CHAPTER ONE

Introduction

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We introduce the study of animal behaviour as a subject of great diversity (many different species of animals going about their lives in a great variety of ways) but unified by four questions that can be asked about any behaviour and at any level from 'whole animal' to neuron.

Wolves excitedly greet each other as members of the pack come together; a bumble bee uses its long tongue to reach the nectar at the base of a foxglove flower; a peregrine falcon stoops at high speed to strike a pigeon flying below; young cheetahs rest quietly together, very close to sleep (Fig. 1.1). The study of animal behaviour is about all these things and much more. It is about the chase of the hunter and the flight of the hunted. It is about the spinning of webs, the digging of burrows and the building of nests. It is about incubating eggs and suckling young. It is about the migration of a hundred thousand animals and the flick of a tail of one. It is about remaining motionless and concealed as well as about leaping and flying. Behaviour involves the static postures and active movements, all the noises and smells and the changes of colour and shape that characterize animal life.

Figure 1.1 Young cheetahs recline sleepily. Inactivity is as much a characteristic of behaviour as activity.

Animal behaviour is a very popular subject, not just with biologists but with the general public – so much so that it has even come to occupy a lot of prime time on television, the surest measure of real popularity! Since our earliest origins, human beings have always been fascinated by our fellow creatures. Apart from this intrinsic interest and the fact, which we hope to demonstrate, that the subject presents us with questions as challenging as any in science, the study of animal behaviour is also of great practical importance. The conservation of wild animals in their natural habitats and the welfare of those other species we have domesticated for our use are both topics which command a lot of public attention.

Experimental studies with animals are now controlled by law in many countries, and rightly so. In the past, we have gained valuable information about behaviour from experiments, for example deafening young birds or isolating a young monkey from its mother, which might now be deemed unacceptable. Nevertheless, we shall describe some such results as part of this book. Not to do so would be perverse, since they have advanced our understanding and by this understanding we are better able to design observations and experiments which are not invasive or cruel in any way. Animal behaviour workers are very conscious of their responsibilities in this regard and go to some lengths to minimize any kind of disturbance to the lives of their subjects. The Association for the Study of Animal Behaviour in the United Kingdom and the Animal Behavior Society of the USA collaborated to publish a collection of papers, *Ethics in Research on Animal Behaviour*, which considers such problems, not only for laboratory studies but also for fieldwork (ASAB/ABS, 2006). Even observing animals from a distance can disturb them and so needs to be done with great care. We are now able to learn a great deal about the behaviour of animals by tagging them for recognition or fitting them with tracking devices. Although the animals may then be released back into the wild, catching them may cause stress and the tracking or marking devices may even alter their behaviour. This means that the way in which we design any study of animal behaviour – experimental or observational – has moral, social and economic implications. The importance of animal welfare is being increasingly recognized around the world as more and more countries now have legislation, codes of practice or other guidance as to how animals should be treated. The study of animal behaviour has a particular contribution to make here, since understanding the behaviour of animals and how it has been evolved under natural selection can help us to improve welfare. Legislation will be effective only if it is based on good information about how animals live and how they respond to their environment.

For example, the captive breeding of cheetahs (*Acinonyx jubatus*) is likely to be one important tactic for the long-term survival of this wonderful animal. Zoos had kept them for many years but their breeding success was pitifully low until we obtained the results of fieldwork in Africa (see Caro, 1994). This showed that keeping males and females together – the standard zoo practice – was doomed to failure. Female cheetahs live and hunt alone, completely separately from males, except for the brief days of their oestrus. Once this aspect of the natural situation was reproduced in captivity, cheetahs proved quite easy to breed and several zoos – the cheetahs in Fig. 1.1 are at London's Whipsnade Wildlife Park – now have good numbers which could be the basis for re-introductions to the wild should this prove necessary.

We opened this chapter with a glimpse at the range of very diverse phenomena we are dealing with. Where in all this diversity do we start? What do people who study animal behaviour actually do and what do they want to find out?

There are two main approaches, the physiological and the 'whole animal'. 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 a 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', as it were. For example, if we want to get at the mechanisms that give rise to the behaviour of singing, or those which organize an animal's responses to visual stimuli from predators.

In practice there is considerable overlap between the approaches. It is now possible to collect urine samples from animals in the wild – only tiny amounts are needed – and then back in the laboratory get an accurate measure of what hormones are circulating in the bloodstream. A few cells from the root of a recently shed hair or feather, or even those shed from the bowel with the droppings or shed from the inside of the mouth of a herbivore and left with its saliva on vegetation, can be cultured for DNA fingerprinting enabling relatedness within a social group to be worked out. The best understanding of behaviour nearly always comes when a combination of approaches is employed for, used well, physiological and 'whole animal' approaches complement each other – behavioural studies sparking off the search for physiological mechanisms and in turn putting physiological studies into a functional perspective. One of our aims in this book is to give some idea of the extent to which this is now possible.

Within the 'whole animal' approach, a distinction is often made between psychologists and ethologists, both of whom could be described as being interested in the behaviour of intact, functioning animals. Psychologists working with animals have traditionally been mainly interested in learning and have tended to work in laboratories on the learning abilities of a restricted range of species, often rats and pigeons. Ethologists have been more concerned with the naturally occurring, unlearnt behaviour of animals, often in their wild habitats. Although this distinction still exists to some extent, there is now a fruitful coming together of the two. Ethologists have become interested in the role of learning in the lives of wild animals and psychologists are beginning to ask evolutionary questions about the learning abilities of a much broader range of species and to study their responses to more natural stimuli. Another of our aims is to show how much psychologists and ethologists are increasingly learning from each other, to mutual advantage.

But nobody – physiologist, ethologist or psychologist – can rely solely on one source of information; they must approach problems at the level which is appropriate for them. Some physiologists like to emphasize that their methods are the more fundamental, and it is true that increasingly it becomes possible to explain certain aspects of behaviour in terms of the functioning of the basic units of the nervous system, the neurons. However, this is effectively a task without end and since the main function of the nervous system is to produce behaviour we must also investigate the end product in its own right. Even if we knew how every nerve cell operated in the performance of some pattern of behaviour, this would not remove the need for us to study it at a behavioural level also. Behaviour has its own organization and its own units which we must use for its study. Trying to describe the nest-building behaviour of a bird in terms of the actions of individual nerve cells would be like trying to read a page of a book with a high-powered microscope. Not only would it be incredibly laborious to discern the boundaries and make out the identity of each printed letter, we might miss out completely on the grouping of letters first into words, then sentences, then paragraphs and so on.

As we illustrated with our opening paragraph, 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, although we are increasingly able to detect them indirectly through brain imaging or recording from single nerve cells. What we see from the outside may be an animal engaged in violent activity or one completely at rest, but both are behaving. The range of phenomena that are called behaviour immediately presents us with the problems of how to observe and how to measure it. In the physical sciences, and often elsewhere in biology, we have universally recognized units – molecules, milliamps, pH units, metres, etc. – for measuring and classifying our observations. When we watch animals we have no such framework. Behaviour is continuous for as long as life persists and so many different things may count. Put this way, the task would seem to be impossible and so to make it manageable, we have to abstract and simplify. In other words, we have to make decisions about what it is important to record and what can safely be ignored. Exactly how we do this may be different on different occasions or for different purposes.

For example, if we are studying the courtship behaviour of sticklebacks or 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 be judged irrelevant for behavioural studies of courtship. However, if we are watching the courtship of newts, the rules are changed. Male newts court females on the bottom of ponds or streams and their courtship is punctuated by trips to the surface to breathe. Halliday and Sweatman (1976) have found that males can postpone breathing up to a point if courtship is proceeding smoothly, but if there are delays or the female moves off they rush to catch up on their breathing. Thus records of breathing are an important part of any study of newt courtship patterns, unlike those of pheasants. The behavioural measures we use must be chosen to suit both the animal and the type of problem under investigation.

Questions about animal behaviour

We can see, then, that animal behaviour presents us with problems of description and selection. There are other difficulties that arise from the very beauty and fascination of the subject which have made it so popular. Natural history TV programmes and books now offer films and photographs of such a high standard that we have become familiar with details of animal behaviour which used to be virtually impossible to observe. We can watch penguins fleeing from leopard seals by leaping up onto an Antarctic ice floe; we can watch in close-up the fantastic courtship displays of male birds of paradise; we can follow from start to frustrating finish the hunting chase of a cheetah who finally pulls down a gazelle only to be immediately driven off its prey by roving hyaenas. All this is splendid, but there can be a considerable temptation simply to gaze and wonder, rather than to think about analysing what remarkable things are happening.

We certainly must not lose our sense of wonder, but in order to use constructively the enthusiasm for further study which it gives us, we have to identify clearly what kinds of questions about behaviour need to be answered. In 1963, Niko Tinbergen, one of the founders of modern ethology, wrote a paper, as valuable today as when it was written, which he entitled, 'On the aims and methods of ethology'. There he suggested that there are four main types of question which we need to ask of an animal's behaviour. They are really four different ways of asking the question 'Why?' and we can get into a very unhelpful muddle unless we clearly understand the nature of the distinctions between them.

Firstly, Tinbergen asserts, we ask why the animal performs a piece of behaviour in terms of its **function**, i.e. how it helps to improve the survival of the animal or its success at reproducing itself. Secondly, we ask about the **evolution** of the behaviour, i.e. how it has changed over the course of evolutionary time, in just the same way that we might study how a whale's flipper or a bat's wing changed from the ancestral limb into what we see today. Thirdly, we have to deal with its **causation**, what factors, both internal and external, lead to the performance of that particular piece of behaviour at that particular moment. Lastly there is the question of the behaviour's **development**, how the behaviour of a young animal changes as it matures and what factors, again both internal and external, affect this process and its end point.

Function and evolution are obviously interconnected and it is by selection acting on the processes of development that behaviour becomes adapted to the environment in which it has to operate. **Adaptation** is a subject we shall examine more closely in Chapter 6; here we may note that it arises by selection between individuals over many generations following genetically based changes, or by modifying behaviour to achieve the best response during an individual's own lifetime. It will often be important to keep in mind the distinction between these two pathways to adaptiveness.

Tinbergen's ideas have been very influential amongst behaviour workers, so much so that 'The Four Questions' have entered into much of our thinking, certainly they have for the authors of this book. We want to integrate some of the diverse ways of studying behaviour, for full understanding can come only when we have answers to each of the questions.

Tinbergen directed his paper at ethologists but we should note that the same four questions can be asked no matter at what level of organization we are working. They are as relevant to studies of physiological mechanisms as to ecological ones.[1]

Of course, when one begins to examine particular cases it rapidly becomes obvious that function, evolution, causation and development are not isolated topics: they overlap extensively and studies directed at one topic will nearly always contribute to the others. Studies at different levels and on different animals will lead to emphasis

1 Confusingly, ethologists and physiologists use the words 'function' and 'adaptation' in rather different ways. For physiologists, 'function' often means the way an organ works – e.g. 'liver function is badly affected by too much alcohol'. They do not mean the contribution that one's liver makes to survival. Again, 'adaptation' to a physiologist often refers to sensory adaptation whereby a sense organ ceases responding to continuous or repeated stimuli, and has nothing to do with good fit to the environment.

being laid on this question or on that, but all will benefit from taking as broad an approach as possible. We can best illustrate this by taking a look at two very contrasted examples of well-studied behaviour patterns – the escape response of the cockroach and the courtship displays of male sage grouse.

The escaping cockroach

Anyone who has handled a cockroach will know that it behaves like greased lightning when an attempt is made to catch it. Toads, which are natural predators of cockroaches, seem to have almost as much difficulty as we do. Probably the first question that springs to mind is that of causation: we want to know how the cockroach manages to avoid the lightning strike of the toad's tongue. We want to explore both the mechanisms inside the cockroach and the stimuli impinging on it from the outside that enable it to detect that it is about to be attacked and to dash away so effectively.

The first clues about causal mechanisms come from watching the behaviour of freely moving cockroaches and toads, or rather analysing film of them because everything happens so quickly that the naked eye cannot follow it. Slowed-down film shows that when a toad is within striking distance then just before its tongue flips out of its mouth, the cockroach will turn rapidly and run. It seems, then, to have some way of detecting in advance that a toad is going to strike and from which direction before it actually does so. The cockroach always turns in the appropriate direction, away from the toad and about 16 milliseconds (ms) before its tongue becomes visible. At this point, the toad is apparently already committed to a particular direction and distance to its target. The cockroach's movement means that tongue may strike in the wrong place.

How does the cockroach predict that the toad is gearing up to strike? The most important cue seems to be tiny gusts of wind produced by the toad's preparatory movements. Camhi *et al*. (1978) showed that these slight air movements are picked up by the cockroach through many tiny wind-sensitive hairs on its cerci, paired appendages which protrude like little tails from the end of its abdomen (see Fig. 1.2). These cercal hairs are exquisitely sensitive and the cockroach will make a false run if a tiny gust of air is blown at a cercus. The smallest gust of air that generates escape behaviour is 12 mm/s with an acceleration of 600 mm/s^2. The hairs have to be physically moved, because if they are immobilized with glue, the cockroach is much less successful at escaping.

In behavioural experiments in which puffs of air were blown at cockroaches, it was shown that they started to show their escape behaviour just 44 ms after a puff started. Then, by measuring the wind generated by a toad when it strikes at prey, it was found that the critical (12 mm/s) gust of wind occurred on average 41 ms before the tongue emerged from the mouth – very close to the response latency of 44 ms shown by the cockroach to an artificial puff of wind. So it is the minute gust of wind generated by a

Figure 1.2 The cockroach *Periplaneta americana*. The cerci at the hind end are indicated by the arrow.

toad preparing to strike that sets off the escape turning behaviour. By waiting until the very last moment before turning, the cockroach evades the tongue that has already started to move and thus escapes because the toad cannot, at that late stage, change the direction of its strike.

So far, we can see that a great deal can be learned about the mechanism of the behaviour by studying the behaviour of whole animals – intact toads and intact cockroaches. Film records of strike and escape, experiments stimulating the sense organs of the cockroach and measurements of the wind stimulus produced by the toad give us a basic idea of the mechanism underlying escape behaviour at this level.

The next stage, and this is often the case with studies of causation, is to go ‘inside the skin’ and look at the same behaviour but at the physiological level. Close examination shows that there are about 220 hairs on each of a cockroach’s cerci and that each hair is hinged so that it can be moved most easily in just two directions at 180° to one another. They move less easily in directions at 90°. Different hairs have different biases, which means that wind from certain directions moves some hairs and wind from other directions moves others. Thus the basis for the cockroach being able to discriminate wind direction so accurately appears to lie in the mechanical construction of the hairs. By recording from sensory nerve cells at the base of each wind-sensitive hair, Camhi *et al*. found that the nervous activity in these cells reflected the directionality of their hairs: the nerve cells responded much more to wind from some directions than from others.

Camhi *et al*. also found that there is a cluster of nerve cells, the terminal ganglion, at the hind end of the cockroach which contains a group of large cells known as Giant

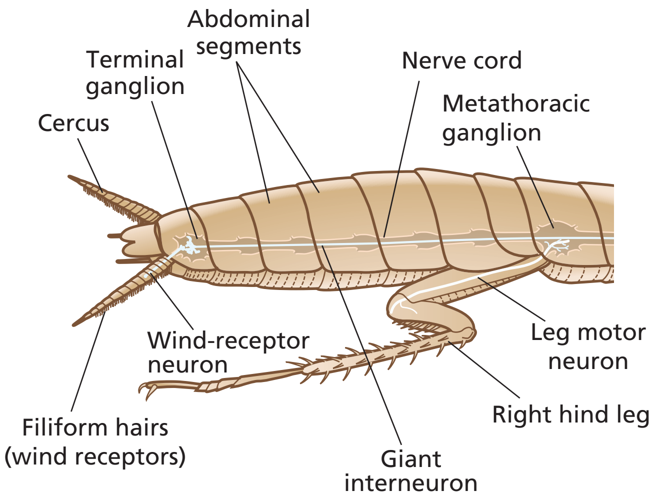

Figure 1.3 Hind end of a cockroach showing the cerci with filiform hairs, which are the wind receptors.

Interneurons (GIs). The GIs run up the nerve cord to the head, on the way passing through the thorax and linking to the motor nerves of the legs that do the rapid escape running. The GIs receive a pattern of information from the sensory nerves in the cerci which conveys the direction of the wind. They pass this on to the nerves which control the leg muscles: these nerves, in turn, command the legs to turn the cockroach and make it run in the opposite direction (Fig. 1.3).

When the insect is stimulated with a wind puff, the GIs become very active (as recorded by microelectrodes inserted into them) and so do the motor neurons to the muscles of the hind leg. It is possible to inactivate some of the GIs by injecting them with an enzyme, leaving other GIs intact. This has the effect of making the cockroach turn in the wrong direction in response to a puff of a wind. So it appears that some sort of comparison between activity in different GIs goes on in the normal cockroach, telling it which of its legs to move.

It is clear that for this piece of behaviour we have made very good progress, at both behavioural and physiological levels, towards understanding **causation**. For relatively few behaviours, particularly in vertebrates, do we understand the mechanisms in as much detail as this, right through from the detection of a stimulus to the command to the limbs. We can also give thoroughly satisfactory answers to the question of **function**, in the sense that we can readily understand how the escape behaviour aids the cockroach's survival. As we shall see, not all behaviour is so easy to interpret. However, note that the cockroach study does enable us to identify aspects of function in considerable detail. Whereas we might have assumed that it would be to the cockroach's advantage to run the instant it detected a toad – it might see its head turn for example – we can now understand the function of that 44 ms delay. It actually improves the insect's chances because it means that the toad's strike is now committed and if the cockroach can move a sufficient distance, the tongue is bound to miss – the toad cannot adjust. Many ethological studies of animals in their natural habitats have revealed just such detailed matching of behaviour to function.

What can we say about the related question, the **evolution** of this piece of behaviour? What were its origins and what sort of escape behaviour did ancestral cockroaches show? Since we have already seen that the function of the very rapid response is to evade predators, there must have been a kind of arms race between them and their prey, beginning with slower cockroaches and slower toads and other predators. Then, as now, both sides won some of the time, but some cockroaches would be a bit faster, perhaps because they had more sensitive cercal hairs which could detect smaller air currents. They would survive better and leave more offspring and sometimes their increased speed would have a genetic basis. When this was the case then their offspring would inherit their parents' extra speed. This would put selection pressure on the predators to become faster at grabbing cockroaches, which would in turn favour even faster cockroaches and so on.

This is a very general story suggesting how the skills of cockroaches became honed to a high degree over millions of generations. In this case it is difficult to be more precise because, for the most part, behaviour does not leave a fossil record and we do not have details of how the escape skills of modern cockroaches compare with those of their ancestors. However, we can deduce something of the course of escape behaviour's evolution by looking at the 'family tree' of such behaviour in living relatives.

Just as with bodily characteristics, so with behavioural ones we can get an idea of evolutionary history by comparing traits among groups of related species. If a wide range of species share a trait then we are fairly safe in assuming that it evolved before the different species diverged from a common ancestor. If a behavioural trait is shared by quite distant relatives then it pushes the time of its origin further back in time. On this sort of criterion we can be confident that the common ancestors of the whole ancient group of orthopteroid insects – the stick insects, crickets, grasshoppers and cockroaches – had escape responses organized very much along the lines just described. All of their descendants have cercus-like structures at their hind ends; all have giant fibres in their ventral nerve cords, often arranged in strikingly similar ways. Not all of them escape by running as does the cockroach; some jump, some may freeze into immobility to evade a predator's eyes, but the basic response and its mediation must have evolved very soon after the first insects appeared.

The last question we must address for the escape response concerns its **development**. As with questions about mechanism, questions about development can be asked at many different levels. Does a newly hatched cockroach escape as effectively from a toad as an adult or does it improve with practice? How do the connections between the sensory nerves and the GIs form so that escape behaviour can be accurate?

In a way, there is a simple and direct answer to all developmental questions: it is always true that an animal's genetic makeup and the environment in which it grows up