Charles Darwin and animal behavior.

Chapter · January 2004

CITATIONS
0

READS
2,957

2 authors:

Gisela Kaplan
University of New England (Australia)
92 PUBLICATIONS **1,291** CITATIONS

SEE PROFILE

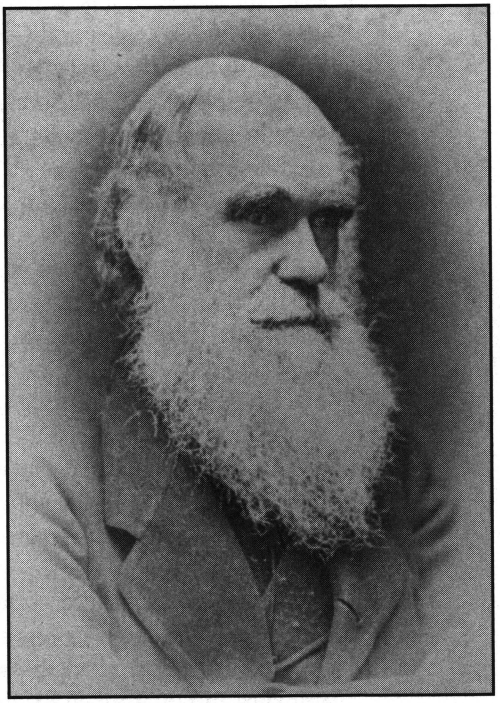
Lesley J Rogers
University of New England (Australia)
316 PUBLICATIONS **17,088** CITATIONS

SEE PROFILE

Darwin, Charles (1809–1882)

Kaplan, G. and Rogers, Lesley J. (2004) Charles Darwin and animal behavior. In M. Bekoff and Jane Goodall (eds.) *Encyclopedia of Animal Behavior*. 3 vols, Greenwood Publishing, Westport, CT, ISBN 0-313-32745-9, vol.2, pp. 471-479 (introductory essay to vol.2).

Charles Darwin's discoveries and theories were of such importance that it is hard to imagine how people perceived things before they were made. Modern evolutionary biology, molecular sciences, and many other new subfields of science would be unthinkable without Darwin's ideas. The idea that humans have evolved is now also very well supported by fossil evidence of hominid predecessors. Conversely, many of Darwin's ideas that were speculative at his own time have now been shown to be true. One such basic tenet was that all organisms are individually unique; that is, they vary from one another by inherited traits. This is *diversity* and diversity has now been shown to exist even at molecular and genetic (chromosomal) levels to an extent totally unknown and unsuspected at Darwin's time. More offspring are produced (by any species) than can survive to adulthood and reproduce, so that only certain traits and characteristics survive—known as *natural selection*. And most importantly, all organisms are connected through a process of evolution: Selection processes favor some variants over others, and their accumulation may lead to new species.



Charles Darwin.
Courtesy of the Library of Congress.

Charles Darwin was born in 1809 in Shrewsbury, England, and died in Downe, near Croydon, England, in 1882. Darwin, as was typical of his class and background, was a man of privilege who did not have to work for a living. He could devote his life to his studies and, because of his social position, was able to converse with and move in circles of scholars without any specific university affiliations. His formal studies of medicine (in Edinburgh) and of theology (in Cambridge) came to nothing. He did not complete his course in Edinburgh and, in Cambridge, Darwin spent probably more time dabbling in scientific hobbies than attending to his lecturers. He never became a man of the cloth as he was meant to do and, instead, escaped on a sea voyage. Just as he had finally completed his Cambridge studies, he was offered a place as a companion to Captain Fitzroy of the H.M.S. *Beagle*. Fitzroy was just 23 years of age when he was given command over the *Beagle*, and Darwin was a mere 22 years old when they sailed from England in 1831. The journey, with the clear task to establish better naval charts, eventually extended over 5 years in a complete circumnavigation of the world. In those years, Darwin turned himself from social companion into a de facto naturalist of the ship, noting down his observations along the way. His meticulousness and his passion for natural history led him to make many discoveries. Among these were the seminal studies of Galapagos finches. He discovered 14 species and drew them all separately, noting

their feeding preferences and beak shapes in particular. Influenced by a new spirit of science that began to ask for reasons (causes) of events, forms, and structures, particularly by authors such as Charles Lyell and his book *Principles of Geology* (1830–1833), Darwin was slowly beginning to doubt that species were immutable and unchanging (see below). The finches seemed to show that variability and adaptability were crucial factors in survival. From these observations, he began to shape his theories and, on return to England in 1836, took another 20 years to perfect them.

The Theory of Evolution and Natural Selection

Before the publication of Darwin's theory of evolution, the study of animal behavior had been dominated by the idea that the species were immutable, or unchangeable. The perception was that God had created living organisms in different but static forms. The scientific study of animals, hence, focused on examining the anatomies of different species. Baron Cuvier, head of the Académie des Sciences in Paris, was one of the most influential advocates of this approach and he collected enormous amounts of laboratory-based data. His ideas and influences suffocated any other more unifying approach to the study of animals and any attempts to develop unifying theories. This led to the famous debates of the 1830s between Cuvier and Geoffroy St. Hilaire, who embraced the trends seen in animals in nature. Within the next two decades, the debates, often bitter, led to the establishment of two disciplines: animal psychology, focused on laboratory testing and analysis as emphasized by Cuvier, and ethology, termed such by the son of Geoffroy St. Hilaire and focused on studying the characters of animals in their natural habitats. On this background, and in 1859, Darwin published the *Origin of the Species*, formulating a unifying theory based on the mutability of species.

Darwin's theory of evolution led to a revolutionary change in the study of animals. For the first time, it made research on animals a natural science relevant to understanding humans and, within the unifying framework of evolution, the behavior of one animal species was seen to be relevant to another. This laid the foundations for comparative studies of animal behavior. By postulating that one species could evolve into another by the gradual accumulation of chance variations in *phenotype* (physical form) and the process of natural selection, Darwin changed our view of ourselves in the context of all animal life. The earlier notion that humans were entirely different from animals, separated from them by an insurmountable barrier, was replaced by the view that the difference between humans and animals was a matter of degree and not of kind. Although natural selection was seen to act on phenotype, the structure of the sensory organs and the brain itself was seen as part of the phenotype, and these aspects are expressed in behavior. For example, in support of Darwin, Thomas Huxley studied the structural differences between the brains of different higher primates and interpreted his findings from an evolutionary perspective.

By the end of the nineteenth century, interest in Darwin's theory of evolution had declined. The theory was seen as largely disproven because geological and paleontological evidence, showing that life had existed on earth for only a short time, indicated that the gradual accumulation of chance variations took too long to account for the appearance of each species. Even Darwin's formulation of the concept of *sexual selection* (referring to preferences in mate choice for particular phenotypes, hence *genotypes*) failed to convince his critics at the time. Study of animal psychology developed at this time when Darwin's theory of natural selection was seen to be of little merit, and it emphasized the value of laboratory experimentation. Not until the 1930s did natural selection move back into a central place in

the theory of evolution. Then, as it had done before and also in more recent times, it was also used by emerging fascist groups and individuals as a political force to oppress Jews, blacks and others. Hence, Darwin's theories have had very seminal and revolutionary impact on the study of animal behavior but, at the same time, some disastrously negative outcomes in the study and theoretical development of research of human behavior (sexism, racism and many other discriminatory theories of present day, as seen, for instance, in the relatively new field of evolutionary psychology) have laid claim to Darwin's theories.

The 1970s, for instance, saw the emergence of sociobiology as a mainstay of Darwin's ideas, and, while its attempts to explain human behavior in divisive genetic terms were hotly contested, its application to animal behavior gained a large following, as is still the case today. At the same time *ethology*, the scientific study of animal behavior, fragmented into neuroethology, behavioral ecology and other subdisciplines. Sociobiologists were entirely focused on genetic explanations of animal behavior, as a direct application of Darwin's theories (natural selection and sexual selection), and they declared large parts of ethology to be irrelevant, especially research on development and causation. In time, sociobiology spawned evolutionary psychology which, by and large, has remained a crude attempt to explain much of human behavior in terms of genetic causes.

Both sociobiology and evolutionary psychology are, it is argued, characterized by reductionist thinking, reducing complex behavior to unitary genetic causes, and they are both used frequently in the service of conservative social and political forces. Although there is a lineage of these ideas directly back to Darwin, the study of behavior has almost disappeared in these accounts, other than as a by-product of the genes. While innovative (but highly problematic in their consequences on the social and political arena of human society), some of these theoretical developments have done little to foster our understanding of animal behavior in the context of its natural environment. In the supposed application of Darwin's ideas, they have often degenerated into pseudoscientific discussions, betraying their political convictions rather than scientific rigor and in that they are very "un-Darwinian."

Darwin and Ethology

The field of ethology has been referred to by Niko Tinbergen, one of its chief modern exponents, as "the biological study of behavior." Many ethologists study the behavior of animals in the wild. Others observe them carefully in captive environments or in the laboratory, always taking into account the known behavior of the species in its natural environment. Ethology is just one approach to the study of animal behavior, and Darwin is not always regarded as the first ethologist. Indeed, evaluations of Darwin in the history of science have at times placed him in the prehistory of ethology. Credit for ethology has been placed either much more recently in the direction of Karl von Frisch, Konrad Lorenz, and Tinbergen, the winners of the Nobel Prize in 1973, or in the hands of their relatively unacknowledged predecessors such as O. Heinroth or C. O. Whitman, who undertook behavioral observations much earlier than the Nobel Prize winners. However, in the English tradition, Darwin has maintained a founding role of the modern discipline of animal behavior, although he is by no means considered the only founder: G. M. Romanes (1848–1894) and C. L. Morgan (1852–1936) have been accorded similar founding status, while the role of Alfred Wallace, despite Darwin's and Wallace's first joint paper on natural selection (1844), was largely eclipsed by Darwin's *Origins* 15 years later. To further complicate matters, some early researchers of animal behavior were decidedly against Darwin (such as J. von Uexküll).

Darwin's own and detailed descriptions of animal behavior are closely linked to animal psychology and usually formulated with reference to human emotions and feelings. Both Romanes and Darwin have been criticized by some writers for a hopelessly entangled anthropomorphizing of animals. On the other hand, recent investigators of higher cognition in animals have seen such approach as less problematic and even valuable.

In the English tradition Darwin's role in ethology is considered central. Although the term ethology had been used over more than a hundred years prior to Darwin's time, it had been used to refer to the study of the ethics or science of building character in humans. It is generally accepted in this tradition that the use of "ethology" as referring to the study of animal behavior began with the publication of Darwin's *The Expression of Emotions in Man and Animals* in 1872, although it was not until well after Darwin that the label ethology was used consistently to refer to a particular way of studying animal behavior. Also, the origin of ethology could be attributed equally to the publication of Darwin's books *Variation of Animals and Plants under Domestication*, published in 1868, and *The Descent of Man*, published in 1871. In all of these he made comparisons between the mental processes of humans and other animals. Further impetus to the study of animal behavior came from the publication, in 1882, of the book *Animal Intelligence* by Romanes, a strong follower of Darwin. Romanes is seen by many as being the key figure in placing the study of animal behavior within an evolutionary framework and making it a comparison between species. He made a considerable move away from the Cartesian view and saw anthropomorphism as a means of understanding the minds and emotions of animals, thus foregrounding the debates that led ethologists of the mid-twentieth century to adopt the opposite position and avoid any hint of anthropomorphism.

Following the influence of Darwin, early ethologists studied animals in their natural habitats, and this focus persisted in the ethologists of the 1940s in Europe and the United States of America, as a clear distinction from laboratory-based comparative psychology. Also, as a direct line of influence from Darwin, the ethologists were largely concerned with instinctual behavior (inherited behavior). Darwin had argued against the division made between animals as being largely controlled by instincts, whereas humans are controlled by reason. His view was that all behavior is partly instinctive and partly dependent on past experience (learning), and it is not a simple matter of balancing off one by the other. In other words, the same animal may display many instinctive patterns of behavior as well as rapid and obvious learning.

Darwin's pivotal role in modern studies of animal behavior was his original combination of evolutionary theory with theories of instinct, even though some of these relationships have never been solved to Darwin's own satisfaction. Social insects, such as ants and bees, posed a major difficulty in his theory of natural selection because a colony contains large numbers of sterile workers that still show a rich diversity of adaptations and hence a complex division of labor. Yet variation in individual reproductive success is the lynch pin in the theory of natural selection, and this is a problem that appeared not to fit the theory (particularly in his detailed observations of the behaviors of ants). While Darwin speaks at length of instincts in the *Origin of the Species*, he points out repeatedly that "instinct" has no clear definition, and that learning by imitation and/or experience may modify inherited patterns of behavior.

Hence, even in the first writings of evolutionary theory (and its postulation of heritability of traits, physical and behavioral), there was room for learning and development—a point that Tinbergen's formulations acknowledged and maintained. In Tinbergen's model, the task of the ethologist is four-fold: namely to address the *ontogeny* (the development of

an animal), the *phylogeny* (the evolution of the animal), the cause, and the function of the animal's behavior. By erecting these four pillars of investigation, ethology had turned away from subjective states, cognitive abilities, or emotions of animals, and hence away from presumed unscientific ways of engaging with animals. Cartesian philosophy, from Descartes onward with its mechanistic reflex theories of animal behavior, thus had strangely combined with the calls of Tinbergen and colleagues for a rigorous science, to maintain a solid taboo over the question of animal intelligence and emotions.

Ethologists studied a wide range of species in their natural environment and emphasized the comparisons between species, the most famous exponent of this approach being Konrad Lorenz. Ethologists saw value in studying each species in its own right. Their approach was a direct application of Darwin's theories, and it contrasted with the approach of comparative psychologists, who focused on experimenting with just a few selected species and conducted laboratory studies on learning, usually with the aim of understanding human behavior rather than animals per se. Some syntheses were attempted between the two directions. Particularly in the second half of the twentieth century, it was discovered that there are methodological ways of studying areas of animal behavior that had been thought to escape scientific scrutiny. Today, there is evidence that many mammals may have higher cognitive abilities that, for a long time, were thought to be uniquely human or, just by proximity to humans, partially present in apes.

Emotions and Cognitive Abilities in Animals

And it is at this point that one ought to return to Darwin and examine what he attributed to animals. In *The Descent of Man*, particularly in chapters 2 and 3, called "Mental Powers of Man and the Lower Animals," Darwin makes a number of observations that, despite certain shortcomings in interpretation (but only when judged against current scientific knowledge), illuminate a field of studies in animal behavior that has been in ascent ever since the 1980s. We shall address his catalog of behavioral attributes in animals in the order in which Darwin described and named them in these chapters (note that page numbers in brackets refer to *The Descent of Man*).

Feelings

First, Darwin addresses the question of feeling in animals. He argues that animals feel pleasure, pain, misery and fear. These claims are now largely supported by research and form the basis of animal ethics codes around the western world. He further claimed that certain species show strong individual differences in temperament. Today, we may not use Darwin's terminology, such as "timidity" or speak of "ill-tempered" or "sultry" animals, as Darwin did, but the study of individual temperament is now being investigated again.

Higher Mental Powers

In the same chapter, he makes an even more daring assumption that complex emotions are common to "higher animals" and humans. Complex emotions, in Darwin's catalog, include jealousy and modesty. This is something that we still have not proven, although owners of companion animals have long since believed that their pets can show such emotions and some researchers are investigating these questions.

Attention and Imitation

In Darwin's view, two particular abilities foster learning and therefore higher cognition: One is the "the power of attention" and the other the "power of imitation" (p.44). If an individual organism can attend to something then it is possible for that individual either to imitate what it has seen or to be taught to do something. Research into a large variety of species (including birds and primates) has shown that both can be present in one species and be part of learning, hence behavior is not based solely on instinct.

Reason

Today we might refer to the powers of reason Darwin described as problem-solving ability. Problems can be solved by trial and error, by learning from others (observation) or by insight. Many authors rather too hastily attributed the problem-solving abilities of apes merely to imitation learning, but there are many more recent reports indicating insight learning. It may well be that only a few individuals within a group or species may possess the power of insight and that others then learn from that individual, by imitation, but this does not negate this ability.

As an aspect of higher cognitive abilities, Darwin also mentions memory and imagination. The ability to recognize an individual after a considerable passage of time or the ability to dream indicated to Darwin that "higher animals," as he called them, possess the rudiments of mind.

Tool Use

Even in Darwin's time there was debate about the existence of tool using in animals; some denied its existence altogether, but Darwin was able to point to a few recorded and published examples of tool using in chimpanzees and baboons. He describes the case of a chimpanzee "in a state of nature" (i.e., not in captivity) using a stone to crack a nut and an orangutan using a stick as a lever or, baboons, in conflict with neighboring troops of another species, using stones in defense, hurling them down a slope against their assailants (p.51). Similarly, Darwin quotes reports by Wallace of orangutans throwing sticks and spiky durian fruit like missiles at the human observer. We now have further evidence that some species use tools, and that such tool using may be more versatile than had once been thought. Elephants are credited with tool using, and the tool using of the great apes is now very well documented. Moreover, tool using has been discovered more recently in birds.

Darwin, to some extent, disagreed with the Duke of Argyll that the fashioning of tools is altogether unique to humans by downplaying the human "invention" of using flint stones and how the first fashioning of such tools may have come about (p.52). Today, we have detailed research accounts of the fashioning of tools by some great apes and by one avian species, the New Caledonian crow, reported in *Nature* and other journals in the 1990s. Such fashioning of tools may be relatively simple—varying the length of a stick to make it fit a tree hole—but also more complex—varying the shape of a tool (creating multistep tools in the case of New Caledonian crows) in order to fulfill a particularly difficult extracting task—or one may think of the detailed descriptions of chimpanzees using an anvil and a rock to crack nuts. The anvil has to be carefully selected or even fashioned so that the nut stays in position while force is applied by a rock hammered from above.

As examples of tool using Darwin also referred to nest building and building of shelters, as had been observed of orangutans and baboons. Some of the examples of tool using today are still hotly debated in the sense that they may have come about as a result of

proximity to humans and can, therefore, not be classified as something peculiar to the species. Darwin's point about tool using acquired because of the presence of humans is still noteworthy because the individuals in question continued to use the tools thereafter in appropriate ways, and sometimes in new and different situations, showing that they had not just mimicked a behavior but that they had understood the function and uses of the tool they were shown.

Property, Art, Culture, Perception of Beauty

Darwin's description of rudimentary presence of a sense of property, art and perception of beauty does not necessarily strike a cord today, certainly not in scientific study of animals. However, we cannot quite dismiss them outright either. He described, for instance, the episode of a chimpanzee hiding his favorite rock with which he liked to crack nuts. Darwin thought that this was evidence of a sense of property. The stone had no direct food value and other stones were available. Research refers to food storing in animals as *caching* and in many of these cases (known in species of various corvids and described in detail in woodpeckers and especially in the nutcracker), such caching becomes a vital survival task; in such cases, food has to be stored for the lean winter months ahead or the individual will starve. However, some crows and ravens simply do not pass up a food offer even when there is plenty about, and they cache it and retrieve it, sometimes on the same day. The important point here, relating to Darwin's claims of a sense of property ownership, is that the caching process in these crows and ravens is accompanied by repeated checking of the environment. If there is another crow that might have watched, the caching individual will at once retrieve the find and try to hide it somewhere else. In other words, there is some understanding that another might desire the same morsel and might take it. Guarding against this could certainly be regarded as taking possession of the food item. It may also indicate that the caching individual is aware of a state of mind of another and, evidently, capable of foreseeing that it could be stolen. Hence, a sense of property ownership might indeed be regarded as a higher cognitive ability.

Sexual Selection

Darwin refers here largely to sexual selection and female choice—the colorful displays of male birds or their complex tunes, in his view, are a sign that the female must have a sense of beauty and will choose the most beautiful one. Modern research regards certain features of display as signaling health, strength and perhaps even intelligence, but not "beauty." However, the case of the bowerbird is somewhat difficult to accommodate in the model of "health," and this is Darwin's clinching argument for a perception of beauty. After all, the bowers that various species of male bowerbirds build are not nest sites. Bowers are purely for display and they can be extremely elaborate structures that serve no known specific purpose other than to attract females. The bowers are often decorated with shapes and objects of bright colors. Some decorate only in one color, others in multiple arrangements. Females come and inspect them in detail and they may consent to a mating or fly off after such inspections. However, there is another way to argue this—a bower can certainly signal the age and maturity of a male bird. Immature and young adult male birds also build bowers, but these are not skillful, even to the human eye, and it takes bowerbirds a long time to perfect the art of building such a bower, usually by watching successfully breeding adult males build their bowers—the age and maturity of the courting male may be the trigger of which the bower is its visible signal.

Culture

Today, scientists take less, or no, offense when the argument is made that certain species of animal, foremost primates, possess something akin to "culture," as Darwin suggested. Culture in animal behavior studies refers to the presence of behaviors or habits that may be specific to a species in one geographical location but not in another, and persist over generations within the same area.

Sociability in Animals

Darwin argues that social animals in particular might well develop higher cognitive abilities and even a conscience, namely, altruism. He writes that animals living in groups tend to perform a number of services for each other, the most common of which is to respond as a group or on behalf of the group in the case of danger. A joint action might ward off a much larger predator. Another is to warn each other of danger. He cites groups of monkeys issuing not only cries of danger but also of safety so that group members can resume normal activities (p.74). He includes mutual touching, licking and grooming among the services, and even such cases as protecting group members when ill or even blind (p.77, final pages of Ch.3, *The Descent of Man*). The concept of altruism gave rise to many debates, especially in the 1970s and 1980s, since sociobiologists could not see how genes encoding altruistic behavior would be passed on from generation to generation.

Darwin's Contribution to Science

In Charles Darwin's theoretical mold, animals are not extraneous to us, in the sense that we are not separate from the animal world, but one of the evolutionary extant outcomes of this process. Darwin's influence on the study of animal behavior is as diffuse as it is distinct. His theories have been misused and taken at face value in alluring pseudoscientific justifications for a host of unethical human acts, beliefs and values. We cannot blame Darwin for the latter (even though his views on human cultures were circumscribed by nineteenth century understanding) because he presented us with a way of viewing all living things in such a new light that his contribution is equal to Galileo's. As in the case of the position of the earth in the solar system and the loss of the earth as the center of the universe, Darwin's view took away something of the centrality and importance of human beings. What has been gained instead is a new appreciation of the importance of animal life around us as something that matters for understanding life, including our life. That is part of the reason why we continue to have an abiding interest in animals and in animal behavior. More unsettling is the thought that evolution is an ongoing process and that living organisms will change in the future. The study of animal behavior today is also a study of how these processes have functioned and to discover laws about the existence, preservation or disappearance of certain traits. Yet it is wise to remember that Darwin's many theoretical contributions and astute observations are not easily fitted into a simple formula. It would be nice if we could crystallize Darwin's views on animal behavior into a few simple lines. Unfortunately, as Stephen J. Gould reminded us a decade ago, conceptual complexity is not reducible to a formula "as we taxonomists of life's diversity should know better than most" (Gould 1994, 6774).

See also Anthropomorphism
Cognition—*Cognitive Ethology: The Comparative Study of Animal Minds*

Cognition—*Theory of Mind*
Culture
Emotions—*Emotions and Affective Experiences*
Frisch, Karl von *(1886–1982)*
History—*History of Animal Behavior Studies*
Lorenz, Konrad Z. *(1903–1989)*
Sociobiology
Tinbergen, Nikolaas *(1907–1988)*
Tools—*Tool Use*

Further Resources

Barnett, M. 1981. *Modern Ethology*. London: Oxford University Press.

Boakes, R. 1984. *From Darwin to Behaviourism*. Cambridge, UK: Cambridge University Press.

Darwin, C. 1981. *The Descent of Man, and Selection in Relation to Sex*. Facsimile from 1871 edition held in the Firestone Library, Princeton University, Princeton University Press, Princeton, NJ.

Darwin, C. 1890. *The Origin of Species by Means of Natural Selection*. 6th edn., London: John Murray.

Darwin, C. 1904. *The Expression of the Emotions in Man and Animals*. London: John Murray.

Darwin, C. & Wallace, A. R. 1844. *Evolution by Natural Selection*, Cambridge, UK: Cambridge University Press.

Dewsbury, D. A. 1992. *Comparative psychology and ethology. A Reassessment*. American Psychologist, 47(2), 208–215.

Gould, S. J. 1994. *Tempo and mode in the macroevolutionary reconstruction of Darwinism*. Proceedings of the National Academy of Science USA, 91, 6764–6771.

Heinroth, O. 1985. *Contributions to the biology, especially the ethology and psychology of the Anatidae*. In: *Foundations of Comparative Ethology* (Ed. by G. M. Burghardt), pp. 246–301, New York: Van Nostrand Reinhold.
(original work: 1911, Ornithologen-Kongress, Berlin, pp. 589–702).

Hinde, R. A. 1966. *Animal Behaviour: A Synthesis of Ethology and Comparative Psychology*. London: MacGraw-Hill.

Huxley, J. 1942. *The Living Thoughts of Darwin*. London: Cassell.

Jaynes, J. 1969. *The historical origins of 'ethology' and 'comparative psychology'*. Animal Behaviour, 17, 601–606.

Kaplan, G. & Rogers, L.J. 2003. *Gene Worship*. New York: Other Press.

Lehrman, D. S. 1953. *A critique of Konrad Lorenz's theory of instinctive behavior*. Quarterly Review of Biology, 28, 337–363.

Lorenz, K. 1980. *A personal introductory history of ethology*. The Journal of Mind and Behaviour, 1(2), 171–122.

Page, R. E. Jr. 1997. *The evolution of insect societies*, Endeavour, 21 (3), 114–120.

Plotkin, H. C. (Ed.) 1988. *The Role of Behaviour in Evolution*. Cambridge, MA: MIT.

Rogers, L. J. & Kaplan, G. Eds. 2004. *Comparative Vertebrate Cognition: Are Primates Superior to Non-primates?* New York: Kluwer Academic /Plenum Publishers.

Thorpe, W. H. 1979. *The Origins and Rise of Ethology: The Science of the Natural Behaviour of Animals*. New York: Praeger.

Tinbergen, N. 1951. *The Study of Instinct*. Oxford, UK: Oxford University Press.

Whitman, C. O. 1898. *Animal Behaviour*. Biology Lectures of the Marine Biology Laboratory, Wood's Hole, MA, 285–338.

Gisela Kaplan & Lesley J. Rogers