THE EVOLUTION OF NATURAL SELECTION: DARWIN VERSUS WALLACE

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In 1879 William James took Darwin seriously. He pointed out that consciousness must have some bearing on the ability of an organism to survive. The function of the conscious brain was to select.

I think we may go further and add that the powers of cognition, discrimination and comparison which it possesses, exist only for the sake of something beyond themselves, namely, Selection. Whoever studies consciousness, from any point of view whatever, is brought up against the mystery of interest and selective attention. There are many things which consciousness is in a passive and receptive way by its cognitive and registrative powers. But there is one thing which it does, sud sponte, and which seems an original peculiarity of its own; and that is, always to choose out of the manifold experiences present to it at a given time some one for particular accentuation and to ignore the rest. And I shall show how, from its simplest to its most complicated forms, it exerts this function with unremitting industry. [1]

In 1888 C. Lloyd Morgan suggested that Darwin's phrase "natural selection" had two meanings: (1) Natural elimination,

First elimination by direct action of surrounding conditions; secondly, elimination by enemies (including parasites); and thirdly elimination by competition.

(2) Natural selection,

Natural selection (in the narrower sense suggested) is a much rarer process, and one that only comes into play when intelligence or (since it may be objected that selection is in some cases instinctive) when the mind-element comes definitely upon the scene of life. [2]

In 1913, the sociologist L. T. Hobhouse wrote, "In the biological theory of evolution the development of mind takes a secondary place. The biologist is concerned with the laws of variation and heredity" [3]. It is

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still true today that the evolution of mind is left out of the biological theory of evolution. In the great interdependent trinity of variation, heredity, and natural selection, mind would not involve variation and heredity but would be implicated with natural selection. It is the main point of this essay that a component, perhaps a major component, of natural selection is mental. Furthermore, natural selection is recursive in the sense that it operates on the selectors or organisms that in turn change the nature of what is being selected and hence of natural selection itself. A case in point would be the coevolution of flowers and insects.

A. R. Wallace played both the role of John the Baptist and St. Paul in the drama of Darwinism. When he wrote as John the Baptist, his paper "On the Tendency of Varieties to Depart Indefinitely from the Original Type" pointed the way to Darwin's *Origin of Species*. When he wrote as St. Paul, his book on Darwinism set the major dogmas in place except for his views on man. Between these two singular events, he waged a titanic struggle with Darwin over the place of mind in the trinity of heredity, variation, and natural selection.

Heredity

Darwin was a Lamarckian. Wallace was not.

From the facts alluded to in the first chapter, I think there can be little doubt that use in our domestic animals strengthens and enlarges certain parts, and disuse diminishes them; and that such modifications are inherited. [4]

The hypothesis of Lamarck—that progressive changes in species have been produced by the attempts of animals to increase the development of their own organs, and thus modify their structure and habits—has been repeatedly and easily refuted by all writers on the subject of varieties and species, and it seems to have been considered that when this was done the whole question has been finally settled; but the view here developed renders such an hypothesis quite unnecessary, by showing that similar results must be produced by the action of principles constantly at work in nature. [5]

At the very start, Wallace and Darwin differed on heredity. Another paper would have to be written in order to detail their interactions as Darwin worked out his theory of pangenesis, which was adopted and then rejected by Wallace, who finally ended up in championing Weismann. However, Wallace summarized this history in his autobiography.

Darwin always believed in the inheritance of acquired characters, such as the effects of use and disuse of organs and of climate, food, etc., on the individual, as did almost every naturalist, and his theory of pangenesis was invented to explain this among other effects of heredity. I therefore accepted pangenesis at first, because I have always felt it a relief (as did Darwin) to have some hypothesis, however provisional and improbable that would serve to explain the facts; and I told him that "I shall never be able to give it up till a better one supplies its place."

I never imagined that it could be directly disproved, but M. F. Galton's experiments of transfusing a large quantity of the blood of rabbits into other individuals of quite different breeds, and afterwards finding that the progeny was not in the slightest degree altered, did seem to me to be very nearly a disproof, although Darwin did not accept it as such. But when, at a much later period, Dr. Weismann showed that there is actually no valid evidence for the transmission of such characters, and when he further set forth a mass of evidence in support of his theory of the continuity of the germ-plasm, the "better theory" was found and I finally gave up pangenesis as untenable. But this new theory really simplifies and strengthens the fundamental doctrine of natural selection. [6]

The conclusion of this debate between Darwin and Wallace on the nature of heredity led George Romanes to write,

Those biologists who of late years have been led by Weismann to adopt the opinions of Wallace, represent as anti-Darwinian the opinions of other biologists who still adhere to the unadulterated doctrines of Darwin. Weismann's Essays on Heredity (which argue that natural selection is the only possible cause of adaptive modification) and Wallace's work on Darwinism (which in all the respects where any charge of "heresy" is concerned directly contradicts the doctrine of Darwin)-these are the writings which are now habitually represented by the Neo-Darwinians as setting forth the news of Darwin in their "pure" form. The result is that both in conversation and in the press, we habitually meet with complete inversions of the truth, which show the state of confusion into which a very simple matter has been wrought by the eagerness of certain naturalists to identify the views of Darwin with those of Wallace and Weismann. But we may easily escape this confusion, if we remember that wherever in the writings of these naturalists there occur such phrases as "pure Darwinism" we are to understand pure Wallaceism or the pure theory of natural selection to the exclusion of any supplementary theory. [7, 2:12]

To which Wallace answered "Hence it is that some of my critics declare that I am more Darwinian than Darwin himself, and this, I admit, they are not far wrong" [6, 2:22].

Variation

Both Darwin and Wallace assumed variation, but it was not until this century, when Mendelian genetics was brought into the debates on evolutionary theory, that an adequate theory of heredity and variation was formulated. (The history of this period is well covered in E. Mayr's *Growth of Biological Thought*, especially in his part 3, "Variation and Its Inheritance.")

Natural Selection

It all began publicly when Wallace wrote his paper, "On the Tendency of Varieties to Depart Indefinitely from the Original Type." In this, he described how populations or organisms remained stable until geological changes initiated changes in populations of organisms. "It appears evident, therefore, that so long as a country remains physically unchanged, the numbers of its animal population cannot materially increase" [5, p. 197]. This introduced what I call the ecological theory of natural selection.

The action of this principle is exactly like that of the centrifugal governor of the steam engine, which checks and corrects any irregularities almost before they become evident; and in like manner no unbalanced deficiency in the animal kingdom can ever reach any conspicuous magnitude, because it would make itself felt at the very first step, by rendering existence difficult and extinction almost sure soon to follow. [5]

The effect of this paper on Darwin was such that it led to his publication within a year of the Origin of Species.

For Wallace and Darwin, natural selection was a struggle for existence conditioned by an organism's adaptation to its place in the delicately balanced ecological equilibrium.

However, Darwin reserved another type of selection, "sexual selection," in which no males competed with each other for the female but the female selected the male on the basis of color, dance, and song. This, I claim, was the seed from which the psychological theory of natural selection grew.

These two views, ecological and psychological, are not contradictory, as Darwin held both. However, Wallace, with his desire for clarity, would dispense with the psychological theory.

The term "natural selection" was coined by Darwin in the Origin of Species. It was used metaphorically as Darwin had been greatly influenced in his thinking by the artificial selection carried out by plant and animal breeders.

It is wonderful what the principle of selection by man, that is the picking out of individuals with any desired quality, and breeding from them, and again picking out, can do. Even breeders have been astounded at their own results. [8]

In contrast to the views that artificial selection of domestic breeds gave important clues to evolution, Wallace stated "We see, then, that no inferences as to varieties in a state of nature can be deduced from the observation of those occurring among domestic animals" [5].

In a letter (dated 1866) to Darwin, A. R. Wallace pointed out that the term "natural selection" was causing misunderstanding among naturalists. He thought that the reason for this

arises almost entirely from your choice of the term "Natural Selection" and so constantly comparing it in its effects to Man's Selection, and also your so frequently personifying nature as "selecting" as "preferring" as "seeking only the good of the species," etc., etc. To the few this is as clear as daylight, and beautifully suggestive, but to many it is evidently a stumbling block. I wish, therefore,

to suggest to you the possibility of entirely avoiding this source of misconception in your great work (if not now too late), and also in any future editions of the origin, and I think it may be done without difficulty and very effectually by adopting Spencer's term (which he generally used in preference to Natural Selection)—vis., "survival of the fittest." This term is the plain expression of the fact; Natural Selection is a metaphorical expression of it, and to a certain degree indirect and incorrect, since, even personifying Nature, she does not so much select special variations as exterminate the most unfavourable ones. [9]

To this criticism Darwin replied in a letter written in the same year. "I formerly thought, probably in an exaggerated degree, that it was a great advantage to bring into connection natural and artificial selection; this indeed led me to use a term in common, and I still think it some advantage" [9].

At first glance, this exchange seems a mere quibble over words, but it is the seed that blossomed into deep divisions between Darwin and Wallace over sexual selection and led to a rupture in their relationship over the role of natural selection in the evolution of man and his mind.

Wallace was not unaware of the role of mind in natural selection. His friend Bates, with whom Wallace had embarked to Brazil, had discovered mimicry in butterflies. In the years 1849–1859, Bates spent his life exploring the Amazon. He was an avid collector of butterflies. Of the beautiful colorful patterns on their wings, he wrote,

It may be said, therefore, that on these expanded membranes nature writes as on a tablet, the story of the modifications of species, so truly do all changes of the organization register themselves thereon. Moreover the same colour patterns of the wings generally show with great regularity, the degrees of blood-relationship of the species. [10]

As he collected his butterflies and began to sort them, he found that some butterflies had the same color and wing shape but belonged to different species and even different genera and families. Nature was a masquerade; some butterfly species took on the appearance of poisonous beautiful but unrelated species.

Wallace immediately went back to his collection of butterflies and confirmed Bates's findings. He then wrote,

A more accurate knowledge of the varied phenomena connected with this subject may not improbably give us some information both as to the senses and the mental faculties of the lower animals. For it is evident that if colours which please us also attract them, and if the various disguises which have been here enumerated are equally deceptive to them as to ourselves, then both their powers of vision and their faculties of perception and emotion must be essentially of the same nature as our own—a fact of high philosophical importance in the study of our own nature and our true relations to the lower animals. [11]

In the case of butterflies, this meant that the predator bird was fooled, just as Bates had been, by the mimicry of one butterfly by another.

Darwin was not unaware of this, since he thought that Bates's paper on mimicry was one of the best he had ever read, but it was on sexual selection that he spent his major energies.

Sexual Selection and Psychology

In his communication to the Linnean Society, Darwin announced the principle of sexual selection.

Besides this natural means of selection, by which those individuals are preserved, whether in their egg, or larval, or mature state, which are best adapted to the place they fill in nature, there is a second agency at work in most unisexual animals, tending to produce the same effect, namely the struggle of the males for the females. These struggles are generally decided by the law of battle, but in the case of birds, apparently, by the charms of their song, by their beauty or their power of courtship, as in the dancing rock thrush of Guiana. [8]

The announcement of the role of female choice by Darwin, charmed by song and excited by beauty, set off a long debate between himself and Wallace involving sex-limited inheritance and the role of natural selection. An excellent historical account of this debate has been given by Kottler [12]. Wallace finally stated his position as follows:

It will be seen, that female birds have unaccountable likes and dislikes in the matter of their partners, just as we have ourselves, and this may afford us an illustration. A young man, when courting, brushes or curls his hair, and has his moustache, beard, or whiskers in perfect order, and no doubt his sweetheart admires them; but this does not prove that she marries him on account of these ornaments, still less that hair, beard, whiskers, and moustache were developed by the continued preferences of the female sex. So, a girl likes to see her lover well and fashionably dressed, and he always dresses as well as he can when he visits her; but we cannot conclude from this that the whole series of male costumes, from the brilliantly coloured, puffed, and slashed doublet and hose of the Elizabethan period, through the gorgeous coats, long waistcoats, and pigtails of the early Georgian era, down to the funereal dress-suit of the present day, are the direct result of female preference. In like manner, female birds may be charmed or excited by the fine display of plumage by the males; but there is no proof whatever that slight differences in that display have any effect in determining their choice of a partner. [13, p. 286]

In the case of female choice, what was being fought over was whether or not a female bird had the psychological wherewithal to appreciate beauty of sight or sound consistently. This clearly separated psychology from ecology. It was Darwin's contention that most of man's characteristics were due to sexual selection.

He who admits the principle of sexual selection will be led to the remarkable conclusion that the nervous system not only regulates most of the existing functions of the body, but has indirectly influenced the progressive development of various bodily structures and certain mental qualities. Courage, pugnacity, perseverance, strength and size

of body, weapons of all kinds, musical organs, both vocal and instrumental, bright colours and ornamental appendages, have all been indirectly gained by the one sex or the other, through the exertion of choice, the influence of love and jealousy, and the appreciation of the beautiful in sound, colour or form; and these powers of the mind manifestly depend on the development of the brain. [14; italics added]

According to Darwin, it is a major role of the brain to select. This is a great insight. It is a fact of intellectual history, that Darwin made the fundamental error of invoking psychological factors in variations and heredity that was corrected by Wallace and Weismann. However, his greatest contribution in my view was his isolation of psychological selection from ecological selection. Wallace did not follow him, and most evolutionists have followed Wallace rather than Darwin.

It has always been a puzzle—what is the function of the brain? Take any other organ of the body and the answer is immediate: stomach—digestion, kidney—filtration, heart—pumping blood, and so on. Natural selection can obviously operate on these organs. But the brain—what is its function?

What the brain does, among other things, is to create a model of an animal's world [15]. It is clear that natural selection can operate on an animal's model. If an animal mistakes a predator for an innocuous intrusion into its world, then both the model and the modeler become lunch. However, it is also clear that the model built by the brain of an insect selects a flower, the model built by the brain of a female bird of paradise selects the impressive beauty of her consort. The major problem that one faces is, why do models generated by organisms as different as birds and naturalists give rise to illusions in a similar manner as in butterfly mimicry? In fact, the whole enterprise carried out by naturalists assumes sufficient overlap between the worldviews of the organisms studied and that of the curious human observer. This, in a deep sense, was Darwin's greatest insight. Natural selection has a psychological component. This fact is not simply the result of evolution; it in turn directly affects evolution itself. This psychological factor belongs to a field called metaevolution or, to be more precise, the evolution of evolution.

In the case of heredity and variation, R. A. Fisher said, "Others have considered the bearing of the theory of heredity on evolution. I am going to consider the bearing of evolution on heredity" [16]. (A book detailing precisely such an approach is by C. D. Darlington, *The Evolution of Genetic Systems*.) In a recent symposium, Darlington wrote,

The mutual adaptiveness of all the different aspects in the genetic system introduces too many dimensions for the mathematician to cope with. When I suggested this to Fisher, he never appeared to hear. I think he was quite right not to hear, because no one can cope mathematically with all the effects of

selection when the mechanism controlling selection and the unit that is being selected are both themselves being changed by "selection." [16]

The case of the current debates on the evolution of sex tends to buttress Darlington's argument. Similar self-referential circles occur in mathematical logic. It requires metamathematics to study them properly. In the cases of the evolution of genetic systems and the evolution of natural selection, one is in the field of metaevolution, which has yet to be intensively studied.

Comparative psychology was founded by Darwin. It was Romanes who attempted to legitimize it. Instead, what we got was behaviorism. Behavior is clearly the output of mind. One might use an analogy from digestion. Would one study only the output of the digestive tract without some concern about the input and the mechanism of stomach and intestines? This curious affliction struck the comparative psychologists at the turn of the century. We still suffer from the conceptual straitjacket foisted on us. The problems of the perceptual world of an animal are open to us as mimicry and sexual selection demonstrate. One hundred years without Darwin's comparative psychology is enough.

Man

Charles Sanders Peirce wrote in 1898,

The instincts connected with the need for nutrition have furnished all animals with some virtual knowledge of space and of force, and make them applied physicists. The instincts connected with sexual reproduction have furnished all animals at all like ourselves with some virtual comprehension of the minds of other animals of their kind, so that they are applied psychists. Now not only our accomplished science, but even our scientific questions have been pretty exclusively limited to the development of those two branches of natural knowledge. There may for aught we know be a thousand other kinds of relationship which have as much to do with connecting phenomena and leading from one to another, as dynamical and social relationships have. Astrology, magic, ghosts, prophecies, serve as suggestions, of what such relationships might be. [17]

This is a good summary of what turned out to be the final debate between Darwin and Wallace on man.

In 1864 Wallace wrote a paper on man. In it he pointed out that man was "a being in whom that subtle force we term mind, became of greater importance than his mere bodily structure" [18, p. 181]. This meant that man would no longer be subjected to natural selection, according to Wallace [18]. In 1870 Wallace wrote another paper. He concluded that the mathematical, moral, musical, and philosophical faculties of man could not have been produced "through the action of a law [natural selection] which looks only, and can look only, to the immediate material welfare of the individual or the race" [19, p. 204].

The best argument that Wallace gave for the inadequacy of an ecological selection theory for man was related to the origin of the mathematical faculty. He pointed out that, in primitive societies, the native could not count beyond some finite number. He then puzzled over "how this rudimentary faculty became rapidly developed into that of a Newton, a Laplace, a Gauss or a Cayley. What motive power caused its development?" [13, pp. 466–467]. He concluded "that the present gigantic development of the mathematical faculty is wholly unexplained by the theory of natural selection, and must be due to some altogether distinct cause" [13, pp. 466–467].

This conclusion is echoed in modern times by the logician Kurt Godel. According to Godel, "There are more similarities than differences between sense perceptions and the perceptions of concepts. In fact physical objects are perceived more indirectly than concepts. . . . Godel conjectures that some physical organ is necessary to make the handling of abstract impressions (as opposed to sense impressions) possible, because we have some weakness in the handling of abstract impressions which is remedied by viewing them in comparison with or on the occasion of sense impressions. Such a sensory organ must be closely related to the neural center for language. But we simply do not known enough now and the primitive theory on such questions at the present stage is likely to be comparable to the atomic theory as formulated by Democritus' [20]. There is no good theory for the evolution of the mathematical faculty. Wallace's problem is still alive today.

The inference Wallace drew "from this class of phenomona is, that a superior intelligence has guided the development of man in a definite direction, and for a special purpose, just as man guides the development

of many animal and vegetable forms" [19].

What an irony, that Wallace should invoke artificial selection by superior spirits to bring man into being. Wallace had become a spiritu-

alist in public [21].

Darwin reacted to this in a letter to Wallace. "But I groan over Man—you write like a metamorphosed (in retrograde direction) naturalist, and you the author of the best paper that ever appeared in the Anthropological Review! Eheu! Eheu! —Your miserable friend, C. Darwin" [22].

Thus ended the debate between Wallace and Darwin.

Wallace ended his book on Darwinism as follows:

We thus find that the Darwinian theory, even when carried out to its extreme logical conclusion, not only does not oppose, but lends a decided support to, a belief in the spiritual nature of man. It shows us how man's body may have been developed from that of a lower animal form under the law of natural selection; but it also teaches us that we possess intellectual and moral faculties which could not have been so developed, but must have had another origin; and for this

origin we can only find an adequate cause in the unseen universe of Spirit. [13, p. 478]

Needless to say, very few modern Darwinists would agree with these conclusions.

Wallace, for me, is one of those rare scientists who is in search of origins. As a man of 40 he visited Herbert Spencer in a quest for the answer to the problem of the origin of life.

Soon after my return home, in 1862 or 1863, Bates and I, having both read "First Principles" and been immensely impressed by it, went together to call on Herbert Spencer, I think by appointment. Our thoughts were full of the great unsolved problem of the origin of life—a problem which Darwin's "Origin of Species" left in as much obscurity as ever—and we looked to Spencer as the one man living who could give us some clue to it. [6]

Spencer did not give satisfaction. "That, he said, was too fundamental a problem to even think of solving at present. We did not yet know enough of matter in its essential constitution nor of the various forces of nature" [6].

Spencer, of course, was right. However, Wallace's hunger to know and his search for answers to the deepest questions are evident. He had a courage, rare in scientists of his own age or our own. He paid a price for seeking answers to ultimate questions of origins.

The debate between Wallace and Darwin on heredity, natural selection, and man was between equals and echoes down to our day. Wallace has faded out, being dismissed as a spiritualist by many but not all (see Ernest Mayr's *Growth of Biological Thought*). Yet it is his version of Darwinism that dominates our view. The emergence of man is still debatable, and Wallace's arguments were not foolish. Yet Darwin has been elevated to scientific sainthood and Wallace demoted to a scientific purgatory. The unseen universe of history is not fair in its selection of our heroes.

In summary, Darwin believed in a combination of ecological and psychological factors in natural selection. Wallace believed in the ecological factor (i.e., survival of the fittest). The best way to reconcile the situation would be as follows: In the early ecosystems there was very little psychology; as the ecosystems became more complex, an organ of selection, the brain, appeared, which now selected, and so gradually psychology displaced ecology as the dominant selective factor. With man, the brain so dominated ecological factors that the world is now threatened. Thus natural selection evolved from ecology to psychology.

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