

EATING AND NOT BEING EATEN

Feeding ecology and feeding behaviour interact if we examine more closely a smaller group of species. Let us consider, for example, the feeding habits of the five main species of large herbivorous mammals that inhabit the Serengeti Plains of East Africa.

Feeding in group-living herbivores

Buffalo, zebra, wildebeest, topi, and Thomson's gazelle live together in huge groups which together make up some 90% of the total weight, of mammals living on the Serengeti. At first sight the five all appear to live on the same species of grass, herbs, and small bushes. The appearance, however, is illusory. When Bell and his colleagues analysed the contents of the stomachs of four of the five (they did not study buffalo), they found that each species was living on a different part of the vegetation. These different parts of the vegetation differ in their food qualities: lower down, there are succulent, nutritious leaves; higher up are the harder stems. There are also sparsely distributed, highly nutritious fruits, and Bell and his colleagues found that only the Thomson's gazelle eats much of these. The other three species differ in the proportions of lower leaves and higher stems that they eat: the zebra eats the most stem material; the wildebeest the most of the leaves; the topi is intermediate.

How are we to understand their different feeding preferences? The answer seems to lie in two associated differences among the species, one in their digestive systems and the other in their body sizes. The digestive

systems can be divided into the non-ruminants (the zebra, which is like the horse) and the ruminants (wildebeest, topi, and gazelle, which are like the cow). Non-ruminants cannot extract much energy from the hard parts of the plant; however, this is more than made up for by the fact that food passes much more quickly through their guts. Thus, when there is only a short supply of poor-quality food, the wildebeest, topi and gazelle enjoy an advantage. They are ruminants and have special structures in their stomachs (the rumen); containing special micro-organisms which can break down the hard parts of the plants. Food passes only slowly through the ruminant's guts because ruminating, digesting the hard parts, takes time. The ruminant continually regurgitates food from its stomach to its mouth to chew it up further (that is what a cow is doing when 'chewing cud'). Only when it has been chewed up almost to a liquid can the food pass through the rumen, and on through the gut. Larger particles cannot pass through until they have been chewed down to size. Therefore, when food is in short supply, a ruminant can last longer than a non-ruminant because it can extract more energy out of the same food. The differences can partially explain the eating habits of the Serengeti herbivores. The zebra chooses areas where there is more low-quality food. It migrates first to unexploited areas and chomps the abundant low-quality stems before moving on. It is a fast-in/fast-out feeder, relying on a high throughput of incompletely digested food. By the time the wildebeest (and other ruminants) arrive, the grazing and trampling of the zebras will have worn the vegetation down. As the ruminants then set to work they eat down to the lower, leafier parts of the vegetation. All of

which fits in with the differences of stomach contents with which we began.

The other part of the explanation is body size. Larger animals require more food than smaller animals, but smaller animals have a higher metabolic rate. Smaller animals can therefore live where there is less food, provided that it is of high energy content. That is why the smallest of the herbivores, Thomson's gazelle, lives on fruit, which is very nutritious but too thin on the ground to support a larger animal. By contrast, the large zebra lives on the masses of low-quality stem material.

The differences in feeding preferences lead, in turn, to differences in migratory habits. We have seen (p. 84) that wildebeest follow, in their migration, the capricious pattern of local rainfall. The other species do likewise. But when a new area is fuelled, by rain, for exploitation, the mammals migrate towards it in an orderly pattern. The larger, less fastidious feeders, the zebras, move in first; the choosier, smaller wildebeest come later; and the smallest species of all, Thomson's gazelle, arrive last (Figure 5.1) The later species depend on the preparations of the earlier, for the action of the zebra fits the vegetation for the stomachs of the wildebeest and gazelle.

if we are to understand the feeding habits of the species, therefore, we must consider it in relation to the whole ecology of the species, and its relations to other species. Behaviour is an inseparable part of a whole system, made up (in this example) of body size, gut morphology, and the habits of associated species.

Recognizing food

Given the diet of a species, determined by its ecology, the individual members have two behavioural problems, the best solutions to which will depend on their diet. Food must first be recognized, and then caught. We shall consider these two in the next two sections. First how is food to be found? The environment of an animal contains all sorts of things, some of which are edible and some of which are not. The problem for the hungry animal is to distinguish the former from the latter, and only to put the edible things in its mouth. What is food for one species is often poisonous, or indigestible, for another. Each species must recognize its own kind of food. The complexity of the problem depends among other things on whether the species is a specialist feeder which eats only one or two types of prey, or whether it is an omnivore which eats many kinds of prey.

Let us consider first a fairly specialist feeder, the toad. Toads mainly eat small, dark, flying insects. They stick out their tongue and snap at any insect which flies by. J.-P. Ewert and his colleagues have studied in detail how the toad recognizes its meal. The toad does not recognize insects as such, but recognizes small, dark, moving objects. If a piece of dark paper about $\frac{1}{8}$ inch in length is moved where a toad can see it, it will snap at it just as if it were an insect (Figure 5.2). This recognition system works perfectly well for a toad because any small, dark, moving object in its natural environment is an insect. Only in the laboratory is it fooled by bits of paper. Ewert and his colleagues have also worked out where, in its nervous system, the toad recognizes small dark moving objects. They found neurons

in the retina of the eye which respond differently according to the size of dark objects moving in the field of view. There are three classes of sensory neurons which respond to three different classes of objects. The visual system of a toad is a world of moving dark objects of various sizes and shapes; its gastronomic choice is to put all the objects of a certain size in its mouth.

The toad's response to different sized objects is not much affected by learning; to find cases where leaguings has an influence we must turn to animals with more catholic diets. The first learning phenomenon to consider is a perceptual one, called a search image. Forming a search image means learning to see something which had not previously been seen. It often occurs in humans with photographs of camouflaged animals. To begin with you cannot see the animal at all, but after you have first noticed it, it becomes infirm animal and only then siari the chase During the chase, the dogs of the pack may take turns in leading. When the kill comes they usually all join tn to wear their victim down They are flexible, however, and employ other tech-niques when appropriate. They pay particular attention to prey that straggle or leave the herd. One dog may then try to get between the herd and the straggler, and try to drive it towards the rest of the pack.

5.4.3 A note om domestication

Domestic dogs arc descendants of wolves, to which they show many similarities of appearance and behaviour. Their social habits have fitted them to human society. The exact reasons why dogs were first domesticated by humans are now lost in the past, whether it was the agreeable companionship of an animal that apparently respects its

master much as a dominant member of its hunting pack, the exceptional sensitivity of their whole-body surface, their uses in agriculture, or, most likely, a combination of all such factors. Undoubtedly their ancestry rendered dogs particularly good pets. We still exploit the ancestral habits of dogs in their training. The hunting techniques we have just discussed for wolves and African dogs are made use of in the training of sheepdogs. For instance, young and untrained sheepdogs will often spontaneously run round to the other side of a flock of sheep and try to drive them towards the shepherd. It is only a small step from this to teach the sheepdog to 'circle', to run round the flock and keep the sheep tightly bunched together (Figure 5.5). Sheepdogs are also particularly alert to stray sheep and can easily be taught to drive stray sheep back to the shepherd.

If we imagine that the sheepdog is treating the shepherd as a fellow hunter, then circling and retrieving stray sheep both manifestly resemble the ancestral canine hunting behaviour. Moreover, the most difficult tricks to teach a sheepdog are those most removed from its ancestral hunting skills. Sheepdogs are difficult to teach to drive the flock away from the shepherd the dog has to be restrained from its desire to circle round and drive them back. Sheepdogs are also difficult to teach to leave stray sheep they have gathered, to go and gather more.

The learning abilities of the sheepdog are closely related to its ancestry. It learns most easily what comes naturally to it. This is a general principle in teaching tricks to animals. Circus animals, for another example, learn tricks most easily if those tricks are a simple extension of the animals' natural behaviour patterns.

Avoiding being eaten: active evasion

Any property of an organism that reduces its chances of being taken by a predator will be favoured by natural selection, as it will increase the organism's chance of survival. The resulting anti-predator adaptations are very diverse. In the following four sections we shall examine five different habits used by animals to avoid being eaten: potential prey may actively flee their predators, or they may stay still and try to be invisible, or they may stuff themselves with sickening chemicals and advertise their unpalatability with bright 'warning colours or they may mimic the warning colours of others, and finally, in some circumstances, an animal may make itself less likely to be eaten by living in a group.

Active flight is used by many animals to escape predators, and a particularly elegant study has been made on noctuid moths by Koeder. Noctuid moths are eaten by bats, and have evolved a special pair of ears to warn them of approaching danger. There is one ear on each side of the thorax, and each has a simple structure; two nerves connect each ear with the thoracic ganglion (which is the nearest mini-brain). They are sensitive to the high pitched squeaks used by bats to find their prey, and they have the advantage of the bat, in that the bat emits very loud blasts in order to detect a faint echo. The moth can hear the bat from a greater distance than the bat can pick up the echo from a flying moth; to be precise, a moth can hear a bat about 100 feet away, whereas a bat can detect a moth at a range of less than 8 feet. The moth, moreover, can tell whether the bat is to the right or left (because it has an ear

on each side) and whether it is approaching or moving away. A bat approaching a moth will sound louder and louder as it comes close, and the moth is sensitive to loudness. Bats do not fly in the same direction for long. Therefore, if a moth hears a bat approaching about 100 feet away, its best policy is to fly off in the other direction. That way it may get out of the bat's flight path before it enters the detection range. Once a bat has detected a moth it has the advantage, because bats can fly much faster than moths. The moth's surest means of staying alive, therefore, is not to be detected a moth it has the advantage of advance warning to keep out of the way.

A bat may appear suddenly out of the dark close to a moth. It is then useless for the moth to flee, because it will have been detected and the bat can fly faster than it. When a moth detects a loud bat sound, indicating a bat less than about eight feet away, it puts a different escape tactic into action. It flies in wild loops and spirals, and dives to the ground, a course of flight designed to make it as difficult as possible for the bat to catch it. (The erratic flight may be produced by the moth by just switching off its steering mechanism. Then even the moth will not know where it is going: and the most effective means of confusing someone else about where you are going is not to know yourself.) The moth has two escape responses. If it hears a bat afar, it turns and flees; if it is surprised by one nearby, it goes into a crazy flight. It uses its hearing sense to decide which response is appropriate.

Camouflage

The noctuid moth's defence is to seek escape in active flight. The opposite defence is to sit dead still and try to be invisible. Such is the method of camouflage in which a species evolves to resemble its background. Camouflage is of course an adaptation of appearance and colouration, but the most exquisite

artistry will be wasted if the animal's behaviour is not suited to the camouflage. The world is a patch-work of different colours: the animal is only camouflaged if it settles in the right place. Consider the European grasshopper *Acrida turrita*. It comes in a green form and a yellow form. In nature the green form lives in green places and the yellow form in yellow and brown places, with rare exceptions. In a simple experiment, the German ethologist S. Ergene gave yellow and green grasshoppers a choice between yellow and green backgrounds. The green grasshoppers fittingly tended to go and settle on the green backgrounds, and the yellow grasshoppers on the yellow.

The North American moth *Melanolophia canadaria* faces a more difficult problem in lining up with its background. It has striped wings and lives on the bark of trees. It must line its stripes up with the lines of the bark if it is to be camouflaged. In an experiment, T. D. Sargent allowed the moths to sit on cylinders that had regions of vertical stripes and regions of horizontal stripes.

If the stripes (which were made of black tape, stuck on a white surface) could be felt by the moths, then the moths usually lined up correctly. When Sargent covered up the stripes and surface with a transparent film, the moths no

longer lined up correctly. The moths must be relying on the feel of the surface that they have to line up on. In nature they will be able to feel the stripes of their background, and ensure that they settle in a camouflaged posture.

5.7 Warning coloration and mimicry

Some animals protect themselves against being eaten by containing poisonous or sickening substances. Some such animals make their own poisons; others take them from sources in their environment. The wings of the monarch butterfly, for example, contain powerful heart-stopping poisons called cardiac glycosides. The monarch eats the poisons as a caterpillar, when its food plant is the asclepiad, or 'milkweed', which contains cardiac glycosides. The caterpillar is not harmed by the poisons; it just stores them, and they are then retained by the adult.

For the behavioural problem of defence by poison, we must turn from the prey to the predator. If the defence is to work, the predator must learn not to eat poisonous animals, because natural selection will not favour a trait, by which an animal, after it is dead, makes its attacker sick. If the trait is to evolve, it must ensure survival. The tactic used is to enable predators to learn to recognize sick-making prey, in which case they will avoid them, it is a skill

6.1 Principles of communication

The subject of our remaining four chapters is social behaviour. All social behaviour is mediated and organized by communication, and before we come on to such social, and anti-social, topics as fighting, sex, and altruism, we should consider the means by which these interactions are controlled. We should discuss the principles of animal signals.

Ethologists never have been able to make up their minds about what they mean by communication and signalling. A definition, along the right lines but too broad, is that an animal has signalled when it changes the behaviour of another animal. The definition can be made more accurate, but not wholly satisfactory by specifying that the other animal must have changed its behaviour because it perceived the signal through its sense organs, and was not physically forced. On the former definition, pushing someone in a river would have to be called a signal because it certainly would change his behaviour: but this would be excluded by the definition requiring the influence of the signal to be mediated by the recipient's sense organs.

The criterion of behavioural change is necessary in order to recognize signals by external observation. Most signals have been discovered by simply watching the behaviour of interacting animals. If members of a species consistently perform an activity, such as running away, after other members have performed another recognizable activity, such as baring their teeth, then teeth-baring is probably a threat signal. The evidence of simple observation is not, however, perfectly convincing. It can only establish a correlation between two behaviour patterns; but a correlation can always be explained by both activities being caused by a third, unobserved activity. Experimental evidence is therefore more convincing. Tinbergen, for example, presented model bills of adult herring gulls (*Larus argentatus*) to the chicks of that species; the chicks responded by pecking at the red spot at the top of the bill, which strongly suggests that the red spot is a signal, meaning 'start pecking' (Figure 6.1). (The pecking of the

spot is the chick's signal method of asking for food: if the spot was on its parent's, rather than a model) bill, the chick would receive a meal.) It is difficult to believe that every time Tinbergen presented a model bill to a chick his activity coincided with a third, unobserved variable that was really signalling to the chick to start pecking; that would however be possible for the natural observation that chicks peck when their parent arrives. Scientists therefore require experimental evidence to test between causes and correlations. Now that we have provisionally fixed what a signal is, and how one may be recognized, let us consider some examples of signals — the songs of birds, the pheromones of moths and ants, and the dance of honeybees —before we consider the theoretical question of why signals have evolved in the form that we see in nature.

Bird song

Birds, like mammals, produce sound by blowing air from their lungs over vibratory vocal chords in the trachea, although in birds the vocal cords are situated slightly closer to the lungs than in mammals Bird song is a very familiar kind of animal behaviour. It has been celebrated by poets, and •enjoyed by most people. It is also particularly easy to study, because sound can be recorded and reproduced by a tape-recorder. So, why do birds sing? And why do they sing in the way they do?

Male birds do most of the singing, which gives an immediate clue that singing has something to do with sex. In fact, singing seems to serve two main functions in birds: defending territory, and attracting and stimulating females

to mate. The following experiment shows the importance of song in territorial defence. John Krebs removed the resident pairs of great tits [Parus major L].

from their territories in Wytham Woods near Oxford. Some of the territories he left empty; but in others he placed loudspeakers, broadcasting the song of a great tit. He then watched to see how long it took another pair to occupy the two kinds of territory. It took longer for the territories with loud speakers to be occupied than it did for the silent territories (Figure 6.2). He then took the experiment a stage further. Great tits sing a repertory of one to eight distinct songs. Why do males sing so many songs? What can eight songs do that one cannot? As before, Krebs removed pairs from their territories and put loudspeakers in instead. This time the loudspeakers in some territories broadcast one song, whereas the loudspeaker in other territories broadcast