

ANIMAL BEHAVIOUR (ABG 503) LECTURE NOTES

Aims of the course

1. To understand the general concepts that govern the manner in which animals behave throughout their lives i.e. maximizing 'fitness' through essentially selfish actions.
2. To appreciate the range of mechanisms by which animals adapt to their environmental conditions using behavioural actions.
3. To achieve competence in the skills required to conduct scientifically meaningful studies of animal behaviour.

Brief history of the study of animal behaviour

1. First ethologists (pre-historic humans) studied behavior for practical purposes:
 - i. Prey behaviour was studied for hunting.
 - ii. Domestication - dogs, cats, ox, cattle, reindeer, horses, etc.
2. Natural theologians during the Middle Ages documented behaviour as part of general biology of organisms.
3. From early 1900s - animal behaviour became a formal discipline.
4. From late 1900s and early 2000 - modern studies of animal behaviour.

Introduction

Behaviour can be defined as an expressed course of action produced in organisms in response to **stimulus** from a given situation. It could simply be considered as what the animal does. The fundamental explanation of behavioural activity must begin with a stimulus and end with a response.

Stimulus: Any change in the biotic and abiotic environments capable of eliciting or causing some sort of reaction or response in a living organism. For example, temperature, pressure, radiation, gravity, or activities of other organisms within the immediate environment.

Approaches to behavioural studies

i. Vitalistic approach

Behavioural activities are explained in terms of what animals are seen to do in relation to changes in the environment. It involves total rejection of any study of the animal outside its natural environment. The technique is non-scientific since all the observations relate to past events which cannot be tested experimentally.

ii. Mechanistic approach

It is an experimental approach and involves the study of particular aspects of behaviour under controlled conditions in a laboratory. It was pioneered by Pavlov and used extensively in psychological study. It may be criticized on the basis of the artificiality of the experimental conditions and the way in which results are interpreted.

iii. Ethological approach

Ethology is the scientific study of animal behaviour. It explains responses observed in the field in terms of stimuli eliciting the behaviour. This was pioneered by Lorenz, von Frisch and Tinbergen. Ethologists have so far tried to answer questions about animal behaviour from four major areas:

1. The evolutionary history:

- How did various forms of behaviour evolved? i.e. (Innate/instinctive/genetic or learned?)
- How does the behaviour compare with similar behaviour in related species?

2. Development:

- How does behaviour change with age?
- What are the early experiences necessary for the behaviour to be expressed?
- e.g. How does courtship behaviour develop during the individual's life?
- Does the male in domestic fowl learn the waltz dance?
- Does he practice dancing?
- Is he successful in directing the female?

3. Causation:

What are the stimuli that elicit the response?

How has it been modified by recent learning?

4. Function:

How does the behaviour impact on the animal's chances of survival and reproduction?

I.

Components (types) of Behaviour

Nature/innate

*Instinct or genes
determine behaviour*

Nurture/learned

*Experience and learning
influence behaviour*

1. Learned behaviour

Learning can be defined as an adaptive change in individual behaviour as a result of experience. The degree of permanence of newly acquired learned behaviour patterns depends on memory storing information gained from the experience. Learning alters the range of behaviours shown by an individual, and allows it to adapt to and control its environment.

Types of learned behaviours

i. *Habituation*

Ideally, an animal should recognize important cues or signals in its environment and act in response to them in order to adapt to constantly changing environment. **Continuous repetition of a stimulus not associated with reward or punishment (reinforcement) puts off any response to the stimulus.* E.g. birds learn to ignore scare crow. Particularly important is the reaction to new signals. The importance of these signals have to be assessed, and the animal has to work out how to react to them. This is where learning is important - a suitable response can be learnt, rather than a trial and error effort after each presentation of the same stimulus. Take for example a rat that has just experienced an aversive stimulus (e.g. a very bright light). Immediately after this event, the rat may be extra sensitive to other cues (such as noises or lights) that it would not normally respond to. This is **sensitization**, a period of increased responsiveness following a reward or punishment (or 'reinforcement'). However, if the second stimulus is repeated without the reinforcer, the response of the animal should become reduced, and the stimulus may even be completely ignored eventually. This is habituation. The animal learns not to respond to irrelevant stimuli. This decline in response is specific to a given stimulus. If a new stimulus is presented the animal will react (i.e. it has not ceased responding simply

because it is tired). Animals will not habituate to relevant stimuli e.g. those associated with predators, food or mates.

Habituation is important in the development of a behaviour in young animals and helping to understand neutral elements in the environment, such as movements due to wind, cloud, shadows, wave action etc. It is based in the nervous system and is not a form of sensory adaptation since the behaviour is permanent and no response is ever shown to the stimulus after the period of habituation.

ii. Associative learning

Associative learning simply means that an animal learns to associate an event with a result. There are two types of associative learning: classical (Pavlovian) conditioning, and instrumental (operant or trial-and-error) conditioning.

a. Classical (Pavlovian) conditioning (conditioned reflex):

Pavlovian conditioning involves the association of events over which the animal has no control. It is able to gain prediction of events in its environment. Pavlov's **dog** associated bell with the arrival of food and begins to salivate at the sound of a bell. At first, the dog didn't react to the stimulus alone, but after a few repetitions the stimulus was able to cause salivation, before the arrival of the food being given to the dog.

The animal learns to associate a conditioned stimulus (e.g. a bell), with the onset of an unconditioned stimulus (e.g. the arrival of food). An unconditioned response (e.g. salivation) would only occur in response to an unconditioned stimulus prior to learning.

Birds avoid eating black and orange cinnabar moth larvae because of bad taste and avoid all similarly coloured larvae even though they may be nutritious.

b. Operant conditioning (trial-and-error learning):

Trial-and-error activities give rise to responses which are reinforced either by rewarding (positive) or punishment (negative). The association of outcome of a response in terms of reward or punishment increases or decreases respectively future responses. Instrumental conditioning therefore involves association of events with control.

Possibly the most famous set of experiments examining this sort of learning were done by followers of the school of B.F. Skinner. The classic tool is the Skinner box. Here, the animal is placed in the box, which has some sort of reward for conducting a behaviour. For example, if the animal presses a lever, it receives a food pellet. By trial and error, the animal learns that pressing the lever delivers the reward. In this way, the animal gains prediction and control over events in its environment. The animal learns to associate its own behaviour with a particular outcome. If the outcome is rewarding e.g. access to food, the animal learns to repeat the behaviour that resulted in food access previously. It therefore learns a conditioned response to obtain food (unconditioned response).

iii. Latent or exploratory learning

Animals explore new surroundings and learn information which may be useful at a later stage (hence latent) and mean the difference between life and death. E.g. In mice, knowledge of the immediate environment of its burrow may help it escape from a predator. At the time of acquiring this knowledge, it has no apparent value, hence *not all behavioural activities are apparently directed to satisfying a need or obtaining a reward*.

iv. Insight learning

This is the highest form of learning which does not result from immediate trial-and-error learning but may be based on information previously learned by other behavioural activities. Insight learning is based on advanced perceptual abilities such as thought and

reasoning. Kohlar's work on chimpanzees suggested insight learning: when presented with wooded boxes and bananas too high to reach, the chimps stacked up the boxes beneath the bananas and climbed up to get them. This response appeared to follow a period of 'apparent thought'. Previous experience of playing with boxed (latent learning) may have increased the likelihood of the response.

v. **Imprinting**

A simple and specialized form learning occurring during receptive periods in an animal's life. Imprinting involves young animals becoming associated with, and identifying themselves with another organism, usually a parent, or some large object. E.g. Chicks hatch with an innate tendency to approach and follow their mother. They have already imprinted on her vocalizations. After hatching (24 - 36 hours) they imprint on her visual appearance. Geese and ducklings form social attachments shortly after birth. Lorenz found that goslings deprived of their parents would follow him and use him as a substitute parent. Pet lambs or kids bottle fed show similar behaviour. This may have a profound and **undesirable effect** later in life when the animal finds it difficult in forming normal relationships with others of the same species as exemplified by sexual imprinting (direct sexual behaviour of members of the same species). Individuals raised by another species (cross-fostered), recognizes foster species as its own when sexually mature and will attempt to mate with foster species.

In natural situation, imprinting have **adaptive significance** in enabling offspring to rapidly acquire skills possessed by their parents such as learning to fly in birds, song learning; and features of the environment such as the 'smell' of the stream in which migratory salmon were hatched and to which they return to spawn or reproduce. Imprinting is also important in that it may have effects upon the animal's future choice of a sexual partner.

2. Innate behaviour

Innate behaviour involves a collection of responses that are predetermined by the inheritance of specific nerve or cytoplasmic pathways in multicellular or single-celled organisms. As a result of these 'built-in' pathways a given stimulus will produce invariably, the same response. These behaviour patterns have developed and been refined over many generations (selected) and their primary adaptive significance lies in their survival value to the species. Innate behaviour patterns include orientations (taxes and kinesis), simple reflexes and instincts. Instincts are extremely complex and include biological rhythms, territorial behaviour, courtship, mating, aggression, altruism, social hierarchies and social organization.

Instincts are complex, inborn, stereotyped behaviour patterns of immediate adaptive survival value to the organism and are produced in response to sudden changes in the environment. It can be considered as '*unlearned species-specific motor patterns*' or *species-characteristic behaviour*. These responses are handed down from generation to generation and, having successfully undergone the rigorous test of natural selection, clearly have important survival significance. However, *instinctive behaviour patterns are not completely inflexible* because all aspects of the development in an organism whether anatomical, biochemical, physiological, ecological or behavioural, are the result of the influence of constantly varying environmental factors acting on the genetic framework. In view of this, some behavioural patterns may not be purely instinctive (genetic) or purely learned (environmental), but influenced by a combination of the two.

Motivation

The concept of motivation encompasses a variety of factors that modify the extent and nature of any behavioural response. At any given moment in time, an animal usually has a range of behaviours which it could exhibit. ***What is it that determines which behaviour an animal decides to conduct?*** The study of motivation is interested in determining what the *causal factors* (or *driving forces*) are behind a behaviour. No animal exists in isolation from its external environment. The environment the animal lives in may change, for example, food may appear or disappear, a predator may attack, the temperature could fall, or offspring may start begging for food. These may all cause changes in the animal's behaviour. The same stimulus does not always evoke the same response in the same organism. The difference is always circumstantial and may be controlled by either internal or external factors. E.g. Presenting food to a starved animal will produce a different response from that shown by an animal that has been fed. In between two extremes, responses of varying strengths will be produced depending on the degree of hunger experienced. However, if the act of feeding will place a hungry animal in danger of being attacked by a predator, the feeding response would be stopped until the danger is passed.

Many behavioural responses associated with reproduction have a motivational element. E.g. Many female animals are only receptive to mating attempts by males at certain times of the year which coincide with the period of oestrus and have the adaptive significance of ensuring that mating coincides with the optimum time for fertilization, and therefore the production of offspring at the most favourable time of the year. These behavioural patterns are known as biological rhythms. In many species, the degree of motivation **or drive** coincides in males and females, but in other species, some system of communication between sexes is essential to express the degree of motivation. In many primates, the timing of oestrus is signaled by a swelling and change of colour of the genital area of the female and this is displayed to the male. Such behaviour reduces the likelihood of a male attempting to mate at the time when the female is not receptive. The signals used to bring about a change in behaviour are known as **sign stimuli**. Depending on their origin or function, they are classified as *motivational, releasing or terminating stimuli*.

Motivational stimulus may be external, e.g. increasing day length induces territorial and courtship behaviour in birds, or internal, e.g. depleted food stores in the body results in seeking for food. **Releasing stimulus** may be a simple stimulus or sequence of stimuli produced by a member of a species which evokes a behavioural response in another member of the same species. E.g. Young herring gull chicks normally peck at a red spot on the yellow lower mandible of the parent's bill to signal the parent to regurgitate fish which the young then swallows. **Terminating stimulus** completes a behavioural response and may be external or internal. E.g. External visual stimuli of a successfully completed nest will terminate nest building in birds, likewise, a full stomach will terminate feeding.

It is likely that both internal and external factors often have an effect at once (they interact). For example, chickens will normally forage throughout the day. However, when a hen is brooding eggs, she will be much less likely to feed, even if food is available in the environment. Thus, there is a subtle interplay between current internal factors, and external ones.

Motivation and welfare

Welfare is a measure of how well an animal copes with its environment; If the animal fails to cope or its coping efforts have detrimental effects on the productivity, then the welfare of the that animal is poor. Welfare can also be considered as absence of suffering.

How can an understanding of motivational systems be important to our understanding of animal welfare? In some cases, they can give insights into the causes of behaviours that are potential welfare problems. Many housing systems for husbandry restrict space and foraging ability. In essence, they do not permit animals to perform natural behaviours and contribute to the development of abnormal behaviour patterns, which develop in captive animals housed in inadequate environmental conditions and can cause health problems. Some abnormal behaviours are indicative of reduced welfare in that they act as a 'coping mechanism' to allow the animal deal with a stressful environment. E.g. Dust-bathing is an activity that increases in intensity with an increased period of deprivation. However, in some cases, chickens will go through the actions of dust-bathing, in the absence of dust. This is called a vacuum activity - could be likened to a 'build-up' of motivational energy (Lorenz's model), eventually triggering a behaviour without the correct stimulus being present. A similar example occurs in pigs, which usually build nests prior to giving birth, and the day beforehand is spent rooting up straw etc. to form a nest. If no straw is present, the pigs will nonetheless root, which can lead to facial damage. Understanding the causal factors behind these behaviours may allow us to either stop the behaviour from occurring, or else supply the animal with the correct environment, so that its behavioural repertoire is not compromised.

Another issue where welfare becomes important in the study of motivation is that of rebound activities. If a behaviour is prevented, or the animal is unable to conduct it for a period, when given the opportunity, the behaviour will be performed at a much greater intensity - which again can be likened to the build-up of 'motivational energy' in Lorenz's model. Rebound is seen in a number of situations, such as exploration behaviour in pigs, maintenance behaviour in chickens, social play in rats, aggression in fish, and sleep in humans. By attempting to understand the motivational system behind a behaviour, we can have an influence on the welfare of the animal. Animals may be strongly motivated to conduct a behaviour, but be unable to do so. Or, animals may be able to perform a behaviour, but be prevented from reaching the functional consequences of that behaviour. **Two models** give very different predictions when we examine them from a welfare perspective. *Lorenz's model* states that it is the performance of the behaviour itself that is important. The *homeostatic model*, however, suggests that the goal of the behaviour is important. **By understanding the motivational system, we can alter our husbandry system so that the behaviour itself can be conducted, or so that the goal can be reached.** These all have effects in maximizing the productivity and profit of the livestock farmer.

Summary

- The study of motivation looks at how internal and external causal factors interact to produce behaviour.
- Motivation must be considered as we do not know the exact mechanisms as to why a behaviour occurs.
- Animal welfare and hence productivity is likely to be compromised when highly motivated behaviours cannot be expressed, or when a functional goal is not achieved.
- An understanding of motivation allows us to make predictions about when welfare will be compromised.

Innate behavioural patterns or types

1. Agonistic behaviour

Agonistic behaviour can be defined as a group of behavioural adjustments associated with fighting, which includes attack, escape, threat, defense and appeasement. The simplest explanation of the concept of agonistic behaviour is that it composed of a continuum of behaviours from *threat* to *aggression* to *submission*. Agonistic behaviour has the **adaptive significance** of reducing intra-specific conflict and avoiding obvious fighting which is not in the best interest of the species. Dangers from competition are avoided by agonistic behaviour.

Threat refers to those species-specific vocalizations, odours, postures, facial or body movements that signal the intent to display aggression. In stable social systems, threat causes immediate signs of avoidance or submission. In newly formed or unstable social groups, a threat may cause the recipient to threaten, or a threat may precede an outbreak of aggressive behaviour.

Submission includes species-specific behaviours, vocalizations, postures and odours that signal non-aggressiveness and reduce further attack by the aggressive individual. E.g. In dogs and wolves, an appeasement posture may take the form of the animal lying down on its back or baring its throat to the victor. A submissive behaviour is usually exhibited following either a threat or an aggressive interaction. Therefore, while showing submission, the animal is stressed. Most submissive behaviours are learned behaviours associated with fight (from attack) or appeasement, and that an animal must have been attacked at some time in his life in order to show submissive behaviour. Submissive behaviour may be objectively measured because they always follow either an aggressive behaviour or a threat, and because each species has specific submissive postures.

Aggression is a segment of agonistic behaviour and can be regarded as those species-specific behaviours associated with attacks with the objective of causing physical injury. They are usually directed towards members of the same sex and species and have various **functions**, including the displacement of other animals from an area, usually a territory or source of food, the defense of a mate or offspring and the establishment of rank in a social hierarchy. Most species channel their ‘aggression’ into ritual contests of strength and threat postures which are universally recognized by the species. E.g. Horned animals such as deer and goats may resort to butting contests for which ‘ground rules’ exist. Only the horns are allowed to clash and they are not used on the exposed and vulnerable flank. Siamese fighting fish resort to threat postures involving increasing their apparent size.

Classification of aggressive behaviours common to food animals

Behavioural category	Definition/Example
Inter-specific aggression:	
1. Maternal defense	Mother defends young against potential predators. E.g. Ewe with lamb attacks dog.
2. Defense of territory	Animal attacks intruder. E.g. grazing bull attacks man.
3. Predation	Animal attacks, kills and eats other animals. E.g. Lion catches and eats Zebra.
Intra-specific aggression:	
4. Aggression after grouping	Previous unfamiliar animals are brought together, they fight and a social structure or hierarchy results. Eg. pigs.
5. Inter-male fighting	Adult males generally fight to win mates or territory. E.g. rams or goats fight during breeding season.
6. Resource defense	Aggression increases with limited resources in cattle, etc
7. Inter-gender fighting	Males attempt to mount non-oestrus females, aggressive behaviour

	results. E.g. Non oestrus sows attack boar who attempts to mount.
8. Aberrant aggression	Wool biting in sheep, ear and tail chewing in pigs, cannibalism or killing of young.

1. *Maternal defense*: Aggression towards humans from females is less common, but the lactating female may be a threat to workers due to maternal defense of young.
2. *Territorial defense*: Inter-specific agonistic behaviour is most often a management problem with large farm animals. Aggressive male animals, particularly bulls, boars and rams can be dangerous because they can injure or kill farm workers. Food animals may set up a territory which when violated by a human, provokes attack.
3. *Predation*: Some motor patterns used during predatory attack fit the definition of aggression. Pigs and poultry are considered omnivores and thus may occasionally attack and eat small animals.
4. *Aggression after grouping*: The most common management practice that induces aggression and submission is bringing together unfamiliar animals (especially in poultry, sheep, swine and cattle). This incites high and measurable levels of agonistic behaviour. The agonistic behaviour shown after grouping unfamiliar animals follows the continuum from threat to aggression and submission until a period of social stability is reached, during which only an occasional threat or attack is necessary for an animal to reinforce its dominance. If greater amount of agonistic behaviour is observed, the group may have an unstable dominance order. Inter-specific agonistic behaviour must therefore be managed to optimize productivity.
5. *Inter-male fighting*: Is observed during breeding season in normally un-aggressive flocks of food animals. It may be due to motivation to breed limited number of females or due to seasonal changes in physiology. E.g. high testosterone level.
6. *Resource defense*: When resources are limited in any season, aggression increases. E.g. limited feeder space.
7. *Inter-gender fighting*: Occurs during attempted sexual activity when (1) when a male attempts to mount a female but receives aggression from an anoestrus female or (2) a male attacks a female in search for a receptive female.
8. *Aberrant aggression*: The intent seems to be to cause physical damage as in tail biting in pigs.

Ethogram of agonistic behaviours

An ethogram is a complete catalogue of all behaviour patterns and vocalization occurring in a species.

1. Sheep

They are often viewed as non-aggressive, gregarious animals but do show measurable levels of agonistic behaviour.

Aggressive behaviour (fighting) include: shoving with shoulders, running together and butting. Play butting occurs in young lambs and more damaging aggression in ewes and rams. Most fighting is during breeding season.

Threat postures include: striking the ground, tooth grinding, lateral body presentation, sniffing, mounting and chasing.

Aberrant aggression: Some ewes show aberrant aggression towards their lambs or alien lambs. Wool picking with teeth is common in confined sheep.

2. Cattle

Pre-fight behaviours – Active or passive avoidance leads to fight.

Threat – Close contact, head lowered, ready to fight and butting or active fighting. Butting could be regarded as a non-retaliated blow with the head, while fighting involves reciprocal butts, circling and pushing.

Submissive behaviour – The end of the fight begins with one animal showing submissive behaviour.

Aberrant agonistic behaviour include naval sucking, fence and pen chewing (aggression towards inanimate objects) and ear sucking. These behaviours may be a sign of deficiency.

3. *Swine*

Threat – Head tilt and retreat or avoidance to chase and nose to nose contact.

Aggressive components of agonistic behaviour in the pig are composed of bites and pushes. Head-thrusts in combination with bites and shoulder pushes represent the phase of interaction that seems most intense.

Submissive behaviour is shown by subordinate pig turning its body and either running away or remaining stationary and presenting its rump. Submission may be signaled by lowering of the head.

Abnormal or aberrant agonistic behaviours – Swine occasionally kill their piglets, and growing pigs bite tail and chew ears. High concentration of atmospheric ammonia, dietary factors, floor type and lack of bedding may aggravate tail biting and ear chewing in pigs.

4. *Chickens*

Threat – Chickens show threats associated with fighting, leaping and wing-flapping. The major aggressive act is pecking.

Submissive behaviours are described as retreat.

Aberrant behaviour can be found among confined chickens. Cannibalism could be influenced by diet and management procedures.

Management of aggression

Changes in space allowance and group size may also influence the occurrence of aggression. Some experiments have shown that agonistic behaviour in chickens reduces when the density of chickens within a pen of a fixed size is increased, but others have shown that aggression such as feather-pecking and cannibalism increase as pen size and flock size are increased.

The location of food in the environment is very important. Several feeders should be placed at strategic locations to avoid one individual taking control over the available food. If resources are distributed, there will be less competition over resources.

Some short-term treatments sometimes used to minimize aggression between newly mixed pigs include the use of tranquilizer (azaperone). This does reduce the immediate levels of aggression following mixing. However, once the tranquilizer has worn off, fighting would resume at levels that would have occurred; Presumably, the pigs still have to form their dominance hierarchies. Dosage may also be important, if it is too high, the pigs may be unable to familiarize themselves with new individuals during the period of the drug's effects.

Other methods such as mixing individuals during periods of low activity, or providing food to distract them from each other may have limited effectiveness, but likely postpone rather than prevent aggression.

2. Dominance status

One aspect of social behaviour arising from a group of individuals living together temporarily or permanently is the existence of social hierarchies or pecking orders. A pecking order is a dominance hierarchy in which animals within a group are arranged according to status. E.g. In a group of hens sharing a hen house, a linear order is found in which hen A will peck any other hen in the group, hen B will peck all hens other than A and so on. The position in the hierarchy is usually decided by some agonistic form of behaviour other than fighting. Pecking orders exist only where animals are able to recognize each other as individuals and possess some ability to learn.

Factors determining the position of individuals in the hierarchy include: size, strength, fitness and aggressiveness. Lower order male members may be raised up the hierarchy by injection of testosterone which increases their levels of aggressiveness.

Advantages of pecking order

1. It decreases the amount of individual aggression associated with feeding, mate selection and breeding site selection.
2. It avoids injury to the stronger animals which might occur if fighting was necessary to establish the hierarchy.
3. It ensures that resources are shared out so that the fittest survive. E.g. if a group of 100 hens is provided with sufficient food for only 50 hens, it is preferable, in terms of the species, for 50 hens to be adequately fed and the weaker 50 hens die than for them all to live and receive only half rations, as this might prevent successful breeding.
4. Social hierarchy increase genetic vigour of the group by ensuring that the strongest and genetically fittest animals have an advantage when it comes to reproducing.

3. Territorial behaviour

A territory is an area held and defended by an organism or group of organisms of the same or different species. Territorial behaviour is common to all vertebrates except amphibian but is rare in non-vertebrates.

The exact **function of territory formation** varies from species to species, but in all cases, it ensures that each mating pair of organisms and their offsprings are adequately spaced to receive a share of the available resources, such as food and breeding space. In this way, species achieves optimum utilization of the habitat.

The size of territories occupied by any particular species varies from season to season according to the availability of environmental resources. *Birds* of prey and large carnivores have territories several square miles in area in order to provide all their food requirements. *Herring gulls* and *penguins* have territories of only a few square metres, since they move out of their territories to feed and use them for breeding purposes only.

Territories are found prior to breeding, usually by males. Defense of the area is greatest at the time of breeding and fiercest between males of the same species. There are a variety of behavioural activities associated with territory formation and they involve threat displays between owners of adjacent territories. These threat displays involve certain stimuli which act as releasers. E.g. An adult male robin would attack another adult male displaying a red breast and a bunch of red feathers, but not a young male robin which did not have a red breast. The level of aggression shown by an organism increases towards the centre of the territory. The aggressiveness of males is determined partly by the level of testosterone in the body and this can affect territory size. E.g. the territory size of a red

grouse can be increased by injecting the bird with testosterone. Territories are acquired through threats, gestures and postures in place of actual fighting. Having obtained a territory, many species especially carnivores proceed to mark out the boundary by leaving a scent trail. This may be done by urinating or rubbing parts of the body against objects called scent posts along the boundary of the territory.

4. Altruistic behaviour

Altruism is a form of social behaviour whereby one organism puts itself either at risk or personal disadvantage for the good of other members of the species. In the case of activities associated with and parental care, altruism is not so difficult to comprehend since the action is clearly in the interest of the parents, offsprings and species. E.g. the female baboon protects and cares for its offspring for almost six years whilst most bird species feed and protect their demanding offsprings until they are capable of fending for themselves. What is not so clear is the reason why some organisms give support to organisms which are not their offspring. E.g. birds and monkeys call out warnings to others in danger and female monkeys carry and care for the babies of other monkeys. In insects such as honey bees, wasps and ants, sterile female workers are prevented from producing offsprings, yet they spend their lives looking after their brothers and sisters. Hence, helping their sister (queen) to reproduce, they are effectively aiding in the production of queens, workers and drones with a genetic complement closer to their own than if they had offspring of their own. The conferring of a genetic advantage on closely related organisms forms the basis of altruistic behaviour.

Altruistic behaviour is very common amongst primates and varies from the extremes of social protection which exist between members of the same troop (monkeys), through acts of mutual grooming and food sharing (apes) to deliberate acts of self-sacrifice for family (God for humans). The extent of altruistic behaviour appears to be related to close relatives (kin) such as offspring and siblings (brothers, sisters, cousins) with whom they share certain alleles. Thus the **adaptive significance of altruistic behaviour** is to increase the frequency of those alleles common both to the donor and recipient(s) of the altruistic behaviour.