

Mammals

Adaptive Radiation in Mammals with reference to locomotory appendages:

Introduction –

Mammals occupy the highest position in the ladder of evolution. The structural diversities amongst the different groups of mammals are profound. They vary in size from that of a field mouse barely 2.5 cm in length to that of a whale attaining a length of more than 30 metres.

A shrew, *Sorex minutus* (order Insectivora) is the smallest living mammal weighing about 3 grammes in comparison to whale, the Balaenoptera which is the largest mammalian form of about 122 tonnes in weight. Elephants are largest among the land mammals. The giraffe is the longest for its elongated neck.

Mammals have colonised all environments in course of their evolution. Adaptive radiation at its zenith is encountered amongst the mammals.

During Mesozoic era, the age of reptiles (dinosaurs), mammals were small, generalised and rare. By the end of Mesozoic or beginning of Coenozoic, the dinosaurs vanished and mammals suddenly expanded into varied evolutionary patterns. Early in Cretaceous period, placental mammals became distinct from marsupials.

During Eocene and Oligocene, most of the orders of mammals originated moving into habitats and ecological niches vacated by the extinct dinosaurs. This evolution from a single ancestral species to a variety of forms which occupy different habitats is called adaptive radiation or divergent evolution.

The concept of adaptive radiation in evolution was developed by H.F. Osborn in 1898. Examples often given as evidence include Darwin's finches of the Galapagos Islands, varied limb structure of mammals, Australian Marsupials, etc.

Adaptive Radiation:

Adaptive radiation refers to the adaptation of an organism that enables them to spread successfully or radiate into another environment. Adaptive radiation is the evolutionary process by which many species originate from one species in an area and radiate to different species. The phenomenon of adaptive radiation was first observed by Darwin.

Adaptive radiation, evolution of an animal or plant group into a wide variety of types adapted to specialized modes of life. Adaptive radiations are best exemplified in closely related groups that have evolved in a relatively short time. A striking example is the radiation, beginning in the Paleogene Period (beginning 66 million years ago), of basal mammalian stock into forms adapted to running, leaping, climbing, swimming, and flying. Other examples include Australian marsupials, cichlid fish, and Darwin's finches (also known as Galapagos finches).

Many examples of speciation by adaptive radiation are found in archipelagoes removed from the mainland. In addition to the Galapagos Islands, the Hawaiian archipelago, with its several volcanic islands and relatively small total land area, hosts an astounding number of plant and animal species that are endemic; that is, they have evolved there and are found nowhere else. More than 90 percent of the native species of Hawaiian flowering plants, land mollusks, birds, and insects are endemic.

Locomotion in Mammals –

The mammals are basically quadruped animals. The legs are like the ‘towers of the bridge’ and the backbone is the ‘arched cantilever system’ supported by the ‘towers’. This whole system carries the animal and helps to secure food, shelter and other biological needs.

Mammals exhibit extensive adaptive radiation for locomotion. The skeletal framework becomes greatly modified in relation to diverse modes of locomotion.

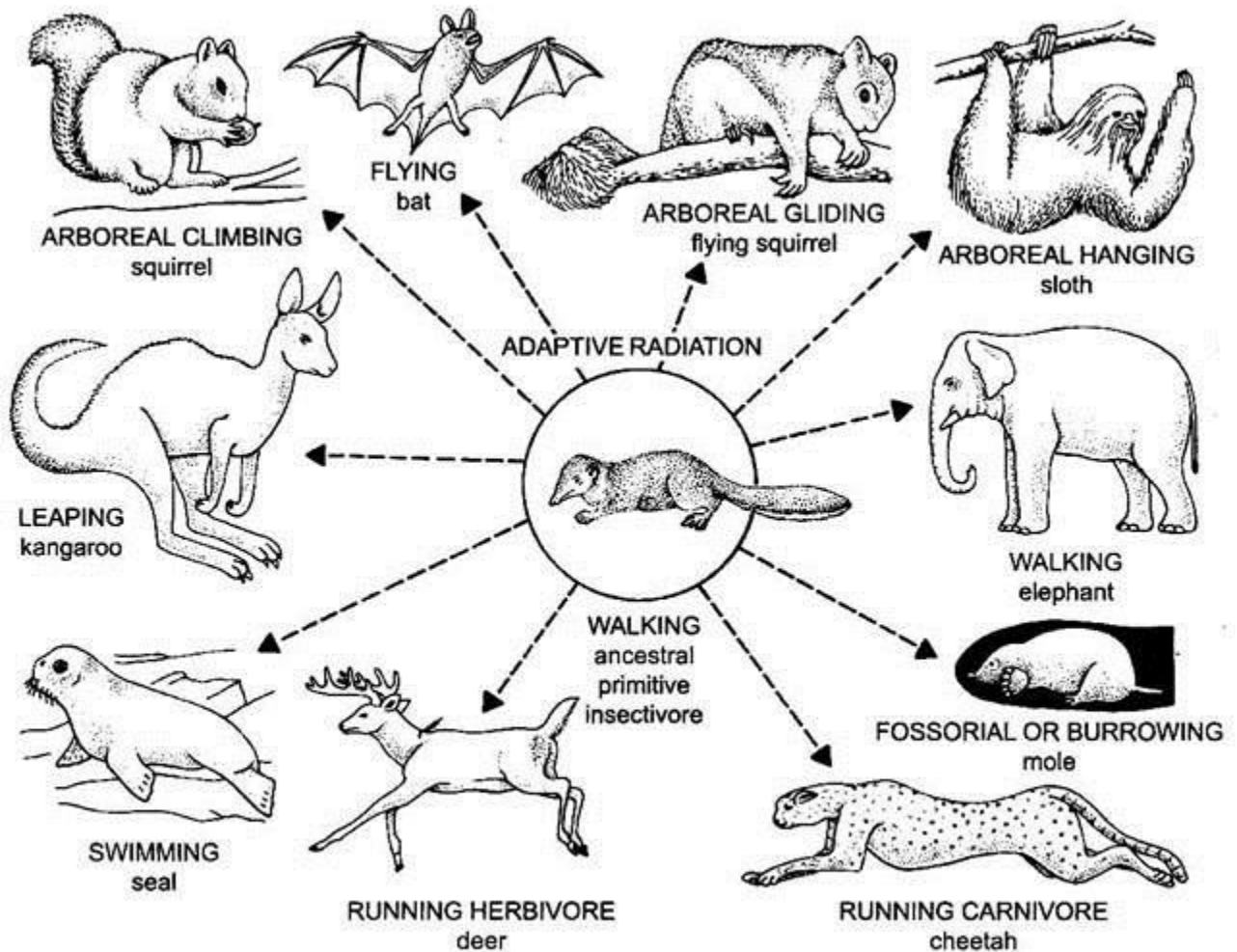


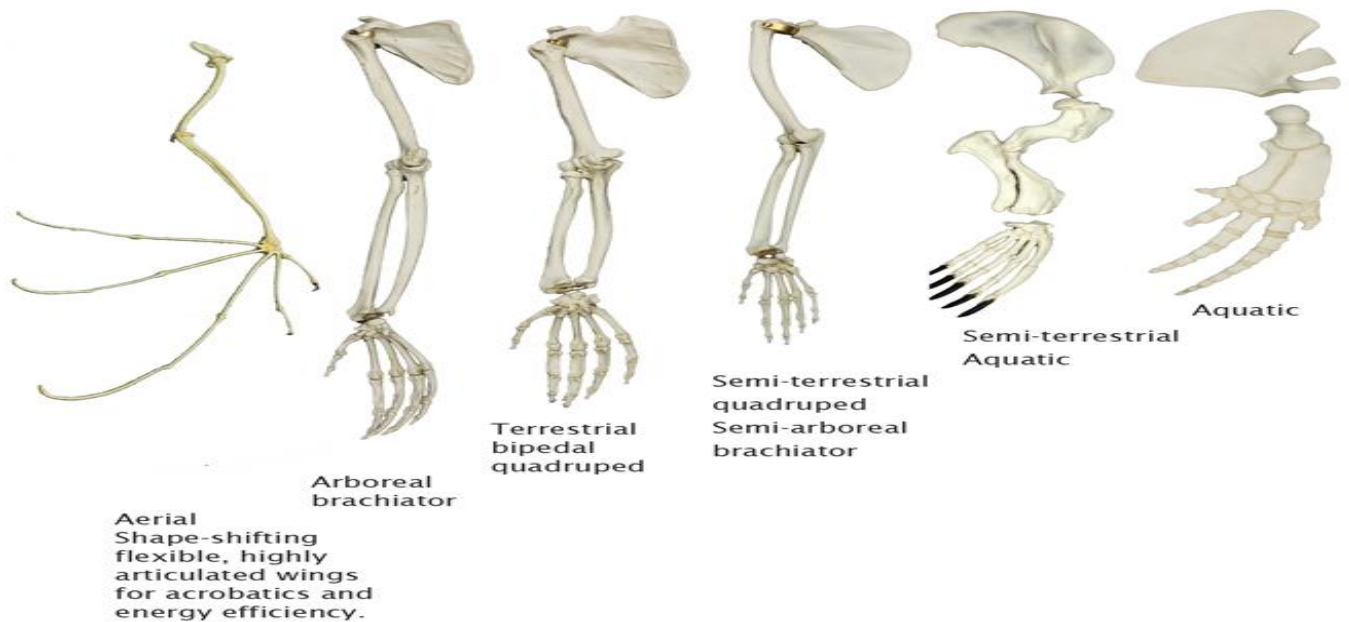
Fig. 33.10. Adaptive radiation or divergent evolution in mammals, based on locomotion.

Plantigrade (Ambulatory)—the central type of locomotion –

The ancestral mammals were plantigrade, i.e., the feet (soles) and toes touched the ground during locomotion. This type of locomotion is observed in human beings. The other mammals which serve as examples of this type of locomotion are: opossums, bears, raccoon, shrews, mice, etc.

This is the central type of locomotion from which other types of locomotion have radiated in mammals. The mammals under this category walk on the entire foot and are typically five-toed. The metatarsals and metacarpals are not fused and are longer than the phalanges.

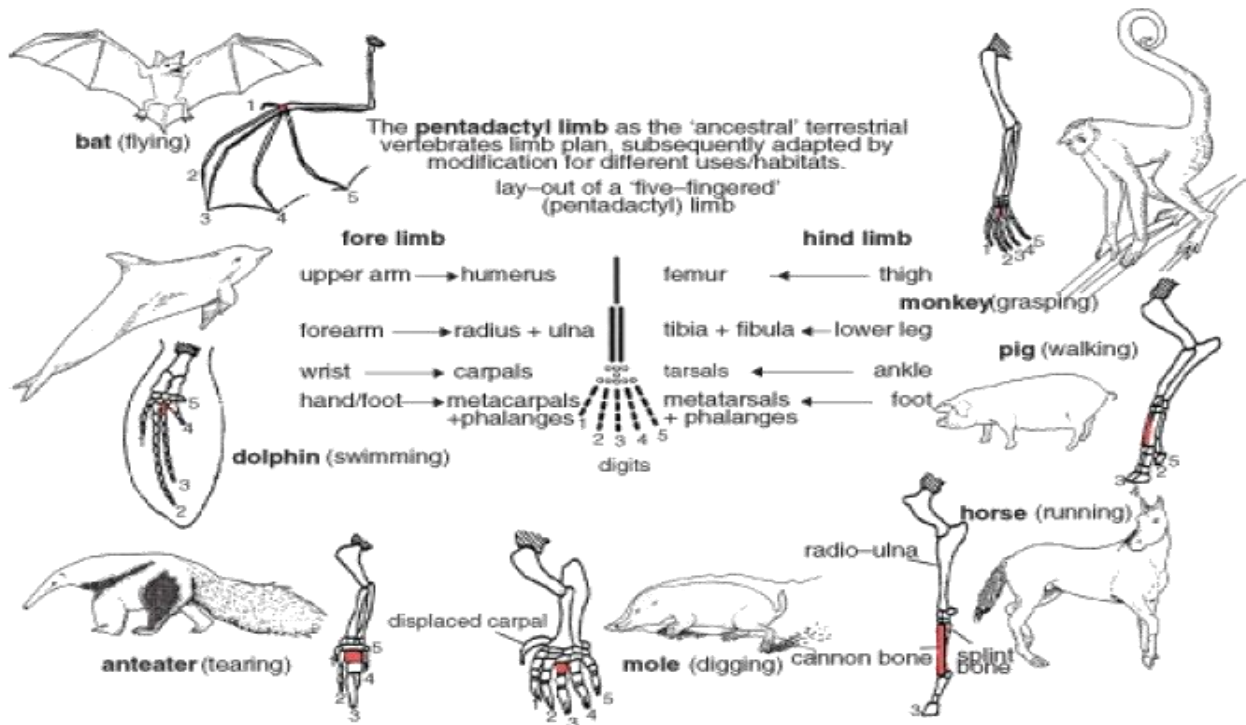
The wrist and ankle bones permit movement in various planes. In larger mammals (exemplified by bears) the locomotion is ambulatory while in smaller forms (e.g., shrews, opossums, etc.) the locomotion tends toward the cursorial types. Human beings practice an ambulatory bipedal plantigrade type of locomotion.



Radiation in Limb Structure of Mammals –

Mammalian limbs are the modifications of the pentadactyl limb. Primitive, ancestral mammals are believed to have been short legged five fingered creatures living on the ground. Their limbs were not modified for any particular type of locomotion. These animals were terrestrial. These terrestrial ancestors formed the ancestors of modern mammals.

These mammals having primitive limb structure are placed in the centre of the figure shown below. Therefore, adaptive radiation occurred in five different lines or habitats with modifications in their limb structure.



From these terrestrial mammals the different lines radiated in the following manner:

1. One evolutionary line radiates to form arboreal forms which have adapted limbs for life in trees (e.g., squirrels, sloths, monkeys, etc.).

2. Another line leads to aerial representing mammals adapted for flight (e.g., bats) Only bats occupy the position at the terminus of this line, since they are the only truly flying mammals Somewhere along this line we can place for gliding mammals such as “flying squirrel. ”

The arboreal and aerial forms not arose independently from the terrestrial forms as shown in the diagram It is believed that the ancestral aerial forms were previously lived in trees having gliding type of locomotion which later gave rise to true flight. Hence, perhaps the gliding formed transitional type of locomotion between climbing and true flight.

3. Third line of radiation gave rise to cursorial forms (e.g., horses and antelopes). They have developed limbs suitable to rapid movements over the surface of the ground. Along this line also developed other mammals with less strongly modified limbs, such as wolves, foxes, hyaenas, lions.

4. Fourth line of radiation formed the burrowing mammals, the fossorial mammals. Some of the fossorial mammals, like the moles, have modified their forelimbs for digging but they are poorly adapted for locomotion on the ground. While others like pocket gophers and badgers are expert diggers but they have retained structures enabling them to move readily on the surface of ground.

5. Fifth line of radiation leads to the aquatic mammals

(i) Whales and porpoises having limbs strongly adapted for aquatic life, but they cannot move about on land.

(ii) While seals, sea lions and walruses have also strongly modified limbs for aquatic life but they are also able to move about on land.

(iii) The third group includes accomplished swimmers such as otters and polar bears which are equally at home in water or on land.

Thus, all the mammals of different radiating lines have limbs more or less adapted for some particular mode of locomotion. All the lines start

from a common centre representing the short, pentadactyl limbs of terrestrial mammals. From the centre, evolutionary lines radiate out in various directions. Hence, adaptive radiation is evolution in several directions starting from a common ancestral type.

Arboreal type:

Many mammals, specially living in forest areas, have become modified to live on trees. This mode of living is named as arboreal. Arboreal mammals are able to climb the trees and use their branches as the highways.

Modifications for holding onto tree branches are observed in these mammals. Tree squirrels and sloths have well-developed claws. Some arboreal mammals possess prehensile tail. The tarsier develops adhesive discs on the front toes.

Sloths spend most of their time hanging upside down the trees and lead a sedentary life. The skeletal system becomes greatly modified. The neck is short with the unusual number of cervical vertebrae (i.e., seven in number) in *Choleopus tridactylus* (two-toed sloth), but in *Bradypus tridactylus* (three-toed sloth) there are nine cervical vertebrae.

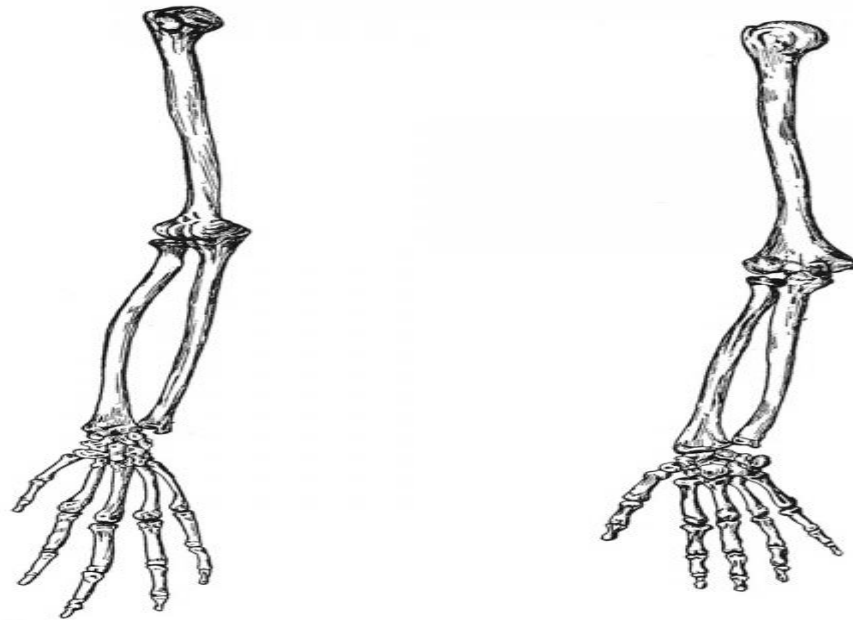
Strong shoulder girdle, well-formed clavicle, increase in the number of ribs are some of the important arboreal adaptations.

The squirrels use the trees for climbing and jumping rather than hanging. In typical forms the body is elongated, the hind limbs have well-developed musculature, well-developed and sharp claws and well-formed sense organs.

Brachiation -

This is a specialised type of arboreal locomotion which means swinging from branch to branch by using the forelimbs only. The forelimbs become greatly lengthened. In gibbons the forelimbs may touch the

ground. The stereoscopic vision is very good which helps a gibbon to have a 12-metre-jump from one branch to another with precision.



Fossorial type:

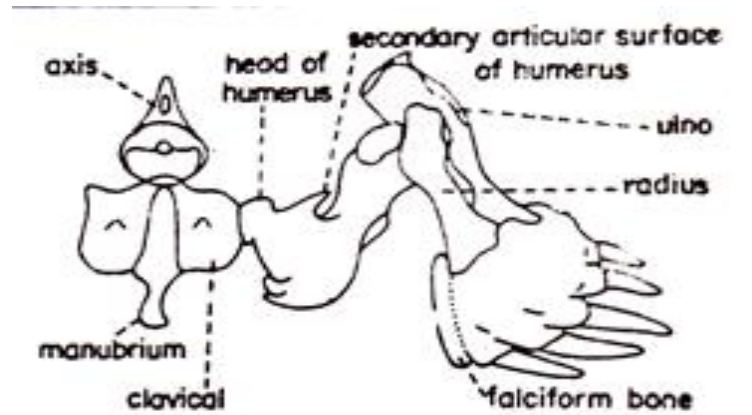
There are many mammals who spend their entire life in the underground. They become specially adapted for this mode of life. The pocket gophers and moles are the typical representatives. Most of them are small in size.

The digging apparatus becomes highly evolved in this group of mammals. There are some semi-fossorial type [e.g., badger (*Taxidea*)] which spends much of its time above the ground. In fossorial mammals the profile of the head is triangular and flat (e.g., *Spalax*). Besides modifications of skull the post-cranial portion of the skeleton becomes also modified.

The forelimbs together with the pectoral girdle are modified for digging efficiency in different ways. The forelimb may be provided with

sesamoid and hetero-tropic bones. In Scalopus the palmar regions are furnished with stiff hairs.

In much semi-fossorial type (Taxidea) the claws become greatly elongated. These claws grow at a quicker rate to make up for the wear and tear for digging. In pocket gopher (Thomomys bot-tae) three centre claws grow 0.23 mm/day or over 0.84 cm/year.

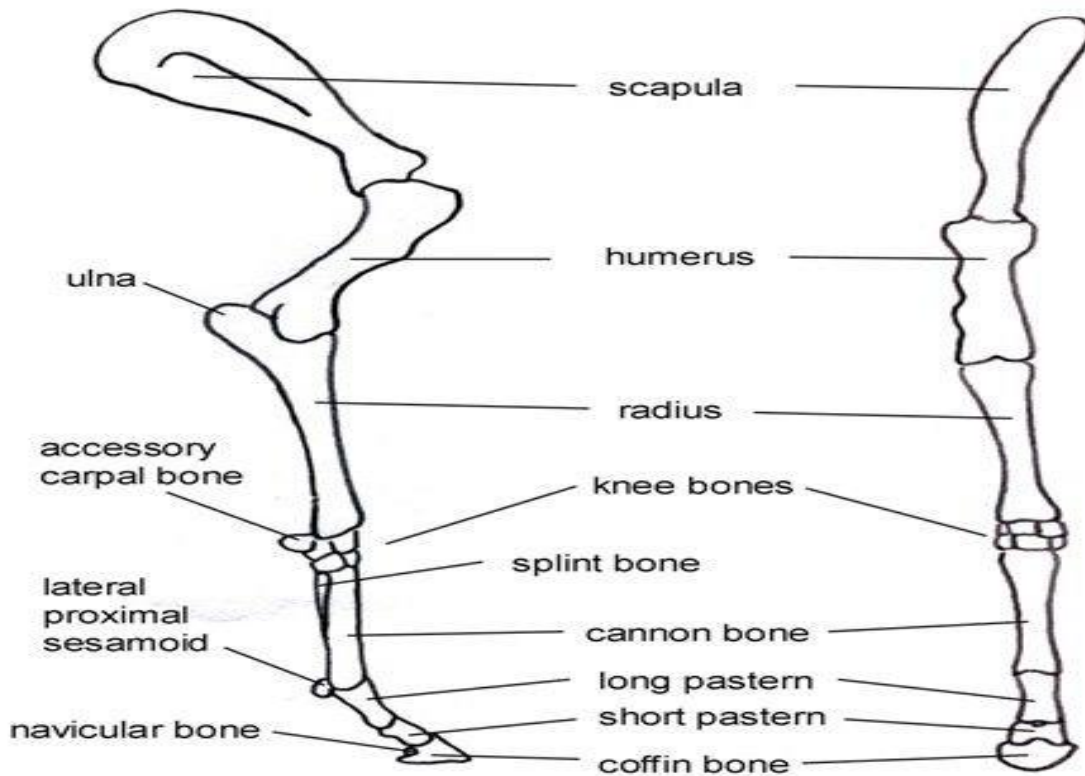


Cursorial (Running):

Surface-oriented larger mammals depending on speed for catching prey or survival show cursorial locomotion. Larger mammals including carnivores, horses, zebras, deer, pronghorn, antelopes, cattle, bison, giraffe show this type of locomotion. Cursorial type of locomotion reaches its peak in ungulates living on the plains. Cursorial mammals have an elongated body and neck.

The elongated neck is used to shift the centre of gravity forward when the animal attains momentum during locomotion. *Odocoileus virginianus* (white-tailed deer) stretches its neck far forward when it moves at its greatest speed.

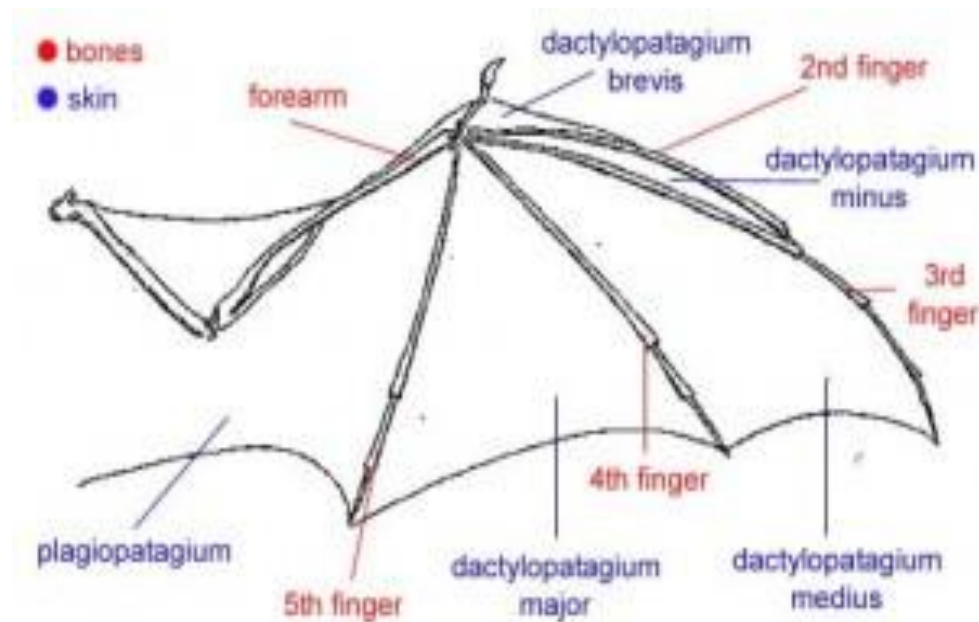
The limbs become lengthened with the tendency towards fusion or loss of metacarpal and metatarsal bones into the cannon bones. The joint surfaces become tongue-and-groove types restricting the movement of the limbs in a single plane parallel to the long axis of the body.



Aerial type:

Several locomotor patterns for climbing are used by arboreal mammals, the grasping ability of which has been enhanced by the presence of either strong claws or prehensile fingers. Many monkeys use a climbing gait similar to the leg sequence of walking. Occasionally, however, they use a leg sequence equivalent to that of a trot. Small-bodied climbers with sharp claws, such as squirrels, climb by the alternate use of forelegs and hind legs; essentially, they hop up a tree. Prehensile-fingered climbers descend backward and generally with a walking type of leg

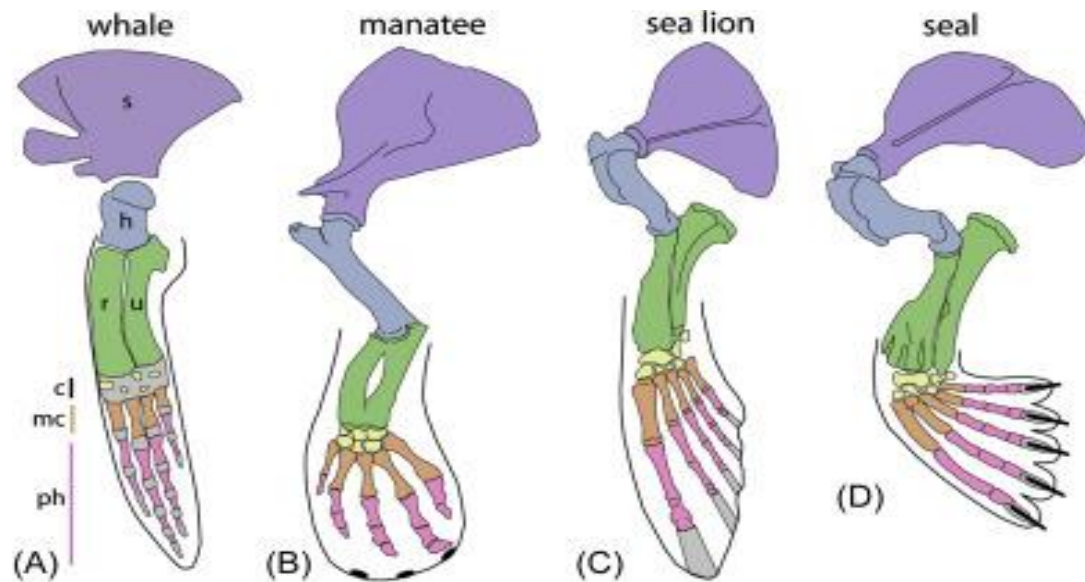
sequence. Sharp-clawed species descend with a similar gait sequence but with the head downward.



Aquatic type:

Swimming mammals, such as whales, dolphins, and seals, use their flippers to move forward through the water column. During swimming sea lions have a thrust phase, which lasts about 60% of the full cycle, and the recovery phase lasts the remaining 40%. A full cycle duration lasts about 0.5 to 1.0 seconds. Changing direction is a very rapid maneuver that is initiated by head movement towards the back of the animal that is followed by a spiral turn with the body. Due to their pectoral flippers being so closely located to their center of gravity, sea lions are capable of displaying astounding maneuverability in the pitch, roll, and yaw direction and are therefore not constrained, turning stochastically as they please. It is hypothesized that the increased level of maneuverability is caused by their complex habitat. Hunting occurs in difficult environments containing rocky inshore/kelp forest communities, with many niches for prey to hide, therefore requiring speed and maneuverability for capture. The complex skills of a sea lion

are learned early on in ontogeny and most are perfected by the time the pups reach one year. Whales and dolphins are less maneuverable and more constrained in their movements. However, dolphins are capable of accelerating as fast as sea lions, but they are not capable of turning as quickly and as efficiently. For both whales and dolphins, their center of gravity does not line up with their pectoral flippers in a straight line, causing a much more rigid and stable swimming pattern.



Echolocation in Micro Chiropterans:

Introduction –

Echolocation is the emission of high frequency sound (ultrasonic sound, about 20 kilohertz) which is utilised for detecting the presence of objects (including food) by the echoes produced. It is a good substitute for vision for those animals, such as bats, which have to hunt in darkness. These high frequency sounds are produced in the larynx (voice box) and

are generally restricted in insectivorous bats of the suborder Microchiroptera.

The mega-chiropterans, that feed on fruit, flower, nectar etc., generally lack ultrasonic orientation. However, some of its members produce orientation sounds that are largely audible and have ultrasonic components that are produced not in the larynx but by clicking the tongue. Bats are not the only mammals possessing ultrasonic orientation sounds. However, in case of bats, it has reached its peak.

Microchiropteran bats are also known as "echolocating bats" because they have the ability to use echolocation in obstacle avoidance and hunting. These bats occur on every continent but Antarctica. Every food preference that is found in bats is represented in Microchiroptera, although the majority are predominately insectivorous. Several notable microchiropteran bats include *Craseonycteris* (Bumblebee Bat), which is one of the smallest mammals in the world, *Thyroptera* (Disc-winged Bats), which attach to leaves using suction cuplike discs on the foot and thumb, and Desmodontinae, which are the only blood-feeding bats.

Microchiropterans navigate with the aid of echolocation, also known as "biosonar." This is similar to the mechanical sonar systems used by humans. A signal is emitted and the returning sound is analyzed to learn about the surrounding environment. Microchiropteran bats are not the only animals that use echolocation. Toothed whales, some insectivores (eg., shrews), oilbirds, and some swiftlets also use echolocation.

Echolocating bats typically emit an ultrasonic (over 15 kilohertz) pulse, and analyze the returning echo to determine the distance to the object as well as what type of object it is. Most bats alternate between emitting sound and listening for returning sound. The frequency, length of call, intensity, and degree of modulations of the emitted sound differs between species, and there may even be differences between individuals within a species.

Echolocation calls are vocalizations that are produced in the larynx (voice box). Calls are emitted through the mouth or the nostrils. Bats that emit calls through the nostrils, such as Phyllostomidae and Rhinolophidae, often have complex folds and/or flaps surrounding the nostrils, which may affect the signal.

A few megachiropterans also use echolocation (e.g., some species of *Rousettus*), but these bats produce sound by clicking their tongues rather than by vocalization. The different method of sound creation is one reason why echolocation is believed to have evolved independently in Microchiroptera and the few echolocating megachiropteran bats. Echolocation is not thought to have been present in the common ancestor of Megachiroptera and Microchiroptera.

The ability to echolocate has allowed many bats to exploit flying nocturnal insects as a food source, as well as to live in dark caves. In neither situation can one successfully rely on vision alone to locate objects due to the limited amount of light. Most likely as a result of increased reliance on echolocation, microchiropterans have reduced vision capabilities, having lost some of the complexity found in the eyes and brains of megachiropteran bats.

While echolocation has many benefits, it also has costs. The most pronounced is that other animals can often hear the signals emitted by bats. Those who are able to hear the sounds include other bats, potential predators, and prey. Some moths have evolved complex ears, apparently for listening to bats. When such a moth hears calls of an approaching bat, it begins evasive maneuvers. Some insects actually emit sounds in response to bat calls. This apparently confuses the bat although it does not directly jam the signal.

All bats, however, possess and utilise low frequency sounds (below 20 kHz — within normal audible range of humans), which are generally used to facilitate social interactions such as territorial spacing among individuals, mother-infant communication, recognition and warning calls.

The echolocation mechanism adopted is not fully understood and certainly is not the same. Lazzaro Spallanzani (1729-1799), an Italian at the age of 64, first experimented and proved that bats did not rely upon their visual sense to fly and capture prey at night. He, however, could not provide a plausible explanation.

In 1920, H. Hartridge reconfirmed the notion of Spallanzani that bats oriented with auditory rather than visual cues. Later, in 1958, Donald Griffin, a Harvard biology student, showed conclusively that the bats emit pulses of high- frequency sounds which strike objects and reflect back to the animals. Thus, bats hunt by echolocation and not by listening to the sounds made by the insects.

Anatomical Structure in Sound Production and Reception:

A. Sound Production:

Micro-chiropterans generate ultrasonic sounds in the larynx. The larynx in micro-chiropterans is proportionately longer than that found in mega-chiropterans and the cartilages are ossified to make a rigid framework. The strong cricothyroid muscles put greater tension on the light vocal cords. The complexity and large size of this sound-producing structure directly relates to the range of ultrasonic sound that it produces.

It is performed by discrete pulses of high intensity and up to 150 kHz frequency which is emitted through the nose and mouth. In the case of horseshoe bats (Fig. 5.19A) there are special resonating chambers and the face is elaborately modified forming a nose-leaf.

B. Role of Nose-leaf:

The role of nose- leaf in echolocation is not well-understood. Rhinolophid and hipposiderid bats possess complex nose-leaf that serve to beam the ultrasonic sounds and help in directing the signal to

a particular direction. The complex flaps and folds also serves to shield the ears from the outbound, nasally emitted signals and so increase their overall sensitivity to returning echoes.

Characteristics of Echolocation Sounds:

Before going into the novelty of chiropteran acoustic orientation, some physical parameters of sound are discussed:

A. Physical Aspects of Sound:

Sound is a form of energy which is manifested in the form of disturbance or vibration in a medium. Sound can be measured in a number of ways.

(a) Wavelength and frequency:

Sound can be measured in frequency which is expressed as Hertz or cycles per second (Fig. 5.21). Another way sound can be characterised is by its wavelength (Fig. 5.21), which is inversely related to its frequency. High frequency sound has a short wavelength. For example, a sound frequency of 50 kHz has wavelength of only 6-8 mm, while a low frequency sound of 34 Hz has a wavelength of about 10 m.

Bats utilise high frequency sounds rather than those of low frequency because:

(i) High frequency sounds get weakened in intensity as they pass through air, whereas low frequency sounds retain their intensity over long distances.

(ii) By using high frequency sounds bats avoid possible interference from environmental background noises such as insect songs, wind or other nocturnal noises that are generally in the low frequency range.

(iii) By utilizing high frequency signals, it provides a means of escaping detection by potential nocturnal predators.

(iv) It may be a way of detecting insect prey without being detected in turn.

It is to be noted that some moths who fall prey to bats, can hear bat's sounds and exercises evasive maneuvers or even produces high frequency sounds of their own to jam an approaching bat's course.

(b) Amplitude or intensity:

Sound contains energy-amplitude, intensity or loudness. Amplitude is represented by the height above and below the zero reference line of the wave form, as shown in Fig. 5.21. It can be estimated by measuring the difference in pressure between the peak and the trough of the wave. This pressure is expressed as Newtons per square meter (Nm^{-2}).

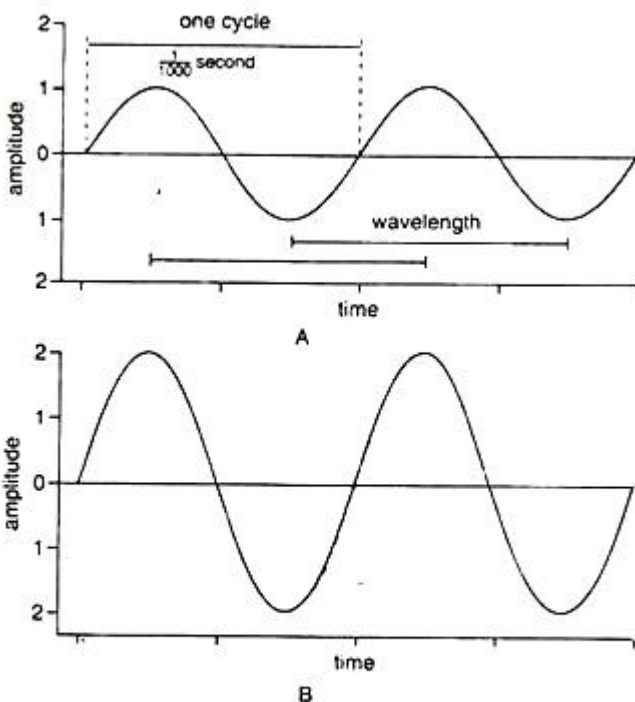


Fig. 5.21 : Physical aspect of sound wave. A. 1,000 Hz pure tone having an amplitude of 1. B. 1,000 Hz pure tone having an amplitude of 2

(c) Harmonics or overtones:

Natural sounds are complex in structure and consist of a collection of several to many frequencies. The different frequencies in a complex sound are called harmonics or overtones. The harmonic structure of a complex sound is not a random assortment of frequencies, but it is rather an ordered sequence of related frequencies (Fig. 5.22).

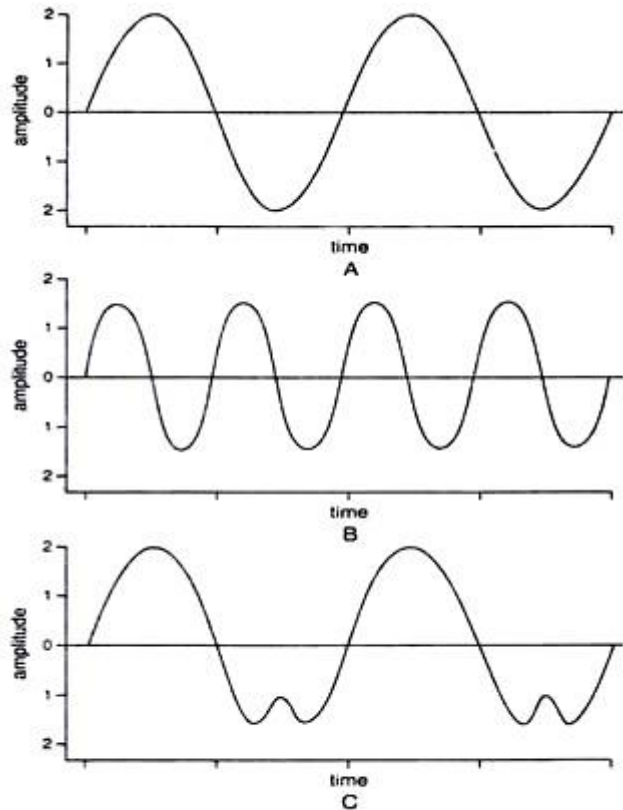


Fig. 5.22 : Simplistic complex sound : A. Fundamental, lowest frequency. B. Second harmonic of A. C. Complex wave formed by the sum of two pure tones (A and B)

The complex sound of Fig. 5.22C consists of two related frequencies. The lowest in this series (Fig. 5.22A) and thereby the fundamental frequency is 1,000 Hz. The next frequency, or second harmonic (Fig. 5.22B) is higher than 1,000 Hz and is precisely 2,000 Hz.

Complex sounds are further complicated by the fact that each harmonic may be produced with different amplitudes or intensities, and, in some cases, harmonics may be 'dropped out' of the sound spectrum altogether.

Harmonics of bats:

Bats produce a variety of complex sounds in their acoustic orientation vocalizations, which comprises of sweeps through several frequencies with accompanying harmonics. These sounds are produced in the larynx and may be filtered or altered by various resonating cavities or

other peculiarities in the vocal tract or nasal passages. The acoustic sounds thus emitted by the bat have a particular structure.

By using orientation sounds with multiple harmonics, bats increase the discriminatory ability of the sound as each harmonic represents a discrete frequency with its own wavelength and target size recognition characteristic.

Such range of harmonics would be of definite value in hunting in a dense, tangled environment (or along solid surfaces) by improving the contrast between echoes reflected from a potential prey item and its background.

B. Echolocation Sounds Produced by Micro-Chiropterans:

Micro-chiropterans produce high frequency sounds that are acoustic signals emitted by the bat for the purpose of gathering vital information about objects in its immediate vicinity. The nature of this biological imaging system, its quality and quantity, varies widely among the various species of micro-chiropterans.

The micro-chiropterans ultrasonic signal is characterised by a combination of several parameters such as:

(i) Duration of signal:

The orientation signal used by bats varies in duration from about 0-2 to 200 milliseconds (ms). The range of this variation is divided into 1. those that are exceptionally short (less than 2 ms), 2. those that are of moderate duration (less than 10 ms but more than 2 ms), and 3. those that are very long (more than 10 ms).

(ii) Harmonic structure of signal:

Bats can incorporate from one to about 5 harmonics in their acoustic orientation signals. Contrary to the above, some species do not incorporate any harmonics in their echolocation sounds.

(iii) Frequency-modulated (FM) component of signal:

The frequency-modulated components comprise of sweeps that starts with a beginning frequency, passes through several to many

intermediate frequencies and, ultimately, ends in some ending frequency that is usually lower than the beginning frequency.

FM components may be:

1. Narrow in band width that sweeps through relatively few frequencies (for example, 55 kHz to 40 kHz = bandwidth 15 kHz), or
2. Broad in bandwidth that sweeps through many frequencies (for example, 100 kHz to 50 kHz = bandwidth 50 kHz).

(iv) Constant-frequency (CF) component of signal:

Constant-frequency signals are echo-location sounds emitted at one frequency. Many bats incorporate a CF component in their acoustic orientation calls.

(v) Sequence of frequency components in signal:

Both CF and FM components are commonly encountered in ultrasonic sounds of micro-chiropteran. Any one of the components may precede the other.

The bio-sonar pulses of micropteran species may differ among the different species within the same genus and these pulses are classified into 3-types. They are constant frequency (CF), frequency modulated (FM) and combined CF-FM.

CF pulses consist of a single frequency or tone, and are found among rhinolopids and some other rhinolophoid bats. Constant frequency pulses are longer (40 – 1000 ms duration) than frequency modulated pulses and are emitted through the nostrils. CF pulse repetition rates are less than 10 per second. FM pulses sweep downward and sound like chirps, observed among vespertilionids and some other bats. These pulses are short (1-5 ms duration) and are emitted through the mouth.

The pulse repetition rate varies from less than 10 per second at rest and above 100 per second when hunting. Combined CF-FM pulses consist of a long constant tone followed by a downward chirp. In many

bats the tones are not pure but consist of a fundamental or first harmonic and several higher harmonics.

Except information about the target the bio-sonar signals can provide varied information with some remarkable details (Fig. 10.66). Doppler Shifts (changes in the frequency of the echo relative to the original signal) convey information not only about the relative velocity of a flying insect but also about its wing beat (Fig. 10.67).

The amplitude of the echo, combined with the delay, indicates the size of the target. The amplitudes of the component frequencies correspond to the size of various features of the target (Fig. 10.66).

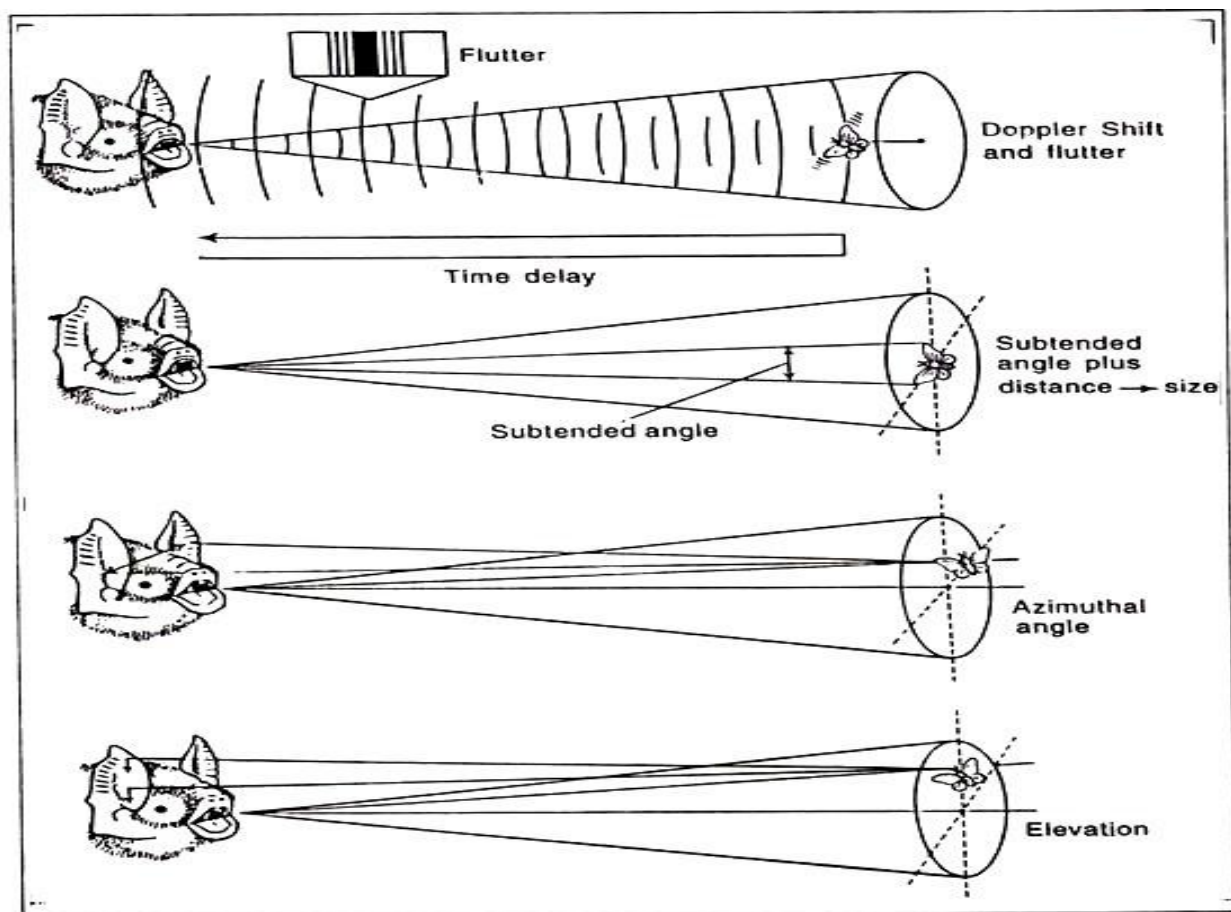


Fig. 10.66 : Varied information can be extracted from biosonar signals. The time delay and Doppler shift of the echo indicate the distance and relative speed of the target. Rapid flutters betray the presence of beating insect wings. Echo amplitude depends on the relative size (subtended angle) and distance of the target. Interaural time and amplitude differences convey the azimuth of the target. Elevation depends on the interference patterns of sound waves (after N. Suga, *Scientific American*, 1990).

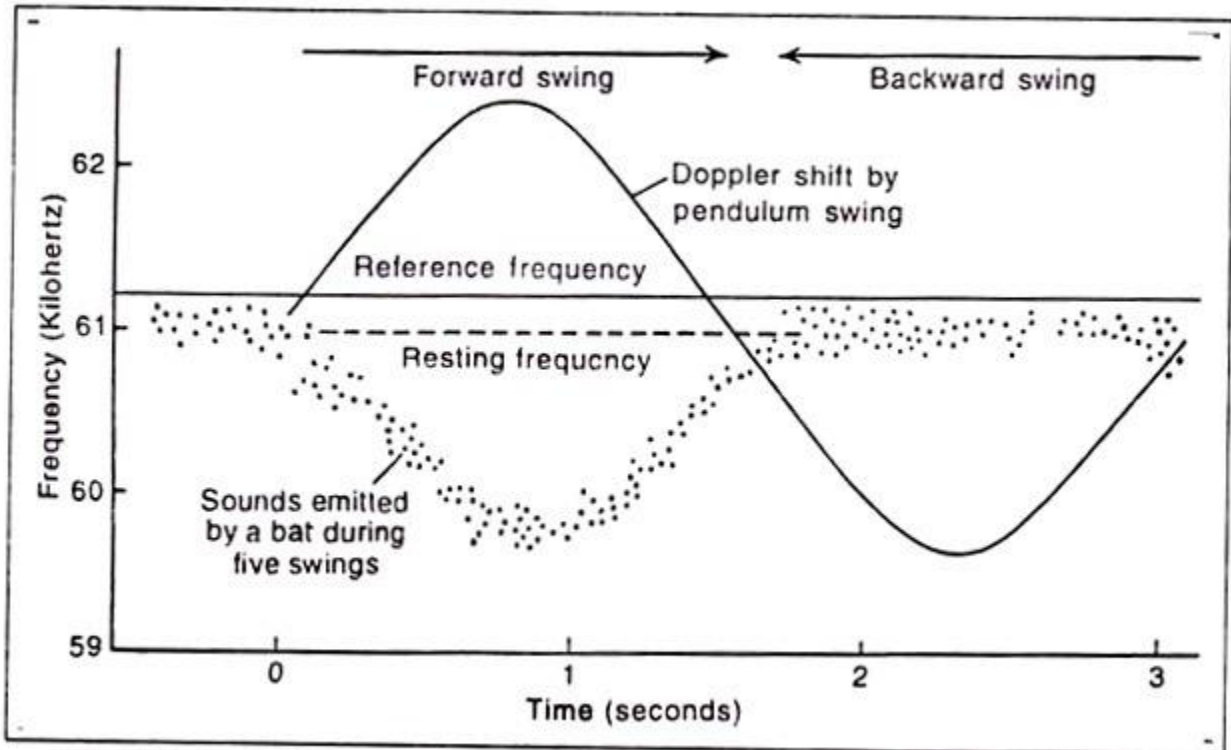


Fig. 10.67 : Doppler Shift compensation of a mustached bat (after N. Suga, Scientific American, 1990).

(vi) Amplitude of signal:

The amplitude (intensity or loudness) of the acoustic orientation sounds of bats are of a wide range. Intensities of $0.1-0.32 \text{ Nm}^{-2}$ have been recorded for the Greater False vampire (Megadermalyra). While the Greater Horseshoe bat and the Mediterranean Horseshoe bat produces intensities of 27.0 Nm^{-2} and 2.0 Nm^{-2} , respectively. The Little Brown bat (*Myotis lucifugus*) produces sounds between 6.0 and 17.3 Nm^{-2} .

(vii) Variations of repertoire:

Each bat may change its acoustic repertoire along one or more of the parameters discussed above. This change may be continuous in nature or it may differ in different foraging situations.

Micro-chiropterans acoustic imaging system is of two general kinds:

1. Time frequency spectrum consisting primarily of broadband, frequency-modulated (FM) signals.
2. Time-frequency structure that consists mainly of narrowband, constant frequency (CF) signals.

(a) Broadband, frequency-modulated signals:

The first broadband acoustic pattern consists of frequency-modulated signals with multiple harmonics. The acoustic orientation of phyllostomids (New World leaf-nosed bats) has been well-studied and they are the most diverse with regards to their feeding habits. Their ultrasonic signals are exceptionally low in amplitude (less than 0.1 Nm^{-2}) and of short duration (0.5-2.5 ms).

Although the band width of each harmonic is relatively narrow (average 20-30 kHz), the abrupt linearity of the frequency sweep causes these harmonics to overlap, thereby creating a rather broad bandwidth for an entire signal.

Such a case is best exemplified in the case of the carnivorous Spear-nosed bat (*Phyllostomus hastatus*), who emits four harmonics (1^o, 35 kHz to 30 kHz; 2^o, 45 kHz to 35 kHz; 3^o, 60 kHz to 45 kHz; 4^o, 75 kHz to 60 kHz). This results in an overall band width of 40-45 kHz.

A second pattern involving broadband is the frequency-modulated signals. It consists of a brief FM sweep (1-3 ms), followed by a short (5-7 ms) constant-frequency component. This FM followed by short CF pattern is found in many tropical and temperate species which are often called as 'FM bats' (example: Big Brown bat, *Eptesicus fuscus*).

(b) Narrowband, constant frequency signals:

The first narrow-band CF patterns consist of multiple harmonic, short CF signals. These signals are of very short duration (0.2-2 ms) and lack any substantial FM sweep. However, they are very much like that of multiple harmonic FM signals.

The fundamental frequency is emitted at or near 20 kHz and is accompanied by four harmonics. These harmonics are all CF or only slightly FM. The acoustic orientation sounds of the Greater False vampire (*Megaderma lyra*) is the best example within this group.

A second narrowband CF pattern consists of a moderately short CF signal (5-7 ms) followed by a brief FM sweep (1-2 ms). There may be one to three harmonics and the FM portions of these are shallow so as to prevent overlap in bandwidths. For example, *Pteronotus gymnotus*, *P. davyi* and *P. personatus* of the family Mormoopidae are of this sort.

A third CF pattern is seen similar to the second except that the CF component is exceptionally long (20 to over 100 ms) in duration. This pattern is common among the species of the old world family Rhinolophidae (*Rhinolophus landeri*) and some members of the Hipposideridae.

(c) Variable bandwidth:

Several insectivorous species of the genus *Tadarida* are quite flexible in their use of acoustic orientation patterns. These bats are perhaps the most versatile echo locators among the micro chiropterans. In uncluttered spaces, these bats hunt with narrowband short CF signals with no FM component. However, while pursuing potential prey, they drop the CF signal while adding a broadband FM component.

One harmonic accompanies this FM sweep. In cluttered or confined situations, these bats employ a multiple harmonic signal with several harmonics that overlap somewhat. The same shifting from essentially FM signals to short CF/FM signals during different phases of prey hunting has also been noted in the case of fishing bats (*Noctilio leporinus*).

Effectiveness of acoustic orientation of bats

(a) Target size discrimination:

Recent experimental studies have revealed that the little Brown bat (*Myotis lucifugus*) is capable of detecting and flying through an

obstacle network of wires 0.28 mm in diameter. The phyllostomids (*Glossophaga soricina*, *Carollia perspicillata* and *Artibeus jamaicensis*) can detect wires ranging from 0.19 mm to 0.175 mm in diameter.

The Mediterranean Horseshoe bat (*Rhinolophus euryale*) and the megadermatid (*Megaderma lyra*) has the ability to detect wires as fine as 0.05 mm and 0.08 mm in diameter, respectively, which is about the thickness of human hair.

(b) Target range discrimination:

Target range (distance) discrimination of echo locating bats varies with the size of the target. For example, the Little Brown bat (*Myotis lucifugus*) can detect wires of 3 mm diameter at range of about 2.25 m. This range decreases to 1.15 m for 0.28 mm wires and 1.0 m for 0.18 mm wires.

Similarly, the Mediterranean Horseshoe bat (*Rhinolophus euryale*) does not detect a 3 mm wire until it is within 1.4 mm distance of the wire, and a wire of 0.05 mm thickness is perceived at a distance of 0.2 m. It has been demonstrated that bats (*Eptesicus fuscus*, for example) have the ability to differentiate between two identical targets (as little as 12-13 mm) placed at different distances.

(c) Target shape and texture recognition:

It has been worked out that bats can differentiate target shape and texture of objects. It has been experimentally proved that the carnivorous phyllostomid, *Vampyrum spectrum*, is able to detect differences in the shape of various spheres and spheroids. Demonstrations in case of the Brown bats has proved their ability of textural discrimination of plexiglass plates with as little as 0.8 mm difference in hole depth.

(d) Feeding rates:

The efficiency of bat ecolocation activity has been evaluated by using feeding rates. It has been observed that the feeding rate of individuals of *Myotis lucifugus* in terms of successful capture of insects in the field is 1 g hr⁻¹.

The prey size varied between 0.2 mg and 3 mg. Thus, this species of bat detects and captures insects, in the wild, at a rate of about 500 per hour or about one insect every seven seconds. The same species, while foraging in a room full of *Drosophila* (about 2 mg), demonstrated a capture rate of 1,200 per hour or one every three seconds.

Working Space and Information Content of Echoes:

The important task an echo locating bat faces is to sort out objects acoustically in its immediate environment. The dimension of this 'working space' vary among species of bats from less than a meter to several meters, depending on flight speed and style, as well as target range discriminatory ability.

Within this working space the bat must be able to differentiate food items and avoid potential obstacles and all this has to be accomplished in a matter of microseconds.

The various echolocation patterns (multiple harmonic FM, FM/short CF, short CF/FM etc. as described above) serve as a carrier of vital information about target size, distance etc. Each of these acoustic patterns is limited by the kind of target imagery that it can convey.

(a) General Pattern of Echolocation:

A generalized sequence of acoustic events appears to be common to all echo locating bats and can be divided into three distinct phases – search, approach and terminal. Each phase of echolocation is characterised by a marked quantitative change in the rate at which the ultrasonic sounds are emitted and the duration of each signal. Fig. 5.23 illustrates the nature of these three phases in four different species of bats. Each of these bats uses a different qualitative pattern of acoustic orientation.

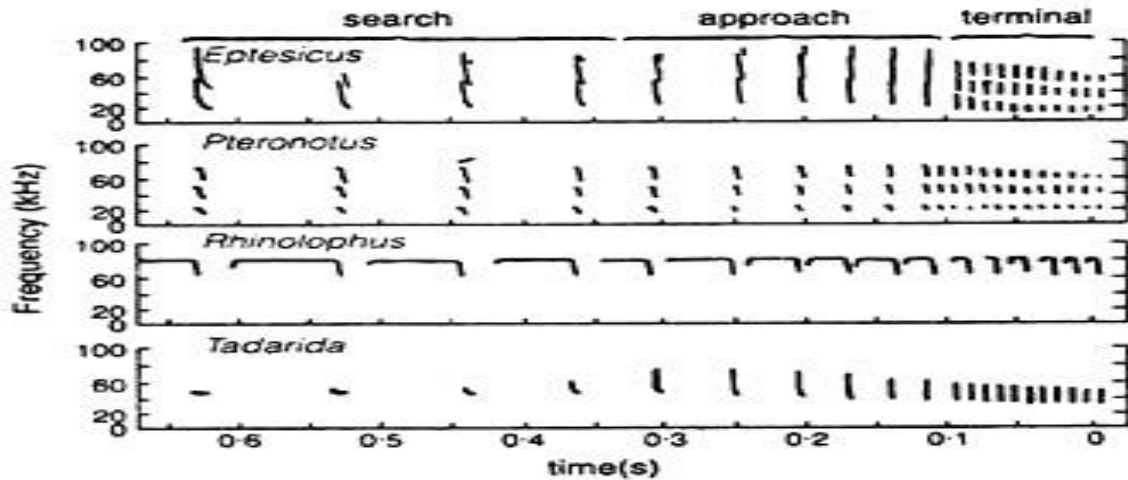


Fig. 5.23 : Diagrammatic representation from sonograms of echolocation signals made by *Eptesicus*, *Pteronotus*, *Rhinolophus* and *Tadarida*, during search, approach and terminal phases of hunting

(i) Search phase:

In most bats, including those given in Fig. 5.23, the search phase is characterised by a signal emission (or pulse) rate of about 10 pulses per second. As ultrasonic sound production is a metabolically expensive process, the repetition rate of the acoustic signals is regulated or balanced against the activity of that moment.

Signals are emitted at a minimal rate, during the search phase, which is just sufficient to survey and screen the area ahead for potential prey items or obstacles. The rate of signal emission in the search phase also appears to be correlated with flight speed and the degrees of environmental clutter.

(ii) Approach and terminal phase:

Goal oriented flight begins once the target has been detected. It gives rise to the approach phase, characterised by 25-50 pulses per second. It finishes with the terminal pulse during which pulse emission may reach as high as 200 or more pulses per second.

The marked rise in signal emission rate during these two goal-oriented phases allows the bat to gather more precise information concerning the speed, direction of movement and other acoustic imagery about

the intended target or obstacle. Due to the rapidity of the terminal phase, it is often termed as the “buzz”.

In many echo locating bats, although the general structure of the signal remains unchanged, the qualitative nature of each signal may be slightly modified, as in the case of *Rhinolophus*, where the duration of the signal is shortened.

In contrast, the Mexican Free-tailed bat (*Tadarida brasiliensis*) and the Long-eared vespertilionid (*Idionycteris phyllotis*), show a marked change in the structure of the acoustic signal during search, approach and terminal phases. During search phase they use a narrowband CF signal.

In the approach phase and while hunting in open areas, they drop the CF component and add a FM component. In complex, cluttered areas, they add multiple harmonics as well. Thus, these bats use different acoustic signals for different hunting situations.

(b) Pulse or Echo Overlap:

During the search phase of echolocation, the initial detection of a target takes place. The position of a target is first perceived when an echo, after getting reflected from the object, arrives back at the bat's ears. The distance of the object can thus be evaluated by the time interval between a pulse emission and the return of its echo.

In some bats, the echo from a pulse arrives at the time when the next pulse emission has already taken place. The Wagner's Moustached bat (*Pteronotus personatus*) emits a search pulse of about 4 ms duration. We know that sound travels through air at 340 mm ms^{-1} , a pulse of 4 ms duration would be 1,360 mm in length.

As the pulse or echo circuit is a two-way journey, and then this species would receive an echo from an object about 680 mm ahead at just about the time when the next pulse was getting emitted. With a flight speed of 1.7 mm s^{-1} and a search pulse rate of 18 (4 ms) pulses per second, the next echo would return or overlap about 0.6 ms into the

succeeding pulse emission. Similarly, the next echo would overlap by 0.12 ms.

However, most species of echo locating micro chiropterans appear to avoid pulse or echo overlaps. On making contact with the target, the pulse duration is shortened. The Little Brown bat (*Myotis lucifugus*) searches its prey at a pulse rate of about 15 per second, with each pulse being about 2.5 ms duration.

These bats can detect targets at about 2 meters distance, but do not attend to them until nearing about 720 mm. The bat, as it approaches its target, shortens the pulse by about 1 ms per 260 mm. Just before contact the pulse may be as short as 0-25 ms with the pulse rate being about 200 pulses per seconds.

(c) Narrowband Target Imagery:

Long CF pulses appear to be associated with searching and target or obstacle detection at generally long distances. Such acoustic signals may be more useful at high altitudes where sound attenuation is reduced. However, these signals are of maximal efficiency in open, uncluttered situations.

As shown in Fig. 5.24A, short CF signals are relatively limited in the information content they can carry. They are good only for the initial detection of a target, but do not convey any other information than the general location of the target.

They are of value mainly during close pursuit of prey, flight in congested conditions and perhaps also in landing. It is, thus, not surprising that there are no bats that use such type of signals exclusively.

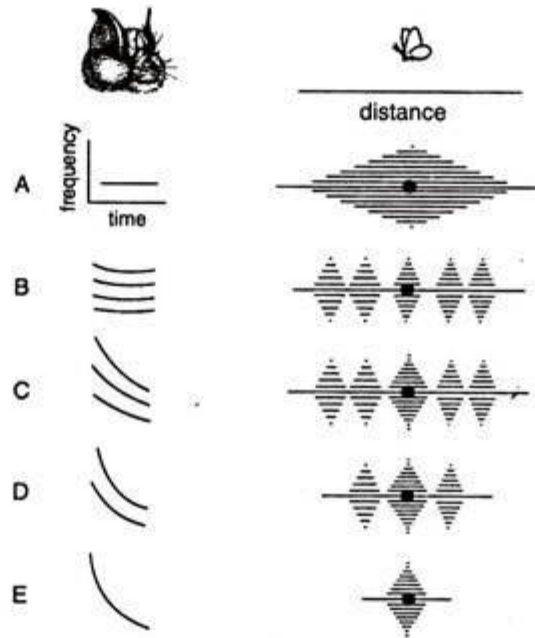


Fig. 5.24 : Diagrammatic relationship between bandwidth and number of harmonics in the ultrasonic signal of bat along with the perceived position of a target : A-E represent the different time-frequency signals. (Target represented by the dot and the shaded area illustrate the bats perception of the image)

Adding several harmonics to the short CF signal (Fig. 5.24B) sometimes improves somewhat the perception of the target's 'true' position. Such crude type of acoustic orientation appears to be used by *Megmaderma lyra*, *rhinopomatids* and *nycterids*.

(d) Broadband Target Imagery:

Bats that move about and forage in complex, cluttered environments use multiple harmonic signals with broadband FM sweeps (Fig. 5.24C). In many bats, the overall bandwidth is large (Fig. 5.24D), while others may use but a single broadband, curvilinear FM sweep (Fig. 5.24E).

However, all FM signals provide better multidimensional acoustic images than do CF signals. Better localisation of a target's 'true' position increases as bandwidth is broadened. This has been amply illustrated in Fig. 5.24C-E.

Use of multiple harmonics and its correlation with the hunting situation can be best exemplified in the case of the genus *Myotis*.

Myotis volcans hunt over the open fields and clearings and uses one prominent harmonic, while Myotis evotis uses narrow fundamental frequency and two harmonics to hunt in tangled vegetation.

(e) Doppler Effect:

Different bats use different methods of echolocation. It can determine the distance to prey by the time required for the signal to bounce back. The echoes coming back from any insect show the Doppler Effect, which is, if a sound source is moving toward us, the sound will have a higher pitch; if it is moving away, the sound will be of lower pitch.

The horseshoe-nosed bat emits a signal at 83-4 kHz. If the echoes coming back from the insect (prey) are at 83-4 kHz, they tell the horseshoe-nosed bat that the insect is flying away from it at the same speed that the bat is travelling (Fig. 5.25).

If the sound comes back lower than 83-4 kHz, the insect is moving away faster than the bat; and if the sound comes back at a higher speed then it means that the bat is closing on the insect. The bat then lowers the frequency of its signal.

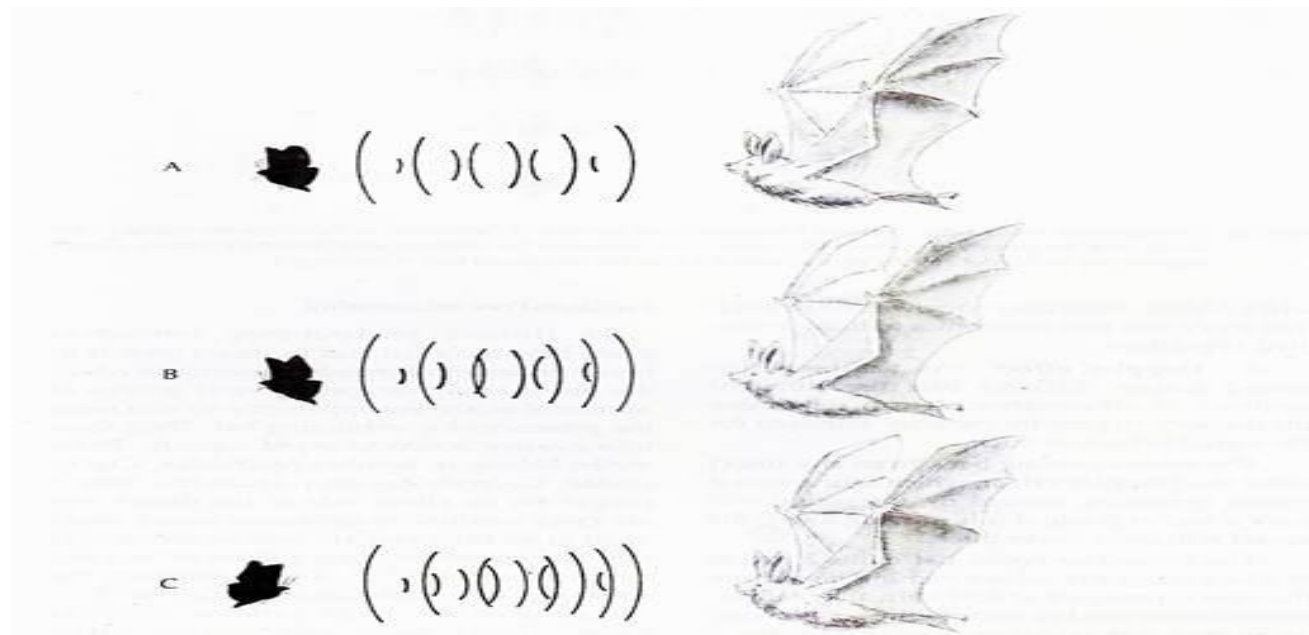


Fig. 5.25 : The Doppler effect by which bats can detect the movements of insect prey relative to themselves : A. The pitch of the echo is the same as the original sound. B. The pitch of the echo is higher than that of the original sound. C. The pitch of the echo is still higher indicating that the moth is flying towards the bat (enhanced Doppler effect)