

Charles Darwin: theory of natural selection

Book or Report Section

Accepted Version

Stack, D. (2019) Charles Darwin: theory of natural selection. In: Shackelford, T. K. and Weekes-Shackelford, V. A. (eds.) Encyclopedia of Evolutionary Psychological Science. Springer, Cham, Switzerland. doi: <https://doi.org/10.1007/978-3-319-16999-6> Available at <https://centaur.reading.ac.uk/87357/>

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To link to this article DOI: <http://dx.doi.org/10.1007/978-3-319-16999-6>

Publisher: Springer

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Title of entry: Charles Darwin: Theory of Natural Selection

Synonyms: Survival of the Fittest

Definition: Natural Selection was the term Darwin used to describe the evolutionary process by which favorable or advantageous traits and characteristics are preserved, and unfavorable or disadvantageous ones discarded.

Introduction

Natural Selection was the term Charles Darwin (1809-1882) used for the main mechanism by which he understood evolution to work. Natural selection was first announced publicly in a joint-reading of his and Alfred Russel Wallace's papers at the Linnean Society in July 1858 (Darwin and Wallace, 1858), and first developed in published form in Darwin's most important book, *On the Origin of Species by Means of Natural Selection, or the preservation of favoured races in the struggle for life* (1859). As the full title of the *Origin* indicates, natural selection was key to Darwin's evolutionary argument and the fourth chapter of the *Origin* was devoted to an exposition of its operation. Darwin's definition of natural selection was deceptively simple: 'This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection' (Darwin, 1859). Packed within the term, however, were a series of assumptions and implications which Darwin had taken over twenty years to work through, and which critics of his thought subsequently sought to pull apart.

At its simplest, natural selection describes a process in which favourable or advantageous characteristics - physical or psychological - are preserved, and

unfavourable or disadvantageous characteristics are discarded. This is a 'natural' process because it is said to occur without the conscious intervention of either the organism which is undergoing change or any external selector. The process of 'selection' is in fact one of preservation and discarding, determined by the utility or disutility of any given characteristic. What is useful is 'selected', in the sense that it is preserved and strengthened across generations; what is useless, is weakened and eventually discarded across generations. Natural selection, therefore, requires an extended timescale and, like all evolutionary theories, depends upon inheritance.

Darwin's theory of evolution by natural selection is premised upon two prior conditions: a naturally occurring *variation* within species, and an ongoing 'struggle for life' among all organisms, in which the fittest survive and the weakest are eliminated. Natural selection occurs only as a result of variation and the 'struggle for life', but is not synonymous with them. As Darwin explained in the *Origin*:

If during the long course of ages and under varying conditions of life, organic beings vary at all in the several parts of their organisation, and I think this cannot be disputed; if there be, owing to the high geometrical powers of increase of each species, at some age, season, or year, a severe struggle for life, and this certainly cannot be disputed; then, considering the infinite complexity of the relations of all organic beings to each other and to their conditions of existence, causing an infinite diversity in structure, constitution, and habits, to be advantageous to

them, I think it would be a most extraordinary fact if no variation ever had occurred useful to each being's own welfare, in the same way as so many variations have occurred useful to man. But if variations useful to any organic being 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. (Darwin, 1859).

This process of natural selection is the core of Darwinism and constitutes the essence of Darwin's distinct contribution to science.

The Origin of Natural Selection

Darwin developed his understanding of natural selection even before he began to use that specific term. Although Darwin first developed a distinctive understanding of evolution in the late 1830s, it was not until the early 1850s that he came to regularly and confidently refer to his theory as 'natural selection'. So enamored of the term did he then become that after he began work on his never-to-be-completed 'big species book' in 1856, he decided that it would be entitled *Natural Selection* (Stauffer, 1975).

In his first unpublished 'Sketch' of his species theory, however, written in 1842, the term 'natural selection' appears only twice - once as a sub-heading and once in the main body of the text - in over 15,000 words. Despite the 'Sketch' covering, in outline, much of the same subject matter that Darwin would later tackle in the *Origin*. The term is only slightly more prominent in

Darwin's also unpublished 1844 'Essay': appearing six times in the 60,000 words that again anticipate the structure and argument of the *Origin* (F. Darwin, 1909). One of the few aspects of the *Origin* that is not anticipated in these earlier renderings of Darwin's theory was the separate consideration of natural selection that formed the fourth chapter of his book.

The relative absence of the term, and the fact that in neither the 'Sketch' nor the 'Essay' did Darwin trouble himself to introduce or explain the term does not diminish the centrality of the underlying idea to both texts, and the strong connecting thread between these two manuscripts and the *Origin*.

Nonetheless, the fact that Darwin used the term only sparingly in the early 1840s, compared with well over 200 times in the *Origin* is striking. What seems to have changed is that Darwin had become accustomed to the term during his studies of domestic breeding. After Darwin's publisher John Murray complained, upon receipt of the manuscript of the *Origin*, about the obscurity of the term 'natural selection', Darwin wrote to the geologist Charles Lyell expressing some surprise. 'Why I like the term,' he told Lyell, 'is that it is constantly used in all works on breeding, and I am surprised that it is not familiar to Murray: but I have so long studied such works that I have ceased to be a competent judge.' (<http://www.darwinproject.ac.uk/DCP-LETT-2439>).

This remark is doubly illuminating: it confirms Darwin's derivation of the term, and that his use of it grew out of his immersion in the world of animal breeders. This is significant because breeders used the term 'natural selection' as convenient phrase to contrast unknown causes of changes in species with

the deliberate changes which they actively sought to engineer. This contrast, and subsequently the analogy, between 'natural selection' (changes that arose without any deliberate action or design on the part of the breeder) and 'artificial selection' (changes that were actively sought, instigated, and accentuated by breeders) was integral to Darwin's understanding.

Modern readers of the *Origin of Species* are sometimes perplexed or amused by the first chapter, 'Variation under Domestication', dwelling so long upon the subject of pigeon breeding, but in this chapter Darwin is both laying the foundations for an analogical argument, and providing an insight into the development of his thought. Having established the principle of modification and selection in breeding, Darwin proceeds, in chapters two and three, to consider first the variability of species in the state of nature, and then the ubiquity of a struggle for existence, before, in his fourth chapter, explaining how 'it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be *naturally selected*' (Darwin, 1859).

In case any reader had missed, or doubted, the analogy, Darwin restated it clearly:

I have called this principle, by which each slight variation, if useful, is preserved, by the term of Natural Selection, in order to mark its relation to man's power of selection. We have seen that man by selection can

certainly produce great results, and can adapt organic beings to his own uses, through the accumulation of slight but useful variations, given to him by the hand of Nature. But Natural Selection, as we shall hereafter see, is a power incessantly ready for action, and is as immeasurably superior to man's feeble efforts, as the works of Nature are to those of Art. (Darwin, 1859).

In his *The Variation of Animals and Plants under Domestication* (1868) - the only part of his unfinished 'big book' to be published in his lifetime - Darwin went further, distinguishing three types of selection: *Methodical* selection, which arose from breeders systematically endeavouring to modify a breed; *Unconscious* selection, 'which follows from men naturally preserving the most valued and destroying the less valued individuals, without any thought of altering the breed;' and *Natural* selection, 'which implies that the individuals which are best fitted for the complex, and in the course of ages changing conditions to which they are exposed, generally survive and procreate their kind.' Unconscious selection, Darwin noted, graduated into methodical selection, and could rarely be distinctly separated. While natural selection was sufficiently strong to come, 'to a certain extent into action, independently of, and even in opposition to, the will of man' (Darwin, 1868).

The strength of natural selection

Darwin's certainty of the strength of natural selection was rooted in his understanding of the forces underlying its operation. As already noted, natural selection was premised on two prior processes: naturally occurring *variations* and an intense *struggle for life*. In order for natural selection to make sense,

that is, one needed to accept (i.) the mutability of life forms and (ii.) the universal prevalence of a competition for the means of survival. Neither idea was new: Darwin's innovation was to bring them together as the foundation of his own, innovative evolutionary mechanism: natural selection.

Darwin's notebooks show that by 1837 he was deeply immersed in the problem of the mutability of species and was trying to understand how the process of the transmutation of species might operate (Gruber, 1974). At this point his growing conviction that evolution occurred was matched by a suspicion of the inadequacy of all previous attempts to understand transmutation (see Stott, 2012).

His breakthrough came in autumn 1838, Darwin later recalled, when he read Thomas Malthus's *Essay on the Principle of Population* (1803), 'for amusement'. Malthus's *Essay* argued that humans had an inherent tendency towards overpopulation, as they reproduced faster than the food supply could be increased, inducing regular struggles for subsistence. It was an argument Darwin encountered with a sense of recognition:

and being well prepared to appreciate the struggle for existence which everywhere goes on, from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable new ones to be destroyed. The result of this would be the formation of a new

species. Here, then, I had at last got a theory by which to work ...
(Barlow, 1958).

Reading Malthus was not merely the midwife to the birth of Darwin's theory of natural selection; the Malthusian struggle was a key constitutive element in his understanding of its operation. Only if there was a 'Struggle for Existence amongst all organic beings throughout the world, which inevitably follows from their high geometrical powers of increase', would Darwin be able to explain why some traits and characteristics were favored, and others eliminated, and this struggle, he told readers of the *Origin*, was 'the doctrine of Malthus, applied to the whole animal and vegetable kingdoms' (Darwin, 1859).

By making overpopulation key to the operation of natural selection, Darwin's theory of evolution was distinguished from that of his predecessors in several important respects. In particular, natural selection made competition, utility, and extinction central evolutionary themes.

Prior to Darwin, the most fully developed theory of evolution was to be found in the writings of the French zoologist Jean-Baptiste Lamarck (1744-1829). Lamarck argued that the transmutation of species occurred by a process of inheritance of acquired characteristics, and that new characteristics were acquired by species through the use and disuse of organs, leading structures to either develop or disappear. The prompt for the increased or decreased use of any particular organ was, in turn, an internal urge, rooted in an innate

tendency to develop in a certain way. Lamarck's understanding, that is, was orthogenetic, with organisms developing towards a predetermined goal.

Evolution by natural selection, by contrast, occurred because certain variations proved advantageous or disadvantageous in the ongoing struggle for life. This made natural selection directionless. The key to which variations prospered or failed was their *utility* in the ongoing *competition* for scarce resources. There was no orthogenetic element to this, as there was no predetermined direction to natural selection, beyond whatever proved most useful. Natural selection was, in contrast to Lamarck's understanding, a brutal and destructive mechanism, which worked by the constant overproduction of organisms, and the recurrent elimination of those less fitted for the struggle for life. So brutal was this process, Darwin asserted, that *extinction* - which Lamarck's account had precluded - was a frequent occurrence under natural selection. Indeed, 'extinction and natural selection,' Darwin declared, 'go hand in hand.' (Darwin, 1859)

Darwin's rooting of his theory of natural selection so firmly in the Malthusian population principle had two contradictory consequences for the reception of his ideas. On the one hand, notions of competition, struggle, and utility were so familiar, especially as adumbrated through the new social science of political economy, that natural selection would have echoed with an almost common sensical familiarity for many readers. On the other hand, however, it immediately threw up many of the same theological problems - not least why would an omnipotent and benevolent deity depend upon a mechanism that

entailed death, destruction, and apparent evil? - that had greeted Malthus's theory (see Pullen, 1987).

Darwin neatly sidestepped this in the *Origin*, arguing that there was 'grandeur' in the view of life which saw 'from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows' (Darwin, 1859). This type of language, self-consciously deployed to give comfort to those with religious sensibilities, could not entirely soften the blow that Darwin had delivered. Taken to its logical conclusion, natural selection meant an end to teleology; an end to special interventions; an end to all notions of Design; and an end to the natural theology associated the name of William Paley. Writing, towards the end of his life, in his 'Recollections', Darwin was clear:

The old argument of design in nature, as given by Paley, which formerly seemed to me so conclusive, fails, now that the law of natural selection has been discovered. We can no longer argue that, for instance, the beautiful hinge of a bivalve shell must have been made by an intelligent being, like the hinge of a door by man. There seems to be no more design in the variability of organic beings & in the action of natural selection, than in the course which the wind blows. Everything in nature is the result of fixed laws. (Barlow, 1958).

Difficulties with the term

Although Darwin himself had become increasingly enamored of the term 'natural selection' prior to the publication of the *Origin*, his confidence in its appositeness received a blow from the initial reaction of his readers. Writing to Lyell in September 1860, a mere ten months after the *Origin* was published, Darwin declared: 'if I had to commence de novo I would have used natural preservation' (<http://www.darwinproject.ac.uk/DCP-LETT-2931>). The problem, he complained, was that too many readers seemed incapable of understanding the term.

In the third edition of the *Origin*, published in 1861, Darwin inserted an extra paragraph at the start of chapter four, to address those writers who had 'misapprehended or objected to the term Natural Selection'. In particular, he sought to correct those who understood natural selection to imply the need for *active* selection, either by the organism itself or by an external chooser. Part of the misunderstanding, Darwin acknowledged, arose from an ambiguity inherent to the term. 'In the literal sense of the word,' he wrote, 'natural selection is a misnomer,' which had allowed some readers to suppose that he understood Nature to be personified into a 'selector' and that natural selection itself was 'an active power or Deity'. This, Darwin complained impatiently, was wrong: natural selection was no more an active power or deity than was gravity. When he referred to 'Nature' he meant only the aggregate action and product of natural laws. The problem, he concluded, was that his readers were failing to understand that 'natural selection' was a metaphor 'With a little familiarity,' Darwin concluded, 'such superficial objections will be forgotten' (Darwin, 1861).

This proved to be a rather optimistic assessment. Five years later, in July 1866, Wallace wrote to Darwin to say that he been 'so repeatedly struck by the utter inability of numbers of intelligent persons to see clearly or at all, the self acting & necessary effects of Nat[ural] Selection,' that he was forced to conclude 'that the term itself', and Darwin's illustrations of it, were at fault. By comparing natural selection to artificial selection, and by personifying Nature as 'selecting' and 'preferring,' said Wallace, Darwin had deployed a metaphor which, instead aiding understanding, was proving to be a 'stumbling block' (<http://www.darwinproject.ac.uk/DCP-LETT-5145>).

Wallace's criticisms were well made. In basing natural selection upon an analogy with artificial selection Darwin encouraged an anthropomorphic conception of selection in which the 'power' which 'acted' could be seen as an active Deity. This was not Darwin's intention. At the time he wrote the *Origin* Darwin was, on his own account, still a theist. The agnosticism (and arguably atheism) of his later years was still some way off, but he did not entertain any notion of an active, interventionist god. For Darwin, nature was a set of fixed laws, and natural selection was directionless beyond favoring whatever was best adapted. Yet his words frequently suggested something else. Thus when he wrote to the US botanist Asa Gray, announcing his new theory, he claimed: 'I think it can be shown that there is such an unerring power at work in Natural Selection (the title of my book), which selects exclusively for the good of each organic being.' (<http://www.darwinproject.ac.uk/DCP-LETT-2136>) Following this introduction to the concept, it is perhaps unsurprising that Gray became

the principal champion among those who sought to reconcile natural selection and natural theology.

Wallace suggested a way out of such misunderstanding. Darwin, he advised, should abandon the term 'natural selection' and replace it with the phrase 'survival of the fittest'.

This latter phrase, which many now associate with Darwin, had been coined two years earlier as a synonym for 'natural selection' by Herbert Spencer, in an installment of his *Principles of Biology* (Spencer, 1864). Wallace argued that Spencer's term was 'the plain expression of the facts' - nature did not 'so much select special variations, as exterminate the most unfavourable ones' - and, as such, was less liable being 'misrepresented & misunderstood' than Darwin's metaphorical, 'and to a certain degree indirect & incorrect,' natural selection.

Wallace's letter had a limited effect. Darwin did agree to integrate Spencer's phrase into his work. It was too late to make changes to the fourth edition of the *Origin*, which was already with the publisher, but Darwin used 'survival of the fittest' six times in the *Variation*, and sixteen times in the fifth edition of the *Origin* (1869). Nor were these unimportant or incidental uses. Darwin even reworked the title of chapter four of the *Origin*, into 'Natural Selection, Or The Survival of the Fittest', and in the text described 'survival of the fittest' as 'more accurate' than and 'sometimes equally convenient' with natural selection.

Ultimately, however, Darwin was unwilling to give up his own term. In part this was a matter of practicality: the *Origin* had enjoyed such a wide circulation, and natural selection had 'been so largely used abroad & at home,' (<http://www.darwinproject.ac.uk/DCP-LETT-5145>) that Darwin doubted whether its use could be eliminated, even if he had wanted that. And there is no evidence that he did, quite the contrary. Darwin continued to cling to the hope he had expressed to Lyell, that in time his readers would come to understand his phrase. This had nothing to do with the obvious criticism that might be made of the term 'survival of the fittest', i.e. it is a tautology with little explanatory value. Rather, Darwin preferred the term 'natural selection' precisely for the reason that Wallace questioned its use: it was a metaphor.

A number of scholars, principally Robert M. Young (1971), have made the case that the phrase 'natural selection' had an important explanatory role both in the development of Darwin's thought and in his efforts to persuade others to accept his theory. In the absence of any precise understanding of how inheritance worked, Darwin's task in the *Origin* was not so much to show evolution in action, or to provide a complete example of the stages by which it occurred, but to stress the greater plausibility of his theory over all other explanations, principally Lamarckism and all notions of special creation. In those circumstances, language mattered: natural selection was more than just a phrase, convenient for summarizing a complex process. For Darwin, 'natural selection' was a 'theory-constitutive metaphor' (a metaphor which suggests future research strategies), and an 'emphatic metaphor', i.e. one which is

bound up with the cognitive content of the theory it seeks to explain (Al-Zahrani, 2007).

Difficulties with the theory

(i.) Prior to publication of the *Origin*

What troubled Darwin most when developing his theory was the need to square natural selection with some apparently awkward scientific facts. The need to work through possible objections, and reconcile his theory to the existing state of scientific knowledge, accounts, in part at least, for the otherwise extraordinary 'delay' (van Wyhe, 2007) between Darwin's revelatory reading of Malthus and the publication of the *Origin* some twenty-one years later. As a result of the time he took, one feature of the *Origin*, which helped to make it such a compelling argument, was that Darwin led his readers through his own initial doubts and their subsequent resolution. Thus the four middle chapters of the *Origin* are concerned with exploring and resolving various objections and difficulties, including the problems of hybrids, the imperfection of the fossil record, and the problem of producing complex outcomes by a series of insensibly fine gradations.

The 'most serious special difficulty' posed to Darwin's own acceptance of the sufficiency of natural selection, however, came in the form of neuter insects, especially sterile females such as worker ants:

with the working ant we have an insect differing greatly from its parents, yet absolutely sterile; so that it could never have transmitted successively acquired modifications of structure or instinct to its progeny. It may well be asked how is it possible to reconcile this case with the theory of natural selection? (Darwin, 1859).

Part of Darwin's answer to his own question was to emphasize that natural selection applied to 'the family' as well as 'the individual' and that in the case of social insects, such as ants, it was entirely possible for fertile parents to transmit to their fertile offspring a tendency to produce sterile offspring, if that was beneficial to the community. Natural selection, that is, acted upon fertile parents to regularly produce neuter offspring.

The 'climax of the difficulty', however, as Darwin saw it, was not merely that neuters were produced, but that the neuter ants themselves were specialized into two or three 'different castes'. Among Eciton ants, for example, the neuters were divided into worker and soldier ants, 'with jaws and instincts extraordinarily different'. To explain this by natural selection required Darwin to suppose that a graduated series had first been formed, 'and then the extreme forms, from being the most useful to the community, having been produced in greater and greater numbers through the natural selection of the parents which generated them; until none with an intermediate structure were produced' (Darwin, 1859).

It is obvious when reading the *Origin* that Darwin's success in resolving this problem, with which he had wrestled for a considerable period, boosted his

confidence in natural selection considerably. The fact that natural selection could explain the existence of neuter insects proved, for Darwin, the superiority of natural selection over Lamarckism: 'For no amount of exercise, or habit, or volition, in the utterly sterile members of a community could possibly have affected the structure or instincts of the fertile members, which alone leave descendants'. Even in relation to instincts, he argued, there was in nature 'one general law, leading to the advancement of all organic beings, namely, multiply, vary, let the strongest live and the weakest die' (Darwin, 1859).

(ii.) Subsequent to publication of the *Origin*

Although Darwin had satisfied his own doubts about natural selection prior to the publication of the *Origin*, problems remained. There were three principal scientific barriers to winning full acceptance for natural selection, each of which related to the question of inheritance.

First, as compelling as Darwin's argument was, what the *Origin* offered was natural selection as a *hypothesis* for how evolution worked. The 'preservation' of a trait and characteristic occurred by its transmission between generations, with each successive generation accentuating whatever advantage it offered. But, writing before modern genetics, Darwin was not able to explain precisely *how* inheritance worked. In the *Origin* he rather fudged the issue, by making natural selection refer to both the evolutionary *effect* (the favored trait or characteristic) and the *mechanism* (preservation in struggle and hereditary transmission).

In the *Variation*, however, Darwin did attempt to flesh out what he called a 'provisional hypothesis' of heredity, which he called pangenesis. Pangenesis brought together an ancient tradition stretching back to Hippocrates with some of the latest thinking in cell theory, in an unconvincing amalgam. According to the pangenesis theory, all parts of the body produced tiny particles (gemmules) which circulated in the blood, but migrated to the gonads, and were passed on to offspring, before developing as the offspring matured. Because these gemmules were continually produced, it was possible for both somatic and behavioural traits to be inherited (Darwin, 1868).

Unfortunately, Darwin's attempt to shore up his theory of natural selection with pangenesis tended to weaken his own theory by opening up space for the very Lamarckian interpretation he had set out to counter. Pangenesis suggested that alterations to body parts would, in turn, alter gemmules and, therefore, that an inheritance of acquired characteristics would be possible.

From our perspective it is easy to see what was missing from Darwin's hypothesis: he lacked a particulate theory of heredity, a distinction between somatic and germ cells, and a concept of dominance. i.e. he lacked modern genetics and molecular biology. It was to take the rediscovery of Mendel's laws of inheritance in the early twentieth century, and their integration with evolutionary theory, to firmly establish the *mechanism of* natural selection. Ronald Fisher's *The Genetical Theory of Natural Selection* (1930) and Theodosius Dobzhansky's *Genetics and the Origin of Species* (1937) were particularly important in this movement, which became known as the 'modern synthesis', and gave us natural selection as it is now understood.

The second principal challenge natural selection faced was how to explain the preservation of favourable variations when inheritance was widely believed to involve 'blending'. The engineer Fleeming Jenkin (1833-1885) became a trenchant and troubling critic of Darwin on this point, arguing in an 1867 review of the *Origin* that any advantageous mutations would be swamped and diluted out of existence within a few generations. Certainly no change could survive across the hundreds or thousands of generations that would be required to bring about Darwin's process of evolution by natural selection (Jenkin, 1867). As with inheritance more broadly, this problem would eventually be overcome by the integration of Mendel's theory of particulate inheritance, but Darwin's initial reaction was concern and a hurried attempt to give a partial answer in the fifth edition of the *Origin*.

What gave Jenkin's criticism added bite was that it chimed with the third challenge to Darwin's theory of natural selection: doubts about the age of the earth.

As Jenkin noted, a process of incremental change required preservation across a huge span of generations, but in the years immediately following publication of the *Origin* the depth of geological time necessary for natural selection was called into question. William Thomson (later Lord Kelvin) argued that the crust of the earth had solidified no more than 100 million years ago. Darwin was 'rattled' by this claim, lamenting Thomson's work as 'an odious spectre' and identifying it as 'one of my sorest troubles' (Browne, 2002). In response, the fifth and sixth editions of the *Origin* placed an increased emphasis on use and

disuse explanations of evolution, alongside natural selection, as a means of accelerating aspects of the evolutionary process.

Natural selection and other evolutionary mechanisms in Darwin

This 'speeding up' was possible because Darwin had always left room for other factors working alongside natural selection. As he reminded readers of the introduction to the 1874 edition of his *Descent of Man*:

even in the first edition of the 'Origin of Species,' I distinctly stated that great weight must be attributed to the inherited effects of use and disuse, with respect both to the body and mind. I also attributed some amount of modification to the direct and prolonged action of changed conditions of life. Some allowance, too, must be made for occasional reversions of structure; nor must we forget what I have called "correlated" growth, meaning, thereby, that various parts of the organisation are in some unknown manner so connected, that when one part varies, so do others; and if variations in the one are accumulated by selection, other parts will be modified. Again, it has been said by several critics, that when I found that many details of structure in man could not be explained through natural selection, I invented sexual selection; I gave, however, a tolerably clear sketch of this principle in the first edition of the 'Origin of Species,' and I there stated that it was applicable to man. This subject of sexual selection has been treated at full length in the present work, simply because an opportunity was here first afforded me. (Darwin, 1874).

Darwin's defence here was a little disingenuous. With the publication of *The Descent*, in particular, a significant change had occurred in his thought.

In the first edition of the *Origin*, the overwhelming emphasis on natural selection was supplemented by a small section in the fourth chapter, which considered 'Sexual Selection', and a brief discussion in chapter five of the evolutionary effects of use and disuse. In both cases Darwin found these other mechanisms to be subsidiary and supplementary to the overriding importance of natural selection. Sexual selection, which Darwin defined as 'a struggle between the males for possession of the females,' was, he said, 'less rigorous than natural selection,' and, for the most part, merely reinforced its more powerful counterpart: 'Generally, the most vigorous males, those which are best fitted for their places in nature, will leave most progeny' (Darwin, 1859). It was the same with use and disuse. Darwin allowed that changed habits could produce an inherited effect, and speculated that moles and cave dwelling fish, for example, may have lost their sight this way, but Darwin also implied, that natural selection was the underlying cause of every change, and that use and disuse contributed only by accelerating a process that natural selection might have effected, albeit more slowly, on its own.

When Darwin turned to the question of human evolution, however, in *The Descent of Man, and Selection in Relation to Sex* (1871), he identified sexual selection as, in some instances, more powerful than and independent of natural selection.

Natural selection and human evolution

Darwin had not addressed human evolution directly in the *Origin*, limiting himself to the gnomonic prediction: 'Light will be thrown on the origin of man and his history' (Darwin, 1859). This deliberate omission certainly helped Darwin finish his book, and probably helped to minimize the controversy that the *Origin* provoked. It also, however, meant that by the time Darwin was ready to publish his thoughts others had already begun the process of applying his theory to human evolution.

Two ideas, in particular, had taken hold in the twelve years that elapsed between the *Origin* and the *Descent*. The first was Wallace's argument, outlined in his 1864 paper 'The Origin of Human Races and the Antiquity of Man Deduced from the Theory of "Natural Selection"', that the human brain effectively removed humans from the bodily effects of natural selection, and that natural selection now operated exclusively on the human mind and intelligence. The second, promulgated most prominently by Darwin's half-cousin Francis Galton was that the trappings of civilisation seriously impeded or completely prevented the operation of natural selection - physically *and* mentally - and that, in consequence, human evolution was threatened with a reverse process of degeneration (Galton, 1869).

Darwin acknowledged this fear in a section of the fifth chapter of the *Descent*, entitled 'Natural selection as affecting civilised nations'. 'We civilised men,' he began, 'do our utmost to check the process of elimination; we build asylums for the imbecile, the maimed, and the sick; we institute poor-laws; and our medical men exert their utmost skill to save the life of every one to the last moment.' As a result, those who would have been eliminated by the free

operation of natural selection were allowed to breed, and 'this must be injurious to the race of man' (Darwin, 1871). Despite this doom-laden language, which foreshadows the arguments of the later eugenics movement, Darwin's overall conclusion was positive. Whatever impediments society might erect to its operation, Darwin argued, much as he had in the *Variation*, that natural selection was always sufficiently strong to act 'independently of, and even in opposition to, the will of man' (Stack, 2012).

When explaining physical differences between different human groups, however, rather than reassert the primacy of natural selection, Darwin turned to sexual selection. 'For my own part,' he wrote, 'I conclude that of all the causes which have led to the differences in external appearance between the races of man, and to a certain extent between man and the lower animals, sexual selection has been by far the most efficient.' Darwin still thought that natural selection played the primary role in accounting for the development of man's 'intellectual and moral or social faculties', but doubted its ability to explain racial divergence. Natural selection, Darwin noted, depended upon utility, but 'as far as we are enabled to judge (although always liable to error on this head) not one of the external differences between the races of man are of any direct or special service to him' (Darwin, 1871). If racial differences were predominantly ornamental or aesthetic, Darwin concluded, they could be better explained by sexual selection.

Human groups, tribes, or races, Darwin suggested, had become their own selectors, breeding themselves to their own ideal:

We have seen that with the lowest savages the people of each tribe admire their own characteristic qualities,—the shape of the head and face, the squareness of the cheek-bones, the prominence or depression of the nose, the colour of the skin, the length of the hair on the head, the absence of hair on the face and body, or the presence of a great beard, and so forth. Hence these and other such points could hardly fail to have been slowly and gradually exaggerated from the more powerful and able men in each tribe, who would succeed in rearing the largest number of offspring, having selected during many generations as their wives the most strongly characterised and therefore most attractive women. (Darwin, 1871).

It was a similar story when Darwin came to explain differences in the mental powers of the sexes. 'With respect to differences of this nature,' Darwin wrote, 'it is probable that sexual selection has played a very important part.' Again Darwin did not entirely discount natural selection: male intellect, he argued, had been honed both in the competition of natural selection (from which females had been relatively sheltered) *and* sexual selection, the struggle 'for the possession of the females' (Darwin, 1871). The result, when supplemented with Darwin's use and disuse argument that it was the age at which a characteristic was strengthened which determined when it would be transmitted (thus males inherited distinctively male, and females distinctively female, characteristics), was that Darwin's mix of natural selection, sexual selection, and use and disuse explanations, combined to produce an evolutionary basis for male 'superiority'.

Male genius, Darwin maintained, had

been developed in man, partly through sexual selection,— that is, through the contest of rival males, and partly through natural selection, — that is, from success in the general struggle for life; and as in both cases the struggle will have been during maturity, the characters thus gained will have been transmitted more fully to the male than to the female offspring. Thus man has ultimately become superior to woman. (Darwin, 1871).

Here we can see that Darwin's dilution of natural selection as the main mechanism for human evolution went hand-in-hand with arguments that gave a naturalistic basis to the social inequalities of the late-Victorian world, and tended to justify racial and sexual inequality (Goodman, 2019). This may not have been his conscious intention, but it is striking that the normally cautious Darwin offered firm conclusions despite the fact that, by his own admission, his views 'on the part sexual selection has played in the history, want scientific precision' (Darwin, 1871).

A useful contrast can be made here with Wallace, an advocate of equality, who despite his misgivings about the term remained steadfast in his commitment to natural selection, to the exclusion of all other evolutionary mechanisms. In his rendering of their shared discovery, *Darwinism: an exposition of the theory of natural selection, with some of its applications* (1889), Wallace argued for the 'overwhelming importance of natural selection over all other agencies.' and rejected Darwin's account of sexual selection. Indeed so unrelenting was he in his advocacy of a 'pure Darwinism' that George J. Romanes characterized

Wallace as a 'neo-Darwinian' for 'seeking to out-Darwin Darwin by assigning an exclusive prerogative to natural selection' (Romanes, 1895). This was never Darwin's position.

Summary

Natural selection was the term Darwin used to describe both the mechanism and the effect of the evolutionary process by which favorable or advantageous traits and characteristics are preserved, and unfavorable or disadvantageous ones discarded. The 'selection' process is 'natural' in the sense that it occurs without any conscious intervention (there is no 'selector') in response to an ongoing 'struggle for life'. Traits and characteristics favorable to survival in that struggle are preserved and developed. This, for Darwin, is the basis of evolution. Key to the process is inheritance but, as he was writing without knowledge of modern genetics, Darwin's presentation of natural selection did not include any detailed understanding of how inheritance worked.

Although Darwin succeeded in winning acceptance for the general notion of evolution, the mechanism of natural selection remained controversial. Partly this was due to a lack of direct evidence. Besides the absence of any precise understanding of genetic inheritance, Darwin struggled against gaps in the fossil record, the elusiveness of transitional forms, and his inability to demonstrate direct instances of natural selection in operation.

His major work, *On the Origin of Species by Means of Natural Selection*, presented 'one long argument' in favor of his mechanism, but critics pointed out that swamping, blending, dilution, and the uselessness of incipient

structures would all tend against the process he described. A further challenge came from William Thomson's work on the cooling of the earth, which suggested that the planet was too young to have witnessed the magnitude of species development, wrought by incremental change, which Darwin suggested. Other readers misunderstood what Darwin meant by natural selection, and supposed an active selector to be at work. This led some of Darwin's allies, most notably Wallace, to suggest abandoning the term.

Darwin refused, and continued to favor 'natural selection' as a metaphor. Nonetheless, in his later works, and even in later editions of the *Origin*, Darwin was keen to stress that, although the most powerful, natural selection was not the only mechanism by which the evolutionary process occurred. Especially in the case of humans, discussed by Darwin in *The Descent of Man*, use and disuse and sexual selection were given greater prominence. One consequence of this was that although an acceptance of evolution flourished in the late-nineteenth century, an understanding and acceptance of Darwin's mechanism of natural selection was less widespread.

The success and prevalence of natural selection that we know today has its roots in the 'modern synthesis' of the early twentieth century, which united Darwin's hypothesis of natural selection with the understanding of genetics that he lacked.

Cross-References: Sexual Selection; Lamarckism; Alfred Russel Wallace;

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