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NATURAL SELECTION AND HEREDITY

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原书缺页

nature of the gene and human evolution, to mention only a few.

The most important topic I have omitted, perhaps unwisely, is the evolution of the chromosomal system of heredity itself, on which depends the orderly distribution of the genes and, consequently, the course of subsequent evolution. I have not specifically covered this subject, other than discussing the effects of polyploidy and inversions, because it has been brilliantly covered by C. D. Darlington in his book *The evolution of genetic systems* and because space does not allow its adequate treatment here.

While writing this book I have been influenced by three considerations: (i) to explain principles, (ii) to avoid giving the impression that most problems concerned with natural selection are solved and that controversy no longer exists, an idea which elementary books often impart to their readers, (iii) to reach a standard sufficiently advanced to allow those who wish to follow up the ideas in this book to do so by reading original papers.

In order to achieve these objectives I have reduced the number of examples to the minimum and have tended to pick well-known groups of animals to illustrate my points. Consequently the Lepidoptera (butterflies and moths) are well represented, for this group is as well known to most people as any, with the possible exception of the birds. Moreover, they have been extensively used in evolutionary studies and I myself have worked with them on occasion. I have included in the text some hypotheses which are supplementary to, or alternatives to, those that are generally accepted, thus emphasizing the incompleteness of our knowledge a hundred years after the Darwin–Wallace lecture. I have not hesitated to use scientific terms where this leads to brevity, as familiarity with them is necessary for reading, without difficulty, more advanced books and papers. Space does not allow me to give a glossary but the technical terms are explained in the text. Nor can I give full references for all my statements, but I have often given the author to whom I am referring. The actual reference can usually be found from the books and papers listed at the back of this book.

I am most grateful to Dr. A. J. Cain who drew the illustrations and found time to read the manuscript in detail. His many comments have been of the greatest use to me. Dr. E. B. Ford, F.R.S., has also spent much time and trouble in reading the manuscript, and I am deeply indebted to him for his encouragement and constructive criticisms. Without the help of Dr. H. B. D. Kettlewell and his kindness in allowing me to use unpublished data the account of industrial melanism would not have been nearly so detailed or accurate. I also wish to acknowledge the help and advice I have received from Dr. L. P. Brower, Dr. C. A. Clarke, Sir Julian Huxley, F.R.S., Professor K. Mather, F.R.S., Professor R. J. Pumphrey, F.R.S., Dr. S. Walker and Dr. M. Williamson. I am entirely responsible for the choice of subjects and for any omissions or errors which may occur. However, without the help of so many colleagues and friends the text would have been less comprehensible and several errors might have been included. I also wish to thank Miss B. Sanderson for the care with which she typed the manuscript and the editors of *Genetics* for allowing me to reproduce Figure 6.

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I

NATURAL SELECTION

JULY 1st 1858 marks a turning point in biological thought, the immense importance of which could hardly have been appreciated at the time. It was on this date that the Darwin-Wallace lecture was delivered before the Linnean Society of London. Subsequently it was published in the third volume of the Society's Journal.

Both Charles Darwin and A. R. Wallace independently put forward the view that species (p. 181) are not individually created and unchanging, but that each could give rise gradually to new species during the course of time. That species are not immutable but can change, or *evolve* as we would now say, was not a new view. However, the point which was new (it had been put forward before in a tentative way but with little detailed argument and evidence to back it) was the hypothesis that natural selection is the essential agent directing and controlling such change.

Before discussing the hypothesis in more detail, it is desirable to mention briefly some of the beliefs held by biologists at that time. Broadly speaking, there were two schools of thought on the origin of the various forms that have inhabited, or still inhabit, the earth. One school maintained that species are individually created and are unchanging. It was agreed by many that slight deviations from the normal form occurred from time to time. However, it was also held that in the end these variations always reverted to the original form, and could not be sufficiently distinct to constitute new species. The other group, which included such men as Erasmus Darwin (Charles Darwin's grandfather), and the great French biologist Lamarck, held the view that species could change gradually into new species, in other words that they could evolve.

Lamarck's great contribution to biological thought was to support the theory of evolution with cogent arguments. He also put forward an hypothesis as to the factors controlling evolutionary change. He maintained that living matter had an inherent capacity to alter gradually over many generations from a simple structure or organization to a more complex and perfect one. Over and above this, he noted that organs which are much used tend to become larger and more highly developed as the result of this use, compared with those in an individual in which they are not so extensively exercised. Moreover, he observed that when they are not used at all, they tend to diminish in size. He assumed that such modifications, acquired by an organism during its own lifetime, may be inherited to a certain extent by the offspring. Consequently he accounted for the remarkably delicate and complex structure of many organs, which is so well suited to their particular function, by modification during the course of generations as the result of inheritance of these 'acquired characters'. For example, he postulated that water birds, in their efforts to swim, extended their toes and so stretched the skin between them. The stretched condition would be inherited, he thought, and the process repeated in the offspring of the birds, and in subsequent generations, until a webbed foot had been evolved. Thus species would gradually become well suited, that is *adapted*, to their environment, and once they had done this they would remain constant in structure until conditions changed. He supported his hypothesis by many such examples and, particularly, by pointing out that domestic animals and plants, during their domestication, had departed from their wild ancestors in a remarkable way.

It is greatly to Lamarck's credit that he made out such a strong case for evolution at a time when many of his colleagues believed firmly in individual acts of creation to account for species. It is not surprising that he believed in the inheritance of acquired characters, for this was a reasonable hypothesis to propose at that time. Moreover, the mechanism of inheritance was probably a consideration of secondary importance to him as compared with the task of convincing people that evolution occurred.

It seems probable that Lamarck's insistence that species evolved gradually, a feature essential to his hypothesis, was in part due to his own observations and deductions, and in part to the fact that the sudden appearance of a new species would be too strongly suggestive of special creation. Charles Darwin certainly agreed with Lamarck in the belief that species evolved slowly and, in part at least, for the same reasons. He also followed Lamarck in believing in the inheritance of at least some acquired characters, and it seems not unlikely that Lamarck's work impressed Darwin with the contribution that the study of domestication could make to knowledge about evolution, thus stimulating his own interest in it.

The Darwin-Wallace lecture consists of four papers. The first is a letter from Sir Charles Lyell and Dr. J. D. Hooker stating the circumstances leading up to the reading of both Darwin's and Wallace's papers at the same meeting. They explained that in 1839 Darwin put down his views in a manuscript, which, according to them, was rewritten in 1844 and shown to Hooker. Wallace sent his own paper to Darwin in 1858 with the request that, if it was of any interest, it should be sent to Lyell. Consequently Lyell and Hooker deemed it advisable to put forward both views, which had been independently arrived at, at the same meeting of the Society. Darwin's contribution consists of part of his manuscript together with a letter sent to Professor Asa Gray of Boston in 1857.

In these two papers he gives the reasons which led him to make the suggestion that natural selection was a primary factor in controlling the course of evolution. He had been much impressed with the theoretical work of Malthus on the growth of human populations. He pointed out that animals, like man, produce sufficient offspring to ensure that the population will increase at an enormous rate if all survive. To illustrate this, Darwin gave the following example: 'Suppose in a certain spot there are eight pairs of birds, and that *only* four pairs of them annually (including double hatches) rear only four young, and that these go on rearing their young at the same rate, then at the end of seven years (a short life, excluding violent deaths, for any bird) there will be 2048 birds instead of the original sixteen.' He then pointed out that, as Malthus had realized, in fact populations do not increase in this way but remain on the average fairly constant in size. However, they have the potentiality of increasing their numbers at a great rate, as is demonstrated by the fact that populations of plants and animals under favourable conditions, especially when introduced into a new country, sometimes expand very rapidly, although a stable state is reached in time. He concluded that the numbers of organisms in each country must be kept in check 'by recurrent struggles against other species or against external nature'. It is quite clear that he does not necessarily mean struggle in the physical sense, but simply to express the idea that conditions, or the *environment*, as we now call them, are always harsh, and get worse with increasing population size. Under such conditions there is competition both between species and between individuals of the same species for space, food, protection from enemies, the acquisition of mates and similar commodities in short supply.

Having reached this point, Darwin explains his hypothesis in such a clear way that I cannot do better than quote him. 'Now can it be doubted, from the struggle each individual has to obtain subsistence, that any minute variation in structure, habits or instincts, adapting that individual better to the new conditions, would tell upon its vigour and health? In the struggle it would have a better *chance* of surviving; and those of its offspring which inherited the variation, be it ever so slight, would have a better *chance*. Yearly more are bred than can survive; the smallest gain in the balance, in the long run, must tell on which death must fall, and which shall survive. Let this work of selection on the one hand, and death on the other, go on for a thousand generations. Who will pretend to affirm that it would produce no effect, when we remember what, in a few years, Bakewell effected in cattle, and Western in sheep, by this identical principle of selection?'

Darwin believed that in any environment an organism will accumulate in the course of time the *inheritable* variations which best fit or adapt it to its surroundings. If the environment changes, new variations will become advantageous, will be utilized and will supplant the old less well-adapted forms. Darwin realized that for this 'natural selection' to be effective the variations must be inherited, and that there will have to be a store of them present at the moment when they can be utilized. Noting that variation often appeared when environmental conditions were altered, as in the domestication of wild species, he postulated that a change in conditions brings about the spontaneous production of new variability (now known as mutation, p. 51). We know now that this is not true (if we except the results of an increase in ionizing radiation and the presence of certain chemicals), but that the new variation appears as the result of a change in the direction and intensity of the selection itself. Thus, as is explained in Chapter VI, the change in selection 'releases' inherited variability which, although present before, did not exert a visible effect. Darwin concluded from his arguments that advantageous variations, however small, would be preserved, and that as the result of their accumulation the species would depart further and further from its original form.

Other aspects of selection and evolution more fully dealt with in his later works, including his great book *On the origin of species* published in 1859, were mentioned in his lecture. One in particular must be considered here. Darwin separated sexual selection from other types. He pointed out that there exist in animals which have two sexes, particularly in the male, many attributes which seem unlikely to contribute to the survival of the individual and may even be deleterious to it. He easily explains the presence of these. For example, if a male possesses a structure or behaviour-pattern which stimulates the female in such a way that his chance of securing her for a mate in the presence of a rival is increased, the attribute will put him at an advantage with respect to the number of progeny he leaves. Moreover, such a character will be improved and perfected in the course of time because any variations increasing its stimulating power will put their possessor at an advantage, and these more successful males will leave more offspring to future generations compared with the less successful ones. The character will only cease to change when its sexual advantage is exactly counterbalanced by some mechanical, physiological, or other disadvantage—that is to say, when sexual selection, as Darwin calls it, is counterbalanced by equal and opposite natural selection. In this way he explained the otherwise inexplicable development of many secondary sexual characters, such as the plumes of Birds of Paradise or the peacock's tail.

Darwin clearly over-emphasized the importance of sexual selection, for he included too wide a category of phenomena under this heading. Many, such as the songs of birds, are as much concerned with the intimidation of other males and the maintenance of territory as with the attraction of a female. However, it is equally obvious that some recent authors have underestimated its importance.

Wallace's paper approached the problem of evolution from the same point of view as Darwin's, but with rather different emphasis. He pointed out that those who thought that species were unchanging entities admitted that variation occurred. However, they held that this variation could not be large enough to constitute a new species, and that new forms always reverted in time to the original species type. Wallace pointed out that little was known about varieties in nature, and that the argument was based on information from domestic forms. He maintained that such generalizations could not be supported by the consideration of domestic species, and that there was no justification in applying information from them to variation found in the state of nature. He then went to considerable lengths to emphasize, as Darwin did, that organisms have the capacity to increase their numbers very rapidly, but that in fact they do not, their numbers tending to remain fairly constant over considerable periods of time. Moreover, the common species are not necessarily the ones which have the greatest fecundity. Consequently he argued that population size depended not on the potential reproductive capacity of the species, but on other factors, particularly food supply.

Wallace was undoubtedly correct when he maintained that in general factors other than reproductive potential control population size. Food shortage may often be such a factor,[48] but Wallace clearly put too much emphasis on this particular item. Modern ecologists know of many others, for example interactions between the density of predator and prey, and host and parasite, to mention only two (*see* p. 174). Wallace suggested that if we knew enough about such factors, we would be able to determine why one species was common and another closely allied form was rare. It is a sobering thought that 100 years later in not a single instance are all the controlling factors for a