

## EVOLUTION OF BEHAVIOUR

Probably the most important question in comparative psychology is the following: “Why do the members of any given species behave in a certain way?” There are usually several different answers to that question. For example, some species of birds may sing in the spring because this attracts mates for breeding purposes, which is important for the preservation of the species. However, they may also sing because the increasing length of the day in the spring triggers off changes in hormone levels.

Tinbergen (1963) developed this line of argument. He argued that there are often *four* kinds of answers to the question of why the members of a species behave as they do. We will follow Krebs and Davies (1993) in considering these four kinds of answers with respect to the issue of why starlings sing in the spring:

1. Survival value: starlings sing to attract mates for breeding.
2. Causation: starlings sing because of the hormonal changes produced by the lengthening day in spring.
3. Development: starlings sing because they have heard their parents and other starlings singing.
4. Evolutionary history: starlings sing complex songs as a result of evolutionary change from previous generations of birds singing simpler songs.

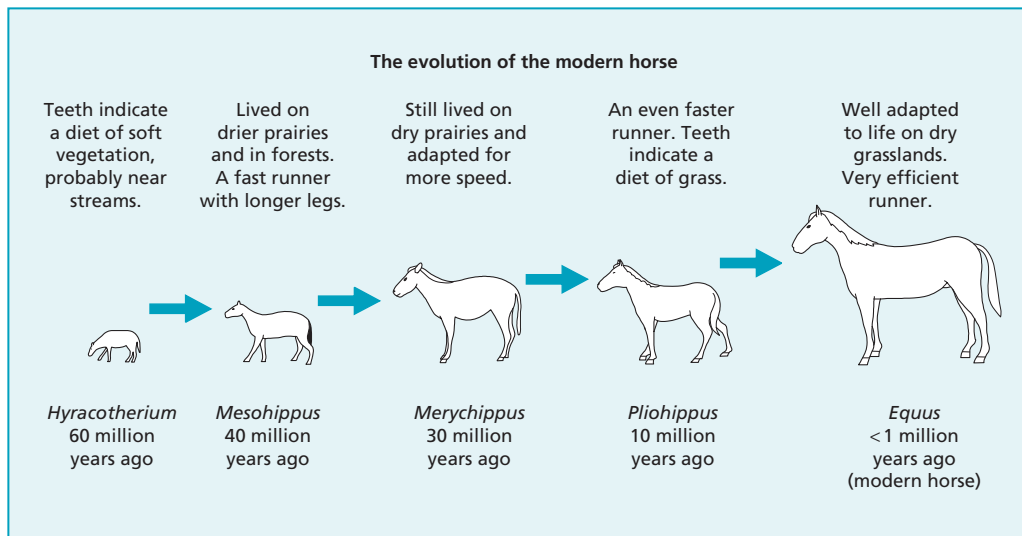
It is tempting to ask which of these four answers is the correct one. In fact, *all* of the answers are correct. There are various levels of explanation for animal behaviour, and all of these levels need to be considered in order to provide a complete account. In this chapter, however, we will focus mainly on the impact of a species’ evolutionary history on the current behaviour of its members.

### Species: Fixed or changing?

It used to be argued that every species is separate from every other species, and that it remains fixed over time. This argument seems to be supported by the evidence of our own eyes. During the course of our lifetime, there are no obvious changes in the cats, dogs, and other species of animals we encounter. However, there is overwhelming evidence that species do change substantially over much longer periods of time than a human lifetime. There are at least three main kinds of evidence supporting the notion that species evolve over time: the fossil record; geographical variation; and selective breeding.

#### *Fossil record*

Examination of the fossil record reveals that there have been progressive changes over time in the size and shape of many species. However, the fossil record is limited in a number of ways. First, the record is usually very incomplete. Often only some of the bones have been preserved, and there may be gaps in the record extending over thousands or tens of thousands of years. Second, the fossil record at best provides evidence only about the hard parts of an animal, and so it is often not easy to work out in detail what the animal looked like. Third, the fossil record cannot tell us about the behaviour of the



members of a species. It is sometimes possible to make well-informed guesses about their behaviour, but that is all.

## Geographical variation

The notion that each species remains unchanged over time seems improbable in the light of geographical variation. As Ridley (1995, p.21) pointed out:

*At any one place, species do appear as discrete groups of organisms, but if a species is traced across the world its appearance can usually be seen to change from place to place. House sparrows, for example, vary in size, bodily proportions, and colouration across the United States, and the house sparrows of North America visibly differ from those of Europe.*

Charles Darwin travelled thousands of miles on the scientific survey ship *HMS Beagle*, and his observations of geographical variation within species played a part in the development of his theory of evolution.

## Selective breeding

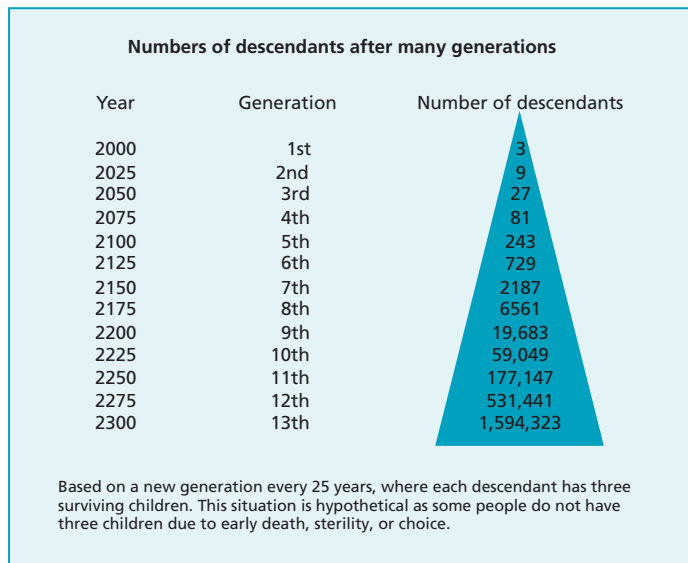
Selective breeding also supports the view that species can change over time. Darwin (1859) was impressed by the way in which breeding programmes can produce, for example, either race horses that are light and lean or farm horses that are large and strong. Darwin himself bred pigeons, and observed changes in them from one generation to the next. He argued that the changes produced artificially by selective breeding are like those that occur under more natural conditions.

Examples of modern selective breeding can be visually obvious (e.g. pedigree dogs) or less so (e.g. strawberries that are resistant to the cold). Modern wheat is the result of over 2000 years of selective breeding from grasses. Can you think of other examples of selective breeding in our current environment?

## Natural selection and adaptation

We have seen that there is convincing evidence that species can change considerably over long periods of time. What is needed is an explanation of the *processes* involved in producing these changes. Darwin (1859) provided such an explanation in his theory of natural selection. This theory was based on five major assumptions:

1. Variation: individuals within a species differ from each other in their physical characteristics (e.g. height) and in their behaviour.
2. Heritability: at least some of the variation among members of a species is inherited; as a result, offspring tend to resemble their parents more than other members of the species.



3. Competition: the members of most species produce far more offspring than can survive. Darwin worked out that a pair of elephants could have about 19 million descendants alive 750 years after their birth if there were no problems of survival. In fact, there is competition for mates, food, and places to live.
4. Natural selection: the members of a species which survive the process of competition and go on to breed will tend to have characteristics that are better suited to the environment than those which do not. Thus, there is natural selection or survival of the fittest (in the sense of survival or reproductive success rather than physical fitness).
5. Adaptation: as a result of the process of natural selection, successive generations will tend to be more and more adapted to their environment. They will possess characteristics that allow them to obtain food and to reproduce.

Darwin was greatly influenced by the work of Malthus (1798). Malthus emphasised the notion that the human population tends to increase considerably over time, whereas the earth's resources (e.g. land; food) either cannot increase or do so only slowly. Malthus worked out what would happen if a couple had three children, all of their children had three children, and so on. After 12 generations, the original couple would have more than 250,000 descendants. After 25 generations, this would increase to over 5 million, a figure that makes me feel guilty at having three children of my own! Malthus and Darwin were both pessimistic about the chances of any species showing reproductive restraint. As a result, Darwin reasoned, what must happen is that there will be ever-increasing competition for finite resources.

### Changes within a species

How do the assumptions of Darwin's theory of natural selection explain changes within a species? The crucial notion is that the environment will often only allow those members of a species having certain characteristics to survive. Suppose, for example, that a speedy predator eats mainly the members of a given species. If only the fast-moving members of the prey species survive, then that species should evolve over the generations in the direction of becoming faster moving on average.

Darwin (1859) assumed that evolutionary change would generally happen relatively slowly over periods of hundreds or thousands of years. However, the fossil record suggests that changes can occur fairly rapidly. As a result, Gould (1981) argued that a species will sometimes have fairly brief periods of rapid development in between long periods of relative stability. He described this notion as **punctuated equilibrium**. Recent research has identified the genes that permit such rapid development.

Grier and Burk (1992) addressed the issue of why it is some aspects of behaviour seem to have changed much more than others during the course of evolution. They identified four main reasons why evolutionary change might be rapid for some categories of behaviour:

1. Changes in those aspects of behaviour may allow a more efficient use of the available resources.
2. Competition may lead to more specialised forms of behaviour.
3. Forms of behaviour that are of use with respect to other members of the same species (e.g. courtship; communication) may be especially likely to show evolutionary change.

#### KEY TERM

**Punctuated equilibrium:** the notion that long periods of relative stability for a species are punctuated by short-lived periods of rapid change.

#### Deep sea octopus

In a study of deep sea life, Wider, Johnsen, and Balsler (1999) described one octopus species that lives at depths of 900 metres and feeds on prey too small to grasp with tentacles. The usual suckers on octopus tentacles are therefore redundant and do not have the muscles in this species that are normal in shallow-water octopuses. Instead, the sucker-like pads have developed light-emitting cells, which produce the bluish light typical of bioluminescence and attract prey.

4. Forms of behaviour between the members of two species (e.g. predator–prey interactions; host–parasite interactions) may be subject to rapid change by both species.

In contrast, forms of behaviour tend to be stable over the generations when there would be no advantage in changing them. They are also stable because a superior form of behaviour has simply not appeared in the species in question.

### *Adaptation is imperfect*

It might be thought that the processes of natural selection and adaptation would tend to make the members of a species almost perfectly suited to their environment. This is not what Darwin actually believed. According to Darwin (1872, p.163):

*Natural selection tends only to make each organic being as perfect as, or slightly more perfect than, the other inhabitants of the same country with which it comes into competition ... Natural selection will not produce absolute perfection.*

Behaviour is sometimes not well adapted to the environment because the environment has changed recently. For example, it is speculated that the behaviour of the dinosaurs became fatally non-adaptive after a large meteor hit the earth 65 million years ago.

It is much harder for species to adapt to their environment when it is changing rapidly. Numerous species have experienced enormous changes in recent years because of the speed at which the human species is destroying their environment. According to Sir Robert May (1998), “Looking towards the immediate future, three different approaches to estimating impending rates of extinction suggest species’ life expectancies of 200 to 400 years.” In contrast, the average lifespan for a species before the arrival of the human species was about 5 to 10 million years. May (1998) pointed out that what is happening “represents a sixth great wave of extinction fully comparable with the Big Five mass extinctions of the geological past [including the one that wiped out the dinosaurs]. But it is different, in that it results from the activities of a single other species rather than from external environmental changes.”

An important reason why species are imperfectly adapted to their environment was identified by Maynard Smith (1976). He argued that natural selection typically produces *stable* behavioural strategies, even when these strategies are not ideal. When an individual animal interacts with other animals, its most adaptive behaviour depends very much on how the other animals behave.

Maynard Smith considered whether it is more adaptive for animals to be hawks (very aggressive and inclined to fight) or doves (avoiding conflict and fighting). In principle, the most adaptive strategy would be for all animals to be doves. However, in the real world, that is a risky strategy because of the danger of invasion by hawks. The most adaptive strategy in practice is for there to be a mixture of hawks and doves, and this is what is found in many species. Maynard Smith referred to this as an **evolutionarily stable strategy**.

#### KEY TERM

**Evolutionarily stable strategy:** a behavioural strategy that works effectively and is stable over time provided that most members of a species adopt it.

#### CASE STUDY: *The Milk Thief*

In 1949 doorstep delivery of bottled milk was becoming increasingly popular. Previously, milk had been decanted into the householder’s own jugs and containers, but the new method involved a glass bottle with a foil cap. Housewives began to complain that someone or something was piercing and peeling back the foil cap, and stealing the cream from the top of the milk. As this epidemic of thefts spread, it was discovered that the culprits were several species of tits, the main offenders being blue tits who had discovered a new food source. The behaviour was widespread for ten years or so, during which time householders learned that a solution was to leave a cup on the doorstep for the milkman to put over the top of the milk bottle. Gradually the milk thefts ceased to be a problem.

However, at about the same time, blue tits began another unusual behaviour. Entering houses and factories, they would embark on an orgy of paper-tearing, ripping up strips of any paper they found: wallpaper, toilet rolls, parcel wrappings, newspapers, and so on. There seemed to be no obvious reward for this behaviour, and scientists were baffled. One explanation put forward by the British Trust for Ornithology was that, because the birds could find so much food so easily, their hunger was satisfied before their hunting drive, so they were imitating tearing bark from trees in search of prey. Before anyone could agree on the true explanation for this odd behaviour, it too died out, and milk-stealing and paper-tearing by blue tits is now almost unknown.

*Do you think the adaptive strategy of a mixture of hawks and doves also applies to the human species?*

This is “a strategy which when adopted by most members of the population cannot be beaten by any other strategy” (Krebs & Davies, 1993, p.149).

## Evidence

**Uniformitarianism.** Most of the evidence for natural selection is rather indirect. The reason for this is because the processes involved occur over such long periods of time that they cannot be observed directly. Those who use the fossil record or other historical evidence endorse the assumption of **uniformitarianism**. This is the notion that biological and physical processes operate in the same uniform way over time. If we accept the notion of uniformitarianism, then our observations in the present allow us to make inferences about the past.

There is a constant danger of observing what a given species is like now and making up an “explanation” that sounds plausible but lacks evidence. For example, we might guess that giraffes have long necks because in the long distant past only those giraffes with long necks were able to reach up high enough to obtain food. Hailman (1992, p.127) was very critical of this approach:

*The colouration, anatomy, physiology, and behaviour of animals seem so well suited to the environments in which they live that natural selection “must” have adapted the animals to their environments. Come on, can’t we do better than that?*

**The peppered moth.** What has often been regarded as fairly direct support for some of the assumptions of Darwin’s theory was obtained by H.B.D. Kettlewell in the 1950s (see Ridley, 1995). He studied two variants of the peppered moth, one of which was darker than the other. The difference in colour is inherited, with the offspring of the darker type being on average darker than those of the lighter type. Both types of peppered moth are eaten by birds such as robins and redstarts that rely on sight to detect them. Kettlewell observed the moths when they were on relatively light lichen-covered trees and when they were on dark, lichen-less trees in industrially polluted areas. The lighter-coloured moths survived better on the lighter trees and the darker-coloured moths survived better on the darker trees.

According to Darwin’s theory, the number of darker moths should increase if there is an increase in the proportion of dark trees. Precisely this happened in England due to the industrial revolution, when pollution killed the lichen and coated the trees with sooty deposits. The proportion of peppered moths that were dark apparently went from very low to over half in a period of about 50 years. However, the evidence that there were few dark peppered moths in the late nineteenth century comes from moth collections. As Hailman (1992, p.126) pointed out, “Those collections were not scientific samples but were made by amateurs ... Perhaps they did not like ugly black moths.”

**Kittiwakes.** Good evidence for the theory of evolution comes from studies on gulls. There are about 35 species of gulls, and most of them show great similarities in their behaviour. Nearly all these species nest on the ground, but kittiwakes nest on narrow ledges which are a long way above ground level. Cullen (1957) found that the chicks of most gull species start to roam about away from the nest within about one day of hatching. In contrast, the chicks of kittiwakes remain in their nests. The evolutionary significance of this difference is fairly clear. The chicks of kittiwakes might kill themselves if they moved around on narrow ledges, whereas the chicks of other gull species can often avoid danger by running away from it.

**Empid flies.** The courtship behaviour of various species of empid flies can easily be explained in evolutionary terms. In some species, male flies give prey wrapped in silk to the female during courtship. This is effective, but has the disadvantage that the male has to exert energy to obtain the prey. In other species, the male gives the female nothing. This has the disadvantage that the male is sometimes eaten by the female, probably because the female is not distracted by the presence of the prey wrapped in silk. In evolutionary terms,

### KEY TERM

**Uniformitarianism:** the notion that biological and other processes operate in the same constant way over time.

the optimal behaviour for the male would be to distract the female without the need to catch any prey. Precisely this happens in other species of empid flies, in which the male gives the female an empty silk balloon (Kessel, 1955).

**Links between environment and behaviour.** One of the best ways of testing evolutionary notions is to study numerous species that differ in their behaviour. The researcher tries to work out which environmental differences have produced the behavioural differences among species. According to Grier and Burk (1992, p.143):

*This approach is considered as strong or nearly as strong as the genuinely experimental method. In essence, one is merely taking advantage of experiments that have already taken place in nature where there is a sufficiently large sample size to reduce the impact of spurious correlations.*

Ridley (1983) made use of this approach. There are numerous species in which the male hangs on to the female for periods of time ranging between days and weeks before fertilisation occurs. This is known as precopulatory guarding, and it is found in arthropods (e.g. spiders and crustaceans), frogs, and toads. Ridley argued that precopulatory guarding might develop through natural selection in species in which the females are receptive for mating for fairly brief but predictable periods of time. On the other hand, precopulatory guarding would not be found in species where the females are continuously receptive for mating or where their receptivity occurs at unpredictable times. His key finding was that these predictions were confirmed in 399 out of 401 species.

## Evaluation

**Mechanisms of heredity.** It is generally accepted that Darwin's (1859) theory of natural selection is essentially correct as far as it goes. However, he did not provide an account of the *mechanisms* involved in heredity. We now know that genes determine what is inherited, and so Darwin's theory can be re-expressed in terms of the involvement of genes. In the words of Krebs and Davies (1993, pp.9–10):

*The individual can be regarded as a temporary vehicle or survival machine by which genes survive and are replicated ... the most successful genes will be those which promote most effectively an individual's survival and reproductive success ... As a result, we would therefore expect individuals to behave so as to promote gene survival.*

Evidence that genetic factors can have powerful influences on behaviour comes from artificial selection experiments. In such experiments, animals are bred so as to produce separate strains that behave very differently from each other. For example, Berthold et al. (1990) carried out a selection study on blackcaps, 75% of whom were migratory and 25% of whom were resident. They mated migratory birds with other migratory birds, and they mated resident birds with other resident birds. After six generations, they produced two separate strains that were either 100% migratory or 100% resident. It is claimed that selection experiments show in an exaggerated form the workings of evolution.

*Can you think of everyday examples of artificial selection?*

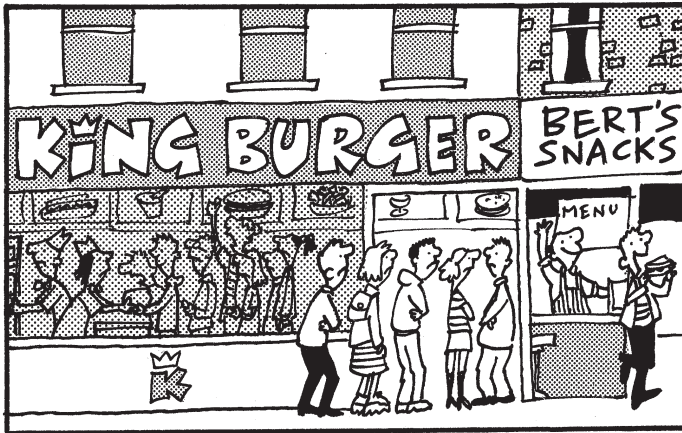
**Altruism.** According to Darwin's theory, individual animals should behave in a selfish fashion to compete successfully against other individuals, and so ensure the survival of their genes in the future. However, animals often seem to show altruistic behaviour, which is behaviour that benefits other animals but at some cost to the animal itself or to its reproductive potential. One of the clearest examples of such altruism is found in social insect societies, in which most of the insects do not try to reproduce themselves.

The existence of altruistic behaviour is contrary to evolutionary theory as put forward by Darwin (1859). However, it can be explained in terms of evolution. The key notion

*Does the kin selection strategy also apply to human beings?*

is that an individual animal's close relatives share many of its genes. As a result, its motivation to ensure that its genes are transmitted to the next generation can be achieved by helping its close relatives to reproduce. This strategy is known as **kin selection**. That seems to explain the apparently altruistic behaviour of social insects.

**Adaptation.** According to Darwin's theory, the characteristics possessed by individual animals serve the function of making them well adapted to their environment. However, some species possess characteristics that do not seem to serve any useful purpose. For example, the long tail or train of peacocks makes them vulnerable to attack by predators because it reduces their mobility. It now appears that peacocks' long tails or trains are more functional than used to be thought. Peahens find the peacock's long train attractive, and so peacocks with long trains have greater reproductive success than those with short trains. Not only do the peacocks spread out their trains as a mating display, they also shake them noisily to draw attention to them.



*Exploitation: the best habitat is not always the one that contains the most resources.*

## COMPETITION FOR RESOURCES

When resources such as food are in short supply, individual animals need to compete for those resources. In nature, there are often several factors that together determine how individuals compete for resources. However, we will start by considering two simple possibilities: competition by exploitation and competition by resource defence. After that, we will consider some examples of species that make use of these forms of competition.

### KEY TERMS

**Kin selection:** a strategy in which an individual animal increases its genetic representation in the next generation by assisting its close relatives.

**Exploitation:** a form of competition for resources in which animals go to the place offering them the greatest access to resources.

**Ideal free distribution:** the notion that animals are distributed so that each individual has equal access to resources; it requires that animals have good information about the distribution of resources, and that they are free to go wherever they prefer.

**Resource defence:** this involves some animals keeping others away from resources by aggressive behaviour or by fighting.

**Territory:** an area that is defended by one or more animals.

## Exploitation

**Exploitation** means using up resources. According to the simplest model of exploitation, individuals go to the place or habitat that offers them the greatest access to resources. The key point is that the best habitat is not always the one that contains the most resources. Krebs and Davies (1993) took the simple example of an environment with a rich habitat and a poor one. Initially, it is best for all individuals to go to the rich habitat. However, the resources of the rich habitat will be increasingly used up as more and more individuals go to it. There will come a point at which newcomers will do better to go to the poor habitat, which has the advantages of less competition and less depletion of resources.

Suppose that we assume that the numbers of animals at each habitat are such that each individual has equal access to resources. This state of affairs is known as the **ideal free distribution**. It is an ideal distribution because it will only happen when the animals have good or ideal information about the availability of resources at the various habitats. It is a free distribution because it is based on the assumption that all of the animals are free to go to whichever habitat they prefer. In nature, animals often defend a habitat in an aggressive way, and so the assumption is not justified.

## Resource defence

**Resource defence** involves some animals keeping others away from resources by displays of aggression or by fighting. What typically happens is that the first animals to arrive at a rich habitat set up territories, which they then defend against animals that arrive later on. A **territory** can be regarded more generally as any area that is defended by one or more

animals. A territory can be set up for feeding purposes, for mating purposes, for raising young, and so on.

Huntingford and Turner (1987) argued that there are four key features defining the existence of a territory:

1. The animal or animals defending a territorial area display aggressive behaviour towards other animals.
2. Animals defending a territory limit their aggressive behaviour to a given area.
3. The territory or defended area is only used by the animal or animals defending it.
4. The aggressive or dominant behaviour displayed by animals defending their own territory changes to submissive behaviour when they enter another territory.

## Evidence: Exploitation

Some studies on exploitation of resources have obtained evidence of an ideal free distribution. Milinski (1979) put six sticklebacks into a tank. Prey were dropped into the water at each end of the tank, with twice as many prey being available at one end as at the other. An ideal free distribution in these circumstances would involve four sticklebacks being at the end of the tank with the greater resources. That was precisely what Milinski found.

The study by Milinski was a controlled laboratory study. Evidence of an ideal free distribution under natural conditions was reported by Power (1984). She studied the behaviour of armoured catfish in a stream in Panama. These fish eat algae, which are found mostly in sunny pools. The catfish tended to gather in the sunny pools, and the relative numbers in sunny and shady pools were in agreement with the ideal free distribution.

It is very common in nature for the competition for resources to involve both exploitation and resource defence. For example, animals may decide which habitat to go to for resources on the basis of exploitation, but the amount of resources obtained by each animal in any given habitat may depend on resource defence.

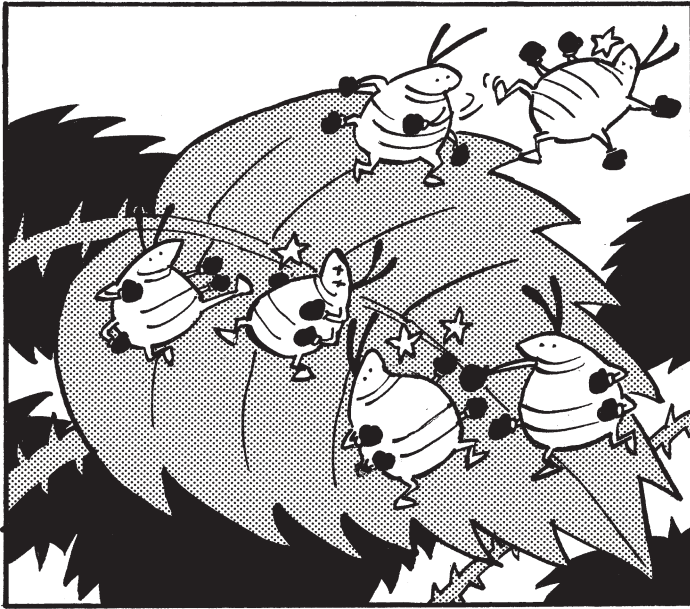
Whitham (1980) studied habitat selection in the aphid. In the spring, females settle on leaves that provide juices they need to reproduce successfully. Larger leaves provide more juices than smaller leaves, and so the largest leaves are the ones that are occupied first. Whitham's findings were in agreement with the ideal free distribution. More female aphids settled on the large leaves than on the small ones, so that the average reproductive success in terms of the number of offspring did not depend on whether the habitat was good or poor.

The findings discussed so far have conformed to the ideal free distribution. However, here even though the *average* access to resources and reproductive success did not depend on the nature of the habitat, there was also evidence that some individuals within any given habitat had access to more resources than others. Some parts of the leaf provide more juices than others, and female aphids kicked and pushed each other in order to

*In your experience, how do pet animals show what they consider to be their territory?*



Milinski's study: at the start, two-thirds of the prey were available at one end of the tank. Subsequently, two-thirds of the sticklebacks moved to the place with greater prey resources, showing an ideal free distribution.



occupy the best positions on the leaf. These findings indicate that resource defence played a part in the competition for resources.

### Evidence: Resource defence

Krebs (1971) reported evidence of resource defence in great tits. Their best breeding habitat is in oak woodland. The oak woodland is filled rapidly with defended territories in the spring, so that late-arriving great tits have to occupy the much poorer habitat provided by hedgerows. When great tits were taken away from the oak woodland, others from the hedgerows moved in rapidly to replace them. This suggests that it was resource defence that forced them to inhabit hedgerows.

The members of some species compete for resources by means of resource defence or defending their territory, but the members of other species do not. What determines whether or not animals make use of resource defence? Brown (1964) argued for the importance of

**economic defendability**, which is the notion that a territory will be defended whenever the benefits are greater than the costs. In the section on territorial contests we will see how a group of red deer stags assesses the costs of defending their territory.

### Size of territory

We have seen so far that the notion of economic defendability is of value in predicting whether animals will defend territories. However, it would be useful to be able to make more detailed predictions. For example, what is the size of the territory that animals will choose to defend? It might be thought that animals would defend a large territory, because

### Gill and Wolf

It is hard in many species to work out the benefits and costs associated with territorial defence. However, this can be done in some species of birds. Gill and Wolf (1975) looked in detail at the behaviour of the golden-winged sunbird in East Africa. Sunbirds extract nectar from *Leonotis* flowers. They can obtain this nectar either by defending patches of these flowers against competitors, or by foraging for it. Defended territories generally consisted of between 1000 and 2500 flowers, and there was more nectar on the defended flowers than the non-defended ones.

Gill and Wolf worked out the costs of territorial defence, foraging, and sitting on a perch in terms of the number of calories per hour they required. Territorial defence used up far more calories per hour than the other activities. However, territorial defence took less time than foraging, and it provided access to flowers containing more nectar. According to the notion of economic defendability, sunbirds should engage in territorial defence when the gain in terms of additional nectar outweighs the cost in terms of using up calories. In general terms, that is exactly what was found by Gill and Wolf. However, it is important to note that the sunbirds did *not* work out the number of calories per hour involved in different activities before deciding what to do. The information actually used by sunbirds when deciding whether to defend their territory or to forage for food remains unclear.

### Discussion points

1. Can psychologists always work out the precise benefits and costs of territorial defence?
2. How could we extend this type of research? For example, we could put small weights on the backs of sunbirds to increase the cost of territorial defence in terms of calories.

#### KEY TERM

**Economic defendability:** the notion that a territory will be defended when the benefits are greater than the costs.

large territories contain more resources than small ones. However, it takes more energy to defend a large territory, and so the benefits of extra resources may be outweighed by the costs of its defence.

This issue was considered by Carpenter, Paton, and Hixon (1983). They studied rufous hummingbirds who were migrating southwards through California, and who needed to make up the weight lost on their journey. These birds often changed the size of their territory between one day and the next. Carpenter et al. found that the hummingbirds showed more weight gain when they defended a medium-sized territory than when they defended one that was either large or small. These findings suggest that the best defended territory is of medium size.

*How might Carpenter et al. have assessed the size of the hummingbirds' territory from day to day?*

## Sharing

All the examples of resource defence considered so far have involved individuals defending a territory. However, there are many cases in which two or more individuals of the same species combine forces to defend the same territory. Davies and Houston (1981) studied pied wagtails. These birds feed on insects washed up on the banks of rivers. Individual wagtails generally go around their territory a number of times each day, taking about 40 minutes each time. Sometimes two pied wagtails defend the same territory, with the territory owner permitting a “satellite” territory owner to join it. This has the advantage that the territory is defended better against intruders. However, it has the disadvantage that each bird is only able to feed on about half of the insects within the territory. Davies and Houston worked out that the advantages of sharing would outweigh the costs when many insects were being washed up on the river bank, and when there were many intruders. As predicted, sharing was much more common in those circumstances than when there were fewer insects being washed ashore and fewer intruders.

## Resource defence: Theory

Most theoretical approaches have focused on the notion of economic defendability, with its emphasis on identifying the benefits and costs associated with resource defence. Huntingford and Turner (1987) identified several benefits and costs that jointly determine whether a territory possesses economic defendability. Some of the main potential benefits of territoriality are as follows:

- Decreased risk of predation (being attacked by predators).
- Food resources last longer, because fewer animals have access to them.
- Renewable food resources are used more slowly, and so can be harvested more efficiently.
- Animals may have greater reproductive success because of the resources available within the territory.
- Offspring are raised in a more favourable environment.

Huntingford and Turner identified the following major costs of territoriality:

- It may be necessary to remove the previous owner before taking over a territory.
- Defending a territory may require the expenditure of much energy.
- Defending a territory may take up considerable amounts of time.
- Defending a territory may risk injury or even death.

It is often thought that animals will typically strive to maintain their territory over long periods of time. However, it follows from the notion of economic defendability that territories will often be abandoned when circumstances change so as to reduce the benefits of the territory and/or increase the costs. This was shown clearly in the study by Davies and Houston (1981) on pied wagtails. Territory owners used four different territorial strategies at different times. When the food resources in the territory were very low, they abandoned it completely. When the food resources were fairly low, they spent all their time in the territory. When the food resources were abundant, but there was much intrusion by other birds, they allowed a second or satellite bird to join them in the

*Do you think Huntingford and Turner's lists of benefits and costs would also have applied to early humans?*

territory (see earlier). When the food resources were abundant, but there was little risk of intrusion, the pied wagtails did not devote time to defending their territory.

### Red deer displays

The red deer colony on the Scottish island of Rhum show clear ritual in their mating and territorial contests. The ritual has several stages, each of which acts as an assessment of an opponent's strength. A stag can leave the contest at any time by backing off and turning away, thereby escaping serious injury. First, the two contesting stags perform a parallel walk, side by side up and down a stretch of land. They appear to be assessing each other visually. If the contest continues, the stags stop walking and stand to bellow or roar. They can make a fearsome amount of noise, which appears to be another way of demonstrating strength. The next stage involves mock rushes at the other animal, followed by physical contact using their bodies and antlers. If contests reach this point, serious injury can result, even leading to the death of an animal, so this final stage is only embarked on when both stags assess their strength and fighting ability as likely to bring success. Because success brings territory and a harem of females, it is a powerful reward.

### Territorial contests

The decision as to whether it is worth defending a territory often depends on the likelihood of the territory owner being successful in a territorial contest against an intruder. In most species, the winner of any territorial contest tends to be the larger animal (Huntingford & Turner, 1987). When the two animals are the same size, then the owner or resident is more likely to win. For example, Burk (1984) studied territorial contests in male Caribbean fruit flies. When both flies were the same size, the owner won just over 70% of the contests.

**Keep-out behaviours.** There are various reasons why territorial contests are rare in many species. One reason is because of the existence of keep-out behaviours that may be visual or auditory. Peek (1972) studied male red-winged blackbirds, who defend their territories by showing off their red and yellow shoulder patches and by loud vocalisations. Blackbirds that had their shoulder patches covered with black polish were less successful at keeping out intruders. In similar fashion, blackbirds that were operated on to prevent them vocalising were also less able to prevent intruders from entering their territory.

**Ritualised aggression.** Another reason why no-holds-barred territorial contests are fairly rare is because of **ritualised aggression**. This involves an animal producing stereotyped aggressive displays to deter other animals from attacking it. One of the key purposes of ritualised displays is that they permit animals to assess each other's fighting ability without serious risk of injury or death. For example, a cat defending its territory will arch its back, erect its fur, and make menacing noises at other cats. Male frogs and toads wrestle each other to decide who has the best territory, and beetles push each other to assess which is the stronger (Krebs & Davies, 1993).

**True aggression.** Ritualised aggression may be the norm, but vicious fighting often occurs when resources are scarce or valuable. For example, up to 10% of male musk oxen die every year as a result of fierce fights over females. More dramatically, male fig-wasps inside a fig fruit often kill each other in fights to decide who will mate with female fig-wasps. According to Krebs and Davies (1993, p.157), one fig fruit “was found to contain 15 females, 12 uninjured males and 42 damaged males who were dead or dying from fighting injuries. Damage included legs, antennae and heads completely bitten off, holes in the thorax, and eviscerated [disembowelled] abdomens.”

## PREDATOR–PREY RELATIONSHIPS

According to Krebs and Davies (1993), there is a kind of “arms race” over time between predators and their prey. Natural selection during evolution should produce predators who are increasingly well equipped to detect and to capture their prey. However, natural selection should also lead to changes in the prey, so that they are better able to avoid detection or to escape from predators. The term **coevolution** is used to refer to the notion that evolutionary changes in predator and prey species depend in part on changes in the other species. According to Grier and Burk (1992, pp.268–269):

*The effects of predator–prey coevolution on animal behaviour and morphology [form and structure] are so pervasive that it has even been theorised to be one of the main factors in, for example, the evolution of the vertebrates.*

### KEY TERMS

**Ritualised aggression:** stereotyped rituals involving aggressive displays designed to deter other animals from fighting.

**Coevolution:** evolutionary changes in predator and prey species that depend on changes in the other species.

There can be serious consequences, leading to extinction of their species, if either predators or prey fail to adapt rapidly enough, so it is of great importance for both predators and prey not to fall behind in the evolutionary arms race. Dawkins and Krebs (1979) argued that the pressures are often greater on the prey rather than on the predators. According to them, “A fox may reproduce after losing a race against a rabbit. No rabbit has ever reproduced after losing a race against a fox. Foxes who often fail to catch prey eventually starve to death, but they may get some reproduction in first.”

In what follows, we will see some of the methods used by predators, as well as some of the defensive methods that have been developed by prey. There is a surprising variety of methods used by both predators and by prey. Some of these methods depend in a direct way on evolutionary change. For example, many species have developed acute senses of seeing, hearing, or smelling. Other species have developed physically, becoming able to move more quickly or becoming stronger and heavier. Other methods are more subtle, depending on various forms of trickery.

There are various stages in the predator–prey relationship. Endler (1991) identified five stages, as follows: encounter; detection; identification; approach; and consumption. Any given adaptation by predators or by prey is typically of most relevance to one or other of these stages.

## Adaptations by predators

### Tactics

Grier and Burk (1992) list seven methods used by predators when trying to catch prey. Perhaps the most obvious method is by simply chasing and pursuing the prey. Another method is to force the prey to keep moving until it is exhausted. This method is often used when the prey might prove dangerous if attacked before it is exhausted.

Stalking and ambushing are used by many species of cats. Some other species (e.g. chameleons; mantids) achieve success at stalking and ambushing by blending in with their background so they are hard to see. An unusual form of stalking and ambushing is used by anglerfish. They display a bait that looks very much like a small fish. If a prey moves close to this bait, the anglerfish moves rapidly to catch it (Pietsch & Grobecker, 1978).

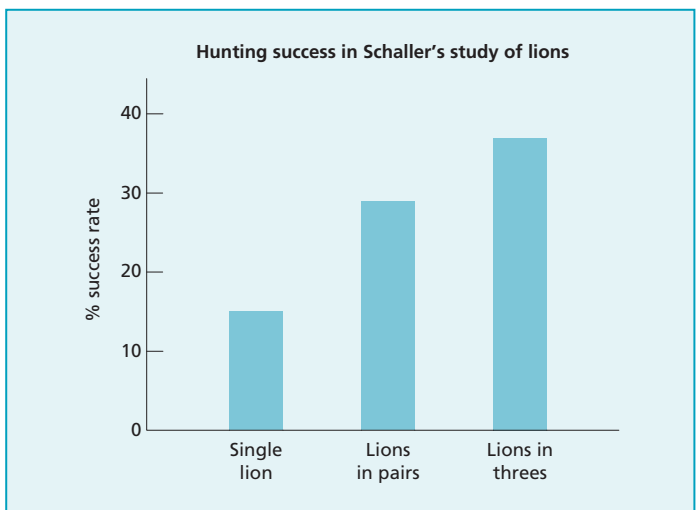
Predators sometimes achieve more success at hunting in groups. Such communal hunting is found in lions, wolves, killer whales, communal spiders, and other species. Detailed evidence on the effects of group size on hunting success in lions was reported by Schaller (1972). When lions hunted gazelle, wildebeest, zebra, or other prey on their own, their overall success rate was only 15%. This increased to 29% when two lions hunted together, and to 37% when three lions hunted together. The success rate decreased somewhat when there were more than three lions in the hunting group.

### Search image

Krebs and Davies (1993) identified additional ways in which predators can become more successful at catching prey. Predators may develop more effective ways of searching for prey by improved visual acuity. Alternatively, they may learn to find prey more easily by forming a **search image**, which involves learning more about the visual features of their prey. Forming a search image may also involve improved attentional processes. Evidence for the development of a search image in chicks was reported by Dawkins (1971). The prey consisted of coloured rice grains which were presented on a background that was either the same or a very different colour to the grains. The chicks initially found it hard

#### Seven methods used by predators to catch prey (Grier & Burke, 1992)

1. Groping and flashing: this involves using feet or feelers.
2. Stalking and ambushing.
3. Chase and pursuit.
4. Interception of flight path.
5. Exhaustion of prey.
6. Tool use to get prey.
7. Communal hunting.



#### KEY TERM

**Search image:** detailed learning about the visual features of prey by predators.

to detect the prey when it was the same colour as the background. After a few minutes, however, they started to detect and to eat the prey more quickly, suggesting that the chicks had formed an appropriate search image.

### *Subduing prey*

Krebs and Davies (1993) also pointed out that some predators become more effective by developing better ways of subduing prey they have caught. Prey can be subdued and killed in various ways. Predators can use their teeth or beak to bite or tear their prey, or they can use their claws to open them up. Another possibility is squeezing or suffocating prey by the use of constriction, as with many species of snakes. Finally, predators such as stingrays, venomous snakes, and scorpions use stinging or poison to subdue and kill their prey.

### *Success rates*

Predators are often not very successful at catching prey. Success rates are hard to calculate accurately, in part because it is not always clear to an observer whether an act of predation has been tried. In addition, success rates vary considerably depending on the predator and prey species involved. However, a typical hunting success rate for a predator is about 30% (Grier & Burk, 1992), indicating that about two-thirds of predation attempts end in failure. In the next section, we consider some of the ways in which prey manage to avoid being caught by predators.

## **Adaptations by prey**

### *Tactics*

According to Grier and Burk (1992), there are at least 11 major methods used by prey to defend themselves against predators. The most obvious method is to run, swim, or fly faster than the predator, so that the prey cannot be caught. Another fairly obvious method is for the prey to make unpredictable movements so that it is hard for the predator to follow it. This method is used by moths when trying to escape from bats.

A useful defence method is to develop more sensitive perceptual abilities so that predators can be detected as early as possible. Roeder and Treat (1961) argued that moths' hearing is mainly designed to detect bats' calls and alert them to the need to take escape action. They observed about 400 encounters between bats and moths. The moths that detected the bats and so took evasive action were much more likely to survive than those that did not take evasive action. A different tactic is used by small reef-dwelling fish. They tend to swim in very large tightly packed shoals. This mass may serve to distract predators, but also means that each individual fish has a greater chance of escaping predation.

## **Polymorphism**

Underwing moths do not only have crypsis or camouflage as a defence against predators. The forewings of many species of underwing moths show **polymorphism**; that is, they differ somewhat in colour among the members of that species. Suppose that a predator forms a search image (see earlier) of the colour pattern of the first moth it finds, and then looks for further moths having the same colour pattern. If that is the case, then polymorphism would help prey to avoid detection.

This notion was tested by Pietrewicz and Kamil (1981). Blue jays were presented with slides consisting of either members of only one species of underwing moth or a random mixture of members of two species. The blue jays showed a rapid improvement in their ability to detect the moths when they were all of the same species, but there was no improvement when the moths came from two differently coloured species. These findings suggest that predators who encounter polymorphic prey find it hard to form a useful search image of their prey.

#### **KEY TERM**

**Polymorphism:** the occurrence of a number of forms in a species (e.g. differing wing colour in moths).

## Crypsis

Another defence method that has proved useful in many species is known as **crypsis**, in which the prey's colouring resembles that of the setting in which it is generally found. In other words, crypsis is like camouflage in that it makes it harder for the predator to detect its prey.

Various species of underwing moths have forewings that look very similar to the bark of the trees on which they rest. They generally seem to make the camouflage most effective by orienting themselves so that the patterning on their forewings matches that on the bark as closely as possible. Evidence that crypsis is, indeed, effective in reducing the ability of predators such as blue jays to detect the moths was reported by Pietrewicz and Kamil (1981). They presented slides to blue jays in a testing apparatus. An underwing moth was present in some of the slides but not in others, and the moth was shown against a background that either resembled the moth's forewings or was rather different. The blue jay was rewarded with a mealworm every time it correctly detected a moth. The blue jays detected over 90% of the moths presented against a different background, but only about 10% of the moths presented against a very similar background. These findings show clearly that crypsis or camouflage in prey can be a very effective defence against predators.

It might be thought that crypsis or camouflage in prey will only be an effective defence when it is very hard for predators to detect them. However, this is not so. Erichsen et al. (1980) presented great tits with a mixture of large prey that took a few seconds to detect and small prey that were easy to detect. When the easily detected prey were encountered often, the great tits tended to eat them and to ignore the large cryptic prey. Thus, even fairly poor crypsis or camouflage will be very useful to a species if it makes some other prey more profitable to predators.

## Discussion points

1. Can you think of other species that make use of camouflage?
2. How do you think that crypsis or camouflage developed in those species that possess it?

## Startling a predator

The forewings of underwing moths look like tree bark. In contrast, their hindwings tend to be brightly coloured. In order to escape detection, the moths normally rest with their hindwings covered by their forewings. When they are disturbed by a predator, the moths suddenly expose their hindwings. This may startle the predator, and thus give the moth the chance to escape. The advantage of brightly coloured hindwings may be that they startle the predator more than would hindwings lacking colour.

Schlenoff (1985) tested these ideas. She presented blue jays with models of moths in which the hindwings suddenly became visible. Blue jays who were initially exposed to models with grey hindwings had a startle response to brightly coloured hindwings. However, blue jays who initially saw brightly coloured hindwings were not startled when shown grey hindwings. Thus, brightly coloured hindwings do cause predators to become startled. Schlenoff also found that blue jays were no longer startled when exposed repeatedly to the same brightly coloured hindwings. However, the startle response returned when differently coloured hindwings were presented. These findings make sense of the fact that underwing moths have a great variety of colour patterns in their hindwings.

## Edibility

Some species of prey are brightly coloured all over, and do not show any tendency towards crypsis or camouflage. It is a little puzzling that such prey have colouring that

### KEY TERM

**Crypsis:** a form of protection adopted by prey, in which their colouring resembles that of the normal setting.

makes it very easy for predators to detect them. The puzzle is largely solved when it is realised that such prey are often distasteful. Evidence that it is useful for distasteful prey to be easily detected or conspicuous was reported by Gittleman and Harvey (1980). Chicks were presented with breadcrumbs which had been made distasteful by dipping them in quinine sulphate and mustard powder. Initially, the chicks ate more of the breadcrumb prey when they were easily detected rather than hard to detect or cryptic. However, the conspicuous or easily detected prey were eaten much less than the cryptic prey later on. Presumably chicks find it easier to avoid distasteful prey when it is conspicuous than when it is cryptic.

### *Mimicry and confusion*

The fact that predators learn to avoid distasteful or inedible prey lies behind the development of Batesian mimicry in some species. Batesian mimicry involves the members of an edible species having the same warning colours and patterns as the members of an inedible species. This is found in various beetles and flies. For example, bombardier beetles resemble crickets, and ladybeetles look like roaches. Batesian mimicry generally works best when there are more members of the inedible species than of the mimicking one. If this is not the case, then predators may eat several mimics before encountering a member of the inedible species.

Mertensian mimicry is another way in which prey can defend themselves against predators. It involves the members of a prey species behaving in ways resembling those of a species that is dangerous to the predator. For example, some species of snakes make themselves seem more dangerous by hissing, shaking their tails, or making striking movements (Grier & Burk, 1992). Rowe, Coss, and Owings (1986) found that burrowing owls make hissing sounds that are like those of rattlesnakes.

Another way in which prey can avoid being captured and eaten by predators is by creating confusion effects. Grier and Burk (1992) describe two examples of such effects. Octopuses that are being attacked emit a large amount of black ink, which makes it very hard for predators to see them. Geese that are being attacked by an eagle often use their wings to splash water all around them to confuse the eagle.

*The term “mimicry” suggests that the prey species deliberately adopts a particular pattern or colour. Is this so?*

### **Adaptations and counter-adaptations**

As was mentioned earlier, we can only understand predator–prey relationships by focusing on coevolution. In other words, the evolutionary adaptations of predators depend on the changing behaviour of their prey, and the adaptations of prey likewise depend on the changing behaviour of their predators. We will reconsider some of the evidence in this context.

#### **Counter-adaptation in rabbits**

When rabbits are pursued they zig-zag instead of running in a straight line. This increases the likelihood of escape, as a larger fox or dog may not be so manoeuvrable. Unfortunately this behaviour tends to increase road deaths among rabbits, as they often double back under a vehicle's wheels. Perhaps rabbits are now evolving a different behaviour pattern to deal with this risk.

Predators have adapted in various ways to make it easy for them to detect their prey. Adaptations include improved visual and auditory sensitivity, and the ability to form search images. It is obviously very much in the interests of prey species *not* to be easily detected. This has led to various counter-adaptations by prey species, such as crypsis and polymorphism.

Predators generally want to get as close as possible to their prey before they are detected. This can be done by blending in with their background. It can also be done by approaching their prey slowly and almost silently and/or by making sure they are downwind of their prey. One of the main counter-adaptations by prey species is to develop more sensitive perceptual abilities (e.g. hearing in moths), so that they can detect predators when they are still at some distance.

When predators have detected their prey, they usually move swiftly to capture it. For example, this is the case with lions and tigers. Many prey species have developed counter-adaptations to reduce their chances of being captured after detection. For example, octopuses and geese create confusion effects. Other counter-adaptations include

looking like the members of an inedible species and behaving like the members of a more dangerous species. Some harmless hover-flies have black and yellow striped bodies that resemble wasps.

Many predator species have developed various adaptations so that they can subdue and kill their prey. These adaptations include sharp teeth and/or claws, powerful bodies to squeeze prey, and the ability to sting or poison prey. Many prey species have developed counter-adaptations. Some species of rodents and insects attack predators in an aggressive way. Other prey species develop spines or hard shells which protect them.

## SYMBIOTIC RELATIONSHIPS

As Grier and Burk (1992, p.291) pointed out, “Organisms of most species simply go about their business and do not interact with most of the other organisms surrounding them.” As we have seen, most relationships between members of different species are of the predator–prey kind. However, there are many examples of less aggressive relationships between species. **Symbiotic relationships** involve the members of two different species behaving in ways that benefit each other (the word “symbiosis” means living together). The two most important kinds of symbiotic relationship are mutualism and commensualism. **Mutualism** involves interactions between the members of different species that are of benefit to both the participants. In contrast, **commensualism** involves interactions that are of benefit to one participant but which do not benefit or harm the other.

There is a close similarity between symbiotic relationships on the one hand and reciprocal altruism on the other hand. The main difference is that symbiotic relationships involve individuals of different species helping each other, whereas reciprocal altruism involves mutual helping between members of the same species.

## Evidence

Most symbiotic relationships provide the benefit of food to one of the participants and a different benefit (e.g. protection from predators; bodily hygiene) to the other participant. Some examples of this type of symbiotic relationship will be considered before moving on to other types. For example, there is a symbiotic relationship between groupers and wrasses. Groupers are large fish and wrasses are small cleaner fish. A grouper allows a wrasse to enter its mouth to remove skin parasites and other small eligible items. When the wrasse has finished, the grouper allows it to swim out of its mouth without trying to harm it. The grouper gains because it loses the parasites from its mouth, and the wrasse gains because it is being provided with a meal.

There are other species in which symbiosis involves the removal of parasites. For example, cowbirds often spend much of their time removing insects that have become lodged in the hair or skin of giraffes or other large African animals. In return, cowbirds gain access to a rich source of food.

Isack and Reyer (1989) discussed one of the relatively few cases in which humans are involved in a symbiotic relationship with the members of another species. The greater honeyguide (a species of bird) leads the Borans of Kenya to honeybee colonies or hives, which are often not easily visible from a distance and can be located deep inside hollow trees. The birds do this by flying and perching in such a way as to indicate the direction and distance of a hive. The Borans remove the honey. They benefit because the average time taken to find a hive is 3.2 hours with the assistance of the birds compared to almost 9 hours without their assistance. The birds eat the bee larvae and wax. They benefit because most of the hives are only accessible to them with human help.

Preston (1978) studied a form of mutualism that did not involve feeding. There is a symbiotic relationship between goby fish and shrimp, in that the shrimp digs a hole in which they both live. The goby fish gains the benefit of somewhere safe to live, and the

*Do you think humans have anything approaching a symbiotic relationship with another species? If so, which one(s)?*

### KEY TERMS

#### **Symbiotic relationships:**

cooperative behaviour in which the members of two different species behave in ways that help each other, or which help one participant without harming the other.

**Mutualism:** interactions between the members of two species that are of benefit to both participants.

**Commensualism:** interactions between the members of two species that benefit one participant without harming the other.

shrimp gains the benefit that the goby warns of danger. The shrimp maintains contact with the goby fish by means of its antennae, and the goby gives a tactile warning signal with its fins.

Most symbiotic relationships benefit both of the participants, but such relationships can be exploited by the members of other species. For example, blenny are small fish that look like cleaner fish, and resemble them in their behaviour. As a result of this resemblance, blenny are able to approach closely to host fish. They then take a bite out of the host fish rather than providing a cleaning service.

## How do symbiotic relationships develop?

It is usually easy to see the advantages of symbiotic relationships to the members of the two species involved. However, it is harder to work out how such relationships between different species became established in the first place. It is often hard to form co-operative relationships between members of the same species, and it would seem that this would be even harder to achieve between two species. Thompson (1982, p.61) argued that most symbiotic relationships develop out of antagonistic encounters:

*If it is unlikely that individuals can avoid a specific antagonistic interaction, then selection will favour individuals that have traits causing the interaction to have at least less of a negative effect on them. This selection regime sets the stage for the evolution of the interaction towards commensalism or mutualism.*

Why do antagonistic encounters need to be unavoidable for them to lead to the development of a symbiotic relationship? If such encounters are avoidable, then the members of the weaker species are likely to make use of avoidance behaviours so as to reduce the chances of injury or death.

Springett (1968) discussed an example of a symbiotic relationship developing out of antagonistic encounters. Burying beetles and colliphora flies compete with each other to lay their eggs on dead mice. The flies are more successful in this competition, as the beetle larvae do not survive when flies are present. However, the overall situation is to the benefit of all, because the mites carried by beetles eat the eggs of the flies, and this allows the beetles to survive.

Thompson (1982) argued that the development of symbiotic relationships (e.g. mutualism) depends on various factors in addition to unavoidable antagonistic encounters:

1. The environment should be physically stressful, as for example by providing very limited food supplies; this provides motivation for symbiotic relationships to occur.
2. The level of survival of members of the two species should be intermediate; if it is low, then encounters with other species are too risky; if it is high, then there are no clear advantages in seeking encounters with members of another species.
3. Social species (e.g. social insects; birds) that have various ways of communicating with others are more likely to form symbiotic relationships than are non-social species.

## Evaluation

Thompson (1982) has suggested various factors that are likely to be involved in the development of symbiotic relationships. His suggestions are consistent with most of the evidence, and help to explain why it is that such relationships are more common among social insects and birds than most other species. However, there is an inevitable problem with testing any theoretical ideas about the ways in which