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The Evolution of Animal Behavior: The Impact of the Darwinian Revolution

> *Darwin's theory of natural selection came very late in the history of thought. Was it delayed because it opposed revealed truth, because it was an entirely new subject in the history of science, because it was characteristic only of living things, or because it dealt with purpose and final causes without postulating an act of creation? I think not.* Darwin simply discovered the role of selection, a kind of causality very different from the push-pull mechanisms of science up to that time. *The origin of a fantastic variety of living things could be explained by the contribution which novel features, possibly of random provenance, made to survival. There was little or nothing in physical or biological science that foreshadowed selection as a causal principle.*
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> —B. F. Skinner (1974, p. 36; emphasis added)

People and animals are most remarkable for the things they do. Inanimate objects and forces certainly can impress us, as when a tornado plows through an American prairie town, a volcano erupts in Indonesia, an earthquake wreaks havoc on a Japanese city, or a comet pays a visit to our corner of the cosmos. But most of the objects that we encounter tend to stay in one place unless pushed or pulled in some way by an animal or person.

Living animals and people are different. They can burrow, crawl, walk, run, hop, climb, swim, and even fly to get where they want to go. Many animals engage in complex rituals for attracting mates and employ clever tricks for finding food, avoiding enemies, and raising their young. They build elaborate structures such as spider webs, beehives, coral reefs, bird nests, and beaver dams to provide shelter and to obtain food and store it for themselves and their associates. Some even make and use tools. One particular species, *Homo sapiens*, has transformed a considerable portion of the earth's surface, covering it with farms, highways, parking lots, houses, shopping centers, and skyscrapers.

Watching all this activity, the curious mind must wonder why all these organisms do what they do. Further reflection suggests that there are really two different types of why questions to consider about the behavior of animals and humans. One concerns immediate or *proximate* explanations. In the previous chapter we learned how seeing animate behavior as the means by which organisms control perceived aspects of their environment provides one set of answers to why questions. A cybernetic, control-system perspective allows us to understand purposeful behaviors in terms of the goals they achieve, such as attracting mates, obtaining food, finding (or building) shelter, avoiding enemies, or caring for offspring.

But we have also seen that this goal-based view does not address the ultimate questions having to do with why such goals (and the perceptual control systems that serve them) appeared in the first place. This is a particularly interesting question when we consider the many complex behaviors (and their consequences) of animals and humans.

This chapter focuses on these questions concerning animal behavior and chapter 8 deals with human behavior. We will see how the proposed answers go beyond the model inherited from Newtonian physics to arrive at a very different type of explanation first proposed by a reclusive English naturalist well over a hundred years ago.

The How and Why of Animal Instincts

When we observe the actions of animals we notice two rather distinct types of behaviors. One type consists of acts that every individual of a given species is somehow able to perform without first having to experience them performed by others, and without being in any way guided or instructed in them. Thus a mother rat will build a nest and groom her young even if she is raised in total isolation and has never seen other female rats engage in those acts (Beach 1955). The behaviors involved in the caterpillar's spinning a cocoon, the spider's weaving a web, the beaver's constructing a dam, and the honeybee's sculpting a honeycomb are additional examples of complex behavior that seem to be somehow built into these organisms.

The other type of behavior consists of acts that appear to be influenced by an animal's own particular experiences, and it is here that we notice striking differences in individuals of the same species. A circus performance shows us what dogs, bears, horses, lions, tigers, and elephants can do when provided with certain types of experiences. Dogs do not normally walk upright on their hind legs, bears are not to be seen riding motorcycles through the woods, or seals balancing beach balls on their noses in the Arctic. Yet these creatures can perform these and other unnatural acts if given a special type of environment provided by a circus and its animal trainers.

Similarly, whereas all normal, healthy children manage to breathe, laugh, cry, walk, and even talk without explicit instruction, such is not the case for reading, writing, mathematics, and music performance skills. The development of these latter abilities normally requires many years of explicit instruction coupled with many long hours of practice. Of the two types of behaviors, the first is typically referred to as *instinctive*, *innate*, or *inherited*, and the second as *learned* or *acquired*.

Two interrelated questions can be asked concerning instinctive behaviors of animals. The first deals with their origin and the second deals with their propagation. It is important to address the questions separately, but we will see that the most satisfactory answer we have to each turns out to be very much the same. We will also see that the answer to the ultimate why question provides an answer to the question of how these behaviors originally came about.

Instinct Through Divine Providence

One view of instinctive animal behavior came to us in the Western philosophical tradition through the writings of Aristotle, Thomas Aquinas, and Descartes, and remained popular and virtually unchallenged through the eighteenth century. This view attributes the source of instinctive behavior to an all-knowing creator. As Thomas Aquinas reasoned in the thirteenth century:

> Although dumb animals do not know the future, yet an animal is moved by its natural instinct to something future, as though it foresaw the future. Because this instinct is planted in them by the Divine Intellect that foresees the future. (1265–1273/1914, p. 470)

Later in the eighteenth century the views of followers of Aristotle and those of Descartes differed in many respects concerning animal behavior. But like Thomas Aquinas they agreed that complex animal behavior could be explained by an appeal to instincts that they understood as blind, innate urges instilled by God for the welfare of his creatures.

It is within this tradition of Christian thinking that we find William Paley (1743–1805), an English archdeacon, theologian, and philosopher. The Reverend Paley saw in the instinctive behavior of animals convincing evidence for the existence, goodness, and wisdom of God. He made his point by emphasizing those behaviors that could not possibly have been the result of learning during the lifetime of the organism. Thus he described (1813, p. 306) how moths and butterflies

> deposit their eggs in the precise substance, that of a cabbage for example, from which, not the butterfly herself, but the caterpillar which is to issue from her egg, draws its appropriate food. The butterfly cannot taste the cabbage—cabbage is no food for her; yet in the cabbage, not by chance, but studiously and electively, she lays her eggs. . . . This choice, as appears to me, cannot in the butterfly proceed from instruction. She had not teacher in her caterpillar state. She never knew her parent. I do not see, therefore, how knowledge acquired by experience, if it ever were such, could be transmitted from one generation to another. There is no opportunity either for instruction or imitation. The parent race is gone before the new brood is hatched.

Paley emphasized that if the animal has no opportunity to learn behaviors that are essential to the survival and continuation of a species, the originator of the behaviors must be God. From this supernatural perspective the question of transmission of behaviors to the next generation simply does not arise, since the behaviors are an integral part of the organism as designed by its creator.

Although such supernatural accounts are no longer held by behavioral scientists, providential thinkers such as Paley must be credited for noticing an important characteristic of these behaviors—that they are essential to the survival and reproductive success of the animal, even though it is unlikely that the animal is mindful of their ultimate function. The providentialists saw the mind of God as the explanation, but other scientists of the nineteenth century were seeking more naturalistic, materialist explanations.

Instinct Caused by the Environment

The work of Charles Darwin's grandfather, Erasmus Darwin (1731–1802), offers one materialist alternative to the providential view of instinct. Erasmus Darwin's annoyance with that view can be seen in his observation that from this perspective, instinct "has been explained to be a kind of inspiration; whilst the poor animal, that possesses it, has been thought little better than a machine!" (quoted in Richards 1987, p. 34). He and other "sensationalists" of the time emphasized the role of *sensory* experience. They believed that all behavior was based on the experience and intelligence of the individual organism, and described ways in which apparently instinctive behavior could be explained as such. But this explanation fared less well with behaviors performed immediately after hatching or birth. A French naturalist's theory appeared, at least initially, to do better.

Although early in his career Jean-Baptiste Lamarck (1744–1829) believed that all species had originally come into existence in much the same form as he observed them during his lifetime, he eventually accepted and promoted a theory of transformation by which over long periods of time organisms could change into new species. He also formulated a materialistic account of how the habits of animals of one generation could be changed into the instincts of their descendants, an account that bypassed Paley's God[1] and proposed instead mechanisms of environmental influence on organisms and their response to these factors.

According to Lamarck, changing environmental conditions forced organisms to change their habits. These changed habits involved increased use of certain body structures and organ systems along with the decreased use of others, with resulting organic changes being passed on to succeeding generations. Since behavior is clearly influenced by biological structures including internal organs and appendages, the inheritance of such modified structures would result in the instinctive behavior dependent on the structures in succeeding generations. In this way Lamarck attempted to provide explanations both for the origin and transmission of new instinctive behaviors.

This materialist theory was well in keeping with the growing scientific naturalism of the nineteenth century, as was its one-way cause-effect character. The latter can be seen in its three necessary components. First, the environment causes a change in an animal's behavior (imagine a bird's environment becoming drier, so that it now has to find, crack open, and eat bigger and harder seeds than it did when smaller, softer seeds were more readily available).[2] Second, this change causes structural changes in the animal, both a result of the new behavior and facilitator of it (the bird develops a larger, more powerful beak, better able to crack bigger and tougher seeds). Third, these changes in structure and behavior are transmitted to the animal's offspring who thereby inherit the new high-performance beak and the (now instinctive) behaviors for using it. As Lamarck explained (1809; quoted in Løvtrup 1987, p. 53),

> Everything which has been acquired . . . in the organization of the individuals in the course of their life, is preserved through the reproduction, and is transmitted to the new individuals which spring from those who have undergone these changes.

In his view the environment causes changes in behavior, which cause changes in body structures, which in turn cause changes in the germ (egg and sperm) cells, which cause instinctive behavior in offspring. This causal chain from environment to behavior to bodily structure to germ cells to offspring has the ultimate effect of producing new organisms that possess as instincts the acquired habits of their parents.

But although Lamarck's theory successfully avoids a supernatural creator, it runs into serious problems of its own. First, how is it that a changing environment causes animals to assume adaptive behaviors? If soft seeds are no longer available, how does the environment cause the bird to search out and attempt to eat larger, tougher seeds? Particularly problematic in this regard are behaviors that cannot be imagined as the result of individual learning, as the egg-laying behavior of the moth and butterfly (in Paley's observation quoted above).

Second, according to Lamarck's principle of use and disuse, body parts that are used a great deal will develop and become more adapted to such use, whereas those that are not used will shrink and atrophy. But, to remain with our example, how will a bird's attempting to crack a seed that is too big and tough for its beak cause its beak to become bigger and stronger? We all know from our attempts to repair things that using a tool that is too small or weak will usually ruin the tool (and often what we are trying to fix), not make it bigger and stronger. As another example, consider that our shoes do not grow thicker soles the more we walk in them, nor do they become thin by being left unused in the closet. On the contrary their soles wear out from extended use and maintain their original condition only if not used. Now it is clearly the case that among living organisms we see what appear to be Lamarckian effects of use and disuse, as when someone begins to exercise and develops larger muscles and then stops and loses them again. But something more than a direct physical cause-effect phenomenon must be involved here because these adaptive results are not what we see happening in the objects we use where continued use leads to wear and tear and eventual breakdown, but disuse results in preservation.

Third, we must consider if the structural and behavioral changes an organism undergoes during its lifetime actually cause similar changes in its offspring. Lamarck was so convinced that such acquired changes were passed on to offspring that he wrote that the "law of nature by which new individuals receive all that has been acquired in organization during the lifetime of their parents is so true, so striking, so much attested by facts, that there is no observer who has been unable to convince himself of its reality" (1809; quoted in Burkhardt 1977, p. 166).

Indeed, the belief that acquired characteristics were inherited by one's offspring was well accepted in Britain and Europe throughout most of the nineteenth century, yet it turns out that there was never any good evidence for it whatsoever. A man and a woman who develop large and strong muscles either through hard physical labor or sport do not have a son or daughter who is born with similarly well-developed muscles. A man and woman who both become proficient pianists will not produce a child who can instinctively play the piano. And as German embryologist August Weismann (1834–1914) rather gruesomely demonstrated, chopping off the tails of several generations of mice does not produce successive generations of tailless mice or even mice with shorter tails. Weismann consequently made an important distinction between those cells of the body that are passed on to the next generation in reproduction (germ cells) and other cells that are not (somatic cells). He held that changes to somatic cells could in no way cause corresponding changes to germ cells. Separation of these two types of cells remains today as a generally recognized barrier to Lamarckian inheritance of physical or behavioral characteristics so that the habits acquired by one generation cannot become innate instinctive behaviors in a later one.[3]

So we see that while Lamarck attempted to provide a naturalistic, nonprovidential account of instinctive behavior, his theory (referred to by some as *instructionist*, since it assumes that the environment can somehow directly cause or instruct adaptive changes in behavior) failed at every posited cause-effect relationship, from environment to behavior, from behavior to somatic cells, and from somatic cells to germ cells. Clearly, a radically different explanation was needed.

Instinctive Behavior as Naturally Selected

Just such a radically different explanation was proposed by Charles Darwin. Darwin's initial attempt to explain instincts had much in common with Lamarck's theory. He believed that beneficial habits that persisted over many generations would make heritable changes in the organism leading to instinctive behavior in later generations. Gradually, however, he became dissatisfied with the idea of inherited habits as the sole explanation for instinctive behaviors, particularly when he realized (as Paley had before him but Lamarck apparently had not) that many of these behaviors (such as the moth laying eggs in cabbage) could not have originated as habits. Another example is provided by British natural theologian Henry Lord Brougham who wrote in 1839 about the female wasp who provides grubs as food for the larvae ("worms") that will hatch from its eggs "and yet this wasp never saw an egg produce a worm—not ever saw a worm—nay, is to be dead long before the worm can be in existence—and moreover she never has in any way tasted or used these grubs, or used the hole she made, except for the prospective benefit of the unknown worm she is never to see" (quoted in Richards 1987, p. 136). We know that Darwin was intrigued by this observation since he wrote in the margin of Brougham's book "extremely hard to account by habit." It was, in fact, more than "extremely hard" since "an act performed once in a lifetime, without relevant experience, and having a goal of which the animal must be ignorant—this kind of behavior could not possibly have arisen from intelligently acquired habit" (Richards 1987, p. 136).

So in keeping with his theory of natural selection for the origin of species, Darwin began to see instincts not as results of inherited useful habits but as consequences of the reproductive success of individuals already possessing useful habits (although he never completely abandoned the former idea). Natural selection thus provided an explanation for instinctive behaviors that never could have originated as habits, such as the wasp's egg-laying behavior.

Darwin's selectionist theory of instinct differs fundamentally from Lamarck's one-way cause-effect (or instructionist) theory of evolution. For Lamarck, the environment somehow caused (directed, instructed) adaptive changes in organisms that were passed on to future generations. It is this direct, causal effect of environment on organism that constitutes the one-way push-pull character of Lamarckian theory. But in Darwin's selectionist theory, individuals of a species naturally vary their behavior, with the environment playing no active, instructive role in causing this variation. Instead, the environment's role is restricted to that of a type of filter through which more adaptive behaviors pass on to new generations and less adaptive ones are eliminated. Darwin's selectionist explanation is distinctly different from Lamarck's in that the behaviors offered to the scrutiny of natural selection are not caused by the environment but are rather generated spontaneously by the organisms.[4]

An example may be useful here. Among Darwin's finches in the Galápagos Islands, one particular species, appropriately called the vampire finch, foregoes the vegetarian diet of seeds and nuts of other finches and prefers instead the taste of blood, obtaining it by perching on the back of a booby (a larger bird) and jabbing it with its pointed beak until it draws blood (see Weiner 1994, p. 17). Since this is the only bloodthirsty finch on the islands, it is reasonable to assume that the species descended from birds that did not drink blood. But because of natural variation in the behavior of its ancestors, some of these finches must have tried pecking at other birds and found some nutritional advantage from the practice, producing more offspring than birds that tried pecking at other objects. Within any one generation, these birds would show natural variation in feeding behavior; and after many generations of variation and selection the vampire finch that we know evolved. So unlike Lamarck's theory, which assumed that an animal's learned behaviors were inherited by its offspring, Darwin's selectionist account of instinctive behavior can work only with a *population* whose individuals already vary in their behavior, selecting behaviors leading to greater survival and reproductive success. Darwin, unfortunately but understandably, hadn't a clue as to why individuals of a species varied in form or behavior, or how these variations could be inherited by following generations. Our current knowledge of genetics and the molecular basis of mutation and sexual reproduction provides answers to these questions and strong support for Darwin's conclusion.

But one particularly thorny problem remained for Darwin concerning instinct, that of the evolution and behavior of neuter insects. The *Hymenoptera* order of insects includes bees and ants together with some wasps and flies. Many of these insects live in well-structured societies where survival depends on a specialized division of labor among the members that is reflected in different castes, such as the queen, drones, and workers in a beehive. Particularly intriguing and troublesome for Darwin's theory of natural selection was the fact that worker castes are often made up of insects that are sterile and therefore have no genetic means of passing on their instinctive behaviors to the next generation of workers. This posed a serious threat to Darwin's theory, as he was well aware.

A solution came after he learned how cattle were selected for breeding to produce meat with desirable characteristics. As described in a book by William Youatt published in 1834 and read by Darwin in 1840, animals from several different families would be slaughtered and their meat compared. When a particularly desirable type of meat was found, it was, of course, impossible to breed from the slaughtered animal. But it was possible to select for breeding cattle most closely related to it to produce the desired meat. In like manner, a colony of insects that produced neuters that helped the survival of the community (say, by taking care of young, providing food, or defending against enemies) would be naturally selected to continue to produce such neuter insects even if the neuter insects themselves could not reproduce. Darwin concluded that "this principle of selection, namely not of the individual which cannot breed, but of the family which produced such individual, has I believe been followed by nature in regard to the neuters amongst social insects" (1856–1858/1975, p. 370).

The concept of kin and community selection became powerful in understanding the evolution of altruistic behavior (to which we will return shortly) and it provided Darwin with an explanation for complex and useful instinctive behaviors that could not be explained by Lamarckian inheritance. But where the inheritance of acquired habits seemed conceivable, particularly when Darwin could see no selective advantage for the behavior, he made use of Lamarckian principles. And since for some reason Darwin was unable or unwilling to see survival or reproductive advantages accruing from the expression of emotions, he explained these as inherited useless habits that existed only because they accompanied more useful ones.

Despite the enormous impact that Darwin had on the life sciences during his own lifetime, he had relatively little immediate impact on the scientific study of animal behavior. One reason for this has to do with methodological difficulties of both naturalistic and experimental research on animal behavior. Another was the heavy use of anecdotal evidence and anthropomorphic interpretation practiced by George Romanes (1848–1894), Darwin's young disciple and defender who wrote extensively about animal behavior and mind from a Darwinian perspective while maintaining belief in the inheritance of acquired habits.

It was not until the 1930s that a serious attempt to study animal behavior from evolutionary and selectionist perspectives was begun. Konrad Lorenz (1903–1989) grew up sharing his family's estate near Vienna with dogs, cats, chickens, ducks, and geese. His observations in this setting eventually led to the founding of the field of ethology, which he defined as "the comparative study of behaviour . . . which applies to the behaviour of animals and humans all those questions asked and methodologies used as a matter of course in all other branches of biology since Charles Darwin's time" (1981, p. 1).

As suggested by this definition, Lorenz was primarily interested in finding evolutionary explanations for instinctive behavioral patterns characteristic of a species. For example, it was brought to his attention that greylag geese reared by humans would follow the first person they had seen after hatching in the same way that naturally hatched goslings waddled after their real mother. Lorenz confirmed these findings and extended them to several other species of birds. This pattern of behavior, resulting from a type of bonding with the first large moving object seen by the hatchling, he called imprinting, and it is for this finding that Lorenz is still best known.

By extending Darwin's theory of natural selection to animal behaviors observed in the field, Lorenz posited a genetic basis for specific behaviors that was subject to the same principles of cumulative variation and selection that underlie the adapted complexity of biological structures. In the case of the greylag goose, goslings that maintained close contact with the first large moving object they saw (which would normally be their own mother) would be in a better position to enjoy her protection and nurturance. Consequently, they would be more likely to survive and to have offspring that would similarly show this behavioral imprinting than goslings lacking this behavioral characteristic. In much the same way that we now understand how a tree frog can become so well camouflaged over evolutionary time through the elimination by predators of individuals that are less well camouflaged, we can understand how instinctive behavior can be shaped through the elimination of individuals whose behaviors are less well adapted to their environment.

Another example of Lorenz's conception of instinctive behavior is the egg-rolling behavior of the greylag goose. When the goose sees that an egg has rolled out of her nest, she stands up, moves to the edge of the nest, stretches out her neck, and rolls the egg back into the nest between her legs, pushing it with the underside of her bill. Lorenz called this a "fixed motor pattern" (1981, p. 108), that is, a sequence of actions generated in the central nervous system of the goose that is released or triggered by the sight of an egg (or other egglike object) outside the nest. In other words it is a fixed sequence of actions released by a specific type of stimulus. The purpose of this instinctive act is clearly to return the egg to the security of the nest, and it is easy to appreciate its value for the continued survival of the species.

But a serious problem with this concept becomes apparent when one realizes that an invariant pattern of actions will not be successful in returning a wayward egg to the nest unless all environmental conditions are exactly the same for each egg-rolling episode. This is, of course, the same problem with all one-way cause-effect theories. Instead, for the goose to be consistently successful in returning an egg to her nest she must be able to modify her behavior not only from episode to episode but also within each episode to compensate for variability in conditions and disturbances that she inevitably encounters, such as differences in the distance between herself and the egg at the beginning of the behavior, and irregularities in the terrain between the egg and the nest. This is another instance of consistent outcomes requiring variable means that William James described as the essence of purposeful behavior. And it is for this reason that Lorenz's stimulus-response analysis ultimately fails to explain the typical success of instinctive actions.

Many good examples of the variability of instinctive behaviors that are directed to fixed, consistent outcomes can be found in a book published in 1945 by E. S. Russell entitled *The Directiveness of Organic Activity*. Here are just three.

1. The larva of the caddis fly (*Molanna*) builds itself a protective case made of grains of sand. If this case is overturned, it will try a remarkable range of behaviors to right it. It will normally first extend its body out of the tube of the case and grip the ground with its forelegs in an attempt to flip the case over sideways. If this does not work, the larva will reverse its position and make a hole in the tail end of the case. Then it will either extend its body out the rear of the case and attempt to twist the case around the long axis of its body, or reach under the case and flip the case over its head. If the ground is very fine, loose sand, the larva will produce silk to bind grains together to make a firmer platform for righting its case. Or it may try to pull its case to another spot where the ground provides better traction. If all this fails, the caddis larva may bite a piece off the roof of the case and use that as a platform for its righting attempts, or even remove an entire wing of the case to flip it over. If the larva is still unsuccessful after several hours of work, it will abandon its case and build a new one somewhere else (Russell 1945, pp. 123–124).

2. The burying beetle (*Necrophorus vestigator*) is so called because it buries small dead animals on which it deposits its eggs. These insects often cooperate in this endeavor, working together to remove soil from under the animal so that it sinks into the earth. If the corpse lies on grass-covered soil, they will bite through the impeding stems and roots. If a mat of woven raffia is placed under the corpse, the beetles will cut through that as well. If a dead mole is tethered to the ground by raffia strips, the beetles will start their usual digging, but when the mole does not sink they will crawl over it, find the tethers, and cut them. If a small mouse is suspended by wires to its feet, the beetles will bite through the mouse's feet. If the suspended mouse is large, the beetles will be unsuccessful, although they may work for nearly a week before abandoning the project. Russell also

reported that when a dead mouse was placed on a brick covered with a thin layer of sand, the beetles spent a few hours trying unsuccessfully to bury it. Then they spent several more hours pulling the mouse in various directions until it was finally dragged off the brick and buried (1945, pp. 125–126).

3. The shore crab (*Carcinus maenas*) moves its legs in a fixed progression when walking forward. If one or more legs are amputated, it is still able to move about, but the order of movement of the remaining legs is changed, clear evidence that locomotion is not achieved by a fixed motor pattern that is inherited and unmodifiable. Similarly, "an insect which has lost a leg will at once change its style of walking to make up for the loss. This may involve a complete alteration of the normal method, limbs which were advanced alternately being now advanced simultaneously. The activities of the nervous system are directed to definite end, the forward movement of the animal—it uses whatever means are at its disposal and is not limited to particular pathway" (Adrian; quoted in Russell 1945, pp. 127).

So it appears that Lorenz was mistaken in insisting on innate fixed motor patterns as the basis for instinctive behavior. But he must nonetheless be acknowledged as the first to attempt to provide a Darwinian account of species-specific behavior patterns, and he was recognized for his achievement in 1973 when he shared a Nobel prize with fellow ethologists Nikolaas Tinbergen and Karl von Frisch. In the same way that biologists constructed evolutionary trees (phylogenies) by comparing the anatomical similarities and differences among living organisms and fossils, Lorenz used patterns of instinctive behavior, basing his comparative study "on the fact that *there are mechanisms of behavior which evolve in phylogeny exactly as organs do* (1981, p. 101). His evolutionary perspective also led him to emphasize that understanding animal behavior involved appreciating its purposefulness in preserving the species, its role in the entire repertoire of the animal's activities, and its evolutionary history.

Whereas Lorenz was successful in going beyond a one-way cause-effect view of the origins of instinctive behaviors, he nonetheless maintained a rather stimulus-response view of the actual behaviors performed. He concluded that evolution works in a selectionist manner, resulting in the emergence of those organisms with adaptive stimulus-response systems that contribute to survival and reproductive success. He was apparently unaware of the need for and existence of an alternative to this account that was as necessary as his selectionist explanation of its origins. And he would have no doubt been intrigued by the type of behavior generated by the Gather computer simulation described in chapter 6 that provides a striking simulation of the mother-following behavior of his beloved geese.

Foundations and Misconceptions

Lorenz placed the study of instinctive animal behavior within a thoroughly Darwinian framework, but his work initially had rather limited impact, especially in the United States. One reason for this was his association with the Nazis during World War II (see Richards 1987, pp. 528–556). Another reason was the then-dominant behaviorist paradigm in North America that was much more interested in learned behavior of rats and pigeons in artificial experimenter-controlled laboratory settings than in naturally occurring behavior of a variety of animals in their natural habitats. But Lorenz's Darwinian initiative eventually had an important impact on both sides of the Atlantic.

Before discussing this impact, it will be useful to outline in a bit more detail the necessary components of a standard evolutionary view of instinctive animal behavior. For evolution by natural selection to occur, three conditions must be met. First, there must be variation in the population of organisms making up a species. Although we may be most accustomed to thinking of this in terms of the physical make-up of organisms (morphology) such as size or coloration of body parts, variation in species-typical behavior can also be observed among individuals of a species, such as in feeding and mating behaviors.

Second, this variation in behavior must have consequences for reproductive success. Measured as the number of viable offspring produced, it requires both survival to the age of reproductive maturity (for which obtaining food and avoiding predators and serious diseases are essential) as well as the ability to find mates and, for some species such as birds and mammals, feed and protect one's offspring.

Finally, variation in behavior influencing reproductive success must be heritable; that is, it must be able to be passed on to the next generation.

Although this inheritance of behavior need not be limited to genetic inheritance (since forms of cultural learning are also possible for many animal species), evolutionary accounts usually emphasize the genetic component.

The importance that a Darwinian view of instinct ascribes to survival and reproductive success should come as no surprise for two reasons. First, if variation in behavior exists and behavior can be inherited by the next generation, clearly those behaviors that were not conducive to survival and reproduction would eventually be eliminated from the species. Any male squirrel that attempted to mate only with pine cones or engaged only in oral sex with other squirrels would simply not have any descendants to continue these innovative (for squirrels) sexual practices. Similarly, any mammal (other than humans or mammals raised by humans) that refused to nurse at its mother's breast would not survive long enough to find a mate and produce nipple-avoiding offspring of its own.

Second, the survival or reproductive function of many striking instinctive behaviors that we see among animals are rather obvious. The spider spins an intricate web. Why? If we watch what happens after the web is complete the answer becomes obvious—to obtain food. A wasp paralyzes a caterpillar with her venom and buries it alive with her eggs. Why? So that her hatched larvae will have fresh food (and not decayed, putrid flesh) when they emerge from their eggs. The male ruff, a European shore bird, spreads its wings, expands the collar of feathers around his neck, and shakes his entire body when a female ruff comes in sight. Why? To attract a mate. The parasol ant carries bits of freshly cut leaves back to its nest. Why? To grow a certain type of fungus that it uses for food. Countless other examples could be given, and indeed much of the appeal of books, films, and television programs about nature lies in their portrayal of such instinctive behaviors that have obvious survival and reproductive functions. And although we certainly need not assume that these animals are in any way conscious or aware of the survival, reproductive, or evolutionary consequences of their actions, the survival or reproductive role that most instinctive behaviors play is either initially obvious or made clear by further research into the life and habits of the particular species.

An evolutionary perspective on behavior can be misleading in at least three ways, however. The first has to do with Lorenz's original conception of instincts as fixed motor patterns. As we saw in the previous chapter, invariant sequences of actions cannot be adaptive in an environment containing unpredictable disturbances. An assembly-line robot may be able to assemble an automobile part by repeating the same motion over and over again, but it is successful only to the extent that its environment is carefully controlled to prevent disturbances from affecting the production line. The real world of living organisms, with its changing weather conditions and the presence of many other (often competing and hostile) organisms, is anything but a carefully controlled production line. In its natural environment an animal's action patterns cannot remain invariant if they are to be functional; rather its behavior must compensate for such disturbances. It is now recognized by at least some ethologists that animal instincts are modifiable by feedback received during execution of behaviors (see Alcock 1993, pp. 35–37).

We saw in chapter 6 how organisms organized as networks of hierarchical perceptual control systems can be effective in producing repeatable, reliable outcomes despite unpredictable disturbances. For an evolutionary perspective on instinctive behavior to make sense, we have to discard the commonly accepted notion that specific behaviors can evolve and be usefully inherited, and instead recognize that it is perceptual control systems and reference levels that are selected and fine-tuned for their survival and reproductive value across generations. We also have to be on guard against the behavioral illusion demonstrated in the previous chapter that makes it seem as though environmental factors (or stimuli) cause behavior, when in fact organisms vary their behaviors to control aspects of their perceived environment.

The second potential danger lurking in evolutionary accounts of instinctive behavior is the tendency to regard genes as *determiners* of instincts and consequently to regard instinctive behaviors as essentially inborn or innate. We know that genes do influence an organism's behavior, as it has been shown repeatedly and clearly that certain genetic differences are associated with striking behavioral differences. For example, changing a single gene in the fruit fly *Drosophila melanogaster* results in male flies referred to as *stuck* since they do not dismount from females after the normal period of copulation (Benzer 1973). Another single-gene difference affects the daily activity cycle of fruit flies. Normally this period is twenty-four hours long, but flies with a particular variation of a gene (referred to as an *allele*) have no fixed activity cycle. Flies with a second type of allele have shortened nineteen-hour activity cycles, and flies with a third allele have lengthened cycles of twenty-nine hours (Baylies et al. 1987).

But whereas individual genes and groups of genes have an important influence on behavior, they alone cannot determine behavior since all development and consequent behavior depend on the interaction of genes and environmental factors, the latter including physical factors such as nutrition and temperature as well as various sensory experiences. In this respect, genes can be thought of as a type of basic recipe for building an organism, while the environment provides the necessary materials and additional crucial information in the form of certain sensory experiences. When viewed in this way, questions concerning whether a given behavior depends more on nature or nurture can be seen to be meaningless, as would be asking whether the appearance and taste of an apple pie depend more on the recipe or on the ingredients. Of course, both are crucially and 100 percent important, since without the recipe (or equivalent knowledge of apple-pie baking) the ingredients are useless, as would be the recipe without the ingredients.

Some striking examples of the necessary interaction of genetic and environmental factors in determining behavior have been provided by the common laboratory rat. A mother rat will normally build a nest before bearing offspring and then groom her newborn pups. That she performs these behaviors even if she is raised in total isolation from other female rats, and so has never seen other rats engage in such behaviors, is the reason that such activities are referred to as instinctive. Nonetheless, certain experiences are necessary for these behaviors to take place. For example, when provided with appropriate nesting materials a pregnant rat will not build a nest if she had been raised in a bare cage with no materials to carry in her mouth. Also, a mother rat will not groom her young if she had been raised wearing a wide collar that prevented her from licking herself (Beach 1955). And failure to groom her babies can have serious consequences, since a newborn rat cannot urinate until its genital area has been first so stimulated, resulting in burst bladders for the unfortunate unlicked pups (Slater 1985, p. 83).

These and other findings indicate that instincts are not behaviors that are somehow completely specified in the genome of an animal, as stated by Lorenz. Rather, they are species-typical behaviors that emerge from the interaction of an animal's genes with the usual environmental conditions. As research shows, a change in either genes or environment can result in a change in instinctive behavior.

A final danger to guard against in taking an evolutionary view of animal instincts is thinking that all instinctive behaviors must be well adapted to the organism's present survival or reproductive needs. Although most instincts appear to have current survival or reproductive value, it does not follow from evolutionary theory that *all* such behaviors do. Certain behaviors may be neutral or even maladaptive side effects of other adaptive behavior. Reasons have been advanced for how certain forms of homosexual animal behavior can improve reproductive success; for example, cows mounting other cows may signal to nearby bulls that the cows are sexually receptive (see also Bagemihl 1999 for a comprehensive review of animal homosexuality). Research suggests, however, that at least some forms of homosexuality, such as that among female macaque monkeys, serves no clear direct or indirect reproductive function and may be simply a side effect of natural selection of animals with high sex drives (see Adler 1977). Such "useless" behavior may be tolerated by natural selection if it has negligible effects on ultimate reproductive success. But we should not expect it to persist for long if it has negative effects on survival and reproduction unless it appears as an unavoidable side effect of some other adaptive behavior that compensates for the effects of the maladaptive one.

In addition, because of the long periods of time required for evolution to shape adaptive instinctive behaviors, there is no guarantee that such behaviors are still adaptive today. Moths used the moon and stars to navigate during their nightly forays for millions of years when these celestial bodies were the only nocturnal sources of light. But the appearance of countless sources of artificial illumination in areas inhabited by humans now has moths spending the night flying in dizzy circles around electric light bulbs, into flames, or onto the electrocuting grid of bug zappers. The distinction between the environment in which a behavior evolved and the current environment where it may be less well suited will become particularly important when we consider human behavior in the next chapter.

The Problems of Altruism and Cooperation

Keeping in mind these potential problems of evolutionary accounts of behavior, we can now turn to some other aspects of animal behavior that first challenged and then showed the value of such an approach. The role of instincts in promoting the survival and reproduction of individual organisms (and therefore continued existence of copies of their genes in future generations) puts a distinctive selfish spin on instinctive behavior. It would initially seem that any behaviors that were helpful to others but costly to the originator should simply not evolve as instincts.

So-called *altruistic* acts, such as sharing food or putting oneself at risk by crying out to warn others of an approaching predator, would appear to reduce the ultimate reproductive success of the altruistic donor while increasing that of its recipients and genetic competitors. Yet these and other apparently altruistic behaviors are commonly observed among animals. A ground squirrel emits an alarm call upon noticing a predator, thereby warning other squirrels but putting itself at greater risk of predation (Alcock 1993, p. 517). A vampire bat regurgitates blood for a neighbor that was unsuccessful in finding its own meal (Slater 1985, p. 178). It was this problem of accounting for the evolution of altruistic acts that attracted the attention of a new generation of British and American biologists in the 1950s, 1960s, and 1970s who were interested in solving this and other evolutionary puzzles about animate behavior.

Among these scientists was British geneticist, biometrician, and physiologist J. B. S. Haldane (1892–1964) who in 1955 provided an important clue. He noted that a gene predisposing an animal to save another animal from some danger, with the potential "hero" running a 10 percent risk of being killed in the attempt, could spread in the population through natural selection if the animal thus saved were a close relative of the hero, such as an offspring or sibling. This is because a closely related individual would have a good chance of sharing the same altruistic gene as the hero, so that a copy of the gene in question would likely be saved even if the hero were to perish by his actions. Haldane also noted that such a gene could even spread, although not as quickly, if the saved individual was more distantly related to the hero, such as a cousin, niece, or nephew. "I am prepared to lay down my life for more than two brothers or more than eight first cousins" (reported in Hamilton 1964, 1971, p. 42) was his way of summarizing this phenomenon.

This was the beginning of the formulation of what is known as *kin selection*, the idea that a gene is not "judged" by natural selection solely on its effects on the individual who carries it, but also on its effects on genetically related individuals (that is, kin) who are also likely to carry a copy of the gene. From this perspective, altruistic behavior toward kin can be understood as a form of selfishness on the part of the gene necessary for the behavior, since the related individuals who receive assistance are likely to carry a copy of the same gene and pass it down to their offspring.

As there are different degrees of relatedness (the closest being identical twins; followed by offspring and full siblings; then half siblings, grandchildren, nieces, and nephews; followed by first cousins, etc.) it would make evolutionary sense for altruistic behavior to be scaled according to the degree of relatedness so that it would most likely be directed toward the closest relatives. British biologist William Hamilton developed these ideas in papers published in 1963 and 1964, noting that evolution should be expected to bias altruistic behavior toward close relatives and therefore also select for the ability of altruistic animals to discriminate close relatives from more distantly related individuals so that their acts could be preferentially directed toward the former and not the latter.

But whereas kin selection is an important factor in the evolution of behavior, we also see apparently altruistic acts directed toward unrelated individuals.[5] How can evolution account for this?

The modern answer was first hinted at in 1966 by American biologist George C. Williams in *Adaptation and Natural Selection*, a book that became a classic in evolutionary biology. Williams suggested that beneficent behavior toward another unrelated individual that was initially costly for the donor (for example, giving away food) could in the long run be advantageous if the favor was later returned.

This idea was further developed and refined in 1971 by American biologist Robert Trivers with the theory of *reciprocal altruism*, as in "I'll scratch your back if you'll scratch mine." Here, cooperative and seemingly altruistic behavior can evolve among individuals who are not closely related. Indeed, it can also account for mutually advantageous relationships observed between different species, such as that between cleaner-fish and the larger fish that they clean. During cleaning, the cleaner-fish obtains a meal and the cleaned fish gets rid of troublesome parasites, but only as long as it refrains from gobbling down the much smaller cleaner-fish. Through such symbiotic behavior both cleaner and cleaned profit in ways that would not be possible without mutual co-operation (see Trivers 1971).

Another topic much studied by researchers taking an evolutionary approach to animal behavior is sex differences. No matter how successful an animal is in finding shelter and food and defending itself from disease and enemies, none of these achievements can have evolutionary significance if the animal does not reproduce and have offspring that survive until they in turn reproduce. For sexually reproducing species, reproduction means finding a mate, and offspring of many species require some form of parental care.

The importance of finding a mate and factors determining mate selection were first pointed out by Charles Darwin in *The Descent of Man and Selection in Relation to Sex*, published in 1871. Darwin observed that males often compete with each other for access to females and that females in contrast tend to be choosy in their selection of partners, often preferring males with alluring courtship displays or some physical characteristics that could well interfere with their day-to-day survival. Darwin understood that such selection pressure was responsible for the elaborate “ornaments” possessed by males of many species, such as the bright and striking plumage of the paradise bird and peacock, and deer antlers.

But sexual selection and its consequences for animal behavior were largely ignored for the next century until Robert Trivers’s 1972 paper, which drew attention to the fact that sex cells (gametes) produced by males (sperm) are much smaller and more numerous than those produced by females (eggs). An individual male may well provide enough sperm cells (many millions) during a single mating theoretically to impregnate every female of the species. This is in sharp contrast to the females of most species who produce a much smaller number of much larger eggs (in birds, a single egg may equal from 15 to 20 percent of the female’s body weight). This marked discrepancy in potential reproductive potential (being much greater for males) should have important consequences for differences in sexual behavior, and as we will soon see, it does.

Making Darwinian Sense of Animal Behavior

Darwin's theory of evolution by natural selection turned out to be remarkably successful in providing answers to many ultimate why questions about animal behavior. Animal behavior scientists have repeatedly found that behaviors appearing at first quite puzzling often make good sense when seen from the Darwinian perspective, especially when principles of kin selection, reciprocal altruism, and sexual selection are taken into account. Let us take a brief look at some examples that can be understood using these evolutionary principles.

Since Hamilton's formulation of kin selection, many studies of animal behavior yielded results that are consistent with the theory. Parental care for offspring, such as that often observed in birds and mammals (and also practiced by certain species of insects and fish) is one obvious form. In one setting where it might appear difficult for parents to recognize their offspring, the communal cave nurseries of the Mexican free-tailed bat that may contain many thousands of crowded young pups, mothers find and feed their own offspring greater than 80 percent of the time (McCracken 1984). For certain birds whose young receive assistance from nonparents, these helpers are typically closely related individuals such as siblings (Harrison 1969; Brown 1974).

It was mentioned earlier that insects of the order *Hymenoptera* live in societies with a strict division of labor. Particularly intriguing are workers who diligently care for the queen's offspring and yet are sterile and therefore unable to have offspring of their own—certainly an extreme form of altruism. It turns out that these species are *haplodiploid*, meaning that each female receives the normal half of its mother's genes but *all* of its father's genes. Because of this genetic quirk, sterile female workers are actually more closely related to their siblings than they would be to their own offspring!

Similar societies in which most individuals are sterile and raise the offspring of their mother have been found that are not haplodiploid, for example, the naked mole-rat. Kin selection theory would predict that these altruistic individuals should show a very high degree of genetic relatedness to each other so that the altruistic genes they carry have a high probability of also being present in the individuals they assist even though they have no descendants of their own. This fact was found for the naked mole-rat (Reeve et al. 1990).

Examples of reciprocal altruism in which one individual assists another that is not closely related in order to receive some benefit in return (either at the same time or later) are widely reported in studies of animal behavior. The relationship between cleaner-fish and their cooperative hosts was mentioned earlier. Another interesting example is provided by olive baboons (*Papio anubis*). Sexually receptive females of this species are usually closely attended by a single male consort on the lookout for opportunities to mate. A rival male, however, may solicit the aid of an accomplice male who engages the consort in a fight. While distracted, the rival has uncontested access to a female. What is in this for the accomplice who fights but does not mate? He will likely get his chance at mating the next time when his buddy will take his turn in distracting another consort (Packer 1977).

What about differences in male and female behavior related to the roles they play in reproduction, with males' billions of tiny cheap sperm and females' much fewer, much larger, and much more costly eggs? The huge quantity of sperm cells that a male produces means that gaining access to as many mates as possible increases his reproductive success. But this is usually not the case for a female, whose reproductive success depends more on the fate of her fertilized eggs. This would lead us to expect that males should be more eager to mate and less discriminating in their choice of mates than females, who should be more restrained and more choosy in their selection of mates. And this is just what was found across a very wide range of animal species including insects, amphibians, reptiles, birds, and mammals.

A good example of discriminative mate choice is provided by female insects that demand a "nuptial gift" from the male before allowing copulation to take place. The female black-tipped hangingfly (*Bittacus apicalis*) will reject the advances of any male that does not first offer a morsel of food. And the larger the male's gift, the better the male's chances of inseminating the female, since a quickly consumed tidbit may lead the female to cut short the mating process and seek another gift-bearing male (Thornhill 1976). Such behavior puts selection pressure on males to provide larger bits of food since males with little or no gifts are not likely to have their "stingy" genes represented in the next generation, whereas those with larger gifts are more likely to reproduce.

This is just one example of many in the animal world of eager males having to provide resources to females for sperm to gain access to eggs. But it is not always food that is offered. Many female birds will mate only with males that control a food-producing territory. Female bullfrogs prefer mating with the largest males (as indicated by the strength and pitch of their singing), and it is not likely coincidental that the largest males usually control the breeding locations that are best suited to the development of fertilized eggs. Female birds often select males based on their song repertoire, plumage, size, or courtship ritual, which are indicators of health, strength, and parental ability as well as the likely mating success of male offspring fathered by the male (see Alcock 1993, chapter 13, for many similar examples).

But there are some fascinating exceptions to these typical male-female differences in reproductive strategies. In some species we find a complete reversal of the typical sex roles. Among pipefish of the species *Syngnathus typhle* the male receives from the female the eggs he has fertilized and keeps them in his brood pouch until they hatch. Since females can produce eggs more quickly than males can rear them, brooding pouches are in great demand among females. So as one would expect, it is the male pipefish who is picky about his mates, preferring large, well-decorated females who appear to be able to provide many high-quality eggs for him to carry.

Another interesting example of sex role reversal is the Mormon cricket (which, curiously, is neither a cricket nor Mormon but rather a katydid with no known religious preference). The male produces for his mate a large, nutritious meal in the form of what is called a *spermatophore*. Since the spermatophore may weigh as much as 25 percent of his body weight, he can usually produce only one in his short lifetime, thereby limiting his mating opportunity to just one female. Since he invests so much in his single mating, he is choosy, preferring to mate with large females who carry a greater number of eggs, and females compete for access to him.

These examples are of particular interest since they demonstrate that it is not gender itself or any intrinsic property of egg or sperm cells that normally makes males competitors for and females selectors of mates. Rather it is the gender with the higher reproductive costs that is choosy in selecting a mate, whereas the gender with the lower costs is less discriminative and more competitive. The fact that exceptions are so nicely accounted for by the struggle for survival and maximization of reproduction is an indication of the power of the Darwinian perspective on animal behavior.

A particularly striking example that can be explained from an evolutionary perspective involves the grisly act of infanticide. Hanuman langurs are monkeys found in India that live in bands consisting of one sexually active male and a harem of females with their young. Occasionally, the resident male is expelled from the group by another male after a series of violent confrontations. When this occurs, the incoming male attacks and kills the infants that were fathered by the previous resident male.

Many reasons could be proposed for this behavior. Perhaps high testosterone levels left over from fighting result in heightened aggression and attacks on easy victims. Or maybe the new male makes use of the infants as a source of high-protein food after a period of great physical exertion. Or it could be that infanticide is a pathologial reaction to the high stress accompanying the artificially high population densities of langurs in the many locations where they are fed by humans.

An evolutionary explanation, however, would look first at the reproductive consequences of langur infanticide, and these turn out to be considerable. Nursing females provide resources to the offspring of the previous male. In addition, lactating females do not ovulate and so cannot be impregnated by the new male. So by killing the infants the incoming male both eliminates the reproduced genes of his male rival and makes the females sexually receptive once again. That male langurs have never been observed to eat the infants they kill and that infanticide occurs also in areas of low population density lend support to the hypothesis that infanticide is a means of achieving reproductive advantage (Hrdy 1977). Also consistent with this interpretation is the observation of infanticide in similar conditions by other animals including the lion (Pusey & Packer 1992) and the jacana (Emlen, Demong, & Emlen 1989), a water bird.

Of course male langurs need not be conscious of the reasons for their killing ways, any more than they are conscious of why they have a tail or fingers. It is extremely unlikely that they have figured out that lactating females do not ovulate and that killing infants will make their mothers fertile and sexually receptive. It is more reasonable to suppose that incoming males simply have an instinctive desire to eliminate from their band all infants, a goal (or reference level) that was repeatedly selected in past generations because of the reproductive advantages it conveyed.

These are just a few examples of how an evolutionary perspective focusing on reproductive success provides answers to the ultimate why questions concerning a wide range of animal behaviors. Many other examples could be given showing the survival and reproductive function of behaviors animals use to find and make places to live, obtain food, defend themselves from predators, cooperate with other animals, mate, and care for offspring (see Alcock 1993, and McFarland 1993). Indeed, it can be said that evolutionary theory now provides the core explanatory framework for studies of animal behavior in natural settings. In addition, it is strongly supported by countless experiments in both field and laboratory settings (again, see Alcock 1993, for descriptions of many such studies).

But when invoking evolutionary answers to these ultimate why questions, we must be on guard against the tendency to see specific behaviors as being selected for their survival and reproductive benefits. Instead, we know that what are selected and inherited are not fixed patterns of action but rather goals in the form of reference levels and the physical means to achieve them despite continual and unpredictable disturbances provided by an uncaring Mother Nature.

To illustrate this essential point, let's consider a spider spinning its web. The webs of any given species of orb-weaving spider are all of the same basic design, but actual dimensions must vary because of variations in the locations where they are installed, such as branches of a tree or bush. So it is obvious that no invariant sequence of actions will be successful in installing a web in all locations. Instead, each web must be custom-designed for the site it is to occupy.[6]

The spider is able to fit web to site not by engaging in a fixed pattern of actions but by *varying* its behavior for each stage of web building until certain goals are met before it proceeds to the next stage. First, the spider, perched on a branch, releases a strand of silk into the wind until it catches on another branch. Since the distance to the other branch will be different for each site, the spider cannot release a fixed length of silk each time and therefore it has no fixed sequence of behavior. Instead, it must continually let out silk until it feels that its sticky end is attached to another branch (probably not unlike the way an angler fishing for bottom fish lets out line until he feels the weighted hook come to rest on the bottom of the lake). The amount of silk it will then pull back in for the proper tension must also vary from one web to another, depending on the distance between the branches and the stiffness of the branches themselves. After tying the near end to its branch, the spider uses this first strand to drop a looser second strand and then a third to form a Y configuration with three stands meeting at what is to become the center of the web. The spider then begins to construct additional radials, like the spokes of a bicycle wheel, checking angles between the radials with its outstretched legs and continuing to add radials until the angle between each spoke and its neighbor falls below a certain value. Each radial is also carefully cinched in so that it has the proper tension.

Next, the spiral portion of the web is constructed. Using a temporary nonsticky strand as a scaffold, the spider works first from the center outward and then from the periphery back toward the center, laying down permanent, sticky silk that will trap its future meals. The spider again carefully controls the spacing between spirals, since too much space would allow insects to pass through the web and too little would be wasteful of precious silk. Finally, the spider determines how much the web sways in the breeze. If sway is excessive, it may attach weights in the form of small pebbles or twigs to one of the web's lower corners. If after all this work the spider judges the web to be unsatisfactory, it will abandon the site and construct another web elsewhere.

Due to the nature of web building and the varied conditions in which it occurs, sensory feedback is essential to all stages of construction. It is only by varying its behavior as required to achieve each subgoal that the spider is successful in recreating the same basic design that evolved over millions of years for its prey-catching ability. As noted by William James (1890, p. 7): "Again the fixed end, the varying means!" In the case of the spider's web, the fixed end can be brought about only by achieving a number of subgoals in a particular order. It is these subgoals and the means for achieving them, not the spider's actions themselves, that evolved because of their value in providing the spider with a means for its livelihood.

Learned Behavior

We have seen that instinctive animal behaviors are (and must be) more flexible than originally understood by Lorenz for them to remain adaptive in a world of unpredictable obstacles and disturbances. But these behaviors nonetheless have real limits to their flexibility. A spider's web catches prey, and the spider must custom-build each web to fit its site. But the design it uses is the same basic one that has been successful over many thousands of years. If this design now turns out to be unsuccessful for a particular spider in securing food, the spider cannot make another kind of web, like the more productive one being used nearby by another species. It is stuck with the design of its species in much the same way that it is stuck with having eight legs, a hairy body, and an appetite for juicy insides of insects.

Other animals show more flexibility, being capable of learning. Whereas an insect-eating spider will eat only insects, rats will nibble on just about anything that might be edible and learn to distinguish what is nutritious from what is not (more on this type of rat learning later). Thus individual rats of the same species may have very different diets and food preferences according to their dining experiences. The circus examples given at the beginning of this chapter of dogs walking on their hind legs, bears riding motorcycles, and seals balancing beach balls on their noses are particularly striking cases of animal learning that appear unrelated to such naturally occurring instinctive behaviors as barking, scratching, and catching fish. But these unnatural acts arise only in a specially arranged environment where they are instrumental in obtaining food and achieving other goals. Although psychologists recognize several different forms of learning, we will focus here on the kind that involves acquisition of what appear to be novel behaviors as a result of the animal's particular experiences.

One way of looking at such learning is to see it as a behavioral adaptation to environmental changes that happen too quickly to be tracked by natural selection. Gradual changes in climate or the gradual appearance and extinction of pathogens, prey, and predators can affect instinctive behavior through the differential survival and reproduction of organisms with adaptive behaviors. But more rapid environmental changes taking place from one generation to the next or even within a generation cannot be tracked by evolution. As Skinner (1974, p. 38) observed, "contingencies of survival cannot produce useful behavior if the environment changes substantially from generation to generation, but certain mechanisms have evolved by virtue of which the individual acquires behavior appropriate to a novel environment during its lifetime." These "mechanisms" refer to ways of learning that allow animals to adapt their behavior to unpredictably changing environments.

We considered several approaches to learning theory in chapter 3, including classical conditioning theories of Pavlov and Watson as well as instrumental and operant conditioning theories of Thorndike and Skinner. But since that chapter came before the discussion of perceptual control theory in chapter 5 and before the evolutionary perspective presented in this chapter, it will be worth while to take another look at learning and modification of animal behavior from these new perspectives, focusing on the type of learning that Skinner was interested in.

As described in chapter 3, Skinner included both one-way cause-effect and selectionist components in his theory of how animals acquire new behaviors, in much the same way that Lorenz included both of these in his account of instinctive behavior. The selectionist component for Skinner had to do with the learning process itself; that is, how new behaviors are first emitted (random variation) with certain ones selected by the environment according to their consequences. It is for this reason that Skinner emphatically rejected the frequently applied characterization that his was a stimulus-response theory because of the "unstimulated" nature of the originally emitted novel behaviors.

But despite his protests, an important one-way cause-effect component of Skinnerian theory comes into play after a new behavior has been learned. This is because the new behavior is then elicited or caused by sensory stimuli that are the same as or similar to environmental stimuli experienced when the behavior was originally selected. The rat may stumble upon pushing the lever to obtain food in a haphazard, random way, but after it learns this new way of feeding itself it will immediately approach and push the bar (if hungry) when placed into the same or similar box in which the behavior was learned. It is for this Newtonian-inspired one-way cause-effect conception of performance of already learned behaviors that Skinner's theory was and still is characterized by many behavioral scientists as a stimulus-response theory. This characterization is understandable, if not completely justified, when it is realized that Skinner repeatedly referred to the “stimulus control” of behavior. Although he understood stimulus broadly as the cumulative effects of all previous sensory stimuli experienced by the organism, he emphasized that “the environmental *history* is still in control” (Skinner 1974, p. 74). By control he actually meant cause. This view of behavior is in striking contrast with the circular causality of perceptual control theory, which sees organisms purposefully varying their behavior to control perceived environmental consequences of those behaviors. In other words, instead of Skinner’s selection *by* consequences we have Powers’s selection *of* consequences.

A good way to contrast the difference between these theories of how organisms modify their behavior is to consider an intriguing pattern of behavior Skinner observed. He found that he could obtain very high rates of a behavior (such as a hungry pigeon pecking at a key to obtain food) by gradually *decreasing* the rate of reinforcement. These high rates could be obtained by starting out with a relatively generous reinforcement schedule that provided a grain of food for each key peck, and then using progressively more stingy schedules requiring more and more pecks (for example, 2, 5, 10, 30, 50, 75, and 100) for each reward. Skinner was thereby “able to get the animals to peck thousands of times for each food pellet, over long enough periods to wear their beaks down to stubs. They would do this even though they were getting only a small fraction of the reinforcements initially obtained” (Powers 1991, p. 9).

But if, according to this theory of operant conditioning, reinforcement increases the probability of the behavior that resulted in the reinforcement (note that this describes a *positive*-feedback loop) how could it be that *reducing* the reinforcement leads to an *increase* in the rate of behavior? This puzzle is solved when we see reinforcement not as an environmental event but rather as a goal the organism achieves by varying its behavior as required. If circumstances are arranged so that the hungry Skinner-box-trained rat must perform more bar presses to be fed, and it has no other way to obtain food, it will adapt its behavior by increasing the rate of bar pressing. If the rate of reinforcement is increased to the point at which the rat can maintain its normal body weight, a control-system model of behavior based on circular causality would predict that further increases in reinforcement should lead to decreases in the rate of behavior. This is exactly what happens (see Staddon 1983, p. 241, figure 7.18).

Skinner also believed that any behavior an animal was physically capable of could be brought about through contingencies of reinforcement. He took particular delight in demonstrating the games that he taught pigeons to play, such as the one in which the bird used its beak to roll a midget bowling ball down a miniature alley to a set of tiny pins (Skinner 1958).

But other research on animal learning has discovered clear constraints on the types of behaviors that animals can learn, and that instinctive behaviors can often interfere with learning new ones. Keller and Marian Breland, who worked for many years training animals for commercial purposes, reported several such examples in their informative and entertaining 1961 paper "The Misbehavior of Organisms." Included in their report are accounts of chickens that could not learn to stand on a platform for twelve to fifteen seconds without vigorously scratching it; raccoons that could learn to put one coin in a container but when given two coins would spend minutes rubbing them together and refuse to deposit them; and pigs that, after having learned to pick up and place large wooden coins in a piggy bank, would after several weeks or months begin repeatedly to drop the coin, push it with their snout (called "rooting"), and pick it up again, taking up to ten minutes to transport four coins over a distance of about six feet. Other researchers reported that male three-spined sticklebacks (a North American fish) were successfully trained to swim through a ring to gain access to a female, but they could not learn to bite a glass rod for the same reward since they attempted instead to mate with the rod (Sevenster 1968, 1973)! In all these cases we see the animal's normal instinctive behaviors related to eating and reproduction interfering with the new behavior the researcher wanted it to learn, a phenomenon referred to by the Brelands as "instinctive drift."

Other interesting evolutionary constraints on learning were investigated in the laboratory rat. For example, rats are quite handy with their front paws and so a hungry rat normally learns quite quickly to press a bar to obtain food. But it is very difficult to get a rat to press a bar to avoid a shock (Slater 1985, p. 87). This seems due to the rat's freezing in response to fear, an instinctive behavior incompatible with bar pressing.

Rats also can make certain associations between stimuli and their effects, but not others. If a rat is made sick after consuming a food with a certain taste, it will consequently avoid all foods having the same taste. And if a sound or visual stimulus regularly precedes an electric shock, a rat will associate this as a signal of the impending shock and will learn to make an appropriate avoidance response. But rats cannot learn to associate taste with electric shock or use auditory or visual cues to learn that a food is noxious (Garcia & Koelling 1966; Garcia et al. 1968).

These findings may be puzzling for the psychologist who has no appreciation of the evolutionary past of the rat, but they make quite good sense from an evolutionary perspective. For rats, which often scurry about in dark places and eat an amazing variety of foods, taste is a better indicator of the quality of food than its visual appearance or the sounds they make while eating. In contrast, physical dangers are usually accompanied by visual and auditory signals, not gustatory ones. So it makes sense that evolution would have selected rats that learn what is bad to eat by taste and what is physically dangerous by sight and sound.

That rats can learn food aversion based on taste is itself a quite remarkable adaptation that led psychologists to seriously revise their theories about learning. It was once widely believed (based on Pavlov's and other studies of classical conditioning) that two stimuli had to be presented several times and within a very short time if one was to become associated with the other. But in 1955 John Garcia and his associates fed rats a harmless substance with a characteristic taste and later made the animals sick using radiation (Revusky & Garcia 1970). Contrary to expectations, rats would learn to avoid the new food even if they were made sick several hours after ingesting it. And this food-avoidance learning appeared permanent.

The findings of this and several similar studies were quite surprising to psychologists at the time, although this type of learning ability again makes good evolutionary sense. Rats live in a wide variety of rapidly changing (now usually human-made) environments and consume a wide range of foods, often those intended for humans or discarded by them. Since they cannot know beforehand whether a new food is toxic or nutritious, they are very cautious and at first take only a small quantity of it. And since it may take a few hours for food poisoning to take effect, they have evolved a learning mechanism that can operate over an interval of hours so that they forever avoid the taste of a food that has made them ill just once. This well-adapted learning is why rat poisons have limited success. On the other hand, a rat whose normal diet is deficient in an essential nutrient (such as the B vitamin thiamine) has a stronger inclination to try a new food. If the new addition happens to be followed by recovery from the dietary deficiency, the rat will develop a marked preference for it (Rodgers & Rozin 1966).

These examples of how the learning ability of animals is adaptively constrained by evolution show that whereas theories of learning may be able to provide some answers to proximate why questions about animal behavior (such as why is that pigeon pecking that key? Answer: Because it is hungry and has discovered that it can obtain food by doing so), learning alone cannot provide answers to ultimate why questions. Ultimate questions must consider the evolutionary origin of the animal's learning abilities.

But what exactly is learned when an animal escapes from a puzzle box of the type Thorndike used, presses a bar to obtain food in a Skinner box, or develops a preference for a food that contains some essential nutrient? We saw in chapter 6 and from the preceding discussion of instinctive behavior that fixed patterns of behavior cannot remain adaptive in a world characterized by variable circumstances and unpredictable disturbances. Learning can be adaptive only if learned behaviors remain flexible and permit the organism to obtain its goals in the face of these disturbances.

The hierarchy of controlled perceptions introduced in chapter 6 provides a quite different perspective on learning. It will be recalled (see figure 6.3) that it shows how higher-level goals are achieved through manipulation of combinations of lower-level goals (subgoals). A spider is able to catch prey only by achieving a rather large number of subgoals that involve spinning a web (which itself requires achieving additional subgoals as described earlier), catching prey, and injecting its venom to kill or paralyze it. Fortunately for the spider, it inherits a control system hierarchy in which these goals and subgoals are specified, and so it requires no learning to be able to feed itself. This is what is referred to as instinctive behavior.

But other animals are more adaptable. A rat inherits certain taste preferences, and as long as it can find sufficient quantities of these foods, it may live its entire life without having to try new ones. But a starving rat must try new foods if it is to survive. It will then come to prefer tastes associated with feelings of wellness and avoid those associated with sickness. The rat is not learning specific new eating behaviors, but rather to reset reference levels for lower-level perceptions based on consequences for higher-level goals.

The rat placed in the Skinner box also demonstrates learning, but this involves learning which patterns of proprioceptive, auditory, and visual perceptions lead to the delivery of a food pellet (another perception). A rat's behavior is more flexible than that of a spider in that the rat is able to reset reference levels based on experience, whereas the spider's reference levels are less modifiable. However, we saw that evolution allows certain types of flexibility but not others; recall that a rat quickly learns in a single trial which taste leads to nausea and which sounds are followed by skin pain. In perceptual-control-theory terms, the rat learns to set a very low or zero reference level for these tastes and sounds to avoid the nausea and pain that follow them. But its behavioral flexibility is limited in that it cannot change its reference level for taste based on sound or for a certain sound based on nausea.

Learning from a hierarchical-perceptual-control-theory perspective is actually finding out, by a form of trial and error, which combinations of lower-level perceptions are successful in bringing about a higher-level goal. Powers refers to this process as *reorganization* (1973, p. 179):

> Reorganization is a process akin to rewiring or microprogramming a computer so that those operations it can perform are changed. Reorganization alters behavior, but does not produce *specific behaviors*. It changes the parameters of behavior, not the content. Reorganization of a perceptual function results in a perceptual signal altering its *meaning*, owing to a change in the way it is derived from lower-order signals. Reorganization of an output function results in a different choice of means, a new distribution of lower-order reference signals as a result of a given error signal.

This way of looking at what is normally considered learning combines the two alternative causal processes that provide the major themes of this book. First there is cybernetic circular causality in recognizing the purposeful nature of animal behavior and learning. Animals act on their world based on what they perceive and thereby change their environment and what they consequently perceive of it. Animals also change how they act on the world when old ways are no longer effective in getting what they want. But this change in behavior is based on a Darwinian process involving spontaneous variation and selection; not variation and selection of specific behaviors as conceived by Skinner and his behaviorist followers, but rather variation and selection of goals as the organism discovers which new combinations of controlled lower-order perceptions lead to the attainment of higher-level goals.

We will consider in more detail this notion of within-organism evolution and its purposeful nature in chapters 9 and 10 after we consider the evolutionary bases of human behavior in the next chapter.