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ONE

The science of behaviour

1.1 Introduction

This book is concerned with the science of behaviour. Much of the material is to do with non-human animals but we have also included some consideration of human behaviour. Indeed, throughout the book 'animals' includes humans. We have attempted to show how an understanding of the behaviour of non-humans can help us to understand ourselves better. At the same time, although there are similarities between humans and non-humans, there are very significant differences too. These differences mean that we should be careful not to extrapolate too readily from the behaviour of non-humans to our own behaviour. Equally, we should be careful not to be **anthropomorphic**. To be anthropomorphic is to generalise from humans to non-humans. For example, you might be tempted to think that the rhesus macaque in figure 1.1 is grinning because it is happy. Actually, careful observation shows that quite the reverse is the case. This 'grin' is better named as a 'bared-teeth display'. (Such a label describes what the behaviour looks like, not what its function is guessed to be.) In fact, the behaviour in figure 1.1 is displayed when the macaque would like to flee but is thwarted from so doing – for example, because it is cornered.

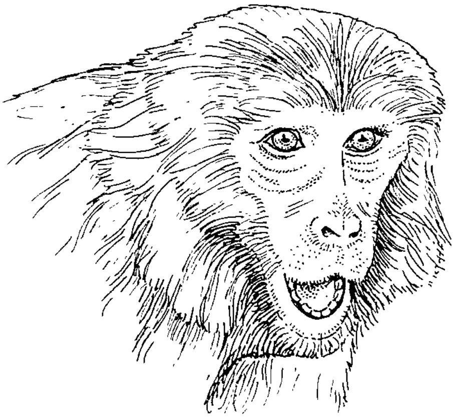

Figure 1.1 The bared-teeth display of a rhesus macaque. It may look as though the animal is grinning happily. Actually, it is fearful.

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While anthropomorphism is not good science, neither is its extreme opposite. Humans, while distinct from other animals, are not utterly different from them. We can learn about ourselves by studying the behaviour of other species.

In this chapter we will look at some of the questions which the science of behaviour attempts to answer and will also outline how those who study behaviour attempt to answer such questions. We begin by looking at the various scientific disciplines that are concerned with the study of behaviour.

1.2 Ethology, anthropology, psychology, sociology and sociobiology

There are a number of different scientific disciplines which look at behaviour. Actually, the boundaries between these various disciplines have shifted over time and nowadays are not as rigid as they once were. Nevertheless, each of these disciplines has its particular focus and methodology.

Ethology is the study of the behaviour of animals – mainly non-humans. The golden days of ethology were from the 1920s to the 1970s and we shall refer in this book to some of the great ethologists such as Konrad Lorenz, Niko Tinbergen, Karl von Frisch and Jane Goodall. The fundamental working assumption of ethologists is that in order to understand behaviour, animals should be studied carefully in their natural environment. Experiments are often performed and are undertaken in the field not in a laboratory. Little equipment is needed beyond a notepad, a pencil and a watch, and the key to success is patience and acute observations. Often observations are carried out over a period of many years, allowing a detailed understanding of the behaviour of the species to be built up gradually.

Anthropology is the study of living people. It has several branches. Cultural anthropologists study the cultures of living peoples. They examine what people make (cultural artefacts), the ways they communicate and how they organise their lives. Traditionally, a cultural anthropologist would spend one or more years away from home living with a foreign people. Many cultural anthropologists were especially interested in peoples whose lives had changed little in recent centuries. So they would study tribespeople, peasants and others relatively unaffected by industrialisation and westernisation. Nowadays, cultural anthropologists, while continuing to study such people, also study cultures nearer to home. There are urban anthropologists who study how city dwelling affects people, and feminist anthropologists who focus their research on the roles occupied by women in culture and society. There are other branches of anthropology. For example, physical anthropologists are interested in how humans evolved. What were the evolutionary pressures that led to our having such large brains, to standing upright and to having so little body hair? How have our bodies adapted to the many environments in which we live?

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Psychology looks both at humans and at non-humans. Psychologists are interested in understanding how animals think and why they behave as they do. Often the emphasis has been on the mechanisms underlying behaviours. How does learning take place, for example? And what precisely is involved in 'seeing'? The answer to this question requires both an understanding of the physiology of the eye and an understanding of how the brain processes the information gathered by an animal's eyes. Traditionally, psychologists studied their subjects under laboratory conditions so that they could precisely control the environment. This allowed psychologists to investigate one question at a time. For example, when an animal is shown a number of objects for a brief period of time, what determines what the animal subsequently remembers? Nowadays psychologists, while continuing to work in the laboratory, also work in less controlled environments.

Sociology is the study of how humans live in society and behave in groups. These groups may vary from the temporary groups formed such as when people are at a sporting event to the longer-term groups that occur at home and in work. A sociologist might study how a person's educational achievements and earning potential are affected by their social class – that is, by the type of job that they have. Or a sociologist might be interested in how different societies are structured by economic, political and other factors. Sociologists are also interested in how people differ in their access to power and in how they make use of their work and leisure time.

Sociobiology burst onto the scene in 1975 when E. O. Wilson produced a book of this title. Sociobiology concentrates on the social behaviour of animals, examining the reasons why animals have evolved to live and behave in groups as they do. Social behaviour often involves helping behaviours, and sociobiologists are particularly interested in explaining the advantages and disadvantages of helping behaviours. They are also interested in understanding the genetic basis of behaviours. In the late 1970s and early 1980s many sociobiologists, including E. O. Wilson himself, enthusiastically extrapolated from the behaviour of non-humans to the behaviour of humans. Sociobiologists argued that many of the differences we see typically between men and women – for example that men are more likely to be aggressive and women more likely to bring up children – were primarily due not to culture but to our genes. This caused tremendous controversy and sociobiologists were often accused of being sexist or racist.

1.3 Tinbergen's four 'Why's'

The Greek philosopher, Aristotle, pointed out that four *causes* can be identified for most objects or events. What causes a house, for example? One answer is the matter from which it is constructed; a second is the builder; a third is the plan of the house; and a fourth is the house's purpose. Similarly, the Dutch ethologist Niko Tinbergen realised that when people ask *why* a

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certain behaviour occurs, they may mean one or more of four things. They may mean:

- what are the mechanisms that enable that behaviour to occur?
- how did the behaviour develop during the life of the individual showing it?
- what is the function of the behaviour?
- how did it evolve over the generations?

Consider, for example, a blackbird singing. We can ask what are the mechanisms that enable singing to take place. (The answer will have something to do with vocal cords and breathing and muscles and nervous control.) Or we can ask how the behaviour develops as a blackbird grows up. (To answer this question we might try tape-recording a blackbird's song to see whether it changes during an individual's life. We might also see whether blackbirds need to hear other blackbird songs before they can sing themselves.) Then we can ask what the function of the blackbird song is. (Is it to attract a mating partner, for example, or is it to proclaim ownership of a territory to rivals?) Finally, we can ask how blackbird song evolved.

The first of Tinbergen's four questions is really to do with physiology and we shall say only a little about it in this book. The last of Tinbergen's questions is the most difficult of the four to answer and we shall say only a little about the evolution of behaviour here. Most of what we cover is concerned with the functions and development of behaviour.

1.4 The functions of behaviour

We shall illustrate the ways in which scientists have investigated the functions of behaviour by considering two of the classic stories of animal behaviour – eggshell removal in black-headed gulls and the reproductive behaviour of sticklebacks.

Eggshell removal in black-headed gulls

During the 1950s and 1960s, Tinbergen led a large research programme into the behaviour of black-headed gulls, herring gulls and kittiwakes. The work on black-headed gulls was done in Cumbria in the north-west of England. Black-headed gulls (*Larus ridibundus*) are social breeders. They crowd their nests together even when apparently suitable nest sites are available elsewhere. The birds are mainly **monogamous**, so that a single female and a single male form a pair. Within the colony there is a system of **territories**, each territory being an area defended by a single pair of gulls (figure 1.2).

Early in spring, the birds gradually return to the breeding colony from their winter quarters. Some birds arrive paired, others only pair up after they arrive at the colony. Once the birds arrive, much calling and posturing

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Figure 1.2 Black-headed gulls (*Larus ridibundus*) defending territories at their breeding colony.

occur as the birds establish territorial boundaries. When a bird intrudes into another pair's territory, the territory owners, particularly the male bird, usually respond by posturing and calling but occasionally by attacking the intruding bird. Typically the intruding bird retreats. Actual fights are rare.

After all the courtship and territory establishment is over, eggs are laid, incubated and eventually hatched. Then, within a few hours of a chick hatching, a small but intriguing piece of behaviour occurs. One of the parents takes the empty shell in its bill, walks or flies away with it, and drops it well away from the nest. It took Tinbergen a long time to become interested in this because it seemed such a minor piece of behaviour. However, as Tinbergen spent longer observing the birds he noticed that predators such as neighbouring black-headed gulls, marauding herring gulls or passing carrion crows were often on the alert for just such occasions when a gull leaves its brood unprotected for a few seconds. The gulls or crows break open eggs or grab and eat a chick. Evidently, eggshell removal has a cost. But what is its corresponding benefit?

Tinbergen came up with a number of rival hypotheses for the function of eggshell removal:

- eggshell removal prevents the sharp edges of an eggshell from injuring the newborn chick (such damage had occasionally been reported in duck hatcheries);
- eggshell removal prevents an empty shell from slipping over an, as yet, unhatched egg, imprisoning the chick inside;
- in the absence of eggshell removal, an empty shell might compete for one of the gull's three brood spots – the defeathered patches on its belly used for incubation;
- disease-causing bacteria grow in empty eggshells;
- empty eggshells have white interiors and attract the attention of predators.

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Tinbergen thought the last of these five explanations especially worth testing for two reasons. First, many predators, including carrion crows and foxes, do take black-headed gull eggs and chicks. Secondly, the kittiwake, a bird closely related to the black-headed gull, rarely removes its eggshells. Kittiwakes nest on very steep cliffs where predation is much less of a problem than with black-headed gulls. Indeed, kittiwake chicks don't even have the camouflaged plumage typical of gull species. Instead of the buff ground colour and speckled dark dots typical in gulls, kittiwake chicks are a beautiful silver-white.

To test whether eggshell removal reduces predation in black-headed gulls, Tinbergen laid out a number of well-scattered, single eggs in a valley next to an area where the gulls nested. Half these eggs were left 'isolated'; the others each had an empty eggshell placed just 5 cm from them. Tinbergen and his co-workers then retired to a hide on a nearby dune-top. Carrion crows, herring gulls and an occasional black-headed gull swooped down and attacked the intact eggs. When about half the eggs had been taken, counts were made to determine which eggs had survived. Many more of the 'isolated' eggs survived. When the effect of distance between the eggs and the eggshells was examined more systematically, a clear pattern emerged (figure 1.3). The greater the distance between an intact egg and a broken eggshell, the lower the chance that a predator would take the intact egg.

Observations of the birds that fed on these eggs showed why eggshell removal is advantageous. On spotting an empty eggshell from afar, a crow or gull alights near to, or walks up to, the empty shell and then starts searching around it. The closer the intact egg, the more likely it is to be found. So here is evidence for at least one function of eggshell removal – it reduces the risk of predation.

Tinbergen's work on eggshell removal is seen as a landmark investigation in *ethology*. He presented clear alternative hypotheses, explicitly considered the costs and benefits of a behaviour, and experimentally tested his ideas.

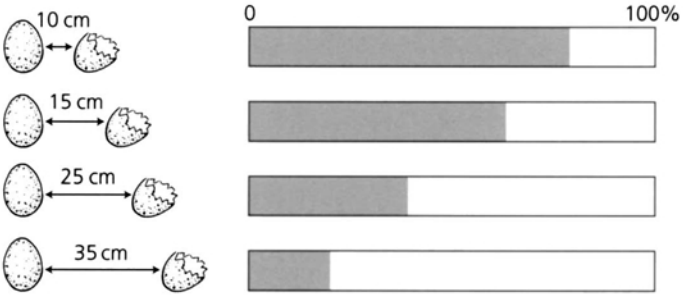

Figure 1.3 The results of Tinbergen's experiment to determine the effect of broken eggshells on the predation of intact eggs. The closer an eggshell is to an intact egg, the greater the risk of predation. The lengths of the shaded parts of the bars show the percentage of eggs taken, within a standard time, for each of the egg-to-eggshell distances indicated.

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Reproductive behaviour in sticklebacks

Sticklebacks are small freshwater fish. In a series of experiments dating from the 1930s, Tinbergen investigated the reproductive behaviour of the three-spined stickleback (*Gasterosteus aculeatus*). Tinbergen's account can be summarised as follows (figure 1.4).

In spring, male sticklebacks set up territories from which they chase away intruders of either sex. At the same time, each male constructs a nest and develops a red belly. The red on a male's belly acts as a **sign stimulus** – that is, it provokes a **stereotyped response**, in this case aggression from a territorial male. Tinbergen found that a realistically shaped but non-red model male stickleback provoked little interest from a territorial male, whereas extremely crude models painted red on their lower surfaces provoked strong aggression!

Once a male's nest is complete, the male becomes interested in females swollen with eggs. When a female appears, he moves towards her in a curious zig-zag fashion (the zig-zag dance). When she sees him, the female responds by swimming towards the male with her head and tail turned upwards, thereby displaying her swollen abdomen. The swollen abdomen acts as a sign stimulus for the male. Realistic model females lacking a swollen belly are not courted, while crude model females provided with a swollen lower surface are.

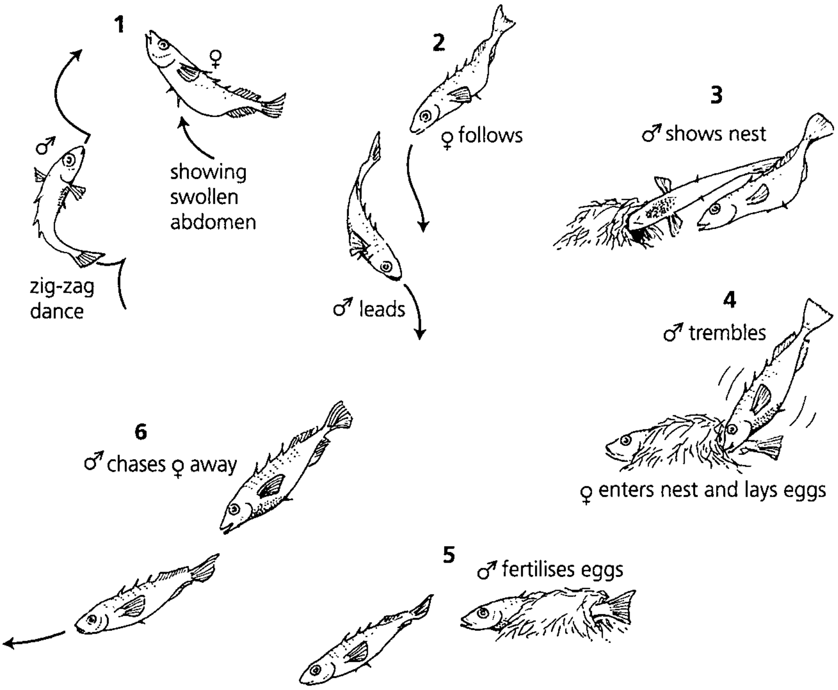

Figure 1.4 Courtship and reproduction in the three-spined stickleback.

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Having displayed her swollen abdomen to the male, he then leads her to the nest entrance and shows it by poking it with his snout. The female enters the nest and the male gives her several prods with a trembling motion to stimulate her to lay her eggs. When she has discharged all her eggs, she leaves the nest and the male enters it and ejaculates sperm over the eggs. He then chases the female away.

A male may mate with as many as five different females. Then, having fertilised several clutches, he loses his readiness to court females. Instead he begins regular ventilation of the eggs by fanning them with his pectoral fins. The time spent in fanning increases daily until the eggs hatch, when it stops. The fanning is to aerate the eggs. Evidence for this is provided by the observation that artificial lowering of the oxygen content of the water induces increased fanning.

The above account was the standard one found in animal textbooks for almost half a century. Then, in the 1980s, the story became modified in a number of significant ways which provide valuable lessons about scientific research. Perhaps the most remarkable finding is that careful experiments have shown that adding red to a model stickleback male makes it *less* likely to be attacked by a territorial male! This, of course, is the exact opposite of what Tinbergen wrote. We can't be certain why Tinbergen got it wrong. Possibly he was so sure what he would find that he failed to record adequately those occasions when his experiment 'didn't work' – that is when a model without red was attacked more than a model with red. In any event, the whole saga emphasises the importance of making and keeping proper records and of testing hypotheses statistically – something that Tinbergen did not do.

Another way in which Tinbergen's account has been modified came about through researchers studying females in the same ways as they studied males. In the wild, females go around in groups. Experimental studies of such all-female groups have shown that there are actually more aggressive encounters per hour in all-female groups than in all-male groups. What is the function of this female aggression? It turns out that females compete amongst themselves for access to males with the best territories. In other words, females cannot be viewed, as Tinbergen had unthinkingly assumed, as the passive recipients of a male's attentions. They too have reproductive interests. Indeed, as we shall see (section 6.4), by and large females in the animal kingdom are more choosy than males about their mating partners.

1.5 The unit of natural selection

You may be used to thinking of natural selection as acting on individuals. For example, one form of a moth may survive and reproduce more successfully than another form. We can talk about some individuals being **fitter** than others, that is, leaving more descendants.

However, there are occasions, as even Charles Darwin realised, when individuals clearly behave in ways that do not maximise their individual fitness. Consider the tens of thousands of worker honey bees in a single colony. None of these workers ever reproduces. Instead they devote their entire lives to helping rear the offspring of the queen. What is the evolutionary explanation for this behaviour? The simple answer is that they are helping to produce not their offspring but their sibs, that is their sisters and brothers. The worker bees themselves are the daughters of the queen. In helping the queen to rear offspring, they are therefore helping their mother to have sons and daughters. These sons and daughters are their sibs. Darwin termed this 'family selection'. Nowadays it is called 'kin selection' and we shall examine it in more detail in section 7.3. For the moment, we shall introduce one more technical term – namely **inclusive fitness**. The idea is that an individual can, in a sense, reproduce via its relatives, as we saw in our example of a worker honey bee. The term 'inclusive fitness' therefore takes account of the helping behaviour an individual gives its relatives. In other words, it is not an organism's individual reproductive success alone that matters, but also the reproductive success of any of its relatives that have been affected by its helping behaviour.

The notion of inclusive fitness is quite a complicated one. Many evolutionary biologists, notably Richard Dawkins, argue that the best way of understanding evolution is not to think about individuals having offspring or even helping relatives to, but rather to think of genes replicating and leaving copies of themselves. You may well have heard of the term 'the selfish gene'. It comes from a book of that title written by Richard Dawkins which is well worth reading.

1.6 Behavioural genetics

If behaviour is to evolve by natural selection, then behavioural differences between individuals need to have a genetic basis. Evidence that behaviours may have a genetic component to their inheritance comes from the many different breeds of domestic dog. We now think that dogs were first domesticated some 140 000 years ago. Most breeds, though, are less than a thousand years old. Even a thousand years, however, has been sufficient time for several hundred generations and this has allowed considerable differences in behaviour to evolve under artificial selection. Think, for example, of the way different breeds of dogs behave towards strangers or react to an object being dropped into water. Even puppies of the different breeds behave very differently, suggesting that the differences are genetic rather than due to training or other aspects of the environment.

One of the earliest demonstrations of the genetic basis of a behaviour involved the nest-clearing behaviour of honey bee workers. Bees in some hives have the ability to perform two behaviours:

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- first, uncapping cells that contain dead pupae;
- secondly, removing the dead pupae from the cells and the hive.

Workers from other hives lack these abilities and ignore cells with dead pupae. Rothenbuhler crossed the two strains and then performed some additional crosses with the hybrid generation. These experiments revealed that the expression of each of the two behaviours was under the control of separate genes called u (for uncap) and r (for remove). Workers that were homozygous recessive for each gene (i.e. uurr) would first uncap cells with dead pupae and then remove them. Workers with one or two copies of the dominant allele of each gene (i.e. UURR, UURr, UuRR or UuRr) would only rarely uncap or remove. Through his genetic crosses Rothenbuhler produced some bees with the genotype Uurr. These were unable to uncap cells but would remove dead pupae provided Rothenbuhler did the uncapping for them!

The above nest-clearing story is an elegant one. However, it is beguiling in its simplicity for at least two reasons. First of all, most behaviours, certainly human ones, are not under the influence of just one or two genes. Any genetic component is much more likely to be polygenic (that is affected by the actions of many genes). Secondly, as we shall see in section 2.1, it is more fruitful to think of behaviours as being the result of an interaction between genetic and environmental effects.

1.7 The evolution of behaviour

Already in our consideration of eggshell removal in birds, we have found ourselves thinking about the differences between black-headed gulls and kittiwakes and so hypothesising on the evolutionary history of the behaviour. A full understanding of a behaviour really requires answers to all four of Tinbergen's questions: What is the function of the behaviour? How does it develop? What mechanisms underlie it? How did it evolve? (section 1.3).

Behaviours do not fossilise in the way that bones do. True, the discovery of fossilised dinosaur nests tells us something about the incubation behaviour of the adults. Similarly, animals sometimes leave behind **trace fossils** as a result of their movements or the homes they have constructed. Nevertheless, the study of the evolution of behaviour relies heavily on the **comparative method**. The comparative method works by comparing the behaviour of related living species and then trying to piece together a possible evolutionary pathway for the behaviour. It is not the most experimental of sciences, though it can make testable predictions.

An elegant example of the use of the comparative method is provided by the study of how a distinctive courtship signal evolved in a small empid fly, *Hilara sartor*. The adult male of this species constructs a hollow silk