

ZL 202 Animal Behaviour Semester – II

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Unit – I

- a) Behaviour: Definition - Innate behaviour, learning, reasoning, motivation, conflict and sexual behaviour.
- b) Migration and homing with special reference to birds.
- c) Communication in animals: Visual, olfactory, auditory and tactile.
- d) Camouflage and Mimicry – types of mimicry

Behaviour: Definition - Innate behaviour, learning, reasoning, motivation, conflict and sexual behaviour

Animal Behaviour is a very popular subject, not just with biologists but with the general public – it occupies a lot of prime time on television (Animal planet, National Geography, Discovery). Human beings have always been fascinated by our fellow creatures. Apart from this intrinsic interest and the fact, the subject presents us with questions as challenges as any other subjects in science, the study of animal behaviour is also of great practical importance.

Behaviour: Behaviour includes all those processes by which an animal senses the external world and the internal state of its body and responds accordingly. Many such processes will take place inside the nervous system and not be directly observable. What we see may involve violent activity or complete inactivity, but all equally rank as behaviour. Behaviour continues as long as life persists; anything and everything may count.

The task of understanding the behaviour fully would seem to be impossible and in fact we can not ever study behaviour unless we abstract and simplify. We have to make decisions about what it is important to record and what can safely be ignored. For example, if we are studying the courtship behavior of pheasants we will probably decide that there is no need to record the number of times that the animals breathe. Breathing is part of that continuous activity which constitutes behaviour but it will often judge irrelevant for behavioural studies of courtship.

Behavior comes in orderly sequences, recognizable patterns of behavior that can be called behavioral "units". The same animal will produce the same pattern of movements again and again; different members of the same species will also behave in recognizably similar ways. Behavior can only be studied because of this fact. A classic example of behavioral unit is the "egg-retrieval response" of the graylag goose.

Regarding the types of behaviour, there are two main approaches the *physiological behaviour* and the *whole animal behaviour*.

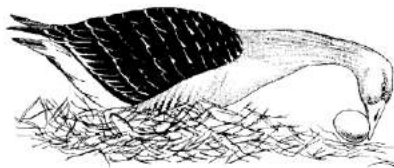
Behavioural physiology is the study of how the body works, that is how the nerves, muscles and sense organs are coordinated to produce complex behaviour such as singing in a cricket or a bird.

The whole animal approach investigates the behaviour of the intact animal and the factors that affect it, for instance what it is in the environment of the cricket or bird that prompts them to sing at particular time or why they sing at all. Whole animal questions of this latter type can be studied both by looking at wild animals in their natural environments and also by observing captive or domestic animals living under more controlled conditions: it depends on the exact question involved.

Physiological investigations often require bringing animals into a laboratory environment because they will involve probing beneath the skin, for example to get at the mechanisms that give rise to the behaviour of singing, etc. In practice there is considerable overlap between the approaches.

Innate Behaviour:

Most animals must perform a large number of quite varied behaviours that they have no opportunity to learn. This may be because they never meet their parents, or any members of the parental generation, to learn from, or because their survival depends upon them being able to perform the behavior very soon after



Egg retrieval by greylag goose. The gull in Figure 3.12 (p. 66) is carrying out a similar task in an experiment. (After Lorenz and Tinbergen)

they hatch or are born, allowing no time for learning. Such behaviours are termed **innate**.

The concept of instinct or instinctive behaviour is still a familiar one. Yawn is a behaviour of fixed action patterns (FAP). An FAP is an instinctive behavior. It is performed perfectly first time, without practice and without any tuition. A yawn lasts for about 6 seconds and involves a fully open mouth and in many cases the closing of the eyes. Once started it is difficult to stop. So FAPs can be described as always running to completion. Therefore (FAP), yawns, have one other important characteristic – something triggers their performance. This trigger or stimulus is usually referred to as a releasing mechanism or a releaser. A yawn is a releaser for another yawn. In fact it is often the case that hearing a yawn or just seeing a photograph of a yawn is enough to release the behavior.

Instinct is often described as patterns of inherited, *preset behavioural* responses which develop along with the developing nervous system and can evolve gradually over the generations, just like morphology, to match an animal's behaviour to its environment. It might be defined in a negative kind of way, as that behaviour which does not require learning or practice. However, they can learn how to behave appropriately and perhaps practice or even copy from others to produce the best response.

Preset behaviour which requires no learning or practice is obviously going to be advantageous for animals with *short life spans and no parental care*. Many insects lead almost totally solitary lives with no overlap between the generations and precious little social contact of any kind.

Example 1: Mason wasps (genera: *Manobia*) construct a series of cells inside the hollow stems of plants. A female wasp emerges from her cell and has a brief moment of interaction with another wasp when she mates with a male. Thereafter, she is totally on her own. She selects a hollow stem and builds a partition of mud mixed with her saliva at the inner end. She then lays an egg attached to the roof of the stem, close to this partition. Next she hunts for caterpillars which she lightly paralyzes with her sting and after repeated excursions, provisions the cell with 5-8 of them; these are the future food supply for the larva when it hatches. This done, she builds another partition sealing off the egg with its food supply and, laying a second egg beyond this,

provisions a second cell, seals that off and so on. In this way 8-10 cells may be constructed in line along the cavity of the stem until the female reaching the outside end, plug this with mud. She then moves off to seek another stem and constructs more cells.

The female wasp lives only a few weeks and carries out this elaborate series of behaviour patterns in total isolation. She could not possibly achieve this tight schedule if she had to acquire everything from scratch by trial and error and she has to rely on pre-set, unlearnt responses. This conclusion is given further emphasis by the fascinating observations made by *Cooper* (1957) on this wasp species. Examining a stem, in which the larvae have pupated prior to their emergence as adults, reveals that all the pupae are oriented with their heads facing the open end. Making the correct choice of end is a matter of life or death, for although sometimes the emerging adults could turn round in the narrow stem, they don't do so but move on ahead breaking through the partitions. Normally the outermost pupae (although they derive from the later eggs of the series of cells) emerge first, leaving a clear passage, as it was, for their siblings from deeper in the stem. Adults emerging from artificially reversed pupae struggle on inwards through the deeper cells and accumulate at the blind end.

How can a larva, about to pupate, make the correct decision? *Cooper's* experiments showed clearly that there was no possibility that they detected, or used gravity or oxygen concentration as a cue. They rely on information left behind by their mothers. As the female wasp retreats outwards building the partitions between the cells, the inner side of each is, of necessity, left as rough mud whilst the outer sides she smooths into a concave form. *Cooper* experimented with artificial grass stems in which he used glass paper to make partitions, rough on one side and smooth on the other, and he could show unequivocally that it is just these characteristics of concavity and smoothness versus roughness which the larva uses: it pushes with its head towards the latter. Information is thus passed from one generation of wasps to its offspring and it must be encoded genetically in a way that allows the larvae and the adult female to develop appropriate behaviour. Again we must recognize that neither the mother wasp's actions nor the response of the larvae can rely on experience.

Example 2: Young herring gulls (*Larus argentatus*) hatch from their eggs able to do little more than sit up. They are completely dependent upon their parents for food and protection for some weeks. Adult gulls feed their young by regurgitating food directly into their beaks and the regurgitation reflex is initiated in response to a releaser provided by the chick when it pecks at the tip of the adult bird's beak. But what stimulates the pecking reflex in the chick in the first place? Niko Tinbergen found that young gulls do not need to see the whole parent to begin pecking, in fact a model of the head and beak of the bird is a perfectly adequate stimulus. Taking advantage of this fact he went on to carry out a number of experimental studies that enabled him to shed further light on some of the general properties of releasing mechanisms. An adult herring gull's beak is bright yellow with a red spot close to its tip. Tinbergen manipulated this very distinctive pattern in his models and found that the presence of the spot was very important. The chicks were far more likely to peck at beaks with spots than those without. They were also more likely to peck at spots that contrasted strongly with the beak color, and interestingly at red beaks rather than yellow ones.

Learning:

Some aspects of the behavior of an animal are performed in a rigidly predictable way such that each time a particular stimulus is presented, a predictable response will be recorded. But all behaviors cannot be characterized in this way. In many situations flexibility of response is a definite advantage, and so it should come as no surprise that many behaviors may be permanently modified as a result of experience. This modification can be attributed to learning.

Habituation: It is an extremely simple form of learning, in which an animal, after a period of exposure to a stimulus, stops responding. The most interesting thing about habituation is that it can occur at different levels in the nervous system. Sensory systems may stop, after a while, sending signals to the brain in response to a continuously present or often-repeated stimulus. Lack of continued response to strong odors is a common example of sensory habituation.

Habituation is important in filtering the large amounts of information received from the surrounding environment. By habituating to less important signals, an animal can focus its attention on the most important features of its environment.

A good example of this is species that rely on alarm calls to convey information about predators. In this case animals stop giving alarm calls when they become familiar with other species in their environment that turn out not to be predators.

Birds learn not to waste energy by taking flight at the sight of every leaf blowing in the wind. Squirrels learn not to respond to the alarm calls of other animals if these calls are not followed by an actual attack. This may also help us understand why animals avoid predators, while ignoring common, harmless species.

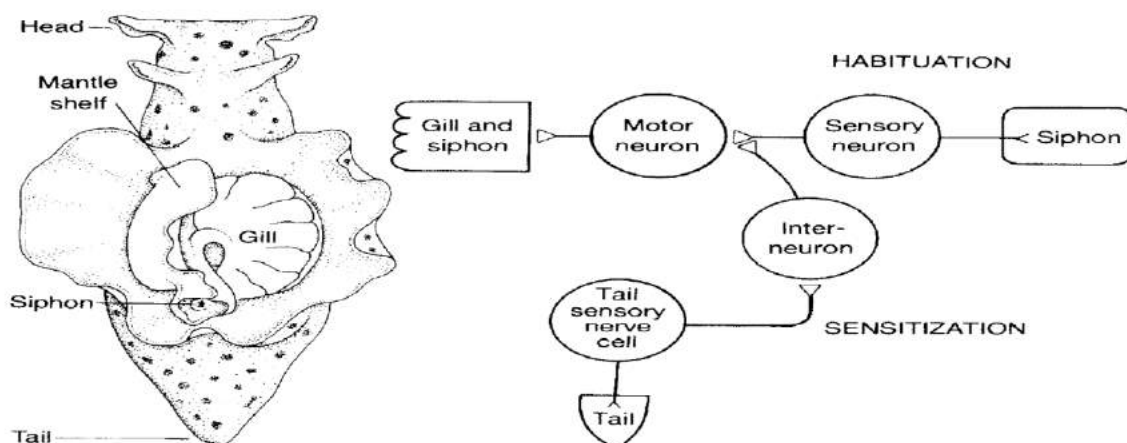
Example: The process by which a stimulus detected by the sensory hairs on the abdomen of a crayfish can result in the animal performing a powerful tail-flip that projects it through the water at speed. The purpose of this behavior is to enable the animal to escape from the source of the stimulation that could in many cases be a predator.

If a crayfish is tapped on the abdomen repeatedly (about one tap per minute) the probability that a tail-flip will occur diminishes quickly. In fact after just 10 taps the response can diminish to zero – habituation has taken place and recovery from it can take several hours. The lateral giant interneuron (LGI) involves in regulating the tail-flip.

Habituation and sensitization are two of the main kinds of non-associative learning. For example, the sea hare *Aplysia* breathes through its gills, which are situated in a region called the mantle cavity; the gill's enclosure opens to the outside through an opening called the siphon. If an experimenter prods the siphon, the *Aplysia* withdraws siphon and gills and folds them up within the mantle cavity. This is called the siphon (or gill) withdrawal reflex, and is simply a protective reaction. After a while, if undisturbed, the *Aplysia* puts its siphon out again, and if it is then prodded a second time, it will show the same withdrawal reflex. However, it will not do so an indefinite number of times. If it is repeatedly prodded, it comes to ignore the stimulus, and leaves its siphon and gills out. This is the kind of

behavioural change called **habituation**: the *Aplysia* has learned not to respond to an apparently harmless stimulus.

Sensitization is the opposite kind of change. Habituation means to become less sensitive to a stimulus, sensitization more so. If an *Aplysia* receives an alarming stimulus such as an electric shock on the tail, it then responds more readily to other stimuli that it would otherwise have been less responsive to. It has become more sensitive. The sensitization of siphon withdrawal by a tail shock depends on a number of factors. One is whether siphon withdrawal is already habituated (i.e., the animal does not withdraw its siphon when prodded); if it is, the tail shock immediately "dishabituates" the reflex so that the siphon will now be withdrawn if prodded. The dishabituation of the siphon withdrawal reflex appears within 90 seconds of the tail shock.



If siphon withdrawal is not already habituated, a tail shock has little or no effect on siphon withdrawal after 90 seconds. The habituation and sensitization of the siphon withdrawal response in *Aplysia* are understood neurophysiologically. The nervous control of the gill withdrawal reflex is a simple unit of one sensory neuron and one motor neuron. The siphon contains the sensitive end of the sensory neuron which, at its other end, is directly connected at a synapse with a motor neuron that controls the muscles of the mantle cavity. When the sensory neuron is stimulated, it fires the motor neuron, and the siphon and gills are withdrawn.

How does the system habituate? There are two possible mechanisms for regulation in so simple a system: either a change in the amount of neurotransmitter released by the sensory neuron, or a change in the sensitivity of the motor neuron to constant doses of neurotransmitter. In the

case of *Aplysia* the former possibility is the real one. It is as if repeated activity in the sensory neuron exhausts its supply of neurotransmitter, making the system as a whole less responsive.

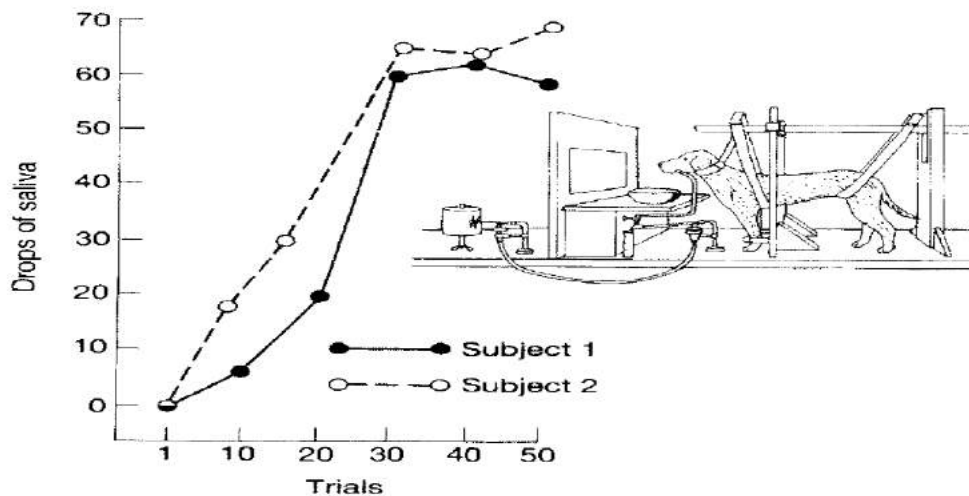
Two more kinds of neurons are needed for sensitization. The dangerous stimulus is sensed by another sensory neuron, which is connected by a synapse to one or more interneurons, which eventually connect with the synapse of the motor neuron that controls the mantle muscles. When the sensory neuron (for instance, in the tail) becomes active, it fires the interneuron, which in turn causes a series of chemical changes in the motor neuron and the effect of those chemical changes sensitize the system.

Conditioning:

There are two main kinds of conditioning, called classical conditioning and operant conditioning. Classical conditioning was first studied in dogs by the Russian physiologist Ivan Pavlov (1849-1936). Pavlov's interest was in digestion. In 1904 he won the Nobel Prize for his work on the physiology of digestion, after which he turned to study the conditioning of digestion. In a typical experiment Pavlov would sound a bell when bringing a dog its food. As the dog learned the association between the sound of the bell and being fed, it salivated on hearing the bell in expectation of its meal. Soon Pavlov could make his dog salivate just by sounding the bell, even without bringing its food. He claimed the salivation of the dog had been conditioned. Classical Pavlovian conditioning is advantageous to the animal, because it can respond more rapidly or appropriately to important environmental stimuli, such as those associated with food or other members of its species.

Operant conditioning: It is goal-directed behaviour. We learn to perform a particular response as a result of what we know will happen after we respond. For example, a child may learn to beg for sweets if the begging is usually successful. There is no single stimulus that elicits the begging behavior, but instead it occurs because the child knows that this action may result in receiving treats. Every time the child receives sweets after begging, the behavior is reinforced and the tendency of the child to beg will increase.

During the 1930s, American psychologist and behaviourist *Burrhus F. Skinner* performed several important experiments into operant conditioning. Using what is now termed a *Skinner Box*, he trained rats to press levers to receive food. A hungry rat would be placed in a box containing a special lever attached to concealed food. At first the hungry rat would wander around the



box, investigating its surroundings. Eventually it would accidentally press the lever thereby releasing a food pellet into the box. At first the rat would not show any signs of associating the two events, but over time its exploring behaviour becomes less random as it begins to press the lever more often. The food pellet reinforced the rat's response of pressing the lever, so eventually the rat would spend most of its time just sitting and pressing the lever. This type of learning is based on the idea that if a behavior is rewarded, the behavior will occur more frequently. There are four main types of operant learning:

Positive Reinforcement: The more often the subject performs the action, the more the stimulus is reinforced (for example, pressing a lever for food)

Negative Reinforcement: Performing an action removes an undesirable stimulus, i.e. wrong performance will provide negative reinforcement.

Punishment: Performing an action elicits an undesirable stimulus (for example, receiving a shock by pressing a lever)

Omission Training: Performing an action prevents the delivery of a pleasant stimulus.

Multiple-Response Learning: When we learn skills, we must first learn a sequence of simple movement-patterns. We combine these movement-patterns to form new, more complicated behavioral patterns with stimuli guiding the process. For example, efficient typing requires us to put together many finger movements, which are guided by the letters or words that we want to type. We must first learn to type each letter, and then learn to put the movements together to type words and then phrases.

To investigate this type of learning, psychologists have observed animals learning to run through mazes. An animal first wanders aimlessly through the maze, periodically coming to a choice-point, where it must turn either left or right. Only one choice is correct, but the correct direction cannot be determined until the animal has reached the end of the maze. By running through the maze numerous times, the animal can learn the correct sequence of turns to reach the end. It has been found that the sequences of turns near the two ends of the maze are learned more easily than the parts near the middle. Similarly, when we try to learn a list of items, we usually find the beginning and the end easier than the middle.

An extension of multiple-response learning is latent learning, where learning occurs in the absence of an immediate reward. If rats are allowed to repeatedly run a maze without a reward at the end, they will learn the maze quite slowly. However if they have first been allowed to run the maze without reward, and then food is placed at the end, these rats will learn the maze very quickly. This shows that learning had been occurring the entire time, but did not become evident until it was activated by a reward.

Insight learning and Reasoning:

Insight learning is widely regarded as the most advanced form of learning. Responses produced by insight are those resulting from a rapid appreciation of relationships in which animals solve problems too quickly to have gone through a trial-and-error process. The animal seems to arrive at a solution by reasoning (defined as 'the ability to combine spontaneously two or more separate or isolated experiences to form a new experience, which is effective for obtaining a desired end).

A common experimental procedure used to test for reasoning involves an animal's ability to make detours in a maze. Shepard found that once rats had learned a maze, they quickly capitalised on newly created short-cuts (created by removing partitions, so that what was previously a blind alley became a quicker route to the goal box). Tool use, e.g. chimpanzees reaching bananas high up in their cage by piling boxes on top of each other or joining lengths of stick together, provides another possible instance of reasoning.

Cognition (conscious mental process):

Solving a problem involves using prior experience, observation, and insight to find the solution. You should be able to add any two, randomly chosen, numbers together to obtain the correct sum, even if you have never encountered that particular pair of numbers before. We tend to judge "intelligence" in animals by the animals' ability to solve problems at which humans are proficient. Many animals have superior navigational abilities to humans', and can solve complex navigational problems that would confuse a human through a combination of better sensory abilities and more sophisticated use of simple navigational tools like path integration.

In recent decades it has become apparent that the cognitive skills of many animals are greater than previously suspected. Part of the problem in research on cognition in animals has been the intrinsic difficulty in communicating with or testing animals, a difficulty that makes the outcome of a cognitive experiment heavily dependent on the cleverness of the experimental approach.

Another problem is that when investigating the non-human primates, the animals whose cognitive skills are closest to that of humans, one cannot do experiments on large populations because such populations either do not exist or are prohibitively expensive to maintain. The result is that in the area of primate cognitive research reported experiments are often "anecdotal", i.e., experiments involving only a few or even a single animal subject.

But anecdotal evidence can often be of great significance and have startling implications. In 1985, Matsuzawa reported experiments with a female chimpanzee that had learned to use Arabic numerals to represent numbers of items. This animal whose name was "Ai" can count from 0 to 9 items, which she demonstrates by touching the appropriate number on a touch-sensitive monitor. Ai can also order the numbers from 0 to 9 in sequence.

The authors report that the chimpanzee Ai can remember the correct sequence of any 5 numbers selected from the range 0 to 9. Ai's performance shows that chimpanzees can remember the sequence of at least 5 numbers, the same as (or even more than) preschool children.

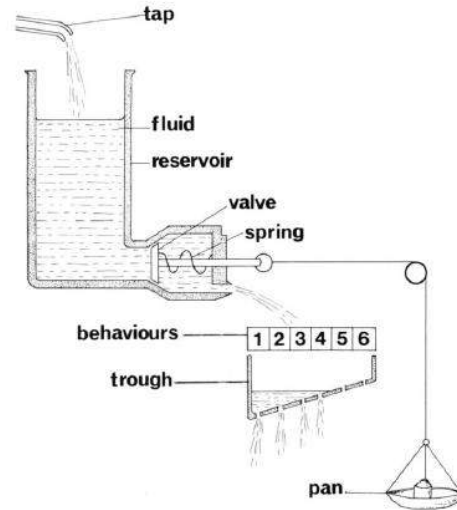
Motivation:

It is a matter of common observation that an animal does not respond to a stimulus in the same way every time that stimulus is encountered. We only have to think of the lion moving through the bush and coming upon a herd of wildebeest. On some occasions such an encounter results in the lion stalking and perhaps killing one of the wildebeest. On others, the lion walks casually past apparently ignoring the presence of potential food.

A male chaffinch, during winter, vigorously defends his territory against conspecific intruders of either sex. In spring, however, he selectively admits and courts females while continuing to drive off other males. Something about the lion and the chaffinch in these two examples has changed between one encounter with food or a female and another. But what has changed? Since there is no difference in the stimulus itself, we are left with the possibility of some internal change in the animal. That internal change we can conveniently label **motivation**.

An another example, one can remove the endocrine organ responsible for testosterone production, the testes, and inject known quantities of testosterone to study how plasma testosterone precisely governs the response of males to agonistic situations (presence of rival males) or sexual stimuli (presence of receptive females). Testosterone is present over a long time course, and can be considered a general factor governing arousal in animal. The presence of a male or a female can be clearly identified as the external stimuli that might elicit a behavior, given that sufficient testosterone is present to allow for the underlying motivational state to be reached.

Figure 2.1a: Lorenz's Hydraulic Model of Motivation.



Testosterone is used by both of the sexes to generate a heightened state of sexual arousal, but in females an additional hormone is required for receptivity, estrogen. Thus, hormones may require synergistic interactions to generate the motivational states.

Hormones do not necessarily have to be present for long periods to alter an animal's motivational state. For example, the "flight-or-fight" neurohormone, adrenalin, effectuates changes in motivational state of animals within seconds.

Conflict and sexual behaviour

Of course, it is conceivable that two or more motivational systems will become equally aroused. Example, a female has just returned to a large clutch when a predator appears on the horizon and is torn between incubation and escape. What should she do? In practice what she might do is neither; instead she preens! It is one example of what ethologists dubbed conflict behaviour.

Sexual Behavior

The question 'what is the difference between the sexes?' is not as easy to answer as it seems. Certainly we have little difficulty identifying males and females among most animals. Males may possess various secondary sexual characteristics like facial hair, manes and deep voices. Clearly, external morphology is an unreliable guide. What, then, is the basic distinction between males and females? The answer is their gametes.

In general, the role of hormones in the control of sexual behavior is well known. Beach (1976) has emphasized that female behavioral patterns are much more complex and the full range of female behavioral patterns ought to be considered. Beach divides female behavior into three phases: (1) attractivity, the female's stimulus value in evoking sexual responses from the male; (2) proceptivity, reactions by the female that constitute her initiative in establishing and maintaining the sexual interaction (e.g., soliciting); and (3) receptivity, the female's postural responses that are necessary and sufficient for the achievement of copulation by the male.

In a study of female rhesus monkeys, Johnson and Phoenix (1976) found different effects of hormones on the different behavioral patterns. Female attractiveness was enhanced by estrogen, female proceptivity was heightened by both estrogen and androgen; and female receptivity was stimulated by estrogen but not androgen.

Hormones play a role in the control of sexual behavior. Pituitary hormones, ACTH, and related peptides have been reported to affect male copulatory behavior (Bertolini, Gessa, & Ferrari, 1975). Even the hypothalamic releasing factors, such as LH-RF, appear to have direct effects on copulatory behavior (Moss & McCann, 1973).

In zebra finches, like in other vertebrates, male sexual behavior is dependent on androgens. Castration of adult males, or pharmaceutical blocking of testosterone production, leads to the loss of song, but the song can be restored with testosterone replacement treatment.

Testosterone mediates the transition from plastic to fully crystallized song and is implicated in maintaining adult song stereotype. Experimental manipulation of adult males' testosterone titers decreases the fundamental frequency of males' song and the latency to first song upon introduction of a female. Song rate and androgen titers are positively correlated.

Migration and homing with special reference to birds

Migration is the movement of animals in large numbers from place to place. Migration is distinct from dispersal in that migratory animals typically move from one geographic region to another without using the intervening habitat. Navigation is a key to orientation and migration. Migrations are associated with specific seasons, and tied to reproduction and endocrine system. A key issue underlying migration is how animals navigate the huge distances or orient to natal areas. Migration is classically associated with birds; however, many other groups undertake long migratory movements.

Many different types of animals migrate, and depending on the animal, the trip may last as long as an entire lifetime or as short as a few months. Some animals follow a specific route during the course of a migration, while others may follow a path less direct. Many stops may be made along the way depending on the breeding or feeding preferences of the migratory animals. Whether daily, seasonal, annual, or only twice, migration remains a spectacular and mysterious event. Mainly the animals migrate to find food, to escape seasonal changes, and to breed.

Examples: Whales swim from the Arctic to give birth in warm Mexican waters. Bats migrate each spring to specific caves. Wildebeests constantly migrate to find food. Monarch butterflies take several generations to complete a seasonal migration. In many cases, the primary reason for a seasonal migration is to find suitable grounds for reproduction.

Dolphins have been known to migrate, although their migration routes are usually not as well defined as whales. While many dolphins stay in the same area throughout their lives, some populations have been known to move over great distances. Orcas, the largest member of the dolphin family, can be seen demonstrating this behavior. These marine mammals form transient groups, which travel long distances, and resident groups, which remain local and follow predictable migratory paths. Other dolphins that have been seen migrating include the bottlenose, common, pacific white-sided and risso's dolphins. Like whales, dolphins migrate in search of food and better environmental conditions.

The Pacific salmon lay their eggs and then die in the headwaters of the streams of Oregon, Washington, western Canada and Alaska. The eggs hatch and the young fish live there two years before they go downstream and out to sea. There they gorge themselves and grow rapidly for two more years. Then each fish returns to the mouth of the river from which it came and fights its way back upstream, jumping up over water falls and dams, until it reaches the same tributary where it was hatched. There they mate, lay their eggs, and die.

Many birds migrate every year from their winter feeding grounds to their spring and summer breeding grounds. Studies show that birds begin to orient in the direction of their migration path some weeks before the start of migration. Migratory birds follow certain general directions, most often north-south movements, from winter habitats to nesting areas and return travel to their post-nesting quarters. These “routes” are not necessarily an exact course made by individual birds or a path followed by a species with specific geographic or ecological boundaries. The bar-tailed godwit (*Limosa lapponica*) is an example of a migratory species that crosses several flyways during its annual cycle.

Types of migration:

Seasonal wandering:

There are many examples of birds that show from banding returns a remarkable degree of seasonal wandering without much evidence that the movements follow a consistent directional migration pattern. The returns from Redhead Ducks banded at Bear River Refuge in northern Utah indicate a widespread dispersal in almost every direction where suitable habitat occurs. While such movements are seasonal in nature, there appears to be no correlation with either a directed species movement or a consistently better habitat at different seasons of the year.

Food migrations:

The peculiar wanderings of the Red Crossbills have been coordinated with food supplies. Being highly specialized for conifer-seed extraction they seem to be largely dependent upon the conifer seed-crops for sustenance. The inconsistency of seed production makes sedentary living in a given spot almost impossible. Apparently then, they have developed a wandering or

migratory habit not correlated with seasons but rather, with the occurrence of seed-crops in various localities, which enables them to adjust their movements to the vagaries of seed production. Thus, their movements do not show regular migration rhythms, but do seem to indicate a definite pattern of movements that take them to the areas where and at the time when seeds are available. They are probably in the nature of food migrations correlated with very irregular cycles of food production which of course, are mainly seasonal.

Altitudinal migration:

Altitudinal migration occurs in many mountainous regions. It is a well-known phenomenon in the mountains of the western United States and occurs in the Himalayas in Asia. The significant thing about altitudinal migration in temperate regions is that it gets temperature effects similar to latitudinal migration in much shorter distance without noticeable change in day length. Chickadees kinglets, rosy finches and juncos are believed to illustrate this type of migration in the Wasatch Mountains of Utah and the Black Redstart and White Redstart in the Himalayas of Asia. In mountainous regions of the tropics where day length as well as temperature are relatively more uniform, there would theoretically be less expectation of altitudinal migration than in temperate-zone mountains.

Vertical migrations:

Seasonal effects seem much less pronounced upon aquatic animals, but nevertheless, seasonal rhythms do exist. Certain vertical migrations seem to be correlated with changes in surface temperatures of water. In temperate regions, some animals such as fishes, lobsters, crabs, prawns and squids living along the shores when surface waters are warmer than underlying waters, descend in to deeper waters when surface waters become cooler than those underneath.

Anadromous migrations:

Perhaps the most outstanding ocean migrations for purposes of this work are the long-distance migrations of fishes that take them from ocean to freshwater and vice versa across great osmotic barriers. Many freshwater fishes migrate up small streams to spawn.

In the case of anadromous fishes such as salmon, the young fishes hatched in the small freshwater creeks or tributaries at the heads of large rivers make their way slowly downstream more or less independently of the current despite the fact that they are going with it. Eventually, they reach the mouth of the river and enter the ocean without any apparent difficulty with the problem of osmosis. After development in the ocean over a period varying from one to several years, the sexually mature adult individuals make their way back to the mouths of the rivers (may be the same rivers), across the osmotic gradient and make their way up the stream against the force of the current to the headwaters of the stream where spawning takes place.

Catadromous migrations:

In the case of catadromous fishes, such as the Atlantic eels, the process is reversed. The newly hatched conger eels in the deep waters of the Atlantic Ocean between Bermuda and the West Indies make their way slowly over a period of three years toward the North American and European coasts where they also cross the osmotic gradient into freshwater streams. Ascending the rivers, the eels spend from five to twenty years in development before they undertake a return migration. After reaching the ocean, the adults must make a long journey before reaching the spawning deeps between Bermuda and the West Indies.

Longitudinal migration:

East-west migrations are, of course known to occur in animals. It has recently been established from the in Great Salt Lake that young California Gulls reared in rookeries on islands in the lake migrate westward to the Pacific coast in late summer and fall.

Latitudinal migrations:

Most important of all are the seasonal migrations that are primarily latitudinal movement. The seasonal response has had a much larger outlet on land via latitudinal movement than by altitudinal, and longitudinal responses. A number of southern-hemisphere nesting birds that move northward for their winter with the numbers of northern-hemispheres nesters that move southward.

Arctic breeding ground migration:

An area occupied by birds in summer for nesting in the polar regions north of the arctic circle would have almost continuous daylight during the early part of the summer, after which the day length would gradually decrease to twelve hours by late September and finally to continuous darkness by late December. This would be accompanied by a generally equable climate in summer, in which the fluctuations between day and night temperatures would be much less than that expected in temperate climates. The long daylight periods of summer would give the green food-making plants opportunity for long hours of work, resulting in rapid growth of food, part of which would be quickly transformed into insect, rodent or other animal life. Thus the arctic nesting ground furnishes to the bird nesters an equable climate for rearing the young, long hours of daylight in which to tend the young and a rapidly multiplying food supply at the time when the young are growing vigorously and increasing tremendously the demand on the food supply. After September, conditions rapidly change – the days grow shorter, the nights get colder, the food supply diminishes, cold-blooded animals hibernate or perish, and much of the area becomes covered with snow. The ideal conditions of summer are almost completely reversed thereafter.

The Hormonal trigger for the initiation of migration

Migratory behaviour is triggered by seasonal photoperiodic cues. Cues are integrated by centers in the brain, which induces secretion of hormones that triggers migratory movements. In amphibians this movement is called the *water drive*. In experiments very similar to the lobster studies, demonstrated that newts (tailed amphibian) also use a magnetic field to move to and from their breeding ponds.

A phylogenetic analysis of the evolution of endocrine regulation in amphibians enriches our understanding of trade-offs and the origins of behavioral traits like migration and maternal care in other vertebrates. In all vertebrates, migration is controlled by prolactin. In addition, if parental care is present, this is likewise controlled by prolactin. Thus, migration and parental care are often coupled in a given life history, largely because of the regulatory effect of prolactin on both behaviors.

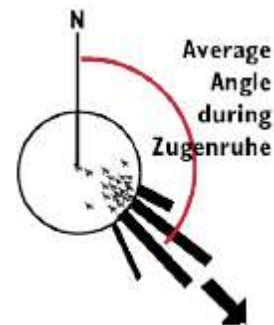
Many physiological functions of vertebrates are controlled by the Hypothalamic-Pituitary (HP) gland, which involves a series of endocrine

cascades such as those governing reproduction. The HPGonadal-Adrenal axes interact to achieve organismal homeostasis during reproduction. Migration and parental care are also controlled by a system involving prolactin.

In terrestrial adults, the HP-prolactin-growth hormone regulates a behavior called water drive, which induces adults to migrate back to water and to reproduce. Prolactin modulates migratory behaviors in all vertebrates. Prolactin releasing hormone (PrRH) triggers the release of prolactin (Prl), which travels to targets throughout the body and triggers migration. The same life history trade-offs on migration apply to migratory birds, and mammals. It should be noted that in birds and mammals prolactin is the trigger for parental care as well as migratory behavior.

Avian migration and navigation: *Zugruhe* response

How do we assess the cues that bird use for orientation? Birds indicate the direction that they wish to fly by a well-known phenomenon called the *zugruhe* or nighttime restlessness. ***Zugruhe*** refers to the sharp jump in nighttime activity that occurs at the onset of the migratory response. Birds migrate at night, but are not normally active at night during other times of the year. Another aspect of *zugruhe* is that birds orient strongly in the direction in which they are to migrate. A clever apparatus consisting of a cone shaped cage with a mesh top, and an inkwell at the bottom has been developed to record the directionality of the *zugruhe*.



The birds hop up and down trying to take flight, and end up leaving a complete record of each hop, as well as the direction of the hopping relative to magnetic north. In the example of black cap migration, the researchers used the *zugruhe* response and the Emlen funnel to determine genetically predetermined migration directions of fledged young.

Homing

Orientation is the use of external cues to move in the environment. Orientation can come about by fixing a position and then using cues to determine the appropriate direction to move in. *Navigation* involves a little more sophistication in that a map sense (a sense of where you are) in addition to a compass sense (a sense of the appropriate direction in which to move) is a requirement for a complete navigational system. Many studies have demonstrated orientation, but few have demonstrated that animals have a map sense.

True navigation

An animal can be considered to have true navigation if, after displacement to a location where they have never been, they can determine their position without relying on familiar surroundings, cues that come from the destination, or information collected during the outward journey.

Navigation is simply put the movement of animals in their environments. The fact that animals move in different spatial scales, from the very local to the global, adds complexity to the topic. Animals "home" when they return to a central place, such as their nest or their territory.

Homing is a frequent activity, occurring after foraging bouts or other relatively local movements. This distinguishes homing from migration, which is a long distance movement between two distinct habitats. The key element to understand homing behaviour is determining which cues provide the directional information that allows animals to move between their home and other locations. Also, animals may use environmental information hierarchically, so that one type of homing information is important when they are distant from their home, and others become more important as they come closer to their goal.

The major navigational clues used by homing animals seem to be the same as those used in migration (sun angle, star patterns, etc.), but homing may occur in any compass direction and at any season. The best-known examples of strong homing ability are among birds. Simple visual clues may also be used for short distances or over familiar territory.

Homing behavior in pigeons, *Columba livia* is interesting because pigeons find their way home from unfamiliar sites up to thousands of kilometers from their nests. Pigeon races may feature releases of birds from France, for example, which then find their way home to sites in England or the Netherlands. The extraordinary reliability of homing pigeons makes them excellent subjects for studies of navigation.

The map sense: In familiar surroundings locations from which pigeons have previously homed or landscapes through which they have flown landmarks play a predominant role in homing. Pigeons learn visual features of the landscape and use these visual features to determine their current position (map location) relative to their roost.

While pigeons clearly use visual landmarks, because pigeons orient better in familiar landscapes when other sensory inputs, such as olfaction, are eliminated, direct tests of landmark usage are difficult. Experiments manipulating visual landmarks are generally not feasible. One can hardly bulldoze mountains or cut forests as part of an experimental design, and interference with the eyes, such as using contact lenses, may be so much of a general disruption to the pigeon that it confounds tests of landmark perception in orientation.

How do pigeons produce a map sense when they are released in a completely unfamiliar location? The answer is that they use olfactory cues. In their roost, they associate odors with wind directions. When released, they assess the odor of their new location and extrapolate the map location from their roost-gained knowledge of winds and odours. Pigeons in visually unfamiliar territory whose sense of smell has been disrupted (by cutting olfactory nerves or treatment of the nasal passages with zinc sulfate solution) have a great deal of difficulty homing. Similarly, if the roost is blocked from winds and provided with filtered air, homing fails. Pigeons may home better if they have some time to olfactory experience their new surroundings prior to release.

The compass sense: The primary compass information of pigeons comes from the position of the sun in the sky. By integrating their internal clock with the sun's position, they compensate for the apparent movement of the sun across the sky. Pigeons whose time sense is shifted by keeping

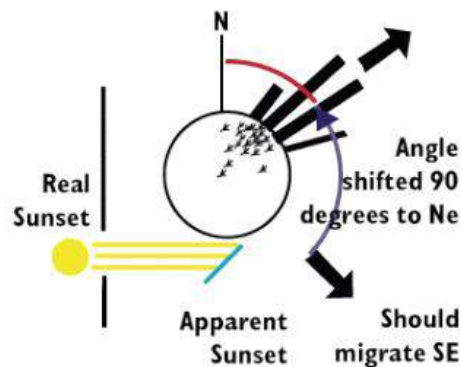
then under artificial lights display incorrect orientations when released. For example, if "sunrise" comes for the pigeons 6 hours prior to actual sunrise, then their orientation shifted counterclockwise. If their "sunrise" is later than the actually sunrise, then their orientation shifts clockwise.

Consider the European starling that has a normal migration route that is in a SE direction. It is easy to shift the direction of zugenruhe by using mirrors to alter the true direction of the sun at sunset by 90° clockwise or counterclockwise. Starlings in aviaries that see such a frame-shifted sun end up leaving tracks that are 90° frame shifted in the right direction.

Pigeons homing: Pigeons use several different cues to find their way back to their home lofts after being released many miles away. There are three important cues viz. **geomagnetism**; i.e. the earth magnetic field varies place to place, **sun compass**; i.e. the height of sun varies with north-south latitude and **star compass**; i.e. the height of stars varies with north-south latitude. Pigeons also appear to have an internal topographic map of territory they fly over frequently, and may use that information to navigate closer to home. In some cases (and places) they may also use olfactory cues provided by scents in the wind - though this seems to be used only in areas when the winds are fairly constant.

Note: Theoretical, behavioral and physiological evidence supports two magnetic sensing hypotheses: a magnetite-mediated magnetic sense and/or a vision-mediated magnetic compass. The magnetite-mediated mechanism seems to act as part of a magnetic map-sense, which could provide the animal with information about its geographic position, whereas the vision-mediated magnetic sense seems to be a pure compass sense. Together the systems can confer true navigation.

The light-dependent magnetic compass hypothesis suggests that magnetic modulations in photoreceptor molecules in the birds' eyes provide orientation by sensing magnetic field lines. Putative sensor molecules



(cryptochromes), which possess the required biophysical properties, are expressed in the retina of migratory birds. In garden warblers, *Sylvia borin*, the retinal ganglion cells, which express cryptochrome, along with a neuronal cluster called "Cluster N", which is located in posterolateral regions of both forebrain hemispheres, show high neuronal activity during zugenruhe. The expression of the gene ZENK turns on and off during night versus day to confer magnetic orientation.

Communication in animals: Visual, olfactory, auditory and tactile.

Communication is something that all animals, including humans do. Communication is said to occur when one animal responds to the signals sent out by another animal. Communication is an adaptation that helps animals to survive. An important aspect in sociobiology is to understand what information animals perceive, process and transfer, and how they coordinate their behaviour with other group members.

Animals use communication to *define and maintain territories.* Food and water sources must be shared; assembly sites announced. Hierarchies within a group may need to be established, and activities synchronized. Warnings are vital to alert others of danger. Migration timetables and routes must be coordinated. Mates must be found and courted; bonds established; rivals discouraged. Signals of surrender or submission may control aggression. Parents and offspring need to recognize each other. Juveniles express hunger, pain, or frustration as they seek attention from adults, who pass on essential skills. Animals communicate many messages in an amazing number of ways: *visual, auditory, tactile, olfactory,* and even vibrations.

There are two types of communication: **verbal and non-verbal.** A wolf's howl may either communicate a warning signal or other message to the group. A migrating whale communicates with others to keep in touch. These are examples of verbal communication - using sounds to give a message to others, whether of the same species or with other animals. Non-verbal communication employs body movements and gestures. Dogs wag their tails when happy, bees "dance" to show their fellow workers where flowers are located and peacocks spread their tail feathers to signal their readiness to mate.

Visual communication: Much visual communication is unintentional, especially that conveyed by the "badges" that aid species recognition and individual identification. Variations in pigmentation or pattern may indicate gender, physical condition, or position within the group. Colorful features and breeding plumage advertise mating availability and genetic potential. A characteristic pattern reminds a would-be predator of venom or a foul taste. Color change can signal an emotional state. Spots or lighter colors may allow

immature animals to act in a manner forbidden to adults. These structural signals are delivered unconsciously. But when displays highlight particular attributes, visual communication becomes behavioral.

Behavioral communications are initiated by the sender in response to certain circumstances or stimuli. Light flashes are employed by some invertebrates and fish. Facial expression and body language, however, are most important for vertebrates. Nestlings' open mouths indicate hunger. Primates' flexible faces can convey a variety of moods. Carnivores' laid-back ears and barred teeth might indicate that fear is holding aggression in check, while a stiffness in the legs and body of any animal can mean attack is imminent. The position of a tail can be a signal to follow or retreat, and the speed with which it wags can show the intensity of an emotion. Within a group, attitudes may indicate social standing.

There seems to be universality about some postures. A threatening animal usually enlarges its body by whatever means possible: back arched, hair bristling, wings spread, throat sac inflated, collar or hood extended. Conversely, to indicate submission, animals attempt to appear smaller by cowering or cringing low to the ground. These stances are understood across species. Many animals adopt childish poses to appear non-threatening, and males may even masquerade as females. An animal feigning injury may well confound a predator, while predatory insects often mimic another species to lure its members to their death. Most visual messages are transitory, but some are longer lasting. Dung piles can indicate the boundaries of a territory. Scratches on a tree show the presence of an animal and also indicate its size by the height at which they were made. Some males present gifts or build elaborate structures to advertise their worthiness. Mating rituals are often elaborate, and courtship displays and dances can be extremely complex. But few routines are as impressive as the honeybees' dances that communicate both the distance and direction to a nectar source, while visual communication is generally effective.

It has limitations and disadvantages. Unless it involves light, it is inefficient in the dark, and its success depends on proximity, a clear line of sight, and the attention of the intended recipient. Visual signals may also attract unwanted attention.

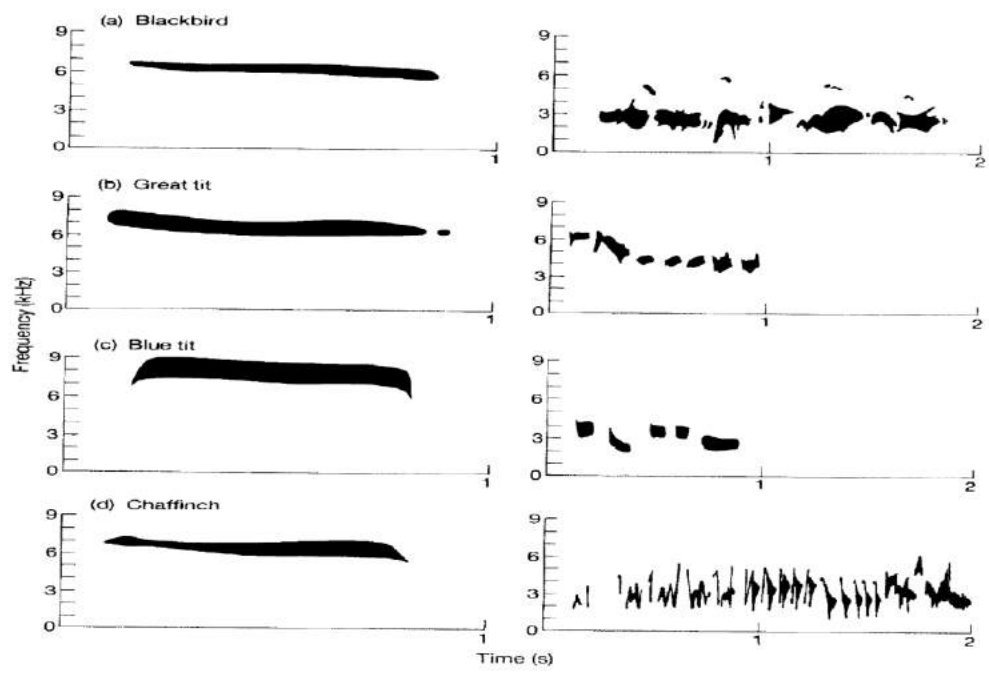
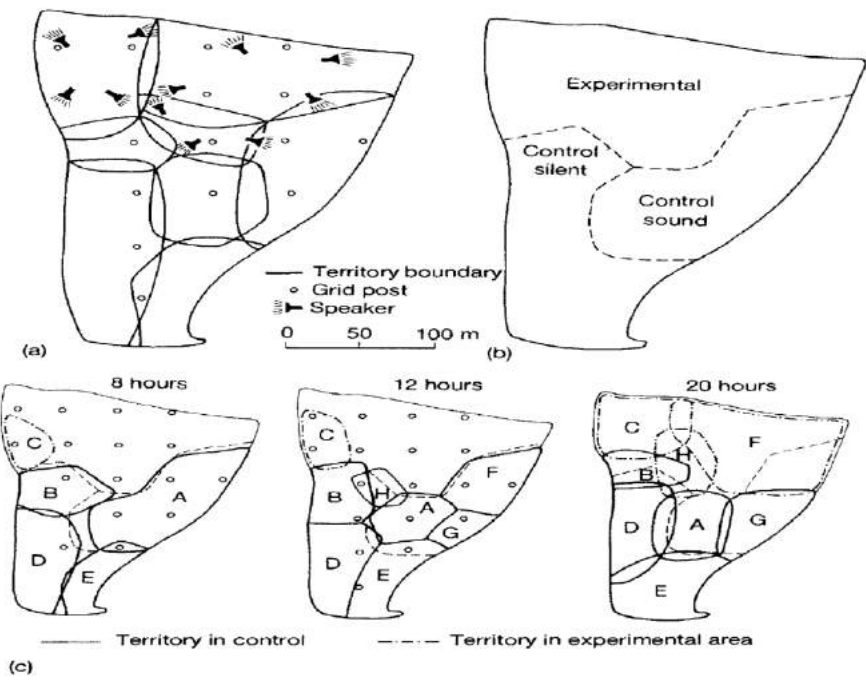
Olfactory communication: Chemical communication is generally acknowledged to be the most widespread mode of communication among insects, but it is more prevalent among all animals than was formerly thought. Characteristic odours identify individuals and species. Unpleasant smells or tastes discourage predators. But the most highly developed form of chemical communication involves **pheromones**: chemicals that bring about a specific response in others of the same species. First discovered in 1959, pheromones are liquids produced by relatively simple glands on or near the body surface, or by more complicated glands deep inside. They may be smelled or tasted, assessed by the Jacobson's organ, or taken in by receptors on the skin or antennae. Some pheromones evaporate very quickly, others have a wax or oil base that lasts longer. Pheromones can be dispersed by air, often to attract a mate. On the ground, they leave trails for others to follow. Added to wastes, pheromones can mark boundaries and convey information about gender, age, ranking, or sexual receptiveness. Pheromones can be extremely complex. Different combinations of chemicals relate to aggregation, dispersal, alarm, trail marking, kinship recognition, and sex. For animals living in cooperative groups, pheromones are believed to synchronize estrus cycles. Research suggests that for some social animals, pheromones produced by a queen or alpha female not only suppress reproduction by other colony members, but also induce subordinates to care for infants not their owns. Pheromones are probably produced at all times, but released only in response to certain stimuli, such as hormones, emotional states, or environmental conditions.

Auditory communication: Sound, on the other hand, offers multiple advantages. Because sound fades quickly, it leaves no trace to give away location. Some animals use frequencies that other species are unable to hear. Sound carries in darkness, over distances, and under water. Auditory communications can be initiated or discontinued instantaneously, allowing for rapid exchanges that can be corrected quickly. Sound can reach many individuals at once, and an animal can advertise ownership of a territory without visiting its borders.

Auditory communication includes non-vocal noises: chest beating, tail slaps, foot thumps, hoof beats, bill clacking, buzzing, stridulation (the shrill, creaking noise produced by rubbing together special bodily structures, most

commonly created by male insects). But non-vocal messages usually lack the potential for elaboration, whereas vocalizations can be varied by pitch, clarity, volume, duration, and rate of repetition, making intricate codes possible. Because water is very efficient for sound transmission, aquatic animals rely on sound as their primary means of communication. The complex songs of whales and dolphins are well documented. Insects, too, have alternative systems to detect vibrations, as do snakes. Although snakes cannot hear, they can be heard, and may hiss or rattle to ward off threats. Except for long-range communication, land mammals rarely use auditory signals in isolation. At close range, sounds usually accompany postures or displays. However, vocal communications alone can convey very specific information. Vervet monkeys, for example, can tell whether a cry of alarm indicates the presence of a snake, leopard, or eagle.

Bird vocalizations are sometimes divided into calls or songs. Calls are simple, almost monosyllabic, and their uses include begging, roosting, alarm, and individual recognition. Even short calls can be quite distinctive. Bird songs are more complicated and may transmit complex messages. Males are the primary singers, and they gain attention by repeating a pattern of notes over and over. The same song can attract females and repel other males, a dual message whose meaning depends on its receiver. Research suggests that songs may accelerate ovarian growth in females and synchronize reproduction in an entire colony. Some birds have extensive repertoires, up to 150 songs. Those that mimic may include bizarre imitations: car horns, telephones, farm machinery. Although the reason for this is obscure, it may be that females associate quantity with maturity and experience, making the more accomplished bird the more desirable mate.



Tactile communication: As a mode of communication, touch is used mostly with kin, or among members of the same species that live in social groups. Touch is important in courtship, bonding, and displacement of anger. With some species, particularly insects and arachnids, it is a primary means of recognition. Ants recognize nest members by a sequence of antenna taps, and male spiders tap on a female's web or body as a prelude to mating. Elephants use their sensitive trunks extensively for greeting and in child rearing. Other animals nudge, cuff, or nip their young to keep them in line. Grooming, neck rubbing, and tail twining maintain relationships and, perhaps, reduce aggression.

Camouflage and Mimicry – types of mimicry

Mimicry

Camouflage and mimicry are adaptations some animals use as protection from predators. An animal that uses camouflage looks like things in its environment. It might look like a leaf, a twig, or a rock. Animals that use mimicry use colors and markings to look like another animal.

In ecology, mimicry (sometimes called mimetism) describes a situation where one organism, the mimic, has evolved to share common outward characteristics with another organism, the model, through the selective action of a signal-receiver. The model is usually another species, or less commonly, the mimic's own species, including automimicry, where one part of the body bears superficial similarity to another. The signal-receiver is typically another intermediate organism, e.g the common predator of two species. As an interaction, mimicry is always advantageous to the mimic and harmful to the receiver, but may either increase or reduce the fitness of the model.

Though mimicry is most obvious to humans in visual mimics, they may also use olfactory (smell) or auditory signals, and more than one type of signal may be employed. Mimicry may involve morphology, behavior, and other properties. In any case, the signal always functions to deceive the receiver by providing misleading information. Mimicry differs from camouflage in which a species appears similar to its surroundings. In evolutionary biology terms, this phenomenon is a form of co-evolution involving an evolutionary arms race, and should not be confused with convergent evolution, which occurs when species come to resemble on another independently due to similar lifestyles.

Mimics may have multiple models during different stages of their life cycle, or they may be polymorphic, with different individuals imitating different models. Models themselves may have more than one mimic, though frequency dependent selection favors mimicry where models outnumber mimic. Models tend to be relatively closely related organisms, but mimicry of vastly different species is also known. Most known mimics are insects, though other mimics including mammals are known.

1. Batesian
2. Müllerian
3. Mertensian
4. Peckhamian/Aggressive
5. Bakerian
6. Vavilovian
7. Automimicry
8. Other

Batesian: The mimic (palatable) resembles the model (unpalatable) and only the mimic benefits. A drone fly exhibits Batesian mimicry by resembling a honey bee. Batesian mimicry is named after Henry Walter Bates, an English naturalist whose work on butterflies in the Amazon rainforest was pioneering in this field of study. In this type of mimicry the mimic sends similar signals to model species, but does not share the attribute that makes it unprofitable to predators (e.g. unpalatability).

Examples: The Ash Borer (*Podosesia syringae*), a moth of the Clearwing family (Sesiidae), is a Batesian mimic of the Common wasp because it resembles the wasp, but is not capable of stinging. A predator that has learned to avoid the wasp would similarly avoid the Ash Borer. Several palatable moths produce ultrasonic click calls to mimic the unpalatable tiger moths.

The False Cobra (*Malpolon moilensis*) is a mildly venomous but harmless snake which mimics the characteristic "hood" of an Indian cobra's threat display. The Eastern Hognose Snake (*Heterodon platirhinos*) similarly mimics the threat display of poisonous snakes.

Octopuses of the genus *Thaumoctopus* (the Mimic Octopus and the "wunderpus") are able to intentionally alter their body shape and color so that they resemble dangerous sea snakes or lionfish.

Müllerian: Named after Fritz Müller, where the mimic resembles the successful species and shares the anti-predation attribute (dangerous or unpalatable.) This type of mimicry is unique in that both the mimic and the model benefit from the interaction, which could thus be classified as mutualism in this respect.

Examples: The Monarch Butterfly (*Danaus plexippus*) is a member of a Müllerian complex with the Viceroy butterfly (*Limenitis archippus*) in shared coloration patterns and display behavior.

The Viceroy has subspecies with somewhat different coloration, each one very closely matching the local *Danaus* species. E.g., in Florida, the pairing is of the Viceroy and the Queen Butterfly, and in Mexico, the Viceroy resembles the Soldier Butterfly. Therefore, the Viceroy is a single species involved in three different Müllerian pairs. This example was long believed to be a case of Batesian mimicry, with the Viceroy being the mimic and the Monarch the model, but it was more recently determined that the Viceroy is actually the more unpalatable species, though there is considerable individual variation. *Danaus*

species tend to be toxic rather than just repugnant, due to their different food plants.

The genus *Morpho* is palatable but they are very strong fliers; birds - even species which are specialized for catching butterflies on the wing - find it very hard to catch them. The conspicuous blue coloration shared by most *Morpho* species seems to be a case of Müllerian mimicry. Many unpalatable tiger moths make ultrasonic clicking calls to detract bats.

Mertensian: Mertensian mimicry is named after the late German herpetologist Robert Mertens, and is often considered a subtype of Müllerian mimicry. In this case harmless and deadly mimics resemble a dangerous but not usually deadly species (if the predator dies, it cannot learn to recognize a trait, e.g. a warning coloration).

Examples: Some Milk Snake (*Lampropeltis triangulum*) subspecies (harmless), the moderately toxic False Coral Snakes (genus *Erythrolamprus*), and the deadly Coral Snakes all have a red background color with black and white/yellow stripes. In this system, both the milk snakes and the deadly coral snakes are mimics, whereas the false coral snakes are the model.

Peckhamian/Aggressive: Named after Elizabeth Maria Gifford Peckham; also called aggressive mimicry, where the mimic resembles a harmless species in order to lure prey.

Examples: The Alligator Snapping Turtle uses its tongue to lure fish. Female fireflies of the genus *Photuris* copy the light signals of other species, thereby attracting male fireflies which are then captured and eaten. The Alligator Snapping Turtle (*Macrochelys temminckii*) is a well-camouflaged ambush predator. Its tongue bears a conspicuous pink extension that resembles a worm and can be wriggled around; fish that try to eat the "worm" get in turn eaten by the turtle.

Bakerian: Named after Herbert G. Baker, where the mimic resembles members of its own or other species in order to lure pollinators or reap other benefits, although the mimicry may not be readily apparent due to the fact that the members of the same species may still exhibit sexual dimorphism.

Examples: Common in many species of *Caricaceae*. Their flowers have little or no nectar but resemble nectar-producing flowers. Pollinators will be

fooled into visiting them and thus fertilization is ensured without having to produce a reward for the pollinator.

Vavilovian: Vavilovian mimicry is named after Nikolai Ivanovich Vavilov, a prominent Russian botanist and geneticist who identified the centres of origin of cultivated plants and later died in prison during the days of Lysenkoism. In this form of mimicry, the mimic comes to resemble a domesticated plant through generations of artificial selection, and may eventually be domesticated itself. This type of mimicry does not occur in ecosystems unaltered by humans.

Examples: *Echinochloa oryzoides* is a species of grass which is found as a weed in rice (*Oryza sativa*) fields. The plant looks similar to rice and its seeds are often mixed in rice and difficult to separate. This close similarity was enhanced by the weeding process which is a selective force that increases the similarity of the weed in each subsequent generation.

Automimicry: Where the mimic has some part of its body resembling some other part. Examples include snakes in which the tail resembles the head and show behavior such as moving backwards to confuse predators and insects and fishes with eyespots on their hind ends to resemble the head. The term is also used when the mimic imitates other morphs within the same species such as some males looking like females or vice versa.

Examples: Many insects have filamentous "tails" at the ends of their wings which are combined with patterns of markings on the wings themselves to create a "false head" which misdirects predators (e.g., hairstreak butterflies). Several pygmy owls bear "false eyes" on the back of their head to fool predators into believing the owl is alert to their presence.

Unit – II

- a) Ecological Aspects of Behaviour: Habitat Selection, food selection and optimal foraging theory, anti-predator defenses, aggression, territoriality, dispersal, host-parasite relations.
- b) Social Behaviour: Aggregations – Schooling in Fishes, Flocking in Birds, Herding in Mammals; Group Selection, kin selection, altruism, inclusive fitness, and social organization in insects and primates.

Ecological Aspects of Behaviour: Habitat Selection, food selection, optimal foraging theory, anti-predator defenses, aggression, territoriality, dispersal, host-parasite relations

Habitat-selection studies have recently assumed a new urgency, partially as a result of the importance of incorporating both habitat and demographic information into conservation planning. The dictionary defines habitat as "the native environment of an animal or plant". The thesaurus lists related words like abode, dwelling, residence, domicile, estate, environment and ecosystem. Habitat is the complex of physical factors required to provide food, water, and cover for a plant or animal. These factors must be in sufficient quantity and quality to provide a never-ending supply of life's necessities.

To study the habitats of animals, we often rely on naming the habitats to help narrow the number of species included in each study. Habitats include:

1. Alpine (typical high mountain), including tundra (between ice cap and tree line) and alpine transition;
2. Coniferous Forest, including fir and pine species;
3. Deciduous forest, including mountain riparian (river bank), desert riparian, and aspen (a poplar with leaves that rustle and flutter in the breeze); Pygmy or Pinyon-Juniper Woodland;
4. Shrub lands, including mountain sagebrush (a North American plant), mountain shrub (oak, maple and associated species), low elevation sagebrush, cold desert shrub, and joshua tree (flowering desert plant);
5. Grasslands, including mountain meadows, arid grasslands, pastures, and lowland meadows;
6. Wetlands including mudflats, salt flats, shoreline, marshes, rivers, streams, lakes and reservoirs;

7. Barrens, including cliffs, bluffs (group of trees in a broad face of cliff), and dirt banks;
8. Developed areas, including orchards, croplands, and building sites; urban areas, residential areas, city parks, commercial areas, and industrial areas.

The distinctions between the terms 'habitat use' and 'habitat selection' are often unclear. 'Habitat' refers to a distinctive set of physical environmental factors that a species uses for its survival and reproduction. 'Habitat use' refers to the way in which an individual or species uses habitats to meet its life history needs. The study of 'habitat-use patterns' describes the actual distribution of individuals across habitat types.

'Habitat selection' refers to a hierarchical process of behavioral responses that may result in the disproportionate use of habitats to influence survival and fitness of individuals. Habitat selection carries an association of understanding of complex behavioral and environmental processes that habitat use does not; habitat-use patterns are the end result of habitat-selection processes. Nest-site selection is a subset of habitat selection focusing solely on nest sites.

There are two aspects of habitat selection that are crucial to understand the adaptive significance of disproportionate use of habitats; demonstration of choice and an assessment of the fitness consequences associated with the choice.

Habitat selection is a decision-making process and researchers need to make an attempt to describe how the observed patterns reflect an individual's choice. That attempt can be improved by the recognition that individuals are faced with choices that differ not only in terms of habitat quality, but also in terms of the costs and benefits of acquiring space.

Habitat preferences are assumed to be adaptive without demonstration of increased fitness in preferred habitats. There is no guarantee that the presence of individuals in a given habitat is positively related to habitat quality. In the absence of behavioral or life-history information, there is no way to know the habitat choice.

In addition, many non-habitat related phenomena influence habitat selection in birds, including nest predation, competition, intraspecific attraction, and food limitation. There needs to be explicit understanding of how those phenomena affect both the choices made by individuals and the fitness consequences of those choices.

There are many factors that are involved with an organism's choice of habitat. Here are some key points to consider regarding habitat selection.

First, habitats are heterogenous. 'Rich' habitats give higher fitness to the organisms living there where 'poor' habitats give lower fitness. The quality of the habitat has many variables such as food availability, predator occurrence, ease of defense, likelihood of offspring survival, microclimate changes, distance to human settlements, and many others.

Second, one should consider how habitat selection can relate to conservation issues. Why do animals choose to live in an area that only appears to have large benefits but in reality damages their fitness? Some theories include the presence of a dominant individual in the source areas, conspecific attraction, and the reception of false signals of habitat quality.

Example of Habitat Choice: Charles Darwin visited the Falkland Islands in the South Atlantic during his 1831-1836 globe-girdling expedition in H.M.S. Beagle. He reported: "Two kinds of geese frequent the Falklands. The upland species (*Anas magellanica*) is common, in pairs and in small flocks, throughout the island. The rock goose, so called from living exclusively on the sea-beach (*Anas antarctica*), is common both here and on the west coast of America, as far north as Chile."

These two closely related species each live, as Darwin described, in a different range of habitats.

Birds are nearly ideal subjects for studies of habitat selection, because they are highly mobile, often migrating thousands of miles, and yet ordinarily forage, breed, and winter in very specific habitats. Indeed, the lives of small migrant songbirds are replete (fully equipped) with habitat choices – where to feed, where to seek a mate, where to build a nest, where to stop to replenish depleted stores of fat when migrating, and so on.

Choices can be so finely tuned that often the two sexes of a species use habitats differently. In grassland, male Henslow's Sparrows forage farther from the nest than females; in woodlands, female Red-eyed Vireos seek their food closer to the height of their nest (10-30 feet), and males forage closer to the height of their song perches (20-60 feet).

Many studies have demonstrated the special habitat requirements of different species. Belted Kingfishers choose nesting sites at those points along streams where particular kinds of riffles shelter fish.

Example: To better understand the relationship between animal behavior and habitat choice, let's walk through a hypothetical scenario. Imagine a male bird that lives near a large marsh. Where should he spend his time during the day? If it is the mating season, one question would be Where are the females? Females may prefer the safety in the reeds, so perhaps our male should go there. The

reed
area,



however, may be home to organisms that parasitize this bird species, so there are both costs and benefits to staying in the reeds. Courting a mate is energetically expensive, and it may be that preys are not found in the reeds, but over the marsh water, so there might be reason to spend time over the marsh first. However, predators may also prefer the area over the marsh, so, as with the reed area, there are costs as well as benefits to spending time over the marsh.

The decision-making process is complicated, as it now includes mates, food, and predators. Other factors may also play a role in determining where our bird goes. Temperature will vary both across the day and across the marsh, and this may affect where the bird spends time. Let's imagine that in deciding where to spend his time, our bird ends up flying between the reeds and the marsh water but does not spend that much time in any one area and does not stop others from using any of the areas it frequents. In such a case, we might speak of those areas being his home range.

Suppose that our bird flies between the reeds and the marsh area but that he regularly returns to a particular area in the central part of the reeds and

actively tries to keep intruders outside of this area. Now we can speak of this bird as having a territory — an area occupied and defended by the bird.

Habitat choice: Imagine a red-winged blackbird deciding where to form a territory. All sorts of factors—mates, temperature, predators play a role in the decision making. Another factor in habitat choice is the availability of prey, such as the presence of dragonflies shown flying above the marsh.

Food Selection and Optimal Foraging Theory:

A central concern of ecology has traditionally been foraging behavior. In its most basic form, optimal foraging theory states that organisms forage in such a way as to maximize their energy intake per unit time. In other words, they behave in such a way as to find, capture and consume food containing the most calories while expending least amount of time possible in doing so. The understanding of many ecological concepts such as adaptation, energy flow and competition hinges on the ability to comprehend what, and why, animals select certain food items.

MacArthur and Pianka (1966) developed a theoretical and empirical construct, the optimal foraging theory (OFT), which led to a better understanding of foraging behavior. Emlen (1966) published a paper on foraging behavior at the same approximate time. Optimal foraging theory uses predators as the object of analysis. There are four functional classes of predators:

True predators attack large numbers of their prey throughout their life. They kill their prey immediately, or shortly after the attack. They may eat all or only part of their prey. True predators include tigers, lions, plankton eating whales, seed eating birds & ants and humans.

Grazers attack large numbers of their prey throughout their lifetime and eat only a portion of their prey. They harm the prey, but rarely kill it. Grazers include cows, locusts, leeches and mosquitoes.

Parasites, like grazers, eat only a part of their prey (host) but rarely the entire organism. This much more intimate relationship is typical of tapeworms, and liver flukes.

Parasitoids are mainly typical of wasps (order Hymenoptera), and some flies (order Diptera). Eggs are laid inside the larvae of other arthropods which hatch and consume the host from the inside, killing it. This intimate predator-host relationship is typical of about 10% of all insects. Many viruses that attack single-celled organisms (such as bacteriophage) are also parasitoids, in that they reproduce inside a single host that is inevitably killed by the association.

The OFT attempts to explain predator behavior since no predator eats everything available. This is typically due to habitat and size constraints, but even within habitats, predators eat only a proportion of what is available.

'E' is the amount of energy (calories) from a prey item. 'h' is the handling time which includes capture, killing, eating and digesting. 'h' starts once the prey has been spotted. E/h is therefore the profitability of the prey item.

Optimal foraging and diet breadth: The predator attempts to maximize $E/(h+s)$, where 's' is the search time involved. For a range of prey, the predators average intake rate is $E_{\text{average}}/(h_{\text{average}}+s_{\text{average}})$. Where E_{average} is the average energy of all prey items in the diet, h_{average} is the average handling time and s_{average} is the average search time.

When the predator has found an item it doesn't currently eat, it has two choices. It can eat the new item, in which case there is profitability $E_{\text{new}}/h_{\text{new}}$ or it can leave it and search for an item already in its diet, in which case we use $E_{\text{average}}/(h_{\text{average}}+s_{\text{average}})$. The predator should eat this new item when $E_{\text{new}}/h_{\text{new}} \geq E_{\text{average}}/(h_{\text{average}}+s_{\text{average}})$ because the new item increases its energy intake per unit time.

New insights: Predators with short handling times and long search times should be *generalists* and include a wide range of items.

Specialists have a longer handling times and short search times; they are choosy. Lions, for example, have a very low search time but a high handling time, which can be prohibitively large for some prey.

Predators should be generalists in unproductive environments and specialists in productive environments. Predator-prey co-evolution often makes it non-profitable for a prey item to be included in the diet, since many anti-predator defenses increase handling time. Examples include porcupine quills, the palatability and digestibility of the poison dart frog, and other predator avoidance behaviors.

Since there is a search time for each item, when predator density increases the search time depends on the density of the prey. There is also a handling time which is species specific. At low prey densities the predator is searching most of the time and eating every prey item it finds. At high prey densities, each new prey item is caught almost immediately. The predator spends almost all of its time catching, eating or digesting the prey. It chooses only those individuals with the highest E/h. As the prey density increases, they become less limited by search time and more limited by handling time.

Food Choice: One of the simplest issues in foraging decisions is picking the food that leads to the highest rate of energy acquisition. How large a prey item should an organism attempt to eat.

Rule number one: Never eat anything bigger than your head.

Rule number two: Eat items that lead to the highest gain in Energy/Time. (Assuming that you are maximizing energy) i.e. Profitability = Energy Gain/Unit of Time.

Optimal Clam Size in the Foraging Crow: Richardson and Verbeek studied Crows foraging on clams in the intertidal and noticed that they left quite a few clams behind after digging them up. If they go to the trouble of digging them up in the first place why not eat them? The answer lies in handling time - how long it would take them to open the clam.

Mussel Size Selection by Oyster Catchers: A similar problem is faced by Oyster catchers trying to open mussels. Optimality model that only considers Energy maximization predicts that Oyster Catchers should choose the largest clams that they encounter. However, Oyster Catchers do not always choose the largest mussels, often leaving them untouched. Why leave the biggest items? The handling time for the largest mussels leads to a dramatic drop in profitability and Oyster Catchers should avoid them from the start.

Foraging Distance: Foraging refers to the mammalian behavior associated with searching for food. The optimal foraging theory assumes that animals feed in a way that maximizes their net rate of energy intake per unit time. An animal may either maximize its daily energy intake (energy maximizer) or minimize the time spent feeding (time minimizer) in order to meet minimum requirements. Herbivores commonly behave as energy maximizers and accomplish this maximizing behavior by choosing food that is of high quality and has low-search and low- handling time.

The *central place theory* is used to describe animals that collect food and store it in a fixed location in their home range, the central place. The factors associated with the optimal foraging theory also apply to the central place theory. The central place theory predicts that retrieval costs increase linearly with distance of the resource from the central place. Central place feeders are very selective when choosing food that is far from the central place since they have to spend time and energy hauling it to the storage site.

Anti-predator Defense

Mimicry and warning color are antipredator adaptations. Colour patterns in mimicry are often determined by relatively few pattern-regulating loci. A strong purifying selection on these genes must explain accurate resemblance as well as monomorphic color patterns within species. Mimicry has diversified at every taxonomic level; warning colour has evolved from cryptic patterns, and there are mimetic polymorphisms within species, multiple color patterns in different geographic races of the same species, mimetic differences between sister species, and multiple mimicry rings within local communities.

Flocking: Predators may hunt lone individuals more successfully than individuals in flocks because individuals in flocks can collectively assess their surroundings more reliably. Sharing of sentry duty means, the individual spend less time for vigilance and more time for such tasks as foraging. An individual may lower its probability of being captured simply by associating with other equally attractive prey. Predators most likely attack prey at the flock's edge, so that centrally located individuals should be relatively safe. Birds in large flocks are less vigilant than birds in smaller flocks. Birds in large flocks devote more time to activities other than vigilance. If food is scarce and energy demand high, birds in the center of large flocks devote more time for foraging than do peripheral birds. In large flocks high status birds occupy central positions.

Number dependent selection mimicry and warning colour: Muller was the first to formulate the benefits of mimicry explicitly, using mathematical intuition from a natural history perspective. He assumed that, while learning to avoid the color pattern of unpalatable species, a predator complex killed a fixed number of individuals per unit time (n_k). Mullerian mimicry is favored, therefore, because the per capita mortality rate decreases when another unpalatable species shares the same pattern. If this traditional naturalist's "number dependent" view of mimicry is correct, it leads to two interesting predictions, only the first of which Muller himself apparently appreciated. First, although Mullerian mimicry of this kind should always be mutualistic, a rare species ultimately gains far more from mimicry than a common one. Second, a novel mimetic variant in the rarer species resembling the commoner is always favored because the common species generates greater numerical protection.

Aggression

Aggression is a multi-dimensional concept, but it can be generally defined as behavior that inflicts pain or harm on another. Psychopaths demonstrate high levels of this behavior without any apparent goal or reason. At a basic level, aggression in humans may be physical (e.g. hitting out) or verbal, while in animals it may be manifest as a threat or as an attack. There are therefore various 'kinds' of aggressive behavior.

Aggression is a common occurrence in the world of marine mammals. Aggressive displays or agonistic interactions are often seen among members of a group or between individuals of different species. Sounds that declare a readiness to fight may be produced during aggressive displays. Animals can listen to these sounds to assess an opponent's willingness to fight or fighting ability. Loud sounds may also be used to startle or defend against a predator.

Various categories of animal aggression:

1. **Territorial defense** - when animals attack intruders who enter their 'territory'
2. **Predatory aggression** - when an animal attacks prey. This form of aggression is not believed to be hunger-induced, but rather involves the lateral hypothalamus and the specific 'trigger' stimuli (the animals it typically feeds on - the prey).
3. **Inter-male aggression** - occurs when another (stranger) male is present. Androgen (hormone) is believed to be important in this form of aggression.
4. **Fear-induced aggression** - always preceded by attempts to escape. This form of aggressive behavior is most evident when the animal is 'cornered' and is afraid. They will almost always react with aggression before they attempt to escape. The lateral hypothalamus is believed to be important here.
5. **Irritable aggression** - this will be evoked by any attackable object or other animal. The ventromedial hypothalamus is believed to be the crucial brain structures here.
6. **Maternal aggression** - when a female reacts with aggression in order to protect her young from harm.

7. **Instrumental aggression** - when aggression was used successfully in a given situation in the past the animal will use this behavior again (in the same or similar situation - therefore the behavior has been reinforced via learning).

Additional Note:

Aggression clearly plays a major role in success during a contest. But aggression is a two-edged sword in that there are clear benefits and costs to fighting. In this regard, mechanisms have evolved that modulate levels of aggression.

Aggression is very often restricted to the adult phase and the breeding season. Territorial aggression is often tightly governed by circulating levels of hormones. Given that there are winners in contests and hormone levels might predict winning, what hormonal changes alter the behavior of the loser in the long-term? What causes retreat from contests in the short-term? An understanding of the neuroendocrine bases of behavior is necessary to understand these issues of contest and conflict.

No hormone receives more attention as an aggression inducer than the gonadal steroid testosterone. In males, testosterone is secreted in the testes in response to gonadotropin, a protein hormone, which is produced by the anterior pituitary. The anterior pituitary is an important control region of the brain that produces a many behaviorally relevant hormones. Testosterone is also involved in a classic negative feedback loop in which higher levels of testosterone produced by the testes will cause gonadotropin secretion by the brain to be suppressed. Given the interaction between gonadotropin control of testosterone, and vice versa, it is not surprising that gonadotropins such as Leutenizing Hormone (LH) can alter male aggression.

Male elephants enter a behavioral state known as musth during the breeding season in which aggressive charges to rivals are common. Injection of LH into sub-adult male elephants appears to trigger this behavioral state as well as a concomitant rise in plasma testosterone (Lincoln and Ratnasooriya 1996). In males, testosterone seems to increase the likelihood that behaviors are expressed, but it is important to realize that testosterone does not directly control specific behaviors. Testosterone and protein hormones such as LH that modulate testosterone can be considered one of the many factors that contribute to the heightened arousal that is associated with aggression.

Testosterone influences a diverse set of behaviors in males. However, contrary to popular belief that the 'male hormone' is testosterone and the 'female hormone' is estrogen, testosterone has potent effects on females, even though most female vertebrates appear to have far lower levels of testosterone than males. In females, the low levels of testosterone promote many female behaviors and appear to be responsible for female sex drive. It is also not the case that testosterone is invariably related to aggression.

Groups of white-browed sparrow weavers breed in cooperative groups and participate in defending their communal territory from other groups. Territory defense involves regular boundary patrols that are punctuated by a characteristic chorus singing elicited by all group members in concert. Wingfield and Lewis (1993) simulated territorial intrusions by placing a caged group within a territory and playing back tape-recorded choruses through a speaker placed adjacent to the cage. The target group responded with a dramatic increase in territorial aggression by all group members. Plasma levels of testosterone were not elevated during intrusions. However, plasma levels of LH were elevated in breeding females after challenge. This suggests that aggressive behavior in females may not result from elevated testosterone, but from the upstream effects of LH.

Despite these important exceptions to the role of testosterone in promoting aggression, testosterone has a broad spectrum of effects that also serve to enhance the physical abilities of males in particular.

Testosterone is in part responsible for triggering the development of special sound producing muscles in male fish, and amphibians (Kelley and Gorlick 1990).

Testosterone not only triggers the development of vocal structures, but it is also responsible for sensitizing certain targets in the brain and thus increases the likelihood of song. In free-living red-wing blackbirds, *Agelaius phoeniceus*, natural variation in the rate of song production on their territories is correlated with the level of testosterone circulating in their plasma.

Territoriality:

It is a type of intraspecific or interspecific competition that results from the behavioral exclusion of others from a specific space that is defended as territory. This well-defined behavior is exhibited through **songs and calls, intimidation behavior (to frighten), attack and chase, and marking with scents**. This form of defense proves to be very costly for animals. So one is forced to ask, why do animals take part in such interspecific competition?

In order to understand this question one must take a cost-benefit approach to territoriality. The proximate reasons for such defense vary. For some animals the reason for participating in such elaborate protective behavior is to acquire and protect food sources, nesting sites, mating areas, or to simply attract a mate. The ultimate cause of this behaviour may be attributed to the increased probability of ***survival and reproductive successes***. In defending a territory an animal is ultimately securing that it will have a habitat in which to forage for food and to successfully reproduce, thus increasing the animal's overall fitness. This ultimate theory is strengthened when one considers the instances in which territoriality increases; in times of depleted resources the presence of territoriality increases. The presence of territoriality often forces less fit animals to live in sub optimal habitats, thus reducing their reproductive success.

Though territoriality offers immense reproductive and nutritional benefits, it also comes at a cost. Defending territory is not easy. Territoriality cost time and energy and can often interfere with other fundamental activities as parenting, feeding, courting, and mating. For these reasons territoriality may not be seen as a benefit in all animals. Animals must be able to reap the fruits of territoriality, while expending the least amount of energy. For these reasons if resources are abundant and predictable it would be disadvantageous to defend the territory. On the other hand, if resources are scarce and undependable it would be advantageous to exhibit territoriality.

An animal chooses its territory by deciding what part of its home range it would like to defend. In selecting a territory the size and the quality play a crucial role in determining an animal's habitat. Territory size generally tends to be no larger than the need of organism to survive, because with an increase in territory comes an increased in energy expenditure. For some animals the territory size is not the most important aspect of territoriality, but rather the quality of defended territory. The quality is considered to be fundamentally important due

to amount of food availability and superior nesting sights. Animals depend on these features to ensure their superior fitness.

Animals invest a lot of time and energy in defending their territories, and for this reason they fight vigorously to defend their territory at all cost. Researchers suggest for this reason that when a rival challenges a territory holder, the owner almost always wins the contest. This phenomenon could be attributed to an evolutionary stable strategy which asserts that rules for behaviour is controlled by an inherited proximate mechanism such that the differences between individuals in their strategies are linked to differences in their genes. Territory plays an important role as a mechanism of population regulation, insuring the success of fit animals, and aiding in the eradication of less fit animals. Territorially also plays a fundamental role as an indicator of carrying capacity; it also serves as an indicator of how much habitat is necessary to support viable populations.

Defending a territory:

Some animals defend their territory by fighting with those who try to invade it. Fighting, however, is not often the best option, since it uses up a large amount of energy, and can result in injury or even death. Most animals rely on various threats, either through vocalizations, smells, or visual displays. The songs of birds, the drumming of woodpeckers and the loud calls of monkeys are all warnings that carry for long distances, advertising to potential intruders that someone else's territory is being approached. Many animals rely on smells to mark their territories, spraying urine, leaving droppings or rubbing scent glands around the territories' borders. Approaching animals will be warned off the territory without ever encountering the territory's defender.

On occasion, these warnings may be ignored, and an intruder may stray into a neighboring territory, or two animals may meet near the border of their adjacent territories. When two individuals of a territorial species meet, they will generally threaten each other with visual displays. These displays often will exaggerate an animal's size by the fluffing up of feathers or fur, or will show off the animal's weapons. The animals may go through all the motions of fighting without ever actually touching each other, a behavior known as **ritual fighting**. The displays are generally performed best near the center of an animal's territory, where it is more likely to attack an intruder, and become more fragmented closer to the edges, where retreating becomes more of an option. This spectrum of performances results in territorial boundaries, where displays

of neighbors are about equal in intensity, or where the tendency to attack and the tendency to retreat are balanced.

Actual fighting usually happens in overcrowded conditions, when resources are scarce. Serious injury can result, and old or sick animals may die, leading to a more balanced population size. Under most natural conditions, territoriality is an effective way of maintaining a healthy population. The study of social behaviors such as territoriality in animals may help us also to understand human society, and to learn how individual behavior affects human populations.

Dispersal:

Biological dispersal refers to those processes by which a species maintains or expands the distribution of a population. Dispersal implies movement away from an existing population (population expansion) or away from the parent organisms (population maintenance). In the latter case, dispersal may simply involve replacement of the parent generation by the new generation, with only minor changes in geographic area occupied. In either case, dispersal is important because new life must replace old, and the two generations cannot easily occupy the same physical space during the transition. More significantly, dispersal enables the species population to occupy much of the available habitat, thereby maximizing resources in its favor and awareness local adverse events. There are five key causes of dispersal: ***competition avoidance, inbreeding avoidance, kin-competition avoidance, breeding dispersal, and colonization dispersal.***

Key causes of dispersal:

1. Competition dispersal (habitat depletion). This is probably a key cause of dispersal in plants, as resources such as light, root space, and nutrients are depleted by the parental plant. In animals it also plays a key role in many species and recurs as a theme in this outline. Infanticide is a common response to habitat depletion in rodents and can be thought of as the result of resource competition. Infanticide is performed by females and males that are unrelated to or are unfamiliar with the pups. In crowded populations of related mice and voles infanticide is much less likely.
2. Inbreeding avoidance. It was observed in meadow voles that they were more likely to disperse from plots occupied by siblings than from plots occupied by non siblings.

3. Kin-competition avoidance. This is really difficult to discriminate from inbreeding avoidance because the result is essentially the same; close kin end up not living near one another.
4. Breeding dispersal. Gravid females may leave social groups or natal areas to find more appropriate places to give birth and feed their offspring. The motivation for this overlaps with other causes of dispersal--habitat depletion could stimulate movement, colonization could be a goal of movement.
5. Colonization dispersal. Selection may favor colonization of new habitats. Individual fitness can be enhanced for plants or animals that find a vacant habitat patch.

In most cases, organisms (plants and especially sedentary animals) have evolved adaptations for dispersal that take advantage of various forms of kinetic energy occurring naturally in the environment: water flow, wind, falling (response to gravity). Animal species need to disperse themselves for similar reasons as plant species. If there are too many individuals of a particular animal species in the same area, they will be in competition with each other. Eventually, either one or more of the following reasons will contribute to the death of many individuals in the population: **lack of food, lack of oxygen, build up of waste, which can cause disease**. Overcrowding, this would allow disease to spread quickly through the population.

Host-Parasite Relations:

A parasite is an organism that lives on or in the body of another organism, deriving benefit at the expense of the latter. Here only one of the partners is benefited and the other is harmed or injured. The organism which harbours the parasite is called the host. The parasite is always benefited in this association and the host is injured or harmed. Parasites are found in different groups of the animal kingdom. When the parasite lives on the surface of the body of the host it is called ectoparasites e.g. *head louse, ticks, mites, bedbugs, leeches*, etc. When the parasite lives inside the body of the host, it is called endoparasite e.g. *malarial parasite* or *plasmodium* in the red blood cells. Liver-fluke *Faciola hepatica* is found in the bile ducts of sheep, causing the disease liver-rot in sheep. The life cycle of certain parasites may be completed in a single host e.g. *Entamoeba histolytica*. But in many endoparasites like *liver-flukes, tapeworms* etc., the life history may be completed in two or more hosts.

The host in which the parasites reaches sexual maturity is known as the **definitive host** and the host in which the parasite undergoes early developmental stages is known as **intermediate host**. As a result of the parasitic mode of life, a number of parasitic adaptations are found in these parasites, especially in endoparasites. These adaptations are indeed in the form specializations associated with parasitism.

The specializations associated with parasitism especially in endoparasites have altered many of the basic characters of the group to which these endoparasites belong. For example, endoparasites like liver-fluke (Trematoda) and tapeworm (Cestoda) possess powerful cuticle capable of resisting the action of digestive enzymes of the host. In liver-fluke suckers are present in addition to the spines in the cuticle for the purpose of attachment. In tapeworm hooks and suckers are present. Locomotor organs are absent in endoparasites, which do not move about in search of food since they get plenty of digested food in the digestive systems of their hosts. Sense organs are also absent in these endoparasites. Digestive glands are absent in liver-fluke since these are not required by the parasite. In tapeworm digestive system as a whole is absent. Digested food materials are simply absorbed through the body surface. The reproductive system is complicated in these endoparasites. They are hermaphrodites. The life history of these endoparasites is very complex involving specific intermediate hosts and involves number of risks.

Social Behaviour: Aggregations – Schooling in Fishes, Flocking in Birds, Herding in Mammals; Group Selection, kin selection, altruism, reciprocal altruism, inclusive fitness, and social organization in insects and primates

Aggregations

Aggregation occurs in the smallest organisms – bacteria and the largest – whales. Territorial animals need to engage in *information transfer*, however no need for group structure. At the other end are highly integrated, long-term associations between individuals possible. Honeybee hives and human communities are examples of these highly integrated groups. In these systems, established pathways of long-term communication between known individuals (siblings, reciprocating group members), at predetermined locations (the hive, the calving grounds, the dinner table), may supplement immediate sensory contact.

Schooling (shoaling) in Fishes

Everyone has heard of a school of fish or aggregation of fish. Schools of fish may be either polarized (with all the fish facing the same direction) or non-polarized (all going every which way). There are some factors that can make it advantageous to hang out with other fish.

Antipredator: by hanging out with other fish, each individual fish may gain an advantage in not being eaten by other fish.

Confusion effect: A large school of fish may be able to confuse a potential predator into thinking that the school is actually a much larger organism.

Dilution effect: If a fish hangs out with a lot of other fish and a predator does come around, the predator must usually select one prey item. With so many choices, the chances are that it will not be you. This is known as the 'selfish herd'.

Predator detection: A bunch of fish has many times the eyes and other senses than a solitary fish; so a school of fish may be better at detecting predators. But a school may also attract predators due to its large size.

Spawning Aggregation: Many species of fishes form schools only at the time of mating. They will form a huge school and release their eggs and sperm in mass quantities. Releasing a massive onslaught of fertilized eggs in the water

may be advantages over a solitary egg, because a massive onslaught may be enough to overcome the egg predators. The predators will eat as many as they can, but some eggs will inevitably survive.

Enhanced Foraging: A school of fish may have better abilities to acquire food. With many more eyes to detect food, many more meals may be found; but there would also be many more mouths to feed. By working as a team, the school may be able to take larger food items than any one individual could manage to capture.

Migration: The migration abilities of fish in schools may possibly be enhanced due to better navigation, etc.

Hydrodynamic efficiency: Due to the complex hydrodynamic properties of water, a fish may gain a swimming advantage by being in a school. The slipstream (a current of air/water behind a quickly moving object such as a car travelling extremely fast or an aircraft or fish) from the fish ahead of it may make it easier to pass through the water. Good for all the fish except for the ones in front.

Flocking in Birds

It's true that 'birds of a feather flock together'. You've probably seen a flock of birds flying in the sky, wheeling gracefully this way and landing elegantly as a single unit, and wondered to yourself, "How do they do that?" Do they have a leader, or if they don't, how do they all democratically decide to do the same thing at the same time?

You and a friend can do a little experiment in flocking behaviour with pigeons. All you need is a good supply of bread, and some pigeons. Try throwing the bread to the pigeons every five seconds, but get your friend to do it every ten seconds. At the very beginning, half of the birds will go to you, and half to your friend. But within two minutes, the pigeons will realise that you're the better food supply, and two-thirds of the birds will be clustering around you. And then, when you and your friend exchange your feeding rates, so your friend gives them twice as much food, it'll take the flock of birds another two minutes to readjust. Your friend will then have two-thirds of the birds.

How do the birds know how to flock from you, to your friend, and back again - without a leader? Well, we do know that all sorts of creatures flock -

birds, bacteria, slime moulds, fish, whales, elephants and wildebeest, as well as sheep. It turns out that there is a whole bunch of advantages to being in a flock.

Another advantage is that if you are little, but there are many of you, you can sometimes band together collectively against a larger common enemy - and successfully repel it.

Another advantage of the flock is the "collective intelligence". People who spend a lot of time looking at European starlings returning to their roost in California have noticed that a small flock will get lost more frequently than a big flock.

There are claims that birds in a flock do get improved aerodynamic efficiency. It's because of the vortices (a mass of air or water that spins around very fast and pulls objects into its empty centre), of spinning air coming off the tips of the wings. One strange thing about most flocks of creatures is that they don't seem to have one single leader.

Herding in Mammals

A herd is a large group of animals. The term is usually applied to mammals, particularly ungulates. Other terms are used for similar phenomena in other types of animal. For example, a large group of birds is usually called a 'flock' and a large group of carnivores is usually called a 'pack'. In addition, special collective nouns may be used for particular taxa: for example a flock of geese, if not in flight, is sometimes called a '**gaggle**'. However, in theoretical discussions in behavioural ecology, the generic term "herd" is used for all these kinds of assemblage.

When an association of animals is described as a "herd", the implication is that the group tends to act together, but that this does not occur as a result of planning or co-ordination. Rather, each individual is choosing behaviour that corresponds to that of the majority of other members, possibly through imitation or possibly because all are responding to the same external circumstances. A herd can be contrasted with a coordinated group where individuals have distinct roles.

The question of why animals group together is one of the most fundamental in sociobiology and behavioural ecology. As noted above, the term "herd" is most commonly used of grazing animals such as ungulates, and in these cases it is believed that the strongest selective pressure leading to herding

rather than a solitary existence is *protection against predators*. There is clearly a tradeoff involved, since on the one hand a predator may hesitate to attack a large group of animals, while on the other a large group offers an easily detected target. It is generally believed that the most important protective factor is *risk dilution* - even if a predator attacks the herd, the risk for any individual that it will be the victim is greatly reduced. In the case of predators, it is often unclear whether the term "herd" is appropriate, since there may be some degree of coordination or role differentiation in group hunting. Predator groups are commonly smaller than grazing groups, since although a pack may be more effective at pulling down prey than a single animal, the prey then has to be shared between all members.

A herd is by definition relatively unstructured. However, there may be one or a few animals which tend to be imitated by the rest of the members of the herd more than others. An animal taking this role is called a "control animal", since its behaviour will predict that of the herd as a whole. It cannot be assumed, however, that the control animal is deliberately taking a leadership role.

Altruism:

The word 'altruism' comes from the Italian *altrui*, was coined in 1851 by *August Comte* to refer to benevolence (kindness). Although not everyone agrees today on what precisely altruism involves, the most basic definition is *seeking the welfare of others*. This definition is often extended, however, to include the necessity of some personal sacrifice on the part of the altruist; *Edward O. Wilson* defined altruism as "*self-destructive behavior performed for the benefit of others*". Under Comte's definition, altruism signified an unselfish regard for the welfare of others. Altruism is helping others at our own expense. People are not entirely self-interested. If they were, then families would be nonexistent. There is also an idea of reciprocal altruism, which is self-sacrificing behavior with the expectation that the favor will be returned eventually. If this behavior is motivated by the desire for future reward, it does not really fit the generally accepted definitions of altruism.

In nonhuman animals, altruism is mainly seen in the form of one animal sacrificing or risking its life to save another. Studies of animals by researchers like Hamilton who worked with bees who sacrifice themselves to allow the queen to produce offspring with their genetic makeup have led to an evolutionary explanation of altruism. One explanation of altruism in the animal kingdom is *kin selection* that an animal will sacrifice its own life only if as a result, its genes have a greater chance of being passed on.

The animal world also is filled with animals that appear to help other creatures. Vampire bats are pretty altruistic, too, regurgitating blood for members of the group that haven't eaten. In numerous bird species, a breeding pair receives help in raising its young from other 'helper' birds, who protect the nest from predators and help to feed the fledglings. Vervet monkeys give alarm calls to warn fellow monkeys of the presence of predators, even though in so doing, they attract attention to themselves, increasing their personal chance of being attacked.

Of course, we are ignorant as to exactly what goes on inside the heads of animals and humans. Animal altruism troubled Charles Darwin, who popularized evolution in the 1800s. Darwin wrote that "natural selection will never produce in a being anything injurious to itself, for natural selection acts solely by and for the good of each. No organ will be formed, as Paley has remarked, for the purpose of causing pain or for doing any injury to its possessor". Natural

selection leads us to expect animals to behave in ways that increase their own chances of survival and reproduction, not those of others.

Why should wolves share their kill; or sparrows draw attention to themselves by issuing a warning call when they spot a hawk? If a bird helps a breeding pair in building their nest and feeding their young, without breeding itself, then it would seem to be a loser in the struggle for life. While this individual is busy helping others, it is missing out on the opportunity to produce heirs (offspring) of its own. How, then, do evolutionists account for altruism in animals?

From the point of view of a sociological analysis, one of the puzzles of social behavior has been **the existence of altruism - sacrifices by one individual that increase the survival - and reproductive chances - of another individual.** How could altruism have evolved, if it reduces the altruist's chances of reproduction?

An evolutionary explanation for altruism was provided by Hamilton's concept of inclusive fitness. The argument is that since related individuals share genes with each other, a sacrifice of reproductive chances by one individual might actually increase the overall chances of that individual's genes being passed on.

If the altruism benefits a relative carrying the same genes. Hamilton's formula indicates that inclusive fitness increases if the altruist's cost is less than the benefit to the beneficiary x the coefficient of relatedness between them.

$$c < b \times r \text{ (higher inclusive fitness)}$$

where c = cost of altruist, b = beneficiary's gain, r = relatedness of altruist and beneficiary

Reciprocal Altruism

Though much altruism in nature is kin-directed, not all: there are also many examples of animals behaving altruistically towards non-relatives, and indeed towards members of other species. Kin selection theory cannot help us understand these behaviours. The theory of reciprocal altruism developed by Trivers (1971) is one attempt to explain the evolution of altruism among non-kin. The basic idea is straightforward: it may benefit an animal to behave altruistically towards another, if there is an expectation of the favour being

returned in the future. The cost to the animal of behaving altruistically is compensating by the likelihood of this return benefit, permitting the behaviour to evolve by natural selection. For obvious reasons, this evolutionary mechanism is termed 'reciprocal altruism'.

For reciprocal altruism, there is no need for the two individuals to be relatives, nor even to be members of the same species. However, it is necessary that individuals should interact with each more than once, and have the ability to recognize other individuals with whom they have interacted in the past. If individuals interact only once in their lifetimes and never meet again, there is obviously no possibility of return benefit, so there is nothing to be gained by behaving altruistically. However, if individuals encounter each other frequently, and are capable of identifying and punishing 'cheaters' who have refused to behave altruistically in the past, then reciprocal altruism can evolve. A non-altruistic cheater will have a lower fitness than an altruist because, although he does not incur the cost of behaving altruistically himself, he forfeits the return benefits too - others will not behave altruistically towards him in the future. The concept of reciprocal altruism is closely related to the Tit-for-Tat strategy. This evolutionary mechanism is most likely to work where animals live in relatively small groups.

Trivers (1985) describes a remarkable case of reciprocal altruism between organisms of different species, a phenomenon known as 'mutualism' or 'synergism'. On tropical coral reefs, various species of small fish act as 'cleaners' for large fish, removing parasites from their mouths and gills. This is not pure altruism on the part of the cleaners, for they feed on the parasites which they remove. So the interaction is mutually beneficial - the large fish gets cleaned and the cleaner gets fed.

However, Trivers notes that the large fish sometimes behave altruistically towards the cleaners. If a large fish is attacked by a predator while it has a cleaner in its mouth, then it waits for the cleaner to leave before fleeing the predator. This is clearly altruistic - surely the large fish would be better off just swallowing the cleaner and fleeing straight away. Trivers explains the larger fish's behaviour in terms of reciprocal altruism. Since the large fish often returns to the same cleaner many times over, it pays to look after the cleaner's welfare, i.e. not to swallow it, even if this increases the chance of being wounded by a predator. In short, the larger fish behaves altruistically towards the cleaner, by

allowing him to escape before fleeing, because there is an expectation of return benefit - getting cleaned again in the future.

Group Selection

Natural selection: Process of adapting to environment, i.e. according to Darwin, the process by which organisms best suited to survival in their environment achieve greater reproductive success, thereby passing advantageous genetic characteristics on to future generations.

Evolutionists have suggested that 'natural selection' involves "group selection," whereby a member of a group of animals would do something for the biological benefit of its entire group. In this way, evolutionists argue, the fittest group will survive.

'Natural selection' is daily and hourly scrutinizing the slightest variations; rejecting those that are bad, preserving and adding up all that are good; it is silently and insensibly working, whenever and wherever opportunity offers.

It is possible that *altruism* may be advantageous at the group level. A group containing lots of altruists, each ready to subordinate their own selfish interests for the betterment of the group, may well have a survival advantage over a group composed mainly or exclusively of selfish organisms. Thus, group selection allows the altruistic behaviour to evolve.

Within each group, altruists will be at a selective disadvantage relative to their selfish colleagues, but the fitness of the group as a whole will be enhanced by the presence of altruists. Groups composed only or mainly of selfish organisms go extinct, leaving behind groups containing altruists.

In the example of the Vervet monkeys, a group containing a high proportion of alarm-calling monkeys will have a survival advantage over a group containing a lower proportion. So conceivably, the alarm-calling behaviour may evolve by between-group selection.

Kin Selection

Kin Selection, the first proposed explanation for the existence of altruism, explains how altruism may arise between close relatives. When adult animals risk their life to distract potential predators away from their offspring they are exhibiting this form of altruism. Such behaviour is evolutionarily stable since although it decreases an animal's chances of survival, it increases the chances for its offspring.

Although most obvious in the case of direct offspring, kin selection can operate between any animals that are relatives in proportion to their coefficient of relatedness (the proportion of genes that two individuals share by common descent). Where the exact relationship is unknown to the animals involved, it seems likely that they attempt to estimate the degree of relatedness on the basis of apparent similarity.

The basic idea of kin selection is simple. Imagine a gene which causes its bearer to behave altruistically towards other organisms, e.g. by sharing food with them. Organisms without the gene are selfish – they keep all their food for themselves, and sometimes get handouts from the altruists.

Clearly the altruists will be at a fitness disadvantage, so we should expect the altruistic gene to be eliminated from the population. However, suppose that altruists are discriminating in who they share food with. They do not share with just anybody, but only with their relatives. This immediately changes things. For relatives are genetically similar and they share genes with one another. So when an organism carrying the altruistic gene shares his food, there is a probability that the recipients of the food will also carry copies of that gene (how probable depends on how closely related they are).

This means that the altruistic gene can in principle spread by natural selection. The gene causes an organism to behave in a way which reduces its own fitness but boosts the fitness of its relatives – who have a greater than average chance of carrying the gene themselves. So the overall effect of the behaviour may be to increase the number of copies of the altruistic gene found in the next generation, and thus the incidence of the altruistic behaviour itself.

Though this argument was hinted at by *Haldane* in the 1930s, it was first made explicit by *William Hamilton* (1964) in a pair of seminal papers. Hamilton demonstrated rigorously that an altruistic gene will be favoured by natural selection when a certain condition, known as Hamilton's rule, is satisfied. In its simplest version, the rule states that $b > c/r$, where c is the cost incurred by the

altruist (the donor), b is the benefit received by the recipients of the altruism, and r is the co-efficient of relationship between donor and recipient. The costs and benefits are measured in terms of reproductive fitness.

The co-efficient of relationship depends on the genealogical relation between donor and recipient – it is defined as the probability that donor and recipient share genes at a given locus that are ‘identical by descent’.

In a sexually reproducing diploid species, the value of r for full siblings is $\frac{1}{2}$ (0.5), for parents and offspring $\frac{1}{2}$ (0.5), for grandparents and grand offspring $\frac{1}{4}$ (0.25), for full cousins $\frac{1}{8}$ (0.125), and so-on.

The higher the value of r , the greater the probability that the recipient of the altruist will possess the gene for altruism. So what Hamilton's rule tells us is that a gene for altruism can spread by natural selection, so long as the cost incurred by the altruist is counterbalance by a sufficient amount of benefit to sufficiently closed related relatives.

Though Hamilton himself did not use the term, his idea quickly became known as ‘*kin selection*’, for obvious reasons. Kin selection theory predicts that animals are more likely to behave altruistically towards their relatives than towards unrelated members of their species. Moreover, it predicts that the degree of altruism will be greater, the closer the relationship.

In the years since Hamilton's theory was devised, these predictions have been amply confirmed by empirical work. For example, in various bird species, it has been found that ‘helper’ birds are much more likely to help relatives raise their young, than they are to help unrelated breeding pairs.

Similarly, studies of Japanese macaques have shown that altruistic actions, such as defending others from attack, tend to be preferentially directed towards close kin.

In most social insect species, a peculiarity of the genetic system known as ‘haplodiploidy’ means that females on average share more genes with their sisters than with their own offspring. So a female may well be able to get more genes into the next generation by helping the queen reproduce, hence increasing the number of sisters she will have, rather than by having offspring of her own. Kin selection theory therefore provides a neat explanation of how sterility in the social insects may have evolved by Darwinian means.

Kin selection theory is often presented as a victory of the '**gene's-eye view of evolution**', which sees organic evolution as the result of competition among genes for increased representation in the gene-pool, and individual organisms as mere 'vehicles' that genes have constructed to aid their propagation. The gene's eye-view is certainly the easiest way of understanding kin selection, and was employed by Hamilton himself in his 1964 papers.

Altruism seems abnormal from the individual organism's point of view, but from the gene's point of view it makes good sense. A gene wants to maximize the number of copies of itself that are found in the next generation; one way of doing that is to cause its host organism to behave altruistically towards other bearers of the gene, so long as the costs and benefits satisfy the Hamilton inequality. But interestingly, Hamilton showed that kin selection can also be understood from the organism's point of view. Though an altruistic behaviour which spreads by kin selection reduces the organism's personal fitness (by definition), it increases what Hamilton called the organism's **inclusive fitness**. An organism's inclusive fitness is defined as its personal fitness, plus the sum of its weighted effects on the fitness of every other organism in the population, the weights determined by the coefficient of relationship r .

Social organization in insects:

Many animals live together as a group, but they are not necessarily social (e.g. a school of fish) because there is a very precise definition when it comes to sociality. True sociality (eusociality) is defined by three features: 1). There is *cooperative brood-care* so it is not each one caring for its own offspring, 2). There is an *overlapping of generations* so that the group (the colony) will sustain for a while, allowing offspring assist parents during their life, and 3). That there is a *reproductive division of labour*, i.e. not every individual reproduces equally in the group, in most cases of insects, this means there is one or a few reproductive(s) ("queen", or "king"), and workers are more or less sterile.

Degrees of sociality: Obviously not all insects are eusocial. Michener (1969) provided some other classifications of various stages of social insects:

- a) *Solitary*: showing none of the three featured mentioned above (most insects)

- b) *Subsocial*: the adults care for their own young for some period of time (cockroaches)
- c) *Communal*: insects use the same *composite nest* without cooperation in brood care (digger bees)
- d) *Quasisocial*: use the *same nest* and also show *cooperative brood care* (Euglossine bees)
- e) *Semisocial*: in addition to the features in quasisocial, also has a *worker caste* (Halictid bees)
- f) *Eusocial*: in addition to the features of semisocial, there is *overlap in generations* (Honey bees)

Eusociality was considered extremely rare in the whole animal kingdom, and even in insects it was only found in *Hymenoptera* (ants, bees, and wasps) and *Isoptera* (termites). However, recently this has expanded to a few more groups: in gall *aphids* (Homoptera) there are sterile soldiers who would sacrifice their lives to their clone sisters who can reproduce, so they are considered eusocial because these soldiers do not reproduce while others do. This is also the case for social thrips that are gall-forming (Thysanoptera). In non-insects, eusociality only appeared twice: in a mammal and a marine animal. *Naked mole rats* live in complex underground tunnel systems in Africa and animals in the same nest are closely related, only one female (the queen) reproduces, although workers, normally sterile, can ovulate when removed from the nest, presumably due a lack of inhibition from the queen.

Snapping shrimp (*Synalpheus regalis*) lives inside sponges and each 'colony' has 200-300 individuals, but only one queen reproduces, again the caste is probably not fixed - the workers remain totipotent and can potentially become a queen when the queen shrimp is removed.

Evolution of eusociality: How could eusociality evolve? Darwin, in his "Origin of Species" (1859) thought that sterile workers in a bee colony, being unable to transmit their genes, represent a special challenge to his theory of natural selection. This is because natural selection depends on the transmission of 'traits' that convey selective advantages to the individuals, and these traits have to be determined genetically (so they are heritable). If workers are sterile, how can they transmit the "helping traits" to the next generation?

Genetic explanations: This problem continued to trouble biologists until William Hamilton (1964) found an ingenious way to explain how a trait can be inherited without direct reproduction. Hamilton introduced a brave new concept, 'inclusive fitness', which basically says someone could still have a

reproductive fitness, even if he/she has no direct offspring. This is while the **'traditional fitness'** only count how many children one has, but **inclusive fitness takes account of all others who share genes with the person** (or animal). For example, I should share approximately 50% of gene with my full brother, therefore if I decide not to marry and have kids, but I help my brother to raise 4 children, it is equivalent to my self having two children. **This inclusion of anyone elses' fitness, who shares common genes by descent, factored by a coefficient of relatedness, is called inclusive fitness.** Therefore although workers do not reproduce, if they share genes with their mother (the queen) to raise more sisters (future queens) their genes would be transmitted too to the next generation.

In fact in honey bees and other hymenoptera, the relatedness among sisters is higher than among other animals. This is because of the **haplo-diploidy** sex determination: drone develop from unfertilized eggs and carry one copy of chromosomes (haploid) from their mother only (no father), while females are fertilized and carry two copies of chromosomes (diploid). Haploid drones do not have the complimentary copy of genes to do exchange, so all the sperms produced by a single drone are identical. Assume the queen is mated to a drone, then all her daughters will share 50% genes from the father, but 25% of their genes from the mother. The coefficient of relatedness among the offspring is therefore 0.75. This is much higher than the 0.5 for sister-sister in a diploid organism (such as humans). **The workers who share the same father and mother, are therefore also called 'super-sisters' because of this higher relatedness.** This theory of one can pass genes through relatives and gain fitness is called 'kin selection'.

Hamilton postulated that because supersisters share 75% of their genes, it is actually a better deal to be a worker, to whom a new queen would have 75% of genes by common descent with her, whereas from the queen's point of view, she only transmitted 50% of her genes to the new queen. In this sense, the inclusive fitness is actually higher for the sterile worker sisters, than for the fertile mother.

One difficulty with the above argument is that the honey bee queen actually mates with more than one male (drone), in some cases as many as more than 30 drones, because half-sisters (workers who share the same mother, but fathered by different males) are only related to one another by 0.25 the average

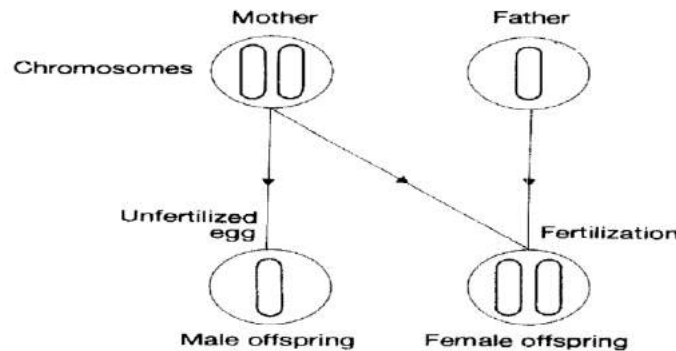
relatedness among the workers in such a colony is close to the average between 0.75 and 0.25, which is 0.5, not different from other diploid organisms.

It is easy to see though, that eusociality can evolve easier in groups within which individuals are highly related, either due to haplodiploidy, or due to mating systems. In both termites and the naked mole rats, animals within a group are all highly related, perhaps due to inbreeding, although it is known in

naked mole
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members are 'clones' because the mother can reproduce asexually (parthenogenesis). However, the marine shrimps do not show high degrees of inbreeding.



rats, some
would migrate
nests to
periodic
outcrossing,
might be
to reduce the
inbreeding. In
colony

Relatedness under haplodiploidy

<i>Relationship</i>		<i>Relatedness (r)</i>
• Mother	daughter	$\frac{1}{2}$
• Mother	son	$\frac{1}{2}$
• Father	daughter	1
• Father	son	0
• Daughter	mother	$\frac{1}{2}$
• Son	mother	1
• Brother	sister	$\frac{1}{2}$
• Brother	brother	0
• Sister	sister	$\frac{3}{4}$
• Sister	brother	$\frac{1}{4}$

Social Behavior in Primates

A group of individuals of the same species organized in a cooperative manner beyond sexual and parental behavior is known as *society*. It is composed of *mothers, daughters, sisters, aunts and nieces*. Male dispersion is more common than female dispersion. Complex social organization exists in many mammals. Social behaviour in mammals is associated with large body size, large brain size, open habitats, and diurnal behavior. Sociality is often considered to increase survival & fitness, cooperative predator avoidance, ready access to mates, kin selection, and thermoregulatory benefits. But, there are also disadvantages, competition for food, mates and space, increase in conspicuousness to predators, and spread of disease and parasites.

Social Structure: Most primates, including humans, spend their lives in large social groups. In the case of [semi-terrestrial](#) species, such as baboons, being in a large community helps provide protection against predatory cats, dogs, and hyenas. It also helps protect scarce food resources. This is especially true for non-human primates when the food is fruit. Leaf-eaters like langurs, tend to form smaller social groupings since there is little competition for their food. The very few nocturnal species of primates are mostly small, relatively solitary hunters.

Most non-human primate communities are more or less closed to contact with members of other communities. Most often, they are tied to particular surroundings and rarely migrate outside of their home range. This unfriendliness from other troops prevents high concentrations of individuals which could result in rapid depletion of local resources. Communities usually avoid each other and are aggressive towards outsiders. As a result, social interactions between members of different troops are usually very rare, especially for females. Chimpanzees are a notable exception. When chimpanzees from different troops come together, there is often an exciting, friendly encounter lasting several hours, following which, some of the *adult females switch groups*. Apparently, they are seeking new mates.

Interactions within non-human primate communities are usually unlimited. All members of a community have daily face to face, casual communication. The most common type of subgroup consists of a mother and her young offspring.

In some forest living primates, contact between groups of the same species is in the form of a specialized territorial defense behavior. Instead of avoiding each other, groups actively converge near their common territorial border and make aggressive displays. Howler monkeys and gibbons all produce exceptionally loud vocalizations for this purpose. This is a ritualized, essentially harmless form of aggression that is intended to intimidate members of the neighboring community. All these species live in home ranges that are usually so small that the food resources of neighboring territories can be seen and become attractive.

Non-human Primate Social Group Composition: While there is considerable variation in social group composition among the primates, there is very little variability within each species. In fact, most non-human primate species are limited to only one of the following basic patterns:

Single Female and Her Offspring: The single female and her offspring group pattern is a rare for primates but common for other mammals. However, they come together with females occasionally for mating. The males of these species generally have large territories that overlap those of several females.

Monogamous Family Group: Monogamous groups consist of an adult male and female with their children. When they are grown, the children leave to create their own nuclear families. While this group pattern is the most common one for humans, it is rare for non-human primates. It is found among the small Asian apes as well as some of the New World monkeys. Specifically, monogamous family groups are the common pattern for gibbons and monkeys.

Polyandrous Family Group: The smallest New World monkeys, form both monogamous and polyandrous family units. They generally start with a monogamous mating pair. Later, a second adult male may join the family and assist in child rearing. When this occurs, both adult males will potentially mate with the adult female. This polyandrous mating pattern is extremely rare among non-human primates.

One-Male-Several-Female Group: One-male-several-female groups have *polygynous* mating patterns. That is to say, one male regularly mates with more than one female. Polygyny is generally not a promiscuous mating pattern. Rather, the male and his female mates form a distinct mating and child rearing group. This pattern is found among baboons, langurs, howler monkeys, and gorillas.

It would be a mistake to automatically assume that non-human primate one-male-several-female groups are dominated by males. Among them females largely control the social group. This is despite the fact that the males are larger, stronger, and more aggressive. Mothers, sisters, and aunts act as a team in chasing off other unrelated females. They also collectively select their mutual mate among a number of potential suitors roaming in and out of their territory. The male that is chosen usually is one that does not act abusively towards them and is willing to cooperate with them in defending their territory. The relationship with any particular male may be short term. The stable core of the community is the group of related females. This is a long way from stereotypical male domination.

One-male-several female groups may take a different form when predator pressure is a problem. In open grasslands, baboon communities are much larger, often consisting of a number of polygynous families. In such multiple one-male-several-female group societies, males are the dominant, controlling members. The adult males not only "herd" their own sexually mature females, but also maintain order and protect the community from predators.

In contrast, gorillas rarely have to be concerned about predator dangers. Subsequently, their communities consist of a single dominant adult male, his mates, and their children. When males reach maturity, they usually are driven off by the dominant silverback male. These exiled males ultimately form their own one-male-several-female groups.

Multimale-Multifemale Group: The most common social group pattern among semi-terrestrial primates is the multimale-multifemale group. With this pattern, there are no stable heterosexual bonds – both males and females have a number of different mates. This is characteristic of baboons, macaques, as well as some monkeys.

Multimale-multifemale groups commonly have a dominance hierarchy among both males and females. Each individual is ranked relative to all other community members of the same gender. This tends to reduce serious violence within the community since everyone knows in advance who they must defer to and who must be submissive to them. Among rhesus macaques, one's position in the dominance hierarchy is determined by the rank of his or her mother. The top ranking individuals are referred to by primatologists as the **alpha male** and the **alpha female**. All other community members defer to them. A female's

rank in the hierarchy stays with her throughout life. However, most young adult male rhesus macaques leave their natal community and ultimately join others to find mates. When they do so, they start at the bottom of the male dominance hierarchy again. Alpha males usually mate more often than others. This makes the social organization superficially look like one-male-several-female group. However, younger females often sneak off to mate with males lower down on the dominance hierarchy. The stable core of rhesus macaque communities is the group of female relatives. They stay within their natal community throughout life and work as a team to defend it against other females.

Fission-Fusion Society: A fission-fusion society is one in which the social group size and composition changes throughout the year with different activities and situations. This is the social pattern typical of chimpanzees. Individuals enter and leave communities from time to time. Adult males occasionally wander off and forage alone or join a few other males in a hunting party. Females casually change membership from one group to the other. This occurs especially when females are in [estrus](#) and seeking mates. As a result, foraging and sleeping groups reform frequently. Male chimps are the relatively stable core of the community since they rarely join other troops.

Unit – III

- i) Reproductive Behaviour: Evolution of sex, reproductive strategies, mating systems, courtship, sperm competition, sexual selection and parental care.
- ii) Hormones and behaviour, pheromones and behaviour.

Reproductive Behaviour: Evolution of sex and reproductive strategies, Mating systems, Courtship, Sperm competition, Sexual selection, parental care

In order for sex to be evolutionarily advantageous, it must be associated with a significant increase in the fitness of offspring. One of the most widely accepted explanations for the advantage of sex lies in the creation of genetic variation. There are three possible reasons this might happen.

First, sexual reproduction can bring together mutations that are beneficial into the same individual (sex aids in the spread of advantageous traits).

Second, sex acts to bring together currently deleterious mutations to create severely unfit individuals that are then eliminated from the population (sex aids in the removal of deleterious genes).

Last, sex creates new gene combinations that may be fit than previously existing ones, or may simply lead to reduce competition among relatives.

Yet, we never learn exactly when or how independent male and female sexes originated. Somewhere along this evolutionary path, both males and females were required in order to ensure the procreation that was necessary to further the existence of a particular species. But how do evolutionists explain this? When pressed to answer questions such as, “Where did males and females actually come from?”, “What is the evolutionary origin of sex?” evolutionists become silent.

How could nature evolve a female member of a species that produces eggs and is internally equipped to nourish a growing embryo, while at the same time evolving a male member that produces motile sperm cells? And, further, how is it that these gametes (eggs and sperm) conveniently “evolved” so that they each contain half the normal chromosome number of somatic (body) cells?

(Somatic cells reproduce via the process of mitosis, which maintains the species' standard chromosome number; gametes are produced via the process of meiosis, which halves that number)

'Sex is the queen of problems in evolutionary biology. Perhaps no other natural phenomenon has aroused so much interest; certainly none has sowed as much confusion. 'Evolutionary biologists are much teased for their fascination with why sex exists. This "mystery" of sex deserves serious consideration in light of its "widespread" prevalence today.

Evolutionists freely admit that the origin of the sexual process remains one of the most difficult problems in biology. Scientists have proposed a simple solution by suggesting that sex is a historical accident - i.e. a kind of "accidental leftover" from the era of single-celled organisms. They claim that the maintenance of sex is therefore a "nonscientific" question that "leads to intellectual mischief and confusion. This implies, however, that sex is useless, and that it has been retained through the years merely by accident.

Evolutionists have practically been forced to admit that there must be "some advantage" to a system as physiologically and energetically complex as sex-as Mark Ridley admitted when he wrote: It is highly likely that sex has some advantage, and that the advantage is big. Sex would not have evolved, and been retained, unless it had some advantage.

Sir John Maddox, who served for over twenty-five years as the distinguished editor of *Nature*, the prestigious journal published by the British Association for the Advancement of Science (and who was knighted by Queen Elizabeth II in 1994 for "multiple contributions to science"), authored an amazing book titled 'What Remains to be Discovered' in which he addressed the topic of the '*origin of sex*'.

The overriding question is when (and then how) sexual reproduction itself evolved. Despite decades of speculation, we do not know. The difficulty is that sexual reproduction creates complexity of the genome and the need for a separate mechanism for producing gametes. The metabolic cost of maintaining this system is huge, as is that of providing the organs specialized for sexual reproduction (the uterus of mammalian females). What are the compensating benefits? The advantages of sexual reproduction are not obvious. What is that "purpose"? And how can evolution (via natural selection) explain it? As it turns out, the common "survival of the fittest" mentality cannot begin to explain the

high cost of first evolving, and then maintaining, the sexual apparatus. Sexual reproduction requires organisms first to produce, and then maintain, gametes.

The *Origin of Sex – from Asexual to Sexual Reproduction*: Many single-celled organisms reproduce asexually. Asexual reproduction is the formation of new individuals from cells of only one parent, without gamete formation or fertilization by another member of the species. Asexual reproduction thus does not require one egg-producing parent and one sperm-producing parent. A single parent is all that is required. Sporulation (the formation of spores) is one method of asexual reproduction among protozoa and certain plants. A spore is a reproductive cell that produces a new organism without fertilization. In certain lower forms of animals (e.g., hydra), and in yeasts, budding is a common form of asexual reproduction as a small protuberance on the surface of the parent cell increases in size until a wall forms to separate the new individual (the bud) from the parent. Regeneration is another form of asexual reproduction that allows organisms (e.g. starfish and salamanders) to replace injured or lost parts.

Evolutionists have suggested four different theories, known in the literature as: (1) the Lottery Principle; (2) the Tangled Bank Hypothesis; (3) the Red Queen Hypothesis; and (4) the DNA Repair Hypothesis.

The Lottery Principle: It was first suggested by American biologist George C. Williams in his monograph, *Sex and Evolution*. Williams' idea was that sexual reproduction introduced *genetic variety in order to enable genes to survive in changing or novel environments*. He used the lottery analogy to get across the concept that breeding asexually would be like buying a large number of tickets for a national lottery but giving them all the same number. Sexual reproduction, on the other hand, would be like purchasing a small number of tickets, but giving each of them a different number.

The essential idea behind the Lottery Principle is that since sex introduces variability, organisms would have a better chance of producing offspring that will survive if they reproduce a range of types rather than merely more of the same. The point being made by those who advocate the Lottery Principle is that, in their view, *asexual reproduction is poorly equipped to adapt to rapidly changing environmental conditions* due to the fact that the offspring are exact duplicates of their parents, and thus inherently possess less genetic variation. Therefore, sex brought the variations that could allow organisms to survive.

The Lottery Principle suggests that sex would be favored by a variable environment, yet a close inspection of the global distribution of sex reveals that where environments are stable (such as in the tropics), sexual reproduction is most common. In contrast, in areas where the environment is unstable (such as at high altitudes or in water bodies), asexual reproduction is widespread.

The Tangled Bank Hypothesis: It suggests that sex evolved in order to prepare offspring for the complicated world around them. The “tangled bank” phraseology comes from the last paragraph of Darwin’s Origin of Species, in which he referred to a wide assortment of creatures all competing for light and food on a “tangled bank”. According to this concept, in any environment where there exists intense competition for space, food, and other resources, a premium is placed on diversification. As Zimmer described it: In any environment – a tidal flat, a forest canopy, a deep-sea hydrothermal vent - the space is divided into different niches where different skills are needed for survival. A clone specialized for one niche can give birth only to offspring that can also handle the same niche. But sex shuffles the genetic deck and deals the offspring different hands. It’s basically spreading out progeny so that they’re using different resources.

The Red Queen Hypothesis: It was first suggested by **Leigh Van Valen** in an article titled “A New Evolutionary Law” in *Evolutionary Theory*. His research suggests that an animal constantly must run the “**genetics arms race**” being able to ***chase its prey, elude predators, and resist infection from disease-causing organisms***. That is to say, they constantly have to “***run to try to improve***” (and the development of sex would be one way of accomplishing that). Yet doing so provides no automatic guarantee of winning the struggle known as “survival of the fittest.” Currently, the Red Queen Hypothesis seems to be the favorite of evolutionists worldwide in attempting to explain the reason as to the “why” of sex.

The DNA Repair Hypothesis: We argue that the lack of ageing of the germ line results mainly from repair of the genetic material by meiotic recombination during the formation of germ cells. Thus our basic hypothesis is that the primary function of sex is to repair the genetic material of the germ line. [Somatic cells die, but the germ line seems to be practically immortal.]

DNA can be damaged in at least two ways. First, ionizing radiation or mutagenic chemicals can alter the genetic code. Or, second, a mutation can occur via errors during the replication process itself. Most mutations are

deleterious. In an asexual organism, by definition, any mutation that occurs in one generation will be passed on automatically to the next. Mark Ridley compared it to what occurs when you photocopy a document, then photocopy the photocopy, and then photocopy that photocopy, etc. Eventually, the quality deteriorates severely. Asexual organisms, as they continue to accumulate mutations, face the unpleasant prospect of eventually becoming both unable to reproduce and unviable-neither of which would be at all helpful to evolution.

But sexual reproduction allows most plants and animals to create offspring with good copies of two genes via crossover and would thus, help eliminate this downward ratchet since mutations, although they might still be passed on from one generation to the next, would not necessarily be expressed in the next generation.

Reproductive strategies

Although every organism struggles to survive, individual survival is not enough to ensure continuation of the species. Individuals must reproduce. Reproduction takes extra energy, and so it would seem that those organisms best suited to capture energy in the environment are those most likely to leave numbers of descendants. Survival of the fittest helps to keep animals and plants strong and adapted to their environments.

Scientists have identified two strategies for leaving living descendants. These strategies are called the r-strategy and the k-strategy. Some organisms, animals and plants, use one strategy or the other: some seem to tend towards one but are closer to a sort of mid-point. Let's compare these strategies. Remember that R stands for Rapid so that you will remember which strategy is which. R-Selected parents rapidly produce many descendants, but do not provide care for them.

We see that r-selected organisms have many babies, but most of these youngsters never become adults. Frogs are a good example of r-selected organisms. Frogs lay many eggs and leave them in the water to hatch into tadpoles. Some of the eggs get eaten, and many of the little tadpoles are eaten, too, by dragon-fly larvae and fishes and fishing birds. When the tadpoles become frogs, many animals are waiting on shore to eat them: foxes, snakes, cats, and many other small predators. If one frog from a hundred eggs lives to be a parent, his/her survival is really outstanding. But frogs go on because they lay so many eggs.

Elephants are examples of K-selected animals. Female elephants have babies about three years apart, and they have only one each time. The whole group looks after the youngsters, and protects them through childhood and adolescence. By reproducing at a rate that holds their numbers close to constant, elephants are able to survive in stable ecosystems. Because they ensure the survival of a good percentage of their young, elephants do not need to produce many elephant babies.

Reproductive Strategies	
r-selected	K-selected
mature rapidly	mature slowly
short-lived: most die before they reproduce	tend to live long lives: low juvenile mortality rate
have many offspring - tend to overproduce	have few offspring at a time
invest little in individual youngsters	care for their young
most pest species are r-selected	most endangered species are K-selected
population not regulated by density: boom and bust population figures	population stabilizes near carrying capacity
opportunistic - invade new areas	maintain numbers in stable ecosystems

Mating System

Monogamy: male and female defend a territory against solitary individuals both range together mate as a pair and often live as a pair, e.g. lemur, monkeys, gibbons - may have two females or two males and one doesn't breed. Monogamous species of males and females pair for the breeding season. In some cases, the individuals may pair for life.

Polyandry: Mate with more than one male - the smaller animals (females) need more help raising offspring and thus get more paternal care (carrying the infants and supplementing their food).

Polygyny: One male mates with more than one female - have pressure to increase group size in order to defend resources, e.g. howler monkeys, leaf monkeys, gorillas. In polygynous species, males have multiple female partners in a single breeding season. In some cases a male may control a large group of females in other cases there may be sequential polygyny, in which a male visits

with successive females. Multi male polygyny - when number of females start to increase, one male cannot keep other males out, therefore multi male polygyny occurs, e.g. howler monkeys, capuchins, baboons, macaques, leaf monkeys.

There are also subcategories of polygynous and polyandrous mating systems that are defined in terms of whether the mating systems are *resource based or non-resource based*. In a resource based polygynous mating system a male defends some resource that might sustain several females. In a non-resource based mating system like a lek, females aggregate in regions with sole purpose of choosing a mate. Males aggregate in these locations and display in order to gain access to females.

Lek Paradox: In the evolution of a resource based mating system, females end up settling on a male's territory or depositing eggs on a male's territory because of the quality of his territory. Females come around and pick from the available males. The paradox of the lek is that they usually mate with one male. However, many females line up and mate with one male. The real paradox is why the other males bother to come to the lek at all if only a single male is going to get copulated. These males would do far better to go in search of females because they would at least get one or two copulations and not up end as big losers. Many species form leks - fish, insects, birds. It is nearly a winner take all form of mating. There are big winners and big losers.

Courtship

Courtship is a complex set of behaviors in animals that leads to mating. Courtship behavior communicates to each of the potential mates that the other is not a threat. It also reveals information to each animal that the species, gender, and physical conditions of the other are suitable for mating. Pre-mating activities are for the most part ritualistic. They consist of a series of fixed action patterns that are species-specific. Each fixed action triggers an appropriate fixed reaction by the partner, with one action stimulating the next. Courtship allows one or both sexes to select a mate from several candidates. Usually, the females do the choosing. In some species of birds, males display in a lek, a small communal area, where females select a mate from the displaying males. Males, generally, compete with each other for mates, and females pick the best quality male available. The danger of courtship is that it can attract predators instead of mates.

Several basic factors influence a female's choice of mate. First, if a female provides parental care, she chooses as competent a male as possible. For example, in birds such as the common tern, the female selects a good fish catcher. As part of courtship, the male birds display fish to the female, and may even feed them to her. This demonstrates his ability to feed the young. In addition, females tend to select males with resources such as food or shelter which help a mating pair to produce more offspring that survive.

In the long-jawed long-horned beetle that lives in the Arizona desert, males battle each other for saguaro cactus fruit. The females mate in exchange for access to the fruit. A male endowed with large mandibles can defeat other males, take over the fruit, and thus attract females. Genetic fitness is another important factor in mate selection.

In species that lack parental care, offspring rely for survival on qualities that they inherit from their parents. During courtship, energetic displays and striking appearance indicate good health. Vigorous, attractive parents generally pass immunities to their offspring. Attractiveness may depend on the intensity of secondary sex characteristics, which in birds, for example, include colorful plumage and long tails. Another advantage is that inherited attractive features make offspring desirable to mates.

Courtship and Mating of Birds: A bird without a mate is a bird without offspring. Because natural selection has placed the burden on each bird to leave descendants, birds have evolved into creatures that use a variety of methods to meet the challenge of providing the next generation. Courtship and mating rituals are among the most varied and fascinating of all bird behaviors. The sequence and variety of courting behaviours vary widely among species, but they typically begin with territorial defense and song followed by mate-attraction displays, courtship feeding, and selection of a nest site.

The mating displays of North American songbirds are essential steps on pair formation and can be extremely interesting to watch. A male songbird, establishes its nesting territory by singing repeatedly from different perches, announcing its presence to competitors and potential female mates alike, and by vigorously chasing away intruders. In some species the male initially treats the female as an intruder to be chased away. Eventually, the male establishes a peaceful coexistence with neighboring male of its own species. In many species females arrive on breeding grounds after males each spring, and to some extent have the privilege of choice among prospective mates. The female may base its

choice on the song or appearance of the male, on the size or quality of the territory the male defends, or on aspects of compatibility not apparent to us. Whatever the method the female uses, the goal is the same: to find a mate likely to provide the offspring with the best chance of survival and continued reproduction.

The potential pair may then engage in a series of displays by one or both birds over the next several hours, days, or weeks, to initiate and strengthen a bond between them. The early displays may be slight, or they may be quite noticeable. Mating displays can also be quite spectacular, as in the sky dance of the Northern Harrier. Over fields or marshes across North America in April you may see this usually low-flying hawk climbing skyward on powerful wing strokes, and then plunging toward the ground while uttering a faint chipping call. The dive is usually repeated in a continuous series by the male, who traces a deep U-shaped pattern or cartwheels in the sky.

Bird Courtship Nests: Some species use other methods to attract mates or develop pair-bonds. The male Marsh Wren builds several almost spherical courting nests and each nest is sturdily woven of grasses and contains a small side entrance. While the male sings and displays, the female enters its territory and inspects the nests. If the female accepts the male, it adds a lining to one of the courtship nests to prepare it for a clutch of eggs. The female may judge a male's potential as a mate by the number and quality of his nests.

Courtship Variety: Every species of bird performs a slightly different courtship ritual. These differences help to ensure that only birds of the same species will mate. Males and females also perform different and complementary roles, thus only attracting members of the opposite sex. Before mating season, many male birds grow colorful plumage. They then show off to attract a mate. Birds that are less colorful, such as species of the warbler, show much less variety of plumage between the sexes. Instead, they use extremely complicated and individual songs to identify themselves and to attract a mate.

Male Dandies (attractive display may be with fashion): Usually it is the male that plays the leading role in courtship by showing off his plumage to the duller colored females. For plainer birds such as the house sparrow, the males display may consist of puffing out his chest or tipping his head back to emphasize his dark bib. Exotically feathered species such as the male peacock often put on a stunning display. The male peacock will fan his tail to present a dazzling array of blue, green, and golden feathers in one of the showier displays of any bird.

Gift Giving: Many birds perform a ritual known as courtship feeding or gift giving. Usually the female will spread her wings and open her beak, behaving like a young bird begging for food. This ritual not only allows her to build up her strength for the demanding job of laying and incubating the eggs, but it also assures her that the male will be a good provider for the chicks. Instead of food, some species of bird present their partners with nesting material. Herons give their mates large twigs which are offered up with ceremonial bowing. Gift giving is probably a symbolic show of the males nest building abilities.

Mutual Display: Plumage of similar color across the sexes means that they are more equal in their courtship displays. Albatross, for example, perform complex joint rituals which look like a courtly dance. The longer the display lasts, the closer the bond formed between them. Some species perform courtship displays in the air. Lapwings try to impress their mates by tumbling through the air as if they were about to crash. Male skylarks fly high into the air singing loudly. Many birds of prey court each other by displaying their hunting skills in mock aerial combat. The female peregrine falcon will often fly on its back as the male swoops overhead; the pair briefly touches claw to claw. The male may even pass food to the female during similar encounters.

Birds often begin their courtship awkwardly. They become more skillful as they progress. Once the ritual is performed perfectly, the birds will often mate. Mating is not the only goal of the courtship ritual, however; many pairs remain together to share the tasks of building nests, incubating eggs, and raising young.

Sperm Competition

Sperm competition is "competition between sperms of two or more males for the fertilization of an ovum". Sperm competition is often compared to having tickets in a lottery; a male has a better chance of winning (i.e. fathering offspring) the more tickets he has (i.e. the more sperm he inseminates a female with). However, sperm are costly to produce and the energy may be spent elsewhere such as defending a territory to the exclusion of other males; the distribution of resources is called strategy.

Sperm competition may lead to evolutionary adaptations for producing more sperm, such as larger testes. Such adaptations cost and so species with low sperm competition invest in mate competition instead. Other means of sperm competition could include improving the sperm itself or its packaging materials (spermatophore).

In primates relative size of testes compared to body mass against the mating system and it reveals that promiscuous chimpanzees have larger testes compared to polygynous gorillas.

A few researchers have even suggested that sperm competition per se could lead to the "fittest" sperm reaching the egg. The sperm is free-swimming and must reach the egg before it dies. The sperm of highest quality might also be carrying high quality genes to the egg. Thus a female that participates in multiple mating might be setting up a sperm competition in which the sperm from many males compete and the best sperm wins the race. The female not only gets offspring that might be of superior genetic quality, but she also gets offspring that are quite variable.

Sexual selection

Sexual selection is the theory proposed by Charles Darwin that states that the frequency of traits can increase or decrease depending on the attractiveness of the bearer. Biologists today distinguish between "male to male combat" (it is usually males who fight), "mate choice" (usually female choice of male mates) and "mate compulsion" (forced mating).

Traits selected for by 'male combat' are called "weapons", and traits selected by 'mate choice' are called "ornaments". Much attention has recently been given to cryptic female choice, a phenomenon in internally fertilizing animals such as mammals and birds, where a female may simply dispose of a male's sperm without his knowledge. The equivalent in male-to-male combat is sperm competition.

The exact effect of sexual selection depends on the sex ratio, which is usually slightly biased in favour of the "limiting" sex (typically females). Male to male combat is also classified as intrasexual competition, while mate choice and mate compulsion are also known as intersexual competition.

Females often prefer to mate with males with external ornaments - exaggerated features of morphology. These can plausibly arise because an arbitrary female preference for some aspect of male morphology initially increased by genetic drift, creating in due course, selection for males with the appropriate ornament. This is known as the **sexy son hypothesis**. Alternatively, genes that enable males to develop great ornaments may simply show off greater disease resistance or a more efficient metabolism - features that also benefit females. This idea is known as the **good genes hypothesis**.

The success of an organism is not only measured by the number of offspring left behind, but by the quality or probable success of the offspring: *reproductive fitness*. Sexual selection is the expansion on the ability of organisms to differentiate each other at the species level, interspecies selection.

Males of almost all animals have stronger excitement than females, and "The female with the rarest of exceptions is less eager than the male, she is coy" (shy / reserved). Darwin wrote these words 140 years ago, in his book 'The Descent of Man and Selection in Relation to Sex'. He theorized that these male/female characteristics result from females choosing mates who are "vigorous and well-armed, just as man can improve the breed of his game-cocks by the selection of those birds which are victorious in the cock-pit."

"Males, who can produce many offspring with only minimal investment, spread their genes most effectively by mating promiscuously. Female reproductive output is far more constrained by the metabolic costs of producing eggs or offspring, and thus a female's interests are served more by mate quality than by mate quantity."

Females look for males with the best genes, whereas males want to fertilize as many females as possible. Genetically superior males distinguish themselves as the winners of male-male contest, as having the most expensive and beautiful ornaments, as among peacocks. These male and female profiles, together with the cheap sperm/expensive egg justification, comprise what biologists call "sexual-selection theory."

According to sexual-selection theory, more sex is always better for males. Males who mate whenever the opportunity presents itself, and make their own opportunities when possible, will sire more progeny. Mammals seem to follow this pattern. About 90 percent of mammal species are polygynous, with one male servicing many females. However, monogamy not only exists, but is quite common.

Fully 90 percent of bird species are economically monogamous - a male and female bird cooperates in raising the eggs together in their nest. Often some of those eggs are sired by neighboring males, and females deposit some eggs in adjacent nests, so that parental relationships are distributed in neighborhoods. Thus, in birds economic monogamy often occurs without reproductive monogamy. Turning to monogamous mammals, males contribute to parental care by building a den, burrow, or lodge, defending the family's feeding territory, feeding his mate, etc. Although not as common as in birds, mammalian monogamy does happen. Most wild canines, as well as 15 percent of primates, are faithful to a single mating partner. Monogamy too contradicts sexual selection.

Sexual selection views mating as solely for conception. But the point of mating is not usually to make babies; it usually serves a social function. Mating occurs too often relative to number of offspring produced to be solely for conception. The intimacy of sex strengthens relationships between adults, defuses social tensions, and helps keep groups together, as in our closest living relatives. Strong social bonds help ensure males and females will work well as a team to protect and raise young.

Parental Care

Parental Care carries several distinct benefits, and it is curious why it is not pervasive in the animal kingdom. An organism that gives its offspring a boost would be at a tremendous advantage over another that provided less parental care. Parental care can even include extra energy added to eggs when they are laid in organisms without parental care. This strictly material provisioning benefits the offspring tremendously. Bigger is usually better. Thus, the arguments described below are equally applicable to animals with and without parental care.

Lack's Hypotheses: David Lack reasoned that parental care or provisioning is a relatively expensive proposition. There is a cost of reproduction that forms some sort of limit on how much an animal can do to provide care to its offspring. *Lack* also came up with an experimental paradigm for testing whether such costs of reproduction exist in birds.

Lack manipulated clutch size and he reasoned that the parental bird would work harder to fledge the extra young and the extra cost of parental care would lead to increased mortality to the next breeding season. Since Lack's time, researchers have documented such costs of reproduction. They have also found that survival costs were not the only way energy limitation might manifest itself as a drop in fitness. In experiments with some species, the researchers found that they did not have a dramatic impact on the survival of the parents. Rather, they found that the size of fledglings or the number of fledglings that survived was reduced in nests that received extra eggs compared to control nests. Fledgling size or perhaps fledging survival was enhanced in nests where eggs were removed.

The second result suggests that there is a trade-off between the number and quality of offspring that a bird can produce. African elephants exhibit overlap promiscuity. This strategy is employed by over sixty percent of mammal species. Some of the reasons overlap promiscuity is so common are that it is the ultimate strategy for males, food resources on a home range are not defensible, predations threats are low, and males can randomly mate and without the responsibility of future parental care. For this strategy to develop, females must be able to raise offspring without the help of a father. Females benefit from promiscuity because they can care for their young alone, it reduces the chance of inbreeding, and they receive good genes from successful males as well as resource gifts from competing males.

The minimum amount of parental care is none, beyond the nutritional investment in the egg. Investment beyond the minimum comes in the forms of guarding the eggs and young, providing further nutrition, and the social transmission of information.

The fundamental balance, which can be modeled as a game, is whether more reproduction will be gained through producing more offspring or through caring for the offspring which are already present. For most animals, though, this game is very much biased by evolutionary history; species which produce highly dependent offspring do not exercise a range of potentially successful choices that includes abandonment of neonates.

Even if evolution has already resolved many of the issues, continued conflict over the balance between present and future reproduction is well known in birds and mammals. These conflicts center on issues like the timing of weaning, the timing of dispersal of juveniles, and the balance between the benefits of social foraging and the costs of feeding a larger social group.

In general, if there is substantial parental care the female is the caregiver. Male mates may remain with the female to ensure paternity, particularly if other opportunities to mate are not present, and the male presence sometimes extends to helping with defending the young and collecting food. Most biologists view this asymmetry of involvement in parental care as an extension of the differences in gametic investment.

In many terrestrial and some aquatic animals the female carries the developing zygote internally prior to laying an egg or giving birth. This gives the male ample opportunity to leave the female, perhaps to search for other mates. In a sense, the female is "stuck" with parental care after laying the eggs or giving birth, because her mate has abandoned her.

In exceptional cases, such as seahorses and midwife toads, males are the primary caregivers. These are interesting examples of how evolution can be driven to unusual solutions.

African elephant calves depend on their mothers for the first three to five years of life. Researchers compared the interaction behaviors of young male elephants to those of young female elephants. Female elephants stay with their birth family for life while males live with the group until reaching puberty, between the age of nine and fifteen. Common calf activities include feeding, resting, and traveling. As calves mature, more time is required for feeding and

thus traveling and resting time decrease for both males and females. Males spend more time suckling and playing than females. During the first two years of life milk is the primary means of nutrition for young calves, weaning takes up to four years and often is completed after the birth of a new sibling. The major interaction between immature elephants can be categorized as playing, which includes chasing, mounting, rolling, trunk wrestling, and sparring. The rates of play decrease significantly, especially among family members, after the first year of life. Aggressive encounters are observed occasionally and included pokes, shoves, slaps, chases, and threats; the number of competitive interactions increases with age, particularly among males.

As calves of both sexes get older, the mean distance between child and mother increases consistently, though males tend to be more independent of their mothers. Female calves interact with mothers at a constant rate, however, the male rate of interaction declines with age. This research provides evidence that the generation and maintenance of behavioral sex differences among juvenile elephants develops as a consequence of, and to reinforce, divergent adult social organization.

The strong genetic and social bonds within family groups provide the opportunity for interactions between calves and older female siblings as well as family members. Animals other than the mother often care for young calves by providing protection, interaction, and assistance. Allomothering helps maintain matriarchal societies and enhances calf survivorship.

During the first three months of live calves are completely dependent on their mothers for survival. Calves learn to feed independently after the age of two, therefore the period between three and twenty-four months in age is most significantly influenced by allomothering. Complete weaning occurs around the age of five, until this time calves are rarely found more than two meters from a family member. Young elephants interacted by touching, greeting, playing, rubbing, comforting and suckling.

Aggression rates between calves and young adult males were higher than the rate of aggression between allomothers and calves. If a calf vocalizes distress, an immediate response by a family member is observed.

Nearly all interactions between calves and allomothers (including occasional interactions from unrelated females) are helpful, affectionate, and positive. Known siblings cared for calves more often than distantly related

females. Claves of young, inexperienced mothers needed more assistance from allomothers than experienced mothers.

Hormones and behaviour, Pheromones and behaviour

Operating alongside the nervous system is a specialised group of organs called **endocrine glands**. These glands provide another means of communication within the animal's body, via **hormones**.

Hormones are secreted by the glands into the bloodstream in response to specific **stimuli**. Because they operate via the circulatory system, hormonal messages are much slower than the electrical messages of the nervous system. They also have longer-lasting effects on their **target** organs, some effects persisting for months.

In vertebrates the most important endocrine glands affecting behaviour are the **pituitary gland**, the **gonads** and **placenta** and the **adrenal gland**. Hormones of the **thyroid** and **parathyroid** glands, **pancreas** and **gastrointestinal mucosa** have no direct behavioural effects.

The pituitary gland is situated under the hypothalamus on the floor of the brain. It plays an important role as the central controller of the endocrine system. The pituitary's anterior and posterior lobes secrete hormones which indirectly affect blood pressure and water absorption (**vasopressin**), gamete production and the secretion of sex hormones (follicle stimulating hormones, luteinising hormone).

In response to luteinising hormone (LH), testes secrete male hormones or androgens (**testosterone** and **androsterone**). One of these, **testosterone**, influences the development and maintenance of the male reproductive tract, the formation of secondary sexual characteristics and various aspects of behaviour, particularly aggression.

In females, LH stimulates the ovaries to secrete **oestrogens** and **progesterones**. Between them they perform analogous functions to the androgens in males.

The paired adrenal glands are situated next to the kidneys and have two anatomical components, the **medulla** and the **cortex**. The medulla secretes **adrenalin** and **noradrenalin** which play important roles in producing 'fight or flight' reactions in emergencies.

In response to adrenocorticotrophic hormone (ACTH) from the pituitary, the adrenal cortex secretes a range of 28 steroid hormones which aid metabolism and resistance to infection.

Hormonal Actions Affecting Behaviour

The effects of hormones on behaviour can be traced to three major sites of action. These are: (1) the nervous system, (2) sensory perception and (3) effector organs and structures.

Hormonal Effects on the Nervous System:

Hormones affect many aspects of the nervous system including its anatomy, biochemistry and transmission capabilities.

Sexual dimorphism in the anatomy of certain neurons in the rat hypothalamus appears to be mediated and the maturation of reflex connections within the CNS is accelerated by high levels of thyroxin.

Corticosteroid and sex hormones, by virtue of their effect on calcium metabolism, indirectly affect nerve conduction in which calcium ions play an important role.

Hormones may actually induce inhibition. Oestrogens inhibit aggressive behaviour in female hamsters. Among invertebrates, the sexual receptivity of female grasshoppers (Orthoptera) is inhibited by hormones.

Hormonal Effects on Sensory Perception:

Many studies suggest that hormones affect an animal's sensory capabilities. In doing so, they alter the animal's perception of its environment and the way it responds to certain stimuli.

During the spring, male three-spined sticklebacks migrate from the sea to their freshwater breeding grounds. Migration is brought about by changes in hormonal output by the pituitary and thyroid glands. In particular, thyroxin alters the fishes' salinity preference from salt water to freshwater, thus providing the impetus for migration.

In many female mammals, sensory perception is influenced by the oestrus cycle. Female rats fluctuate in their ability to detect certain odours according to the levels of oestrogen and progesterone.

Similarly, visual sensitivity in female humans varies with the stage of their menstrual cycle. Visual sensitivity, as determined by ability to detect a small light, is most acute at around ovulation and least acute during menstruation.

Sensory perception in males is also influenced by hormones. Experienced male rats prefer the odour of urine produced by oestrous females to that produced by females in dioestrous. This preference disappears in castrated males. Androgens produced by the testes therefore modify the animals' response to standard olfactory stimuli, although the effect is partly confounded with those of experience.

Hormonal Effects on Effector Organs and Structures:

Animals use a variety of their structural components in the execution of behaviour. Hormones may affect these structures and hence the efficacy of the behaviour in a number of ways. Good examples are the secondary sexual adornments of male birds. These may be just bright plumage or bill colorations or they may be elaborate and gaudy structures like combs and wattles.

Secondary sexual adornments appear to serve a variety of functions including the attraction of mates, the deterrence of sexual rivals and the declaration of reproductive condition. The production and maintenance of these adornments depend on androgen levels.

For example, comb and wattle size in newly-hatched male and female domestic chicks can be increased to proportions normally found in sexually mature males by injections of testosterone.

Bill pigmentation in many species fluctuates in intensity with the time of year. In both sexes of house sparrow (*Passer domesticus*), the bill changes from pale brown to black at the beginning of the breeding season. Removal of the gonads in either sex inhibits the deposition of melanin and results in a cream-coloured bill.

Androgens are also important in determining seasonal changes in plumage patterns. Castrated male ruffs (*Philomachus pugnax*) and black-headed gulls (*Larus ridibundus*) fail to assume their characteristic breeding plumage. In red-necked and Wilson's phalaropes (*Phalaropus* spp.), in which females instead of males acquire brightly coloured breeding plumage, pattern changes are also controlled by androgens.

Similar breeding and competitive status changes are found in mammals. Horn and antler size in certain male artiodactyls is used as a deciding factor in sexual disputes and mate choice and appears to be at least partly under the control of androgens. In these cases, the effects of hormones on sexual and aggressive behaviour may be mediated through their effects on relevant bodily structures.

Developmental Effects of Hormones:

Hormones, however, have profound effects on the development of young animals and impart some characteristic features to their behaviour. At a very direct level, hormones affect embryonic development. Hormone mediated anatomical and physiological changes are important in the development of sexual behaviour.

In guinea pigs, testosterone levels influence the development of the genitalia. Treatment of pregnant females with testosterone proportionate results in female offspring with male-like genitals.

In rats, analogous effects occur after birth rather than *in utero*. If female rats are treated with testosterone when about four days old, their oestrous cycle and sexual behaviour as adults are suppressed.

The CNS in neonatal rats seems to be relatively undifferentiated as far as sexual behaviour is concerned, although there is a tendency towards characteristically female patterns. It is only by the direct action of testosterone that male behaviour develops.

The rat and guinea pig examples illustrate an important characteristic of developmental hormonal effects on behaviour. The effects are exerted during species-specific 'critical periods'. The presence of an appropriate hormone during the critical period determines anatomical and behavioural characteristics for life. No amount of therapy with oestrogen and progesterone will revive female sexual behaviour in female rats treated with testosterone during their postnatal critical period. Developmental hormonal effects are therefore irreversible.

The increase in aggression shown by female mice after treatment with androgens.

Differences in the effects of hormones are even more marked between species. Progesterone induces sexual receptivity in female rodents but inhibits receptivity in some primates.

In Japanese quail, testosterone enhances sexual behaviour in males but has hardly any effect on females. On the other hand, oestrogen produces normal female behaviour in females but both male and female behaviour in males.

Seasonal effects:

In red deer (*Cervus elephus*), the administration of testosterone in winter brings about full rutting behaviour. A similar administration in late spring has no effect at all.

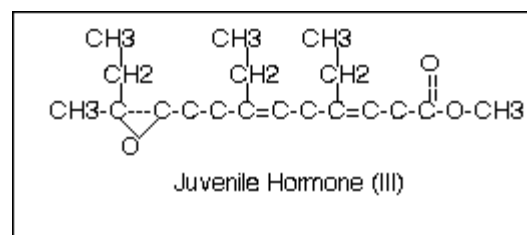
Even the animal's past experience can influence hormonal effects. Copulatory actions in castrated male cats tend to be more protracted if they have copulated in the past. Inexperienced animals show reduced copulatory vigour. Clearly, hormonal influences on behaviour are not simple and readily predictable.

Juvenile Hormone:

Juvenile hormone (JH), produced by the corpora allata, regulates two important processes in insects. The first is development; as an insect develops, the degree juvenility of the next stage is determined by the amount of JH in the blood; the lower the JH, the more adult the next stage. Experimental removal of the corpora allata results in premature development of adult characteristics. JH occurs in several forms; the most common is JH-III, which is shown here.

The other function of JH is, in many insects, to regulate the production of eggs in the female's ovaries. Because mating behaviour is often synchronized with the ovarian cycle, it makes sense for mating behaviour and pheromone production to be linked with JH. In some insects, including species of cockroach this is exactly the case.

In other species the role of JH has evolved one step further, so that the linkage with ovarian activity is lost. In the most intensively studied species, the honey bee, many scientists think JH regulates the behavioral activities of workers through their life.



Aggressiveness of guard bees is correlated with their blood JH levels. Even though guards have high JH levels, their ovaries are relatively undeveloped. JH titers in worker honey bees progressively increase through the first 15 or so days of the worker's life. During this period workers perform tasks inside the hive, such as nursing larvae, constructing comb, and cleaning cells. JH titers peak around day 15; workers this age guard, remove dead bees from the colony, and fan at the colony entrance to cool the nest. Older workers forage for pollen and nectar.

This behavior prevents robbing of honey from the nest by bees from other colonies. It is not an easy trick for the guards to tell which incoming bees to attack and which to not. They do this by smelling odors on the surface of the incoming bees; the bees that do not smell like nestmates are attacked.

Allohormones: In the case of hormones transferred from one partner to another, advocate the use of the term allohormone (*allos* – arousal by another), which refers to a substance that induces a direct behavioural response, bypassing sensory structures. Allohormones are distinct from pheromones, which are signaling compounds that are detected by sensory structures and then transferred to salient integrating centers of the central nervous system.

Allohormones alter target tissues such as the reproductive system, just like hormones, and in many cases allohormones are derived from the same biosynthetic pathways as hormones produced by the targeted individual. An allohormone is found in the garden snail *Helix aspersa*, which enhances male fertility. In the dusky salamander, *Desmognathus fuscus*, the male secretes a substance from the mental gland and then transfers it to the females back, only after having scraped the female's back raw with specialized maxillary teeth. The substance from the mental gland is directly transferred to the female's bloodstream and it appears to make the female more receptive.

Pheromones and behaviour

Pheromones are the molecules used for communication between animals. A broader term for chemicals involved in animal communication is *semiochemical*. Pheromones are a subclass of semiochemicals, used for communication within the species.

Pheromones were originally defined as substances secreted to the outside by an individual and received by a second individual of the same species in which they release a specific reaction for instance a definite behaviour (releaser pheromone) or developmental process (primer pheromone).

The word pheromone comes from the Greek *pherein*, to carry or transfer and *hormon*, to excite or stimulate. The action of pheromones between individuals is contrasted with the action of hormones as internal signals within an individual organism. Pheromones are often divided by function, for example into sex pheromones and aggregation pheromones. *Bombykol*, a substance secreted by female silk moth attract the male moth for reproduction.

One of the best known pheromones is *bombykol*, the sex-attractant of the silk moth. A receptive female emits a small quantity of *bombykol* molecules into the air and sits tight. The molecules drift downwind where they are detected by a wandering male. Because of the extraordinary sensitivity of the male's antennal sense cells, he needs only 200 molecules to strike the antenna within a second to be able to orientate and home in on the female. Unlike the male, the female silk moth is insensitive to *bombykol*. Her antennae are small and thin compared with the male's elaborate, feathery structures.

Other well-known pheromones include the complex scented secretions of mammals. Urine and faeces, as well as specialized scent glands, may be used to mark objects, conspecific territory boundaries or even to scent the air. Species, sex, age, motivational state, may all be coded in various secretions.

Semiochemicals acting between individuals from different species are called *allelochemicals* and are further divided depending on the costs and benefits to signaler and receiver.

Pheromone signals can be over smelled by unintended recipients: for example, the predatory beetles use the pheromone of their bark beetle prey to locate them. The predators are using the bark beetle pheromones as *kairomones*. Kairomones is a substance released by one species that benefits members of another.

Animals of one species can emit signals that benefit themselves at the cost of the receiving species. Chemical signals used in such deceit (misleading) or propaganda are termed *allomones*. Example, bolas spiders synthesize particular moth pheromones to lure male moths of those species into range for capture.

Semiochemicals benefiting both signaler and receiver in mutualisms, such as those between sea anemones and anemone fish (clownfish), are termed *synomones*.

Unit IV

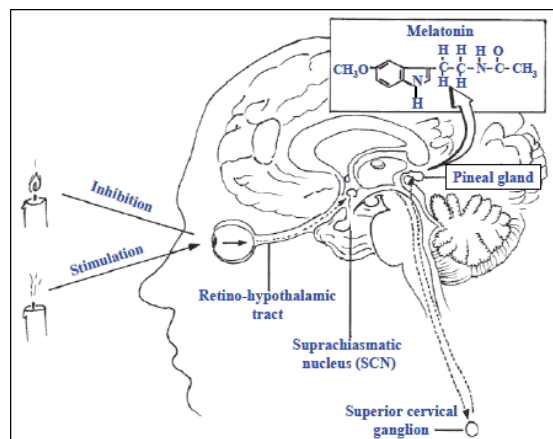
- Biological rhythms: Circadian, circannual, tidal/lunar, ultradian, infradian rhythms, synchronization of biological rhythms, phase shift.
- Photoperiodism with reference to birds and mammals - human circadian rhythms.

Biological rhythms: circadian, circannual, tidal/lunar, ultradian, infradian rhythms, synchronization of biological rhythms, phase shift

Biological Rhythms: A biological rhythm is any cyclic change in the level of a bodily chemical or function. It includes cyclic pattern of physiological changes or changes in activity in living organisms, most often synchronized with daily, monthly, or annual changes in the environment.

Biological rhythms can be internal (*endogenous*) controlled by the internal biological clock e.g. body temperature cycle; or External (*exogenous*) - controlled by synchronizing internal cycles with external stimuli, e.g. sleep/wakefulness and day/night. These stimuli are called *zeitgebers* - from the German meaning "time givers". These stimuli include environmental time cues such as sunlight, food, noise, or social interaction. *Zeitgebers* help to reset the biological clock to a 24-hour day.

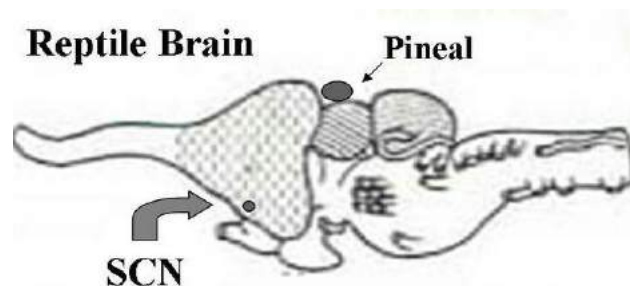
Circadian Clock: In humans (and other mammals), a circadian clock is located in the **suprachiasmatic nuclei** (SCN). The SCN is in the **hypothalamus**. It is a tiny cluster of about 10 thousand nerve cells. The internal mechanism by which such a rhythmic phenomenon occurs and is maintained even in the absence of the apparent environmental stimulus is termed a biological clock. When an animal that functions according to such a clock is rapidly translocated to a geographic point where the environmental cycle is no longer synchronous with the animal's cycle, the clock



continues for a time to function synchronously with the original environmental cycle.

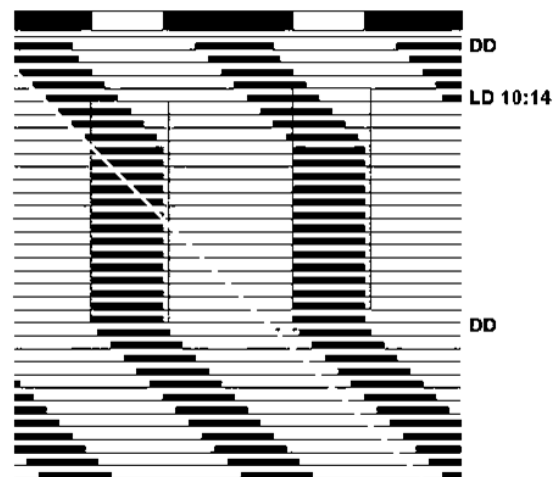
Circadian rhythm: A rhythm with a 24-hour cycle is called a circadian (from Latin *Circa*, “about”; *di*, “day”—i.e., “about a day”), solar day, daily rhythm. Circadian rhythms are physiological and behavioral rhythms which include: – sleep/wakefulness cycle – body temperature – patterns of hormone secretion – blood pressure – digestive secretions – levels of alertness

Two specific forms of circadian rhythms commonly discussed in research are *morning* and *evening* types. There is a direct correlation between the circadian pacemaker and the behavioral trait of morningness - eveningness. People considered morning people rise between 5 a.m. and 7 a.m. go to bed between 9 p.m. and 11 p.m., whereas evening people tend to wake up between 9 a.m. and 11 a.m. and retire between 11 p.m. and 3 a.m. Majority of people falls somewhere between the two types of circadian rhythms.



Evidence has shown that *morning types have more rigid* circadian cycles evening types who display more flexibility in adjusting to new schedules. One theory is that evening types depend less on light cues from the environment to shape their sleep/wake cycle, and therefore exhibit more internal control over their circadian rhythms.

Circadian Organization in Non-mammalian Vertebrates: Non-mammalian vertebrates (fish, amphibians, reptiles and birds) have more complex circadian systems than mammals. While the suprachiasmatic area remains a site of circadian pacemakers, it is, unlike in mammals, not the only such site. The **pineal organ**, which in mammals is a purely secretory organ, is directly photosensitive in other vertebrates (with the exception of snakes) and is a site of a circadian pacemaker. Retinae of the eyes are also sites of circadian pacemakers in at least some non-



mammalian vertebrates. Thus, the non-mammalian circadian system is composed of multiple pacemakers (eyes, pineal, SCN). These structures communicate with each other neurally and humorally and provide a single synchronized output in the rhythmic behavior of the animal.

Entrainment:

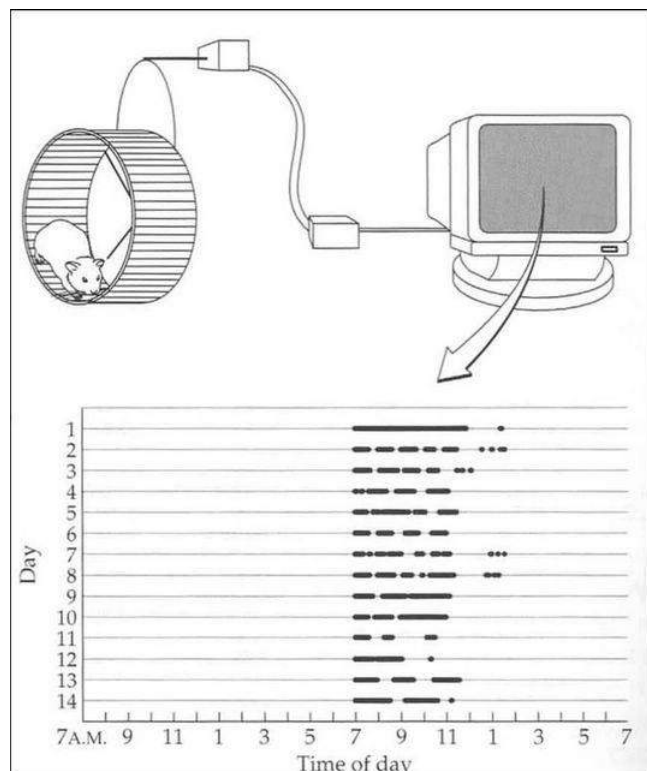
The natural, endogenous period of circadian rhythms, as measured in constant conditions, is almost never exactly 24 hours. In the real world, however, the light-dark cycle provided by the Earth's rotation around its axis is exactly 24 hours long. Utility of biological clocks is in retaining a constant phase between environmental cycles and activities of the organism. Thus, a mechanism must exist to synchronize the internal clock to the environmental cycle, in other words, to force the biological clock to assume a period of exactly 24 hours. The phenomenon of synchronization of biological rhythms by external cues is called *entrainment*.

Freerun:

The length of the period of a biological rhythm in the absence of environmental cue is called freerun.

Laboratory setup:

Here is an example of a laboratory setup for studying circadian rhythms in rodents. A hamster, in this case, is housed in a cage that contains a running wheel. The running wheel has a switch that registers every revolution of the wheel and sends that information to a computer. The computer puts a time stamp on each data point, and collects the data over long periods of time. For visual analysis of the data, computer software is available which will present the data in a graphical format called an



actograph. As you can see in the figure, an actograph has 24 hours of the day plotted on the X axis. The data from the first day are plotted on the top, the

second day is plotted immediately below the first day, the third day data below the second, etc. Each time point (e.g., in 10-minute bins) is depicted either as white or black. White denotes times when wheel was not moving. Black denotes times when the hamster was running in the wheel.

Ultradian rhythms:

Ultradian rhythms are defined as an endogenous rhythm pattern that occurs on a **shorter time scale than circadian rhythms**. As a result of the brief cycle time the frequency of occurrence is much higher. A prime example of an ultradian rhythm is feeding patterns. For the average person this cycle repeats about 3 times a day. Unlike diurnal rhythms ultradian rhythms are share no overlapping relationship with circadian rhythms.

Infradian rhythms:

Infradian rhythms are defined as an endogenous rhythm pattern that a cycle has duration **longer than circadian rhythms**, i.e. more than 24 hours per cycle. Due to the longer time frame for each cycle the frequency of occurrence in these cycles is lower than that of the circadian rhythms. The female **menstrual cycle** is an example of an infradian rhythm. It is a cyclical biological event that occurs in a fairly regular pattern on a monthly basis. Similar to the ultradian cycle, the infradian rhythms are not directly linked to circadian rhythms.

Circannual rhythms:

It includes **bird migrations, reproductive activity, and mammalian hibernation**. Daily cycles or circadian rhythms are in part a response to light or dark cycles, and circannual cycles in part responses to changes in the relative length of periods of daylight.

A mechanism for governing biological seasonality is the circannual clock. In many organisms (even when kept in constant conditions in the laboratory), certain events, e.g., reproductive maturation and behaviour, occur with a precise rhythm whose period is close to (usually a little shorter than) 365 days.

Deletion of the SCN in rodents does not eliminate circannual rhythms, for instance, suggesting that circannual clock is a separate mechanism from the circadian clock and is also located elsewhere in the brain or body of the animal. Not much is known about the physiology of circannual rhythms.

Freerunning circannual rhythms have periods too different from 365 days to be accurate on their own. They have to be entrained to the actual year, in a

manner similar to the way circadian rhythms need to be entrained to the day/night schedule. Circadian rhythms can be entrained by a large variety of cues (e.g., temperature cycles, noise, social cues, etc.), but by far the strongest cue is light.

How about circannual rhythms? Depending on the geographic region, a number of environmental cues serve as dominant triggers for annual physiological changes. Rain (e.g., monsoon), temperature and social cues can trigger reproductive maturation and behavior, entry into hibernation, or start of annual migration. These cues are sometimes called "proximal cues" as they more or less directly affect the onset of annual biological events. However, the proximal cues can only work if the organism is already 'prepared' for them. In almost constant environments, e.g., at the poles and at the equator, the plants and animals may follow freerunning circannual rhythms. For instance, elephant seals have a breeding season every ten months, thus falling in a different month every year.

Migrations of birds are conspicuously rhythmic phenomena. As a rule, they occur at certain seasons and certain times of day and thus are manifestations of an approximately annual (circannual) as well as an approximately diurnal (circadian) rhythmicity. Both of these rhythms reflect basic adaptations to environmental cycles and serve as biological clocks to cope with the annual and daily fluctuations in external conditions.

Many bird species, such as warblers, migrate exclusively at night. When kept in cages provided with an appropriate arrangement of perches, the birds' locomotor activity can be measured by means of microswitches mounted underneath the perches. With this widely used experimental method, it has been shown that locomotor activity in summer and winter is restricted to daytime, i.e. it occurs exclusively in the light portion of the light:dark (L:D) cycle.

In autumn and spring, however, the seasons corresponding to natural migratory activity, the birds exhibit additional locomotor activity at night. The rhythm is usually accompanied by variations in migratory fattening (indicated by an increase in body mass) and followed by a moult in winter and a phase of reproductive activity in summer. In the typical case, the period of the rhythm is longer or shorter than 12 months under such constant conditions, attesting to its endogenous circannual nature.

In migratory birds, endogenous daily (circadian) and annual (circannual) rhythms serve as biological clocks that provide the major basis for their temporal orientation. Circannual rhythms are responsible for the initiation of migration both in autumn and spring. This function of timing migrations is particularly important for birds that spend the winter close to the equator where the environment is too constant.

In normally day-active but nocturnally migrating birds, circannual signals cause alterations in the circadian system leading to the development of nocturnal activity. Although the nature of these signals is unknown, there is evidence that changes in the diurnal pattern of melatonin secretion by the pineal gland are associated with, and possibly causally involved in, the waxing and waning of nocturnal activity. These changes in the melatonin pattern presumably also affect general synchronization properties of the circadian system to Zeitgebers in such a way that circadian rhythms adjust faster to new conditions after long flights.

Phase-Shifting by Light

In order to look at relationships between the external environment and endogenous rhythms, numerous studies using rodents, humans, and other organisms have been performed to study the behaviour and adaptation of circadian rhythms (e.g., temperature), following phase advances or delays of the LD schedule. A major characteristic of circadian rhythms, as well as of many ultradian and infradian rhythms, is a labile phase. In other words, the phase can be moved (phase-shifted) to occur earlier or later. A change in the phase during one or more cycles in reference to previous cycles is called phase-shifting.

For example, the peak in the circadian body temperature rhythm is in the afternoon for most humans that are 24 h synchronized with sleep at night. However, when a person living in central North America crosses seven time zones by traveling quickly to Central Europe by jet airliner, the afternoon peak in his or her body temperature will, after about 5–7 days of transients, have advanced by about 7 h to occur again during the afternoon at the new destination. Stated more simply, the phase is shifted from its location in the original time zone so that the rhythm is similarly synchronized to a new time zone.

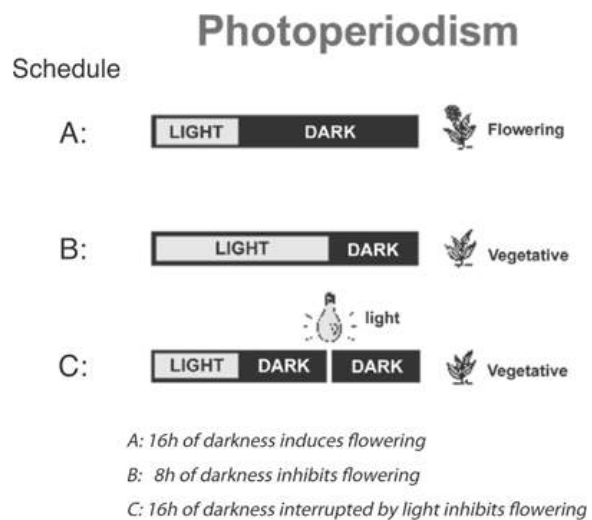
Photoperiodism with reference to birds and mammals - human circadian rhythms

Native plants and animals have become adapted to the seasons of their environment by responding to the changes in the lengths of daylight and night and these responses are associated with the seasons of the year, involve a physiological process known as *photoperiodism* (photo - light, period - duration, ism - process). *Photoperiodism* is a broad topic that is one of the basic principles of biology.

In the context of biological rhythms, photoperiodism can be defined as a *response of an organism to the timing and duration of light and dark*. Response to photoperiod often centers on reproduction and survival, such as the production of flowers, the migration of birds, etc.

For example, a given species of plants will produce flowers if the length of the light span is 15.5 h or less, but not if it is over 15.5 h. Likewise, for gonadal enlargement in the spring, a certain species of birds may require a light span of 8.5 h or more, but not less. Regardless of the type of response, timing is a *critical feature* of photoperiodism, especially how light and darkness succeed each other.

Importance of timing in photoperiodism illustrated by the effects of three LD schedules on the flowering response of a hypothetical short-day plant (SDP). Note that the total hours of L (8 h) and D (16 h) are similar in schedules A (8 h) and C (7.75 h _ 15 min), but the timing of L is different. The responses (vegetative or flowering) are illustrated to show that flowering during A, but not during conditions B and C.



In nature, each daily 24-h cycle consists of a single light span followed by a single dark span, both of which change in duration throughout the year. When one span lengthens, the other span shortens. The changes in the spectrum of light (red vs. far-red) during these transitions from one span to the other (light to dark: dusk and dark to light: dawn) may also allow organisms to better

discriminate the lengths of day and night due to photoreceptors (e.g., the pigments known as phytochromes).

A short-day plant (SDP) will remain vegetative (no flowers produced) if the dark span is interrupted by light, even though all plants receive a total of 8 h of light and 16 h of darkness. What makes the difference? The answer is not the total duration of light or darkness, but the duration and timing of individual light and dark spans (e.g., the single dark span of 16 h was divided into two dark spans of 7.75 h and 8 h separated by a 15-min span of light). Generally, in cases such as the one above where short days and long nights are required for floral induction of a SDP, the duration of the uninterrupted dark span is very important. Even in long-day plants (LDPs), which flower in response to long days and short nights, the dark span continues to be important.

Response Types

Photoperiodic requirements of organisms for the induction of a response are referred to as “**response types**.” Two scientists from the U.S. Department of Agriculture introduced the term photoperiodism, as well as the two categories known as short-day and long-day plants (Garner & Allard, 1920). Of special interest was how a soybean (*Glycine max*) cultivar (variety) known as Biloxi, and a tobacco plant (*Nicotiana tabacum*) called Maryland Mammoth responded to the duration of light and darkness. In the fields near Washington, DC, Biloxi soybeans would flower in September, regardless of whether the seeds were sown in April or July. Their observations of Maryland Mammoth were equally astonishing, since these plants tended to remain vegetative when grown in the field during the summer, but flowered when kept in a greenhouse during the winter. However, the plants remained vegetative during winter if the duration of the light span was lengthened with electric lamps.

Based upon their requirements for floral induction, both Biloxi soybean and Maryland Mammoth tobacco were designated as short-day plants. Plants such as radish (*Raphanus sativus*) and hibiscus (*Hibiscus moscheutos* L.) which require a longer light span to flower were called long-day plants.

A third response type or category, called daylength-indifferent (DI) or dayneutral, is used when there appears to be no relationship between development and photoperiodism. A truly day-neutral plant, which should flower regardless of daylength, is not as common as the short- and long-day

plants. Exceptions abound in all of these categories, since even some SDPs may not flower if the light span is too short.

Critical Daylength

Distinguishing between a short-day and a long-day response is not based upon the absolute length of the light span, but upon a value called the *critical daylength*. For example, a SDP could have a critical daylength of 14 h, while a LDP could have a critical daylength of 9 h. The clue to this seeming paradox lies upon what occurs before and after the critical daylength.

Responses that occur when the light span is shorter than the critical daylength are called short-day, while responses that occur when the light span is longer than the critical daylength are called long-day. Because of the importance of the dark span, reference sometimes is made to the *critical nightlength*, rather than the critical daylength.

Latitude

Often the role of photoperiodism in the life of a given species is not realized until an organism is moved to a different latitude. Historically, these differences were noted when groups of people moved north or south, bringing with them their domestic plants and animals. A number of plant and animal breeding programs have focused on producing and selecting organisms that are better suited for different latitudes.

Light and Photoreceptive Regions

In most instances, the photoresponsive region of an organism is located some distance away from the photoreceptive region. For example, flowers arise from a photoresponsive region known as the shoot meristem, but the photoreceptors are in the leaf. Some SDPs maintained under long-days will produce flowers when leaves from SDPs maintained under short-days have been grafted onto them.

Extraretinal Photoreceptors

It is easy to assume that the eyes are the sole photoreceptors in animals, since they convey information about environmental light conditions to the brain. However, the perception of light cycles is usually coupled to a complex system.

For example, circadian rhythms in some blinded animals can remain synchronized to an environmental light–dark cycle and free-run in constant darkness. Results from such studies provided one of the early clues to scientists that extraretinal photoreceptors in the brain, rather than just the eyes, could participate in photoperiodic timing.

While the circadian rhythm in perching activity of blinded house sparrows (*Passer domesticus*) free-ran in continuous darkness with periods longer than 24 h. A photoperiod of 12 h of light with intensity as low as 0.1 lux entrained the rhythm to 24 h in 50% of blinded house sparrows (and in all sighted birds). If the light level was reduced even further to a sub-threshold intensity, the activity rhythm in blinded birds again free-ran with a longer cycle. This rhythm could again become synchronized when feathers from the top of the head were plucked in order to increase the amount of light penetrating the skull to the brain, while injection of India ink under the head skin prevented sufficient light to penetrate the brain and the rhythm again free-ran.

Extraretinal photoreception has also been demonstrated by normal testicular recrudescence (renewed growth) in blinded sparrows exposed to artificial long days. When sighted birds that had their head feathers plucked and India ink injected under the skin of their heads in order to prevent light from penetrating the brain were exposed to the same lighting regimen, there was very little increase in their testis size, indicating that the eyes do not participate in those photoperiodic aspects of light detection that influence gonadal changes associated with reproduction. In addition, extraocular, nonpineal brain photoreceptors have been found to be involved in photoentrainment of amphibians, fish, and reptiles.

Pigments

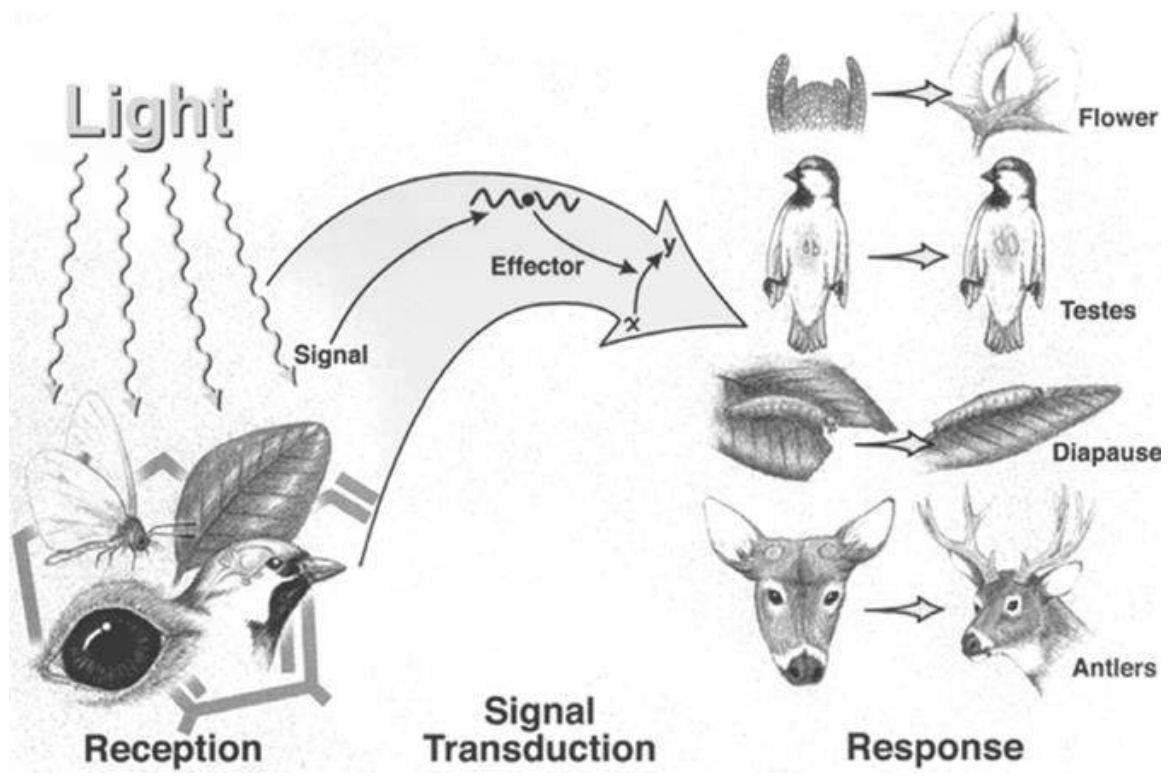
The visible light that is effective in most photoperiodic responses lies within a spectrum that spans from violet to far-red. Certain wavelengths of radiant energy that reach an organism are preferentially absorbed by receptor molecules known as pigments. Great diversity exists in the molecular structure of pigments, as well as in their associations with proteins, but each has a light-absorbing portion called a chromophore (Gr. *chroma* - color, *phoros* - carrying). Phytochromes, which constitute a major class of pigments that function in the photoperiodic response of plants, have a chromophore that consists of four rings (*tetrapyrrole*).

In higher animals the major visual pigment is *rhodopsin*, a molecule that contains a light absorbing part of a molecule (chromophore) called *11-cis retinal* and a protein known as *opsin*. The molecular structure of 11-cis-retinal is similar to the molecular structure of vitamin A, which is converted to 11-cis-retinal. However, these photoreceptive pigments are not necessarily limited to eyes. For example, 11-cis-retinal has been found in the pineal of rainbow trout.

Cryptochromes

Cryptochromes represent another group of pigments that also function in biological timing. These pigments, which are found in plants, are also found in the eyes of mammals and have a role in circadian photoreception. Mechanisms of photoentrainment, however, very likely involve multiple ocular photopigments and reactions. Included here would be melanopsin, an essential component in the phototransduction cascade in the retinal photoentrainment pathway that has been identified in retinal ganglia and the pineal and deep brain of higher animals.

Diagram: Photoreceptive regions (e.g., leaf, brain, eye, and head), signal transduction (sequence from light signal (h) to timer (oscillator) to chemical signal (“inactive” X producing active “Y”) to an intercellular messenger (e.g., hormone), which activates the responsive or target regions and responsive regions (apical shoot meristem, testis, larva, and head). Note changes in morphology, such as floral induction, testis development, diapause, and antler production.



Human Circadian Rhythm

Biological rhythms are common phenomena of life and are found in all major groups of organisms, but are often overlooked. The length of time required to repeat a rhythmic cycle is called the period, a characteristic that has been used to categorize rhythms into three major groups: circadian (20–28 h), ultradian (<20 h), and infradian (>28 h).

Much of the early work on biological rhythms focused on cycles in which the period was 24 h. These rhythms are referred to as *circadian rhythms* because they reoccur with a period of 24 h during usual light–dark conditions, and can continue with a period close to 24.0 h when the organism is isolated from external cues.

Circadian rhythms are usually synchronized by cyclic changes in light and darkness and/or temperature. When isolated from such environmental cues, the rhythm continues (free-runs), but usually with a period slightly longer or shorter than precisely 24.0 h.

Kleitman (1963) was the first to study human circadian rhythms. In 1938, he performed an experiment on two subjects deep within an underground cave, the Kentucky's Mammoth Cave considered as the longest known cave on earth. These people were shielded from periodic environmental cues and lived on non-24-hour sleep/wake, light/dark and meal schedules. They were kept out from the influence of the earth's 24-hour day. He measured the daily rhythm of their body temperature and revealed that in one of the subjects, the circadian temperature rhythm was endogenously generated, persisting for a month with a near 24-hour period despite imposition of a 28-hour rest/activity schedule. These facts strongly suggest that a physiological rhythm could oscillate even in the absence of periodic changes in the environment. This study therefore established the endogenous and physiologic nature of human circadian rhythms for the first time.

Among various rhythms in human body, sleep/wake cycle is perhaps the most overt manifestation of circadian rhythms. Other rhythms control much of the human body's normal functions, including performance, behaviour, endocrine secretions, heartbeat, and body temperature.

Interestingly, most human babies are born predominantly in the early morning hours. While these patterns do not necessarily indicate that the events are driven by the circadian pacemaker, they do suggest temporal order in the

functioning of the human body. This temporal organization appears to be beneficial; the human body is prepared for routine changes in state, such as awakening each morning, rather than simply reacting after shifts in demand. In addition, these regular cycles in the body present considerations for diagnosis

of

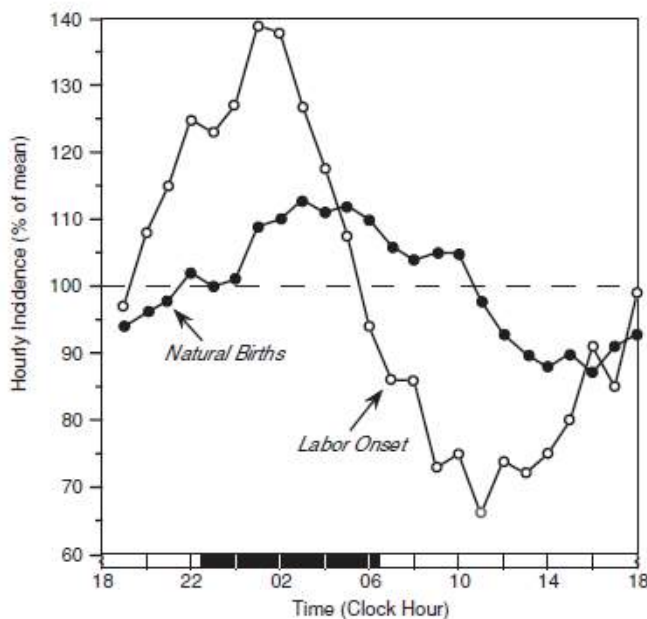
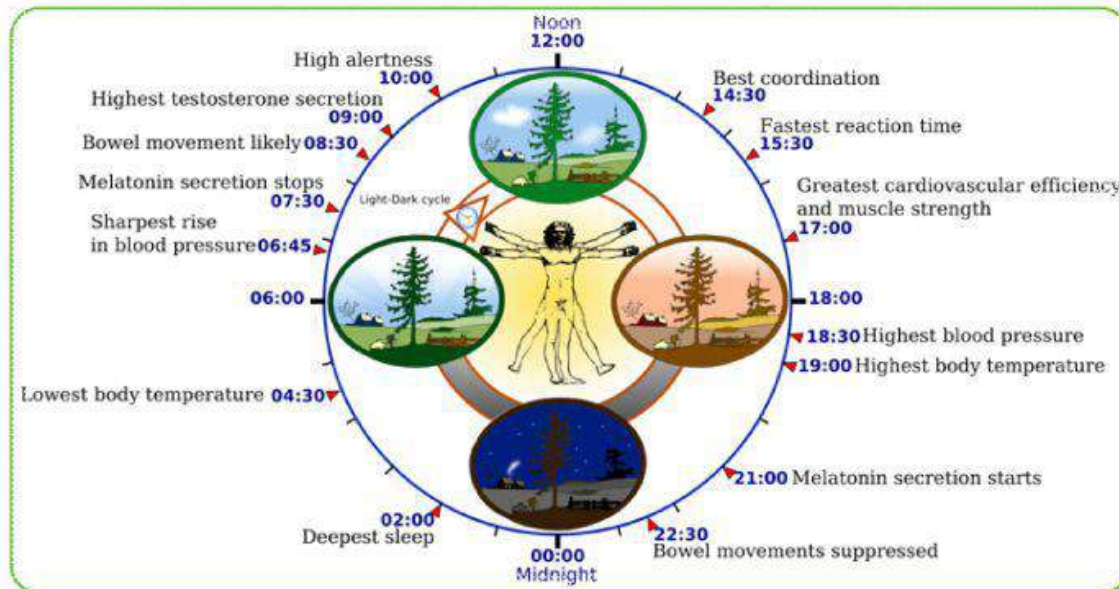


FIGURE 1.8. Comparison of the circadian (*circa* = about, *dies* = day) waveform for the onset of labor and birth in humans, illustrating a natural sequence of events beginning with a peak in the onset of labor early in the night (dark bar) followed by a peak in natural births early in the morning. Hourly incidence of onset of >200,000 spontaneous labors and >2,000,000 natural births (redrawn from Smolensky et al., 1972).

health problems and for the timing of medical treatment.

Examples of circadian rhythms: body temperature in humans, onset of labour and birth in humans, rise in blood pressure, high alertness etc.