the pupal stage of blow fly. Developing wasps feed on the pupa, and the developed flightless males mate with the females developed from the natal clutch. Since, male sibs try to mate with the same sisters, it is called **local mate competetion.** From evolutionary point of view, the breeding system among close relatives makes little sense, because this lowers inclusive fitness. In such situation the operational sex ratio is female biased.

- **Maternal health or Bateman gradient and sex ratio :**

According to a model based on maternal health condition proposed by Trivers and Willard (1973) called Bateman gradient sets the stage for possible deviation from 1 : 1 sex ratio. The model assumes the mothers in the best physical condition produce healthier offsprings that are more able to compete for mates and other resources. For example, male Antarctic fur seal pups are heavier, grow faster and weigh more at 60 days than their sisters. Trivers and Willard (1973) argue that reproductive success of male offsprings should be high if their mothers are in good health, but low, perhaps zero, if their mothers are in poor shape.

9.4 Mating systems

The male biased or female biased operational sex ratio may set the stage for different types of adaptive mating systems as reproductive strategies. The different types of mating strategies can be tabulated as follows.

Mating systems	Characteristics
(1) Monogamy	(1) It refers to bond during mating between one male and one female at a time. Neither sex is able to monopolize more than one member of the opposite sex.
(2) Polygamy	(2) It incorporates all multiple-mating and **nonmonogamous** mating systems.
(3) Polygyny	(3) It refers to bond between one male and more than one females in single breeding period.
(4) Polyandry	(4) It refers to bond between one female and more than one male at a time.
(5) Promiscuity	(5) It refers to the absence of any prolonged bond and to multiple mating by at least one sex.

- **Monogamy and its adaptive value :**

When the habitat contains scattered ecological resources or scarce nest sites, monogamy is the most likely strategy. The formation of long term pairing also seems advantageous, because less time is needed to spend finding a mate during each breeding season. Long-lived birds, such as sea gulls that breed with former mates have higher reproductive success. Probably because of less aggression between rival mates and better synchronization of sexual behaviour.

- **Polygyny and its adaptive value :**

The males usually during their breeding season can produce sperm continuously, which is an astronomically large figure. Owing to such physiological potential, one male can fertilize several egg clutches in different breeding females. This type of polygynous strategy may be practised at the availability of frequent females. The polygamy may be of the following types :

(1) Resource-defense polygyny :

Males defend areas containing the feeding and nesting sites important for reproduction, and a female's choice of a mate is influenced by the quality of the male and its resource of the territory.

Thus, some males with good territorial resource may get two or more mates while others get none. For example, male walnut flies defend sites that are used by females to lay eggs.

(2) Female-defense polygyny :

It occurs when females are gregarious for reasons unrelated to reproduction. Some males, monopolize females and exclude other males from their **harems.** In many species of seals, the females gather on a particular site to give birth, and they mate soon after. The females are gregarious because there are a limited number of suitable breeding sites, and the male monopolize the females for breeding.

(3) Male-dominance polygyny :

If males are not involved in parental care, and have little opportunity to control resources or mates, **male dominance** polygyny may occur. If female movements or their areas of concentration are predictable, the males may concentrate in these areas advertise their quality and courtship signals. These areas where males congregate and defend small territories in order to attract and court females are called **lek**. For example, the males of baya weaver birds *(Ploceus phillipinus)* congregate on tree and display their quality through the well formed nests in order to attract prospective mates.

(4) Scramble polygyny :

In this case, male actively search for mates without overt competition. Female wood frogs *(Rana sylvatica)* congregate in small temporary ponds, often during a single night in early spring. Large number of males rush about attempting to mate with fecund females, sometimes dislodging weaker, already mating males.

Polyandry : In polyandrous systems, females control access to more than one male. Because female investment in eggs exceeds that of males in sperm. The lionesses are polyandrous, because paternity uncertainty may protect the cubs from infanticide by the adult males of the pride. The honey bee queen is polyandrous, and collects large number of sperms in her spermatheca from several males to fertilize large number of eggs. In honey bee society, usually drones/males die after mating and sperm transfer, but queen/fertile female is long-lived and iteroparous in breeding habit.

9.5 Courtship mating behaviour

The courtship refers to the behavioural interaction between male and female usually before the act of mating. **De Morris** defined courtship as the heterosexual **communication system leading to consummatory sexual act. It is often called species stereotyped and instinctive in nature.**

Varied activities forms a part of the courtship behaviour and has a specific function in form of display. One of the most important functions of displays is to attract and bring potential mates at the right time in order to mate. Once a male and female have come together, the male commonly displays and his behavioural pattern may make female sexually receptive.

The success of courtship depends on the fulfillment of four major functions :

(1) Mate finding (2) Persuation (3) Synchronization and (4) Reproductive isolation.

(1) **Mate finding :** In animals mate finding is a highly organised process, which involves one or more of the channels of communication such as olfactory, optic, auditory and tactile devices. In birds, specific calls and songs are helpful in mate finding. In insects, pheromone related chemical interactions are useful in attracting their mates. Fire flies and many of the deep-sea dwelling animals could detect their mates by means of specific light of light producing organ.

(2) **Persuation** : In some group, meeting of male and female leads almost immediately to mating. But in other groups after locating a potential mate, the next hurdle for the male is to bring the female in proximity and make her sexually receptive. In some cases, the female attacks the male and eats him (e.g. some mantis spiders). In these case, male courtship behaviour may serve not only to stimulate the female sexually receptive but also to suppress her non-sexual trophic behaviour.

(3) Synchronization : The occurrence of a same motivation in different individuals at the same time leading to a specific interactive behaviour is called synchronization. Precise synchronization of male and female courtship behaviour is most important factor in reproduction.

(4) Reproductive isolation : The correct and precise follow-up of the process of mate finding, persuation and synchronization results reproductive isolation, which preserves the species uniqueness.

◆ **Some examples of courtship :**

(1) Courtship and mating behaviour of *Drosophila sp* :

Mating behaviour *of Drosophila* consists of species specific fixed action pattern. Such patterns are known as courtship displays and involve a number of elements or signals which are performed sequentially. The visually observable courtship signals and orientation movements of both sexes are performed by specific movement of body.

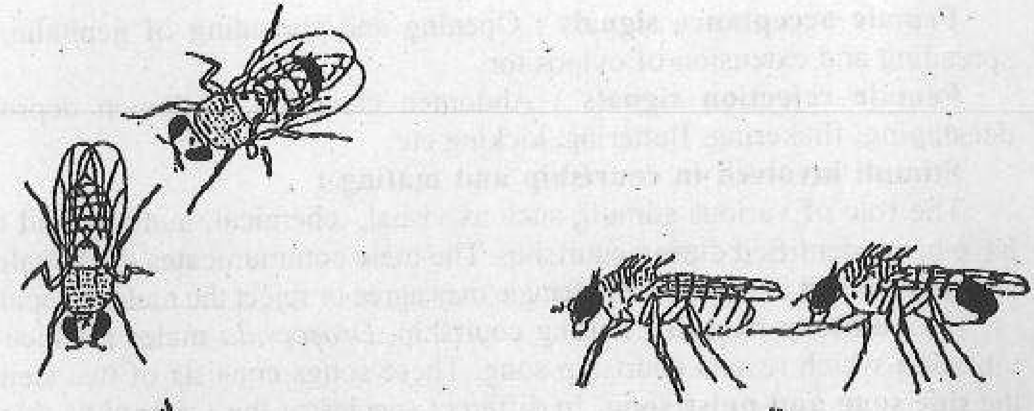
Courtship behaviours that normal sexually mature male performs in response to virgin female.

Male actions are of two types :

(1) Male to male encounter and (2) male to female encounter. In most of the cases, **the forelegs, wings, mouthparts of the male serve as signalling structures.** The female signals are more limited as compared to those of the male and are produced by the **wings, legs, genitalia and movement of the abdomen.** Females perform these signals into two phases : rejection phase and acceptance phase. During courtship, the orientation movement can be described as follows.

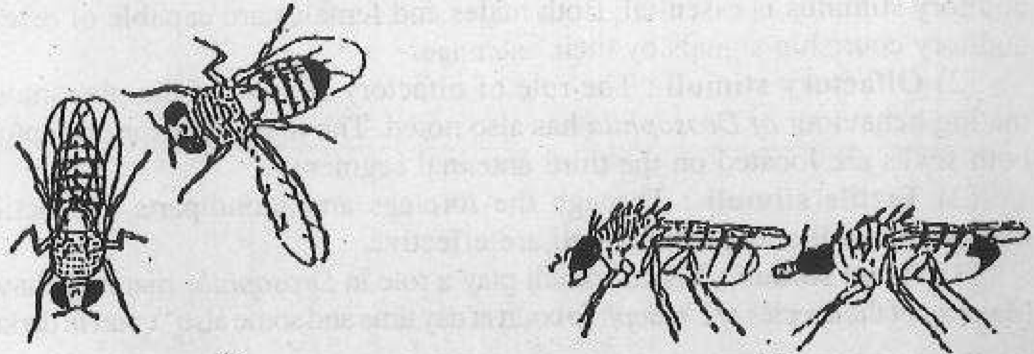
The male initially moves to face the prospective mate and turns toward abdomen of the mate and usually taps the abdomen of the mate. Copulation occurs only if the female responds by displaying acceptance signals. The male positions to the genitalia of the female when she shows readiness for copulation. The male mounts and copulates by curling the tip of the abdomen underwards, simultaneously lunging upwards, and forward pushing his head under or between the female's wings (Fig. 1). Near the end of copulatory phase, the female kicks vigorously backward with her hind legs against the face and thorax of the male. The male withdraws and detached away from the female, falls inertly to the substratum and remains inactive for a short period.

Male courtship elements : Tapping, wing flicking, wing fluttering, wing scissoring, wing vibration, leg vibration and licking.



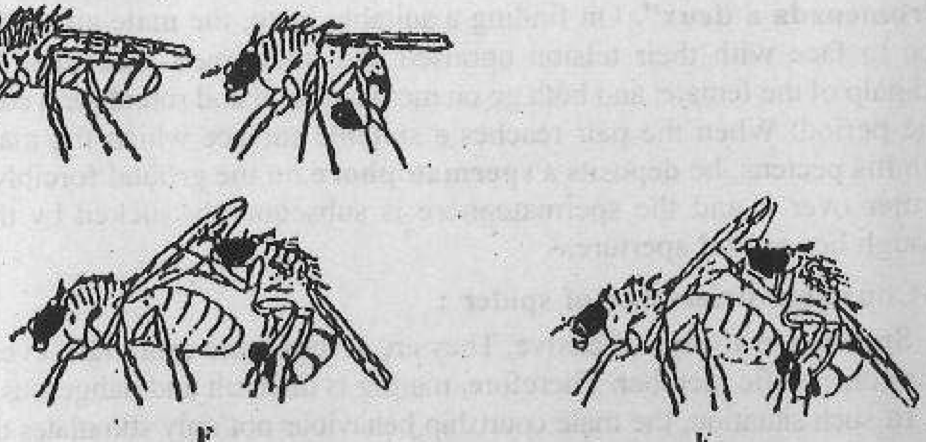
A
Orientation

B
Tapping and Following



C
Wing Vibration

D
Licking



E
Attempted Copulation

F
Copulation

Fig .1. Different Stages of courtship behaviour in *Drosophila*.

Female acceptance signals : Opening and spreading of genitalia, wing spreading and extension of ovipositor.

Female rejection signals : Abdomen elevation, abdomen depression, decamping, flickering, fluttering, kicking etc.

Stimuli involved in courtship and mating :

The role of various stimuli, such as visual, chemical, auditory and tactile have been identified during courtship. The male communicates the female with such stimuli and in response the female may agree or reject the male in copulation.

(1) **Auditory stimuli** : During courtship, *Drosophila* males produce wing vibration which results courtship song. These songs consists of two elements, the **sine song and pulse song.** In different species of the *Drosophila* this song types are of different characteristics. Thus, for species recognition such type of auditory stimulus is essential. Both males and females are capable of receiving auditory courtship signals by their antennae.

(2) **Olfactory stimuli** : The role of olfactory stimuli of the pheromone in mating behaviour *of Drosophila* has also noted. The main olfactory receptors of both sexes are located on the third antennal segment.

(3) **Tactile stimuli** : Through the forelegs and mouthparts the tactile or mechanostimuli and chemostimuli are effective.

(4) **Visual stimuli** : Visual stimuli play a role in *Drosophila* mating behaviour. Majority of the species *of Drosophila* court at day time and some also "court in darkness.

- **Courtship behaviour of scorpions :**

In scorpions, courtship takes place in the form of a dance known as **"Promenada a deux".** On finding a suitable mate, the male and female stand face to face with their telsion upraised and interwined. The male seizes the pedipalp of the female, and both go on moving round and round for a considerable time period. When the pair reaches a suitable surface which the male detects with his pectens, he deposits a **spermatophore** on the ground forcibly jerks his partner over it and the spermatophore is subsequently sucked by the female through her genital aperture.

- **Courtship behaviour of spider :**

Spiders are always offensive. They are invertebrate cannibals; even they eat their conspecific member. Therefore, mating is difficult and dangerous for male.

In such situation, the male courtship behaviour not only stimulates the female sexually but also inhibits the trophic nonsexual behaviour. Among web making spiders, the male vibrates the female's web with some specific signals indicating that he is a potential mate instead of prey items. In some cases, male spider presents the female with a nuptial gift containing a prey item wrapped with cob-web. The mating procedure is quite interesting. Male makes a pad of silk on which a drop of sperm is deposited and is sucked by modified pedipalps. In due course of time, this is inserted into the genital chamber of the female.

- **Birds :**

In birds, the display of courtship behaviour is varied and complex. In some birds, a song is often an important feature to attract and stimulate the female in copulation. Lek behaviour and territorial aggressiveness is the common feature of some birds.

The great crested grebe *Podiceps crestatus* shows elaborate type of courtship (Fig. 2). The courtship ceremony consists of series of behavioural patterns, such as

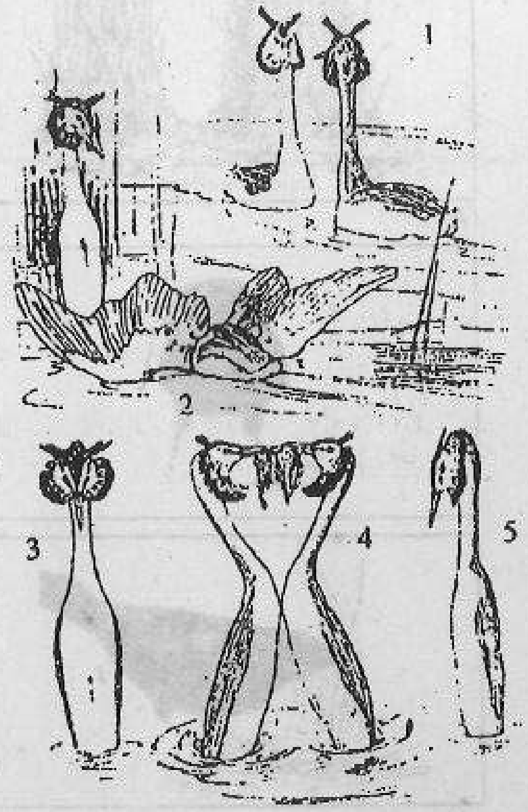


Fig. 2. : Incidents in the courtship of the great crested grebe. 1. Mutual head shaking. 2. The female is displaying before the male who has dived and shoots out of the water in front of her. 3. and 4. Further views of the male rising from the water. 5. Both birds have dived and brought up weeds..

head shaking ceremony; dive; cat display; mutual gretting and penguin dances. The courting birds go through a head shaking ceremony in which they raise their conspicuous head crest, face each other and shake their heads emphatically from side to side. Sometimes when a pair come together, one bird dives when other waits in a cat attitude. The diver then emerges with its back to the waiting bird and closes to it. This often follows penguin dances in which both the birds dive and reappear with bunches of weeds held in their bills. They swim to wards one another, and then spring upright like penguin and move together shaking their heads in a typical pattern.

Fig. 3. : *Ptilonorhynchus* sp. constructs a bower with arched twigs.

The male stain bower birds *(Ptilonorhynchus* sp.) of East Australia (Fig. 3) constructs a bower with arched twigs. One side of it is a display arena in which things like blue parrot feathers, mollusc shells, papers, wasp nests, broken glass etc. as display materials. The male stands on his territory making a whirring round, display his tail in a fan like manner and stiffens his wings. The prospective courting female rounds a few guttural sounds. In the mean time, the female may arrange the disordered twigs of the bower. The male then snatches up one of the display objects and hops arounds.

The Indian peacock, while courting, it spreads its beautiful tail feathers at the approach of a peahen, as she comes near him, he takes an about turn, showing her his rear part. This courtship display may be repeated several times before mating.

9.6 Mechanisms of sperm competition

Sperm competition does not involve individual sperm actually fighting it out to gain access to eggs, rather it involves a selection pressure after mating that has led to two opposing types of adaptation in males. **First, that reduces the chances that the second mate's sperms will be used for fertilization (first-mate advantage). Secondly, that reduces the chances that the previous mate's sperms will be used (second mate advantage).** On the other hand polyandrous female may select among the sperms of different males after copulation, a device called **cryptic female choice.**

- **First-mate devices :**

First-mate devices include, **mate-guarding behaviour** and deposition of **copulatory plug,** both of which reduces the chances of sperm displacement by a second male. In mate-guarding device the male mate prevents his female mate from copulating with other male mate. More commonly, male remains near or physical contact with his female mate ready to react aggressively to the arrival of other male mate. Among mammals, **copulatory plugs** occur in rodents and some primates. In these species males control further insemination of their mated females by other males by sealing the female's genital opening with various secretions. Such sealing of genital opening is called **copulatory plug.** Such plug formation is found in guineapig *(Cavia porcellus}* and deer mice *(Peromyscus maniculatus).*

In fruit flies *(Drosophila melanogaster),* first male mate may also transfer to mated females **antiaphrodisiac** substances that inhibit courtship by other males.

- **Second-mate devices :**

The second mate devices may include **'sperm scooping'** of previous mate and 'dilution of sperms' of the previous mate by frequent ejaculation of large amount of sperm from a second male. Sperm scooping is most evident in damselflies and dragonflies. The male first grasps the front of the female's thorax with specialized claspers at the tip of his abdomen. A receptive female swings her abdomen under the male's body and places her genitalia over the male's penis equivalent, which occupies a place on the underside of his abdomen adjacent to thorax.

The male then rhythmically pumps his abdomen up and down; during this time his penis acts as a scrub brush, sweeping and drawing out any sperm already stored in the female's sperm storage organ or **spermatheca.** In the dunnock *(Prundla modularis),* a small European sparrow like bird, when a male's mate is likely to have mated with another male previously, the present male repeatedly pecks at the cloaca of his mate until she reverts it, sometimes ejecting a sperm bundle. He then reinseminates her (Fig. 4).

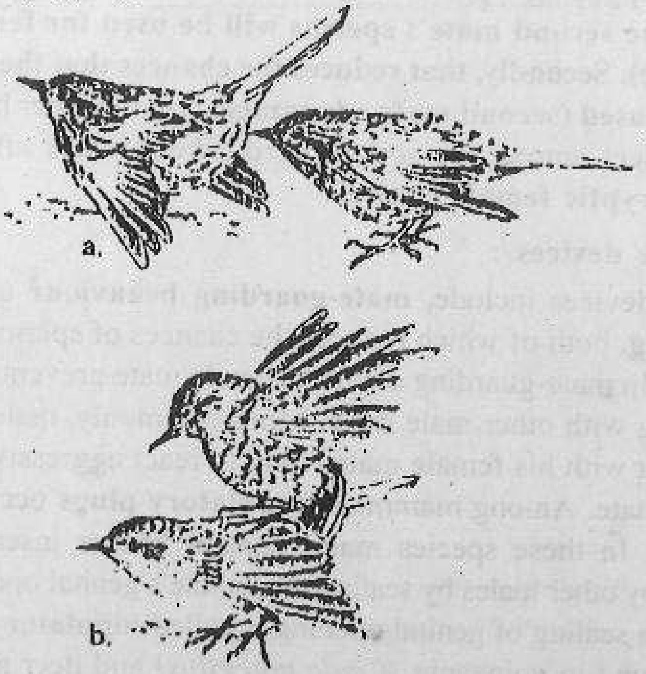


Fig. 4. : Cloaca-pecking in dunnocks. (a) Prior to copulating with a female, the male repeatedly pecks her cloaca, sometimes causing her to eject sperm from a previous copulation, (b) During the very brief copulation, the male appears to jump over the female, and cloacal contact lasts, for a fraction of a second.

In mammals, adaptation of second male is probably restricted to dilution of the first male's sperm by frequent ejaculation of large amounts of sperm from a second male. Females of the rocky moutain bighorn sheep *(Ovis canadensis)* usually mate with more than one male during estrous. Dominant rams guard estrous females from forced copulations by subordinate males. If a subordinate male copulates a already mated female, the dominant male immediately copulates with that female, probably reducing chances that the subordinate male's sperm will fertilize the eggs.

- **Cryptic female choice device :**

In most animals, especially in insects, the male does not place his sperm directly on the eggs, instead places them in some sort of sperm storage organ of the male, usually known as **spermatheca**. In such species, sperm transport and storage is under the control of the female, and when the female mates with more than one male, she has the potential to control which male's sperm fertilizes her eggs. In many species of insects, the male continues to perform courtship displays during and after copulation. These displays function to improve the chances that the female will use the sperm fim horn rather than some other males.

9.7 Sexual selection

The success of potent individual is measured by the number of offsprings it produces. In this respect, the success of male depends on whether he will be allowed or selected by the female/females to fertilize her/their eggs. On the other hand, success of female depends on the selection of good mates with good traits ensuring survival of the offsprings. Darwin (1871) introduced the concept **of sexual selection** traits (in the form of morphological and behavioural traits) that affect an individual's ability to acquire mates. Darwin was not able to explain why it was usually males that competed for access to females in order to mate with them, while females usually seemed to be choosing among males as mates. The explanation was given by Bateman (1948) and Trivers (1972). **Bateman argued that the fertility of the female is limited by the production of developmentally active eggs (fertilized eggs in case of diploid organism and unfertilized egg in case of haploid organism). While in males, fertility is limited more often by the number of female-mates.**

Trivers (1972) generalized Bateman's concept and argued that the **mating systems** and adult **sex ratio** that controls **sexual selection** are function of a single variable-Parental **investment.** Trivers (1972) defined parental investment as **"any investment by the parent in an individual offspring the increases the offsprings chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offsprings" (expected future offsprings).**

The female's general parental investment may be enumerated as **nutritive egg production; selection of good egg-fertilizing mate; energy and time and other costs for raising offsprings in the form of parental care.**

On the other hand the general parental investments of male are fertilization of eggs of a single female (in case of monogamous strategy) different females (incase of polygynous strategy) and additional investments in case of monogamy are nest building, protection and feeding of offspring etc. From the aforesaid discussion it is apparent that, generally the female's parental investment is most cost effective from both sides of male and female. Since, the fertility fitness of both sexes depends on the development of eggs to viable offsprings. Hence, the females have to play most important role, and to pay more costs for parental investment than male. It is also apparent from the afore-made discussion that the **sexual selection** by the females to have good fertilizing genes in order to produce quality offsprings is a parameter of **parental investment.**

The supply of fertilizing -sperms having good genes may be done by the sexual selection either at the level of **intersexual selection** (among the opposite sex) or at the level of **intrasexual selection** (among the members of the same sex).

- **Intersexual selection :**

Darwin proposed that, in animal kingdom males as sexual partner compete among themselves displaying some characters to attract the females for copulation and females choose selectively someone as her breeding partner. Therefore, intersexual " selection is synonymous to **'choice of female'.** Most naturalists after Darwin discounted the importance of mate choice in evolution, but in the last two decades it has become widely accepted as an important evolutionary force. Subsequently various views have been put forward to explain the phenomenon. These are discussed as follows :

- **Runaway selection hypothesis :**

Fisher (1958) proposed a model for sexual selection of male's **epigamic traits**

The character of an animal which is concerned in sexual reproduction other than the gonads and their associated systems which convey the gametes, e.g. bird song, antlers of deer, plumages of bird by females using birds as an example. Suppose a plumage characteristic in males, such as a longer tail, is attractive, for some reason (for e.g. owner is better parental investor) to female. Second condition is that, tail length is heritable in males and preference for the tail length of male sex is also heritable in females. Hence, the development of tail-length trait will proceed in males as will the preference for the female, resulting in a self-reinforcing, **runaway selection process** (Fig. 5). An extreme result of this process is seen in peacock.

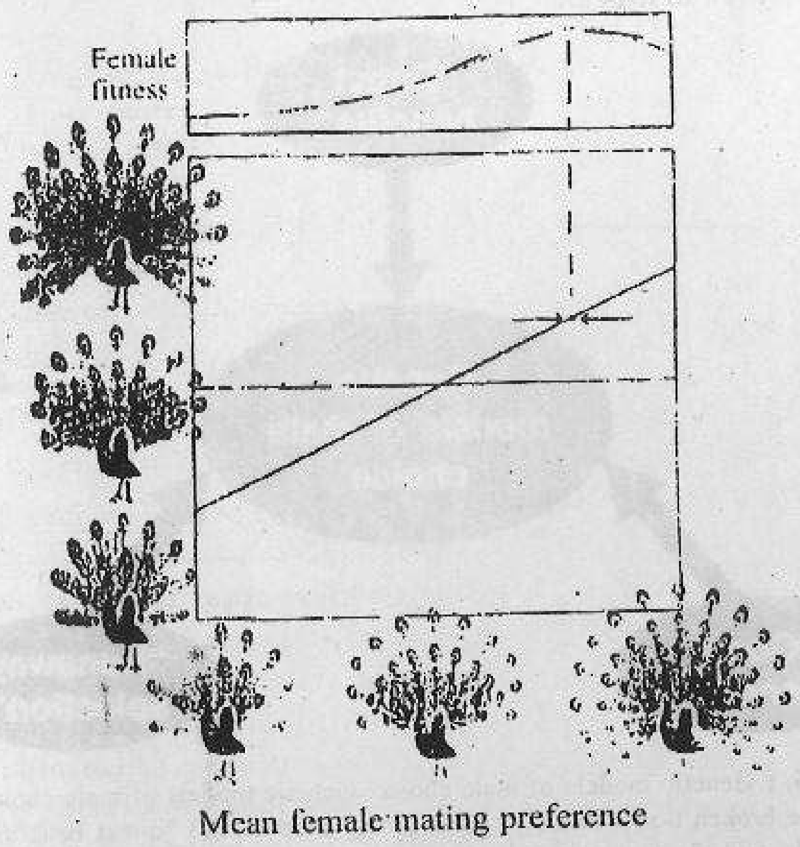


Fig. 5. : A graphical representation of the direct benefits model of female mate choice. Here males provide a direct benefit (food, safety, and so on), and females choose males based on how the benefit affects their fitness.

- **Selection for 'Good genes' hypothesis :**

  Selection for 'Good genes' assumes that the eigamic trait favoured by females, in some way indicates male's fitness. The phenomenon is explained by Zahavi (1975) by his **handicap hypothesis.** Some traits preferred by females in males are detrimental to survival and both costly to produce. For example, the conspicuous and costly to produce tail feathers of some birds, or a stag that can afford to spend energy on a huge bony growth of antlers, are equally detrimental to their survival value because such handicaps could make them easy victims of predators. In spite of these **handicaps,** if they are able to survive and breed, these **handicaps** must be linked to their **over all genetic fitness.** The important notion of this hypothesis is that **"truth in advertising"** and the apparently handicapped traits are reliable index of the male's over all fitness.

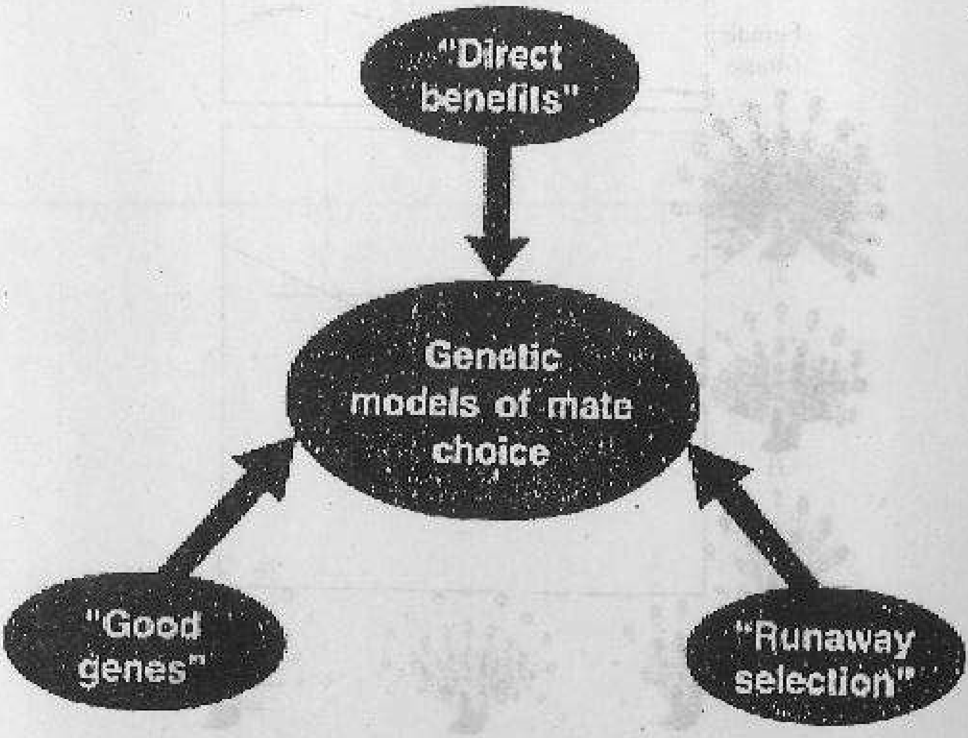


Fig. 6. : Genetic models of mate choice. Genetic models of mate choice can be broken down into (t) "good genes" models, (2) "direct benefits" models, and (3) "runaway selection" models.

- **Intrasexual selections :**

It is the direct competition between the males. It is an event of male rivalry. Rivalry among females is rare in animal kingdom. In red deer *Cervus elaphus* stags grow antlers each year during breeding season. They fight each other for the winning of females which usually do not have antlers. The winner takes possession of all the females of a herd. Now the females have no choice in selection of mates. In this case, the female's mate selection is done by the intrasexual selection by males indirectly.

In is to be noted that, since stags do not have antlers during non-breeding reason and since females do not have antler at all, it is unlikely that antlers are protective arms against predators, rather it is an organ necessary for the intrasexual selection among stags.

Although Darwin, Fisher, Zahavi thought that sexual selection is a process distinct from natural selection, some biologists argue that both are inseparable.

9.8 Parental care

Parental care is a component of **parental investment.** In **iteroparous** animals, parental care is cost an effective phenomenon, since the parents invest energy and time at the cost of future offsprings. Since, parents increase **direct fitness** through the protection of self-offsprings it seems to be a **selfish behaviour** rather than **altruistic approach.** Some authors (Metcalf *et al*) define parental care as an altruistic behaviour from the gene-centric point of view. Since, parents are loosing the perpituation of some genes as they render parental care to their present offsprings at the cost of some future offsprings. Indeed, from the gene-centric point of view both the parental care and altruistic behaviour through kin-selection is out and out selfish in nature as the main objective of both strategy is to perpetuate the genes of the self.

The phenomenon of direct parental care is not a universal strategy in animal kingdom. The act of parental care depends on mating systems, mode of fertilization and ecological factors.

- **Ecological factors :**

Ecologists have attempted to relate environmental conditions to parental care. These can be categorised as **k-selected strategy** and **r-selected strategy.**

k-selected strategy : Species adapted to stable environments have a tendency toward larger body size, slower developmental rate, longer life span and having youngs at intervals **(iteroparity)** rather than all at once **(semelparity)**; such stable conditions favour production of small number of youngs that receive extensive parental care and thus have a low mortality. Such species are said to be k-selected, in reference to the fact that populations are usually at or near 'k'—the carrying capacity of the environment. Example—Mammals.

r-selected strategy : The species, that are adapted to fluctuating environments have high reproductive rates, rapid development, small body size - and need little parental care. Such populations are controlled by physical factors, and mortality rate is high. This is said to be **r-selected,** where 'r' refers to the reproductive rate of the populations. Example—insects and some fishes like salmons.

- **Mating systems and parental care :**

The relation of parental care to mating systems, if present, can be tabulated as follows :

Mating systems	Participant of Parental Care
Monogamy	Both the parents
Polygyny	Only female
Polyandry	Only male

- **Mode of fertilization and parental care :**

The relationship between mode of fertilization and parental care can be discussed by the following hypotheses :

(1) The "Low reliability of paternity" hypothesis :

Mart Gross and Richard Shine proposed this hypothesis based on the fact, that females are more likely to be the parent of an offspring when internal fertilization occurs in a polygynous mating system. In this case, when a female lays a fertilized egg or gives birth to an offspring, this progeny will definitely have 50 percent of her genes. In **polygynous** system, a male has no such assurance, especially if his partner practices **internal fertilization.** Therefore, the male runs the risk of caring for progeny other than his own; his potential gain from parental care is uncertain. At the same time the maternal care will be assured fully.

(2) The "order of gamete release" hypothesis :

According to this hypothesis **internal fertilization** should be linked with **exclusive maternal care,** because after a male inseminates a female, he can departs at once in polygynous system.

In this case, the female would be forced to provide maternal care at the absence of her mate. In contrast, when fertilization is external, females often deposit their eggs before males shed their sperms. Thus, female will flee, leaving the males to face the responsibility of parental care. Data on the relationship between mode of fertilization and parental care in fishes and amphibians are consistant with the **'order of gamete release' hypothesis.**

- **Cost of parental care for male and female :**

Male typically pay a mating cost for parental care; losing fitness when caring for youngs interferes with matings of new mates. In contrast, for female, parenting may involve an unmitigated fertility cost in terms of loss of future egg production. When a female gives parental care to one brood she cannot eat as much as she could by foraging freely and so cannot grow as rapidly as she might otherwise. This loss of growth sometimes damages the fecundity power of the female, since it increases exponentially with increasing body size. In other words, for each unit of growth loss a female pays an especially heavy price in loss of eggs produced in the future.

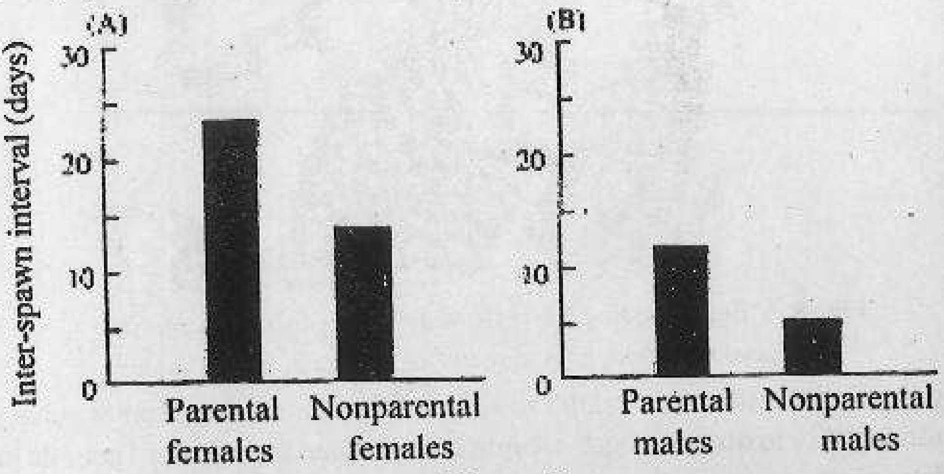


Figure 7. :

The cost of parental behaviour for males and females can be observed in a mouth-brooding Cichlid St. Peter's fish, in which either male or female may care for their youngs by orally incubating the fertilized eggs. In this case, both sexes lose body weight when mouth brooding, since they cannot feed. Furthermore, the interval between two spawnings increases for both parental male and female, compared with male and female whose clutches are experimentally removed from their mouths (Fig. 7). The mean nonreproductive interval is greater for brooding females than for brooding males. Moreover, parental females produce fewer young in their next clutch than non parental females. Whereas parental males are able to fertilize same number of eggs in their next spawning as nonparental males could do. Thus, although both sexes pay a price for parental behaviour, the costs of brood care to females seem especially high.

- **The back-brooding in waterbugs :**

Among the exceptional parental insects are water bugs. In some cases, the male guard and moisten clutches of eggs *(Lethocerus sp.)* that females glue onto the stems of aquatic vegetation above the waterline. Males in some other genera of water bugs (e.g. *Abedus, Belostoma)* permit their mates to lay eggs directly on their backs, after which the males take the responsibility for the welfare of the eggs. A brooding male *Abedus,* spends hours perched near the water surface, diving up and down of water surface repeatedly and to keep well-aerated and moistening the eggs by turns.

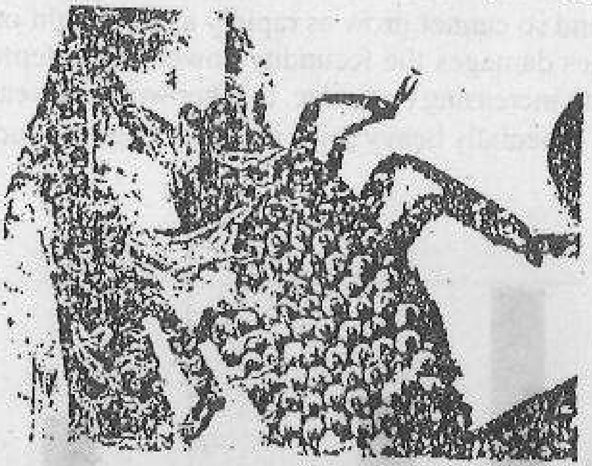


Fig. 8. : Egg brooding by male water bug *(Abedus herberti)*. The female lays the eggs directly on the back of the male.

Bob Smith has studied the adaptive value of these unusual parental behaviour. Smith notes that belostomatid eggs are much larger than the standard aquatic insect eggs. Water bugs are among the world's largest insects, and this huge size is achieved only by five to six molts rather than several molts. It is also noted that about 50 percent of the growth is done only after hatching from egg, which is invariably larger in size. To reach the 50 percent initial growth, the metabolic rate should be high in embryonic development. But the relatively low surface to volume ratio of a large aquatic egg leads to an oxygen deficit in metabolism under water. Since, oxygen diffused through air much more easily than through water, laying eggs out of water on vegetation can solve the problem. But this solution creates another problem, the risk of desiccation. Thus, the solution is done by moistening and aerating the eggs alternately by the male's repeated diving out and in the water. It is probable that back brooding by female itself is not possible, hence the mating males have to do this peculiar and important job of parental care. (Fig. 8)

Unit 10 ❐ Biological Rhythms or Chonobiology

Structure

10.0 Introduction

Biological rhythms occur when animal activities and behaviour patterns can be directly related to distinct environmental features, that occur with regular frequencies. So, biological rhythms are the external manifestations of **biological clock** and are regulated by them. Biological clocks are internal timing mechanisms, that involve both self sustaining physiological **pacemakers** and environmental cyclic synchronizers **(Zeitgebers).**

In this chapter we first describe the properties/characteristics of biological rhythms. Next, look at pacemaker and its physiology, circadian and circannual rhythms. We then ask questions about the functional significance of biological rhythms. Finally, we cover the significance of biological clocks with particular emphasis on migration of some animals like fishes, turtles and birds.

10.1 Structure and characteristics of biological rhythms

Each biological rhythm is composed of repeating units called **cycles.** The length of time required to complete an entire cycle is the biological rhythm's **period** (24 hrs is the period of circadian rhythm). The magnitude of the change in activity rate during a cycle (the difference between peaks and troughs) is called **amplitude.** Any specified part of a cycle is called **phase** (active phase, passive phase etc.) (Fig.1)

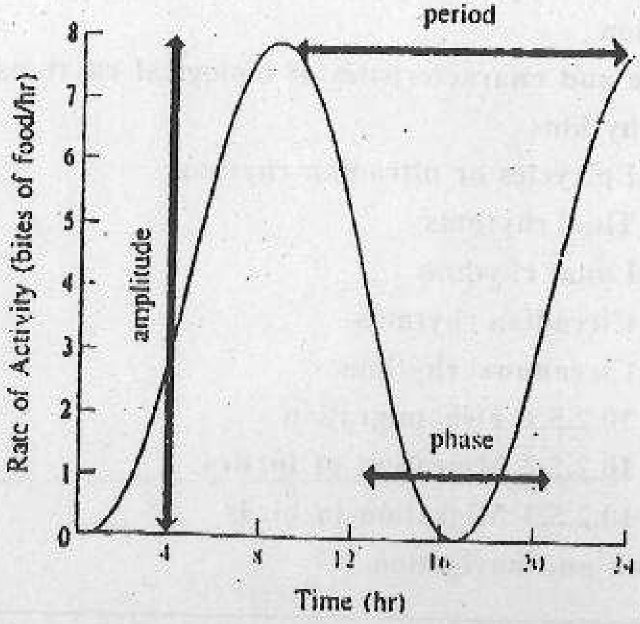


Fig. 1. Biological rhythm : The characteristics of a biological rhythm include period, phase, and amplitude. Phase refers here to the quiet period in terms of activity. Each of these characteristics can vary over time for the same animal, between animals of the same species, or between animals of different species.

The biological rhythms may be characterised by the following properties :

- **Temperature-compensated** : Biological rhythms are relatively insensitive to change in temperature of the environment, especially in endothermous animals. This fact is significant, for if biological rhythms are sped up or slowed down by ambient temperature changes, they would not help the organism keep accurate time.
- **Biological clocks are generally unaffected by metabolic inhibitors** : Biological clocks are generally unaffected by metabolic poisions or inhibitors that block biochemical pathways.
- Biological rhythms occur with approximately the same frequency as one or more environmental features.
- Biological rhythms are self sustaining, maintaining approximately their normal cyclicity even in the absence of environmental cues.

- Biological rhythms can be entrained by environmental cues. The self sustaining, internal pacemaker mechanism may be set and readjusted according to the input from the external environment. The **entrainment** is the process by which a biological clock is set or reset by synchronizing with the period of some external environmental stimulers (e.g. length of photo period etc.).

10.2 Types of rhythms

10.2.1. Epicycles or ultradian rhythms

Some of the organisms exhibit a variety of biological activities with varying frequencies and periods. Some of these cycles are of short duration and are termed **epicycles or ultradian rhythms.** Small mammals like meadow voles *(Microtus pennsylvanicus)* that are active primarily during daylight hours show short cycle of activities followed by a period of rest that vary from 12 minutes to 12 hours.

10.2.2. Tidal rhythms

A unique feature of the seashore is the **ebb and flow of the tides.** Tidal rhythms affect activity periods in many organisms of the seashore. Usually tide is the result of the unequal gravitational forces of the sun and moon, about 12.4 hour period from one low tide to the next low tide (some variation in time period may exists from one location to another). Many species of small crabs *(Uca minax; Uca crenulata* etc.) of the seashore adjust their activity cycle with tides so that they feed on the sandy shore when the tide are out, but return to burrows when the tide flow returns.

10.2.3. Lunar rhythms

The lunar rhythms are based on 29.4 day cycle of the moon. Lunar rhythms are clearly related to tidal rhythms. Some marine insects, like the midge *(Clunio marinus),* coordinate eclosion, mating, and egg-laying activities with the lunar cycle. They lay their eggs at very low tide, thus ensuring that the larvae will hatch in the proper marine environment. .

10.2.4. Circadian rhythms

Circadian means **'about (=circa) a day (=dian)'**. Thus the circadian rhythm means the activities of an organism during the whole light and dark phases consisting about **24 hours day cycle.** This is governed by self-sustaining internal **pacemakers.** In their daily cycle, some animals exhibit peak activity during the day-light hours, called **diurnal;** some are active primarily at night, called **nocturnal;** and others may exhibit peak activity around—**dusk or dawn,** called **crepuscular.**

- **Endogenous pacemaker :**

One of the important characteristics of biological rhythms is the existence of an internal self sustaining **pacemaker** or **internal chronometer.** The following information speaks in support of the existence of internal pacemaker :

1. **Free-running period :**

First, let us consider the case of an animal in constant environmental conditions; for example, in constant darkness. In this constant condition the animal shows normal daily activity pattern, with a period different from that of any known cyclic environmental condition (i.e., normal dark-phase and light phase consisting a daily cycle). This is called **free-running rhythms.** This provides indirect evidence for an endogenous pacemaker. The free running period follows **Aschoff s Rule** (Aschoff, 1960, 1979). When animals are kept in constant darkness, their activity rhythm continues with a period of nearly 24 hour period, but it drifts slightly, becoming shorter or somewhat longer each day. **Aschoff's rule states that the direction and rate of this drift away from 24-hour period are a function of light intensity and of whether the animal is diurnal or nocturnal.** For nocturnal animals, housing under constant dark conditions results in a free-running rhythm period shorter than 24-hours; the activity starts slightly earlier each day. On the otherhand, for a diurnal animal housed under constant darkness, the free-running period is slightly longer each day, and the activity begins slightly later each day.

2. **Isolation :**

Hoffman (1959) maintained lizard eggs under one of three conditions :

(a) 18-hour days consisting of 9 light hours and 9 dark hours, (b) 24-hour days, with 12 light hours and 12 dark hours; and (c) 36 hour days with 18 light hours and 18 dark hours. Lizards hatched from all three groups maintained under constant, conditions, showed free-running activity period of 23.4 to 23.9 hours. Therefore, one could conclude that the component of biological clock mechanism in these lizards is inherited, and is thus endogenous.

3. **Genetics :**

Another evidence for an endogenous pacemaker comes from the study of mutations in the genes that regulate the basic program of biological clocks in various invertebrates.

Recent studies have explored several species of *Drosophila* to understand the genetics of biological clock. *Drosophila* have a diurnal activity phase that is entrained (i.e., seting and reseting of biological clock) by photoperiod. Two types of behaviour rhythms have been studied, **locomotor activity and eclosion** (the process when the adult fly emerges from the pupa). A gene, called **period** (per) mutation can lengthen or shorted, or even abolish circadian rhythm of locomotion or eclosion. The **per** locus is active in the photoreceptor cells of the compound eye, in glial cells of the brain, and in two groups of brain neurons, one in the dorsal cortex and the other near the optic lobes. Recently, a second mutation has been discovered called **timeless (tim)**, flies with this mutation do not exhibit circadian rhythm.

Glossup *et al.* (1999) demonstrated that for the circadian rhythm in *Drosophila* there are two interlocked negative feedback loops involving gene expression (Fig. 2).

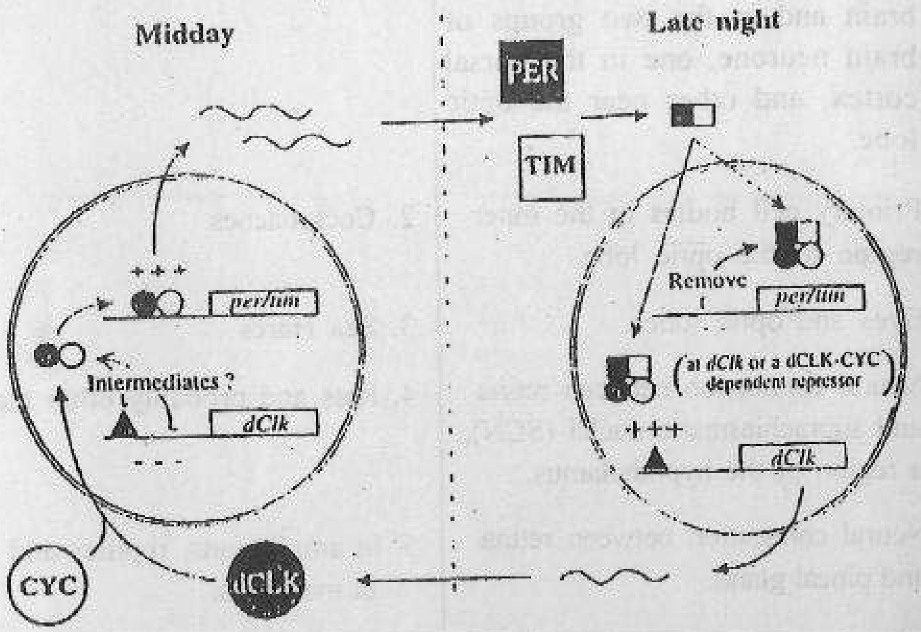


Fig. 2. Model for gene regulation within the *Drosophila* circadian oscillator. During the late evening (right side of diagram), PER-TIM dimers (closed and open squares, respectively) enter the nucleus and bind dCLK-CYC dimers (closed and open circles, respectively), thereby repressing *per-tim* activation. Concurrently, the binding of PER-TIM dimers to dCLK-CYC releases dCLK-CYC-dependent repression ofd*CLK*, thus enabling the *dCLK* transcription via a separate activator or activator complex (triangle). By midday (left side of diagram), high levels of dCLK-CYC (in the absence of PER-TIM) serve to activate per-*tim* transcription and repress *dCLK* transcription (either directly or through intermediate factors). As the circadian cycle progresses, PER-TIM dimers accumulate and enter the nucleus during the late evening to start the next cycle. Dashes denote maximal repression; plus signs denote maximal activation; wavy lines denote mRNA. Dimers are combinations of two molecules.

The two negative feedback loops involve gene pairs with activation or repression of a particular locus by the presence or absence of proteins that are produced from the other member of the gene pair.

The different endogenous self-sustaining pacemakers in different animals are given below :

Pacemakers	Animals
1. Active **per** locus mutation in the photoreceptor cells of the compound eye, the glial cells in the brain and in the two groups of brain neurone, one in the dorsal cortex, and other near the optic lobe.	1. *Drosophila* spp.
2. Primary cell bodies in the inner region of the optic lobe.	2. Cockroaches
3. Eyes and optic lobes.	3. Sea Hares
4. Neural connection between retina and suprachiasmatic nuclei (SCN), a region of the hypothalamus.	4. Rats and probably other mammals
5. Neural connection between retina and pineal gland.	5. In amphibians, reptiles and partly in mammals.

- **Zeitgebers :**

From the previous discussion it appears that under constant environmental condition the biological rhythm generally does not match the normal environmental cycle; it is somewhat longer or shorter. Therefore, endogenous rhythm must be synchronized with the changing external stimulus. The process is called **entrainment.** The environmental stimuli by which biological clocks are reset in variable conditions, called **Zeitgebers ("time givers") Zeitgebers are cyclic environmental cues that can entrain or adjust free-running endogenous pacemaker to their environmental periodicity.**

The different major types of **Zeitgebers** in different animals have been tabulated below :

Zeitgebers	**Animal groups**
1. Photoperiod	1. For most endothermic vertebrates
2. Temperature	2. For most ectotherms
3. Ebb and flow of the tide	3. Tidal sheashore animals

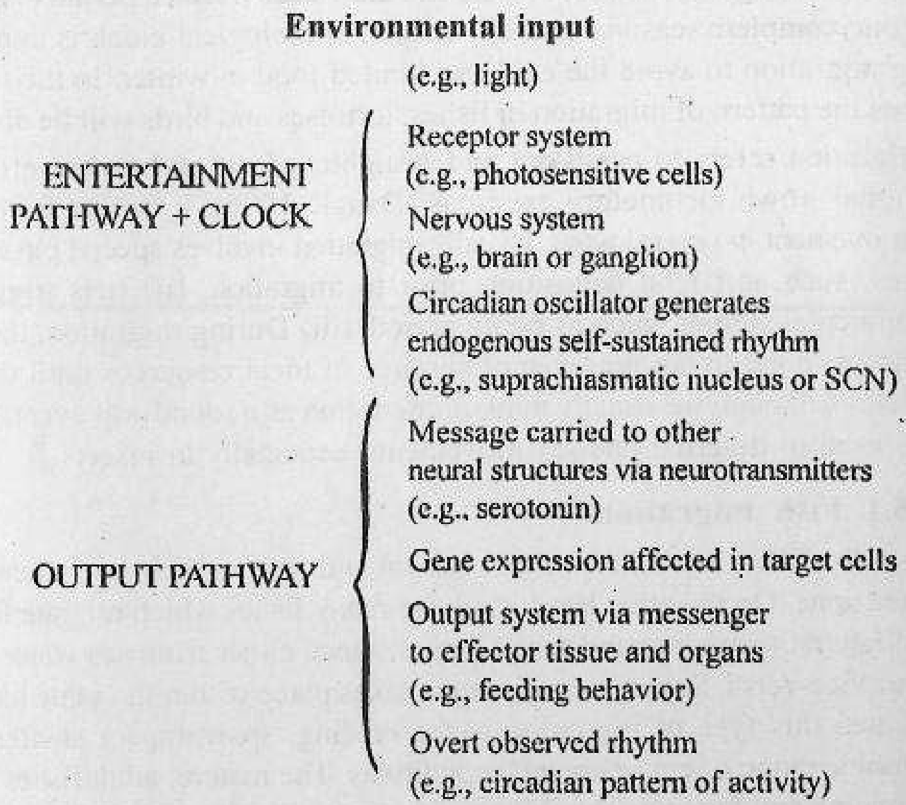


Fig. 3. Model of a mammalian pacemaker system portraying the various component parts and how they may function together, resulting in the overt behavioural and physiological rhythms that can be observed.

- **A model of biological clock mechanism :**

We can construct a model system depicting mechanism of the operation of biological clock. The major elements important for biological time keeping are : (1) an endgenous self-sustaining pacemaker and (2) a system for entrainment to environmental **Zeitgebers.** In this example, we note that some form of environmental input (e.g., light) is sensed from the environment by the appropriate receptor system and transmitted to the circadian oscillator (e.g., suprachiasmatic nucleus in the brain of mammals). From here a message, which may be neural, hormonal, or both is sent to various tissues and organs and results in behavioural rhythmic output. Thus, producing the rhythm we observe.

10.2.5. Circannual rhythms

Circannual rhythms are behavioural and physiological patterns that are governed by self-sustaining internal pacemakers and that occur within a period of about one year (one complete seasonal cycle). An annual biological clock is important in timing migration to avoid the cold and limited food in winter. In the following sections the pattern of migration in fishes, tortoises and birds will be discussed.

Migration refers to persistant and straightened out movement effected by the animal's own locomotory exertions (Dangle 1996). It differs from routine daily movement in several ways. Usually migration involves special physiological changes, such as (i) fat deposition prior to migration, (ii) It is triggered by environmental signals, such as photo period, (iii) During migration, the animal does not respond to the presence or absence of local resources until the trip is complete. Although we usually think of migration as a round-trip event, the term is also used to describe oneway movements, especially in insects.

10.2.5.1 Fish migration

Usually, fishes live in a constant habitat and restrict their movement within a limited zone. On the other hand, there are many fishes which migrate from one type of habitat to another and travel long distance either from sea water to fresh water or vice-versa. Sometimes migration takes place within the same habitat. In most cases this type of migration is for feeding, spawning or shelter within comfortable range of environmental conditions. The mature, adult fishes migrate for spawning and feeding. The following types of migrations in fishes have been observed.

Heape (1931) defined migration as **"a class of movement which impels migrants to return to the region from which they have migrated."**

Fish migration can be typed as follow :

(1) **Alimental migration :** For the need of adequate food.

(2) **Spawning or gametic migration :** For the reproduction and development.

(3) **Climatic migration** : For securing suitable climatic condition.

(4) **Osmoregulatory migration** : For better aquatic condition to have a better osmoregulation.

The migratory fishes can be categorized as follow : -

(1) **Anadromous (away from sea)** : Those fishes which have spend a major part of their lives in the sea but migrate to fresh water during breeding season for **spawning.** Salmon and Hilsa have been found to travel several thousand miles in the sea and then several hundred miles in rivers to reach the spawning ground.

(2) **Catadromous (towards sea)** : Those fishes which spend a major part of their lives in freshwater but migrate to the sea for breeding purposes. *Anguilla,* a freshwater eel, travels several thousand miles from river to the target **spawning ground** of the sea.

(3) **Amphidromous** : Those fishes which migrate from freshwater to the sea, and **vice-versa,** not for breeding but regularly at some other stage of life cycle. Aforesaid three types are collectively called **Diadromous fishes,** e.g., "Asiatic milk fish *(Chanos)*. .,

(4) **Potamodromous** : Truely migratory fishes whose migration is confined within freshwater only e.g., Carps and Trout.

(5) **Oceanodromous** : Truely migratory fishes which live and migrate in the sea, e.g., *Clupea, Scomber.*

- **Migration patterns :**

The migratory movements of the fishes are done by the following mechanisms :

1. **Drifting** : By this method, fishes are carried passively along with the water current. This may result in 'directional movement' if the overall water current is at one direction. The migration of spawns and eggs are done by drifting.
2. **Swimming** : The fishes swim in a particular direction either towards or away from the source of stimulation or at some angle to an imaginary line between them and point of stimulation. Migration by swimming along the direction of water current is called **denatant migration,** and swimming against the water current is called **contranatant migration.**

- **Factors regulating fish migration :**

The factors influencing fish migration may be physical, chemical or biological which are as follows :

1. **Physical factors** : These include water temperature, photoperiod, water current etc. Rise in water temperature in summer of freshwater rivers triggers a stimulus for upstream movement of fishes for spawning. Lampreys and sturgeons migrate during the night hours and herring migrates during full moon. The water current considerably influences the direction of the migration.
2. **Chemical factors** : Chemical factors affecting fish migration are salinity, pH etc. Salinity of water influences fish migration. Most of the freshwater fishes are **stenohaline** (can tolerate a very short range of salinity). Usually they restrict their movement to freshwater only and do not cover large scale migration with a drastic change of salinity. A few species like *Salmon, Hilsa, Anguilla* are **euryhaline** (tolarent to drastic salinity changes), and used to travel long distance from ocean to freshwater river and **vice-versa.**
3. **Biological factors** : In most of the migratory fishes, the internal pacemaker, is an integrated function of gonadal activity and endocrine glands related to reproduction.

10.2.5.2 Migration of turtles

Among the turtles, the most well known migratory turtle is the green turtle *(Chelonia mydas)*. This sea turtle is found throughout the warmer oceans of the world. Adult green turtles are herbivorous. They feed on the so called **turtle grass** that grows abundantly in tropical shallow seas. Green turtles nest only in places where the average temperature of the surface water during the coldest months of the year is above 68°F. In the Atlantic, the northern limit of their nesting range seems to be **Bermuda;** early voyagers to the New World destroyed the colony there. The most Northernly nesting site known in the Pacific is French Frigate Shoal, an outlier of the Hawaiian Islands. These sea-turtles travel thousands of kilometers (about 2000 kms) from their feeding ground of Brazilian sheashore up to the **Ascension Island** in order to complete their breeding. Satellite transmitters have been attached to turtles so that they can be followed day and night. This reveals that they do not need to track the sun's position in order to navigate their journey. Therefore, turtles must make use of some other navigational cues. Probably, the earth's magnetic field can be used in this navigational pattern. To test this hypothesis, Lohmann and associates captured some young turtles, brought them back to the main land, tied them with a rope and reared them into an artificial plastic pool of sea water. The pool was surrounded by a computer driven magnetic coil system that the researchers used to alter the magnetic field around the pool. This simulates the condition that a magnetic field detector animal would experience hundreds of kilometers to the north or south. If the turtles were capable of sensing the earth's magnetic field and using it as a map, then an individual that experienced magnetic field conditions associated with an area 340 kilometers to the north of Melbourne Beach should swim steadily south, rowing along its rope. If the magnetic field was one that the turtle once experienced 340 kilometers to the south of the testing place, then the same turtle should orient in such a way as to head north and continues swimming. In the experimental condition by computerised alterable magnetic field, the turtles did what was expected. Thus, it is evident that **green sea turtle are indeed geomagnetic map navigators.** (Figs..4 & 5).

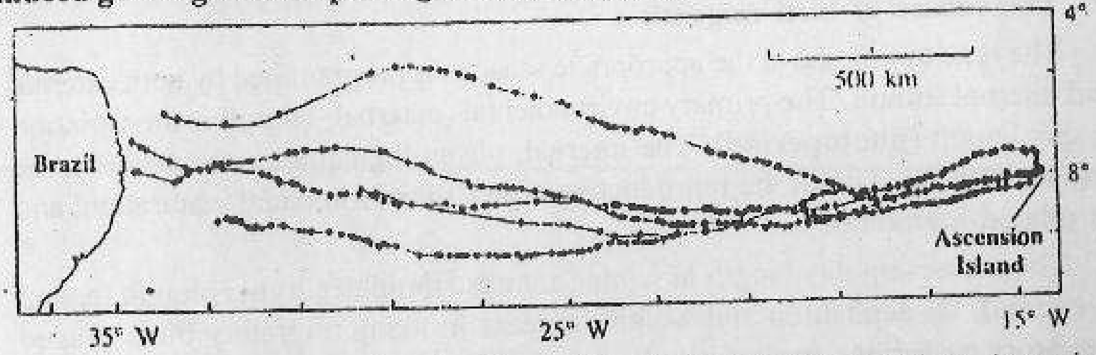


Fig. 4. Migratory routes taken by five green sea turtles that nested on Ascension Island and then returned over 2000 kilometers to feeding areas in the South Atlantic Ocean near Brazil. After Luschi et aL. [753]: photograph by Ursula Keuper-Bennett and Peter Bennett.

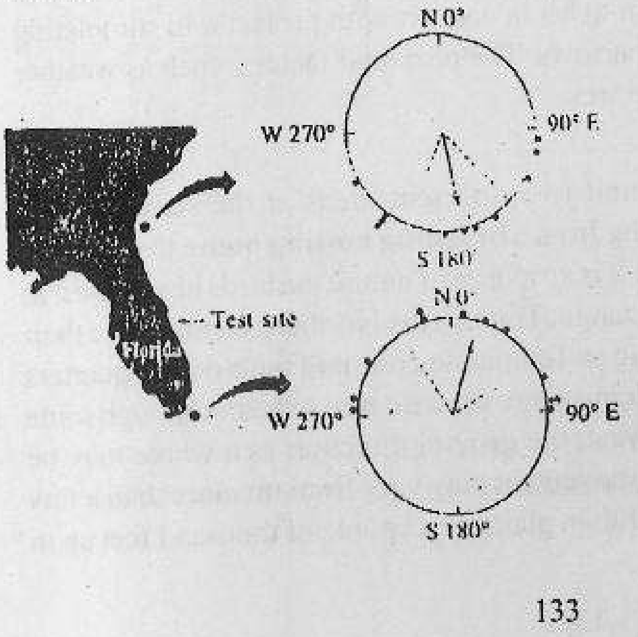


Fig. 5. Experimental manipulation of the magnetic field affects the orientation of green sea turtles. Individuals that experience the magnetic field associated with an area to the north of their actual location swim south; turtles that sense the magnetic field of an area to the south of their actual location swim north. After Lohmann et al.

10.2.5.3 Migration in birds

The subject of migration is one of the most qutralling branches of bird study. The pattern of movements and the regularity and orderness of their occurrence are unique in nature. The entire phenomenon is so reliable that the Red Indians of the Fur countries actually named their traditional calender months after the arrival of the migrant birds.

Landsborough Thomson, an eminent authority, describes bird migration as "changes of habitat periodically recurring and alternating in direction, which tend to secure optimum environmental conditions at all times." Thus the **back and forth** movement is the crucial feature of the bird migration.

- **The causes of bird migration :**

The urge to migrate at the appropriate seasons is programmed by both external and internal stimuli. The primary environmental (external) stimuli is the variation in day length **(photoperiod).** The internal, physiological stimulus seems to be provided by the state of the reproductive organ, mainly gonadal maturation; and its related hormones.

The increasing day length in winter months stimulates **hyperphagia** (eating to excess), fat deposition and weight increase in many migratory birds. Caged migratory passerines predictively become restless just before the times at which they could migrate in the wild. The phenomenon — called **migratory restless or Zugunruhe.** Non migratory birds do not show **Zugunruhe** behaviour. Adrenocortical hormones are known to act in concert with prolactin in stimulating this behaviour in- white-crowned sparrows. The proximal factors, such as weather and food, trigger day to day departures.

- **Types of migration :**

Migration enables birds to inhibit two different areas at the seasons most favourable in each. It involves a swing from a **breeding nesting home** to a **feeding or resting place** in its winter quarter. It is an axiom of nature the birds always nest in the colder portion of their migratory range. Thus, in the Northern Hemisphere their breeding grounds lie nearer the Arctic or Temperate zone and their winter quarters nearer the Equator. In the Southern Hemisphere the case is reversed. Although some migration takes place from east to west, the general direction as a whole may be considered as North and South. The movement may vary from no more than a few kilometers—such as from the north Indian plains to a couple of thousand feet up in

Himalayan foothills—to several thousand kilometers either way as is the case with many'wild-fowl. The longest known migratory journey is performed by the Arctic Tern *(Sterna paradisaea)* which from the Arctic winter travels south acrossing the globe to the Antarctic summer and back again—a distance of about 17,000 km each way (Fig. 6).

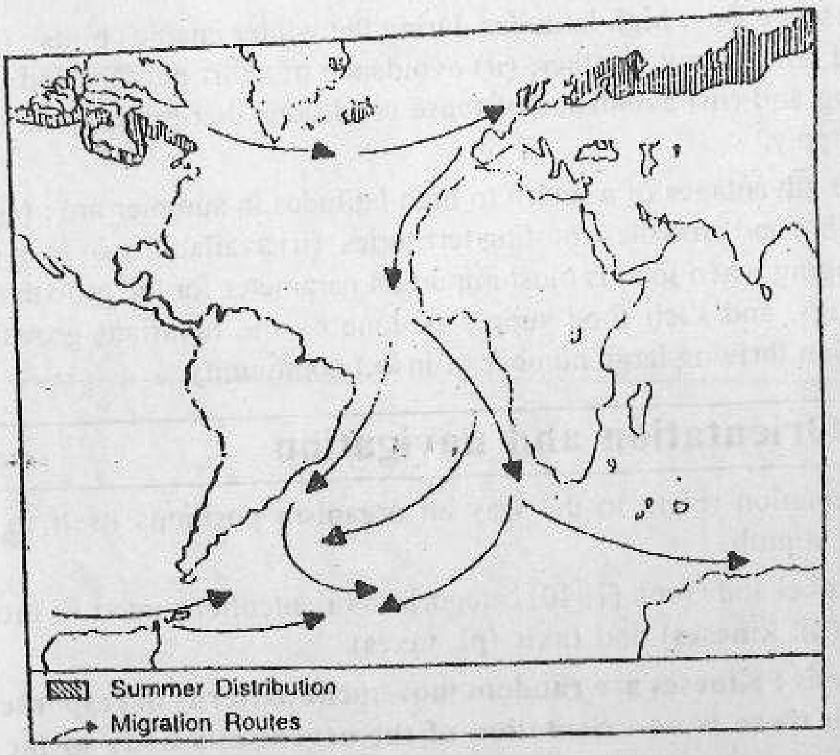


Fig. 6. Figure showing migratory routes of Arctic Terns that breed in Northern Canada.

In the spring, the adult males are the first to arrive on their breeding grounds. They are followed by the adult females, while immature birds that will not breed till the following year follow next. In autumn, the order of departure is reversed; the southward journey is performed more leisurely with many stopovers on the way.

- **Navigation :**

The long distance regular periodicity of bird migration requires precise navigation between breeding territories and wintering stations. Bird ringing method of study proves that individual birds return to a particular tree in Canada after wintering in South America or migrate annually between particular sites in Europe and Africa.

The choice and maintenance of compass direction is the part of accurate navigation is such a hemispheric scale. Ayian navigation system have interactive compass senses including **landmarks, the position of the sun by day and the stars by night, the topology of the Earth's magnetic fields, as well as the position of the setting sun and its bands of polarized light in the evening.**

- **Advantages of bird migration :**

Absence from high latitudes during the winter enables birds : (i) avoidance of cold and stormy weather; (ii) avoidance of short photoperiod available for foraging and (iii) avoidance of those conditions that bring about a scarcity of food supply.

The advantages of a return to high latitudes in summer are : (i) availability of suitable and crowdless nesting territories; (ii) availability of long photoperiod for foraging when food is most important parameter for the growth and survival of youngs, and such food supply is done by the luxuriant growth of spring vegetation thriving large number of insect community.

10.3 Orientation and navigation

Orientation refers to the way an organism positions itself in relation to external stimuli.

Fraenkel and Gunn (1940) categorized oriententions into two broad classes. **kinesis (pi. kineses)** and **taxis (pi. taxes).**

- **Kinesis : Kineses are random movement patterns in response to stimuli in which there is no orientation of the organism's body to the source of stimulation.** The rate of movement increases with the intensity of the stimuli. Although a kinesis is not directed toward or away from the stimulus, it causes to settle organisms in a suitable location. Wood lice *(Porcellio* sp) are commonly found aggregated with least activity under shelters having humid conditions. They cluster in moist areas, because they will die if they are exposed to dry air for a long time due to excessive desication. Under experimental condition, it is proved that more than 70% of the animals were motionless at 90% humidity, but an average of only 20% were motionless at 30% humidity (Gunn 1937). Thus, the rate of movement and clustering increases with the intensity of the stimuli.
- **Taxis** : The simplest directed orientation mechanism is **taxis.** In which generally animals move toward or away from the stimulus. Thus, taxis is based on

the determination of the direction of the stimulus gradient. A taxis can be viewed in different ways. Some categorized taxes according to the response of the animals to the different stimuli. Thus, phototaxis to light; geotaxis to gravity; chemotaxis to chemicals; rheotaxis to a current, or phonotaxis to sound etc. Some describes taxis whether an animal moves toward or away from the stimulus. Thus, an animal that moves toward light and away from gravity is positively phototactic and negatively geotactic respectively.

Different types of animals use different methods to determine the direction of stimulations by moving the receptors appropriately. The maggot of house fly *(Musca domestica)* moves to a dark place at the time of pupation, just orienting head from side to side and sampling the light intensity. If the intensity of light is brighter in one side, moves to the less illuminated side (Fig. 7).

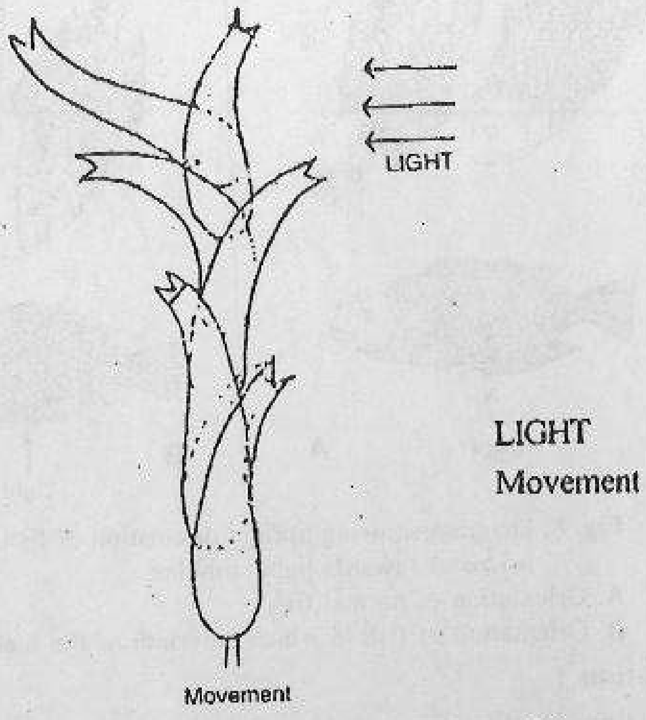


Fig. 7. Diagram to show klino-taxis in the maggot of flies.

Some animals with two receptors senses the intensity of the stimulus on each side and then orient itself so that the receptors are stimulated equally. If such animal displays a positive phototaxis and is blinded in one eye, it will continuously circle to the side of the good eye.

Many aquatic animals orient to light in a manner that helps them swim horizontally. Some fishes may show a dorsal light reaction, one in which the dorsal side is kept toward the light. Others, such as the brine shrimp *Artemia,* show a ventral light reaction in which the ventral side is directed toward the light (Fig. 8).

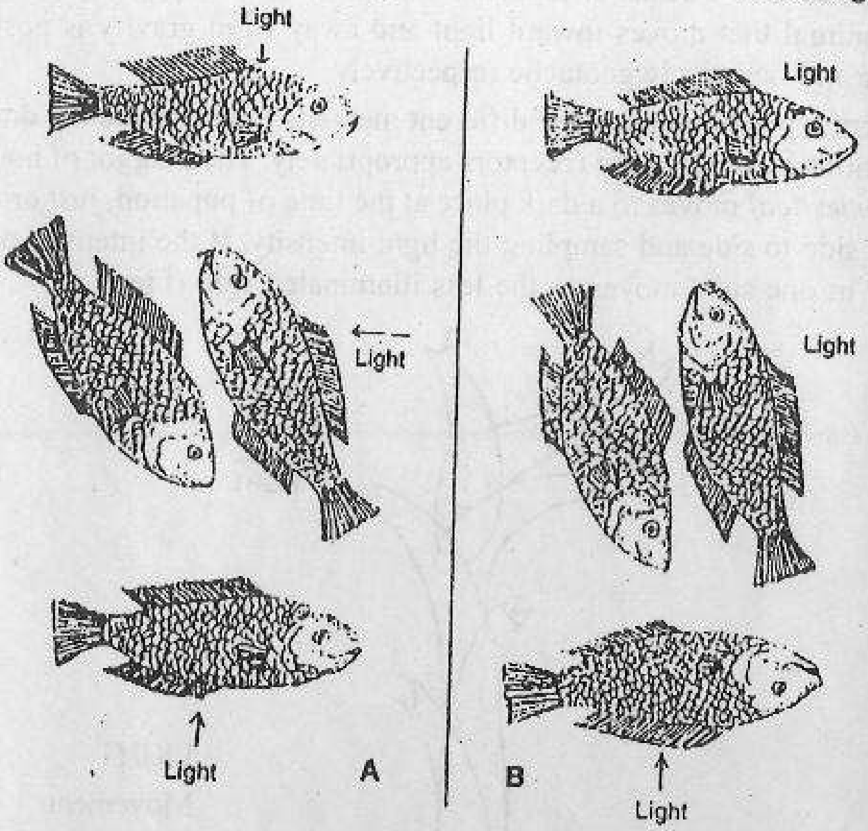


Fig. 8. Diagram showing upright orientation of fish, *Crenilabrus rostratus* towards light stimulus.
A. Orientation of normal fish.
B. Orientation of fish in which labyrinth of the inner ear is destroyed.

- **Navigation :**

Navigation is the process by which an animal uses various cues to determine its position in reference to a known goal (nest, breeding or resting place etc.) as it migrates or homes.

Most mechanisms for navigation involve allocentric, or geocentric cues that require an external frame of reference. These can be placed into three categories : (i) **Piloting**—which refers to the ability to use fixed and familiar reference points or landmarks to orient. (ii) **Compass orientation**—in which the animals uses external cues such as the sun to maintain a heading, (iii) **True navigation**—in which the animals move to a goal in unfamiliar territory in the absence of any sensory contact with that goal. **True navigation requires both a compass and a map.**

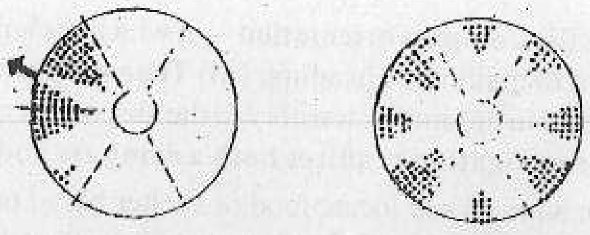
- **Piloting** : Some animals can locate food or shelter based on their relationship to distant, known fixed cues, a mechanism usually referred to as **piloting.** A female digger wasp makes a nest in the ground, then she leaves to capture prey to feed the future young. But before doing so, she circles the hest site several times. When returning with food, she flies straight to the nest. Niko Tinbergen (1951) hypothesized that the returning female uses local land-marks to identify the exact location of the nest. To test this idea, he moved the objects nearest the nest holes a short distance away when female was out for foraging. Upon returning, they invariably searched for their nest hole by the displaced objects. Since, Tinbergen's early work, the use of landmarks has been demonstrated in many species including honey bees, in both field and laboratory.

- **Compass orientation :**

One way to maintain direction in unfamiliar terrain is to use some celestial cues, such as sun, moon, stars etc.

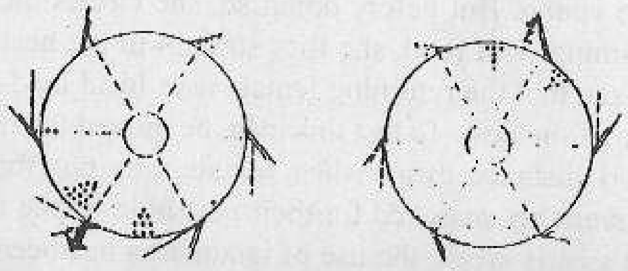
- **Sun :** Sun is not fixed in the sky, the relative movement of the sun across the sky is about 15 degrees per hour. So, some sort of internal clock that help to compensate the movement of the sun is needed. In a classic experiment with the ant *Lasins niger,* Santschi (1911) used a mirror to trick the ants with an altered source of sun light. In this way, the direction of the ant's journey could be changed in relation to "new" position of the sun made by the mirror reflextion for travelling long distances.

Kramer (1950, 1951) showed that European starlings *(Sturnus vulgaris)* placed in an outdoor cage exhibited migratory restlessness in the appropriate direction in the spring and fall (Fig. 9). When mirror was used to alter the apparent position of the sun, the pattern of the starling's migratory restlessness shifted direction in a predictable manner. After the initial discovery of sun compass orientation in birds, theories were put to explain how birds use the sun cue. Some investigators thought that birds use the sun only to gain a compass bearing to head in a particular direction. Others theorized that they use true navigation—the ability to orient toward a goal regardless of its direction and without the use of familiar landmarks.



a. Clear skies

b. Overcast skies



c. Sun's image deflected 90° counterclock wise by mirrors

d. Sun's image deflected 90° clockwise by mirrors

Fig. 9. Use of the sun as a compass by European Starlings.

Bees and other insects, including ants, can receive and interpret information about polarized light. The plane of polarization can provide an axis for orientation for these animals.

- **Moon** : The moon is not as useful as sun in navigation for several reasons. It is visible on an average only half of the night. The moon moves more slowly than the sun (24.83 versus 24 hours/cycle) so that an animal that uses both the moon anc sun have to use two different internal clocks. However, the moon is a prominent feature of the night sky. So, variety of nocturnal animals have a moon compass.
- **Stars** : Most long distance migrants fly at night. When nocturnally migrating birds such as blackcaps *(Sylvia atricapilla)* and lesser whitethroats *(Sylvia curruca* were placed in a outdoor cages with a view of the clear night sky, they exhibited migratory restlessness in a direction appropriate to the seasonal migration (Kramer 1950, Sauer, 1957). Sauer exposed birds to planetorium sky, which permitted him manipulate star patterns experimentally. When he shifted the planatorium's star patterns 180 degrees the direction of the birds activity also shifted. Sauer's experiment

were confirmed both in field and laboratory by Emlen (1967) in Indigo buntings *(Passerina cyanea).*

Emlen rotated the night sky in a planetorium. He conducted an experiment with three groups of young indigo buntings. The birds in group ' 1' were raised in a windowless room, only with diffuse light. Birds of the group '2' were allowed to the normal night sky in the planetorium with a normal rotation of the night stars around the **North star** once every other day. Birds with group '3' were raised in the same way as those in group '2' except that the night stars were rotated around **Betelgeuse, a star in the Constellation Orion.** Later, their migratory orientations were recorded :Two major conclusions can be drawn from this experiment. First, exposure to stellar sky patterns is necessary for normal southward migratory orientation in young buntings. Birds in group '1' exhibited random patterns of orientation when placed under the normal night sky. Second, birds in group '3' oriented 180 degree away from Betelgeuse — as if headed south, using that star to define the southerly direction. Thus, early experience plays a critical role in determining the migratory orientation in buntings, and they may use the sky pattern, they learnt at this stage throughout life. Finally, it should be noted that whether birds are using the stars merely as a compass or whether they are capable of true navigation using stellar configurations is a matter of debate.

- **Magnetic Field :**

The geomatric fields of the earth provide a map of horizontal space, just as gravity and barometric pressures give information about vertical space. The intensity and angle of the magnetic field change with latitude in ways that provide reliable, omnipresent information about geographical orientation and position.

Many migrating bird species navigate by using the Earth's magnetic field. William Keeton (1971, 1972) showed that free-flying homing pegion fitted with bar magnet often did not orient properly on cloudy day, where as control pegion wearing brass bar usually did (Fig. 10). Finally Charles Walcott and Robert Green (1974) fitted homing pigeon with electric cap (containing Helmholtz coils) that produced a magnetic field through **the bird's head.** Such magnetic field can help the bird to find the direction even in the overcast, cloudy sky. The reversal of electric current which reversed the magnetic field, caused the pigeon to reverse its orientation direction on overcast days (Fig. 11).

In birds, one system is a direction-finding magnetic compass based on **photo-pigments in the** eye. This magnetic compass responds to the -poleward' or'

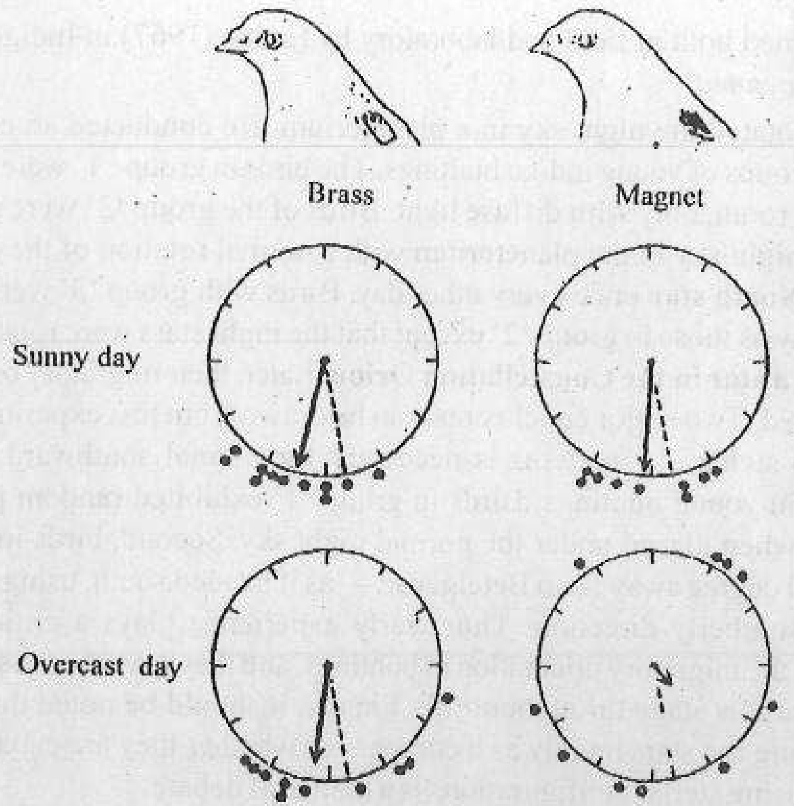


Fig. 10. A bar magnet interferes with a homing pigeon's ability to return to its loft on overcast days. On sunny days, pigeons wearing magnets and control pigeons wearing brass bars both adopt accurate home bearings at unfamiliar release sites. On overcast days when they cannot orient by the sun (their preferred cue), the pigeons wearing magnets become disoriented. The control group, however, orients by means of the Earth's magnetic information. Vectors (arrows) show mean direction and consistency of orientation among individual birds ; long vectors show consistent orientation, and the short vector shows variable orientation. Dots represent bearings recorded for each pigeon tested. The dashed line represents the correct orientation. *[From Keeton 1974]*

'equatorward' angles of inclination of a magnetic field; but not to its "north-south" polarity. The other system, a map location system, is based on **magnetite (Iron oxide) receptors in the ophthalmic branch of the trigeminal nerve.** The magnetite based system enables a bird to determine its location relative to a goal. Such magnetic receptors are sensetive to very small changes in the intensity or topography of the Earth's magnetic fields.

Other than bird, the impact of geomagnetic field in navigation has been proved in whales and turtles.

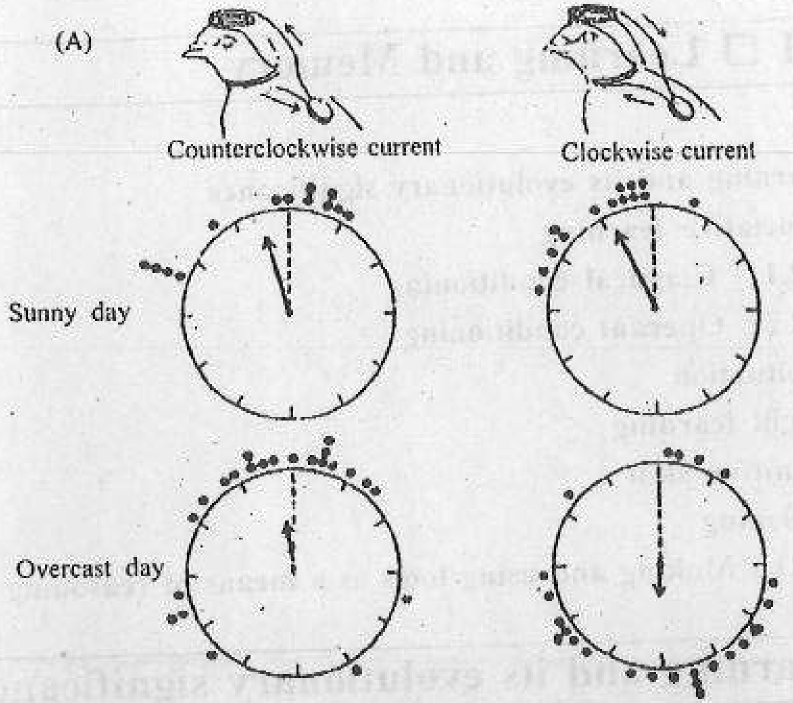


Fig. 11. (A) By attching Helmholtz coils to the heads of homing pigeons, Charles Walcott and Robert Green generated artificial magnetic fields by allowing an electric current to flow through the coils. The reversal of electric current, which reversed the magnetic field, caused the pigeons to reverse their orientation direction on overcast days. Vectors are portrayed as in Figure 10. A homing pigeon equipped with Helmholtz coils. *[(A) After Walcott and Green 1974 and Keeton 1974]*

- **Olfactory and other cues :**

Pacific female salmon migrate from ocean to fresh-water streams for spawning. After hatching the fry develop in the stream during summer and then migrate to the ocean, where they mature. Some *3-5* years later most of the surviving adults return to spawn and die in the stream where they spawn.

The results of numerous experiments conducted over many years (Hasler 1960, 1966, 1978) indicate that young salmon fry are imprinted with the odor of the water of natal stream. When ready to spawn, they apparently respond to minute differences in the odor structure as they move from the ocean into their natal river mouth.

Other cues for navigation may include meteorological parameters and sounds.

Unit 11 ❒ Learning and Memory

Structure

11.1 Learning and its evolutionary significance

When we observe the behavioural patterns of an animal in nature, we find that its behaviour ensures its chances of reproduction and thereby its survival value. Natural selection, as a whole, acts as a mechanism for producing behaviour adapted to environmental conditions. Some biologists consider the concept of **adaptation** only to those behaviours which are shaped by the natural selection. **However, others define adaptation more broadly, including all behavioural traits that increase the inclusive fitness. Adaptation may thus include riot only traits with known genetic causes but also the inherited potential for learning.** Learning is a process in which the animal benefits from experience so that its behaviour is better suited to environmental conditions. So, learning should be viewed here as an **adaptive trait.**

Therefore, we can enumerate the properties of learning as follows :

- The ability of learning affecting behaviour is inheritable.
- The ability of learning is a product of natural selection.
- Learning is adaptive when it ensures the survival of the organism concerned.
- The behavioural change that results from learning is not always expressed immediately. For example, a person may memorize some experience for a particular fact and not demonstrate the result of learning until it may require the same.

Learning is often grouped into different categories, but they may overlap and the distinction between them may not be clear-cut. Nonetheless, categorizing types of **learning is somewhat** useful. The following types of learning may be discussed :

11.2 Associative Learning

Associative learning, sometimes called **conditioning,** is a type of learning in which an association is made **between a stimulus and a response.**

11.2.1 Classical Conditioning

The principle of classical conditioning was first stated by Ivan Pavlov (1927), a Russian physiologist. Pavlov's work began with the common observation that a dog salivates **at the** anticipation of food. He thought that the animal had learned to associate the sight or smell of food and the salivation was due to such, learning. Such inborn response to a certain stimulus is called the **unconditioned (or unconditional) stimulus (US),** because the animal did not have to learn the response to it. On the other hand. Pavlov experimentally proved that in anticipation of food, the dog would begin to salivate to a new stimulus, such as sound, that signaled the arrival of food through the process of learning. A **connection had formed between an inborn response and a learned, new stimulus.** This new stimulus is now called the **conditioned stimulus (CS),** because the animal's response has become conditional upon its presentation. The whole phenomenon is called a **conditioned reflex.** The second, new stimulus is repeatedly presented immediately before the US. After

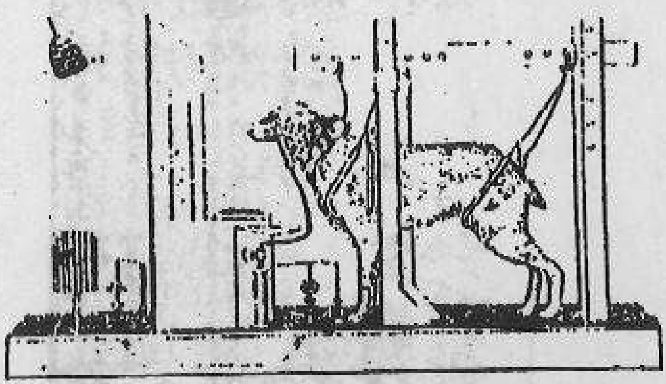


Fig. 1. : Conditioning test apparatus.
Ivan Pavlov discovered classical conditioning through his work on the salivary reflex in dogs using an apparatus similar to this. The dog in the restraining apparatus is ready to be tested using the classical conditioning paradigm.

several pairing, the second stimulus is able to create the response of salivatio through the process of learning only. The order of presentation of the US and C is important. The CS must precede the US. The CS serves as a signal, that th US will appear. Also, the two stimuli must occur fairly close together. If the C is presented frequently without being followed by the US, the association betwee the stimuli is gradually lost. The loss of the classically conditioned response i called **extinction.** (Fig. 1).

11.2.2 Operant Conditioning

Operant conditioning is sometimes called **instrumental learning.** In suc learning, the animal learns to associate its behaviour with the result of th behaviour. When a behaviour has favourable consequences, the probability tha the act will be repeated. This relationship may develop because the animal learn to perform the behaviour in order to be rewarded. This type of learning has bee named **operant conditioning.**

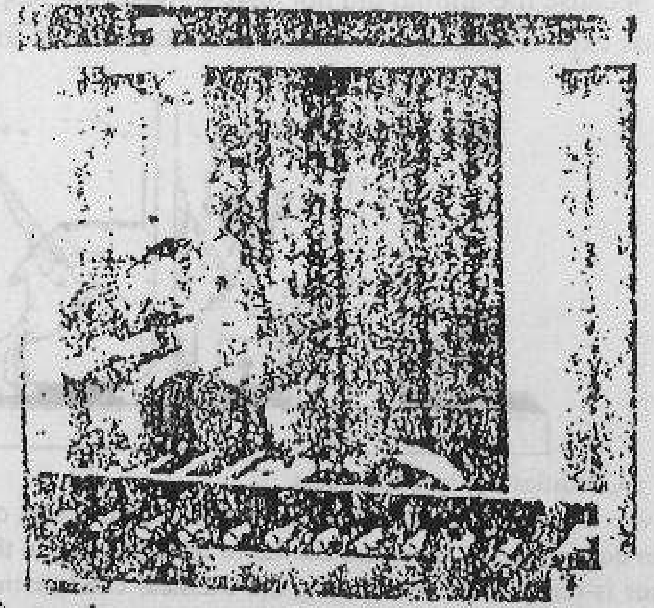


Fig. 2. : Skinner box.

The interior of "the box contains a lever, a light, a food bin. and a grid floor. Additional apparatus for automation and for monitoring the rat's behavior is housed behind the back panel and on the left side of the cage.

B. F. Skinner (1930) devised an apparatus that is still used to study operant conditioning in the laboratory. When a hungry animal is placed into a Skinner box it will move about randomly, investigating each nook and corner. Eventually, it will put its weight on a lever provided in the box accidentally (Fig. 2). When the lever is pressed, a bit of food drops into a tray. The animal will usually press the lever again within a few minutes. In other words, the animal first presses the lever as a random act, and when it is rewarded with food, the probability of repeation of pressing the lever will be increased. A stimulus (e.g. food for hungry animal) that alters the probability that a behaviour will be repeated is called **reinforcer. Positive reinforcers** are those that increase the probability of an act to be repeated against a reward. Examples include food offered to hungry animal or drink to thirsty one. **Negative reinforcers** are those that increase the probability of an act to avoid unpleasant or painful stimulus. For example, an animal will learn to push a panel to stop an electric shock or push a bar to turn off a bright electric light. So, **reinforcement** is best defined operationally to alter the probability of an act. When reinforcement is withheld, the response rate will gradually decline, just as the strength of the conditioned reflex decreases when the CS is presented many times without the US. This process is called **extinction.**

11.3 Habituation

The habituation often considered as the simplest form of learning. The animal learns not to show a characteristic response to a particular stimulus because, during repeated encounters, the same stimulus was proved to be non-effective. **Habituation has been defined more precisely as a "relatively permanent wanning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement. It is specific to the stimulus (Hnide, 1970)".** "Permanent" here means that the effects of habituation are rather long lasting, once they are acquired.

The marine polychaete *(Nereis)* lives in underwater burrows. *Nereis* partially emerges from the tube while feeding. However, certain sudden stimuli, such as shadow may cause it to withdraw quickly in anticipatory approach of predator. They habituate to specific non-harmful stimuli in their environment but retain escape reactions to harmful stimuli.

The benefit of habituation learning is clear : without habituation animals would spend too much time responding to meaningless stimuli rather than foraging or engaging in some other useful behaviour.

11.4 Insight learning

Insight learning is one kind of **Problem-solving abilities.** In insight learning, the animals find new relationships among events. Such relationships were no specifically learned in the past, and they are able to consider the problem as whole, not just the stimulus response association between certain elements o the problem. The animals here, form a mental representation of the problem and then mentally apply trial-and-error patterns to it. An animal could be thinking through the possible responses and evaluating the possibility of success of each trial based on its past experience. The problem-solving ability might seem sudden to observers because they do not have access to the animals mental processes.

A femous example of insight learning comes from the Wolfgang Kohler's (1927) chimpanzee, named as Sultan. In one experiment, Sultan first learned to use a stick as a tool to get a banana on the ground outside his cage. He mastered this trick to get the banana from the outside of the cage with the help of the supplied stick. In the next experiment the same stick was halved into two equal pieces and supplied to the Sultan to collect the banana, but since the sticks were not joined, he could not collect the banana with the stick from outside of the cage. For over an hour, he persistantly tried, and failed to get the banana. Finally, he gave up and began to play with the sticks. Later an intellectual flash struck Sultan. As the chimpanzee was playing with the sticks (Figs. 3, 4) he realized that the end of one stick could be fitted into the other, thus lengthening the stick enough to reach the banana.'Immediately, he ran to the bars of his cage and began to rake the banana. The chimpanzee understood that fitting two sticks together was an effective way to increase the length of the stick enough to obtain the fruit. Kohler believed that Chimpanzee developed insight learning behaviour in a way that he was able to apply the information gained from the experience of playing with the sticks to solve a problem, getting the bananas.

It is to be noted that the concept of insight learning is controversial. Some workers believe that insight learning shows that the animal is thinking, and an animal that thinks about objects or events can be said to experience a simple level of consciousness (Griffin, 1991). An animal that thinks must also form mental representation of objects or events. Therefore, insight has been used as evidence of animal awareness in a chimpanzee.

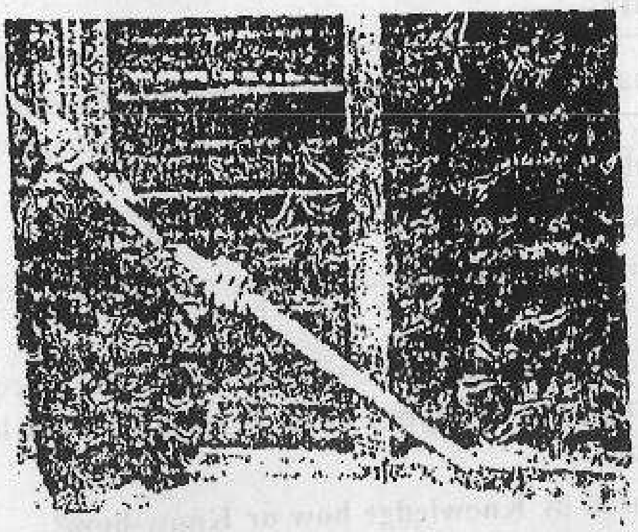


Fig. 3. : Sultan playing with sticks. After playing with sticks, Sultan gained insight into how to obtain the banana placed beyond his reach. The sticks could be fitted together end to end to increase his effective reach.

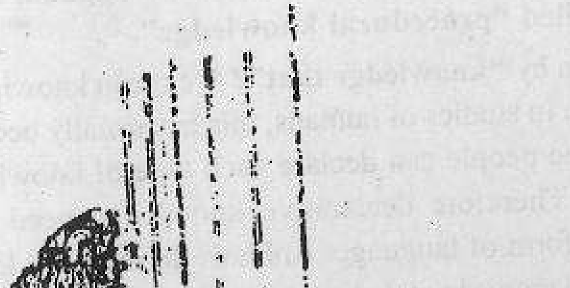


Fig. 4. : A chimpanzee using a stick to obtain an apple.

11.5 Cognitive skill

We have seen that animal can learn to associate two events—the association of **stimulus and response.** There are two basic alternatives about knowledge acquiring process of animals. These are :

(1) The animal can make association between different stimuli.

(2) Animals can acquire knowledge about various relationships in their environment.

Another aspect, which is more important to understand the process of congnitive aspect, is to distinguish two types of knowledge : **"Knowledge-how" and "Knowledge-that".**

What do we normally mean by **Knowledge how or Know-how?**

We mean knowing as a matter of knowing how to do something, such as how to swim, how to ride a bicycle. This type of knowledge cannot be transferred from one task to another, and cannot be articulated. Thus, knowing how to ride a bicycle involves a type of knowledge that cannot be used for anything except riding a bicycle. Riding a bicycle involves a procedure that is implicit. This type of knowledge is generally called **"procedural knowledge".**

What do we normally mean by **"knowledge that"?** We mean knowing about an object, a person, a place etc. In studies of humans, this has usually been called **"declarative knowledge".** The people can declare such type of knowledge by language to another people. Therefore declarative knowledge need a basic communication system in the form of language. Anhnals do not have language abilities, and so cannot have declarative knowledge system. However, some animals (e.g. Honey bees) linguistic equivalent of declarative knowledge. The animals that do not have linguistic-equivalent would only have procedural knowledge. The declarative knowledge is a variety of **explicit knowledge which involves represention**s **of facts that are accessible to many processes.**

An animal that do have explicit representations that it could manipulate to apply its explicit knowledge to a variety of tasks would be capable of some form of **cognition.** Therefore, **cognition,** may be defined as the manipulation of representations of the **explicit knowledge system.**

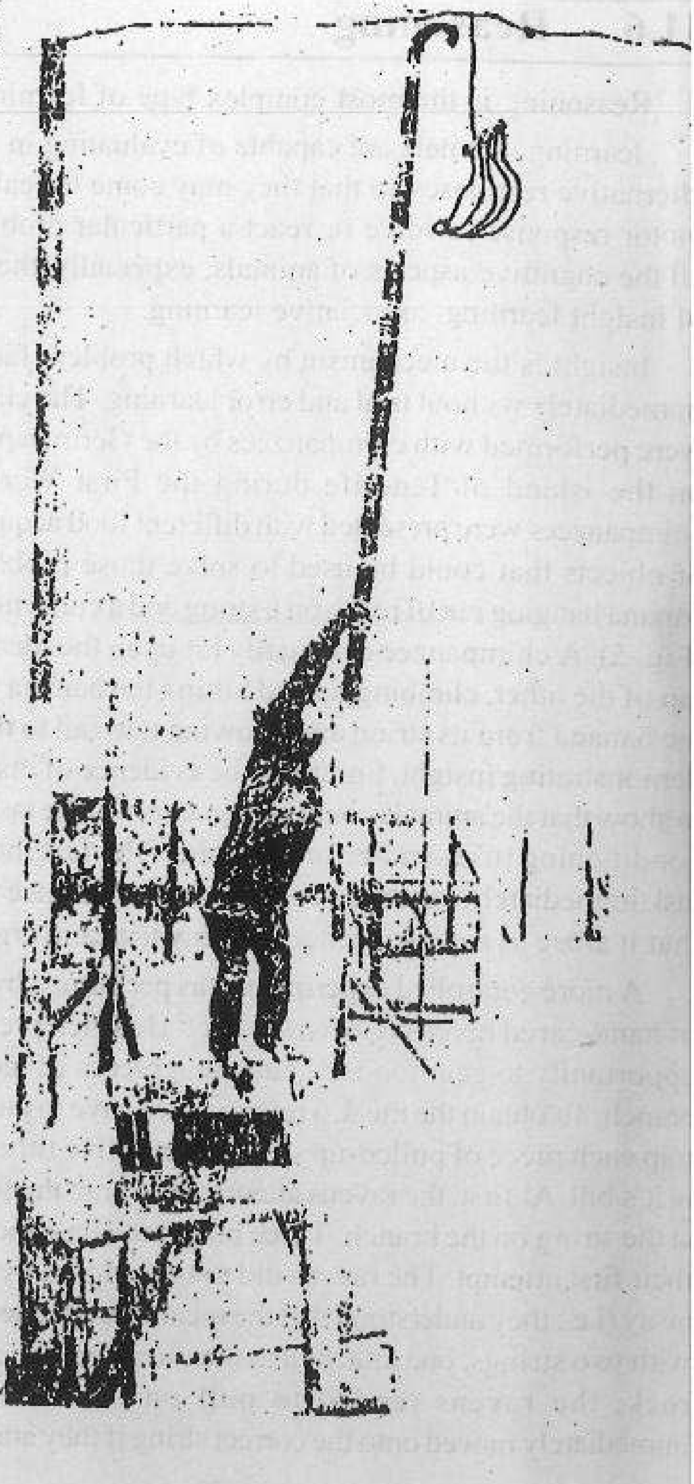
11.6 Reasoning

Reasoning is the most complex type of learning in animals. In this type of learning, animals are capable of evaluating in a comparative manner all the alternative responses so that they may come to realise which would be the right motor response to solve or react a particular problem or event. It may involve all the cognitive aspects of animals, expecially, the problem-solving parameters of insight learning, associative learning.

Insight is the mechanism by which problem faced by the first time is solved immediately without trial and error learning. The classic studies on animal insight were performed with chimpanzees by the German psychologist Wolfgang Kohler on the island of Tenerife during the First World War (Kohler 1925). The chimpanzees were presented with different food acquisition problems, and a number of objects that could be used to solve those problems. A famous example is a banana hanging out of reach on a string and a collection of boxes located underneath (Fig. 5). A chimpanzee eventually hit upon the idea of stocking the boxes one on top of the other, climbing up and hitting the banana with a stick, thereby knocking the banana from its string and allowing it to fall to the ground to be retrieved, thus demonstrating insight. For this to be evidence of insight, however, we would need to show that the animals could not have solved the task by conventional instrumental conditioning (trial-and-error learning). The fact that the chimps did not solve the task immediately, but required extensive experience with sticks and boxes, suggests that it arose as a consequence of many trial and error responses.

A more controlled experiment was performed by Heinrich (1996), with a group of hand-cared ravens *(Corvus corax)*. Heinrich presented his ravens with a novel opportunity to gain food, by attaching pieces of meat to string suspended from a branch. To obtain the meat, a raven would have to pull the string up with its feet, and trap each piece of pulled-up string at least five times before it could grab the meat in it's bill. At first, the ravens attempted to grab the food from underneath or pecked at the string on the branch. Three birds pulled up the string and grabbed the meat at their first attempt. The ravens did not attempt to fly off with the food when chased away (i.e., they understood that the meat was attached to the string). When presented with two strings, one attached to the meat and a second attached to a similar-sized rock, the ravens tended to pull on the string attached to the meat (or immediately moved onto the correct string if they attempted to pull up the string with

Fig. 5. : One of Kohler's chimps standing on stacked boxes to obtain food suspended from above.



the rock attached. When the birds were presented with a novel string (dark-green shoelaces rather twine), the birds almost exclusively pulled on the shoelaces attached to the food. This suggests that the birds did not just form an association between particular string and food, but had generalized to all string like substances to food. This is perhaps a more convincing example of insight than Kohlers chimpanzees as the ravens were hand-reared and therefore Heinrich could be certain that the birds were experiencing the problems and the materials for the first time.

11.6.1 Making and using tools as a means of reasoning :

The propensity to manufacture, transport and use tools was previously thought to be exclusive to humans, but in the 1960s Jane Goodall reported the use of tools by chimpanzees at Gombe, Tanzania. Chimpanzees strip the leaves off tree stems and poke them into termite mounds, thereby extracting termites. The last 30 years have provided numerous examples of tool use in primates in the wild and the laboratory, with different pupulations of chimpanzees using different tools for different uses, e.g., σ wooden anvil and stone hammer to crack open palm nuts, or chewing leaves into a sponge so that it can be used to collect liquids. It has been claimed by some, that these variations in tool use are cultural. However, neither the occurence of social learning nor the mechanisms underlying it can be inferred from observation alone. With field studies one never knows precisely what previous experiences the individuals have had, and whether they have learned by trial and error. The common assumption is that if a particular behaviour must have depended upon the social learning. This is not necessarily the case.

Tool use has not been demonstrated in monkeys and apes to some degree in the laboratory. Visalberghi and colleagues presented Capuchin Monkeys *(Cebus paella)* with a problem that required knowledge of the relationship between objects and tools. The monkeys were given a "trap-tube" problem in which a clear tube contained a hole and well in the middle (Visalberghi & Limongelli 1994). A piece of food was placed next to the well and the monkey was provided with a stick of the correct length to push the food out of the tube. The monkey should have pushed from the side furthest away from the food to avoid pushing the food into the well (Fig. 6a). Infact, only one of the four Capuchins succeeded in the majority of the trials. When the trap was inverted (so that it was no longer a barrier to gaining the food), the monkey that was originally successful used the same technique as previously. This suggests, that this particular monkey was using the rule "always push from the side

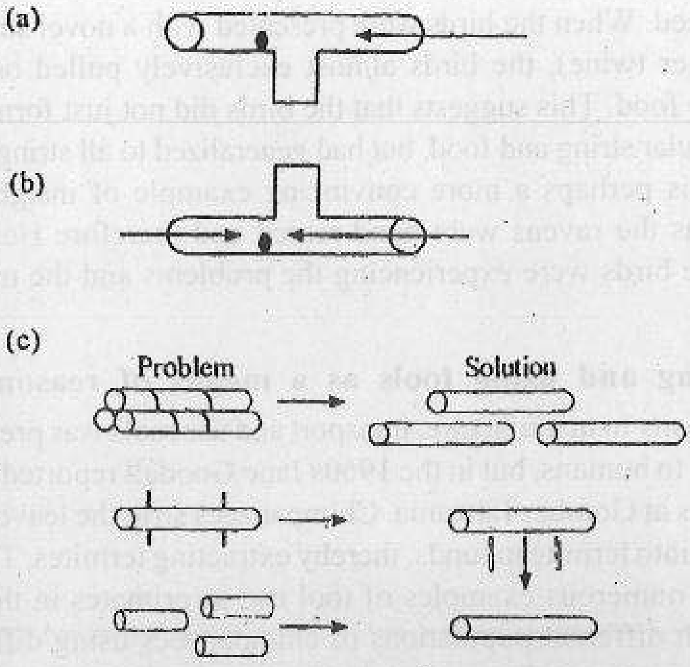


Fig. 6. : (a) "Trap-tube" problem used in capuchin monkeys (Visalberghi & Limongelli 1994), chimpanzees, and more recently New Caledonian crows. The plastic tube is transparent so that the food (black ellipse) can be seen by the subject, and an enclosed trap is located in the center of the tube. To successfully remove the food, the subject must push a stick in the direction of the arrow, i.e., over the trap, (b) In the control condition, the trap is inverted so that it is no longer functional, i.e., it no longer makes a difference from which side the stick is pushed. The subjects are said to not understand the function of the trap if they persistently push the stick from the previously successful side, (c) Additional problems based on changing the physical properties of the sticks : a bundle of sticks tied together (problem) that need to be separated (solution); a stick with small sticks pushed through the center (probiem) that need to be removed (solution) : and three small sticks too small to be functional (problem) that need to be stuck together (solution).

furthest from the food" rather than possessing a conceptualization of how the problem should be solved. Finally, the monkeys were provided with a series of problems associated with the functionality of the sticks were pushed through them, or the monkeys were presented with a series of smaller sticks (Fig. 6c). The capuchins readily learned to solve these additional problems! When the "trap tube" experiment was repeated with chimpanzees, only two of the five performed correctly, thereby suggesting that there are few appreciable differences between capuchins and. chimpanzees in their understanding of tool use in this task.

Tool use in animals is not restricted to primates. For example, Asian elephants *(Elephas maximus)* and African elephants *(Loxodonta africana)* manufacture tools to swat away flies, and the Galapagos woodpecker finch *(Camarhynchus pallidus)* uses sticks to probe for insects in ordinary inaccessible holes in trees. Perhaps the most spectacular use and manufacture of tools is demonstrated by the New Caledonian crow *(Corvus moneduloides).* Hunt observed, four crows manufacture two types of tools and 68 crows carry or use tools in three forests in New Caledonia in order to catch insects in trees or under detritus leaves. Hunt categorized the tools into two main types ; hooked-twing and stepped-cut tools. The hooked-twing tools were made from living secondary twings that were stripped of there leaves and bark, with a hook at their wider end. The stepped-cut tools, in contrast were fashioned from pandanus leaves by tapering the ends into points. Different techniques were employed in using to tools depending on the location of the prey. If the prey was located under detritus, the tool was used with rapid back-and-forth movements, whereas if the prey was located at the base of the holes and leaves, slow deliberate movements were used. New Caledonian crows studied by Kacelnik and colleagues were presented with a tube containing food and a "tool box" containing twings of deffering lengths; the crows consistently chose the appropriate length of twing to push the food out the rather end of the tube. A single crow also fashioned a straight piece of wire into a hook so that it could pull up a small bucket containing food (Weir *ei al.* 2002). This may demonstrate a case of insight as the crows had previous experience of wire that was bent into hooks but not of straight pieces of wire.

Unit 12 ☐ Concepts of evolution and theories of organic evolution with an emphasis on Darwinism

structure

12.1 Introduction

"Nothing in Biology makes sense except in the light of evolution" — Theodosius Dobzhansky.

Evolution in its simplest understanding means change- change between generations. In seventeenth century, the term "evolution" has an embryological origin defined as the "unfolding" of parts and organs in attaining a preformed body plan. It was only in the nineteenth century that people came to use evolution to mean the transformation of species. The evolution also termed as "organic evolution' deals with changes undergone by living things. The form and behavior of organism between generations can be modified from those of their ancestors. The doctrine of evolution assumes that the present day complex animals and plants have been developed in the course of long ages by a process of gradual change in the earlier simpler forms of life. However, not all kinds of biological change can be addressed as evolution: Developmental change within the life of an organism should not be considered as evolution in strict sense and the definition refers to "descent with modifications". In other word, it means change between generations within a population of a species. The evolution of various organisms on this universe is an intricate and elaborative process. The concept of evolution should not include the idea that evolution is always progressive leading invariably from simpler to more complex forms of life. When the members of a population reproduce and new generation is formed, a lineage of population made up of a series of population through time might be formed. Each population is giving rise to the descendant population in the next generation.

Evolutionary modification in living thing possesses some other distinctive properties. It depends on external environmental change and on random genetic innovation. Thus, the form of future change cannot be predictable.

12.2 Thories of orginic evolution with special emphasis on Darwinism

The concepts of evolution though reckoned with Darwin in respect to publication of his very famous book 'On the origin of species". Long before Darwin, attempts were made to explain the obvious diversity of living organisms. People noticed the basic structural and functional similarities, which.exist between organisms. As knowledge has advanced, different concepts have 'evolved' further and at present time also, scientists are arguing for every single details of a particular theory and they are proposing still another theory.

Ideas of evolution developed from the observations of the constant change in the plants and animals of the world.

Empedocles [495 - 443 BC] first stated that evolution in living world occurred step by step. Empedocles is considered as the **father of this concept of evolution.**

Other scientists like **Anaximander [611 - 547 BC], Xenophane** [480 -376 BC], **Aristotle** [384 - 322 BC] worked with the development of egg in chick.

In the Middle Age, **Bacon** [1561 - 1626], **Bonnet** [1720- 1793], **Kent** [1724 - 1780], **Oken** [1776 - 1801] *et al* also worked in this line. Among the other scientists of eighteenth century, **Linnaeus** [1707 - 1778], **Bufon** [1707

- 1780] & **Erasmas Darwin** [1731 - 1802] tried to establish a real picture o
Organic Evolution.

Jean Baptiste De Lamark [1744 - 1829] published a book named *'Philosophic Zoologique'* in 1809 in which he described the theory **"Inheritance of Acquired Character"**. According to this theory - the Plants & Animals undergo physical changes to co-opt with the environment. And these changes are inherited to their future generations, such as -

1. The long neck of giraffe was a result of constant stretching of their neck muscles through generation after generation to collect leaves from high branches.
2. The muscles of left arm of Blacksmith developed due to constant use.
3. Limbs of snakes - Degenerated or disappeared through generations due to lack of use.
4. Degeneration of Eye (visual organ) in animals due to absence of light in caves.

The offspring acquire these developed characters & inherited to their offspring. In this way new species appear after many generations.

Lamarck's ideas had little impact during his lifetime. The contemporary respected zoologists criticized him very much. Lamarck's ideas of how evolution works were wrong but he was the first who proposed a coherent theory of evolution and for that he deserves proper honour.

12.2.1 Charles Darwin [1809 - 1882]

Charles Robert Darwin was the son of an English physician. He studied medicine for a brief period of time and then turned to studying for a career in the clergy at Cambridge University. He was passionately interested in natural history. In 1831 Charles Darwin joined a sea voyage which continued for 5 years in a ship named 'H.M.S. Beagle' and visited every island along the coastal region of South America in the Atlantic Ocean & South Pacific Ocean.

During this voyage, he collected large number of specimens of Plants & Animals & Fossils. Mainly in Galapagos Island he observed a large number of variations in living & fossil Animals & Plants. Especially he observed the finch birds of the island are different from those of the mainland. The variation of beaks & colours of the finches are quite different.

While analyzing the data of his collection he came in contact with R. Malthus in respect to his publication of the article "The Principle of Populations". In his article Melthus expressed the principle for struggle for existence and on the basis of which Darwin wrote the theory of Natural Selection. Almost simultaneously **Alfred Russell Wallace [1823-1913]** published the article "The Tendencies of Varieties to depart from the Original Type". Like Darwin he also visited Malayan Archipelago and observed local flora & fauna. Darwin highly appreciated his theory & they together wrote two articles (i) On the tendency of species to form varieties & (ii) On the perpetuation of varieties by Natural Selection. These two articles were published in the "Journal of Proceedings of Linnean Society" in 1859.

In the same year Darwin published his famous book 'On the origin of species by means of Natural Selection or Preservation of favoured races in the struggle for life'.

12.2.2 Detail account of Darwinism

The idea of Natural selection is simple but its operation is highly complex & extremely subtle. Darwinism is based on three facts of nature from which deduction have been made:

I) Prodigality or fecundity: According to Darwin, all the living organisms have the tendency to increase their numbers rapidly. For example, one female toad may lay as many as 12,000 eggs. It has been calculated that one pair of house flies may have 191,010,000,000,000,000 offspring if all eggs are hatched. We do not see such conditions in reality because of the following limiting factors:

i) Limited food supply
ii) Predatory animals
iii) Disease
iv) Shortage of space

v) Climatic conditions

II) 'Struggle for existence': Each species attempt to produce many more individuals that can live up to maturity under the prevailing conditions. The result is an intense competition among the offspring for food, shelter, mates etc. In this struggle, those will succeed who have favourable inheritable variations.

III) Variations in nature: No two organisms are exactly alike no matter how closely related they are. This is a common observation in nature. Such differences are called variations and are prerequisite for evolution. Without variations no change can occur and evolution cannot occur.

IV) Survival of the fittest: Best fitted organism in a changed environment can survive the change and will propagate successfully in the future. Nature selects the best adapted individuals and select out the less adapted ones.

V) Origin of species: The triumph of nature is the emergence of new species from the older ones. This is achieved by natural selection. So by natural selection evolution works.

VI) Mutations as raw material for natural selection: Mutation is one of the ways by which variations can emerge and thus it acts as raw material for natural selection.

12.3 Suggested questions.

a) Give an idea of Lamark's theory on 'Inheritance of aquired character'?

b) How do you interprete 'struggle for existance' in the origin of species?

c) 'Mutations as raw material for natural selection'— Justify.

nit 12 ☐ Neo-Darwinism

tructure

3.0 Introduction

The theory of evolution as proposed by Darwin has been modified in the ight of evidences from genetics, molecular biology, palaeontology, ecology and ehavioural biology and is known as neo—Darwinism [neo, new]. This theory tates that the organic evolution occurs by the Natural selection of inherited haracteristics.

Following are the prerequisites to accept neo-Darwinism:

a) **Past evolution** : establishment of the fact that change or evolution has taken place in the past

b) **Natural selection of genes:** demonstration of a mechanism which results in evolution

c) **Evolution in action:** observation of the fact that evolution is happening today

Evidences for the past evolution come from fossil records and by estimating the order of the rock formation.

Evidences for the mechanism of genes in action and natural selection of genes come from Mendel's works of genetics.

Finally, evidences for the action of evolution at present time come from the study of speciation in herring gull and also the results of artificial selection and genetic engineering, as in the case of cultivation of wheat etc.

13.1 Hardy-Weinberg law of genetic equilibrium

Darwin believed that there was a blending of characters of parents among their offspring and he considered the variation as continuous variation. On 1871, Galton opposed this notion and proposed the Concept of discontinuous variation. After the rediscovery of Mendel's work in 1900, it became evident that there is no mixture of any parental characters when they produce their offspring and the characters maintain their identity throughout the generations. This is known as the particulate inheritance.

Another shortfall of Darwinism is that it cannot explain the reasons for emergence of variations. The **Germ-plasm theory of Weismann and the Mutation theory of De Vries** were the two cornerstones of the development of neo-Darwinian era and' the proposition of synthetic theory later on. The Germ plasm theory stated that the continuity of germplasm was the main criterion for inheritance of characters. This was in contrast to the pangenesis theory proposed by Darwin. While Darwin believed in the continuity of variations, it was Hugo de Vries who proposed that the discontinuous variations were more important than the continuous one and this saltatory variations or mutations were the ultimate source of new and different genetic material appearing in a population. Mutations arise spontaneously and are not directed by the environment. Environmental influences can affect the mutation rate but they cannot induce a mutation to take place. Mutation is the source of variations on which natural selection may act upon.

The modern synthetic theory of evolution is the result of the works of a number of population geneticists, namely. T. Dobzhansky, R. A Fisher, J. B. S. Haldane, Sewll wright, Ernt Mayr and G. L. Stebbins. They opined that mutations and natural selection both are important for organic evolution. They gave emphasis on the study of population for understanding the flow of any particular gene. The population can be defined as a group of organisms belonging to the same species inhabiting a certain area. Population expresses most direct hereditary and reproductive relationships among individuals and it distinguishes a sort of evolutionary unit.

Hardy and Weinberg independently formulated the founding theorem o population genetics. This law states that the process of heredity does not change either gene frequencies or genotypic frequencies at a particular gene locus in case of a random mating population unless acted upon by external forces such as mutations, genetic drift etc.

Before entering into the detailed account of the Hardy Weinberg Equilibrium, we should start with the definition of the important terminologies:

Gene pool; A gene pool is the total variety of genes and alleles present in a sexually reproducing population.

Allele frequency: The alternative or several forms of a particular gene is known as allele. The number of organisms in a population carrying a particular allele determines the allele frequency.

Genotype frequency: The number of individuals of particular genotypes in a population determines the genotype frequency and it is used in predicting possible outcomes of particular mating or crosses.

An English mathematician G.H. Hardy and a German physician W. Weinberg developed the mathematical relationship between the frequencies of alleles and genotypes in populations independently in 1908. The relationship, known as the Hardy-Weinberg equilibrium is based upon a principle that states that '**the frequency of dominant and recessive alleles in a population will remain constant from generation to generation provided certain conditions exist.**'

These conditions are:

i) the population is large;

ii) mating is random;

iii) no mutations occur;

iv) all genotypes are equally fertile, so that no selection occurs;

v) generations do not overlap;

vi) there is no emigration or immigration from or into the population, that is there is no gene flow between populations.

Any changes in allele or genotype frequencies must therefore result from the introduction of one or more of the conditions stated above. Thus the factors or forces that destabilize the equilibrium are

a) Natural selection, b) Mutation, c) Genetic drift, d) Migration, e) Meiotic drive.

Hardy-Weinberg equation provides a simple mathematical model of how genetic equilibrium can be maintained in a gene pool and also helps to calculate the allele and genotype frequencies of a population i.e. the two basic aspects population genetics deals with.

Now, first of all consider a large population of sexually reproducing diploids and suppose that at some autosomal locus there are two possible alleles, A and a. There will be three possible genotypes, AA, Aa and aa. Let us imagine that we count a large sample size, N, of the population having these above genotypes with the following distributions of individuals:

Genotypes	**AA**	**Aa**	**aa**	**Total**
Number	**n1**	**n2**	**n3**	**N**
Frequency	**P= n1/N**	**Q= n2/N**	**R=n3/N**	

From the numbers, we can calculate the genotype frequencies, P. Q, and R. P+Q+R = 1.

Now we can define the frequency of the allele A as the number of A genes in the population, divided by the'total number of genes. Thus, if p is the frequency of A gene of a diploid organism, the frequency of other allele, a will q where $q = 1\text{-}p$ or. $p + q = 1$.

Therefore, $p = 2n1+n2/2N$

$q = n2 + 2n3/2N$ 1

or, equivalently,

$p = P + ½ Q$; $q = ½ Q + R$ and 2

obviously, $p + q = P+Q+R = 1$ 3

This definition can easily be extended to any number of alleles at a locus.

Example: In a population of 10,000 individuals, one person is albino that is. the frequency of albino genotype frequency is 1 in 10,000. Since we know the albino condition is recessive, the albino person is homozygous recessive for albino allele, i.e., aa. If the frequency of.that recessive allele is q, the aa individual has genotype frequency q^2 (as two a alleles are present in that individual). Thus

$q^2 = 1/10,000$

$= 0.0001$

so, q = VO.0001 I

$= 0.01$

Then p, the frequency of the dominant pigmented allele in the population will be

$p = 1 - q$,[since $p + q = 1$]

so, $p = 1 - 0.01$

$= 0.99$

So, the frequency of the dominant allele in the population is 0.99 or 99%.

Since,

$$p = 0.99$$

$$p^2 = (0.99)2$$

$$= 0.9801$$

the frequency of the homozygous dominant genotype in the population i 0.9801, or approximately 98%

Since,

$$p = 0.99 \text{ and } q = 0.01$$

$$2pq = 2 \times (0.99) \times (0.01)$$

$$= 0.0.198$$

the frequency of the heterozygous genotype is 0.0198 or, approximately 2% o the population carry the albino allele either as heterqozygotes or albino homozygotes.

13.2 A detailed account of destabilizing forces

The Hardy Weinberg principle states that in a given condition the allele frequencies remain constant from generation to generation. Under these conditions, a population will be in genetic equilibrium and there will be no evolutionary change. However, the Hardy-Weinberg principle is purely theoretical. Following are the factors that can change or destabilize the equilibrium of a population:

(i) Natural selection, (ii) Mutation, (iii) Genetic drift, (iv) Migration, v) Meiotic drive.

13.2.1 Natural selection

Natural Selection is the mechanism by which new species arise from a preexisting species. This hypothesis/ theory was proposed by Darwin & Wallace and was based on three observations and two deductions:

1) Individual within a population produced on average more offspring than are needed to replace themselves.

2) The numbers of individuals in a population remain approximately constant.

3) Variation exists within all population.

The deductions are

1) Many individuals fail to survive or reproduce. There is a 'struggle for existence' within a population.

2) In the 'struggle for existence' those individuals showing variations best adapted to their environment have a 'reproductive advantage' and produce more offspring than less adapted one.

The second deduction offers a hypothesis called 'natural selection' which provides a mechanism accounts for evolution.

13.2.2 Mutation

Mutation is a particularly important process in evolution because it is the original source of genetic variation in a population. It is a multilevel process & may involve change in a single nucleotide, several nucleotides. part of a gene. part of a chromosome, a whole chromosome or sets of chromosomes. The immediate cause of a mutation may be a mistake in DNA.replication, an insertion of a transposable element, a physical breakage of the chromosome or a failure in disjunction of meiosis. Mutagens are the agents. chemicals or radiation that induce & cause mutation. For example, the chemical ethylmethanesulfonate (EMS) causes the replacement of a cytosine with a thymine; UV radiation causes the formation thymine dimmers & the subsequent insertion of the wrong nucleotides during replication. These are the agents that cause the artificial mutations. Spontaneous mutations are the mutations for which the immediate causes are not known. Mutation is a very slow process that changes the genetic constitution of population at a very low rate. If mutation be the *only* process of genetic modification, evolution would occur at an impossibly low rate. Mutation will change the gene frequencies and will destabilize the Hardy-Weinberg equilibrium.

13.2.3 Genetic drift

Variation in gene frequencies can occur within the population by chan This is known as random genetic drift or Sewall Wright effect (named after t American geneticist who realized its importance in evolution) may be an mporta mechanism in evolutionary change in small or isolated populations. In a sm population all the alleles that are representative of that particular species m not be present. Chance events would result in the elimination of particular alle from the population when the size of that population is not large. Similarly, it equally possible for an allele to drift to a higher frequency. Random genetic dr in a small population may lead to the extinction of population or result in t population becoming better adapted to the environment. It may help the populati to become divergent from the parental population. In due time, this may lead the origin of new species by natural selection. Genetic drift is thought to ha been an important factor in the origin of new species on islands and in oth reproductively isolated populations.

Associated with this, there is another phenomenon called **Founder's effe** This refers to the fact that when a small population becomes split off from t parent population, it may not be true representative of the parent population terms of alleles. Some alleles may be absent and others may be disproportional represented. Continuous breeding within the pioneer population would produc a gene pool with allele frequencies different from that of the original populatio Continual mating within a small population decreases the proportion c heterozygote and increases the number of homozygote.

While genetic drift may lead to a reduction in variation within a populatio can increase variation within the species as a whole. If the small isolate populations have a selective advantage when environment changes, they may b selected in by natural selection & develop into a new species.

13.4 Migration

Migration or gene flow occurs when individuals move from one populatio another and interbred with the latter. Migration does not change allele frequencie for the whole species but may change them locally when the allele squencies i the migrants are different from those in resident.

Let us assume that individuals from surrounding populations migrate certain rate into a local population and they interbreed with the residents. The proportion of migrant is *m,* so that in the next generation (1-m) of the genes are descendants of residents and *m* are descendants of migrants. Also assume that in the surrounding population a certain allele X_1 has an average frequency P, while in the local population it has the frequency p_0. In the next generation. the frequency of X_1, in the local population will be

$$p_1 = (1 - m)p_0 + mP$$

$$= P_0 - m\,(P_0 - P)$$

i.e. the new allele frequency will be the original allele frequency p_0 multiplied by the proportion of reproducing individuals that are residents (1 - *m),* plus the proportion of reproducing migrant individuals *(m)* multiplied by their gene frequency P.

13.2.5 Meiotic drive

There are several well-known genetic systems in animals in which heterozygous individuals do not produce equal proportions of their two different alleles in gametes, as predicted by Mendelian segregation. This phenomenon is generally called meiotic drive or segregation distortion.

It is an example of ultra-selfish genes that interfere with the function of other genes and there by increase their own frequency. In heterozygotes, the selfish chromosome interacts with the normal chromosome to either destroy their gametes or make them non-functional. The well-known examples are the t allele in the house mouse, SD allele in *Drosophila melanogaster* etc. The distortion from normal segregation proportion takes place only in males and in general such meiotic deviations take place in one sex.

To understand the effect of meiotic drive on allele frequencies, assume that the male heterozygote produces a proportion k of the driven allele A_2 and 1 - k of wild type allele A_1. Therefore the allele frequency of A_2 after one generation, assuming half of the alleles come from females with normal segregation and half from males with meiotic drive, is

$$q_1 = \tfrac{1}{2}(p_0q_0 + q^2_0) + \tfrac{1}{2}(2kp_0q_0 + q^2_0)$$
$$= q_0\,[p_0\,(k + \tfrac{1}{2}) + q_0]$$

The change in allele frequency is

$$\Delta q = q_1 - q_0$$
$$= pqk^*$$

where $k^* = k - 1/2$ the deviation from normal segregation.

13.3 Suggested questions

a) Define gene Pool, allele frequency and genotype frequency?

b) Give a detailed account of destabilizing forces of neo-Darwinism?

c) What is meiotic drive?

d) Discuss the Hardy-Weinberg Law of genetic equilibrium?

Unit 14 ❒ Quantifying genetic variability

Structure

14.0 Introduction

There are two different ways in which a population may respond genetically to a changed environment. One, suggested by the examples of melanism insecticide resistance, is as follows. When the new conditions first arise, required mutations are either absent or very rare. There is an inevitable deb in the response of the population while the required mutations occur and increase from their initial low frequencies. Even for a fully dominant gene, takes three times as long for a frequency to increase from, say, 1 in 100,001 to 1 in 100 as it does from 1 in 100 to 1 in 10: the subsequent increase fror 1 in 10 will be rapid. During the first period, little observable change in the population would occur.

There are two main sources of information about genetic variability in natural populations.

1. Response to artificial selection
2. Study of protein variability

If a sample of sexually reproducing species is brought into the laboratory, will be found to respond to artificial selection for almost any trait.

The most widespread measure of genetic variability in a population is th amount of heterozygosity. Individuals in diploid species are either heterozygou or homozygous at a given locus and thus this measure represents a biologicall useful quantity.

The expected Hardy-Weinberg heterozygosity of a population for a particula locus with n alleles can be calculated as

$$H_E = 1 - \sum_{i=1}^{n} p_i^2$$

which is one minus the Hardy-Weinberg homozygosity.

14.1 Genetic structure of natural populations

In most species, populations are often subdivided into small units because o geographical, ecological or behavioural factors. For example, the populations o fish in pools are subdivided because suitable habitats for these species are no continuous . Behavioural aspects are also responsible for the subdivision of population such as in troops of primates.

A population may have substructure depending on the differences in genetic variation among its constituent parts. For example, a population may have localized subpopulations in which there is genetic drift. Exchange of individuals may not have equal probabilities in a population or selection may have different effects in different part of the population. There are several models studying the effect of population structure on the pattern and amount of genetic variation, the simplest of which is the continent - island model. Other model is the general model of population structure. Such models may not precisely fit a particular biological example, but they give close simulation to many incidences and allow an evaluation of the effect of limited gene flow.

14.2 Phenotypic variations

The basis of Natural selection is the performance of different phenotypes in a particular environment. Phenotypic variability may be caused by genotypic variability, but even a single genotype can produce different phenotypes in different environments. This is known as **phenotypic plasticity.** The reaction to a particular environment may reflect the developmental and physiological program expressed by the genotype to produce a specific phenotype during ontogeny. It is called **developmental reaction norm.** The reaction norm is the property of the genotype and may be subject to natural selection. For example. in a rapidly fluctuating environment it may be advantageous to buffer the metabolism and show an integrated response, while in a slowly changing environment it may be better to closely follow the environmental change. Thus, an organism's reaction norm should be related to fitness.

The predictability of a habitat is also an important ecological factor. If the environment changes in a predictable fashion (e.g. in an annual cycle), genotypes can be well adapted to this pattern. By reacting phenoypically to environmental changes, organisms can be optimally adapted to various environments in contrast to a generalist genotype that would be sub optimally adapted under all conditions. Adaptive phenotypic plasticity has been demonstrated frequently in freshwater organisms.

14.3 Models explaining changes in genetic structure of populations

As stated earlier, there are two distinct models to elucidate the effect of population structure on the pattern and amount of genetic variation: The Continent-Island model and General model.

14.3.1 The Continent - Island model

There are many examples of unidirectional gene flow such as occurs from a continent to an island population. Such examples include species with population on land island and nearby large land masses i.e. continents, aquatic species in ponds with a lake as the source of gene flow and peripheral populations of any species that are continuously replenished by the main part of the species range.

To formulate a model for this situation, let us assume that an island population receives migrants from a large source (continental) population as shown in Figure 1.

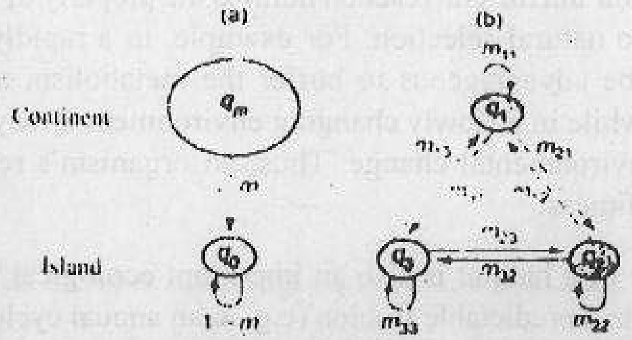


Fig. 1 Illustration of (a) the continent —island model and (b) population structure with three sub-populations.

Here we neglect the reciprocal gene flow though it may occur. We also assume that the island population is large enough that the effect of genetic drift is small relative to that of gene flow. Let the proportion of migrants moving into the island population each generation be m and the proportion of nonimmigrant (residents) be 1-m. If the frequency of A_2 in the migrants (the continents) is q_m and the frequency of A_2 on the island before gene flow is q_0, the allele frequency after gene flow is

$$\begin{aligned} q_1 &= (1 - m)q_0 + mq_m \\ &= q_0 - m(q_0 - q_m) \end{aligned}$$

14.3.2 General model

The continent - island model examines the allele frequency change only in the island population and assumes that only gene flow to the island is important. A more general model, assumes that gene flow can occur among all. parts of a population with many substructures.

Assume that a population consists of k subpopulations and that the proportion of individual migrating from subpopulation *j* to subpopulation *i* every generation is m_{ij}. As a result, there is a matrix of gene flow parameters. called the backward **migration matrix** by Bodmer and Cavalli-Sforza. This describes the gene flow pattern among subpopulations. The proportion of nonmi grants or residents for subpopulation I is given by m_{ii}. Each row of this matrix sums to unity because it describes the proportion coming from even other possible subpopulation to that particular subpopulation or

$$\sum_{j=1}^{k} p_{ij} = 1.0$$

14.4 Suggested questions

a) What is Hardy-Weinberg homozygosity?

b) What do you mean by phenotypic plasticity?

c) Discuss "the Continent-Island model" in the light of genetic structure of population?

Unit 15 ❐ Molecular population genetics

Structure

15.0 Introduction
15.1 Patterns of change in nucleotide and amino acid sequences
15.2 Ecological significance of molecular variations
15.3 Emergence of Non-Darwinism—Neutral hypothesis
15.4 Suggested questions

15.0 Introduction

A thorough understanding of population genetics is a must to comprehend the evolutionary process. Population genetics is a field that has had periods of great interest and growth and other periods in which there was less innovation and fewer contributions.

This area of study attracted such scientific geniuses as Ronald A. Fisher, J. B. S. Haldane, and Sewall Wright. They provided the theoretical basis to population genetics and formed much of the paradigm still used today. Population genetics includes facets of several different disciplines and various approaches to scientific knowledge. The advent of enzyme electrophoresis and molecular biological techniques enabled the scientists to get the first population molecular data and to interpret these fundamental data in the light of molecular population genetics and evolutionary biology. Understanding the evolutionary significance of the data of DNA variations that exist both within and between species is the new challenge for a population geneticist. Furthermore, the role of this molecular variation in adaptive differences in morphology, behaviour, and physiology and nonadaptive variation in complex genetic diseases is a topic to which population genetics can make fundamental contributions.

There are three different approaches that can be used to investigate phenomena in population genetics:

a) Empirical, b) Experimental and c) Theoretical

Empirical approaches are traditional extensive observations of genetic variation of a gene or genes of interest.

Experimental tests can provide necessary support for hypotheses developed from empirical data about the effect of particular factors on levels and patterns of genetic variation.

Using the information gathered either from empirical or experimental studies; one can construct a general theoretical model. This model may also provide a general framework as well as allows scientists to make predictions. However, caution is necessary to extrapolate the prediction to the reality.

15.1 Patterns of change in nucleotide and amino acid sequences

With the spectacular development of biochemical and molecular biological techniques, nucleotide and amino acid sequences of individuals within populations have become available for a number of genes. Understanding the basis for the patterns of this variation within populations, between populations, and between species is basis of study molecular population genetics.

The simplest way to measure the amount of nucleotide variation is to determine the number of nucleotide sites that are variable in the sample of sites examined. If a sample of DNA sequences are examined and let the number of nucleotide sites that are segregating be S and the total number of sites compared be N then the proportion of nucleotide sites that differ in the population is

$$ps = S/N$$

$$V(ps) = p(1 - p)/N$$

This value is called p distance for nucleotide sequences.

One of the first estimation of nucleotide diversity was for the Adh gene in *Drosophila melanogaster.*

Similarly the proportion of aminoacid sites that are different or segregating in the population can be estimated by

$$ps_{aa} = S/N$$

Where S indicates the number of amino acid sites that differ among sequences and N is the number of codons compared.

15.2 Ecological significance of molecular variations

From 1960s onward, biological realism was advocated in population genetics. The hope was that a broader discipline of population biology would be created through the application of population ecology in the field of population genetics and vice versa. The idea implies that relative fitness value does not depend only on a particular genotype but also on the environment in which the genotype exists. For example, in one environment, relative fitness of a given genotype may be high, whereas in another environment, it may be low. Environmental factors that potentially influence relative fitness are physical factors such as temperature, moisture, and soil type; biotic factors such as inter specific competitors, predators or prey, and hosts or parasites. In order to assess the ecological significance of variation, first we have to assume that the selective values are environmentally dependent and that the environment may vary over time or in space. Such an analysis is particularly appropriate in case of the effect of physical factors of the environment. Secondly, we consider the selective effects of different genotype frequencies within a population. The effects of population numbers of the same species can be examined by using an extension of the logistic equation from population ecology that allows density-dependent selection.

A number of approaches have shown apparent associations between genetic variation and environmental factors. One of the most thoroughly investigated polymorphisms is that of colour and banding patterns in the shell of the snail *Cepaea nemoralis.*

There are differences between the effects of spatial and temporal variation in the environment on genetic variation. If the environment varies over time– for example, one year is wet & the next is dry - then every individual must endure every different environment whether they are genetically adapted to it or not. However, if the environment varies over space for example, one area is wet & another is dry - then only part of the population encounters a partial'. —' environment at a given time. In fact most of the substantive cases of genetic - environmental associations are related to spatial environmental heterogeneity rather than two temporal variations in the environment.

15.3Emergence of Non-Darwinism—Neutral hypothesis

With the spectacular development of enzyme purification, protein separation. and molecular biology in 1960s, it became possible to study evolution all molecular level. The amino acid sequences of the same protein in a number of different species were becoming available and the size of difference in the sequence suggested the presence of 'molecular clock'. It means the proteins evolve at a constant rate. The rates are different between proteins. Some proteins evolve faster than others-but the rate for any one protein appears to be almost constant.

Protein electrophoresis, a sensitive process by which variation of protein structure can be assessed faithfully, made it possible to study the variation exists in a natural population. It was observed that many more variants exist for each protein than had been assumed. Lewontin was one of the first to apply gel electrophoresis in this way. The important consequence of these early observations that they led Japanese theoretician, Moto Kimura, to propose a radical hypothesis about the force driving molecular evolution. In 1968. Kimura opined that molecular evolution was mainly driven not by natural selection but by random drift among equally well-adapted sequence variants. This famous theory is known as Neutral theory of evolution. According to this theory, the great majority of evolutionary mutant substitutions at the molecular level are caused by random fixation, through sampling drift, of selectively neutral mutants under continued mutation pressure. This view is in sharp contrast to the traditional neo - Darwinism theory of evolution.

According to Kimura, when one compares the genomes existing species, the vast majority of molecular differences are selectively "neutral." That is, these differences do not influence the fitness of either the species or the individuals who make up the species. As a result, the theory regards these genome features as neither subject to, nor explicable by, natural selection. This view is based in part on the genetic code according to which sequences of three nucleotides (codons) may differ and yet encode the same amino acid *GCC* and *GCA* both encode alanine for example). Consequently, many potential single-nucleotide changes are in effect "silent" or "unexpressed". Such changes are presumed to have little or no biological effect. However, it should be noted that the original theory was based on the consistency in rates of amino acid changes, and hypothesized that the majority of those changes too were neutral.

A second assertion or hypothesis of the neutral theory is that most evolutionary change is the result of genetic drift acting on neutral alleles. A new allele arises typically through the spontaneous mutation of a single nucleotide within the sequence of a gene. In single-celled organisms, such an event immediately contributes a new allele to the population, and this allele is subject to drift. In sexually reproducing multicellular organisms, the nucleotide substitution must arise within one of the many sex cells that an individual carries. Then only if that sex cell participates in the genesis of an embryo and offspring does the mutation contribute a new allele to the population. Neutral substitutions create new neutral alleles.

Through drift, these new alleles may become more common within the population. They may subsequently decline and disappear, or in rare cases they may become "fixed"—meaning that the substitution they carry becomes a universal feature of the population or species. When an allele carrying one of these new substitutions becomes fixed, the effect is to add a substitution to the sequence of the previously fixed allele. In this way, neutral substitutions tend to accumulate, and genomes tend to evolve.

According to the mathematics of drift, when looking between two species or two isolated populations, most of their single-nucleotide differences can be assumed to have accumulated at the same rate as individuals with mutations are born. This latter rate, it has been argued, is predictable from the error rate of the enzymes that carry out DNA replication - enzymes that have been well studied and are highly conserved across all species. Thus, the neutral theory is the foundation of the molecular clock technique, which evolutionary molecular biologists use to measure how much time has passed since species diverged from a common ancestor. While the mutation rate is no longer considered a constant, diverse and more sophisticated clock techniques have emerged.

Many molecular biologists and population geneticists besides Kimura, contributed to the development of the neutral theory, which may be viewed as an offshoot of the modern evolutionary synthesis.

15.4 Suggested questions

a) What are the approaches that can be used to investigate phenomena in population genetics?

b) What are the patterns of change in nucleotide in the population genetics?

c) Discuss the neutral hypothesis in the emergence of Non-Darwinism?

Unit 16 ❐ Genetics of Speciation

Structure

16.1 Phylogenetic and / biological concept of species

What is a Species?

Small almost imperceptible changes in an existing species lead to the shifts that at length are manifested in the appearance of new species. The species provides a common ground where micro- and macroevolution meet. In this role, the species is the critical unit in evolution. New species must come from old if there is to be evolution. To a considerable extent two new species arising from one original parent species would constitute the first step in evolutionary change.

Species/Subspecies

Earlier definition of species is: a species is a community, or a number of related communities, where distinctive morphological characters are in the opinion of a competent systematise sufficiently definite to entitle it, or them, to a specific name.

Later. Mayr as defines it: Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups. Given reproductive isolation, distinctive morphological characters usually will arise in due course.

Subspecies are geographical races of a species and stands one step forward of an existing species. They are genetically open populations.

Evolutionary Significance of Subspecies

Several contrasts exist between species and subspecies:

1. Members of different species do not ordinarily interbreed when they come into contact; members of different subspecies within one species ordinary do so.
2. Different species frequently occupy separate territories, but the territories may overlap, in which case intermediate separate territories that do not overlap, and if the territories come into contact intermediate or transitional forms are frequently found.
3. Structural differences between species are usually greater than those between a subspecies.

However, isolating mechanisms are primary need towards the establishment of subpopulations, which later will develop into subspecies or species.

Biological Species Concept

Species have independent reality and are typified by the statistics of populations of individuals. It differs from both by stressing the populational nature and genetic cohesion of the species and by pointing out that the species receives its reality from the historically evolved shared information in its gene pool.

As a result, the members of a species form a *reproductive community.* The individuals of a species of animals recognize each other as potential of devices ensure intraspecific reproduction in all organisms. The species is also an *ecological unit* consisting of a large, in temporary vessel holding a small portion of the contents of the gene pool for a short period of time. These 3 properties show that species are biological populations. The biological species definition, which result from this theoretic species concept is as follows: *A species is a group of interbreeding natural populations that is reproductively isolated from other such groups.*

The development of the biological concept of the species was one of the earliest manifestations of the emancipation of biology from an inappropriate philosophy based on the phenomena of inanimate nature. This species concept is called biological not because it deals with biological taxa but because the definition is biological. It utilizes criteria that are meaningless in the inanimate world.

A species is a protected gene pool; it is a Mendelian population shielded by ts own devices *(isolating mechanisms)* against unsettling gene flow other gene pools. Genes of the same gene pool form harmonious combinations because hey have become coadapted by natural selection. Mixing the genes of two different species usually leads to a high frequency of disharmonious gene combinations; mechanisms that prevent this are therefore favored by selection.

This makes it quite clear that *the word* species *in biology is a relational term:* A is a species in relation to B and C, because it is reproductively isolated "from them. This concept has its primary significance with respect to sympatric md synchronic populations (nondimensional species), and these are precisely he situations where the application of the concept poses the fewest difficulties. The more distant two populations are in space and time, the more difficult it becomes to test their species status in relation to each other but the more biologically irrelevant this status becomes.

The biological species concept (BSC) also solves the paradox caused by he conflict thai made Linnaeous deny evolution and Darwin denies the reality of species (Mayr 1957). The biological species combines the discreteness of the local species at a given time with an evolutionary potential for continuing change. The importance of the biological species concept lies in the fact that it is the concept employed in the largest number of biological disciplines, particularly ecology. physiology and behavioral biology.

All species mat conform to the biological species concept are evolutionary species. but not au evolutionary species need conform to the biological species concept (Eodkr 1989; Templeton 1989).

Biological species are real, but not in same sense that "hydrogen" is real. A nolecule of hydrogen found anywhere, and formed at any time, in the universe would be a member of the class hydrogen. By contrast, an organism that looks ike a tiger another planet unless the two organisms shared a common ancestor, viewed in this way, we can see that classes are defined by convergences, whereas individuals are defined by homology. So the typological view and the purely populational view of species are nonevolutionary, because they are based on homoplasy and evolutionary descent involves homology (common ancestry: Wiley 1989).

Under this "species as individuals" view, the most important characteristic of a species is that its members are bound together by unique common ancestry, and not that its members are reproductively isolated from members of other species. The evolution of a single species is analogous to the development of a single organism; just as an organism changes its appearance without losing its identity during development, so a species can change its appearance without loosing its identity during evolution. Over time, distinct historical trajectories emerge from the speciation process, each differing to some degree from its ancestor and closest relatives, but retaining some of its ancestry in the form of synapomorphies. We take advantage of this historical mosaic nature of the attributes of organisms that comprise species when we use synapomorphies to reconstruct phylogenetic trees (fig. 16.1).

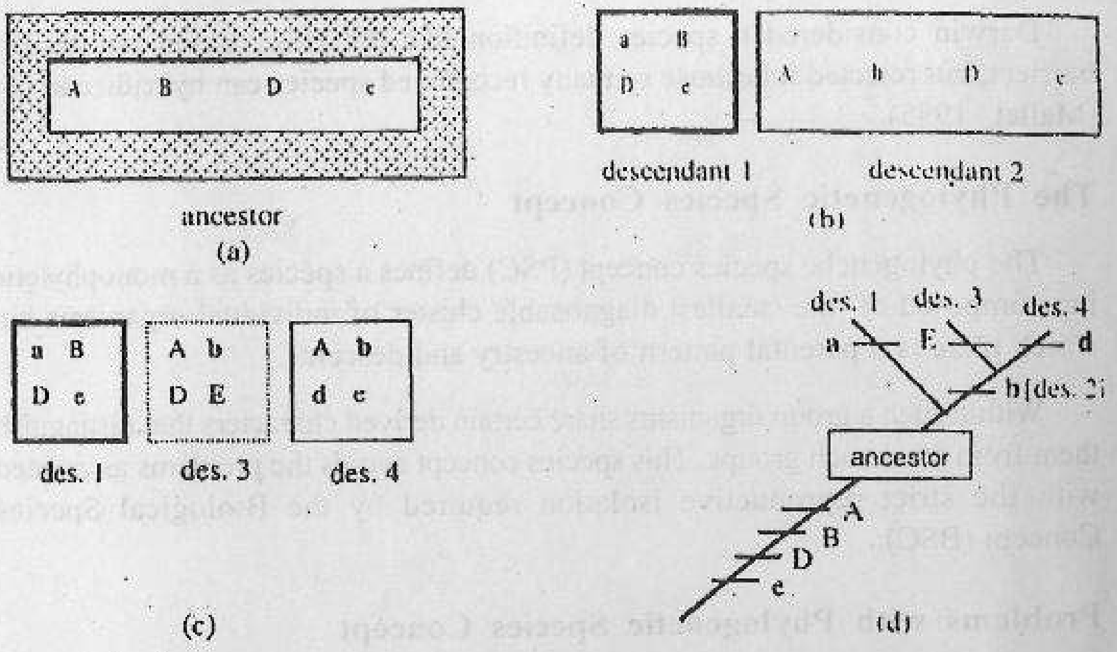


Fig: 16.1. Species are a mosaic of ancestral and derived traits, but only synapomorphies distinguish phylogenetic relationships. *Bold letters* = derived traits, (a) Ancestral species, (b) Ancestral species divided, descendant species 1 and 2 produced, (c) Descendant species 2 divided, specie; 3 and 4 produced, (d) Phylogenetic tree depicting the relationships between the ancestor anc all its descendants. Notice that descendants 1 and 2 are sister species (possession of charade: c); descendants 3 and 4 are sister species (possession of character b). Autapomorphies (a, d, E) distinguish individual species, but not phylogenetic relationships.

Problems with the biological species concept (BSC)

Not all organisms occur in groups within which there is sexual interbreeding and between which gene flow is prevented.

1. *Asexual organisms:* Absence of sexual recombination is rare but does occur in some groups of organisms. Because the BSC refers by definition to sexual reproduction, asexually reproducing organisms (agamous species) cannot be considered for BSC.
2. *Interspecific hybridization:* The BSC is also problematic when species are sexual, but barriers to interspecies breeding are not strong. Interspecies mating producing fertile hybrids are not common among related animal species, but they are frequent in plants and fungi.

Darwin considered a species definition like the BSC, based on sterility barriers, but rejected it because so many recognized species can hybridize in tire (Mallet, 1995).

The Phylogenetic Species Concept

The phylogenebc species concept (PSC) defines a species as a monophyletic iup composed of 'the smallest diagnosable cluster of individual organisms hin which there is a parental pattern of ancestry and descent'.

Within such a group organisms share certain derived characters that distinguish them from other such groups. This species concept avoids the problems associated with the strict reproductive isolation required by the Biological Species Concept (BSC).

Problems with Phylogenetic Species Concept

First, it is not clear how many shared derived characters a monophyletic aup of organisms should have to be classified as a separate species. If one searched hard enough with high-resolution molecular methods, an established species could be split up into many very small groups of individuals that each shared a common derived character. Clearly, giving species status to all such small groups is not meaningful, for in this way any newly derived trait would produce a new species and the number of species would explode. Recently the phylogenetic species concept has started to be modified to avoid extreme division of species, which may well lead to an attractive or addition to the biological species concept.

Evolutionary Species Concept

Some authors, particularly paleontologists, are not satisfied with the biological species concept because of its strict applicability only to the nondimensional situation. Simpson (1961) therefore proposed the following definition: "An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies."

The principal weakness of the so-called evolutionary species definition is that it ignores the core of the species problem - the causation and maintenance of discontinuities between contemporary species - and concentrates instead on trying to delimit species taxa in the time dimension.

Neither Simpson, Wiley, nor Hennig has solved the problem of how to deal with the relationship of descendant populations in a single lineage. Hennig (1966) arbitrarily terminated every evolutionary species when a daughter species branched off the parental lineage, ignoring the fact that a peripatric speciation event usually leaves the parental species unchanged.

16.2 Patterns and mechanism of reproductive isolation

Production of divergence

Three basic phenomena play important roles with regard to the production of divergence.

1. Random incidence of mutations: The origin of diversity in living organisms is due to mutations. But most of the inherited diversity actually seen in different populations is due not so much to the appearance of one mutation here and another there, as to the continual shuffling and recombination by true sexual reproductions, of different mutations.

II. Genetic drift: A second process leading to divergence under certain conditions, is known as genetic drift. It may be described very briefly as the cumulative effect of random sampling errors. In large populations genetic drift can not take place and selection is the principal agent producing changes. But in a large population, subdivided into numerous partially isolated groups, both adaptive and non- adaptive differentiation are to be expected and such conditions are most favourable for evolution.

III. Natural selection: Evidence of the roles played by natural selection in producing geographical variation and divergence is very considerable in importance. There are four main lines of evidence, stable clines, the enological rules, the study of overlaps and direct investigations of selection.

Stable clines are smooth character gradients that are subjected to the approval of natural selection.

Many different species show the same sort of variation under the same ecological conditions and such regularities of variation are explicable only by the action of natural selection. Some ecological rules provide evidences.

Two closely related species come to overlap for part of their ranges, or when part of a species escapes from its coexisting relatives by colonizing a distant district.

It is possible to estimate the selection coefficients involved for effectiveness of natural selection. Since no two localities on the earth are identical in every feature, and even slight differences between localities can produce considerable selective differences between populations inhabiting them the production of geographical diversity in populations by local selection is only to be expected.

Mechanism of Reproductive Isolation

1. If two populations are ecologically isolated for a long enough time, differential mutation, drift, and selection will ultimately lead to gene combuations producing reproductive isolation.
2. If two formerly ecologically isolated populations become sympatric, selection will operate against any hybrids produced by accidental interbreeding and favor and reinforce all reproductive isolating mechanism.

3. If the genetic controls of hybrid sterility are correlated with genetic features with a positive selection value, then genetic incompatibility will result from any crosses.

4. If sterility - producing genes are neutral or even nonadaptive, they may become fixed by genetic drift in small populations.

Table 16.1 Summary of the most important isolating mechanisms, which separate species of organisms.

A. Prezygotic mechanisms : Prevent fertilization and zygote formation.

1. **Habitat**: The populations live in the same regions, but occupy different habitats.
2. **Seasonal or temporal** : The populations exist in the same regions but are sexually mature at different times.
3. **Ethological (only in animals)** : The populations are isolated different and incompatible behavior before mating.
4. **Mechanical.**: Cross-pollination is prevented or restrict differences in structure of reproductive structures (genitalia in animals flowers in plants).

B. Postzygotic mechanisms : Fertilization takes place and hybrid zygotes formed, but these are inviable, or give rise to weak or sterile hybrids.

1. **Hybrid inviability or weakness.**
2. **Developmental hybrid sterility :** Hybrids are sterile because gonads develop abnormally, or meiosis breaks down before it is completed.
3. **Segregational hybrid sterility :** Hybrids are sterile because of abnormal segregation to the gametes of whole chromosomes, chromosome segments, or combinations of genes.
4. **F_2 Breakdown** : F_1 hybrids are normal, vigorous, and fertile , but F_2 contains many weak or sterile individuals.

16.3 Models of speciation (Allopatric, Parapatric, Sympatric)

14.3.1 Allopatric Speciation

"Allopatric" speciation is a generic term for models that invoke the comp geographical separation of two or more populations of an ancestral specie initiate speciation.

Allopatric speciation mode I

Usually called **vicariance**, or geographic speciation, allopatric speciaation mode I combines gene flow among populations prior to separation with a passivate role for range changes in the ancestral species. It occurs when an ancestral species is geographically separated into two or more relatively large and isolated populations, with subsequent lineage divergence by the isolated descendant populations. The speciation rate will depend on the degree of variation in the ancestral species prior to isolation and the rate of origin of evolutionary novelties in the subdivided populations.

Three predictions from this model are of interest to students of speciation :

(1) The phylogenetic tree for the group will be predominantly dichotomous because the fragmentation of the ancestral species and concomitant interruption of gene flow among the isolated populations make is unlikely that either of the descendant species will be identical to the ancestor or to each other. In this case, the ancestor experiences "extinction through total speciation."

(2) The points of geographical disjunction between sister species will correspond to the historical boundaries established'by the geological changes. Based on this, the ancestral range may be estimated by combining the distributions of the descendant species, assum substantial range expansion or contraction following speciatioin (Fig. 5.2).

(3) A multitude of ancestral species, fragmented in the same way by the same geological event, could all theoretically speciate subsequent to

the event, because the mechanism initiating speciation is independent of any particular biological system.

Hence, we would expect to find the same biogeographical distribution pattern shared by a number of different clades. The research program called "vicariance biogeography" relies on this mode of allopatric speciation to detect episodes of parallel biological and geological evolution.

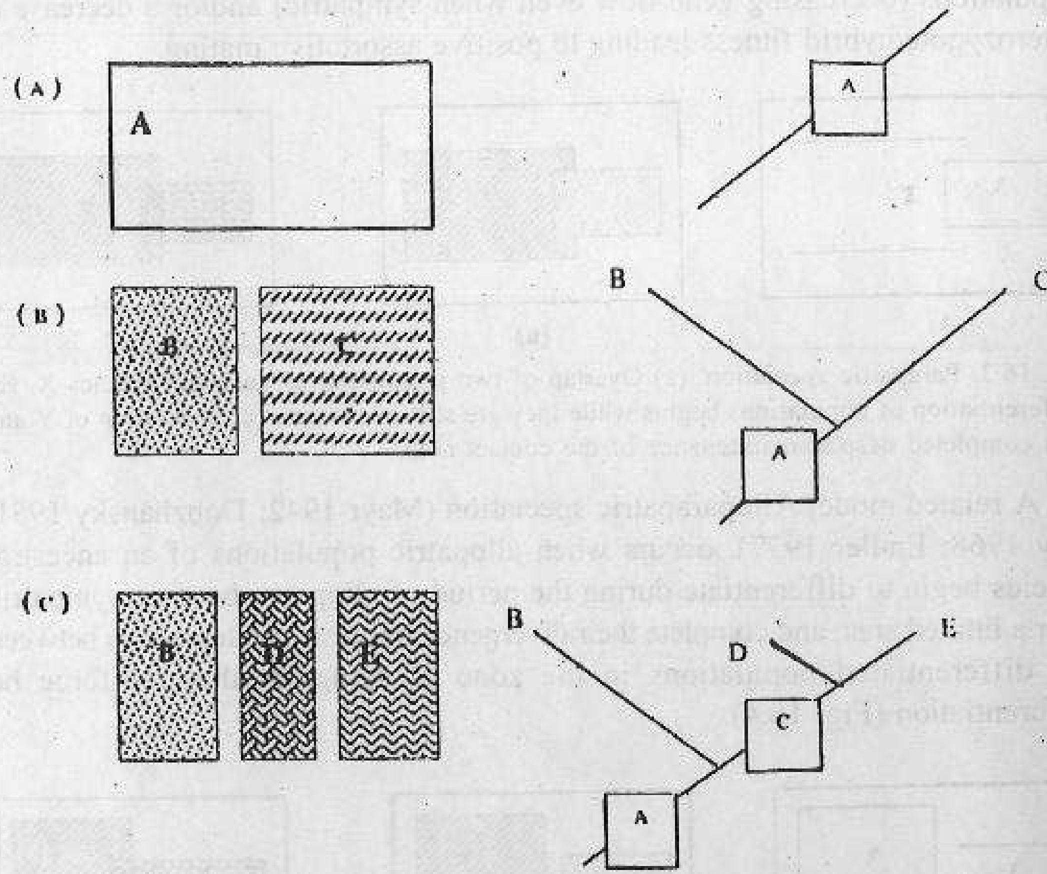


Fig. 16.2. Allopatric speciation mode I. (a) Species A extends throughout a geographical area.(b) The species is divided by the appearance of some geographical barrier preventing gene flow; the two populations continue to evolve independently of one another, producing new species B and C. (c) Species C undergoes another geographical upheaval, gene flow is eliminated, and changes continue in isolation, leading to the eventual production of new species D and E. The outcome of this division of space through time is the production of three extant species (B, D, and E) and the extinction through total speciation of two ancestors (A and C).

16.3.2 Parapatric Speciation

Parapatric speciation occurs when two populations of an ancestral species differentiate into descendant species despite the maintenance of some gene flow and geographical overlap during the process (Fig. 16.3). Stochastic events (e.g., drift) and/or adaptive responses to local selection pressures initiate the differentiation, which is then promoted by low vagility among members of the populations (decreasing gene flow even when sympatric) and/or a decrease in heterozygote/hybrid fitness leading to positive assortative mating.

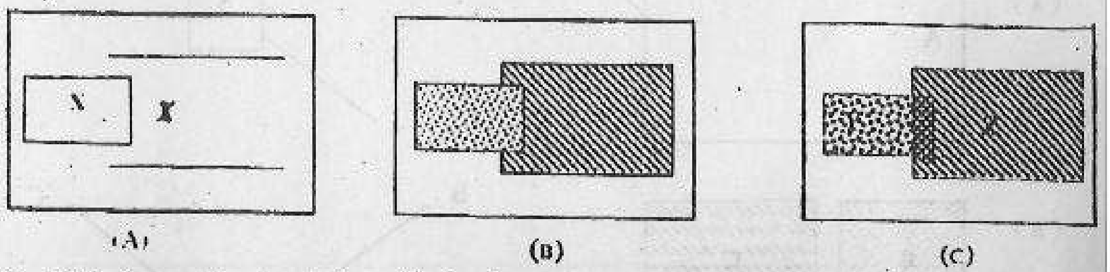


Fig. 16.3. Parapatric speciation. (a) Overlap of two population of ancestral species X. (b) Differentiation of populations begins while they are still in contact, (c) Speciation of Y and Z is completed despite maintenance of the contact area.

A related mode. Alloparapatric speciation (Mayr 1942; Dobzhansky 1951; Key 1968: Endler 1977). occurs when allopatric populations of an ancestral species begin to differentiate during the period of allopatry, become sympatric over a limited area, and complete their divergence because of interactions between the differentiated populations in the zone of sympatry that reinforce he differentiation (Fig. 16.4).

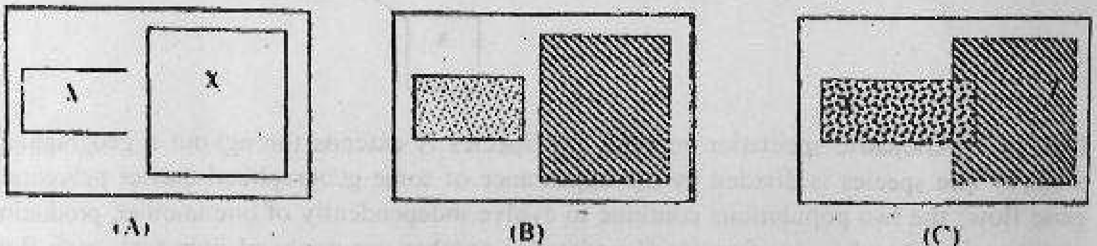


Fig. 16.4. Alloparapalric speciation. (a) Two populations of ancestral species X are separated geographically, (b) Differentiation of populations begins while they are allopatric. (c) Speciation of Y and Z is completed when contact is established between the diverging populations.

16.3.3 Sympatric Speciation

Sympatric speciation (Maynard Smith 1966; Dickinson and Antonovics 1973; Felsenstein 1981; Gittenberger 1988) occurs when one or more new species arise without geographical segregation of population (Fig. 16.5). Unlike the allopatric models, which postulate that gene flow between populations is initially served by factors extrinsic to the biological system, sympatric speciation requires the involvement of biological processes intrinsic to the system, for example hybridization, ecological partitioning, the evolution of asexual or parthenogenetic. populations, or a change in mate recognition. Additionally, differentiation must occur "within the dispersal area of the offspring of a single deme [the cruising range]" (Mayr 1963:257).

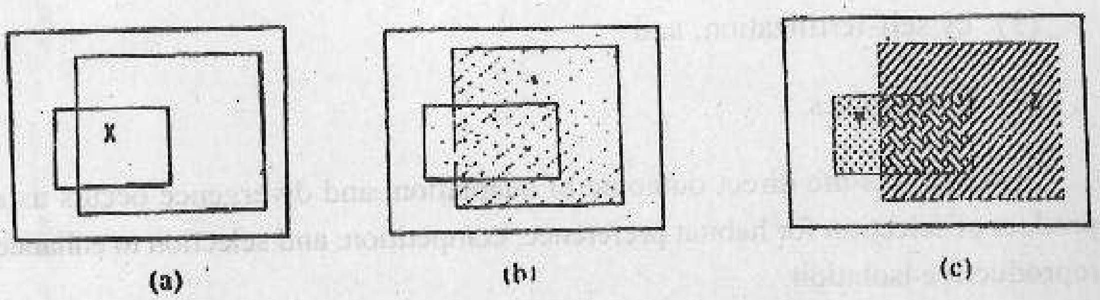


Fig. 16.5. Sympatric speciation. (a) Extensive overlap of two populations of ancestral species X. (b) Differentiation of populations begins while they are still in contact, (c) Speciation of Y and Z is completed despite maintenance of the contact area.

Although this was the mode originally preferred by Darwin (1859), support for sympatric speciation wavered when population geneticists demonstrated that the effects of gene flow among populations would tend to swamp out or homogenize any novel traits arising within a population. If gene flow were restricted or interrupted, as in the allopatric or parapatric speciation models, the novel trait would have a better chance of becoming fixed within a deme, and the whole process would operate much more smoothly. The work of the population geneticists was coupled with the earlier recognition that most "related" species (this usually meant members of the same genus) exhibited allopatric distributions, and this combination provided a strong foundation for the hypothesis that most speciation was allopatric. However, in recent years there has been a revival of interest in the possibility of sympatric speciation modes, as researchers have intensified investigations of mechanisms of phenotypic plasticity, disruptive selection, and chromosomal divergence. One of the most eloquent supporters of this and other nonallopatric models has been Guy Bush, who suggested that it is unnecessary to postulate a link between speciation and adaptation in allopatric speciation models, while in nonallopatric models (Bush 1982).

Sympatric speciation may occur, at least among higher plants, in four principal ways:

(1) by polyploidy;

(2) by hybridization between distinct species;

(3) by self-fertilization; and

(4) byapomixes.

Speciation is the direct outcome of adaptation, and divergence occurs as a product of selection for habitat preference, competition, and selection to enhance reproductive isolation.

Sympatric speciation requires observations of the sympatric distribution of sister species that differ in some special ecological or genetic characteristics that could, in themselves, produce independent species. Phylogenetic trees reflecting incidents of sympatric speciation may be either dichotomous or polytomous, depending on whether or not the ancestor persists. Biogeographically, this mode requires that sister species be broadly sympatric today and *at the time of speciation.* Observing that the two species are sympatric today is not sufficient evidence of either sympatry in the past or a sister-group relationship.

The elementary processes in microevolution are genetic changes-first mutations, then changes in gene frequencies driven by selection, migration, and drift. Phenorypes with better reproductive success get more copies of the genes

Relationship between allopatric and sympatric speciation

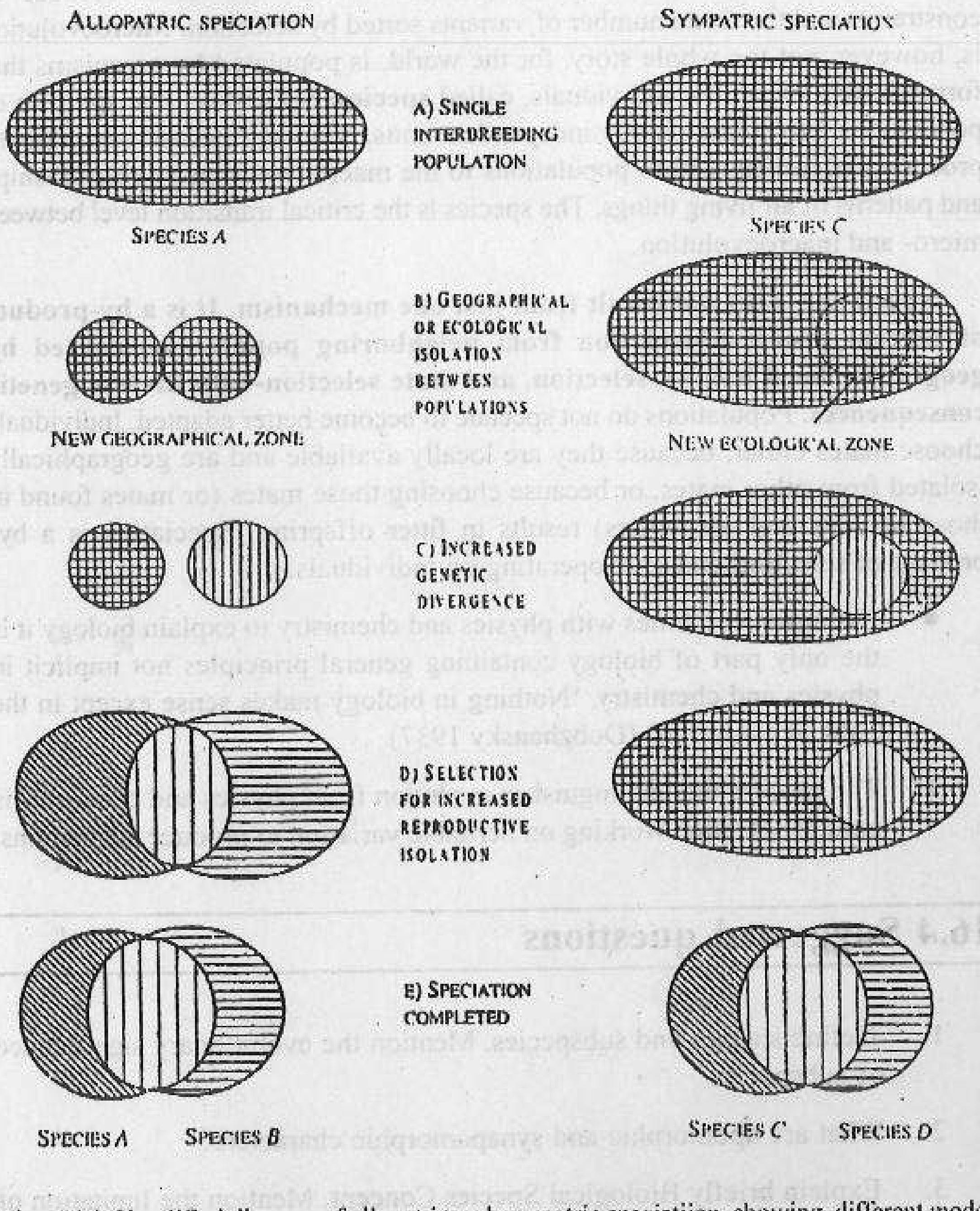


Fig : 16.6. Simplified diagram of allopatric and sympatric speciatiion, showing, different modes of divergence.

they carry into future generations, leading to inherited changes in the design of phenotypes. Adaptation-occurs but perfection does not result because of constraints and the finite number of variants sorted by selection. Microevolution is, however, not the whole story, for the world, is populated by organisms tha form clusters of similar individuals, called **species.** Speciation, the splitting of populations into evolutionarily independent units, connects the microevolutioary processes occurring within populations to the macroevolutionary relationships and patterns of all living things. The species is the critical transition level between micro- and macroevolution.

Speciation does not result from just one mechanism. It is a by-product of several processes-isolation from neighboring populations caused by geography, local habitat selection, and mate selection-with diverse genetic consequences. Populations do not speciate to become better adapted. Individuals choose mates either, because they are locally available and are geographically isolated from other mates, or because choosing those mates (or mates found in those habitats and not others) results in fitter offspring. Speciation is a by-product of selection and drift operating on individuals.

- Evolution combines with physics and chemistry to explain biology it is the only part of biology containing general principles not implicit in physics and chemistry. 'Nothing in biology makes sense except in the light of evolution' (Dobzhansky 1937).
- The process that distinguishes evolution from physics and chemistry is natural selection working on heritable variation to produce adaptations.

16.4 Suggested questions

1. Define species and subspecies. Mention the evolutionary significance of subspecies.
2. What are apomorphic and synapomorphic characters?
3. Explain briefly Biological Species Concept. Mention the limitation of this concept.

4. 'Species are a mosaic of ancestral and derived traits' - explain.

5. Define Phylogenetic Species Concept. Why this concept is not applicable to all kinds of species?

6 What are the sources of divergence in a population? Briefly categorize the mechanism of reproductive isolation.

7. Tabulate the important isolating mechanisms that separate species.

8. What is vicariance? Explain a model of Allopatric speciation.

9. Characterize parapatric speciation. Describe the process of sympatric speciation with the help of diagram.

10. Describe with the help of a flow chart the relationship between allopatric and sympatric speciation.

11. Compare the processes of allopatric and parapatric speciation.

12. What do you mean by evolutionary species concept?

Unit 17 ❐ Origin of higher categories

Structure

17.1 Phylogenetic gradualism and punctuated equilibrium

Evolution of different characters at different rates within a lineage is called **mosaic evolution.** It is one of the most important principles of evolution, for it says that an organism (species) evolves not as a whole, but piecemeal: many of its features evolve quasi-independently. (There are important exceptions; for example, features that function together may evolve in concert.) This independence is seen not only in comparisons among distantly related taxa, but even within a species: characteristics usually vary independently among different geographic populations of a species. These observations largely justify the theory of evolutionary mechanisms, in which we analyze evolution not in terms of whole organisms, but in terms of changes in individual features or even individual genes underlying such features.

Because of mosaic evolution, it is inaccurate or even wrong to consider one living species more "primitive" or "advanced" than another. Although it is in - accurate to describe a living taxon as more primitive than another, it is often useful to speak of a BASAL lineage, one that branches off a phylogenetic tree below others with which it is compared.

Evolution is gradual

One of the most difficult issues in evolutionary biology, still a matter of contention is whether or not Darwin was right in arguing that evolution proceeds by small" successive changes (GRADUALISM) rather than by large "leaps (SALTATIONS).

Innumerable observations on both living and fossil organisms indicate that gradual evolution is common, and is likely to be the pattern in many cases in which evidence is lacking. Cases of mosaic evolution show that the various features of a higher taxon evolve piecemeal, not all at once. Cases of GRADUATION of individual characters among species imply that characters usually evolve by sma steps, not by large, discrete jumps.

The limits of higher taxa are often arbitrary points along a continuum. Many higher taxa can be defined only because gaps do exist, at least among living species.

Another line of evidence in favor of gradualism is that the same discrete characters that clearly define certain higher taxa frequently vary within or among closely related species in another taxon.

There is nothing intrinsic to a particular character that makes it diagnostic of higher taxa rather than species. Hence, it is reasonable to assume that features that now distinguish higher taxa (such as cotyledon number) arose as variations at the species level. Features that distinguish closely related species also vary within species. Thus, at every level of comparison of adjacent taxonomic levels- within vs. among species, species vs. genus, genus vs. family, etc.- many instances of gradation and of mosaic change are known. This pattern implies CONTINUITY of evolutionary change, from slight to great differences.

Arguments for Gradualism

Darwin was well aware of "sports"-what we now call mutations with large, discontinuous effects on one or more features-but held that most evolution is based on the slight individual differences that we observe within populations (which we now recognize as polygenic variation). This gradualist position was reaffirmed by neo-Darwinians such as Ronald Fisher (1930), and has been the majority opinion ever since (reviewed by Maynard Smith 1983). The *chief* *arguments of contemporary- gradualist* are based on (1) intermediates among both living and extinct species; (2) functional considerations; (3) fitness effects of mutations; and (4) the genetics of species differences.

Punctuated Equilibrium

The highly controversial idea of **punctuated equilibrium,** introduced by Eldredge and Gould (1972) and elaborated both by them (e.g., Gould and Eldredge 1977, 1993) and by Steven Stanley (1979), consists of both a *claim about the pattern of change* in the fossil record and a *hypothesis about evolutionary processes.* Many or most phenotypic characters change little over extended spans of geological time (equilibrium, or stasis), but when they do evolve, they change relatively rapidly from one static state to another (that is, the stasis is punctuated by change). The *hypothesis* that Eldredge and Gould introduced is that characters evolve primarily in concert with true speciation. Moreover, if, as Mayr hypothesized new species (reproductively isolated entities) evolves rapidly in small, isolated populations, the transitional stages in the divergence of these populations will seldom be preserved in the fossil record. Eldredge and Gould, suggested that the widespread ancestral form does not change very much because of genetic "constraints" that prevent features from changing, even if natural selection would favor new features. If a newly arisen species becomes widespread and abundant, its new features likewise become stabilized, and little further evolution occurs unless it in turn buds off new "daughter" species.

Eldredge and Gould contrasted their model with what they look to be the traditional view in paleontology - which features evolve slowly, steadily, gradually, without any particular association with speciation. They called this the "phyletic gradualism" model. Another possibility, which Malmgren *et al.* (1983) called "punctuated gradualism," is that character evolution may not necessarily be associated with speciation, but may nevertheless slow rapid transitions between long-stable states (Fig. 17.1).

Gould and Eldredge (1993) have concluded that punctuation and stasis is the most common pattern in the fossil record, but some other researchers (Levinton, 1988) disagree.

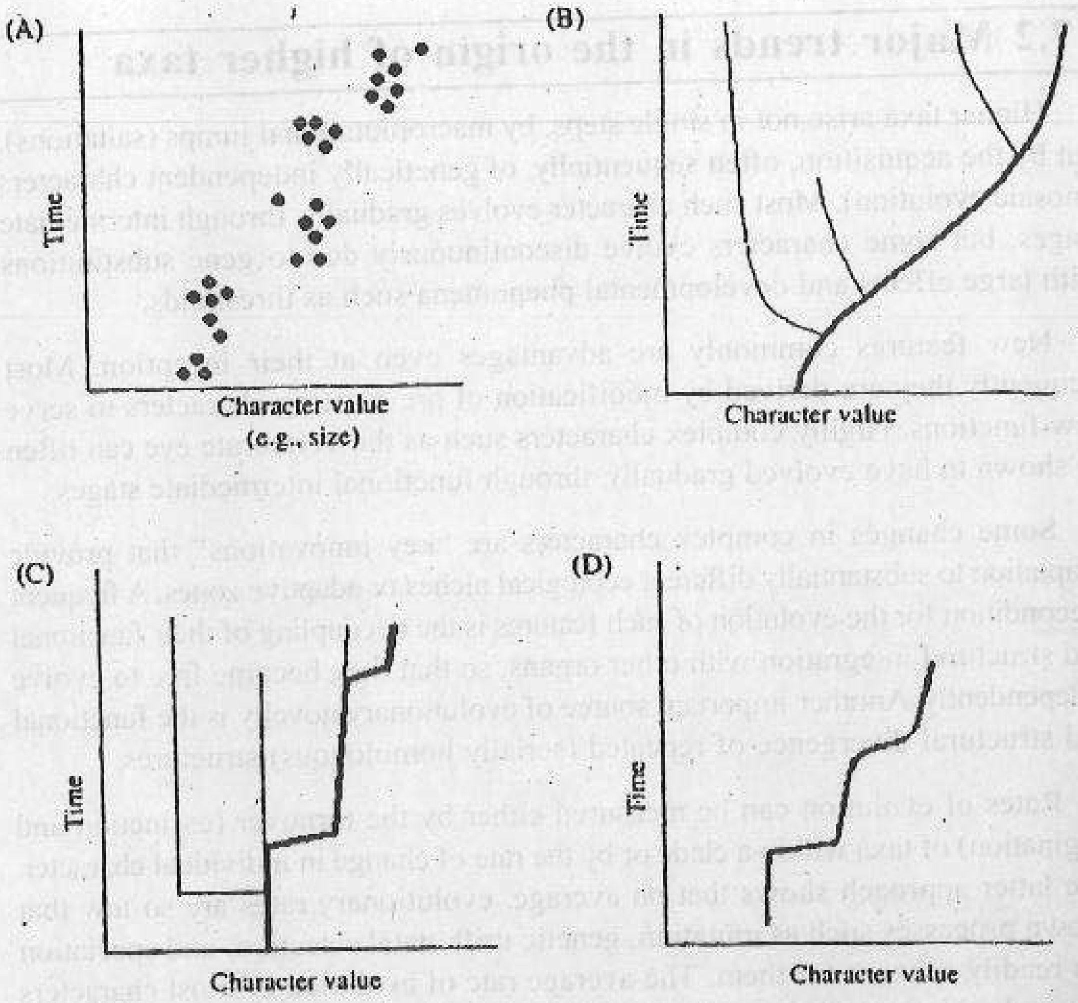


Fig. 17.1. Three models of evolution, as applied to a hypothetical set of fossils (A). (B) The “phyletic gradualism” model, said by Eldredge and Gould to be the traditional paleontologicalj model. The data in panel A might correspond to the boldly darkened line. Evolutionary change is not associated with speciation. (C) The “punctuated equilibrium” model of Eldredge and Gould, in which morphological change occurs in new species, while the parent species remain' unchanged. Morphological evolution, although rapid, is still gradual, as shown in the inset, which illustrates the shift in the mea of the variable character. (D) The “punctuated gradualism” model of Malmgren *et al.* (1983), in which a lineage rapidly evolves from one equilibrium to another, but speciation need not occur. The absence of intermediates between successive morphologies is attributed to the imperfection of the fossil record.

17.2 Major trends in the origin of higher taxa

Higher taxa arise not in single steps, by macromutational jumps (saltations), but by the acquisition, often sequentially, of genetically independent characters (mosaic evolution). Most such character evolves gradually, through intermediate stages, but some characters evolve discontinuously due to gene substitutions with large effects and developmental phenomena such as thresholds.

New features commonly are advantages even at their inception. Most frequently they are derived by modification of pre-existing characters to serve new functions. Highly complex characters such as the vertebrate eye can often be shown to have evolved gradually, through functional intermediate stages.

Some changes in complex characters are "key innovations" that provide adaptation to substantially different ecological niches or adaptive zones. A frequent precondition for the evolution of such features is the decoupling of their functional and structural integration with other organs, so that they become free to evolve independently. Another important source of evolutionary novelty is the functional and structural divergence of repeated (serially homologous) structures.

Rates of evolution can be measured either by the turnover (extinction and origination) of taxa within a clade or by the rate of change in individual character. The latter approach shows that on average, evolutionary rates are so low that known processes such as mutation, genetic drift, natal selection, and speciation can readily account for them. The average rate of evolution of most characters is very low because long periods of little change ("stasis") are averaged with short periods of rapid evolution; but known processes such as natural selection can readily explain even the rapid shifts.

Origin of higher categories

The term "higher categories" refer to the units of classification called genus, family, order, class and phylum. Families, and even more strikingly orders, consist of groups of animals that have a characteristic similarity in their manner of life and occupy certain envirormental (ecological) "niches". A comparable figure of speech for the broader limits of adaptation characterizing families and orders is ADAPTIVE ZONE (Simpson 1953). The processes of speciation will lead to the formation of families (and orders) if a species is fortunate enough to find a broad adaptive zone open to it. For most species this opportunity will not be present; for them the processes of speciation lead to adaptation to narrower environment niches. Such niches may continue to exist for a long time, or they may disappear as the environment changes. If they disappear, occupants of the niche usual become extinct, though a small minority may be able to shift to another niche another way of life. But occasionally a species is offered a larger opportunity.

A higher category is higher because it *became* distinctive, varied, or both to a higher degree and not directly because of characteristics it had when it was arising. Modern members of genus *Equus* and their prehistoric relatives ancestors are included in the family Equidae. How do such families arise evolution? In effect, there was no family Equidae when eohippus *(Hyracotherim)* lived. The family and all its distinctive characters developed gradually as time went on. There is no particular time at which the Equidae became a family rail . than a genus or a species; the whole process is gradual and we assign the categorical rank after the result is before us (Simpson 1953).

Broad adaptive zones are frequently divided into subzones, and so at am given time a taxonomic family is likely to contain subdivisions adapted to these subzones. So in the early Pliocene we find three-toes browsers in the forest and three-toed grazers on the plains. In other words, adaptive radiations occur. *Miohippus*, for example, in addition to giving rise to *Parahippus* was ancestral to *Anchitherium andArcheohippus*, two "horses" we have not mentioned previously. They became extinct; only *Parahippus* gave rise to a higher type of horse: *Merychippus*, a three-toed grazer. *Merychippus*, in turn, was ancestral to at least six lines of descendants, most of them three-toed grazers; but one of them, *Pliohippus*, was the first one-toed grazer.

When we turn our attention from families to orders we find that adaptive zones are still broader. Most orders of mammals, for example, consist of assemblage of families that have some striking characteristic in common-some adaptive trait that characterizes them all. The multitudinous members of the order Rodentia, for example, all have gnawing incisor teeth. Members of the order Catacea, whales and porpoises, have their well-known adaptations for aquatic life. The order Proboscidea, elephants, mastodons and their ancestors, we have already discussed. Bats, of the order Chiroptera, have wings. Members of the order Carnivora - e.g.. cats of all kinds, wolves, bears, weasels, and skunks- have teeth adapted for flesh eating. And so it goes. Of the orders we mentioned especially Perissodactyla, the odd-toed hoofed mammals, and Artiodactyla, the even-toed hoofed mammals. Both orders are herbivorous and have developed long legs for running away from enemies.

Both perissodactyls and artiodactyls are believed to have arisen from Paleocene condylarths. The fundamental difference between the two lines was in the manner in which the weight of the body was distributed in the limbs. In perissodactyls the weight-bearing axis runs through the third digit. In artiodactyls the weight is borne equally by the third and fourth digits. Presumably this difference in the manner of body support arose among the condylarths. Condylarths starting the trend toward prominence of the third digit gave rise eventually to rhinoceroses, tapirs, horses and so on. Condylarths starting the trend toward equal prominence of the third and fourth digits gave rise eventually to antelopes, deer, cattle, pigs, buffalo, camels and their numerous relatives-a much larger assemblage than that of the perissodactyls.

In the above example we have assumed that all perissodactyls had one common ancestor and that ariodactyls had one common ancestor. In the case of orders, and especially of classes, there is always the possibility that not all the organisms placed in one order or class did in fact inherit the distinctive trait from a single ancestral group. We must never forget the possibility of parallel evolution. In the case of the class Mammalia itself we noted that several lines of therapsid reptiles became essentially mammalian. The question of whether a given taxonomic group is *manophyletic* (composed of organisms all inheriting form a common ancestor) or *polyphyletic* (composed of organisms of diverse ancestries) is much debated.

The evolution of vertebrate novelties

Structural novelties (or "key innovations") are associated with adaptive radiations into new ecological territories. The movement of vertebrates onto land is tied to the evolution of the tetrapod limb; the escape of insects into their adaptive range required the evolution of wings. The distinctive molar tooth shape has evolved indecently several times in association with herbivory. Other novelties such as feathers and butterfly scales permit the display of colors and color patterns used for communication or predator avoidance' (Carroll *et al.* 2005).

New structures require the evolution of new developmental programme "novelty" is defined as a structure or pattern element, or even an entire body plan that has a new adaptive function.

Quantitative morphological variation, even when extreme, is not consider novel unless it encompasses a fundamental functional shift. Thus me homologous body parts are not considered novelties, even when the range of a vertebrate forelimb, for example, extends from the gigantic size of a whale flipper to the tiny arm of a tree shrew.

The success and ecological dominance of the vertebrates can be attribute to several unique traits that arose during the evolution of vertebrate lineage include the following:

- The notochord
- Populations of cranial placodes and neural crest cells
- Jaws
- Paired pectoral and pelvic limbs

By comparing the morphology, ontogeny developmental genetics and fossil history of vertebrates and other chordates (such as the cephalochordate amphioxi and urochordate ascidians), it is possible to trace the evolutionary origins of these structures. Conserved regulatory genes control the pattern of these new developmental fields and tissues, revealing once again that new developmental programs have evolved through the co-option of existing regulatory genes and circuits and the expansion of ancestral patterning roles.

Evolution of the notochord - an example of origin of higher taxa

The evolution of the notochord involved the co-option of an ancestral regulatory gene, *Brachyury (T),* a member of the T-box class of transcription factor (Fig. 6.2). In vertebrates, 7 is expressed in developing notochord cells and other mesodermal derivatives and is required for notochord differentiation. Similarly, the urochordate (ascidian and larvacean) *T* genes are expressed in cells that form the notochord and are sufficient to confer notochord fate. In larvaceans as well as hemichordates and invertebrates that lack a notochord, homologs of the *T* gene are expressed in posterior gut tissues. This expression may reflect the ancestral function of *T* before the evolution of the notochord. This gene began to play a new role in notochord development after the chordate and hemichordate /echinoderm lineages became separated, as the hemichordate *T* gene is not expressed in the stomochord (a possible precursor of the notochord).

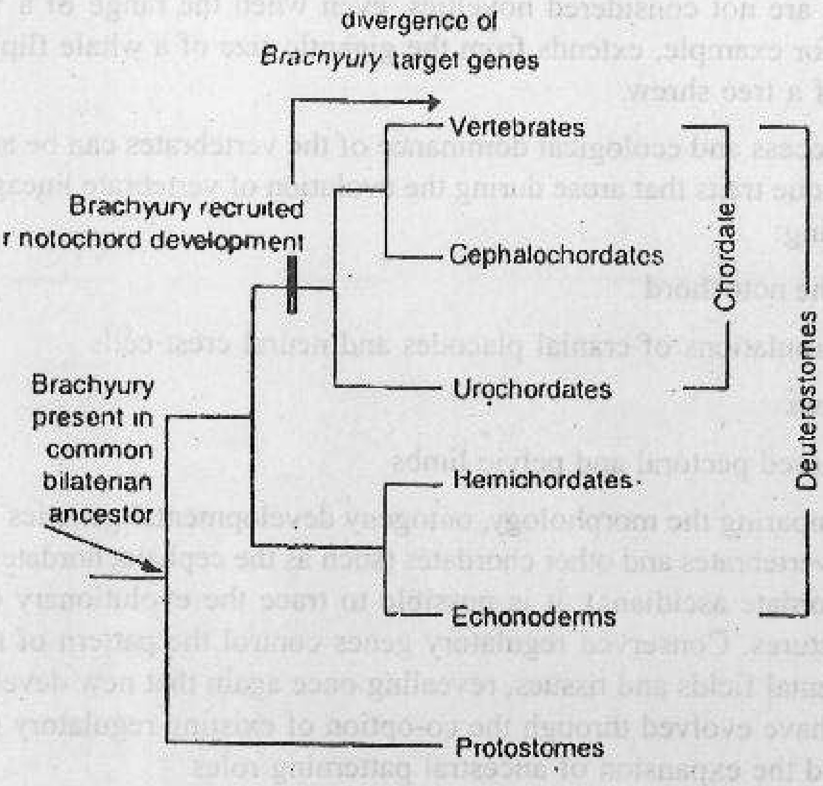


Figure 17.2. Recruitment of the *Brachyury* gene during evolution of the notochord

The *Brachyury (T)* gene predates the origin of the chordate notochord. During the early evolution of the chordates, expression of the *T* gene was recruited to pattern the notochord. Targets of the *T* gene have evolved as the chordate lineages have diverged (after Carroll *et al.* 2005).

17.3 Micro and Macroevolution

One of the most important tenets of the theory forge during the Evolutionary Synthesis of the 1930s and 1940s was that "macroevolutionary" differences among organisms - those that distinguish higher taxa - arise from the accumulation of the same kinds of genetic differences that are found within species. Opponents of this point of view believed that "macroevolution" within species, and are based on a totally different kind of genetic and developmental repatterning. The iconoclastic geneticist Richard Goldschmidt (1940), who held this opinion, believed that the evolution of species marks the break between "microevolution" and "macroevolution"- that there is a "bridgeless gap" between species that cannot be understood in terms of the genetic variation within species. Genetic studies of species differences have decisively disproved Goldschmidt's claim. *Differences between species* in morphology, behavior, and the processes that underlie reproductive isolation all *have the same genetic properties as variation within species;* they occupy consistent chromosomal positions, they may be polygenic or based on few genes, they may display additive, dominant, or epistatic effects, and they can in some instances be traced to specifiable differences in proteins or DNA nucleotide differences. *The degree of reproductive isolation between populations,* whether prezygotic or postzygotic, *varies from little or none to complete.* Thus, *reproductive isolation, like the divergence of any other character, evolves in most cases by the gradual substitution of alleles in populations.*

The causes of evolution within populations and species may be considerable over the course of sufficient time; they are often referred to as *Microevolution.* The principles of *Macroevolution* deal with the origin and diversification of higher taxa. Many biologists consider the study of species and speciation to constitute the bridge between microevolution and macroevolution. Macroevolution can be defined as the pattern at above the species level, including most of fossil history and much of systematics. On the other hand, microevolution is the process of evolution within populations, including adaptive and neutral evolution.

Population and quantitative geneticists think about microevolution, which occurs within populations over relatively short period of time; about the effects of changing the frequency of the different forms that one gene can take (its alleles) or holding these frequencies at a stable intermediate level. The main aspect is to understand what maintains genetic variation. Microevolution describes how populations change in the relative abundance of genes or phenotypes. Two concepts and a link between them explain microevolution. The two concepts are heritable variation in traits and variation in reproductive success among individuals within a population. The link is the correlation between the two types of variation. These three elements explain both adaptive and neutral evolution. When the correlation between reproductive success and a trait is positive or negative, natural selection is operating on that trait, for natural selection consists precisely of variation in reproductive success correlated with variation in a trait. When that correlation is zero, natural selection disappears, even though variation in reproductive success may remain, and is termed as neutral evolution.

Macroevolution describes patterns perceived in the comparisons of species and larger groups - families, orders, and phyla. How microevolution connects to macroevolution is an important question that has not yet been answered satisfactorily. A promising approach suggests that the microevolution of developmental mechanisms produces constraints on the further evolution of the organisms containing those mechanisms. Different lineages evolve different developmental mechanisms. All the species sharing developmental mechanisms may therefore also share similar body plans and evolve under similar constraints. This is probably why we can recognize major groups of organisms by their body plans, what Darwin called Unity of Type.

Evolutionary change: adaptive and neutral

Microevolution describes how populations change in the relative abundance of genes or of phenotypes. Two concepts and a link between them explain microevolution. The two concepts are heritable variation in traits and variation in reproductive success among individuals within a population. The link is the correlation between the two types of variation. These three elements explain both adaptive and neutral evolution. When the correlation between reproductive success and a trait is positive or negative, natural selection is operative on that trait, for natural selection consists precisely of variation in reproductive success correlated with variation in a trait. When that correlation is zero, natural selection disappears, even though variation in reproductive success may remain, and what is left is neutral evolution.

The production of surviving offspring is achieved through the number of offspring born, their survival, the survival of the parents to reproduce again, the number of offspring they have in their second and subsequent breeding attempts, the survival of those offspring, and so forth. Variation in reproductive success is made up out of variation in all these components.

On the one hand, if there were no variation in reproductive success, neither the distribution of genes nor the distribution of phenotypes would change. (This statement excludes mutations, which affect the variation in reproductive success of molecules). Note that there is always some variation in reproductive success in natural populations. For example, in Newton's (1988) study of sparrow hawks in southern Scotland, 72% of the females that fledged died before they could breed, 4.5% tried to breed but produced no young, and the remaining 23.5% produced between 1 and 23 young apiece.

On the other hand, if there is no heritable variation in a trait, there will also be no evolutionary change-even if there is variation in reproductive success-for the differences in performance exhibited by the parents will not be reflected in the offspring. Only if there is some variation both in the trait and in reproductive success can there be a correlation between the two producing natural selection. Both conditions are necessary for adaptive change. Both are also necessary for neutral change, in which case the correlation between the two must be near zero.

When there is both heritable variation and variation in reproductive success, it is the correlation between them that determines the type of evolutionary change that occurs. If there is little or no correlation between heritable and reproductive variation, then the things that are inherited and that do vary, whether genes or traits, will fluctuate randomly in the population within the limits of the available variation. This is **neutral evolution.** If the correlation between reproductive success and heritable variation is strong, then evolutionary change in the gene or trait will not be random but will move in the direction of increasing adaptation. This is **adaptive evolution.** The engine of adaptive evolution, **natural selection,** consists of two of the three parts of the evolutionary mechanism: variation in reproductive success and the correlation between reproductive success and the trait under consideration. It does not include the heritable variation that enables a response to selection.

17.4 Suggested questions

1. What do you mean by mosaic evolution? What is basal lineage?
2. Explain the concept of phylogenetic gradualism.
3. Enumerate 'punctuated equilibrium' concept introduced by Eldredge and Gould and compared it with model proposed by Malmgren and coworkers.
4. What is 'macromutational jumps'? Define stasis. Why 'key innovations' are important in evolution?
5. Explain with a suitable example how higher taxa originates.
6. What are 'evolutionary novelties' ? Mention some important examples.
7. Write a short note on evolutionary novelties.
8. What do you mean by evolutionary turnover?
9. Distinguish between macro- and microevolution. What phenomenon can be considered as bridge between them?
10. How you can distinguish between neutral evolution and adaptive evolution?
11. Describe the process of microevolution.
12. Analyze the process of macroevolution.

Unit 18 ❑ Molecular Phylogenetics

Structure

18.1 How to construct phylogenetic trees

18.2 Phylogenetic inference-Distance methods, Parsimony methods, minimum likelihood method

18.3 Immunological Techniques

18.4 Amino acid sequence and Phytogeny

18.5 Nucleic acid phylogeny

18.6 Molecular Clocks

18.6 Suggested questions

18.8 Glossary

18.9 Suggested references

18.1 How to construct phylogenetic trees

Systematics estimates the relationships among taxa to get working hypotheses in the form of phylogenetic trees. A phylogenetic tree records the history of a group.

To construct a phylogenetic tree, one first determines which characters are homologous, measures them on all the taxa being analyzed then codes the measurements for analysis. Different coding can produce different results.

Trees are built from data using methods that can produce different trees. If all methods yield the same branch of a tree in a large and reliable data set, then that branch can be regarded with confidence. If the data are equally consistent with several branching patterns, judgment about relationships should be suspected.

Phylogenetic analyses are becoming increasingly reliable. They are producing surprises about both relationships and character evolution.

Molecular systematics is not only used to build trees of relating species; it is also used to construct the history of single genes. The trees constructed from different genes in the same organisms often have different structures because each gene has had a different evolutionary history. For events occurring within a species, the recovery of a reliable gene genealogy must be done in sequences with little or no recombination, such as the mitochondrial genome, because recombination produces nets, not branches. A gene genealogy can differ from a species phylogeny because mutations do not occur simultaneously and are not constrained to occur during speciation (Fig. 7.1). One gene may have diverged prior to a speciation event; another gene may have diverged after that speciation event. Thus genes have different genealogies, and only some genealogies have the same structure as the phylogeny of the species in which the genes occur.

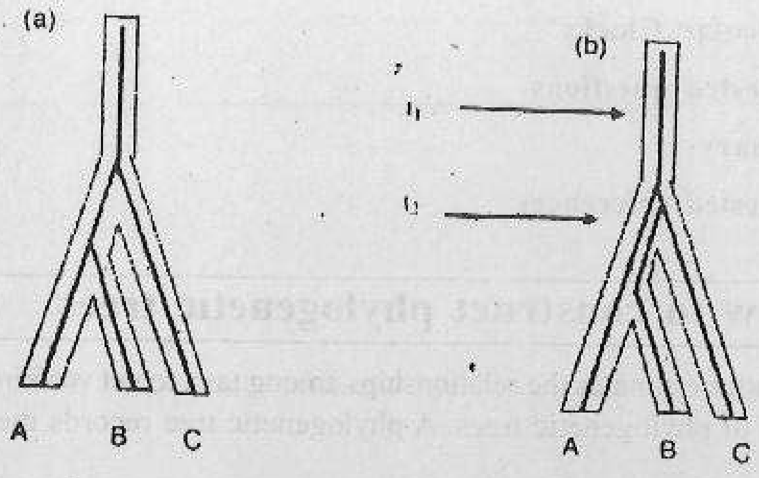


Fig. 18.1. Phytogenies of species and genealogies of genes. The species tree is described by the large outer figure and is the same in both cases. The lines contained within the tree describe the gene genealogy. Whenever more than one line is present, the gene is polymorphic. In both cases there is a mutation at rime t_1, prior to the speciation event, (a) The gene tree and the species tree have the same branching pattern, i.e. the second mutation occurs between the first and the second speciation event, (b) The genes and species have different branching patterns. The second mutation event occurs shortly after the first mutation event at time t_2, and the genealogical spilt predates species divergences (Avise 1994).

A Hypothetical ***Example:***

Unrelated person AAGCTTCATAGGAGCAACCATTCTAATAAT

Suspect A	AAGCTTCACCGGCGCAGTTATCCTCATAAT
Suspect B	GTGCTTCACCGACGCAGTTGTCCTTATAAT
Rape victim	GTGCTTCACCGACGCAGTTGCCCTCATGAT

Using a computer program, one can prepare a phylogenetic tree based on these four sequences. The program examines all the possible trees and delivers the one that implies fewer mutations in nucleotides than any other (Fig. 7.2).

This tree clearly suggests that the Suspect B infected the rape victim. The conclusion is supported by four changes in sequence that are shared by the Suspect B and the victim at position 1, A®G; at position 2, A®T; mat position 12, G®A; and at position 20, A®G. since the rape occurred the virus has continued to evolve in both suspect and victim. In the Suspect there has been a change at position 25,C®T; and in the victim there have been two changes, at position 21,T®C and at position 28, A®G.

This example is artificial but shows how to construct a genealogical tree.

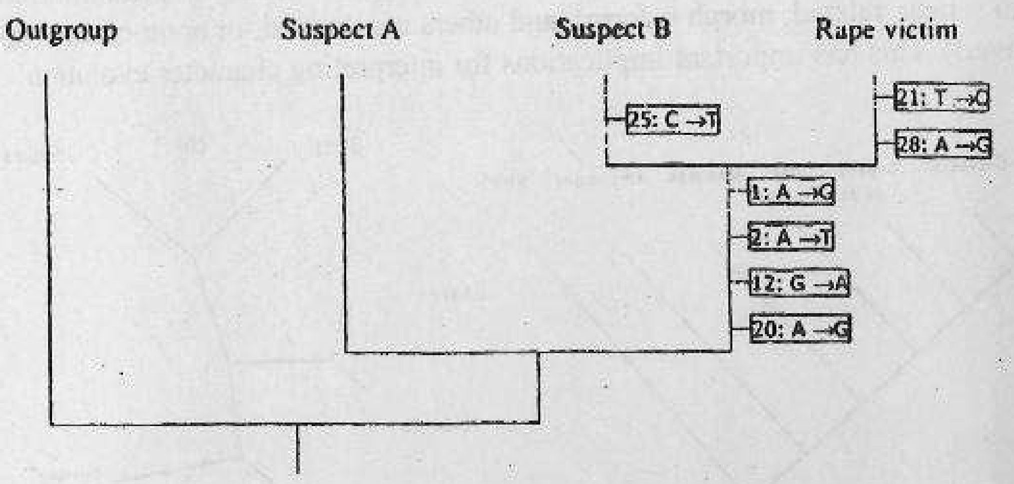


Fig. 18.2. The phylogenetic tree based on the nucleotide sequences in the text that implies the fewest changes overall. The tree is rooted using the unrelated person, and it clearly identifies the Suspect B as the probable rapist. The character changes that support each branch unambiguously are listed (Prepared by C. Baroni-Urbani).

What is phylogeny?

A phylogeny is a hypothesis about relationships expressed as a tree diagram. All parts of a tree are inferred except for the tips of the branches, which are the observed and described species, living or fossil. The usual phylogenetic methods assume that there is no hybridization or horizontal gene transfer through microbial vectors once speciation is complete (this is certainly not the case for many bacteria). Fossils, which help to test, support, and calibrate phylogenetic trees, are usually interpreted as tips of dead branches, not as direct ancestors of living species.

Types of phylogenetic trees

Phylogenetic trees may be rooted or unrooted (Fig 18.3). To root a tree, one uses an outgroup that is clearly not in the group being analyzed; a sister group is best if it can be identified reliably. Thus the outgroup for a phylogeny of the tetrapods should be a fish, probably a lungfish, not an echinoderm. The connection to the outgroup defines the root of the tree. If the tree is unrooted, then one cannot identify the outgroup or-as in the tree of life-there is no outgroup because cellular life is thought to have originated only once. Rooting a tree is an important step, for rooting introduces the notion that some character states are ancestral, or plesiomorphic (plesio = near, related; morph = form), and others are derived, or apomorphic (apo = derived). This has important implications for interpreting character evolution.

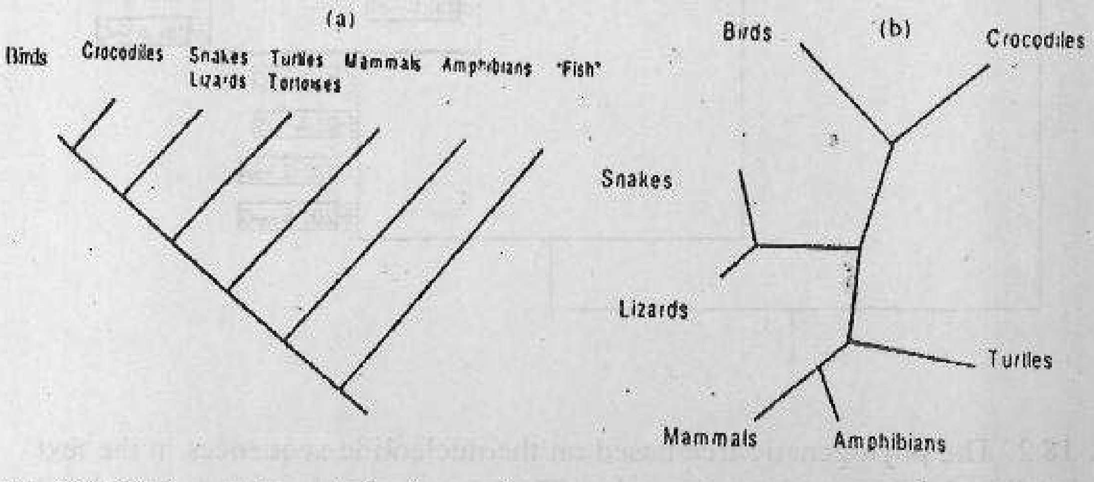


Fig. 18.3 (a) A rooted tree of the living tetrapods. The evolutionary sequence is clear, and the outgroup ('fish') is specified, (b) An unrooted tree. There is no outgroup, and the evolutionary sequence is obscure.

Hennig introduced several important Greek terms that are now commonly used in systematics:

PLESIOMORPHY (adjective, plesiomorphic): An ancestral (primitive character state (with reference to another, derivied, state).

SYMPLESIOMORPHY: An ancestral character state shared by two or more taxa.

APOMORPHY: A derived ("advanced") character state (with reference to another, ancestral, state).

SYNAPOMORPHY: A derived character state shared by two or more taxa.

AUTO POMORPHY: A derived character state possessed by only one of the taxa under consideration.

COMMON ANCESTOR: A species that at some past time split into two (or more) species, each of which gave rise to one of the clades under discussion. Because all organisms are believed to have descended from one remote common ancestor, any two taxa have had a common ancestor at some time in the past. (For example, even though no amniote vaguely resembling either a human or a snake existed 300 million years ago, this is the minimal estimate of the time since these lineages diverged; the synapsid reptiles, from which mammals evolved, were by this time distinct from the diapsid lineage that much later gave rise to snakes.)

NODE: A branch point in a phylogenetic tree. It represents a common ancestor at the time of divergence into two or more lineages.

TERMINAL TAXA: Taxa at the tips of a phylogenetic tree, such as whale and human. The term *operational taxonomic unit* (OUT) is approximately synonymous.

SISTER GROUPS (or SISTER TAXA): Two groups with the same immediate common ancestor. (Either group may contain one or more than one species.)

STEM GROUP and CROWN GROUP (used especially in discussing taxa with a fossil record): A stem group is an ancestral group, with relatively primitive characteristics, from which a crown group with relatively "advanced" characteristics has evolved. Often the crown group is extant and the stem group is extinct.

GROUND PLAN: The set of character states typical of relatively unmodified members of a clade. For example. the ground plan of mammals includes teeth differentiated into incisors, canines, premolars, and molars. Some mammals, such as anteaters and whales, have evolved away from this ground plan, having homogeneous teeth or none.

18.2 Phylogenetic inference-Distance methods, Parsimony methods, minimum likelihood method

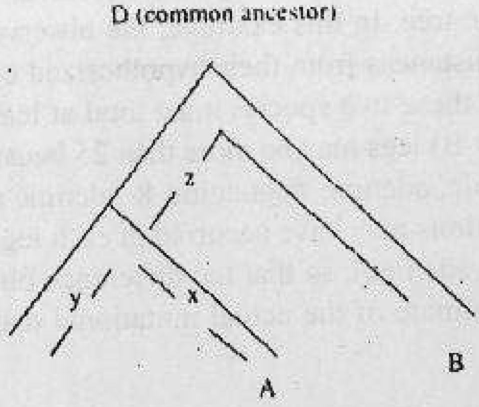
There are three commonly used methods for building trees; parsimony, distance, and maximum likelihood. Parsimony methods apply the logic of cladistics to molecular data, morphological data, or both together. Distance and maximum likelihood methods are usually applied to DNA sequence data where homoplasy is common.

Parsimony methods

This family of methods is based on cladistics; simpler hypotheses are preferred to more complicate ones, and shared derived similarity is decisive. As much similarity among taxa as possible is explained by common ancestry. In most data sets, some characters will conflict with this explanation, making necessary assumptions of homoplasy (convergence, parallelism, or reversal). When parsimony is applied to sequence data, evolutionary rates must be small or nearly equal in different lineages if the method is to yield trees that approach the true tree with increasing amounts of data. Otherwise, the information needed will be washed away by repeated mutations to one of the only four possible nucleotide states (this effect is also called saturation).

The Parsimony Principle, also known as "Occam's razor." Parsimony has the advantage that a true hypothesis generally involves fewer assumptions than a false hypothesis; for example, we can better explain a phenylalanine codon (UUU) as deriving from a single nucleotide substitution in a serine codon (UCU ® UUU) than as deriving from a triple nucleotide substitution in a glutamic acid codor (GAA®UUU). Note that "unparsimonius" explanations are not necessarily false, but, *in the absence of further information*, choices are made on the bases of parsimony.

Given parsimoniously determined evolutionary distances between species, resolving their phylogenetic relationships can follow. For example, if the minimum or most parsimonius mutational distance for a particular protein comparison between species A and B is 25, between A and C is 20, and between B and C is 30, then the two most closely related species are obviously A and C. If we assign legs *x*, *y* and z to represent the numbers of mutations responsible for their divergence, we can portray the phylogenetic relationship among the three species as follows:

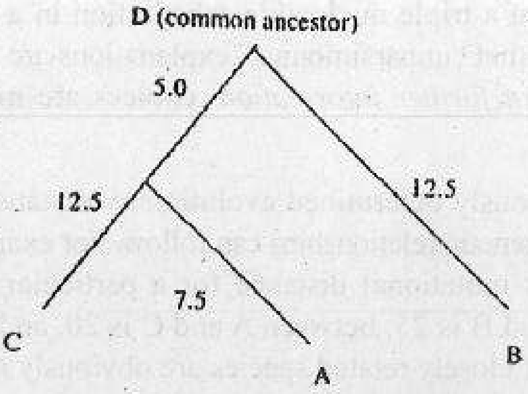


We can determine the lengths of these legs by noting that the A-B distance (25) is less than the C-B distance (30), hence the leg x must be 5 mutations less than y. since $x + y = 20$ and $y - x = 5$, we can subtract one equation from the other and solve for x :

$$x + y = 20 - (-x + v = 5) \quad 2x = 15 \qquad x = 7.5,\ y = 12.5$$

The leg z must therefore equal the A-B distance minus x (or the C-B distance minus y); that is, $z = 25 - 7.5$ (or $30 - 12.5$) $= 17.5$.

These mutational distances therefore yield.



It is to be noted that an important condition of the parsimony method is the observed mutational distance between two species must be less than or equal to the sum of the distances from their common ancestor to each species in the projected phylogenetic tree. In this example, the observed distance between A and B is 25, and the distances from their hypothesized common ancestor at the triangular apex (Di to these two species must total at least 25, if not more. The sum of the (D-A) + (D-B) legs may be more than 25 because undiscovered **back mutations** (for example, adenine ® guanine ® adenine may exist in these two legs, or **parallel mutations** may have occurred in each leg (for example, cytosine ® adenine; guanine ® adenine). so that the difference observed between A and B is really an underestimate of the actual mutational distance.

Distance methods

A distance is the number of differences in character states between two taxa. All distance methods start by calculating the distances between all pairs of species. Common methods include cluster analysis, neighbor-joining, and optimality methods.

Cluster analysis

Cluster analysis is simple and fast but flawed. It assumes that changes occur at the same rate along all branches of the tree, whichi9s questionable, and that grouping on the basis of total similarity is logically valid, which ignores the cladistic distinction between informative synapomorphies and uninformative plesiomorphies.

Neighbor joining

Neighbor joining is the most important of the methods that yield additive trees, trees in which it is assumed that the lengths of the branches between any pair of taxa can be summed to yield the amount of evolutionary change that has occurred between them. It proceeds by linking the closest pair of nodes, which converts the new common ancestor into a terminal node on a smaller tree; then continuing. This method can deal with trees in which changes are occurring at different rates in different branches.

Optimally methods

There are several definitions of optimality and ways to find the best tree. Optimally methods produce estimates of the uncertainty with which we can view - the various parts of trees.

Maximum likelihood methods

Maximum likelihood methods find the most likely tree given the data. That tree is found be considering a large set of hypothetical, candidate trees-all possible trees or a representative sample of them. For each candidate tree the probability is calculated that a given initial state will yield a given final state at the end of a defined interval of time. The probabilities for all changes in the tree are then multiplied to yield the total likelihood of the tree. In making those calculations, branch lengths play an important role. The best tree is then the one with the maximum likelihood (Felsenstein 1988). The method is logically appealing and computationally expensive. Its range of application is increasing as computers improve.

18.3 Immunological Techniques

Comparative molecular methods use immunological techniques in which antibodies produced in a particular host (usually a rabbit) against proteins (antigens) of one-species are measured for their activity against proteins of other species. For example, if antibodies against species A precipitate much of the protein in species C but little of the protein in species B, then researchers presume the A and C proteins have more similar molecular configurations (antigenic components) and are more evolutionary alike (smaller **antigenic distance**) than those of A and B.

Using a variety of antibodies, one can analyze immunological data by various mathematical rules (algorithms) to construct a phylogenetic tree that best correlates the antigenic distance between species with the length of time since they shared a common ancestor. If species A and C are aritigenically closer to each other than to species B, we can presume species B broke off earlier from the common stem that all three originally shared. Successive comparisons are then made between all possible combinations of species until the entire phylogenetic tree is obtained.

Other immunological techniques, such as the **microcomplement fixation** (Sarich and Wilson 1966). involve measuring antibodies produced against specific proteins found in blood serum (albumin and transferrins) or enzymes such as lysozyme. Antigenic distances, which can be detect by measuring the amount of antigen-antibody reactions provide data that generally support the phylogenies we can obtain by other taxonomic methods, although some differences occur. In microcomplement fixation, rabbits immunized with a protein antigen from one species produce antiserum that gives a strong reaction against that antigen (homologous antigen) but not against the same protein from another species (heterologous antigen). The degree of antigenic difference is then measure between the two species by the concentration to which the antiserum must increase for the heterologous antigen to react like the homologous antigen.

18.4 Amino acid sequence and Phylogeny

Amino acid sequences

One of the first molecular phylogenetic analyses (Fitch and Margoliash, 1970) used the amino acid sequence of cytochrome *c* to describe the phylogeny of numerous vertebrates and other taxa. The characters used are either the amino acid sequences themselves or the nucleotide sequences of the encoding genes, inferred from the genetic code.

Popular, approach to molecular phylogeny is sequencing the amino acids in proteins by biochemical methods and comparing such sequences for the same protein in different species. Among the first proteins to yield its amino acid sequence was **hemoglobin,** and it probably still remains one of the most investigated of all proteins. The basic unit of hemoglobin consists of an iron-containing porphyrin (heme) that reversibly can bind oxygen attached to a globin. polypeptide chain that is usually no less than 140 amino acids long. The demonstration that hemoglobin-like molecules appear in a wide range of organisms, from invertebrates to vertebrates, and even in plants, fungi and bacteria (Hardison) indicates their origin far back in the history of life. In vertebrates, hemoglobins are usually the primary protein of red blood cells, making them relatively easy to isolate and purify in large amounts.

Red blood cell hemoglobin of normal human adults is a four-chain molecule or tetramer, consisting of two pairs of polypeptide chains, one pair bearing the a sequence and the other pair mostly bearing the b sequence (a_2b_2). Some adult hemoglobin uses d chains instead of b's (a_2d_2), and a common form of embryonic hemoglobin has two a's and two g's (a_2g_2). Other types of hemoglobin chains also occur (for example, e), and hemoglobin-like molecules such as **myoglobin** appear in other tissues. All these chains are distinguished by their somewhat different properties and different amino acid sequence.

That a species can possess different kinds of globin molecules and each such molecule can differ among different species, points to two major kinds of globin evolution:

- Different kinds of globin chains arose during evolutions, producing the variety carried by a particular vertebrate (a differs from b, which differs from g, and so on).
- Each particular globin chain followed its own evolutionary path, leading to changes in its amino acid sequence in different species (a chains are different in different species, as are b chains, and so on).

The figure given below portrays the genetic phylogeny of the five globins in terms of the numbers of nucleotides necessary to account for the amino acid differences, along with the chronological periods in which evolutionists presume each duplication occurred (Fig. 18.4). We can see that duplication events led to the early coexistence of myoglobin with an a-like chain, the former probably assuming (or maintaining) an intracellular function and the latter probably assuming a circulator function.

When a duplication of the a-like gene further evolved into a b-like gene, the advantage of having two pairs of different chains in a tetramer hemoglobin molecule must have been sufficiently great to account for preserving tetramer organization in the circulating blood of most vertebrates. After the b-like gene formed, a translocation separated it from a and transferred it to a different chromosome. Duplications then occurred in the b-like gene, eventually yielding the modern b. g. and d genes.

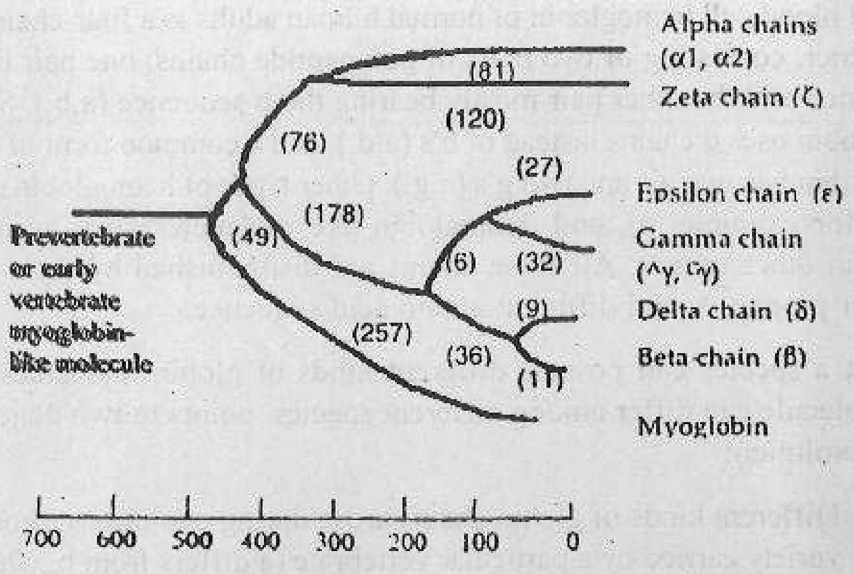


Fig. 18.4. Phylogenetic relationships between globin type proteins found in humans, showing the estimated times at which they originally diverged from each other. The estimated number of nucleotide replacements necessary to cause the observed amino acid changed in each branch of the lineage is given in parentheses.

18.5 Nucleic acid phylogeny

DNA-DNA hybridizaton : The thermal stability of heteroduplexes formed by complementary strands of DNA from two species is taken as a measure of the overall similarity of their DNA. The similarity is measured by a *single number* quantifying similarity or its complement, "distance". Many cladists object to the use of "distance value" for inferring phylogeny, partly because one does not have information on the state of each individual character (i.e., each base pair), so one cannot determine how much of the overall similarity is due to synapomorphies, and how much to simple-siomorphies. Advocates of the technique respond that averaged over millions of nucleotide sites, differential rates of evolution are likely to cancel each other out, so that overall similarity should accurately reflect recency of common ancestry. Two groups of investigators have independently used this method to assess relationships among humans and apes (Sibley and Ahlquist, 1987); Caccone and Powell, 1989). and both arrived at the same phylogeny that has been derived from DNA sequence data.

The two strands of the DNA double helix become separated (denatured) at high temperature, and reestablish their structure (reanneal) when the temperature is lowered. The heat required to denature a DNA sequence depends on the degree of complementarity of the two strands: the more bases of one strand are mismatched with those of the other (i.e.. the greater the number of departures from A-T and G-C pairing), the less heat is required.

A genome that has been fragmented by restriction enzymes can be heated to produce single strands. These DNA fragments are then bound to a filter, and the filter is exposed to another, similarly treated but radioactively labeled, preparation of DNA fragments. The filter bound DNA might be from one species and the radioactively labeled DNA from another. As the temperature is lowered, the free fragments "hybridize" with the filter-bound fragments to which they are complementary, forming double-stranded (duplex) DNA. The *rapidity* of such "hybridization" depends on how likely a fragment is to "find" a complement; this is more likely for a highly repetitive DNA sequence, so the dynamics of reannealing can measure the proportion of the genome that consists of highly or moderately repetitive sequences. The *stability* of the hybridizes duplexes, measured by how much heat is required to separate them again, is a measure of how complementary their base pair sequences are overall. This technique may be used, for instance, to measure the overall sequence similarity of the DNA of two different species.

- **Restriction enzyme sites.** A certain DNA sequence (e.g., mitochondrial DNA) may show either presence or absence of a specific restriction site (i.e., a four- or six-base sequence that is cleaved by a specific enzyme). Each restriction site is treated as a character with two states, and the data can be analyzed by a standard cladistic method.

A number of enzymes have been isolated, mostly from bacteria, that recognize specific, short (e.g., four or six base pairs) DNA sequences ("restriction sites") and cut the DNA within these regions. These restriction enzymes can be used to cut into fragments either a whole (nuclear, mitochondrial, or chloroplast) genome or a specific DNA fragment isolated from such a genome. The resulting DNA fragments can be separated by size by placing the preparation on a gel (e.g., of agarose) and applying an electrical current (electrophoresis). The fragments can be "visualized" by several methods, including AUTORADIOOGRAPHY: radioactively labeling the DNA, and then exposing the gel to a radiation-sensitive film. The size of each fragment (in number of base pairs) is measured by its mobility relative to known standards, and the sum of the fragment sizes equals the size of the sequence that has been cut. By comparing the fragments produced by combinations of different restriction enzymes with those produced by each enzyme singly, it is possible (although rather complicated) to map the different restriction sites, i.e., to specify their order and the number of base pairs between them. These restriction sites can then be used as genetic markers for relatively short sequences of DNA, just as mutant alleles are used as genetic markers in traditional genetics.

- **DNA sequences.** A sequence of DNA from minute samples of tissues, sometimes from long-preserved museum specimens or even certain fossils, can be amplified by the polymerase chain reaction (PCR) and then sequenced. The most difficult step is extracting the particular gene one wishes to sequence, but once this has been done in one species, copies of the sequence (primers) can be used to extract the sequence from closely, or sometimes distantly, related species. This has become the most popular molecular method in systematics.
- **Nucleotide sequence comparisons and homologies.** A more precise method of phylogenetic determination is to compare known nucleotide

sequences from different organisms rather than to infer relationships from hybridization studies for restriction enzyme maps. This procedure offers advantages in comparing changes between protein-coding and noncoding DNA sequences and in determining the extent of synonymous and non-synonymous nucleotide substitutions in the amino acid coding regions.

A large amount of information on nucleotide sequences (on some 2.5 million DNA sequences) has recently been accumulated from a. number of organisms ranging from viruses to eukaryotes. Among the nine sequenced prokaryotic genomes, a number of interesting evolutionary features have appeared which shows:

- Extensive horizontal gene transfer between genomes
- Considerable amounts of gene duplication - as high as 25 percent in the *Bacillus subtilis* genome
- Greater similarity of archaebacterial protein sequences to eubacterial proteins rather than to eukaryotic proteins
- Proteins used in replication, transcription, and translation show a reverse relationship: greater similarity between archaebacteria and eukaryotes
- As much a 50 percent or more of genes in some genomes are "orphans" with no known function
- Based on the 480 genes in *Mycoplasma genitaliurn,* that number or even smaller may represent the minimal set of genes necessary for cellular life.

18.6 Molecular Clocks

The rate of evolution of DNA sequences can be shown in some cases to be fairly constant ("molecular clock"), such that sequences in different lineages diverge at a roughly constant rate. In such cases, degrees of similarity can indicate phylogenetic relationships. The absolute rate of sequences evolution ca sometimes be calibrated if fossils of some lineages are known.

All molecular methods indicate that non-interbreeding evolutionary lineag (species and higher taxa) become steadily more different with time. The theo of population genetics predicts that if natural selection does not favor on molecular variant over others, DNA or protein sequences should diverge, *o* *average,* at a constant rate. Early in the history of molecular phylogenetic studie the data suggested that macromolecules might indeed evolve and diverge at constant rate. This concept has been dubbed the **molecular clock** (Zuckerkand and Pauling 1965). If it were true, it would have two important implications f the study of evolutionary history.

First, if the rate of overall divergence is constant, phylogeny can be inferre directly from the *overall similarity* of species (or, conversely, "distance", whic includes the autapomorphies that cladists consider anathma). One could the legitimately use phenetic methods to infer phylogeny from "distance measures such as those yielded by DNA-DNA hybridization, when information is lackin on the ancestral and derived states of individual characters (such as base pairs

Second, if one could calibrate the clock-if one could discover how fast it "ticking"-one could *estimate the absolute time* since different taxa diverge The clock might be calibrated by, say, information from the fossil record on th absolute time of divergence of certain taxa, and it could then be used to estima the divergence times of other taxa that have not left a good fossil record. Be in mind that the phylogenetic trees we have considered so far portray *relativ* times of divergence (the branching *sequences)* of taxa, not absolute times.

Initially, we need to calculate the number of differences (e.g., in base pair that have accrued among pairs of species since their common ancestor. This ca be estimated by plotting on our estimated phylogeny where each change too place. For example, figure 18.5 shows 76 autapomorphic changes between *Hom* and its common ancestor with *Pan* (e.g., site 6374), 14 synapomorphic change between that common ancestor and the *Gorilla* branch (e.g., site 5365), and 9 autapomorphies along the *Gorilla* branch (e.g., site 6374). Since the commo ancestor of all three species, there have been 94 changes leading to *Gorilla,* 7 + 14 = 90 changes leading to *Homo,* and 92 + 14 = 106 leading to *Pan.* From th more remote common ancestor of these species and *Pongo*, there have been 160 changes to *Homo*, 176 to *Pan*, 178 to *Gorilla*, and 199 to *Pongo*.

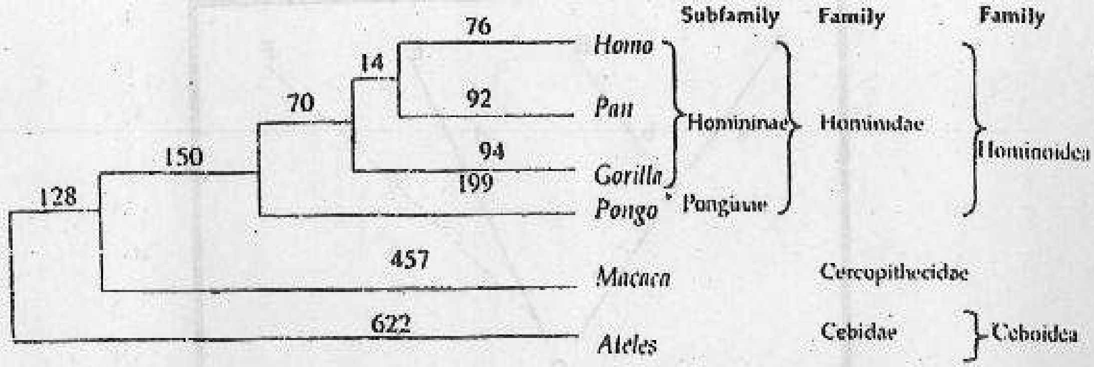


Fig. 18.5. Evidence for phylogenetic relationships among primates, based on the yh-globin region (Goodman et al. 1989). The most parsimonious (shortest) phylogeny based on yh-globin sequence, using *Ateles* as an outgroup. The minimal number of changes is indicated along each branch. A tree that split up the *Homo-Pan-Gorilla* clade would be 65 steps longer, and one that split *Homo* and *Pan* would be 8 steps longer. Note that from the common ancestor of apes and Old World monkeys *(Macaca)*, the number of changes along the branches leading to Human (310) or any ape is less than that in the branch leading to *Macaca* (457). The figure also includes the classification proposed by Goodman et. al. 1989.

The *average rate of base pair substitution* in any lineage can be calculated if we have an estimate of the absolute time of divergence. For example, the oldest fossils of cercopithecid monkeys are dated at 25 million years ago (My). Thus the divergence between *Macaca* and the hominoids is at least this old. This is a *minimal* estimate of divergence time, because it is possible that older cercopithecids (and hominoids) exist that has not yet been found in the fossil record. If, however, we take this date as the age of the cercopithecid / hominoid divergence, we can calculate the average rate of sequence evolution. The number of substitutions per base pair per million years for the cercopithecid lineage *(Macaca)* is 457/10,000 base pairs sequenced / 25 My = 0.0457 substitutions per base pair / 25 My = $1.83'\ 10^{-3}$ per My, or $1.83'\ 10^{-9}$ per year. From the common ancestor to *Homo*, the average rate has been 310 / 10,000 / 25 = $1.24'\ 10^{-3}$per

My, or 1.24´ 10^{-9}per year. Figure 7.6 explains relative rate test for constancy the rate of molecular divergence in a hypothetical model.

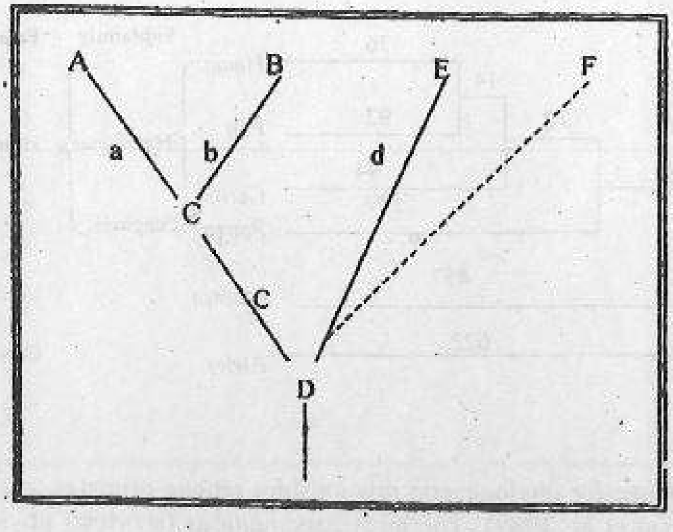


Fig. 18.6. The relative rate test for constancy of the rate of molecular divergence. Sequence are obtained for living species A and B and for outgroup species E (perhaps also F). C an D represent common ancestors. The genetic distance (e.g., in terms of nucleotide differences between A and E is $D_{AE} = a + c + d$. that between B and E is $D_{BE} = b + c + d$. If th rate of nucleotide substitution is constant, a = b, so $D_{AE} = D_{BE}$. If rate constancy hold throughout the tree, the distance between any pair of species that have D as a commo ancestor will equal that between any other such pair of species (e.g., $D_{AE} = D_{BF}$).

18.7 Suggested questions

1. What is molecular systematics and phylogeny?
2. Explain how a phylogenetic tree is constructed (use a hypothetica example).
3. What are plesiomorphy and symplesiomorphy?
4. Define terminal taxa, sister taxa, stem group, common ancestor an ground plan.

5. Explain 'rooted' and 'unrooted' phylogenetic tree.
6: Define Parsimony method for detection of phylogenetic distance. Explain how mutational distances are derived in this method.
7. Write notes on Distance methods and Maximum likelihood methods for construction of phylogenetic tree.
8. What are antigenic distance and micro complement fixation?
9. Why molecular phylogeny is important in studying evolution. Cite an example where amino acid sequences is used in phylogenetic analysis.
10. Elucidate with example that DNA-DNA hybridization can explain nucleic acid phylogeny.
11. What do you mean by Restriction enzyme sites? How this can help in constructing molecular phylogeny?
12. How the average rate of base pair substitution is calculated (use any example).
13. Define molecular clocks. Elucidate the significance of molecular clocks in molecular phylogenetic analysis.

18.8 Glossary

Adaptation: A state that evolved because it improved reproductive performance, to which survival contributes. Also the process that produces that state.

Adaptive evolution : The process of change in a population driven by variation in reproductive success that is correlated with heritable variation in a trait.

Antagonistic pleiotropy : One gene has positive effects on fitness through its impact in one trait but negative effects on fitness through its impact on another trait.

Apomixis : A form of clonal propagation in which progeny genetically identical to the mother are formed without genetic recombination.

Bootstrapping : A statistical method to estimate our confidence in a pattern.

One takes random samples of the original data (with replacement to get a data set of the same size) and repeats the calculations with the new, artificial data sets many times. The patterns that do not change, or only rarely change, receive our confidence.

Canalization : The limitation of phenotypic variation by development mechanisms. It can be demonstrated by disturbing developmental control to reveal the underlying genetic variability that had been canalized.

Clade : A branch of the evolutionary tree containing all the species descended from a single common ancestor.

Cladogenetic : Evolutionary change occurring during speciation events. Usually applied to fossils.

Cline : A spatial gradient in train values or gene frequencies.

Coevolution : Evolutionary changes in one thing-genes, sexes, species-induce evolutionary changes in another, which in turn induce further evolutionary changes in the first, and so forth.

Comparative trend analysis : The relations of two or more traits among higher taxa are analyzed with proper control for phylogeny and covariates such as body weight.

Conserved function : A property of paralogous genes with high DNA sequence homology that code for proteins with similar function in distantly related organisms.

Convergence : Two species resemble each other not because they shared common ancestors but because evolution has adapted them to similar ecological conditions.

Cyclical parthenogenesis : A life cycle typical of aphids, rotifers, cladocerans, and some beetles, in which a series of asexual generations is interrupted by a sexual generation are often adapted to resist extreme conditions and to disperse.

Density-dependent selection : Selection that favors different things at different population densities.

Density-independent selection : Selection that favors the same things at all population densities, or that has always occurred at the same population density so that density effects did not occur.

Derived : Defined relative to ancestral: originating later in evolution than the ancestral state.

Directional selection: Selection that always acts in a given direction; for example, always to increase the value of a trait, or always to decrease it.

Disruptive selection: Selection that favors the extremes and eliminates the middle of a frequency distribution of trait values; for example, increasing the frequency of small and large individuals and reducing the frequency of medium-sized individuals.

Divergence : Related species no longer resemble each other because evolution has adapted them to different ecological conditions.

Downstream gene : A gene under the control of a regulatory gene; the genes downstream from a regulatory gene constitute a regulatory pathway.

Drift: The random walk of gene frequencies that occurs in both large and small populations when variation in genes is not correlated with variation in reproductive success.

Effective population size : The size N_e of an ideal population consisting of individuals with equal reproductive output that would experience the same amount of genetic drift as a real population of size N'. This defines effective population size for drift; there are other definitions for unequal family sizes, subdivided populations, differences in male versus female reproductive success, and variable population sizes.

Epigenetic inheritance : Somatic inheritance of the differentiated state of the cell through cycles of cell division.

Exon : The part of a eucaryotic gene whose DNA sequence is preserved in post - transcriptional splicing and is represented in the spliced mRNA and in the resulting amino acid sequence of the protein product. Exons occur in eucaryotes but not in prokaryotes.

Founder effect: Major changes in gene frequencies that occur in a population founded with a small sample of a larger population.

Frequency-dependent selection : A mode of natural selection in which either rare types (negative frequency-dependent selection) or common types (positive frequency-dependent selection) are favored.

Genealogy : A tree describing the history of a single gene, as opposed to a phylogeny, which uses information from many genes or traits to reconstruct the history of a set of species.

Gene flow: Genes flow from one place to another when organisms born in one olace have offspring in another place that survive to reproduce there.

Gene frequency : The frequency of an allele in a population. If there are 100 individuals in a population of diploid individuals, and we consider one locus (one gene) that is present in tow forms (two alleles), *A* and *a*, then if 20 of the individuals carry two copies of A (they are *AA* homozygotes), 60 of the individuals are *Aa* heterozygotes, and the remaining 20 individuals are *aa* homozygotes, then the gene frequencies are calculated as the number of each allele divided by the total number, in this case. (40 + 60)/200 = 0.50 for both alleles.

Gene substitution : The process by which a new mutation becomes fixed in a population.

Genetic bottleneck : A reduction in population size to a low-enough level for long enough that many alleles are lost and other are fixed.

Genetic diversity: The probability that two homologous alleles chosen at random from a population differ.

Genetic drift: Random change in allele frequencies due to chance factors.

Genetic imprinting : Genes marked by DNA methylation in the germ line of parents; some are marked in mothers, others in father. Methylated genes are not expressed in the early development of the offspring.

Genomic conflict : Occurs when genes affecting the- same trait experience different selection pressures because they obey different transmission rules.

Genochorism : Having separate sexes; individuals are either males or females, not both; used for animals.

Heterogametic : The sex having tow different sex chromosomes; for organisms with chromosomal sex determination; mates are XY in humans.

Heterozygosity : The proportion of a population that is heterozygous at a locus; also the average proportion of loci heterozygous per individual.

Hitch-hiking : Changes in the frequencies of neutral traits that are pleiotropically lined to other traits that are under selection; or changes in the frequencies of neutral genes that are linked on chromosomes to changes in other genes that are under selection.

Homeobox : A 180 base-pair sequence in important regulatory genes that codes for a protein segment that binds to DNA as a key part of a transcription factor.

Homogametic : The sex having two similar sex chromosomes; for organisms with chromosomal sex determination; females are XX in humans.

Homology : Identity of one trait in two or more species by descent form a common ancestor.

Homoplasy : Similarity for any reason other than common ancestry. The commonest cause of homoplasy in morphological trait s is probably convergence; in DNA sequences, simple mutation.

Inbreeding depression: The reduction in the survival or reproduction of offspring of related parents caused by the expression as hemozygotes of deleterious recessive genes that were present in the parents as heterozygotes.

Infinite-allele model: A model in the neutral theory of molecular evolution that assumes that every mutation is unique in the sense that it does not already exist in the population; plausible for long DNA sequences.

Intron : A sequence within a gene that is removed after transcription and before translation by gene splicing; its DNA sequence is not represented in the RNA sequence of the spliced mRNA or the amino acid sequence of the resulting protein; introns occur in eucaryotes but not procarytes.

Kin selection : Adaptive evolution of genes caused by relatedness; an allele causing an individual to act to benefit its relatives will increase infrequency if that allele is also founding the relatives and if the benefit to the relatives more than compensates the cost to the individual.

Lek : A traditional display site where males gather to defend mating territories and females come to mate; Swedish for sports field or display.

Lineage-specific developmental mechanisms : Developmental mechanisms found within all organisms of one lineage but not I other lineages, responsible for the morphology that characterizes the lineage. They limit the genetic variation that can be expressed in the lineage.

Macroevolution : The pattern of evolution at and above the species level, including most of fossil history and much of systematics..

Meiotic drive : Distortion of the fairness of meiosis by nuclear genes to increase their representation in the gametes at the expense of other alleles.

Mendelian lottery : A particular allele will or will not be represented in the offspring because of the segregation of alleles at meiosis and the random chance that any particular gamete will form a zygote. Most easily seen with small family sizes. Think about single children.

Microevolution : The process of evolution within populations, including adaptive and neutral evolution.

Molecular clock : The approximately constant rate of nucleotide substitution for particular genes and classes of genes within particular lineages. The constancy of the rate depends on the randomness with which particular neucleotides mutate and then drift to fixation.

Monophyletic : All species in a monophyletic group are descended from a common ancestor, and all species descended from that ancestor are in that group.

Multigene family: Sets of multiple copies of genes derived by duplication from a common ancestor gene and retaining the same function.

Multilevel evolution : Adaptive evolution occurring simultaneously at several levels of a biological hierarchy, e.g. nuclear and cytoplasmic genes.

Narrow-sense heritability : The fraction of total phenotypic variance in a trait that is accounted for by additive genetic variance; measures the potential response to selection.

Neutral evolution : The change and occasional fixation of alleles caused by the drift of alleles not correlated with reproductive success.

Paralogy : DNA sequence homology plus conserved functions.

Paraphyly : A group does not contain all species descended form the most recent common ancestor of its members.

Parsimony : A criterion used in cladistic tree-building: the best tree has the fewest changes in character states and the least homoplasy.

Phenotypic differentiation : The differentiation of phenotypes in separated gene pools during and after speciation.

Phenotypic plasticity : Sensitivity of the phenotype to differences in the environment. Less precise than reaction norm.

Phylogeneit ctrait analysis : A comparative method in which one constructs a phylogenetic tree, plots character states (traits) on the tree, and infers transitions in character states from their position on the tree. Geographical locations of taxa can be plotted onto the tree to infer the location of ancestors.

Phylogeny : The history of a group of taxa described as an evolutionary tree with a common ancestor as the base and descendent taxa as branch tips.

Pleiotropy : One gene has effects on two or more traits.

Pleisomorphic : Ancestral, relative to a derived, or apomorphic, state.
Polyphenism : A form of induced response in which the phenotypes are discrete.

Polyphyly : A group is polyphyletic if its species are descended from several ancestors that are also the ancestors of species classified into other groups.

Population genetics: The discipline that studies changes in frequencies of alleles in populations; issues include mutation, selection, inbreeding, assortative mating, gene flow, and drift; suitable when genetic differences at one locus can be detected as phenotypic differences.

Punctuated equilibrium : A pattern seen in many but not all lineages in the fossil record, in which a long period of stasis is broken by a short period of rapid change. In some cases the rapid change is associated with speciation.

Quantitative genetics : Studies changes in traits in populations when genetic differences at one locus are too small to detect in phenotypes and when many genes affect one trait; common themes are heritability, genetic covariance, response to selection.

Regulatory gene : A gene that turns another gene, or group of genes, on or off. Small changes in regulatory genes cause large changes in phenotypes.

Replicator: The organism in its role as information copier, the mechanism that copes the DNA sequence of the parent and passes it to the offspring.

Reproductive success : A measure of fitness defined as the number of offspring produced per lifetime. I, can be extended through several generations; for example, one could define it as the number of grandchildren tha, survive to reproduce.

Reproductive value : The expected contribution of orgamsms in that stage of life to lifetime reproductive success.

Residual reproductive value : The remaining contribution to lifetime reproductive successes after the current activity has made its contribution.

Segregation distortion : Deviation from the Mendelian ratios that give equal chances to homologous alleles in meiosis; unfair ratios can be caused by nuclear genes that intertere with meiosis or with the products of meiosis to improve their own chances at the expense of their homologs.

Sexual selection : The component of natural selection that is associated with success in mating.

Sibling species : Species that are reproductively isolated but cannot be distinguished, or can be distinguished only with difficulty and by experts, using morphological criteria.

Species : Either a set of organisms that could share grandchildren (the biological species concept), or the smallest diagnosable cluster of individual organisms within which there is a parental pattern on ancestry and descent (the phologenetic species concept).

Stabilizing Selection : Selection that eliminates the extremes of a distribution and favors the center.

Stasis : A long period without evolutionary change.

Strict consensus tree : A phylogenetic tree derived form a set of equally parsimonius trees and constructed by only including the groups that are supported in all the equally parsimonious trees.

Synapomorphy : A shared, derived character state indicating that two species belong to the same group.

Synergism : A non additive interaction between two or more factor.

Synonymous mutation : A point mutation (change in a single nucleotide) does not change the amino acid for which the DNA triplet codes.

Terrane : A piece of continental crust that did not originally belong to the continent on which it is found but moved there from elsewhere.

Trade-off : A change in one trait that increases fitness causes a change in the other trait that decreases fitness.

Transcription factor : A gene product that binds to DNA at a specific site and regulates the expression of genes downstream from that site.

Transduction : A virus that infects bacteria picks up some bacterial DNA from one host and transfer it to the next host, which may incorporate the DNA if it scurvies the infection.

Wild type : A term used in classical genetics to designate the standard genotype in the population form which mutations formed rare deviations. Modern molecular data have destroys the concept by revealing so much variation that the concept has become meaningless.

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