

The challenge of instinctive behaviour and Darwin's theory of evolution

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In the Origin of Species (1859), Darwin argued that his revolutionary theory of evolution by natural selection represented a significant breakthrough in the understanding of instinctive behaviour. However, many aspects in the development of his thinking on behavioural phenomena indicate that the explanation of this particular organic feature was by no means an easy one, but that it posed an authentic challenge - something that Darwin himself always recognized. This paper explores Darwin's treatment of instincts within his theory of natural selection. Particular attention is given to elucidate how he tackled the difficulties of explaining instincts as evolving mental features. He had to explain and demonstrate its inheritance, variation, and gradual accumulation within populations. The historical and philosophical aspects of his theory are highlighted, as well as his study of the case in which the explanation of instincts represented a 'special difficulty'; that is, the sterile castes of social insects.

Summary

Darwin's treatment of instincts within his theory of evolution by natural selection is exposed and discussed. The first section reconstructs the historical background of the studies of instincts in natural theology and naturalism in order to put Darwin's theory in context. The second section exposes Darwin's notion of instinct. The third section exposes Darwin's demonstration of the evolution of instincts by natural selection. The fourth section argues that Darwin hold an emergentist view of instincts. The last section exposes Darwin's solution of his 'one special difficulty': the evolution of instincts and body of sterile insects.

Introduction

A possible view of Darwin's approach to behaviour is that it was a simple inclusion of an organic feature under the scope of his theory of evolution.¹ However, a deeper analysis reveals that it was more complex than that, especially with instinctive behaviour. Darwin himself pointed this out. In the Origin of Species (1859), he listed what he considered to be the four main difficulties of his theory. The third was the explanation of instincts: 'can instincts be acquired and modified through natural selection? What shall we say to so marvellous an instinct as that which leads the bee to make cells, which have practically anticipated the discoveries of profound mathematicians?.² He did not overcome the challenge of explaining the evolution of instincts straightaway once he conceived his theory of natural selection in 1838. Rather, he developed and refined solutions cautiously over several years.³ His mature views appeared mainly in the chapter VII ('Instinct') of the Origin. Here he advanced that, despite being mental, instincts can be adequately explained as if they were corporeal structures of the organism since they meet the necessary conditions to evolve by means of natural selection. Moreover, based on this perspective, he was able to solve the historical difficulties of a particular type of instincts dubbed 'wonderful instincts,' including those of the sterile castes of social insects.

This paper explores Darwin's treatment of instincts within his theory of evolution by natural selection. Particular attention is given to the difficulties of explaining instincts as evolving mental features. Darwin had to show that instincts varied, these variations were heritable, and beneficial variations could accumulate gradually in populations. In the following two sections I briefly consider the historical background and Darwin's context regarding the studies and opinions on instinctive behaviour. I argue that this context, in addition to his scientific goal of explaining the evolution of the vast diversity of species, determined his notion and definition of *instinct*. In the next section, I expose the evidence and arguments put forward mainly in his Origin in order to sustain that instincts evolve by natural selection. One interesting issue which is sometimes neglected in the studies of Darwin's theories of behaviour is the underlying

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of Medicine, 41: 24–43. Available online 3 February 2016

 $^{^2}$ Darwin, C. R. (1859). On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. London: John Murray. p.172.

³ Burkhardt R.W. (1985). Darwin on Animal Behavior and Evolution. In: Kohn, D., ed. The Darwinian Heritage. New Jersey: Princeton University Press. pp. 327–365; Richards, R. J. (1987). Darwin and the Emergence of Evolutionary Theories of Mind and Behavior. Chicago: The University of Chicago Press. pp. 83–110.



Figure 1. Portraits of William Paley (left) and Charles Darwin (right) at the Dining Hall, Christ's College, University of Cambridge, Cambridge, U.K. Photo courtesy of Dr. Richard Bellon.

philosophical commitment to the body/mind problem. This matter, in relation to instincts, will be addressed in the next section followed by an exposition of his brilliant solution to the 'one special difficulty.'

Historical background and context

The notion that living beings can display certain behaviour without consciousness and without individual experience has been present throughout the history of Western thought.⁴ In many cases, this kind of behaviour has been contrasted with man's reasoning capacity. It has been thought that since humans think, learn and act deliberately, then we behave rationally rather than instinctively. Hence, the roots of the study of instincts can be traced back at least to the ancient Greeks who conceived a dualism of man's rationality on the one hand and animals' natural and blind impulses on the other.⁵ Interestingly, this proposed classification had an important impact in the religious worldviews of medieval Europe like Christian philosophy which adopted it as a basic notion. For theologians such as Thomas Aquinas, instincts show the manifestation of the divine providence since God has 'planted' in animals beneficial instructions.⁶ Also, the description of animals as instinctive instead of rational creatures justified the image of man as the only of God's creature with a soul and an afterlife in Heaven or Hell.

In the eighteenth and nineteenth centuries, natural theologians continued reflecting about instinctive behaviour and the divine providence in light of the vast increase of knowledge on natural history. The world was being enthusiastically explored by Europeans and it was not rare for naturalists to join naval expeditions to investigate nature in remote lands. They typically published their findings and stocked museums with their collections of specimens. The Anglican clergyman William Paley (Figure 1) reflected on this outpouring of new information in his classic work Natural Theology, published in 1802 and avidly read by the young Darwin. Paley, like Thomas Aquinas, thought that diverse and complex instincts provided compelling evidence that nature is divinely designed.⁷ In the same vein, other natural theologians pointed to various instincts whose complexity in their view provided irrefutable proof of God's interventions in nature. William Kirby and Henry Lord Brougham, in works that Darwin read closely, used the honey bees' hivebuilding instinct, the bird's nesting instinct, and the instincts of the sterile insects as pillars in their arguments for natural theology.⁸

Although the discussion on instincts was restricted to the theological domain for a considerable time, an important and revolutionary change happened. A new philosophical and scientific program emerged in the Enlightenment of the eighteenth century which rejected religious dogmatism and sought explanations of physical phenomena in natural rather than supernatural causes. René Descartes, whose ideas were founders of this movement, proposed an influential view on animal behaviour which largely fostered the pre-nineteenth debates on instinct. He and his disciples argued that animals function and behave like organic automata governed by the laws of mechanics.⁹

 $^{^4\,}$ For a thorough historical reconstruction see Wilm, E. C. (1925). The Theories of Instinct: A Study in the History of Psychology. New Haven, CT: Yale University Press.

⁵ Beach, F. A. (1955). The Descent of Instinct. *Psychological Review*, 62(6): 401–410; Wilm (1925). op. cit. note 4.

⁶ See, for instance, Thomas Aquinas (1265–1274). Summa Theologica. Part I-II (Primae Secundae). Q.40, Art.3, Ad. 1.

⁷ Paley, W. (1802). Natural Theology; or, Evidences of the Existence and Attributes of the Deity, Collected from the Appearances of Nature. London: Taylor and Wilks. pp. 324–345.

⁸ Richards, R. J. (1981). Instinct and Intelligence in British Natural Theology: Some Contributions to Darwin's Theory of the Evolution of Behavior. *Journal of the History of Biology*, 14(2): 193–230. pp. 209–226.

⁹ Rosenfield, L. C. (1941). From Beast-Machine to Man-Machine: Animal Soul in French Letters from Descartes to La Mettrie. New York: Oxford University Press; Wilm, 1925, op. cit. note 4. pp. 78–84.

Antagonist views of Cartesianism were hold by sensationalists and neo-Aristotelians. Sensationalists thought that the equation of animals with machines misses out important mental faculties which play a role in the execution of behaviour such as ideas, memory, judgements, and so on. Meanwhile, neo-Aristotelians refused to divorce from the traditional notion of soul. They considered that animals have a sensitive soul and that their behaviour is guided by sensory faculties.¹⁰

A revolutionary idea arose amidst these debates in natural history. Naturalists such as Erasmus Darwin (grandfather of Charles). Jean Baptiste Lamarck, and others, thought that species can experience organic modification throughout time.¹¹ The traditional conception of instincts as fixed was irremediably challenged: either instincts are likely to change or they are not organic features at all. Although the work of each of these naturalists was ambitious and interesting in its own right, the most elaborated and compelling pre-Darwinian theory, as well as influential, was what came to be known as 'Lamarckism.' Within his evolutionary approach, Lamarck introduced two core theories: the inheritance of acquired characteristics and the use-disuse dynamics. Both theories can give an account of the evolution of behaviour - something that Darwin appreciated and echoed in his own views to some degree (see Section: Darwin's theory and instinctive behaviour).¹² In fact, long before he graduated from Cambridge University in 1831, ideas about the evolution of behaviour were commonplace if still outside of the scientific mainstream. In this sense, his was a voice among others, although the one that launched a new scientific paradigm whose heritage has largely influenced the modern behavioural sciences, particularly ethology and psychology.¹³

Darwin's notion of instinct

In many aspects, Darwin's definition of instinct and instinctive behaviour coincided with the vernacular of his epoch. In general, these terms were used to point out those behavioural characteristics, or the qualities that influence behaviour, which were not learnt or acquired by experience but that one was 'born with them.' Hence, Mozart had an instinctive skill for music and the caterpillar's ability to weave its cocoon is an instinct.¹⁴ An initial worry of this use of non-specialist terms in scientific work is that it might be harmful for its development leading to imprecise results. However, in the case of Darwin, instinct thus defined was consistent with his main purpose, that is, to explain the mechanism and factors involved in the evolution of the innumerable species on Earth. So, arguably, there was no need to aim for a technical definition. In all of his work, he only devoted one paragraph in the Origin to stipulate

details and clarifications of what he meant by *instinct*, and although it would seem unhelpful by judging the very first sentence, is sufficient to comprehend his notion.

I will not attempt any definition of instinct. It would be easy to show that several distinct mental actions are commonly embraced by this term; but every one understands what is meant, when it is said that the instinct impels the cuckoo to migrate and to lay her eggs in other birds' nests. An action, which we ourselves should require experience to enable us to perform, when performed by an animal, more especially by a very young one, without any experience, and when performed by many individuals in the same way, without their knowing for what purpose it is performed, is usually said to be instinctive.¹⁵

Leaving aside the essential characteristics of innateness and unconsciousness, there are some further points worth noting. First of all, instincts are heritable. Although this might not be conflicted with the natural theology's view,¹⁶ Darwin argued that inheritance is an important reason to think that instincts are subjected to evolution rather than fixed at Creation. Secondly, Darwin thought that they are 'mental powers' which function is to predispose the organism to behave in certain ways and in certain directions; hence there are many different instincts and they can only be identified and classified by appealing at the different purposes they serve. He provided examples which included the nesting instinct, the migration instinct, the comb making instinct, and the fear instinct.¹⁷ Thereby, they can be interpreted as the inheritable units or patterns of behaviour. Another important point is that Darwin thought that not only instincts are responsible for the displays of innate behaviour, but that there are other innate factors such as intuitions, sensations, emotions and senses that may play a role, and although they are not the patterns of behaviour, nonetheless it can be said that they are instinctive. Finally, instincts are stereotyped. Either in the whole species, in local groups, in the genera or in the family, instincts 'are performed by many individuals in the same way.' Although Darwin's notion of instinct might be ordinary in the sense that it largely coincided with the laymen's view, it was his explanation of the phenomenon what was extraordinary - as we shall see in the following section.

Darwin's theory and instinctive behaviour

When Darwin returned to England in 1836 after circumnavigating the southern hemisphere aboard H.M.S. Beagle (1831–1836), he began to consider seriously that species are not immutable as the natural theologians and most naturalists believed. To understand why he thought evolution plausible, first we have to see Darwin as a naturalist

¹⁰ Richards, R. J. (1979). Influence of Sensationalist Tradition on Early Theories of the Evolution of Behavior. *Journal of the History of Ideas*, 40(1): 85–105.

¹¹ See Corsi, P. (2005). Before Darwin: Transformist Concepts in European Natural History. Journal of the History of Biology. 38(1): 67–83.

 ¹² Lamarck, J. B. (1963). Zoological Philosophy; an Exposition with Regard to the Natural History of Animals. In: Elliot H., tr. New York: Hafner Publishing Company. pp. 106–127.
¹³ For a very brief summary of Derwin's influence and Euclideate C. M. (2000).

¹³ For a very brief summary of Darwin's influence see, Burghardt, G. M. (2009). Darwin's Legacy to Comparative Psychology and Ethology. *American Psychologist*, 64(2): 102–110.

¹⁴ Darwin (1859). op cit. note 2. p. 208–209.

¹⁵ Darwin (1859). op cit. note 2. p. 207.

¹⁶ See, for example, Paley (1802), "Of the Succession of Plants and Animals". op. cit. note 7. pp. 41–44.

¹⁷ These were some of the most discussed instincts by the intellectual communities of the epoch, including Darwin. Besides the Origin of Species, he also discussed them in his Essay on Instinct (1883), The Descent of Man, and Selection in Relation to Sex (1871), The Expression of the Emotions in Man and Animals (1872), in his Notebooks (1836–1844), Private Correspondence (url: http://www.darwinproject.ac.uk) and others.

in its broadest sense. He was interested in every type of natural phenomena that fell under his view. Geology, anatomy, physiology, and biogeography all absorbed his attention. During the expedition, he collected a wide array of botanical and zoological specimens.¹⁸ Moreover, he began to recognize patterns and relationships in the biological diversity he encountered. He realized, for instance, that the living and extinct species of South America were spatiotemporally related. 'It was evident,' he wrote in his *Autobiography*, 'that such facts as these, as well as many others, could only be explained on the supposition that species gradually become modified; and the subject haunted me.'¹⁹

Since the beginning of his speculations on the origin of species, Darwin assumed that instincts are subjected to evolution. Before conceiving the principle of natural selection, he suggested an early mechanism for the modification of species in which instinctive behaviour was the main cause. In his Transmutation Notebooks (1836-1838), he viewed instincts as 'lapsed intelligence.' If living beings intelligently change their habits in order to adapt to their living conditions and if these habits are displayed by several generations, then they can become hereditary instincts. As a consequence, the morphological structures of the organism can be modified in a way that better suit the execution of the new behaviour. As he stated: 'According to my views, habits give structure, therefore habits precede structure, therefore habitual instincts precede structure.²⁰ If this dynamics continued for a long time, then new species with new adaptive characteristics emerge. This 'early theory' suspiciously resembled Lamarck's two theories of inheritance. The first one says that only the corporeal traits used are inherited and developed (or as Darwin put it, 'habits precede structure') while those disused are not. The idea that individuals can practice new habits and then transmit them to their offspring coincides with Lamarck's second theory of acquired traits.²¹

This approach, however, lost its centrality in 1838 when Darwin read Malthus's *Essay on Population*. He realized then that Malthus's principle of 'struggle for existence' applies in natural conditions and to every species. The line of reasoning is straightforward. 'A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase,' he wrote in the *Origin*. 'Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life.²² Although it has been argued that Darwin just extended the Malthusian notion of 'struggle' to nature, he actually reformulated it when he insisted that there are various overlapping arenas of competition: intra-species, inter-species and species with the environment.²³

Based on a scientific method broadly influenced by John Herschel and William Whewell, Darwin proposed that the mechanism of evolution, the vera causa or true cause of the organic world, is the natural selection.²⁴ As he summarized it: 'if variations useful to any organic being ever do occur. assuredly individuals thus characterised will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance, they will tend to produce offspring similarly characterised. This principle of preservation, I have called, for the sake of brevity, Natural Selection.²⁵ Like the artificial selection of domesticated plants and animals, the 'selected' corporeal or behavioural variations can gradually accumulate in subsequent generations of the species. This whole process, Darwin insisted, explains the richness of the living world. Over the course of millions of years, and from at most a few primordial forms, life had diversified into a complex web of interdependent species through natural selection working on heritable variation. Here it is important to emphasize that although Darwin devoted the rest of his scientific work to this new idea, he clearly continued holding his early 'habit theory.' However, he began to think that habits just produce variations ultimately subjected to selection, as he explained in the Origin: 'I believe that the effects of habit are of quite subordinate importance to the effects of natural selection of what may be called accidental variations of instincts; - that is of variations produced by the same unknown causes which produce slight deviations of bodily structure.²⁶ With this revolutionary theory, instinctive behaviour, which was previously thought to be central for the evolution of species, was then regarded as an organic feature with the same importance as any other.

Darwin famously could not explain the mechanism by which variations emerge. Although he advanced that, besides habit, external conditions of life and the principle of correlation might influence the process, he always recognized that the laws governing the appearance and inheritance of variation remained little known.²⁷ Despite this, he argued that variation operates in the same way in all of the organic features, including behavioural.

¹⁸ See Darwin, C. (1838–1843). The Zoology of the Voyage of H.M.S. Beagle. Edited and Superintended by Charles Darwin. London: Colburn; Darwin, C. (1839). Journal of Researches into the Geology and Natural History of the Various Countries Visited by H.M.S. Beagle. London: Colburn. ¹⁹ Darwin C. (1987). Activity of Variations, J. C. (1987). Activity of Variations, J.

¹⁹ Darwin, C. (1887). Autobiography. In: Darwin F., ed. (2010). The Autobiography of Charles Darwin. London: Bibliolis Classics. p. 80.

²⁰ Darwin, C. Notebook C. MS p.199. In: Barret, P. et. al. (1987). Charles Darwin's Notebooks, 1836–1844. Geology, Transmutation of Species, Metaphysical Enquiries, Cambridge: Cambridge University Press. p. 301.

²¹ Lamarck, J. B. (1809). Zoological Philosophy. In: Elliot, H. (1963), tr. New York: Hafner Publishing Company. p. 113. For a discussion of the theories of behaviour of Lamarck, Darwin and also George and Frederick Cuvier see Burkhardt, R. W. (2011). Lamarck, Cuvier, and Darwin on Animal Behaviour and Acquired Characters. In: Gissis S. B. and E. Jablonka, Transformations of Lamarckism. From Subtle Fluids to Molecular Biology, Massachusetts: MIT Press. pp. 33–44. Additionally, George Grinell argues that Kirby also influenced Darwin's early views: see Grinnell G. J. (1985). The Rise and Fall of Darwin's Second Theory. *Journal of the History of Biology*, 18 (1): 51– 70.

²² Darwin (1859). op cit. note 2. pp. 63–64.

²³ See Bowler, P. (1976). Malthus, Darwin and the Concept of Struggle. *Journal of the History of Ideas*, 37 (4): 631–650.

²⁴ Ghiselin, M. (1969). The Triumph of the Darwinian Method. Berkeley: University of California Press; Ruse, M. (1975). Darwin's debt to philosophy: An examination of the influence of the philosophical ideas of John F.W. Herschel and William Whewell on the development of Charles Darwin's theory of evolution. Studies in History and Philosophy of Science Part A, 6(2): 159–181.

²⁵ Darwin (1859). op cit. note 2. p. 127.

 $^{^{26}\,}$ Ibid. p. 209. Additionally, previous reflections on the relationship between habits and natural selection can be found in his *Sketch* (1842, pp. 17–20) and his *Essay* (1844, p. 120); which were the first long expositions of his theory of natural selection. In Darwin, F. ed. (1909). The Foundations of the Origin of Species. Two Essays Written in 1842 and 1844 by Charles Darwin, Cambridge: Cambridge University Press.

²⁷ See Winther, R. (2000). Darwin on Variation and Heredity. *Journal of the History of Biology*, 33 (3): 425–455. pp. 427–441.

Corporeal structures left morphological and palaeontological traces of their evolutionary development such as fossils, bones and other organic material. In contrast, the variations of instincts do not leave any physical vestige. Because they are mental rather than structural, they are absent from the fossil record and invisible to the anatomist. Therefore, the most accurate analysis has to be done by observation of live individuals to 'find in the collateral lines of descent some evidence of such gradation; or we ought at least to be able to show that gradations of some kind are possible; and this we certainly can do.'²⁸ Additionally, many instincts occur only at a certain age, certain seasons of the year and certain situations, so the observation of instinct needed to be meticulous.

In his posthumous Essay on Instinct (1883), Darwin described and reflected in detail a number of instances that were only briefly discussed in the Origin.²⁹ An interesting one was the birds' nesting instinct. The proof that this instinct varies. Darwin thought, is found in the fact that taxonomically allied birds (sometimes in the same species) which inhabit different places build different nests which diverge in shape, material, position, size, so forth in accordance with the local conditions.³⁰ Darwin thought that only cross-comparative analysis between allied populations could demonstrate that instincts, just like the bodily features, present slight and accumulative variations. He claimed in the Origin that 'if it can be shown that instincts do vary ever so little, then I can see no difficulty in natural selection preserving and continually accumulating variations of instinct to any extent that may be profitable.³¹ A more critical view on this matter however was advocated by Alfred Russel Wallace, co-discoverer of natural selection. Although he also thought that instincts are subjected to evolution, he was more reluctant to classify a behaviour as instinctive without analysing it critically and experimentally first. He suggested that many patterns of behaviour which are unquestionably labelled as instincts might actually be the products of other processes like learning, experience or habits. He stated in his 1867 essay on 'The Philosophy of Birds' Nests' that he did not believe that birds built their nests by instinct. Drawing an analogy with the dwellings built by human groups in different countries, he stated: 'Each species uses the materials it can most readily obtain, and build in situations most congenial to its habits'.³²

Emergentism of instincts

The Darwinian revolution was also philosophical. On the one hand, Darwin denied the essentialist position that

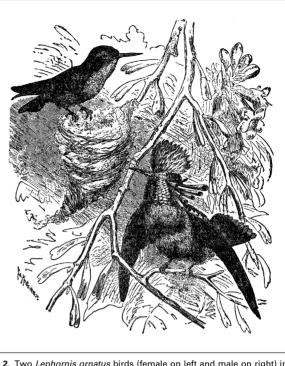


Figure 2. Two *Lephornis ornatus* birds (female on left and male on right) in their nest. Illustration from Darwin, C. (1871), *The Descent of Man, and Selection in Relation to Sex*, London: Murray. Fig. 48, p.76. Flickr's The Commons: Public Domain Image.

assumes that species are entities with a unique and fixed ontological status. Instead, he proposed that change underlies the organic world and that all the numberless living beings that have inhabited this planet are evolved from one or a few primordial forms; a species in his view was 'any form ... sufficiently constant and distinct from other forms, to be capable of definition; and if definable ... sufficiently important to deserve a specific name.³³ He explained the diversity of species without appealing to direct supernatural interventions. The chance emergence of profitable variations and the natural selection accounted for the apparently premeditated 'design' of organisms.³⁴ Moreover, in the case of instinctive behaviour, there is an additional philosophical issue. Darwin's explanation of both the corporeal structures of living beings and their instincts (mental powers) using the same theory was only possible by arguing that instincts have the same properties as the corporeal structures, so they can evolve by means of natural selection, and these are: (1) that slight variations emerge in the succession of generations of species, like in the case of bird's nesting behaviour performed in different places; (2) that these variations are inherited to the offspring and gradually accumulated; and (3) that the variations have a significant survival value in the struggle for existence. This raises the question of what was Darwin's

²⁸ Darwin, (1859). op. cit. note 2. p. 210.

²⁹ This essay was published by the evolutionary psychologist and Darwin's protégé George J. Romanes as an Appendix of his *Mental Evolution in Animals, with a Posthumous Essay on Instinct by Charles Darwin* published in 1883. The essay was based on several notes and drafts on instinctive behaviour written and provided by Darwin to support Romanes' research.

³⁰ Darwin, C., Essay on Instinct. In: Romanes, G. J. (1883). Mental Evolution in Animals, with a Posthumous Essay on Instinct by Charles Darwin, London: Kegan Paul Trench & Co. pp. 355–384. See pp. 364–372.

³¹ Darwin (1859), op cit. note 2. p. 209.

³² Wallace, A. R. (1867). 'The Philosophy of Birds' Nests', *Intellectual Observer* 11 (6): 413–420. pp. 413, 415. For a discussion and comparison of opinions and treatment of instinct between Darwin and Wallace see Costa, J. (2014), Wallace, Darwin and the Origin of Species, Cambridge MA: Harvard University Press. pp. 81–87; 120–125.

³³ Darwin (1859). op cit. note 2. p. 484. Hull, D. L. (1965). The Effect of Essentialism on Taxonomy: Two Thousand Years of Stasis (I). *The British Journal for the Philosophy of Science*, 15(60): 314–326; Hull, D. L. (1965). The Effect of Essentialism on Taxonomy: Two Thousand Years of Stasis (II). *The British Journal for the Philosophy of Science*, 16: 1–18; Mayr, E. (1988). Toward a New Philosophy of Biology: Observations of an Evolutionist. Cambridge MA: Harvard University Press.

³⁴ For an integral discussion on the matter see Sarkar, S. (2007). Doubting Darwin? Creationists Designs on Evolution. Malden: Blackwell Publishing.

philosophical position on the mind/body problem with relation to his approach to instincts.

There is one obstacle to fully understanding Darwin's stance on the mind/body problem. He did not discuss his views publicly, hence his ideas can be found only in his Notebooks and some random marginal annotations. The motive for his avoidance could be to prevent controversies and censorship of his scientific work. The American psychologist Howard Gruber stressed in 1974 that 'it must be remembered how bitter and pervasive the struggle against philosophical materialism was in [Darwin's] days, and how much of the argument against it rested on the belief that the human mind was not subject to natural law.³⁵ The scientific progress that characterized the Enlightenment in the eighteenth century also provided the basis for new radical philosophical worldviews. French philosophers (or *philosophes*) such as Julien O. de La Mettrie, Denis Diderot, Baron d'Holbach, and others, championed a monist ontology in favour of atheism and against philosophical idealism. They thought that science can only explain what is governed by physical laws and that only what can be explained scientifically exists; thus the universe only contains matter and motion. This view, commonly referred as French materialism, denied the existence of God and the notion of soul and mind as something different from matter. By the nineteenth century, these ideas were still very influential but also intensely controversial.³⁶ Darwin's theory was already provocative so he probably preferred to avoid discussing his materialist position publicly.

Darwin's position regarding the link between instincts and the brain comes with his early 'habit theory.' As discussed previously, the theory suggests that if new intelligently acquired habits are repeated by subsequent generations, eventually they can be passed down to the offspring. But additionally, Darwin proposed a mechanism that enables their inheritance. He thought that in the very process of repetition, the brain structure is altered correspondingly: 'An habitual action must some way affect the brain in a manner which can be transmitted.³⁷ The generations that inherit the new cerebral structure will perform the habit innately, becoming then an instinct with a material locus in the brain. However, it is important to notice that Darwin actually did not have any empirical evidence on habits altering the cerebral structure. He proposed this hypothesis to tackle the difficulty of explaining the inheritance of instincts by reducing it to the explanation of the inheritance of bodily structure. Darwin indeed considered this materialist. In a marginalia in his copy of John Abercrombie's Inquiries Concerning the Intellectual Powers and the Investigation of Truth (1838), he jotted: 'By materialism, I mean, merely the intimate connection of kind of thought with form of brain. - Like kind of attraction with nature of element.'38

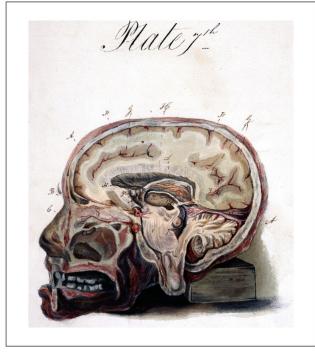


Figure 3. The human brain as illustrated by the anatomist and Darwin's colleague Sir Charles Bell. Illustration from Bell, C. (1802), *Plate VII, in: The Anatomy of the Brain, Explained in a Series of Engravings*, London: T.N. Longman and O. Rees [etc.]. p. 40.

Image courtesy of the Wellcome Library, London.

It is true that because Darwin's Notebooks and marginalia were personal study tools not meant to be published, there is ambiguity in the exposition of ideas. Furthermore, Darwin was not a philosopher in the strict sense of the word and although he was aware of the implications of his views, his philosophical statements lack depth. Therefore, the logical structure of Darwin's materialism has to be deciphered. One option is to interpret it as a 'mind/brain identity.' This theory asserts that mental traits are identical to cerebral traits. Gruber apparently thought of Darwin's materialism in this way, writing: 'more generally, Darwin's materialism is not at all crude: for instance, he considers a mental act to be a brain event, which can in turn serve as the material cause of some other event.³⁹ However, this interpretation fails to account for the fact that Darwin approached and studied instincts independently from the brain, giving no credit to sciences such as anatomy or physiology in this task. Another possible interpretation is that his materialism was an epiphenomenalism. This stance asserts that mental traits are epiphenomena; that is, adjacent by-products of material processes that have no influence in the material world. Then, behaviour is not caused by instincts, but by other physical organic process; instincts are in a different dimension and are incapable to produce any effect in living beings. However, Karl Popper and John Eccles argued that 'the mental system has, clearly, its evolutionary and functional history, and its functions have increased with the evolution from lower to higher organisms. It thus has to be linked with the Darwinian point of view. But

³⁵ Gruber, H. (1974). Darwin on Man. A Psychological Study of Scientific Creativity; Together with Darwin's Early and Unpublished Notebooks. Transcribed and annotated by Paul H. Barrett, London: Wildwood House. p. 203.

³⁶ Ibid. pp. 35–45; 201–217.

³⁷ Darwin, C. N Notebook. MS p.42. Transcribed by De Barret, In: Gruber, H. (1974). op cit. note 32. p. 338.

³⁸ See Ibid. p. 201

³⁹ Ibid. pp. 307–308.

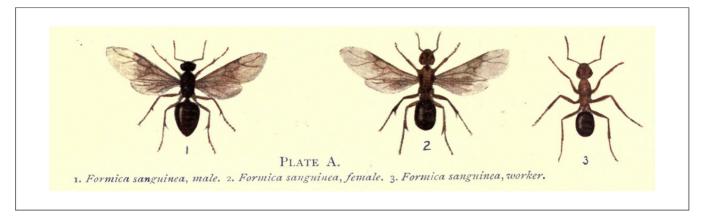


Figure 4. The different castes of *Formica sanguinea*, one of the species of ants studied by Darwin. Detailed illustration from Saunders E. (1907), Plate A. In: *Wild Bees, Wasps and Ants*, London: George Routledge and Sons. frontispiece. Wikimedia Commons: Public domain image

epiphenomenalism cannot do this.⁴⁰ In other words, if instincts lack a role in the 'struggle for existence,' then natural selection is not applied to them and would not have evolved, then they should not exist as we know them now.

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Many aspects in Darwin's approach indicate that he conceived instincts as emergent properties of the brain. There are at least four basic theses of emergentism: (1) that reality is ultimately composed of matter; (2) that a system can exhibit higher levels of organization until forming properties essentially different from the system itself; (3) that the emergent properties are not predictable from and reducible to the system from which they emerged; and (4) that there is a downward causation; i.e., the emergent properties causally affect the lower levels of organization.⁴¹ Darwin's treatment of instincts is in agreement with these four theses. Firstly, he thought that matter, in this case the brain or a similar structure, is the ultimate reality because instincts cannot exist without the brain, but it can be coherently argued that the brain can exist without instincts. Secondly, he studied instincts separately because as 'mental powers' he considered them different in its organization. Thirdly, even though instincts and brain are closely related. Darwin never attempted to reduce the former to the latter and he did not advance upward predictions, so instincts can vary regardless of the brain. Finally, there is a downward causation: if instincts change, then the corresponding cerebral structure is consequently changed and heritable. This approach to instincts was of great importance because it provided Darwin the framework in which he studied them evolutionarily as something different from matter.

Darwin's 'one special difficulty'

I have exposed in some depth how Darwin's theory was capable of explaining the evolution of instinctive behaviour and how he dealt with some implicit difficulties. But the challenge is not yet exhausted. Some specific instincts – 'the most wonderful instincts with which we are acquainted,' as Darwin called them – were so extraordinarily complex that they seemed as resistant to evolutionary explanations as the 'organs of extreme perfection and complication' epitomized by the eye.⁴² Among these 'wonderful instincts' were the hive-building instinct of honey bees, whose particularity lies in the sophisticated mathematical structure of the hive cells to contain the most honey with the least wax and the enslaver instinct of ants, which in some species has become so fundamental for their survival that they irremediably perish without slaves. Darwin thought that these cases, like complex organs, were not real difficulties. Their evolution could be demonstrated by deductions from the evidence of their gradations.⁴³ So instead of being puzzles, these instincts reassert the power of natural selection to direct the evolution from simple to complex. Nonetheless, the sterile castes of social insects provided an authentic challenge to Darwin's theory. He confessed that this 'one special difficulty ... at first appeared to me insuperable, and actually fatal to my whole theory.'44

Ants, bees and termites have a complex social system with fertile and sterile castes endowed with unique characteristics to undertake specific functions in the colony's division of labour.⁴⁵ Darwin focused on two characteristics of ants which were applicable to other social insects. First, sterile ants are very different from their parents morphologically and in their instinctive behaviour. Second, not all the sterile ants are similar to each other even though they are the offspring from the same parents, but they are divided into castes (e.g. soldiers, middle size workers, normal size workers, and so on) with their own characteristic morphological structure and behaviour. He studied several species of ants including *Formica sanguinea* (see Figure 4). The gist of the difficulty was that, despite being sterile, these ants apparently have evolved instinctive and bodily variations to such a degree that they are completely different from their parents and from the other castes.

⁴⁰ Popper, K. R. and Eccles, J. C. (1977). Materialism Criticized. In: The Self and its Brain. New York: Springer International. p. 74.

⁴¹ El-Hani, C. N.; Pereira, A. M. (2000). Higher-level Descriptions: Why Should We Preserve Them? In: Andersen, P. B., et.al. eds. Downward Causation: Minds, Bodies and Matter. Aarhus: Aarhus University Press. p.133.

⁴² Darwin (1859). op.cit. note 2, pp. 186–194, 209.

⁴³ Ibid. pp. 216–235.

⁴⁴ Ibid. p. 236. Richards suggested that the task of resolving this difficulty might explain Darwin's delay of twenty years for publishing his theory. See Richards, R. J. (1983). Why Darwin Delayed, or Interesting Problems and Models in the History of Science. Journal of the History of Behavioural Sciences, 19: 45–53. pp. 51–52.

⁴⁵ This kind of dynamic is now called 'eusociality' or real sociality. It is not only characterised by the presence of sterile workers, but many other features. See Plowes, N. (2010). An Introduction to Eusociality. Nature Education Knowledge, 3(10): 7. Retrieved from http://.nature.com/scitable/knowledge/library/an-introduction-toeusociality-15788128.

Darwin's theory asserts that variations must be inherited so evolution by natural selection occurs gradually, then how is it possible that there is great variation in the succession of only two generations and also that sterile individuals are divided in castes?

Darwin solved this problem by broadening the target of natural selection from the individual to the group. His solution indeed was kin or community selection. By analysing ants not as individuals but as a whole more than the sum of its parts, then he could argue that the colonies are the ones which have been evolving by natural selection. Those colonies which have the most beneficial properties for their conditions of life have been thriving while others less fit haven not. Therefore, if sterility and division of labour by castes are beneficial for the community, then natural selection favoured colonies with such characteristics. As Darwin put it: 'I believe that natural selection, by acting on the fertile parents, could form a species which should regularly produce neuters, either all of large seize... or lastly, and this is our climax of difficulty, one set of workers of one seize and structure, and simultaneously another set of workers of a different seize and structure.⁴⁶ Although fertile ants were the producers of colonies, Darwin tried to show that their fitness depended upon the broader fitness of the colonies they produce, including the sterile castes. Selection, therefore, is applied to the community, not the individual. For Darwin, the

instincts and morphology of sterile castes of social insects severely challenged the validity of his views, much as the eye had; so he presented the solutions to both problems as compelling evidence for the explanatory power of the theory of evolution by natural selection.⁴⁷

Final comments

This paper does not exhaust all discussion of Darwin's treatment of instinctive behaviour, of course, but it demonstrates – and hopefully encourages more scholarship on the subject – that deeper analyses reveal interesting information for getting a better insight of Darwin's work. After he proved that instincts evolve by natural selection, he engaged in new challenges of a different order. In the *Descent of Man* (1871), he developed a theory of human nature in which he attempted to prove that humans share instincts with related species (particularly with other high primates): 'As man possesses the same senses as the lower animals, his fundamental intuitions must be the same. Man has also some few instincts in common... But man, perhaps, has somewhat fewer instincts than those possessed by the animals which come next to him in the series.'⁴⁸

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⁴⁶ Darwin, (1859). op. cit. note 2. p.241.

⁴⁷ For a discussion of the current replies of Darwin's solution see Ratnieks, F. L.; Foster, K. R.; Wenseleers, T. (2011). Darwin's Special Difficulty: the Evolution of "Neuter Insects" and Current Theory. *Behav. Ecol. Sociobiol*, 65: 481–492.

⁴⁸ Darwin C. (1871). The Descent of Man, and Selection in Relation to Sex. Vol. 1, London: John Murray. p. 36.

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