Essential Animal Behavior

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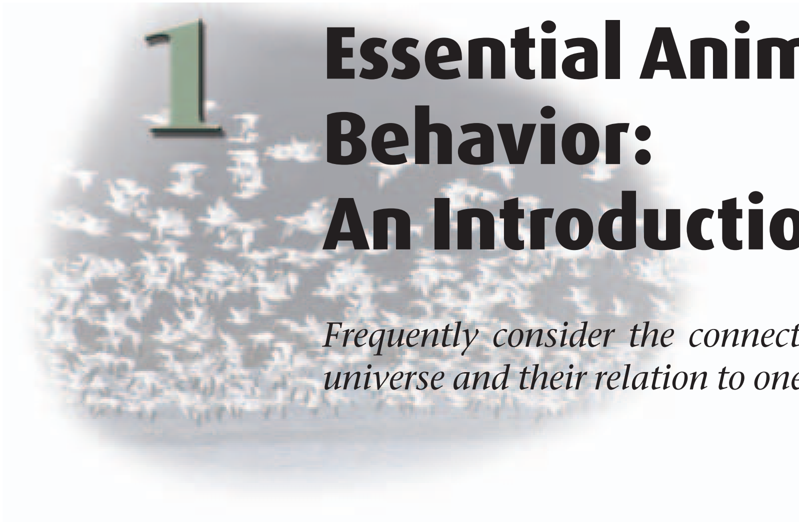

1 Essential Animal Behavior: An Introduction

Frequently consider the connection of all things in the universe and their relation to one another.

Marcus Aurelius AD 121–80

People have probably always been fascinated by the behavior of animals. Indeed an understanding of the behavior of prey animals must have been essential to our early ancestors; their paintings on the walls of caves suggest that they could have been fairly familiar with behavioral concepts such as herd size and migration. The earliest stock-farmers would have needed to understand the behavior of the charges in their care just as their modern counterparts do today.

Some members of society (and even some biology students) may wrongly think of the study of animal behavior in an academic context as being a soft science or even an easy option.

Key points

- The field of animal behavior is diverse and may be studied from a variety of perspectives.
- It is useful to consider behaviors as adaptations.
- A single behavior will not serve, or serve the same purpose in all situations, and behaviors are adapted to be effective in the environment of the animal performing them.
- It is wrong to think of animal behavior as a general interest or a purely academic subject. The study of animal behavior is an important science which has a clear applied context.

Contents

However, I hope to show you in this introduction to the subject that it is an important and rigorous science and that it has a clear application to some of the problems that we face in the modern world.

Cephalopod inking behavior

Many species of octopus and squid are known to exhibit a particularly effective behavior that enables them to escape from predators. In the region of their intestines the animals have a special sac-like organ. In the wall of this sac there is a gland which secretes a brown or black liquid rich in the pigment melanin, this is ink. When threatened the animal has the ability to compress the ink sac and squirt a jet of the liquid from its anus. It is thought that the cloud of ink hanging in the water forms a dummy squid termed a pseudomorph, which attracts and holds the attention of the predator allowing the animal to dart away to safety. The deception is made all the more effective because long thin species produce long thin pseudomorphs and more round species produce rounder clouds of ink (Plate 1.1).

Squid and octopus are molluscs, taxonomic relatives of the garden slug and snail. Can you imagine a slug squirting out ink to leave a pseudomorph hanging in the air to decoy a bird predator while the slug made its escape? Of course you can't, for the simple reason that this behavioral strategy can only work when the animal is surrounded by a medium that will support the ink cloud for a sufficient period to allow the escape. In water this works, but in the less dense medium of air it would not.

Plate 1.1 An animal this shape should produce a long, thin pseudomorph. © C. Waller.

Some species of octopus and squid are inhabitants of the ocean depths. Here light penetration from the surface is minimal or zero and the seawater is a constant inky black. Obviously the ink-dummy strategy would be no more effective here than it would be in air. The pseudomorph would hang in the water column, but it is unlikely that an ink-black shape would be seen against the inky-black backdrop. In this situation species such as the deep-water squid *Heteroteuthis* secrete a luminescent ink, creating a brief flash of light which is thought to confuse a potential predator just long enough for an escape to be affected.

From this example I hope that I have made a few key points about behavior. Firstly, that behaviors are adaptations which serve specific functions, and we will consider this point further later in this chapter. Secondly, that a single behavior may not serve, or serve the same function, in all situations (a point to be borne in mind throughout this book). Finally, behaviors are adapted to be effective in the environment of the animal performing them.

What is behavior?

Before investigating the amazing diversity of behaviors that animals exhibit, it is necessary for us to gain some insight into the concept of behavior itself. We need to decide what the word **behavior** means to us in the current context and to examine the various avenues open to us for the study of animal behavior.

So what is behavior? Dictionary definitions of the word typically include phrases such as "acting or functioning in a specified or usual way." This suggests to us that behavior is a predictable thing. Another common phrase is "the response of an organism to a stimulus." This suggests that behaviors are **made** to happen by something. In the case of this definition the "something" concerned is not specified, and may be internal or external to the animal involved. Each of these ideas is in its own way an adequate response to the question. Behaviors are in many cases predictable given sufficient information concerning their context (although many appear initially to be highly unpredictable). Similarly behaviors are often linked to a stimulus in an immediate sense at some level. The shortcoming of such definitions, however, is that they attempt to narrowly confine behavior in an easily described and highly specific way. Given the diversity of behavior such an approach may not be appropriate, because as humans we often think of different behaviors in very different terms.

Take for example breathing, swimming, and learning. Each of these words describes a behavior for which the definitions presented above would be sufficient. However as humans we would probably not think of them as being equivalent conceptually. We would consider breathing to be an involuntary process and may not even consider it to be a behavior at all because of that. Swimming, on the other hand, is clearly an active process, we tend to think of it as having a motivation or goal. Learning we think of in different terms again. We have a tendency to place it into a higher class of processes, which require a higher level of mental ability (though we shall see in Chapter 4 that this need not be the case). So as a result of our own preconceptions about the words we use to label behaviors, and their obvious diversity, it will be much more useful for us to adopt a very broad definition of behavior in this book.

Put more simply then behavior is a property of all living things and whenever we observe an animal to be engaged in any activity (voluntary or involuntary) we are witnessing behavior. Indeed it could be said that the only animal not behaving is a dead animal!

This is an important point to remember. Although we may feel that a sleeping seal or a motionless sea-snake are doing nothing, they are in fact behaving. The act of sleep is a behavior in its own right, and the snake is quite probably poised to strike at passing prey, tensing a host of muscles in readiness and taking in and processing a wealth of information about its environment. There can be no doubt that it is behaving.

Focus on anthropomorphism

Anthropomorphism is the attribution of human feelings and emotional states to animals. As humans we are aware of three mental experiences: feelings (pain, pleasure, etc.), motivations (the purposes of our actions), and thought. Our current understanding of nonhuman animal species does not allow us to say that they experience the same (of course nor does it preclude common mental experiences). Throughout the development of the field of animal behavior anthropomorphism and the use of anthropomorphic language has been frowned upon by some as a bar to clarity of expression, and in the extreme as a bar to the progression of science. However, given the "human baggage" associated with many of the words we use in describing behavior (e.g. aggression, hierarchy, motivation), it is inevitable that a degree of anthropomorphism will occur.

Throughout this text I have endeavored to avoid unwarranted anthropomorphism; in reading it I would ask that you do the same.

Approaches to the study of animal behavior

The effective study of animal behavior requires observation and experimentation. Before we have any chance of understanding a behavior fully we must observe that behavior, in its natural context, and in its entirety. The careful description of a behavior pattern or a sequence of behaviors allows us to identify all of the relevant components and to link their performance to the wider context of the physical and biological environment of the animal. From such a knowledge base we are able to develop our own ideas about that behavior, to speculate upon its function, and upon the factors which control it. In the language of science we are able to generate testable hypotheses. These are carefully worded questions that we hope to answer via carefully designed experiments where specific factors surrounding behavioral performances are monitored and manipulated. Throughout this book we will consider the results of such observations and experiments.

Animal behavior can be studied at two key levels. At the physiological level we might be interested in the mechanism by which a behavior actually occurs. By this I mean in what way do the biochemistry, nerves, muscles, and senses of an animal interact to result in a particular behavior? Equally interesting, however, are questions related to the whole animal and the world external to it. At this level we might consider the performance of a behavior in relation to the environment in which it is performed, to the wider ecology of the animal, or to its social experiences. This kind of whole animal observation could be carried out in the field – in the natural environment of the animal – or it could be carried out in the laboratory where a controlled environment more readily permits experimentation. In recent times, however, these distinctions have blurred and it is now commonplace to have "field" simulations in the laboratory and experimental manipulations in the field. The most significant recent development in the process of the study of animal behavior must however be the advent of powerful user-friendly computers. Via computer models behavior can be simulated, and "experiments" carried out and evaluated without the involvement of any animal (other than the human operator) and often at a fraction of the cost of a more traditional line of investigation. Such an approach undoubtedly has value, but a model is only as good as the data provided to it, and it will never replace the study of living animals.

Concept
The scientific method

The scientific method is a four-stage approach that we can use to explore animal behavior.

First we make observations of a behavioral phemonenon. Then we use these observations to formulate an hypothesis to explain the behavior. This may lead us to make further predictions concerning the behavior. Finally we design, carry out, and evaluate experiments to test our hypothesis and predictions.

Link
Models enable us to fully explore behavior.
Chapter 6

Asking questions in the study of behavior

As has been previously mentioned, we further the study of animal behavior by posing (and hopefully answering) questions, which are carefully constructed to take into account previous observations (and the answers to previous questions). Although the actual number of specific questions that we can ask is huge, there are a relatively small number of types of question that need concern us:

- **What is behavior X?** The simplest way to answer this question would be to provide a description of the behavior. A more sophisticated answer might consider the raison d'être of the behavior, and in doing so the question would overlap with those below.
- **When does behavior X occur?** We might address this question in a number of ways. Perhaps we are asking at what time of year/day does it occur? Alternatively the question could relate to a life stage (is the behavior performed by mature animals only?). We could also be interested in the position of this behavior within a behavioral sequence (does the animal always do X after Y? or does one animal always do X if another animal has just done Z?).
- **Why does behavior X occur?** This is perhaps the most often asked question during studies of animal behavior and it is certainly the question which is given the most weight.

Tinbergen's four questions

In 1963 Niko Tinbergen, a recognized pioneer of the study of animal behavior, suggested that there are four ways in which we can ask the question "why?" Such is the importance afforded to Tinbergen's four questions (as they are usually referred to) that it is worth spending some time on them so that we can be sure that we understand the subtleties of the distinctions between these four ways of asking "why?" It is also important to remember that no one of the possible answers to the question "why?" that we might discuss is more important than any other. They complement one another and together help us to appreciate the wider picture.

Why do cephalopods ink?

Key reference
Tinbergen, N. (1963) On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, **20**, 410–33.

We started this chapter with a description of the way in which some species of cephalopod mollusc eject a cloud of ink as part of their antipredator behavior. As enquiring animal behaviorists we should not be satisfied with a description of the behavior, we should ask the question why does it happen? Tinbergen suggested that to fully explore the behavior we should ask **why**? in terms of the **causation** of the behavior, in terms of its **evolution**, of its **function**, and of its **ontogeny**.

Causation

What causes a cephalopod to ink? The highly developed sensory organs of the cephalopods allow an animal to continually receive a wealth of information regarding its environment. The animal processes this information and specific environmental stimuli elicit specific responses. If the animal is threatened with immediate danger a sequence of nerve impulses trigger the activity of the ink sac, an effector organ (i.e. an organ which carries out the response to a stimulus). Upon stimulation the ink sac compresses and the duct sealing it from the rectum opens. A jet of ink is expelled through the rectum and out of the anus. In the environment the ink forms either a pseudomorph or a diffuse cloud, depending upon the species involved.

Link
Behaviors are coordinated by the actions of nerves and muscles.
Chapter 2

In thinking about the roles of sense organs, nerves, and muscles we have already considered the mechanics of inking behavior, and so we have begun to examine the causal mechanisms of this behavior in an immediate sense. We might go further, however, to better understand the role of the recent experiences of the animal in the process. Inking is relatively costly because it involves the production of an energetically expensive substance. For this reason it is usually a behavior of last resort. Typically an individual may have attempted to remain undetected through camouflage (crypsis behavior) or to frighten or confuse its attacker by performing one of a range of diematic behaviors. Examples of diematic behavior include changing color rapidly to startle a predator or adopting a threatening body posture. We should therefore consider failure of crypsis and diematic behavior as being causal factors of inking.

Link
An animal may employ a range of different antipredator behaviors.
Chapter 7

Evolution

Behaviors do not fossilize in the same way that body parts do. For this reason we can say little about the very recent evolution of inking behavior, or about its continuing development in the face of improvements in the ability of predators to detect the bluff, as must surely happen. However, by looking at the family tree of the molluscs, and at that of the cephalopods particularly, we can say something about the longer-term evolution of the behavior. Inking is not a general property of the molluscs, it is restricted to the class Cephalopoda. This tells us that the behavior has evolved more recently than at the point at which the cephalopods diverged from the other molluscs. Further investigation reveals that not all cephalopods have an ink sac. The order is subdivided into two subclasses, the Nautilioidea (none of the species of nautilus has an ink sac) and the Coleoidea (most of which have an ink sac). Inking must thus be a relatively recent evolution within the subclass Coleoidea, the squids and octopuses. Further examinations of differences and similarities in inking behavior between the various octopus and squid families would allow us to gain yet more insights into the evolution of the behavior, and may help us to better understand why it has evolved.

Function

The function of inking behavior is very easy to understand. The behavior allows an animal to escape, thereby ensuring its survival and contributing to its fitness. (Fitness in this context equates to reproductive fitness and is a measure of the organism's success in passing on its genes – after all a dead animal cannot pass on its genes.) If inking is so effective why do some octopus and squid use it only as a last resort? As we have already mentioned inking probably has a high cost associated with it, whereas the behaviors involved in crypsis are probably far less costly. It would be better for an individual to rely on less costly behaviors where possible, because by doing so it may save energy with which its fitness might be enhanced. For example, we could speculate that by not using and replacing ink an animal may be able to spend more energy producing a greater number of eggs or sperm.

Ontogeny

We might expect such a useful behavior as inking to be performed by all animals throughout their lives. After all the cephalopods have many predators. However, this is not always the case. The young of the blue-ringed octopus (*Hapalochlaena lunulata*) eject ink during the first few weeks of life, but after that they never do. *H. lunulata* is highly venemous – perhaps this proves a sufficient detterent to predators of adults, but not to those preying upon the young animals. Antipredator behavior must therefore continue to develop and be refined throughout the lifetime of the animal in at least some species. The cover of this book shows just how striking the blue-ringed octopus is.

Link
The modification of behavior may continue throughout the life of an individual.
Chapter 3

Behaviors as adaptations

As biologists we are used to talking about adaptations such as the development of antibiotic resistance in bacteria, or about organs like feathers and wings as adaptations for flying, but we perhaps do not think about behaviors as adaptations as often as we should.

Imagine for example a population of squid at a time early in the evolution of inking behavior. Faced with predators our hypothetical squid might have been able to do no more than squirt a diffuse cloud of ink, which dissipated in the water relatively quickly and had limited success (but some success) as an antipredator behavior. Now imagine that a genetic mutation occurred in a single animal, which had the effect that a chemical in the ink was altered slightly in its composition so that it became gooey on contact with water. When this animal squirted, the ink formed a rudimentary pseudomorph rather than a cloud. What would have been the effect of this alteration in antipredator behavior? Well perhaps it increased the likelihood of survival for this one animal.

If, however, the mutation was a heritable one that would be passed on to all of the young of that animal then something very important indeed might occur. As a result of its increased survival probability this animal might enjoy better reproductive success than the average squid, and because they inherited its gooey ink gene its offspring might also

Focus on heredity and natural selection

Any student of biology who takes the time to think about the characteristics of populations of individuals should note the following:

- That there is considerable variation among the individuals within a species.
- That this variation is passed from parents to their offspring through their genes.
- That many more individuals are produced than can ever survive to mature and reproduce.

From these basic building blocks, together with a prodigious amount of patient work and probably a touch of genius, Charles Darwin was able to construct his theory of evolution by natural selection. Long before the importance of genes was appreciated he realized that some heritable property of certain individuals placed them at an advantage relative to others of their kind. Through time the differential survival of these individuals could result in a shift in the make-up of the population such that animals without the advantage became increasingly rare (or perhaps disappeared) and those possessing it became more common. He proposed a scenario under which beneficial traits were selected for and detrimental traits were selected against (Fig. 1.1).

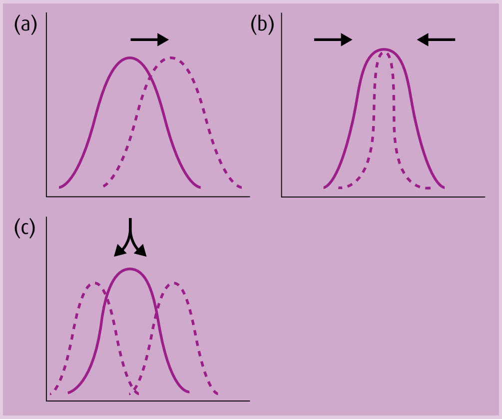

Fig. 1.1 An illustration of the effect of directional (a), stabilizing (b), and disruptive (c) selection upon a hypothetical population. In each case the solid line describes the pre-selection population and the dashed line the post-selection population.

We now understand that selection can be strongly directional in the way that I have just described, leading to the increasing dominance of a trait or to its eradication, or it can act in a disruptive way resulting in the evolution of a population that has two very different but successful phenotypes. Selection can also act in a stabilizing way to maintain the status quo.

Link
There is a genetic component to the performance of behavior.
Chapter 4

enjoy higher reproductive success than average. Through the course of a number of generations animals without the gene would become steadily less common whilst those with the gene would become more common, i.e. natural selection would be taking place. The animals better able to pass on their genes are being selected for, and those that suffer lower reproductive success are being selected against. The end result is the development of pseudomorph production as an adaptation to avoid predation.

Of course this is a purely hypothetical example, and following the course of development of such an adaptation through evolutionary time would hardly be possible. However there have been a number of studies that attempt to use real animals in their natural environments to better understand behavioral adaptation.

Perhaps the most widely quoted of these involves the work of Niko Tinbergen as part of his research into the behavior of various species of seabird. In the course of observations of a breeding colony of black-headed gulls (*Larus ridibundus*) he noticed two things. Firstly that the eggs in a nest do not all hatch on the same day, and secondly that parent gulls habitually remove the broken shells of their recently hatched eggs and deposit them some distance from their breeding area. In performing this behavior, however, it seemed to Tinbergen that the parent bird must place its newly hatched chick at risk because unattended chicks can and do fall easy prey to predatory birds including neighbouring gulls. So in 1967 Tinbergen asked the apparently simple question "why do black-headed gulls remove empty eggshells from their nests?" (Plate 1.2).

Tinbergen assumed (as I am sure would you) that the birds must remove the eggs because it was more advantageous to do so than to leave them in the nest. However, because all black-headed gulls perform this behavior it was not possible for him to simply compare the relative fitness of birds which did and did not remove eggshells. Instead he constructed an artificial colony of nests that he was able to manipulate. Some of the nests contained whole eggs only with some eggshells placed a fixed distance from the nest (to simulate nests from which the shell of the first hatched eggs had been removed). Others nests contained whole eggs and a broken eggshell (i.e. nests from which removal had

Plate 1.2 Black-headed gulls build their nests in close proximity to one another. © P. Dunn.

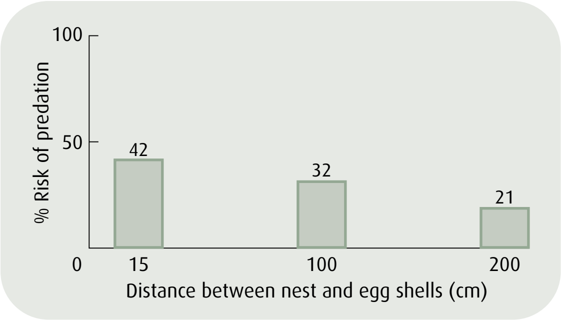

Fig. 1.2 The further away from the nest Tinbergen placed the eggshells, the lower the risk that the nest would be discovered by crows and the eggs eaten. (Data from Tinbergen, N. (1963) The shell menace. *Natural History*, **72**, 28–35.)

not taken place). After a period of observation he found that the nests from which the eggshells had been removed were the most successful (and that the further the eggshells were taken from the nest the more successful was the strategy, see Fig. 1.2). Predators such as crows and other species of gull were far more likely to eat the eggs from the none-removal nests than from the removal nests. From this we could deduce that if a "mutation" in eggshell removal behavior were to occur in which parent birds did not remove, then selection (in the form of increased predator risk) would act against it. This is an excellent demonstration of the usefulness of the **experimental method** as a tool for the study of behavior.

If removal does confer a selective advantage then surely parent birds should remove the eggshells as soon as the chicks hatch rather than waiting for a short period of time prior to removal (which they are observed to do). Further experiments revealed the reason for this delay. Newly hatched chicks are wet and take a short time to dry out. During this period neighbouring black-headed gulls can easily swallow them. If the parent were to leave the nest to remove the eggshells during this crucial period, it is likely that the advantage of removal (the benefit) would be outweighed by the disadvantage of cannibalism (the cost). This kind of reasoning is a vital tool for students of behavior and is termed a **cost–benefit analysis**.

Further confirmation of the role of predators as a selective agent in the shaping of eggshell removal behavior comes from the use of another key study method available to students of behavior. In 1957 Esther Cullen compared the behavior of the kittiwake (*Rissa tridactyla*) with that of a range of closely related gull species. She found that eggshell removal was a behavior common to the majority of gull species, but that it was never performed by the kittiwake. She suggested that the reason for this was that whereas all of the other gulls were ground-nesting birds who would be vulnerable to aerial predators such as crows, the nests of kittiwakes are constructed on the sides of high and sheer cliff faces and are not at risk. Thus this methodology, termed the **comparative approach** (because it involves comparing one species or group of species with another), also points to predation as a selective force in the adaptation of eggshell removal.

Throughout this book we will consider the design and the results of a number of studies similar to those I have described above. We will investigate the way in which the environment has played a part in the shaping of behavior and we will consider behaviors in an adaptive sense. By doing so we will gain new insights into the behavior of animals and into the process of behaving itself.

Why study behavior?

I opened this chapter with the observation that as a species we have a fascination with the behavior of animals (including ourselves). Personally I think that the "it's fascinating argument" is all the justification I need when friends and colleagues ask me why I study animal behavior, but I do regularly find myself having to provide other reasons when pressed. In fact the study of animal behavior has an application to a number of areas of modern life.

As a very obvious example, there is no doubt that an increased understanding of behavior does contribute to an increased understanding of ourselves as an "animal." Comprehension of the physical basis of human memory and brain function has certainly been advanced as a result of breakthroughs made using nonhuman animal models. The other main applications of behavior are however a little less obvious, and it is these areas that I want to draw to your attention in the remainder of this chapter and in the form of specific case studies throughout the remainder of this book.

Behavior and animal welfare

During the closing decades of the twentieth century large numbers of people became vociferous advocates for the welfare of animals. Initially the movement concerned itself with the welfare of captive animals; those species reared on farms, exhibited in zoos, and kept as companions by humans. More recently there has been a shift towards concern for the welfare of wild animals: those that are hunted or trapped, and those that are managed for conservation. In the case of the latter group a dilemma has presented itself as to when we should intervene and when we should "let nature take its course." Essentially the role of animal behavior in this area has been to play a part in the identification of examples of poor welfare, to explore and explain behavioral manifestations of poor welfare, and to provide potential solutions.

Key reference
Spedding, C. (2000) *Animal Welfare*. Earthscan Publications, London.

At a simple level we can think of welfare as equating to a state of well being or some form of contentment, and lack of obvious suffering as a result of cruelty. But welfare is more than that. An animal that enjoys good welfare will not want for food, water, or shelter. It will have space to move and opportunities for socialization appropriate to its needs. It will have the opportunity to express its natural repertoire of behavior. A deficiency in any of these will result in stress, a physical response to poor welfare.

The consequences of stress can be extreme. If a wild male rat blunders into the territory of another male the dominant resident will attack it. The intruder will flee, and once it is clear of the territory it will be safe from further attack. But if we were to replicate this scenario in the laboratory, in an enclosure from which the intruder could not escape, we would see just how extreme the effect of unmanageable stress can be. In this situation the intruder rat's physical health would deteriorate very quickly and it may well die as a result of just a few hours of intermittent attacks, even though it had sustained no significantly damaging wounds. Fortunately the results of stress are rarely so severe this quickly. But even short-term stress can be sufficient to have a negative impact upon the immune system and a sufferer of prolonged stress will often exhibit physiological, physical and psychological damage. It is often the case that an individual will exhibit behavioral indicators of stress, useful cues to poor welfare, and in some cases an early warning system that can be used to mitigate a problem before it gets out of hand.

Animals that are confined for prolonged periods in suboptimal conditions may develop characteristically stereotyped patterns of behavior that they will repeat and repeat and repeat. These stereotypies might be as uncomplicated as repeatedly pacing a fixed route, or they may be quite elaborate involving a set routine of paces, head weaving, and other gestures. In some cases stereotypical rubbing, digging, biting, and chewing, etc. can even result in the performing animal damaging itself physically. Exactly what is going on in these situations is however the subject of some debate. Stereotypies will persist long after the circumstances that led to their development no longer apply, and so identifying where exactly poor welfare applies is often difficult. At a physiological level there is evidence that the performance of stereotypies actually reduces some of the symptoms of stress and so might be thought of as a coping strategy. (I'm sure that you have paced, or rocked, or chewed your nails, subconsciously, when waiting for important news or to face a difficult situation – all coping strategies to relieve stress.) This does not mean though that we can dismiss the poor welfare of an animal engaged in stereotypic behavior because it has solved the problem itself – it has not and we must not!

One approach that we might adopt in determining the optimal husbandry conditions for animals, and thereby ensure high welfare, might be to take a lead from the animals themselves. As a general rule of thumb when they are given a choice we should expect animals to choose what is good for them. They may even demonstrate that they are better able to make such choices themselves than we are to make them on their behalf. For example, in response to a UK government recommendation that battery cages for hens should have floors made of a heavy gauge rectangular mesh rather than a thinner hexagonal one because the latter would be uncomfortable, choice tests were carried out. The hens chose the hexagonal mesh, and it turned out that this flooring

Case study Re-kindling a cheetah's motivation to hunt

Cheetahs (*Acinonyx jubatus*), in contrast to most members of the cat family, depend upon speed rather than stealth when hunting. Chases are generally short but they are clearly exhausting, because after a successful hunt a cheetah will rest for up to 30 minutes before eating (presumably only absolute exhaustion would delay feeding in an environment full of competitors ready to steal a kill). In captivity cheetahs are not given the opportunity to hunt live prey, to do so would be considered inhumane and would almost certainly be offensive to the viewing public. Quite apart from this, in countries such as the UK it is illegal. The lack of hunting opportunity in captivity results in lethargy, boredom, poor physical condition, and increased likelihood of stereotypies. In the case of the cheetah, a species whose liver is adapted for sudden mobilization of energy, lack of exercise may also be a major contributory factor in the development of liver disease. This is one of the main causes of death amongst captive cheetahs.

In an attempt to counter these problems the captive cheetahs at Edinburgh Zoo, Scotland, have been the subjects of a program of environmental enrichment. By providing the animals with a simulated hunting opportunity the research team involved hoped to increase the diversity of the behaviors exhibited by the animals (combating lethargy and boredom) and provide exercise opportunities. As an additional consequence, of course, the "improvement" in the behavior of the cats would increase their interest to the viewing public.

Prior to enrichment the animals were fed one rabbit per day and their food was thrown onto the floor in front of them. This particular cheetah enclosure is built on sloping ground. During the period of enrichment the mode of food delivery was modified. The rabbits were suspended from a wire that ran the length of the enclosure, parallel to the slope. Because the rabbit was introduced up-slope, gravity pulled it along the wire until it reached the fence at the down-slope end of the enclosure where a system of pulleys yanked it out of the cheetahs' reach. After a suitable period of training the cats learned to hunt and catch their "prey" before this happened.

During enrichment the animals would crouch some 5 meters from the point of rabbit delivery as soon as they saw the approaching keeper. Then they would wait until the rabbit had traveled some 10 meters along the wire before beginning their pursuit. Within 25–30 meters the cheetahs would draw level with their prey and fell it with a swipe of the forepaw, just as they would in the wild.

When the enrichment device was in use the cheetahs were seen to sprint three times as often as they had under their old feeding regime. So in terms of its aim to increase the exercise taken by the animals the program was a success. Enrichment did not increase the total range of behaviors exhibited by the animals, but it did change the relative proportions of time devoted to each of them and so it did increase the overall diversity of behaviors that were recorded. The way that the animals used the space available to them changed too. They used the various areas of their enclosure in a more diverse way and one that the research team felt represented improved space utilization. Perhaps most significantly the animals spent an increased amount of their time engaged in observation behavior following enrichment. In this context this meant that they spent more time on an elevated area of the enclosure staring outwards. In the wild cheetah use this technique to locate potential prey. In this study their gaze was directed almost exclusively towards an adjacent paddock stocked with blackbuck (*Antilope cervicapra*). Presumably the enrichment experience had re-kindled in them a motivation to hunt.

Williams, B.G., Warran, N.K., Carruthers, J. & Young, R.J. *et al.* (1996) The effect of a moving bait on the behavior of captive cheetahs (*Acinonyx jubatus*). *Animal Welfare*, **5**, 271–81.

provided their feet with better support than the "higher welfare" option that had been suggested.

Choice tests like these do, however, need to be carefully designed and evaluated if they are to prove useful. Care should be taken that the animals involved are aware of the choices available to them, and that they are "free" to exercise those choices. A great many species will for example avoid a novel situation and such behavior might compromise a test outcome. Hens given the choice between a familiar battery cage environment on the one hand and an unfamiliar outside run on the other will initially chose the familiar (against the predictions of most animal lovers). But if the test is repeated they will eventually modify the choice and take to the outdoor life.

Behavior and conservation

Traditionally conservation biology has been considered more the preserve of ecologists than of animal behaviorists. However, during the last decade a realization has developed that information about the behavior of animals, either as individuals or as part of a population of individuals, is invaluable in a wide range of conservation contexts.

Key reference
Caro, T. (1999) The behavior–conservation interface. *Trends in Ecology and Evolution*, **14**, 366–9.

As one of the main pressures contributing to increased rates of species extinction is habitat destruction and fragmentation it should come as no surprise that one of the main foci of conservation biology has been the design of nature reserves and protected areas. The theoretical background to the debate about reserve design has been grounded in island biogeography theory, and so the main questions asked have related to how big a reserve should be and how reserves should be arranged spatially. Is it better to have one big reserve or several smaller ones? Should reserves be isolated from one another, or connected via corridors to permit animal movements? Questions like these cannot be adequately answered without information about the dispersal patterns of individuals or about the likelihood that they will actually use the corridors as highways rather than perceiving them to be unsuitable "edge" habitat that they will not enter.

Another concern of conservation biology is the management of populations of animals, often with target population sizes in mind (relating to the carrying capacity of an area or to the minimum viable population of a species). In this context there is a tendency to consider all of the members of a population as being equivalent when in fact this is often not the case. Overexploitation of male animals in general may make it difficult for females to find and acquire mates. But the effect will be more marked in those species where females exercise mate choice based

Link
Not all of the members of a sex are equally attractive as potential mates.
Chapter 8

on ornamentation (horns, etc.) that also determine a hunter's choice of target.

I cannot think of a better example of the need to be fully aware of the reproductive behavior and mating system of an exploited animal than the case of the lion. In a number of reserves the licensed hunting of "trophy" lions (males) represents an important income stream that contributes to the continued existence of the reserve. But shooting males necessarily increases the rate at which prides of lions are taken over by new males. New males commit infanticide to ensure that they do not raise the young of their rivals and to ensure that the pride females will come into estrus as soon as possible. This of course means that the impact upon the population of shooting one male is larger than the removal of that male. It is likely that this problem could be further exacerbated if males are repeatedly shot in the same area, perhaps because it offers ease of access to the hunter.

As a strategy of last resort managed populations are often augmented by the reintroduction into the wild of stock raised in captivity. During the captive breeding component of these programs failures may be the result of inadequate opportunities for effective courtship, particularly if male–male competition is important and too few animals are available. When young are produced the captive situation often results in a failure on the part of the parent to raise them. In these situations animals may be raised by a surrogate species, or by humans. This leads to the risk that they will imprint upon an inappropriate model "parent" and as adults will exhibit inappropriate reproductive behaviors. For example as a result of experiments that involved using sandhill cranes (*Grus canadensis tabida*) to foster whooping cranes (*Grus americanus*), a generation of cranes that had difficulty forming relationships with their own kind was produced. As a conservation "product" these animal were clearly of limited value. In the case of this particular species the problems that imprinting can cause have been successfully overcome by the International Crane Foundation in Wisconsin. Young chicks are reared in isolation using glove puppets that mimic the heads of their parents. The chicks are then moved to a suitable habitat where they are exposed to model cranes and to a human attendant wearing a crane costume. This person guides the birds to suitable feeding areas whilst playing tape recordings of crane contact calls. Occasionally the birds will also be played a crane alarm call to coincide with the appearance of an uncostumed human just to make sure that they will learn

Concept
Imprinting

As a concept imprinting was first described in birds. It refers to a particular form of learning that occurs during a usually very short **sensitive period** early in the life of an individual. At this time critical information like species identity, the identity of one's parent, the identity of suitable reproductive partners, and in some cases the characteristics of an appropriate habitat in which to live, are learned.

to avoid people in future.This is an extremely labour-intensive procedure, but given that the result has been birds able to survive in the wild, to join flocks of wild birds, and to learn appropriate migration routes, it does work.

Summary

In this chapter behavior has been defined and a broad overview to the methodologies that we use when we study it has been provided. Specifically the idea that animal behavior is a robust science has been reinforced through a demonstration that it follows the tried and tested scientific method of observation leading to hypothesis generation and experimental testing. It has been shown that it is essential that we consider behaviors as being adaptations, the products of evolution by natural selection. In addition, the study of animal behavior has been demonstrated to have a clear relevance to several areas of our daily lives.

Questions for discussion

As a group imagine that you have been moved from your terrestrial environment to a life in the deepest ocean. In what ways would you need to modify your behavior to ensure your survival?

Do you think that squid ink because they are afraid? Remember that fear is a human emotion and that this is an anthropomorphic question.

Which of the following is the best way to study behavior? By direct observation, in an experiment, by a cost–benefit analysis, or by the comparative approach?