Without Miracles

3 The Emergence of Instinct

Providence

Be it that those actions of animals which we refer to as instinct are not gone about with any view to their consequences, but that they are attended in the animal with a present gratification, and are pursued for the sake of that gratification alone; what does all this prove, but that the prospection, which must be somewhere, is not in the animal, but in the Creator?

--William Paley[1]

Instruction

As the penchants that animals have acquired through the habits they have been forced to contract have little by little modified their internal organizations, thus rendering the exercise of [these penchants] very easy, the modifications acquired in the organization of each race are then propagated to new individuals through generation. Indeed, it is known that generation transmits to these new individuals the state of organization of the individuals that produced them. It results from this that the same penchants already exist in the new individuals of each race even before they have the chance to exercise them, so that their actions can only be of this one kind.

--Jean-Baptiste Lamarck[2]

Selection

To my imagination it is far more satisfactory to look at such instincts as the young cuckoo ejecting its foster-brothers,--ants making slaves,--the larvae of echneumonidae [wasps] feeding within the live bodies of caterpillars,--not as specially endowed or created instincts, but as small consequences of all organic beings, namely, multiply, vary, let the strongest live and the weakest die.

--Charles Darwin[3]

Among the most marvelous puzzles of fit are those observed between the behavior of animals and their environments, environments that include not only a world of objects and forces but also other organisms. Indeed, many of the highly specialized structures of animals would be quite useless if they were not coupled to correspondingly specialized behaviors. The marvelously designed wings of a hawk would be of little use without the ability to move them in such a way as to generate lift for flight. The rattlesnake's rattle would be a frivolous accessory without the snake's ability to shake it vigorously to sound its warning. And the adroit human hand with its opposable thumb would be a worthless appendage if it were not coupled with the coordinated movements that allow it to plant crops, throw spears, construct cathedrals, and perform piano sonatas.

When we consider animal behavior, we are first struck by what appear to be two quite separate categories of actions. One category consists of complex behaviors that all the individuals of a given species are somehow able to perform without first experiencing the behaviors 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 from other female rats.[4] Usually, the evolutionary significance of such behavior is quite clear. In the case of mother rat, it is not difficult to see how building a nest to keep her pups warm and secure and keeping them clean increases their chances of survival, thereby enhancing her own reproductive success and the survival of her genes. The behaviors involved in the spider's spinning a web, the beaver's constructing dams, and the honeybee's sculpting a honeycomb are additional examples.

The other type of behavior consists of those acts that appear to result from an animal's *particular experiences,* and it is here that we notice striking differences across individuals of the same species. The circus shows us what dogs, bears, horses, lions, tigers, and elephants can do given the special environment provided by the animal trainer. Dogs do not normally walk upright on their two hind legs, and 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 provided with a special type of environment. Similarly, whereas all normal children manage to walk and talk without formal instruction, this is not the case for reading, writing, and mathematics skills, the development of which normally requires many years of formal schooling.

Of these two types of behavior, the first is typically referred to as instinctive, innate, or inherited, and the second learned or acquired. Both provide countless instances of puzzles of fit. We will examine the evolution of explanations for the fit of instinctive behavior in this chapter, and address learned behavior in chapter 7. These two chapters will also show how traditional theories of behavior fail to account for the full extent of the observed fit.

Instinct Through Providence

Our prehistoric ancestors' survival depended on their understanding the ways and habits of the animals that shared their surroundings. They hunted the animals useful as food, and avoided and repelled those that would have humans as *their* food. This delicate relationship led to an appreciation of the ways in which animal behavior is adapted to survival. The bird's ability to fly, the frog's skill in catching insects with its long, sticky tongue, the beaver's construction of dams and canal systems--these and countless other examples provide evidence of apparently built-in abilities that emerge without long study or labor, and that all normal members of the species share. This adapted nature of behavior led many traditional societies to venerate certain animals as embodiments of divine spirits.

Two interrelated questions must be considered in attempting to understand instinctive behavior. The first deals with the origin of the behavior itself and the second with the propagation of the behavior to new generations. It is important to address both of these questions separately, but the most satisfactory answer to each turns out to be very much the same.

The providential view of instinctive animal behavior came to us in Western philosophy primarily through the influence of Aristotle, Thomas Aquinas, and Descartes, and it remained popular and virtually unchallenged through the eighteenth century. As Thomas Aquinas reasoned:

> 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.[5]

The views of the Aristotelians and Cartesians of the eighteenth century differed in many respects concerning animal behavior. Nonetheless, they agreed that "complex animal behavior (e.g., birds building their nests and bees their cells) should be explained by appeal to instincts, which they understood as blind, innate urges instilled by the Creator for the welfare of his creatures."[6]

Reverend Paley was also interested in using the instinctive behavior of animals as evidence for the existence, goodness, and wisdom of God. He continued his argument from design by emphasizing those behaviors that could not possibly have been the result of any instruction provided during the lifetime of the organism. Thus he described 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.[7]

From this passage we see that Paley put great emphasis on the "unlearnability" of complex behaviors that are essential to the survival and continuation of a species, since if the animal has no way to learn such important behaviors, the origin of the behaviors must lie in God. From this providential perspective, the question of transmission of behaviors to the next generation simply does not arise, since the behavior is seen as an integral part of the organism as designed by the Creator.

The Instruction of Instinct

It is in the work of Charles Darwin's grandfather, Erasmus Darwin (1731-1802), that we find an early alternative to the providential view of instinct. Erasmus Darwin's annoyance with this view can be seen in his observation that from this perspective, instinct "has been explained to be a *divine something*, a kind of inspiration; whilst the poor animal, that possesses it, has been thought little better than a machine!"[8] He and other "sensationalists" of the time emphasized the role of *sensory* experience in the development of behavior. 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 demonstrated immediately after hatching or birth. Here Lamarck's concept of the inheritance of acquired characteristics seems at first consideration to do much better.

Lamarck's understanding of instinctive behavior was intimately tied to his theory of evolution. Whereas today biological evolution is used to explain the emergence of instinctive behavior, Lamarck saw behavior as the motor of evolution.[9] For him, changing environmental conditions forced organisms to change their habits to survive, and changed habits involved the increased use of certain body parts and systems accompanied by the decreased use of others. According to his theory, such organic changes would be passed on to succeeding generations. Since behavior is clearly influenced by biological organs, including appendages, the inheritance of such modified organs would result in the accompanying instinctive behavior dependent on the organs in succeeding generations. In this way Lamarck attempted to provide explanations both for the origin and transmission of new instinctive behaviors.

This theory depends crucially on mechanisms of instruction in at least three ways. The first two we have already considered and rejected; namely, the transmission of instructions from behavior to biological structure without previous selection, and the instructive transmission from the somatic (body) cells to the germ (sperm and egg) cells. We now have to ask how it is that a changing environment results in the animal assuming just those habits that are adapted to the new environment. If a particular source of food is no longer available, what is it in the environment that instructs the animal to adopt a new effective behavior to feed itself? Certainly, a type of instruction is implied, although Lamarck and others of his day did not consider the problems inherent in understanding *how* new adapted behaviors could initially arise. Particularly problematic in this regard are behaviors that cannot be imagined as the result of individual learning, as in the egg-laying behavior of the moth and butterfly (as Paley describes in the first epigraph to this chapter) and the egg-laying behavior of the wasp (mentioned below). So even if Lamarck's theory could account for the transformation of learnable habits into instinctive behavior (which it does not), it still offers no explanation for the origin of those instincts that could not have been acquired as habits during the lifetime of any individual organism in the first place.

The Selection of Instinct

Charles Darwin's initial attempt to explain instinct had much in common with Lamarck's theory of the acquisition of acquired characteristics. Darwin "supposed that habits an animal might adopt to cope with a shifting environment would, during the course of generations, slowly become instincts, that is, innately determined patterns of behavior. Instincts in turn would gradually modify the anatomy of an organism, adapting the creature to its surroundings."[10]10 Thus, habits that persisted over many generations, such as eating berries from a certain bush, and were beneficial to the survival and reproduction of the species would "inscribe themselves in the heritable structures of the brain."[11]

Gradually, however, Darwin became dissatisfied with the idea of inherited habits as the sole explanation for instinctive behaviors, particularly when he realized (as Lamarck apparently had not) that many of these behaviors could not have originated as habits. Another example was provided by British natural theologian Henry Lord Brougham, writing 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." We know that Darwin was intrigued by this observation, since he added the comment "extremely hard to account by habit" to his copy of Brougham's work.[12] 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."[13]

It was clear to Darwin that habit could not be the explanation for such instinctive behaviors. Therefore he considered them to be not the result of inherited useful habits, but rather the *selection of individuals with useful habits,* although he never completely abandoned the former idea. Thus natural selection provided an explanation for instinctive behaviors that never could have originated as habits, such as the wasp's egg-laying behavior; however, one particularly thorny problem remained, that of the evolution and behavior of the neuter insects.[14]

The *Hymenoptera* order of insects includes bees and ants together with some wasps and flies. Many of these insects live in a well-structured society where their survival depends on a specialized division of labor among its members, 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 the worker caste in these colonies often comprise sterile insects *that therefore cannot genetically pass on their instinctive behaviors to the next generation of workers*. This posed no small threat. Indeed, it may well be that "the case of the neuter insects presented the most serious obstacle to his general theory of evolution."[15]

Darwin's answer came to him 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 selectively to breed cattle most closely related to those slaughtered to produce the desired meat. In like manner, a colony of insects that produced neuters that helped the survival of the community (by taking care of young, providing food, or defending the colony against enemies) would be naturally selected to continue to produce such neuter insects. As Darwin noted, "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."[16] The concept of selection by community or kin rather than the individual later became a powerful idea in the understanding of the evolution of altruistic behavior,[17] and it provided Darwin with an explanation for complex and useful instinctive behaviors that could not be explained by Lamarckian inheritance of habits. But where the transmission of inherited habits seemed conceivable, particularly where Darwin could see no selective advantage for the behavior, he made use of Lamarckian principles. And since he was unable or unwilling to see any survival or reproductive advantages accruing from the expression of emotions, he explained these as inherited habits.[18]

The mix of natural selection and instruction may seem like an odd combination to us today, but when seen from Darwin's own perspective it makes rather good sense. Certain instinctive behaviors (as well as the existence of neuter insects) could not be explained by the Lamarckian theory simply because he had no way to conceive how they could have developed *originally* as habits. For these behaviors, natural selection of individuals possessing behaviors leading to reproductive success was the only way to explain their appearance. However, other instinctive behaviors, such as the expression of emotions through facial or postural means, appeared to have no functional value. Since natural explanation is no explanation at all for the development of traits that provide no survival and reproductive benefits, Darwin reasonably concluded that they must have resulted from the inheritance of useless habits accompanying more useful ones.

The Ultra-Darwinians

Others, however, both during and after Darwin's lifetime, completely rejected the Lamarckian idea that acquired characteristics could be inherited. Consequently, they dared to explain all of evolution, including that of complex instinctive behaviors, solely through natural selection. The most prominent of these ultra-Darwinians, as Darwin's young disciple and defender George J. Romanes called them, was fellow British naturalist and codiscoverer of the theory of natural selection, Alfred Russel Wallace (1823-1913). And since they were ultra-Darwinian only in the sense that they discounted all mechanisms of evolution other than natural selection, they are probably more accurately referred to as ultraselectionists.

But Wallace's view of evolution was more than just a rejection of all Lamarckian instruction. He and his fellow ultraselectionists

> viewed each bit of morphology, each function of an organ, each behavior as an adaptation, a product of selection leading to "better" organisms. They held a deep belief in nature's "rightness," in the exquisite fit of all creatures to their environments. In a curious sense, they almost reintroduced the creationist notion of natural harmony by substituting an omnipotent force of natural selection for a benevolent deity.[19]

Wallace's own words express this view quite clearly:

> None of the definite facts of organic selection, no special organ, no characteristic form or marking, no peculiarities of instinct or of habit, no relations between species or between groups of species, can exist but which must now be, or once have been, useful to the individuals or races which possess them.[20]

But this concept posed a special problem when Wallace considered the human intellect. This is because he believed, in contrast to other European intellectuals of his day, that the brains of "savages" were not intrinsically inferior to those of civilized Europeans. He knew of non-European military bands that very capably performed Western music and was much impressed by the very fine singing of Africans who had learned this music in England.[21] So he reasoned that if natural selection can select only behaviors and abilities that are advantageous to the species, natural selection could *not* be responsible for such "latent" intellectual and musical abilities since they served no purpose in their native environment. Therefore, the human brain and the intellectual and moral qualities that it confers could only be the work of a divine provider.

So although both Darwin and Wallace were concerned with the same problem, they arrived at very different conclusions. Darwin saw certain behaviors that to him served no useful function and explained them by inheritance of acquired characteristics. Wallace saw abilities that served no useful function and explained them as the work of God. It was only much later that Darwin's selectionism and rejection of providentialism would be combined with Wallace's selectionism and rejection of Lamarckian instruction to give birth to the modern neo-Darwinian view of biological evolution that we embrace today.

Despite the enormous impact that Darwin's work had on the life sciences during his own lifetime, it had relatively little immediate impact on the comparative study of animal behavior. Two of the reasons for this are the methodological difficulties of both naturalistic and experimental research on animal behavior, and the heavy use of anecdotal evidence and anthropomorphic[22] interpretation practiced by Romanes, who wrote extensively about animal behavior and mind from a Darwinian perspective while maintaining a belief in the inheritance of acquired habits.[23]

The Beginning of an Evolutionary Ethology

It was not until the 1930s that a serious attempt to conduct research on 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. In this setting his observations of animal behavior 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."[24]

As suggested by his definition of ethology, Lorenz was primarily interested in finding an evolutionary explanation for the instinctive behavioral patterns characteristic of a species. For example, it was brought to his attention that greylag geese that were reared by humans would follow them in much the same way that naturally hatched goslings waddled after their mother. Lorenz confirmed these findings for the greylag goose and extended them to a number of other birds as well. This pattern of behavior, resulting from a type of bonding with the first moving object seen by the bird, he called "imprinting," and it is for this finding that Lorenz is still best known today.

By extending Darwin's theory of natural selection to behavior, Lorenz posited a genetic basis for specific behaviors that was subject to the same principles of cumulative blind 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 (usually the mother goose) 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 behavioral imprinting. Those goslings that lacked this behavioral characteristic would be less likely to survive to maturity and reproduce. In much the same way that we understand how a tree frog can become so well camouflaged over evolutionary time through the elimination by predators of those individuals who are less well camouflaged, we can also understand how instinctive behavior can be shaped through the elimination of individuals whose behaviors are less fit to their environment.

Another example of Lorenz's conception of instinctive behavior is the egg-rolling behavior of the greylag goose. [25] 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. This behavior depends on what Lorenz called a "fixed motor pattern," that is, a pattern of activity in the central nervous system of the goose that is released or triggered by the sight of the egg outside the nest. In other words it is a specific fixed response 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 survival of the species.

But a problem with Lorenz's conceptualization of instinctive behavior becomes apparent when one considers that exactly the same pattern of behavior will *not* be successful in returning the wayward egg to the nest unless all environmental conditions are exactly the same for each egg-rolling episode. Instead, for the goose to be successful in keeping her eggs nestbound, she must be able to modify her behavior not only from episode to episode but also *within* each episode to compensate for the variability in conditions and disturbances that she inevitably encounters, such as differences in the distance between her and the egg at the beginning of the behavior, and irregularities in the terrain between the egg and the nest. As American philosopher and psychologist William James noted over 100 years ago, the behavior of all living organisms is characterized by the attainment of *consistent ends using variable means*.[26] And it is for this reason that Lorenz's analysis fails to explain the typical success (and therefore the fit to environment) of instinctive behavior. This essential aspect of adapted behavior will be considered in more detail in chapter 8.

But despite this shortcoming, Lorenz must be acknowledged as being the first to attempt to provide a truly Darwinian (or, more accurately, a purely selectionist) 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 (or phylogenies) by comparing the anatomical similarities and differences among living animals and fossils, Lorenz proposed patterns of instinctive behavior for the same purpose.[27] Indeed, he based his comparative study of animal behavior "on the fact that *there are mechanisms of behavior which evolve in phylogeny exactly as organs do*."[28] His evolutionary perspective also led him to emphasize that understanding animal behavior required one to appreciate its purposefulness in preserving the species, its role in the entire repertoire of the animal's activities, and its evolutionary history.[29] For these reasons, among others, Lorenz regarded with suspicion research on animal behavior being conducted by experimental psychologists using domesticated animals in artificially contrived environments on the other side of the Atlantic. But to understand how animals are able to modify their behavior during their own lifetime, we must turn to the work of these American animal psychologists later in chapter 7.

[1]Paley (1802/1902, pp. 336-337).

[2]Lamarck (translated by Burkhardt, 1977, pp. 170-171).

[3]Darwin (1859, pp. 242-244).

[4]Beach (1955).

[5]Aquinas (1265-1273/1914, p. 460).

[6]Richards (1987, pp. 22-23).

[7]Paley (1813, p. 306).

[8]Erasmus Darwin (quoted in Richards, 1987, p. 34).

[9]This idea was to persist into the twentieth century in the developmental psychology of Jean Piaget.

[10]Richards (1987, p. 94).

[11]Richards (1987, p. 96).

[12]Quoted in Richards (1987, p. 136).

[13]Richards (1987, p. 136).

[14]Darwin's difficulty in formulating a natural selection theory of instinctive behavior that could account for that of the neuter insects may have been an important factor in the long delay between his discovery of natural selection as a general principle in evolution and his first publication of the theory 20 years later in *The Origin of Species* (see Richards, 1987, pp. 152-156).

[15]Richards (1987, p. 145).

[16]Darwin (1856-1858/1975, p. 370). Now it is known that many truly social (eusocial) insects are *haplodiploid*, meaning that females have a double set of genes (that is, are *diploid*, as are humans), but males develop only from unfertilized eggs, so that they have only one set of genes (are *haploid*). As a result, a female worker is more related to her sisters, sharing with them half of her mother's genes and all of her father's, than she would be to her own offspring. Thus it is in the genetic interest of a female worker to forgo having offspring of her own and devote her energies to caring and protecting those of her siblings (see Badcock, 1991, pp. 73-75).

However, haplodiploidy is neither necessary nor sufficient for eusocial behavior since termites and naked mole rats are both eusocial and diploid, and not all haplodiploid insects are eusocial. Nonetheless, kin selection always underlies eusociality in insects or other animals, whether or not it is facilitated by haplodiploidy (see Sherman, Jarvis, & Braude, 1992, pp. 72-73).

[17]See, for example, Axelrod (1984) and Hamilton (1964).

[18]See Richards (1987, pp. 230-234) and Ghiselin (1969, pp. 203-206).

[19]Gould (1980, p. 50).

[20]Wallace (1867; quoted in Gould, 1980, p. 51).

[21] Concerning their ability to sing, Wallace (1895; quoted in Gould, 1991a, p. 57) commented: The habits of savages give no indication of how this faculty could have been developed by natural selection, because it is never required or used by them. The singing of savages is a more or less monotonous howling. . . . This wonderful power . . . only comes into play among civilized people. It seems as if the organ had been prepared in anticipation of the future progress in man, since it contains latent capacities which are useless to him in his earlier condition.

[22]Anthropomorphism refers to the ascribing of human qualities and traits to nonhuman animals or objects.

[23]Burkhardt (1983, p. 433).

[24]Lorenz (1981, p. 1).

[25]Lorenz (1981, pp. 236-237).

[26]James (1890, p. 7).

[27]Burkhardt (1983, p. 437).

[28]Lorenz (1981, p. 101; emphasis in original).

[29]Burkhardt (1983, p. 436).