Darwin and Animal Behavior

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For many thousands of years, at different times and in different parts of the world, humans have studied their fellow creatures in an attempt to obtain a better understanding of their behavior. Toward the end of the eighteenth century, an increasing amount of observational – and occasionally experimental – research on behavior took place in Western Europe. Nonetheless, the foundations of the contemporary science of behavior were mainly provided by the evolutionary theories and the ensuing debates of the nineteenth century. Of these, the key event was, of course, the publication in 1859 of Charles Darwin's 'On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life' (henceforth referred to as '*The Origin*').

From his youth, Darwin continued to maintain a keen interest in behavior. An early hobby was collecting beetles, and it is clear that he was intrigued as much by how they and other insects behaved as by their bodily structures. For decades, he maintained notebooks on behavior, read widely on the subject, and exchanged letters full of questions about the behavior of a wide variety of species, with correspondents throughout the world. Darwin's concern with behavior becomes evident in '*The Origin*' when he discusses what he saw as four major difficulties with his theory. The third of these was that of answering the question: "Can instincts be acquired and modified through natural selection?," and in Chapter 7, he gives his reasons for believing that behavior was as much subject to natural selection as a bodily characteristic. He starts by acknowledging that some forms of instinctive behavior may derive from habits acquired by a previous generation, as Lamarck had argued 50 years earlier. But the core argument of the chapter is that "it can clearly be shown that the most wonderful instincts with which we are acquainted, namely, those of the hive-bee and of many ants, could not possibly have been thus acquired." Spelt out with many examples, his simple but conclusive point is that in a number of insect species various innate behaviors are displayed only by sterile individuals. This means that "a working ant ... could never have transmitted successively acquired modifications of structure or instinct to its progeny." He then proceeds to the "climax of the difficulty; namely, the fact that the neuters of several ants differ, not only from the fertile females and males, but from each other, sometimes to an almost incredible degree." Citing both his own measurements and data from others showing variation in the size and other characteristics of worker ants, Darwin concludes by explaining how natural selection operating on the parents could give rise to two or more kinds of neuter individuals. In so doing, he took the innate behavior of insects from being a key example of God's design to becoming important evidence for the power of natural selection (**Figure 1**).

The '*Origin of Species*' has justifiably been recognized as a magnificent book, and not just an extraordinarily important one. It is confident, passionate, and carefully constructed so as to convince the reader of two ideas: first, that no coherent account of the origin of species by special creation is possible; and, second, that natural selection is the primary process by which species evolve. As Darwin noted later, he deliberately played down issues that might divert attention from his two main arguments; some topics "would only add to the prejudice against my views." These included the importance or otherwise of Lamarckian inheritance and of sexual selection as secondary processes in evolution. He also postponed discussion of what would have been highly explosive in the predominantly religious society of mid-nineteenth century Britain, namely, that human beings were as much a product of natural selection as any other form of life. Famously, he simply notes just before the end of the book: "In the distant future I see open fields for far more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be thrown on the origin of man and his history." In 1859, arguing that other species had evolved was explosive enough.

Darwin's first aim was met within a remarkably short time. By the time the third edition of '*The Origin*' was published in 1861, he could write: "Until recently the great majority of naturalists believed that species were immutable productions, and had been separately created"; he then noted that this was no longer true. This rapid reversal was helped by the effective efforts of several of Darwin's scientific colleagues and friends, notably, Thomas Huxley, who relished the battle with orthodox and religious opinion. Huxley also boldly published the first book to contain a detailed argument for human evolution. His '*Evidence for Man's Place in Nature*' of 1864 started with a provocative and endlessly reproduced frontispiece in which a human skeleton heads a line containing skeletons of a gorilla, a chimpanzee, an orangutan, and a gibbon (**Figure 2**).

Alfred Wallace had developed the idea of natural selection independent of Darwin and, if Wallace's article describing natural selection sent from faraway Indonesia had not shocked Darwin into sudden urgency, '*The Origin*' would not have been published until much later than 1859 and probably in a less satisfactory form. In some ways, Wallace was more of a Darwinian than Darwin. He saw no need to accept any form of Lamarckian process to complement natural selection, and he argued that the idea of sexual selection was also unnecessary. On the other hand, having dismissed all other possible evolutionary processes except natural selection, he was unable to understand how human intellect and morality could have evolved. In 1869, Wallace appealed to supernatural intervention that had been applied to some human progenitor (**Figure 3**).

Figure 1 A portrait of Charles Darwin around the time that he began to develop the theory of natural selection.

This time Darwin was shocked into publishing '*The Descent of Man and Selection in Relation to Sex*' of 1871 (hereafter referred to as '*The Descent*'). Darwin focused on three questions: "Whether man, like every other species, is descended from some pre-existing form"? What was "the manner of his development"? And what is "the value of the differences between so-called races of man"? Since Huxley and the German biologist, Ernst Haeckel, had already spelt out the evidence for evolution of the human body, Darwin concentrated on the human mind and on rebutting Wallace's claim that "natural selection could only have endowed the savage with a brain little superior to that of an ape."

Darwin's deep belief in human evolution went back to the day when, as a young biologist sailing on HMS *Beagle*, he landed on a beach in Terra del Fuego: "The astonishment which I felt on first seeing a party of Fuegians on a wild and broken shore will never be forgotten by me, for the reflection at once rushed into my mind – such were our ancestors." Nearly 40 years later, he took on the task of persuading his now large readership

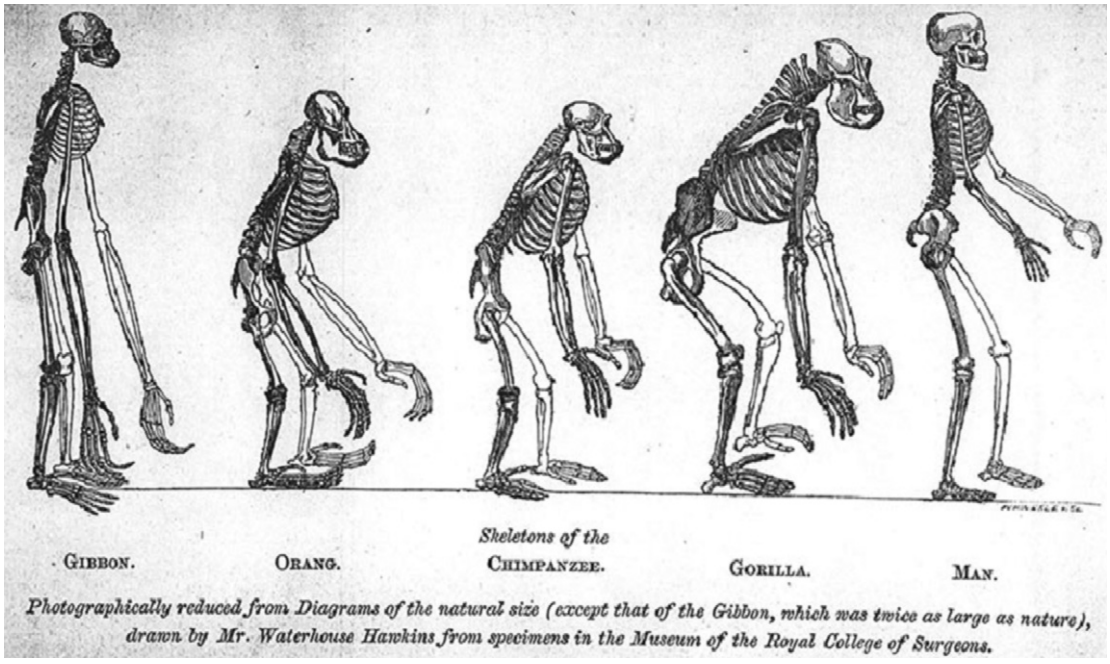

Figure 2 The frontispiece to Thomas Huxley's '*Evidence for Man's Place in Nature*' (1864).

Figure 3 Alfred Wallace.

beyond that belief to the idea that the intellectual and moral sophistication of Europeans was not just related to the intellect and morals of Fuegians but had evolved from simple forms of life.

In arguing for mental evolution, Darwin aimed to undermine the view that animals were incapable of reasoning, did not display emotions, had no form of communication that in any way resembled human language, and never displayed behavior that could be described as 'moral.' In relation to reasoning, he cited various examples, mainly culled from his worldwide correspondence, of problem solving and tool use, mainly by apes. As for the emotional life of animals, he was unreservedly anthropomorphic: He had no doubt that 'elephants intentionally practice deceit' or that 'a dog carrying a basket for his master exhibits in a high degree self-complacency or pride.' In considering language, he pointed to examples of vocal communication in other species and vocal mimicry in birds like parrots. His argument for the evolution of morality took a similar approach, using examples of altruistic behavior in various species. Darwin concluded that "the difference in mind between man and the higher animals, great as it is, is one of degree and not of kind."

This first part of '*The Descent*' lacked the confidence displayed in '*The Origin*.' The evidence he put forward for his views was predominantly second hand, that is, gleaned from correspondence and reading rather than direct observation and experimentation. When in the second part of the book he describes his theories of sexual selection, it is as if with relief that he has reached safer ground. Here, he discusses ideas he had thought about for decades, based on an accumulation of detailed evidence. Having noted that sexual selection is most effective in polygamous species, in the final part of the book he united the two main – and to this point – apparently unrelated themes. In human evolution, he suggests, sexual selection has played a dominant role both in the development of secondary sex characteristics – nakedness and male beards, for example – and intellectual ability. However, the latter is not spelt out. As for the third main question with which '*The Descent*' started, that concerning the significance of racial differences, Darwin had no doubt that all humans were descended from a common ancestor, a view that directly contradicted the influential claim put forward by Louis Agassiz, the most important American biologist of that time.

We have seen that in '*The Origin*' the behavior of insects was deployed as an argument against the adequacy of Lamarckian inheritance. In '*The Descent*,' the behavior of vertebrates was used in the argument for human evolution, albeit with almost no appeal to natural selection but with a great deal to Lamarckian inheritance and some to sexual selection. Only a year after publishing '*The Descent*,' Darwin published the third of his books in which the study of behavior was important. '*The Expression of the Emotions in Man and Animals*' of 1872 (henceforth referred to as '*The Expression*') has the same sense of excitement as '*The Origin*,' with Darwin confident that his account of emotional expression within an evolutionary framework was far superior to its few predecessors.

'*The Expression*' was certainly superior in terms of its empirical base, in that for many years Darwin had been gathering a range of evidence on the topic. This evidence included the innovative use of photographs, ones of angry, fearful, sad, or happy children; of actors simulating such emotions; and even of inmates of an asylum for the insane. These were accompanied by prints – for example, of a snarling dog, a terrified cat, and of monkeys and chimpanzees displaying various moods – to illustrate the argument that human expressions were a product of evolution and that the same principles applied to both human and animal emotions.

These principles were based on the core idea that it is highly adaptive for individuals to signal their emotional states as clearly as possible: "With social animals, the power of inter-communication between members of the same community – and with other species between opposite sexes, as well as between the young and the old – is of the highest importance to them." The first of the three principles was based on the inheritance of "serviceable associated habits." In other words, some form of effective communicative behavior is first learned by a process of trial and error (although Darwin did not use this term), becomes an ingrained habit, and is then passed on via some genetic process so as to become instinctive in later generations. The second is the principle of antithesis: behavior expressing one emotional state – say, affection – is likely to be as different as possible from behavior expressing the opposite state – say, hostility. Remarkably, Darwin did not justify this principle in terms of more effective

communication, as with hindsight we might expect from the author of '*The Origin*.' Instead, he appealed to 'the tendency to perform opposite movements under opposite sensations or emotions.' The third principle appealed to the 'constitution of the nervous system,' an unusual appeal in Darwin's works on behavior. He borrowed from a fellow evolutionist, Herbert Spencer, the idea that 'nervous energy' can overflow into 'less habitual' responses. For example, trembling is explained as the result of intense excitation of the autonomic system.

As in '*The Descent*,' there is almost no mention of natural selection in '*The Expression*.' Instead, the principle throughout is implied: individuals that can communicate better, using their species-specific behaviors, are likely to have more offspring. Darwin stressed the similarities between human and primate emotional expression, but found one example that he decided was uniquely human. Blushing, he argued, required self-consciousness, awareness that someone else might be looking at one's face; and thinking about one's face would automatically increase blood flow to this area (**Figure 4**).

Although Darwin made frequent reference to the acquisition of new behaviors that became habits, he does not seem to have had much interest in the processes by which such learning occurs. In contrast, this topic was of central concern to Herbert Spencer. In the 1860s and 1870s, Spencer was regarded by his peers, as well as by the general public, as important an evolutionary theorist as Darwin. Spencer had coined the term, 'survival of the fittest,' well before Darwin went public with the theory of natural selection. Nevertheless, Spencer maintained throughout his long and eccentric life that Lamarckian inheritance was the main driver of evolution and that natural selection was a secondary process – the reverse of Darwin's belief. As announced in 1855 in his first edition of the '*Principles of Psychology*,' Spencer's main concern was with mental evolution: 'Mind can be understood only by showing how mind is evolved.' He believed that mental evolution is based on the transformation of reflexes into instincts and of instincts into intelligent behavior. In 1855, he proposed that the main driver of such transformations was what later would be known as Pavlovian conditioning. In 1871, in the second edition of his '*Principles of Psychology*,' he added a second learning process, based on the ideas of a contemporary psychologist and philosopher, Alexander Bain. The 'Spencer–Bain principle' stated that a response followed by some pleasant consequence will tend to be repeated.

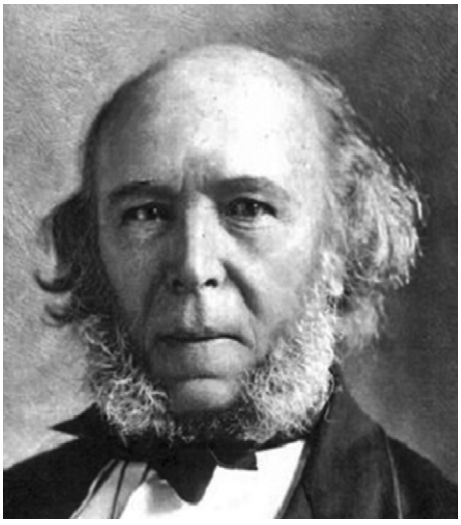

Figure 4 Herbert Spencer.

Toward the end of the nineteenth century, Spencer's work was widely derided. His Lamarckianism, his psychology, his extreme laissez-faire politics, and his system of ethics were attacked from all sides. Yet his influence continued to be highly pervasive. In particular, the Spencer–Bain principle inspired the lively concern with trial-and-error learning that emerged in the 1890s.

Two years after publishing '*The Expression*,' the then 65-year-old Darwin invited to his home in the country a young physiologist, George Romanes. Darwin decided that Romanes was just the person to develop the ideas on mental evolution that Darwin had proposed in '*The Descent*.' Their admiration was mutual. Darwin became a revered father figure for Romanes who for the rest of his life vigorously defended every aspect of Darwin's theories, even those that after Darwin's death in 1882 began to look increasingly dubious, such as his theory of inheritance, 'pangenesis,' and his belief that instinctive behavior could evolve both as a result of natural selection and from inheritance of individually acquired habits. Romanes' aim in life became that of first accumulating systematic data on animal behavior and then using these to construct a detailed theory of mental evolution following the lines that Darwin had sketched (**Figure 5**).

Although as a neurophysiologist Romanes had proved to be a very able experimenter, the data he included in his first book, '*Animal Intelligence*' (1881), were predominantly anecdotal. By the standards of his time, he had reasonable criteria for judging whether to accept a report about some animal's remarkably intelligent behavior or indication that it had experienced a sophisticated emotion. However, the social status of the observer seems to have been as important a consideration as the thoroughness of the observation in assessing the reliability of some anecdote. Despite his self-appointment – and the general perception of him – as 'Darwin's heir,' Romanes' approach owed far more to Spencer. This is seen in his preoccupation with ranking different cognitive processes and emotions. For example, he considered the ability to operate mechanical appliances as indicative of a high level of intelligence and, since he had received many reports of cats operating latches so as to open doors, he ranked this

Figure 5 George Romanes.

Figure 6 Conwy Lloyd Morgan.

species' intelligence as being nearly as high as that of monkeys. Romanes seems not to have entertained the possibility that the relatively high number of reports concerning cats might reflect both the fact that this was one of the few species that a large number of humans observe daily and the fact that few other species have frequent opportunities to interact with mechanical devices.

For Romanes, all creatures that were capable of the most primitive form of learning – for example, including ones that displayed no more than what later became known as 'habituation' – possessed a mind, and this meant that even, say, a snail was to some limited degree conscious of the events impinging on its sensory organs. He believed that consciousness played an important role in instinctive behavior and stressed that instincts could be modified by experience. For example, although there was by then extensive evidence showing that in many species of birds their adult songs were influenced by early exposure to different sounds, for Romanes this was no reason against considering birdsong to be 'instinctive.' Within this framework, it was therefore quite appropriate to refer to the 'instincts of a gentleman.'

Romanes was a generous man. When he received an article sent from South Africa that was critical of his own work, he nevertheless appreciated its quality, supporting its publication and subsequently the career of its author, Conwy Lloyd Morgan. Prior to taking up a teaching position in South Africa, Morgan had studied under Huxley and absorbed his skeptical approach. Six years after returning to England on his appointment as a professor at what was to become Bristol University, Morgan published his important book, '*Animal Life and Intelligence*' (1890), followed by his '*Introduction to Comparative Psychology*' (1895), the first book in English to bear such a title (**Figure 6**).

Morgan's influence on the study of behavior was substantial for three main reasons. The first was his insistence on the need for objective evidence based on careful experimentation or observation and the rejection of one-off anecdotal reports. Although he had become a close friend of Romanes and literary executor when Romanes died, Morgan had no hesitation in dismissing the kind of data on which Romanes had so often relied. Morgan developed many of his ideas from testing his dog, Tony. For example, he repeatedly threw a stick over a fence for Tony to retrieve and was impressed by how slowly the dog improved its ability to maneuver the stick through a gap in the fence. Just as Tony managed once to perform impressively, a passer-by stopped to watch for a few minutes: "Clever dog that, sir; he knows where the hitch do lie." Morgan noted that this was a characteristic – and in this case, entirely false – conclusion to draw from two minutes of chance observation.

Related to the need for careful and systematic observation of behavior was the need for careful interpretation of that behavior. To the extent that he is remembered today, Morgan is best known for his 'Canon.' This was essentially Occam's Razor, the scientific principle of parsimony, applied to behavior; where there are several possible explanations for why an animal behaved in a certain way, one should choose the simplest. What was new was that Morgan appealed to natural selection to justify its application to behavior. If a relatively simple process had evolved to the extent that an individual could respond appropriately in a particular context, then there would be no selective pressure to produce a

more complex process capable of producing the same behavior. Morgan's most common demonstration of how his Canon should be deployed was in the analysis of what Romanes had seen as marks of high intelligence. Based partly on some informal experiments with chicks, Morgan argued that most of such examples could be better understood as the result of trial-and-error learning with accidental success. A key example for Morgan was that of an animal operating a latch to open a door or gate. From his study, Morgan had watched the regular attempts of his dog, Tony, to escape from the garden into the wide world beyond. The dog had repeatedly thrust its head through the fence railings here and there until once, apparently by chance, it inserted its head just below the gate latch and, on raising its head, the gate swung open. From then on, this appropriate action was performed with increasing rapidity to the point when a passing observer who had read Romanes might agree that it was an intelligent creature with some understanding of mechanical devices (**Figure 7**).

The third way in which Morgan made a lasting impact came from his rejection of Lamarckian accounts of the origins of instinctive behavior. This was partly stimulated by experimental work in the 1880s of the German biologist, August Weissman, whose failure to find any evidence for Lamarckian inheritance led him to propose the distinction between 'germ plasm' and 'body plasm' that laid the foundation for modern genetics. Morgan's final break with Lamarckian accounts of instinct came only in 1896 when he developed alternative ways of accounting for the kind of evidence that appeared to support the Lamarckians. The first was inspired by the work of a French writer, Gabriel Tarde, who in 1890 discussed the 'laws of imitation.' This led to the idea that social transmission could result in the rapid spread of some behavior that an individual animal had learned among a population of conspecifics and could support the continuation of that behavior over subsequent generations. When applied to humans, the difference between Fuegians and Europeans that Darwin had attributed to biological evolution was seen to lie in differences in cultural development. Morgan's second principle, 'organic selection,' was also proposed at the same time by at least two other theorists and ultimately one of the latter gained the credit for what became known as the 'Baldwin principle.' This supposes that, when an environmental change threatens the survival of an isolated group, those individuals who have the appropriate learning capacity to change their behavior in an adaptive way will have more descendants than those whose behavior is more resistant to change. Over the generations, the benefits of learning will buy sufficient time for adaptive innate behaviors to evolve by natural selection. The removal of Lamarckian processes meant that Morgan was now able to make a clear distinction between habit and instinct, as in his 1896 book of that name.

Figure 7 Morgan's dog opening the garden gate.

Early in the nineteenth century, biologists such as Darwin and Huxley endured long voyages in sailing ships that had not changed fundamentally in the four centuries since Portuguese mariners first left Western Europe to explore the globe. Later in the nineteenth century, steam ships were regularly plying the world's oceans. The expansion of the United States economy following the Civil War and the unparalleled development of the American university system meant that British evolutionists such as Huxley and Spencer could be paid to make the easy crossing of the Atlantic to give lecture tours. Morgan gave lectures on habit and instinct in Boston in 1896, and these very probably inspired a Ph.D. student at nearby Harvard who was looking for a new thesis topic. Edward Thorndike's subsequent experiments on trial-and-error learning represented the first quantitative studies of vertebrate behavior. His *Animal Intelligence* of 1898 provoked a generation of psychologists to undertake studies of what would much later be termed 'comparative cognition.' It also laid the groundwork for the behaviorist movement with its emphasis on learning theory that dominated American psychology until the 1960s. Ironically these developments occurred at a time when Darwin's theories were seen as outdated, so that the evolutionary framework in which studies of behavior had grown was disregarded.

See also: Animal Behavior: The Seventeenth to the Twentieth Centuries; Body Size and Sexual Dimorphism; Comparative Animal Behavior – 1920–1973; Evolution: Fundamentals; Imitation: Cognitive Implications; Motivation and Signals; Problem-Solving in Tool-Using and Non-Tool-Using Animals; Psychology of Animals; Sexual Selection and Speciation; Social Learning: Theory.

Further Reading

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