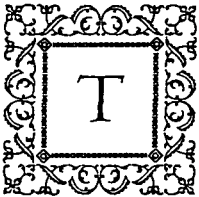


Alfred Russel Wallace's Concepts of Variation

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HE variability of species is one of the most important factors in the theory of natural selection. Both of the naturalists who discovered the theory—Charles Darwin and Alfred Russel Wallace—were uncertain about how best to represent variation within a species. In an earlier article I argued that Darwin used at least two different methods to describe the small individual variations which he saw as the starting point for evolution.¹ Sometimes he spoke as though there were a range of variation for a particular characteristic, with individuals distributed between the favored and unfavored ends of the range; at other times he pictured groups of individuals varying in a number of different directions from the norm. Darwin's exposition of his theory was complicated by the fact that when using the second concept he sometimes implied that the number of individuals varying in a favorable direction was very small. The same two ways of describing variation can also be found in the writings of Wallace, and one purpose of the present article is to illustrate this point. Wallace was far more careful than Darwin in handling the problem of variation since he never underestimated the amount of variation among individuals, whichever mode of representation he used. But Wallace's first paper on natural selection, published in 1858, is difficult to analyze in these terms because the phenomenon of individual variation is mentioned only very briefly—the main description of natural selection is based on a totally different level of variation. Permanent varieties within a species had already been established and were maintaining their differences through successive generations. Wallace may have realized that the struggle for existence among individuals actually produced the permanent varieties (the essence of Darwin's theory), but he described natural selection only in terms of a struggle among the varieties themselves. The very clear recognition of the importance of individual differences in his later writings thus marked a significant development in his thought.

1. 'Darwin's concepts of variation,' *J. Hist. Med.*, 1974, 29, 196-212.

In recent years our knowledge of how Wallace came to discover natural selection has been greatly increased through the works of Barbara Beddall and H. Lewis McKinney,² both of whom refer extensively to unpublished material from the period before 1858. It seems clear that at an early age Wallace accepted the mutability of species, and that his travels to various parts of the world were made with the object of finding clues as to how the organic changes occurred. As a result of his specimen collecting he became increasingly convinced that there was no sharp distinction between varieties and species. Finally in 1858 he remembered Malthus' ideas on population, from which he deduced the struggle for existence and the principle of natural selection. His idea was written out in a fairly brief form and sent to Darwin, with the result that Darwin himself was at last forced to publish. It is not the purpose of the present paper to take the reader once again through the details of Wallace's early career. Instead I want to suggest that the first step in any study of his contribution must be a careful analysis of how he actually presented his idea in the 1858 paper, concentrating especially on the kind of variation that was the basis of natural selection. Strangely enough, such a detailed analysis is provided neither by Beddall nor McKinney, both of whom simply assume that what Wallace eventually discovered was a straightforward equivalent of the Darwinian theory. This assumption is common to most general accounts of the history of evolutionism,³ and was shared by Darwin himself. But there are good reasons for suggesting that Wallace's initial concept of selection differed considerably from Darwin's, or at least was expressed in very different terms. From the beginning, Darwin took as his starting point the existence of individual differences within a species, arguing that the struggle for existence would favor those variants with an advantageous feature. He realized that if the species were subjected to different conditions in the various parts of its geographical range, selection would produce well-marked permanent varieties adapted to these conditions. Further selection would turn the varieties into distinct species, and

2. Barbara G. Beddall, 'Wallace, Darwin, and the theory of natural selection,' *J. Hist. Biol.*, 1968, 1, 261-323. H. Lewis McKinney, 'Alfred Russel Wallace and the discovery of natural selection,' *J. Hist. Med.*, 1966, 21, 333-359, and *Wallace and natural selection* (New Haven and London, 1972). Other biographies of Wallace include Wilma George, *Biologist philosopher: a study of the life and writings of Alfred Russel Wallace* (London and New York, 1964) and Amabel Williams-Ellis, *Darwin's moon: a biography of Alfred Russel Wallace* (London and Glasgow, 1966).

3. For example see Loren Eiseley, *Darwin's century: evolution and the men who discovered it* (New York, 1958); John C. Greene, *The death of Adam: evolution and its impact on Western thought* (Ames, Iowa, 1959); and Gertrude Himmelfarb, *Darwin and the Darwinian revolution* (1959; reprint ed., New York, 1968).

Darwin eventually realized that the varieties themselves might come into conflict, producing a second level of selection in which the fittest varieties would bring about the extinction of the less well favored ones. Wallace's paper, on the other hand, approached selection only through this last phase of the process. He was concerned with the survival of the permanent varieties once they have been formed, not with their actual formation through the action of selection on individual differences. Once this point is accepted, the pattern of Wallace's earlier career as revealed by Beddall and McKinney slips more clearly into place; we can now relate his discovery of selection directly to his interest in the nature of varieties and see how he was able to make the discovery without following Darwin into a long study of individual variation and domestic selection.

The very title of Wallace's paper suggests that its main theme was the differential survival of varieties rather than individuals: 'On the tendency of varieties to depart indefinitely from the original type.'⁴ Wallace began by arguing that the varieties of domesticated species are transitory in that they always tend to revert to the original form, whereas all naturalists agree that in the wild state species exist in the form of 'permanent true varieties' which do not revert. The purpose of his paper was to show 'that there is a general principle in nature which will cause many *varieties* to survive the parent species, and to give rise to successive variations departing further and further from the original type, and which also produces, in domesticated animals, the tendency of varieties to return to the parent form.'⁵ This seems to suggest that Wallace was also concerned with the problem of the original formation of new varieties, and when he went on to describe the struggle which must take place because of overpopulation, he did so at first in terms of the competition between individuals. He proclaimed that there is 'a "struggle for existence," in which the weakest and least perfectly organized must always succumb.'⁶ This might have led him into a Darwinian account of selection acting upon individual differences, but almost immediately he changed the subject by remarking: 'Now it is clear that what takes place among the individuals of a species must also occur among the several species of a group.' Since related species got their livelihood in a similar manner, when they oc-

⁴ A. R. Wallace, 'On the tendency of varieties to depart indefinitely from the original type,' reprinted from *J. Linn. Soc.*, 1858, in *The Darwin-Wallace celebration held on Thursday, 1st July, 1908* by the Linnaean Society of London (London, 1908), pp. 98-107.

⁵ *Ibid.*, pp. 98-99.

⁶ *Ibid.*, p. 101.

cupied the same area, the struggle between individuals must be translated into a struggle between the species in which the least fit would become extinct. But if similar species are in competition, so must there also be a struggle among any varieties which form within a single species. The rest of Wallace's paper is devoted to the competition among 'varieties,' and it is clear from the context (along with Wallace's initial mention of the competition among species) that he is referring to 'permanent true varieties,' not individual differences. Wallace had shifted the concept of variation to a new, and by Darwinian standards, secondary level, where the unit of discussion was a distinct group within the species, not an individual. Wallace made no further attempt to discuss the origin of the varieties from individual differences, and ignored the possibility that the varieties might arise in geographically distinct areas and hence be prevented from coming into competition. He also implied that the appearance of the permanent varieties is a random process, in the sense that groups may appear with both favorable *and* unfavorable characteristics. An antelope species, for instance, might have varieties with both shorter and longer legs, and this factor would have a direct bearing on their ability to escape the attacks of carnivores. Such a factor must inevitably affect the number of individuals making up the variety. A group with a disadvantageous feature would be reduced in numbers, but 'if, on the other hand, any species should produce a variety having slightly increased powers of preserving existence, that variety must inevitably in time acquire a superiority of numbers.'⁷ If now we imagine that changed conditions made it difficult for the species as a whole to get its living,

it is evident that, of all the individuals composing the species, those forming the least numerous and most feebly organized would suffer first, and, were the pressure severe, must soon become extinct. The same causes continuing in action, the parent species would next suffer, would gradually diminish in numbers, and with a recurrence of similar unfavourable conditions might also become extinct. The superior variety would then alone remain, and on a return to favourable circumstances would rapidly increase in numbers and occupy the place of the extinct species and variety.⁸

All that was necessary to complete the mechanism was the assumption that the remaining form would itself in turn separate into a number of new permanent varieties: 'But this new, improved, and populous race

7. *Ibid.*, p. 103.

8. *Ibid.*

might itself, in course of time, give rise to new varieties, exhibiting several diverging modifications of form, any of which, tending to increase the facilities for preserving existence, must, by the same general law, in their turn become predominant.⁹ It is significant, however, that Wallace did not return to individual variation in an attempt to describe how new varieties were formed. The paper merely concluded by arguing that there was no similarity between wild and domestic varieties, since the latter have been chosen for characteristics which would have to be lost immediately if the species were to survive when returned to the wild state.

Wallace's method of describing struggle among permanent varieties differs considerably from Darwin's emphasis on the selection of individual differences. But need we regard this as anything more than an alternative method of presenting the same basic idea? May we assume that Wallace was aware from the beginning that selection acted upon individual differences to form varieties, but that he preferred to discuss competition among varieties because he was more familiar with this level of variation? Or might it be argued that at first he failed to appreciate the primary Darwinian mechanism of selection acting upon individual differences? In later biographical accounts Wallace certainly wrote as though he had discovered the whole theory at once,¹⁰ and it is clear from Darwin's behavior that he saw the 1858 paper as a complete anticipation of his own views. The geologist Sir Charles Lyell and the botanist Joseph Hooker—the two colleagues to whom Darwin turned for advice after receiving the paper—also reacted as though Wallace had proposed the complete theory. Modern historians express the same opinion. Certainly Wallace should have been prepared to appreciate that selection also acted in the formation of varieties, even if his first insight came through the second level of competition. Just before his discovery he confided to Henry Walter Bates—his companion on an earlier voyage to the Amazon—his worry that Darwin might anticipate him by 'proving there is no difference in nature between the origin of species and varieties.'¹¹ The 1858 paper talked of the 'production' of varieties and introduced the struggle for existence at the individual level before making the crucial switch to the second level of variation. This almost certainly would have convinced Darwin that Wallace appreciated the action of selection on individual differences, even

9. *Ibid.*

10. McKinney, *Wallace* (n. 2), quotes Wallace's various accounts of his discovery in appendix 3, pp. 160–163. See, for instance, *Darwin-Wallace celebration* (n. 4), pp. 117–118.

11. Wallace to Bates, 4 July 1858, in James Marchant, ed., *Alfred Russel Wallace: letters and reminiscences*, 2 vols. (London and New York, 1916), I, 54.

though this phase of the mechanism was not elaborated in the rest of the paper. Yet it is strange that Wallace only emphasized the permanent effect of selection on a species in the context of his own mechanism of competition among varieties. He may have preferred to discuss selection at this level, but if he had also understood that the mechanism acted with individual differences, one would have expected him to introduce a far more explicit description of this mechanism at some point in the paper. As it stands, one can at best only infer that he did appreciate the primary Darwinian mechanism. There are, in addition, two points in his main account of selection's acting among varieties which suggest that he may not have been fully aware that such varieties are formed by the action of selection on individual differences, or at least that he had not properly worked out the implications of such selection for his own preferred approach.

Wallace wrote as though the production of permanent varieties were a random process, in the sense that groups might appear with both useful and harmful features. The example of the antelope species' giving rise to varieties with shorter and longer legs was based on the assumption that the shorter legs were a real disadvantage in escaping from predators. In Darwin's theory, however, variation was only random at the level of individual differences; since permanent varieties are formed by the action of selection upon such differences they were always better adapted to the conditions under which they lived. Although two varieties might not be equally matched if they came into conflict with one another, the selective process could not lead to the development of harmful characteristics. Thus variation at the secondary level could not be random in the same way as the production of individual differences, and by ignoring this point Wallace gave the impression that he had not fully understood the mechanism by which permanent varieties are formed by selection. This impression is reinforced when we note that he also wrote as though permanent varieties were in competition with one another in exactly the same way as the individuals involved in the struggle for existence. There is nothing to suggest that he was aware of the role played by factors such as geographical isolation in the formation of varieties and species. Darwin realized from the first that varieties are formed when parts of a species become adapted to the conditions of different areas, and he always believed that this process would be speeded up if the species were isolated into separate groups by actual physical barriers. Under these circumstances the varieties would be incapable of competing with one another. It was only at a later

stage in his thought—after he had discovered the principle of divergence—that Darwin actually came to realize that varieties would at some stage have to compete with one another.¹² The essence of Wallace's mechanism was for Darwin a secondary insight gained some time after he had worked out the primary mechanism of selection acting on individual differences. Furthermore, when Darwin discussed varieties coming into conflict, he pictured this as a geographical effect caused by one form's invading and conquering the territory of the other. Wallace, on the other hand, simply wrote of species splitting into varieties as though this occurred across the whole geographical range, with members of each variety in face-to-face conflict at all points. Wallace's failure to appreciate the role of geographical factors in the formation of varieties again suggests that he may not at first have recognized natural selection as the agency that created the varieties out of individual differences. Or, if he did recognize the action of natural selection on individual differences, he had certainly failed to work out its full implications for his own theory of selection acting among the varieties.

Even if we accept that Wallace must have had at least some insight into the effect of selection on individual differences, the fact remains that this was not the main concern of his first paper. He concentrated instead on the action of selection on varieties already formed—a phenomenon that Darwin recognized, but treated as a second level of selection acting after the primary process had produced the varieties themselves. Almost certainly this was the basis of Wallace's first idea of selection, and there is one point about his early work which suggests why he should have approached the subject from a somewhat different direction than Darwin. In several respects the early careers of the two naturalists were very similar: both began collecting at an early age, and both were able to study the geographical distribution of species by means of journeys to various parts of the world.¹³ McKinney has shown that Wallace actually went abroad looking for clues to the origin of species,¹⁴ and from the beginning he became aware of the importance of permanent varieties. But Darwin made one important additional step after he returned to England; in

12. See, for instance, Charles Darwin, *On the origin of species: a facsimile of the first edition*, introd. Ernst Mayr (New York, 1967), pp. 102–108, 116–122, and 177–178. Darwin's early accounts of his theory contain only a few indirect references to the secondary level of selection among varieties; see for instance the 'Essay of 1844,' in Charles Darwin, *The foundations of the origin of species: two essays written in 1842 and 1844*, ed. Francis Darwin (Cambridge, 1908), p. 209.

13. Wallace lists what he considers to be the similarities in their careers in *Darwin-Wallace celebration* (n. 4), pp. 8–10.

14. See McKinney, *Wallace* (n. 2), pp. 9–12, 54.

search of something analogous to the natural production of species, he turned to the study of artificial selection. Wallace could hardly have taken this step while in the East Indies, and in fact he always refused to recognize the analogy of artificial selection to natural selection.¹⁵ By following this analogy Darwin was led to study the selection of individual differences, since that was how the breeder produced his varieties. Darwin's concept of natural selection thus automatically began at the level of individual differences, with competition among varieties being a secondary phenomenon. Wallace's starting point remained the permanent varieties, and in the beginning he seems to have missed the significance of the fact that sometimes these varieties were characteristic of particular areas. He recognized the Malthusian concept of struggle at the individual level, but immediately translated this into what would happen when permanent varieties came into conflict. The struggle for existence among varieties was thus the keystone to his first insight into the operation of natural selection.

The 1858 paper was certainly enough to start the chain of events that led to the publication of the *Origin of Species*. A copy of Darwin's book reached Wallace in the Far East at the end of 1860, and from this point onward his writings show a much clearer awareness of the action of natural selection upon individual variations. This awareness is apparent in a paper on the variation and geographical distribution of the Malayan *Papilionidae* read to the Linnaean Society in 1864. Here Wallace distinguished carefully among the various senses in which the naturalist spoke of variation, starting with what he called 'simple variability,' that is,

all those cases in which the specific form is to some extent unstable. Throughout the whole range of the species, and even in the progeny of individuals, there occur continual and uncertain differences of form, analogous to that variability which is so characteristic of domestic breeds. It is impossible to define any of these forms, because there are infinite gradations to each other form.¹⁶

Then followed, in increasing order of stability, local forms or varieties, races or subspecies, and finally full species. Wallace emphasized that all

15. See, for instance, the remarks on artificial selection in the 1858 paper (n. 4). Darwin commented on this difference in a letter to Lyell, 25 June 1858; see Francis Darwin, ed., *The life and letters of Charles Darwin*, 3 vols. (New York, 1898), I, 474. See also McKinney, *Wallace* (n. 2), pp. 144-145.

16. A. R. Wallace, 'On the phenomenon of variation and geographical distribution as illustrated by the *Papilionidae* of the Malayan region,' *Trans. Linn. Soc. Lond.*, 1864, 25, 1-71, p. 5. This paper was reprinted in a modified form under the title 'The Malayan *Papilionidae*, or swallow-tailed butterflies, as illustrative of the theory of natural selection,' in A. R. Wallace, *Contributions to the theory of natural selection* (London and New York, 1870), pp. 130-200, see p. 144.

of these forms of variation grade into one another, and that in the later stages it is purely a matter of opinion as to whether two related forms should be regarded as distinct species or merely varieties of one. He also showed a clear recognition of the effects of isolation in helping individual differences to be selected out into varieties.

Under the different conditions of existence in various portions of [the species'] area, different variations from the type would be selected, and, were they completely isolated, would soon become distinctly modified forms; but this process is checked by the dispersive powers of the whole species, which leads to the more or less frequent intermixture of the incipient varieties, which thus become irregular and unstable.¹⁷

Although Wallace's collecting activities should have given him an appreciation of this point, it was lacking in the 1858 paper. Now it is clear that he was fully aware of the action of selection in the actual formation of varieties, although the subject of his paper does not allow him to go into great detail.

The *Papilionidae* paper suggested that it would be virtually impossible to describe the complexities of individual variation, but it was evident that Wallace would have to attempt such a description as soon as he came to write on the details of the selective process. His attempts fell into two basic categories, much the same as those I have described for Darwin: variation was represented both as the modification of groups of individuals in a number of different directions from the norm, and as a range of values for a particular, linear characteristic. His work on protective mimicry led Wallace to use the first of these alternatives in an effort to describe color variation among insects. He admitted that the amount of such variation might appear to be insignificant,¹⁸ but he argued that selection would act in favor of those individuals which had varied in such a way as to acquire a color resembling an inedible species and hence a degree of protection from predators. Thus a certain proportion of the population was pictured as having varied in a particular direction. This mode of representation was subsequently refined by the botanist A. W. Bennet, who criticized Wallace's discussion of mimicry in a letter to *Nature*. Bennet argued that the first stages in the process would be of no real value to the species, so that for selection to begin operating a useful amount of varia-

17. Wallace, 'Phenomenon' (n. 16), pp. 4-5; Wallace, *Contributions* (n. 16), p. 143.

18. A. R. Wallace, 'Mimicry and other protective resemblances among animals,' reprinted from the *Westminster review* for 1867 in *Contributions* (n. 16), pp. 45-129, see p. 67.

tion would first have to be built up by chance. He then calculated the odds against this happening, using as an example the butterfly *Leptalis*.

Suppose there are twenty different ways in which *Leptalis* may vary, only one of these being in the direction ultimately required, the chance of any individual producing a descendant which will take its place in the succeeding generation varying in the required direction is $1/20$; the chance of this operation being repeated in the same direction in the second generation is $1/20^2$ or $1/400$; the chance of this occurring for *ten* successive generations . . . is $1/20^{10}$ or about one in ten billions.¹⁹

Bennet was assuming that ten times the normal amount of variation would be needed before the change became useful and selection began to operate. In his reply Wallace simply denied this and argued that selection could work from the beginning. But he realized that Bennet's attempt to quantify variation was simply an extension of his own approach, his only criticism at this level being that the estimate of one-twentieth varying in the right direction was probably too small.²⁰ Only a few years earlier, Wallace had found himself trying to convince Darwin that he should never imply favorable variants to be rare.²¹ Now he was so convinced of the importance of individual variation that he was prepared to argue for more than one-twentieth of the population's always possessing at least a slight modification in the favored direction.

The method used to represent variation depends a good deal upon the characteristic under study. Color is a complex quality for which many different kinds of variation are possible—hence it is necessary to assume that individuals can vary in many directions from the norm. But this mode of representation entailed certain problems. For instance, it can lead to arguments over the proportion of the population which varies in any particular direction, arguments that would be very difficult to settle objectively. Darwin, Wallace, and Bennet would probably all have agreed that the amount of color change acquired by any individual would be too small to measure properly. One further disadvantage of this concept of variation is that it turns attention away from the effects of negative selection, that is, selection against unfavorable variants. If one-twentieth of the population varies toward a particular, favorable color, and since variation is random, the same proportion must vary toward the other possible

19. A. W. Bennet, 'The theory of natural selection from a mathematical point of view,' *Nature*, 1870-71, 3, 30-33, p. 31.

20. See 'Natural selection—Mr. Wallace's reply to Mr. Bennet,' *Nature*, 1870-71, 3, 49-50.

21. See Wallace's letter to Darwin of 2 July 1866, in Marchant, *Wallace* (n. 11), I, 173.

colors. But none of the other colors seems immediately to represent an actual disadvantage in this context, and hence there is nothing obvious for selection to act against. It is significant that neither Wallace nor Bennet tried to introduce the mechanism of selection against unfavorable variants in their dispute over color mimicry.

Neither of these disadvantages follows from the alternative approach in which variation is represented as a range, with the population distributed between a maximum and a minimum point. Both Darwin and Wallace used this method when dealing with characteristics that could be measured linearly, especially the length of particular organs. An early example of Wallace's using this mode of representation occurs in his critical review of the Duke of Argyll's *Reign of Law* published in 1867. He described selection's action to lengthen the flower of an orchid:

Now let us start from the time when the nectary was only half its present length or about six inches, and was chiefly fertilized by a species of moth which appeared at the time of the plant's flowering, and whose proboscis was of the same length. Among the millions of flowers of the *Angraecum* produced every year, some would always be shorter than the average, some longer. The former, owing to the structure of the flower, would not get fertilized, because the moths could get all the nectar without forcing their trunks down to the very base. The latter would be well fertilized, and the longest would on the average be the best fertilized of all. By this process alone, the average length of the nectary would annually increase.²²

Here the population is seen as spread out in a range on either side of the average, and selection simply acts to shift the average in one direction. Far from concealing the effects of negative selection, this way of representing variation makes it obvious from the start that there will be both favored and unfavored variations for selection to act on. But the great advantage of this approach is that it is almost intuitively obvious that there must be a range of variation in all characters for selection to act upon—there is no way in which favorable variants can be imagined to be very rare. Furthermore the size of the range can be measured fairly objectively, an advantage that Wallace began increasingly to exploit in his later works, endeavoring to show the falsity of the common belief that the amount of significant variation is very small. In his *Darwinism* of 1889 he devoted a long chapter to the 'variation of species in a state of nature,' beginning with permanent varieties but concentrating mainly on the extent of

22. A. R. Wallace, 'Creation by law,' reprinted from the *Quarterly journal of science for 1867* in *Contributions* (n. 16), pp. 264-301, see p. 272.

individual differences.²³ Taking a number of different species, he gave diagrams to show the amount of variation that could be seen in the proportions of various organs, the measurements being taken from specimens captured in the wild. To combat the belief that individuals with any significant degree of variation are quite rare, he gave frequency distribution diagrams, using dots to indicate the number of individuals found in each part of the range. The majority of course clustered around the average, but with significant numbers spread out on either side—a phenomenon that had already been studied by the Belgian anthropologist Lambert Quételet. Finally (but without going into mathematical details) Wallace postulated an idealized frequency curve that would cover the whole population: the bell-shaped normal curve that is so familiar today.²⁴ His chapter on natural selection used mainly examples based on the range concept of variation, although he still used the alternative method of representing color variation in his chapter on mimicry.²⁵

It is clear that in the later stages of his career Wallace was fully aware of the importance of individual variation to selection. He was able to exploit both modes of representation employed by Darwin, using especially the range concept to make a notable contribution to the measurement of variation among wild populations. But all of this occurred after he had read the *Origin of Species*, with its clear descriptions of Darwin's primary conception of selection's acting on the individual differences first to form varieties and then species. His own first paper on natural selection had side-stepped this level of the mechanism and developed a theory of competition among the varieties after they had been formed. This was a valid Darwinian mechanism, but one which to Darwin himself represented a second level of selection which utilized the varieties formed from the selection of individual variations. It may be that from the beginning Wallace also recognized the primary action of selection upon individual differences, and simply preferred to describe the mechanism acting at the second level because he was more familiar with what he called permanent varieties. But even if this were so, there are certain points in the 1858 paper which suggest that he had at least failed to work out the consequences of the first level of selection for his own theory.

23. A. R. Wallace, *Darwinism: an exposition of the theory of natural selection* (London, 1889), pp. 41-64. This work also includes a chapter on variation among domesticated species, although Wallace still implies (p. vi) that it was a mistake on Darwin's part to concentrate so much on the analogy with artificial selection.

24. *Ibid.*, p. 64.

25. See for instance *ibid.*, p. 243.

We cannot deny the importance of Wallace's study of individual variations in later years, but he came to see the need for such a study only after he had read Darwin's work. He always admitted that Darwin was far ahead of him in the amount of work he had put into the theory, but it can also be argued that Darwin's basic conception of selection was sounder than that which occurred to Wallace in 1858.

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