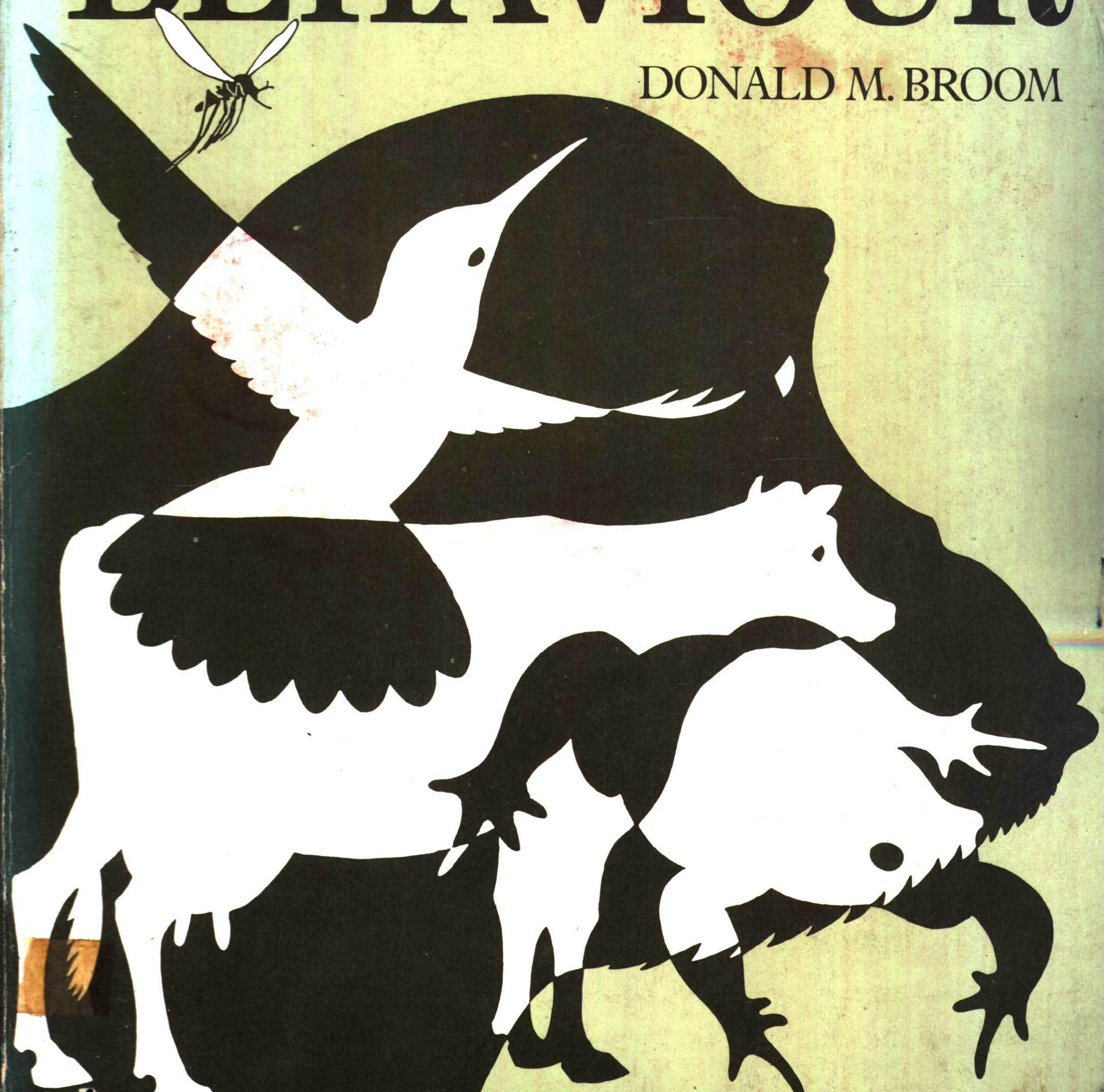
BIOLOGY OF BEHAVIOUR

DONALD M. BROOM



Biology of behaviour

Mechanisms, functions and applications

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WITH ANIMAL DRAWINGS BY ROBERT GILLMOR

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Introduction

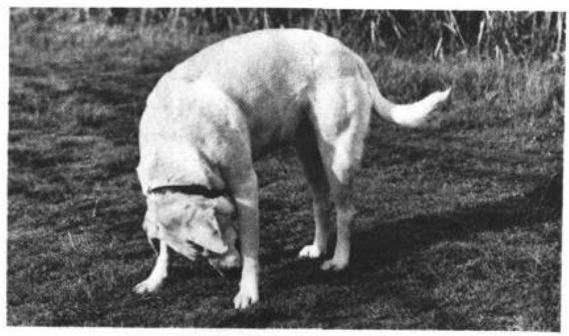
Questions about behaviour

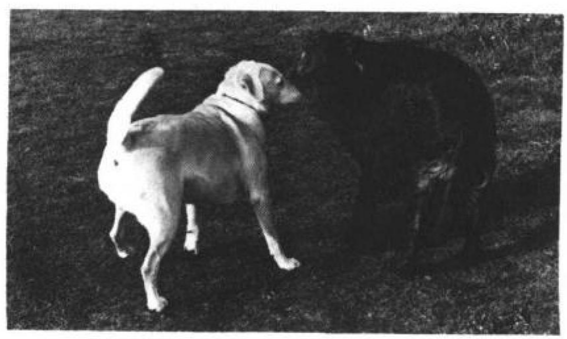
Suppose that you start to watch a dog which, like that in Figure 1, is standing still. What will it do next? What questions can you ask about the dog's behaviour? The behaviour of the dog at any instant depends upon a great variety of factors which interact with one another in a complex way and yet you may be able to predict the behaviour which is most likely. Your ability to predict what the dog will do depends, partly, upon how often you have watched dogs. You will, however, be able to make a reasoned guess based on your experience of other species including our own. We are all expert observers of human behaviour. We can deduce a great deal about the behavioural events which are occurring in any situation and the most likely preceding and succeeding events. Such ability is very important to us in our complex society and we all possess mechanisms which enable us to make predictions about human behaviour and about the behaviour of other species. A first step in trying to understand the mechanisms which control behaviour is to consider what evidence we use when we analyse a behavioural situation. The factors listed below might affect the behaviour of the dog. We consider most of them when trying to predict behaviour. Some of the events which occurred soon after the photograph in Figure 1 was taken, are shown in Figures 2 and 3.

1 This bitch is standing still but her behaviour can be described in terms of leg positions, the way that the head is held, gaze direction, face muscle and ear positions, tail posture, degree of hair erection and so on.

2 The bitch shown in Figure 1 soon started grooming her fore leg.

3 When a male dog arrived, the bitch shown in Figures 1 and 2 responded to him and started investigating him. Compare the head, tail and stance with Figure 1. The dog which arrived was unfamiliar to the bitch and the interaction lasted for several minutes. Two subsequent interactions with familiar dogs lasted for a few seconds only.





Motor ability

The dog's next behaviour is inevitably limited by its physical ability. It can perform only those movements which its muscles and the mechanics of its structure allow. Its movements might be described in a general way as being characteristic of dogs but they will be different according to both genetic variation, such as breed, and to the previous experience of the dog. Muscular function is modified by practice so a dog which has exercised regularly will be different from a dog which has exercised infrequently. It is already apparent that environmental factors, such as the degree and type of exercise, and genetic factors have interacted in the development of the dog to its present state. In describing motor ability it is necessary to consider some sensory and general physiological factors as well, for co-ordinated muscular movements depend upon input from sensory receptors in the muscles and upon the presence of adequate energy sources in the muscle cells.

Sensory input

The world as detected by sensory receptors is continually changing. The dog may stop standing still and initiate a new activity, the nature and timing of which is influenced by the input from a receptor. Some environmental changes might pass undetected but the odour of meat, the sound of footsteps, the sight of another dog, a tactile input due to a flea bite, a feeling of strain in a tendon, or the cooling of the ear tips might elicit different behaviours. The functioning of these receptors, like that of the motor system, will vary according to the previous experience of the dog and its interaction with genetic factors during development up to this time. Input along sensory pathways from receptor cells is not inevitable when a potentially detectable physical change occurs, for sensitivity and analysis of input can be affected at all stages by modifying commands from the central decision-taking areas of the brain. Physiological variables which alter energy availability may also affect input to central analytical areas of the brain.

Attentiveness

When a flea bites a dog the likelihood that the dog will scratch itself and the pattern of movement which it shows will differ according to whether the dog is asleep, drowsy or alert. The scratching probability and pattern will also be different in a dog which is watching an approaching cat, a dog which has heard a sound associated with the advent of food and a dog which is resting quietly. The response to input along one particular sensory channel depends upon the input which is arriving along other channels and the receptivity of central processing mechanisms. The systems concerned here are loosely referred to as attention and arousal. The differences in general responsiveness between sleepy and alert individuals are obvious to us. Attentional mechanisms may function at various levels in the analysis and decision-making systems of the brain. As mentioned above, the functioning of the receptor mechanism itself can be centrally modified. Since there must be a limit to the amount of incoming information which can be processed at any one time, it is essential for the individual to have mechanisms of selective attention. The priorities ascribed to different sorts of input will vary according to the motivational state and will probably differ according to experience during development.

Nutrient levels in the body

Irrespective of any sensory input, the dog might walk towards a place which could be a food source. The likelihood of this behaviour will depend partly on the levels of nutrients within the dog's body, which in turn depend upon the interval since the last meal and the rate of metabolism during that interval. Previous experience of feeding will alter the direction of movement and, perhaps, the posture and gait. Responsiveness to food odours and other sensory input must differ according to nutrient levels in the animal.

Water levels in the body

If internal receptors provide information to the effect that the body is short of water, the dog may go to drink. This factor will interact with others in a way similar to that of nutrient levels. If, as a result of previous drinking and kidney function, its bladder is full, the dog may walk and then urinate.

Body temperature

Like bladder distension, body temperature is monitored by receptors but a change in the input from these receptors may result from physiological changes within the animal and need not be temporally related to any external change. Metabolic activity, or external temperature, may change so that the dog becomes too cold or too warm. It will then modify its behaviour so as to correct that deviation from the optimum temperature range. As with other behaviours mentioned earlier, the precise nature of the behaviour will depend upon the precise interaction of genetic information with environmental factors during the development up to the point of observation.

Hormone levels

Hormonal influences on behaviour become apparent when, for example, responsiveness to sensory input is seen to be different according to hormone levels in the body. A bitch in oestrus would behave towards an approaching dog in a manner which is different from that of an anoestrus bitch. She may vocalise more and stand for longer when sniffed. Sometimes, however, behavioural changes might occur consequent upon hormone levels exceeding a threshold and without any sensory input occurring. In a male dog, when testosterone levels rise during courtship they may affect directly the likelihood that he will attempt to mount the bitch. Other examples include the effects on behaviour of increased adrenaline levels in a dog which had been dreaming and the moulting behaviour which is initiated in some insects by a sudden release of eclosion hormone.

Rhythms

Nutrient levels, water levels, body temperature and hormone levels all fluctuate within limits and the possible effects of such fluctuations on the dog's behaviour have been mentioned. The value to animals of predicting the necessity for action is such that timing mechanisms exist in the body which can initiate behaviour; for example the dog may start to look for food before the nutrient levels in the body initiate such behaviour. If there exists a rhythm of alternate food finding and resting which has a constant wavelength, i.e. which is periodic, then an individual may suddenly walk towards a food source because of the action of this periodic internal process. Most of us are aware of the internal clock which can tell us that it is lunch time, whether or not we have consumed food during the breakfast–lunch interval. A similar periodic process might result in our dog going to sleep at the moment of observation.

Other experiential factors

A dog which is in an unfamiliar place is likely to spend much more time looking around and preparing for rapid movement than would that same dog if the place was familiar. If the dog had been attacked recently in that place it would be much warier than if no attack had occurred. Such effects of previous experience modify behaviour via the sensory, attentional, hormonal and general decision-making systems. The various systems also interact in determining responsiveness to people or to other dogs. The previous social interactions of the dog will alter its responses towards a strange dog and previous encounters with a known dog will affect responses to it. The advent of a person who is recognised as a potential dog-kicker may result in the rapid withdrawal of the dog whereas the sight of a known provider of food may provoke the dog to approach, to bark and so on.

General themes

This book is about observable behaviour, the factors which affect it and its role in the life of the animal. How do the mechanisms which control behaviour work, and what selective pressures have resulted in the existence of all the components of these mechanisms? Many of the answers to these questions can be discovered by ethological investigations. Ethology involves observing behaviour and describing it in detail in order to find out more about how biological mechanisms function. Most people who would call themselves ethologists look for a wide range of actions when observing behaviour. They try to conduct their investigations in situations where the individual or group under observation is not so restricted that much of its behavioural repertoire is impossible. This approach can be applied in laboratory experiments or in farm situations as well as in wild, undisturbed conditions, for many important questions about behaviour cannot be answered by field work alone.

In order to use the information obtained from ethological studies it is often necessary to relate it to physiological or other biological and psychological research. Observational work must also be combined with the construction of theoretical models which attempt to explain the functional system which is being investigated. Thoughts about how a system works are often aided by considering how natural selection may have acted during the evolution of the system to its present state. It is largely as a result of theorising about the evolution of behaviour patterns in relation to the general ecology of species that the important cost–benefit approach to behaviour and other problems has developed. This approach is of use when considering motivational mechanisms as well as, for example, details of feeding behaviour. Another area in which theories about ecology and evolution have lead to exciting advances in our understanding of behaviour is the study of social relationships in groups, as will be discussed later.

One of the themes of this book is that answers to the two questions 'How does it work?' and 'Why does it exist?' are usefully considered together when dealing with any biological mechanism. A second theme is that information which results from different approaches to related problems should be pooled when trying to understand general mechanisms. Physiological studies of sensory or motor mechanisms are relevant to the work of a biologist or psychologist studying what individuals detect and how they respond. Ecological and evolutionary principles, as well as evidence from physiological and psychological experiments and knowledge of biological necessities during development, help to explain how individuals learn what and when they do. A third theme is the importance of applying the results of research on behaviour and related topics to medical, economic and social problems. A better understanding of behaviour means a better chance of preventing or curing behavioural disorders in man and in domestic animals, a better chance of maximising economically important behaviour by farm animals, and a better chance of impairing behavioural function and consequently of reducing the numbers of pest species.

Functional systems and homeostats

For convenience, all activities of animals have been classified in *functional systems* such as feeding, the regulation of body temperature and others listed in this section. Behaviour forms part of several functional systems and behavioural components of these systems are just as important as anatomical or physiological components. The behaviours which are observed during a short period may be part of several systems but, whatever the study, it is useful to consider all possible systems when trying to understand a behaviour sequence. Each of the systems listed below can be subdivided. Their relative importance in the life of an individual varies with time and from species to species.

The term *homeostat*, which is often used in physiological and behavioural studies, requires some comment here. Cannon (1929) coined the word *homeostasis* to refer to the maintenance of constant conditions or steady states in the body by co-ordinated physiological processes. A mechanism which does this is called a homeostat. It may include physiological and behavioural components and 'steady' state really means 'restricted within defined limits'. It is often assumed that homeostats operate by negative feedback, i.e. a corrective mechanism is initiated when a displacement from the steady state is detected. As Hogan (1981) points out, this is only one of several types of homeostat. Others use positive feedback or no feedback at all. In positive feedback the correction is made before the displacement occurs and is of a sufficient magnitude to ensure that an approximately steady state is maintained. An example of homeostasis which involves no feedback is the operation of storage mechanisms which are brought into operation when the concentration of a material rises above a critical level.

Body regulation and maintenance

Obtaining oxygen. All but the smallest animals on land and in water must obtain oxygen from their surroundings by breathing air or ensuring that water passes over their gills. If the oxygen level in the medium drops to a critical level, most animals use behavioural methods which increase the chance of reaching a place where there is sufficient oxygen.

Osmotic. Animals on land have to avoid dehydration whilst those in freshwater have to avoid loss of salts and other dissolved matter into the surrounding medium. Water conservation methods often involve behavioural components, for example going to a place where less water loss occurs. Acquiring water by drinking, on land inevitably involves complex behaviour. There must be receptors which detect changes towards dangerous levels of osmotic state, a decision-making mechanism which receives input from these receptors, a method of acting so as to return the state towards the optimum and receptors which provide an input so that the correcting behaviour can be terminated (see Chapter 5).

Temperature. Behavioural mechanisms and physiological mechanisms combine in regulating temperature. Although especially important in warm-blooded animals, the dangers of being unable to show activity at low temperatures have resulted in the existence of many body-temperature modifying behaviours in cold-blooded animals (Chapter 5). Temperature extremes can often be avoided by locomotion, but methods of temperature regulation will be selected according to the circumstances. For example, in the presence of a predator which can see well, physiological methods such as sweating would be less hazardous but if the predator hunts by olfaction, the prey may be detected if it sweats, so running away may be safer.

Cleaning. Birds must maintain their wing feathers in order that flight will remain possible. Grooming, preening and cleansing behaviour are also important to increase the efficiency of other forms of locomotion, sensory function and display as well as to minimise the effects of disease and parasites.

Feeding

Before they can ingest food, most animals need to search actively for, to recognize, and to acquire it (see Chapter 6). Elaborate behavioural strategies are used when hunting for animal prey or for widely distributed plant sources. Even when the animal is surrounded by food, as is a caterpillar on a host food plant, decisions about which part to eat and when must still be taken.

Hazard avoidance

Chemical. The ingestion of harmful substances and the accumulation of indigestible material or harmful metabolic products within the body must be minimised. The major components of this system are digestion, detoxification and immunological processes within the body but elimination is a frequent behaviour. The time and place of defaecation or urination are often precisely controlled, although the presence of very harmful substances in the gut may over-ride normal constraints on the occurrence of the behaviour. The avoidance of harmful substances when feeding depends, to a large extent, on experience and is discussed in Chapter 6.

Physical. Terrestrial animals encounter hazards such as falling, drowning and being squashed or buried. Aquatic animals may be stranded out of water, they may suffer lack of oxygen, or they may experience large pressure changes. Most of the methods of avoiding or minimising the effects of these hazards are behavioural. Such methods and those for avoiding noxious chemicals, other than those in food, are discussed in Chapter 5.

Predator avoidance

Predators constitute a major hazard for most animal species and their existence has had a large effect on the evolution of behaviour in all species including man (see Chapter 7). Animals avoid large predators by concealment, mimicry, keeping away from danger areas, flight, combat, or combinations of these methods. The depredations of parasites are also countered by using some or all of these methods.

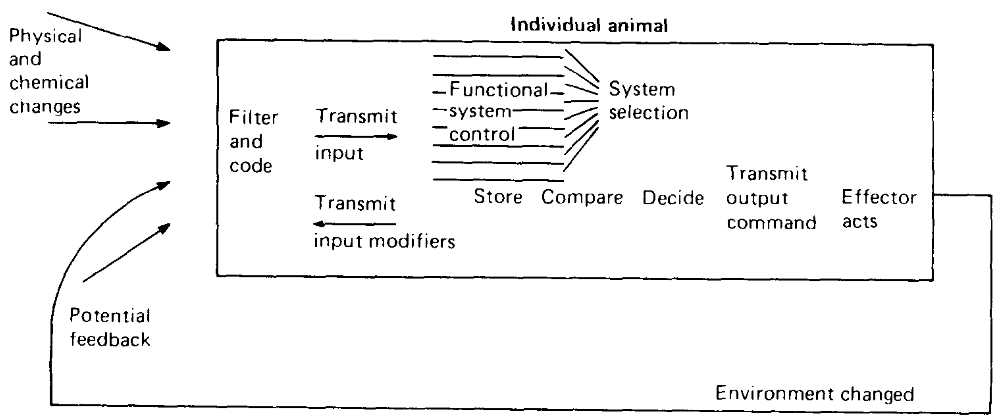
Reproduction

All of the functional systems mentioned so far operate in such a way that individual survival is maximised. The functional system in which reproduction and the survival of offspring or other relatives is promoted operates at the same time as systems promoting individual survival and may conflict with them (see later in this chapter and Chapter 9). The system includes behavioural mechanisms for mate finding, mate recognition, display and other methods of persuasion, mating, parental care, and other means of increasing the chances that offspring and other close relatives will survive and breed. This last function incorporates elements of many of the functional systems which promote individual survival.

Themes of other chapters

In order that any of these functional systems can operate, animals need to detect changes in their surroundings, to make decisions and, sometimes, to modify their behaviour accordingly (Figure 4). Methods of detecting, filtering and coding the effects of physical changes in the environment are discussed in Chapter 2 and the control of movement is the subject of Chapter 3. Since these two chapters, and those which discuss functional systems, include discussions of brain mechanisms, the major parts of the brain are illustrated here (Figure 5). Glands, as well as muscles, are important effectors and the action of hormones is described in Chapters 5 and 9.

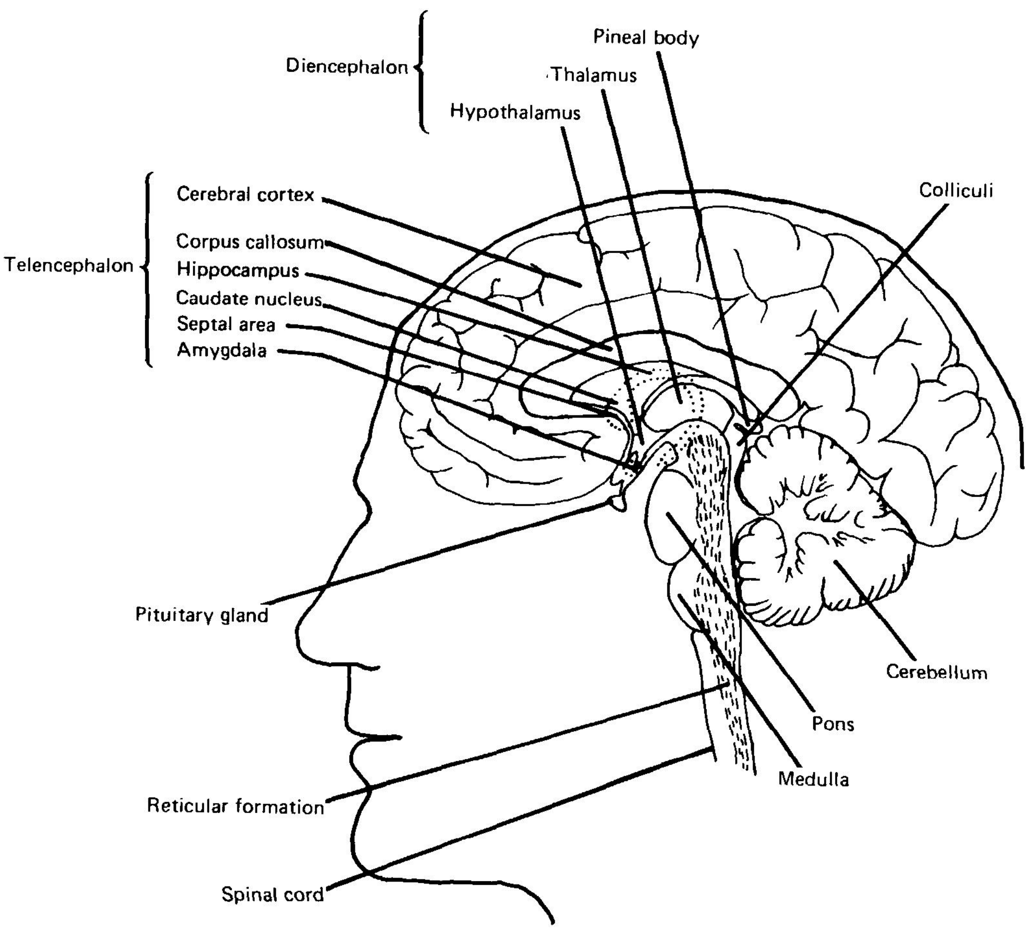
4 Some of the mechanisms within an individual and the relationship of the individual with its environment.



The study of motivation encompasses decisions about which activity to carry out, about the timing of activities and about the amount of energy to expend on an activity. This is a central theme in any attempt to understand behaviour, which psychology departments have long recognised. Consequent upon the work of Hinde (1970) and others, those who teach courses on behaviour for students of zoology or animal science have also come to recognise it. Recent research on motivational mechanisms has demonstrated the importance of considering their biological function and how they might have evolved (McCleery 1978; Toates and Halliday 1981). Mechanisms for deciding which functional system should be in operation and more especially, which behaviour should occur at any moment, are discussed in Chapter 4, on the allocation of resources. For details of storage, comparison and other aspects of decision mechanisms in the brain, books on physiological psychology and cognitive processes should be consulted.

As an example of the importance of biolog-

5 Sagittal section of human brain with certain areas lateral to this section also indicated (dotted). The fore brain is made up of the telencephalon (upper left labels) and the diencephalon (upper centre labels). The mid brain includes the colliculi, part of the reticular formation, the auditory tectum and the optic tectum. The lower right-hand labels refer to parts of the hind brain.



ical priorities in making decisions about behaviour, consider an animal which, while it is feeding, detects a predator. If it does not rapidly stop eating and initiate predator-avoidance behaviour then it is unlikely to survive. Suppose that there were two genotypes within a population of animals such that the possessors of one set of genes were able to switch more rapidly from feeding to predator avoidance than were the individuals with the other set of genes. Provided that a high likelihood of predation impaired individual survival more than did the loss of food, the first set of genes would be more likely to spread in the population than would the second. The decisions which are made today depend upon motivational systems which have evolved and, like any other character, have been influenced considerably in their evolution by natural selection.

Familiarity with an area often facilitates the operation of several functional systems. If some part of that familiar area is modified by secretion or artefact construction, adverse environmental effects may be reduced even more easily. The use of a hiding place or home, which is found or constructed, is discussed in several chapters, especially Chapter 7 on anti-predator behaviour.

Social behaviour forms part of several functional systems and can be advantageous to an individual in various ways. The functions of aggregation and of dispersal behaviour, together with ideas about the evolution of these behaviours, are discussed in Chapter 8. Interactions between mates and between parents and offspring are surveyed in Chapter 9 and the structure and organisation of social groups is the topic of Chapter 10.

Optimality and fitness

In 1966 MacArthur and Pianka wrote: 'There is a close parallel between the development of theories in economics and population biology'. The idea that mechanisms for assessing the costs and benefits of actions are of paramount importance in determining what an animal does at any moment and, as a consequence, how animals are distributed, has become very influential in behavioural and ecological work. This economic view of behaviour bore some resemblance to the thoughts of some psychologists about decision-making mechanisms (e.g. Edwards 1954). MacArthur and Pianka were principally concerned with the utilisation of food resources. They argued that since the present phenotype of an animal, i.e. the body form etc. which results from the expression of its genes, depends upon the results of natural selection over a long period, it is likely to include mechanisms for the 'optimal allocation of time and energy expenditures'. They presented a method of specifying the optimal diet of a predator in terms of the net amount of energy gained from prey capture and the energy expended in searching for the prey. These ideas, and similar ideas by Emlen (1966) about optimal foraging, have been developed considerably and are discussed further in Chapter 6. The general concepts are now applied to all aspects of behaviour. McFarland (1977) applies optimality concepts to mechanisms of decision making and brings together biological, psychological and economic approaches.

In many studies of situations in which a single functional system, usually feeding, was operating, costs and benefits have been expressed in terms of energy units. As an individual is hunting for and then acquiring food, it uses energy. The number of Joules required for these activities can be related to the number of Joules available from the food. When calculating the energetic costs of behaviour it is necessary to include those of basal metabolism during periods of low activity. A hunter which expends very little energy for a long period may die of starvation before catching anything. The total cost of an activity is the product of the time spent and the cost per unit time.

A further factor is the energy required for an activity in relation to the maximum possible energy expenditure. The amount of energy required may be a high proportion of that which is possible for a weak individual but may be a small proportion for a strong individual. The weak individual may not risk that activity, even though the food returns are high, if there is any possibility of failing to get the food and hence dying. The strong individual is very unlikely to die when it carries out that activity so the real cost is less. A simple assessment of the energy required for an activity is not a sufficient estimate of cost, for the risk to the individual must be considered. When predator–prey interactions are considered, the risk of dying is obvious.

The measurement of benefit in terms of the energy gain from food seemed logical in early cost-benefit analyses of feeding but food of a given energetic value might be a life-saver to one individual but not to another. A much better means of expressing costs and benefits is in terms of effect on reproductive potential. A large meal may result in an increase in the number of offspring produced. Such benefits of an action have been thought of by many authors as improvements in the fitness of an individual. This concept of Darwin's encompassed the survival of the individual and its subsequent breeding. Parental care, and other behaviour which benefits close relatives, often involves an obvious cost to the individual showing the behaviour. This behaviour is therefore an example of altruism. W. D. Hamilton's (1963, 1964*a*,*b*) ideas about the actions of genes during the evolution of altruistic behaviour lead to a further sophistication of the idea of fitness. By introducing his concept of 'inclusive fitness', Hamilton not only laid the foundations for a better understanding of the evolution of certain aspects of social behaviour but changed the ideas of many biologists about the level at which natural selection acts.

Ultimately, benefit must be assessed by considering the genes in the population. Behaviour patterns which promote individual survival usually increase the chances that the individual will produce offspring. Those offspring receive half of their genes from that parent. Hence any gene whose expression in the phenotype increases the chances of individual survival, reproduction or the survival of the offspring to breed, is more likely to be present in succeeding generations. Hamilton's example is of a gene causing its possessor to give parental care. Suppose that we are trying to calculate the costs and benefits of a particular behaviour pattern at a particular time in the life of an individual. We are, in fact, considering the many genes whose effects increase the likelihood that the behaviour pattern is shown. Our calculation must include an estimation of the effects that the action might have on the number of individuals in future generations which possess replicas of those genes. If the genes influencing the occurrence of two alternative behaviour patterns are being compared, they may affect individual survival differentially but have no other effect on future reproduction. Thus in some studies of feeding behaviour, simple estimates of energetic costs and benefits are helpful when one is trying to understand why some genes have spread in the population. Where parental care and complex social behaviour are analysed, it is more difficult to estimate costs and benefits. In altruistic behaviour there are apparent costs to one individual and benefits to others but if the net effect of a gene is to promote the spread of its replicas then, by definition, that gene will survive in the population.

One of the consequences of the arguments put forward by Hamilton has been the final demise of suggestions that any characteristic might be present in an individual solely 'for the good of the species'. Although Lack (1954) and Fisher (1958) had rejected the idea of such group selection, Wynne-Edwards (1962) ascribed to group selection a major role in population regulation. Wynne-Edwards' book brought together behaviour, ecology and population genetics and thus served all three disciplines but his theories were strongly contested by Hamilton (1963), Crook (1965), Williams (1966) and by Lack (1968). A gene will not persist in the population because its effects benefit all the members of the species, or some smaller group, unless those effects also promote the spread of that gene. The arguments about group selection and the limited situation in which it could occur are explained by Maynard Smith (1976*a*).

Maynard Smith also explains the concept of kin selection which developed from the inclusive fitness idea. Hamilton had explained that inclusive fitness would be increased if a parent behaved in a way which resulted in its death but, as a consequence, more than two offspring survived to breed. In the same way, for various degrees of relatedness, an individual should die for more than two siblings, more than four grandchildren or more than eight cousins. The degree of relatedness between siblings is 0.5 because each obtains half of its gene complement from each parent but it is not correct to say that the siblings share 50% of their genes because this depends upon the variability within the species. Many genes are the same for all individuals because they code for some essential protein which will not function if its structure is altered. Such variability, or lack of it, is discussed later in this chapter but the actual proportion of genes shared by siblings is always much higher than 50%. Inclusive fitness is a term which refers to individuals as the unit upon which selection acts but as Dawkins (1978) explains, the logical conclusion of Hamilton's arguments is to consider how selection acts on replicators. These replicators are genes or groups of genes, hence the arguments above about the ultimate criterion for assessing costs and benefits.

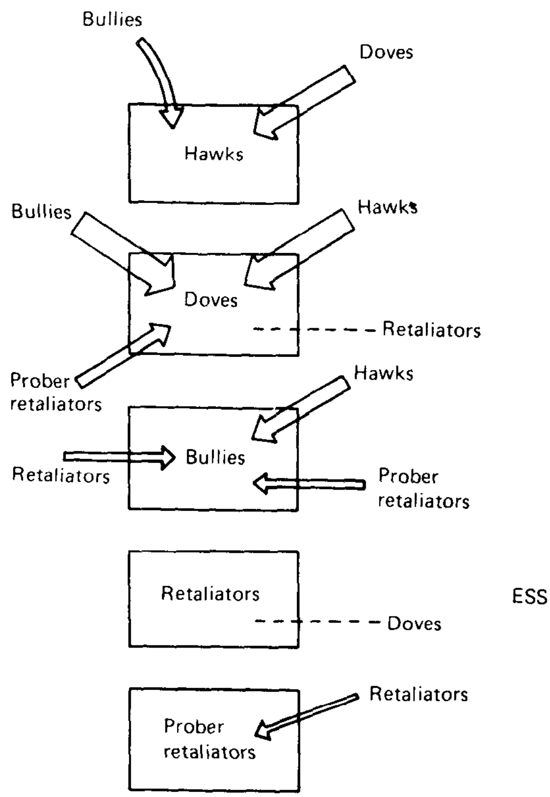
Evolutionarily stable strategies

It is useful to consider behaviour as being the result of the operation of a set of computer programs. This analogy is useful, for the interaction of gene complexes with the environment must be similar in many ways to a computer program which says: carry out this operation, read this environmental input, modify the next step according to which of four kinds of input are received, carry out another operation until a certain type of input is received, etc. The environmental factors which influence the result of this process may be fairly constant among individuals, or very variable, but the fact that such interaction occurs during the development of any characteristic is of fundamental importance. This point will be developed later in this chapter. Examples of such programs might be those which enable a dog which is getting hotter to sweat, or pant, or stand in the wind, or move out of the sun. The dog will utilise these abilities via a decision-making program which determines what it must do when it gets too hot. This program will result in courses of action which depend upon sensory input etc. If a certain combination of inputs exists then a certain pathway is chosen.

The environmental factors which interact with the genetic program will not be the same in each individual so there will be variation in the final form of the expression of that program. Arguments about the evolution of behavioural mechanisms refer to the average individual which has the program and should not be taken to imply that all individuals bearing a particular genetic program will be the same in respect of that behavioural mechanism. It is likely, however, that individuals with slightly different programs will, on average, differ behaviourally. Hence it is useful to consider the way in which natural selection might act in a population which includes more than one alternative program. Taking an example from the Bible, a thirsty man arriving at water might lie face down and lap the water, or scoop up the water with one hand, or scoop up the water with two hands. If the likelihood of predation by lions at water-holes is high, individuals which lie and lap may be less likely to survive until they breed because it is difficult for them to see the stalking lion when they are lying face downwards. Scooping two-handed might be the fastest way to obtain water whilst preserving some vigilance against the approach of a predator so any genetic factors which facilitated this behaviour would become commoner and those which did not would become less frequent. The use of two-handed water-scooping on all occasions is an example of a drinking strategy. A strategy may involve the use of one drinking method in one situation and a different method in another situation.

The way in which selection might act in populations where there are alternative strategies has been considered by Maynard Smith and Price (1973). The question which can be asked when a strategy for dealing with a certain type of situation is present in a population is 'Could a population of a gene-complex which, on average, results in the individuals using that strategy be invaded, during a number of generations, by a gene-complex which results in an alternative strategy?' If lying and lapping was the only strategy for drinking in a human population which was subject to lion attack, when individuals arrived who could use two-handed scooping, they would be at an advantage. Assuming no change in the behaviour of those who lie and lap or of the lions, the population would be invaded by the gene-complex which results, on average, in the new strategy. Maynard Smith and Price discussed intraspecific animal conflicts in their paper. They considered five strategies for contests between evenly matched individuals. The 'Hawk' strategy is to attack as soon as a contest is initiated, thus inevitably incurring quite high costs but sometimes benefiting by victory. 'Doves' threaten initially when a contest starts but always give in, with consequently low costs but no victories against attackers. 'Bullies' attack initially but give in if the attack is returned. 'Retaliators' threaten initially and attack only if they themselves are attacked. 'Prober-Retaliators' threaten initially, attack if threatened weakly, threaten if threatened strongly or if retaliation occurs but retreat if the contest is prolonged. When assumptions were made about the costs and benefits of serious injury, slight injury, winning, and saving or losing time, the average net result of each possible encounter could be calculated. These are summarised in Figure 6 and they indicate that whilst a population of 'Hawks' could be invaded by 'Doves' and 'Bullies', a population of 'Retaliators' would not be invaded by any one of the other strategies. Hence 'Retaliator' is an Evolutionarily Stable Strategy (ESS). The term 'invade' seems particularly appropriate in this example but in its general sense an ESS is a strategy which will persist in the population because the gene complex which usually results in it cannot be replaced due to invasion by a gene-complex for another strategy. Put in Hamilton's terms, the inclusive fitness of the ESS is higher than that of any alternative strategy.

6 Conflicts between animals of equal fighting ability. Populations in which the strategy named in the box was shown, would be invaded by gene-complexes which resulted, on average, in individuals which played the strategies at the base of the arrows. Arrow width indicates ease of invasion. 'Retaliator' is an Evolutionarily Stable Strategy but 'Dove' could co-exist with it (dashed line). Data from Maynard Smith and Price (1973).



The Evolutionarily Stable Strategy in the competitive interaction example used by Maynard Smith and Price can be calculated mathematically but various assumptions must be made. The ESS idea is just as useful in the strategies for drinking mentioned above but it is more difficult to calculate the ESS. In no case is it possible to be sure that all possible alternative strategies have been considered in a real biological situation. Hence it is best to refer to a strategy as being an ESS if it cannot be replaced by any known alternative. The concept is then of value in considering any aspect of biology which has been examined sufficiently rigorously to make possible the understanding of alternative strategies. The area in which the ESS concept is particularly useful is that in which the playing of a particular strategy has consequences as to which alternative strategy by another individual is subsequently most effective. Examples of such situations, where there is interaction between individuals, include competition for food or for other resources as well as direct encounters. The optimum strategy for food acquisition from an area is likely to be different according to what strategies are being used by competitors in the same area. As Maynard Smith (1976*b*) put it 'If everyone else is eating spinach it will pay to concentrate on cabbage'.

Behavioural diversity and reproductive strategies

Man is a large, long-lived species capable of repeated reproduction but with a prolonged juvenile period under parental care. Some species of fly, on the other hand, are small, develop from egg to adult in a few days, breed once producing many eggs, and then die. Fisher (1930) wondered how 'apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism' and 'what circumstances in the life-history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction?' Such questions of strategies in reproduction and life history have been discussed by ecologists for some time but it was not until MacArthur and Wilson (1967) introduced their ideas of *r*-selection and *K*-selection that some order appeared in these discussions. These ideas from ecology and their developments, are also fundamental to an understanding of certain aspects of behaviour. The rate of increase, *r*, in the numbers of individuals in a population has a maximum, *r* max, in an ideal environment. If the fly mentioned above is in an ideal environment, as it might well be at the beginning of the favourable season, its population will increase at r max. There will be little competition between individuals except in the number of offspring they can produce. A gene favouring faster rate of offspring production (higher *r* max) will spread in the population but selection may not alter the proportions of alternative genes concerned with many other characteristics because all individuals survive almost equally well. Such selection is best called *r* max-selection.

If the environment is not favourable enough to make possible very rapid population growth, genetic factors which increase the chances that an individual will survive until breeding and those which promote the chances that the offspring will survive until breeding, become much more important. As soon as there is extensive competition between individuals for essential resources, a different type of selection mechanism operates. The population is maintained at or near the carrying capacity (*K*) of the environment in *K*-selection. More efficient utilisation of resources, such as greater net energy gain from food supply, may alter *K* but most of the major effects of natural selection will be in situations where one strategy might be better than another in a competitive situation. Some of the consequences of *r* max- and *K*-selection are discussed by Pianka (1970) and Brown (1975) and are summarised in Table 1. As Pianka emphasises, there is a continuum between *r* max- and *K*-selection and it is possible to have a mixed reproductive strategy. The most obvious differences in behaviour, according to the type of selection which operates, are in the timing of first reproduction, the amount of parental care and the dispersal mechanisms. If selection leads to early reproduction, no parental care and extensive dispersal, the species is very different from one like our own. Less obvious consequences for behaviour are that strategies for a variety of competitive interactions are likely to be most elaborate in *K*-selected species and, as a result, behaviour in total will be more complex.

Functional aspects of species differences in relation to life-history variables have been extensively reviewed by Wilson (1975). Differences in parental care in relation to number of offspring produced, life expectancy etc. are described further in Chapter 9. It is apparent that closely related species may differ in their strategies, for example the work on deermice (*Peromyscus*) species reviewed by Brown (1975). A dramatic contrast is that between lemmings (*Lemmus*) which breed very fast and migrate in a spectacular way, and beavers (*Castor*) which are long-lived, disperse two years or more after birth, have low birth and death rates, and extensively modify their surroundings. Any comparative psychological or biological study must take into account the fact that selection may result in changes in different directions in different species.

The universality of environmental effects on behaviour

Environmental factors and genetic programs

An important point, which is made earlier in this chapter, is that the operation of genetic programs always involves interaction with environmental variables. Research on genetic expression in cells and during morphogenesis has provided some evidence as to how genetic programs operate. The end result of the operation of a program may vary greatly from individual to individual or may be relatively constant

Table 1. *Summary of some aspects of* r *max- and* K*-selection.* (*Modified after Brown 1975*)

	r max-selection favouring a higher population growth rate and higher productivity	*K*-selection favouring more efficient utilisation of resources
Defining characteristics		
1	Conditions of occurrence far below *K*	At *K*
2	Little competition for resources among and within species	Much competition
3	Often transient habitats	Long-lasting habitats
4	Frequent and large population fluctuations	Infrequent and small population fluctuations
Consequences		
1	*r* max higher	*r* max often lower
2	*K* rarely approached	*K* raised
3	Higher birth and death rates	Lower birth and death rates
4	Rapid development	Slower development
5	Earlier reproduction	Later reproduction
6	Shorter life	Longer life
7	Less parental care	More parental care
8	Good dispersal	Poor dispersal