VI

SEXUAL REPRODUCTION AND SEXUAL SELECTION

The contrast between sexual and asexual reproduction. The nature of species. Fission of species. Sexual preference. Sexual selection. Sex limitation of modifications. Natural Selection and the sex ratio. Summary.

To all who are engaged in Psyche's task, of sorting out the seeds of good from the seeds of evil, I dedicate this discourse. FRASER.

The contrast between sexual and asexual reproduction

A GROUP of organisms in which sexual reproduction was entirely unknown might none the less evolve under the action of natural selection. This condition cannot, I believe, be ascribed with certainty to any known group. Yet, since it is impossible to draw any sharp distinction within a whole series of asexual processes, from individual growth at the one extreme, through the regeneration of injured or lost parts, to vegetative reproduction by budding; it is tempting to believe that asexual reproduction was the primitive condition of living matter, and that the sexual reproduction of the predominant types of organisms is a development of some special value to the organisms which employ it. In such an asexual group, systematic classification would not be impossible, for groups of related forms would exist which had arisen by divergence from a common ancestor. Species, properly speaking, we could scarcely expect to find, for each individual genotype would have an equal right to be regarded as specifically distinct, and no natural groups would exist bound together like species by a constant interchange of their germ-plasm.

The groups most nearly corresponding to species would be those adapted to fill so similar a place in nature that any one individual could replace another, or more explicitly that an evolutionary improvement in any one individual threatens the existence of the descendants of all the others. Within such a group the increase in numbers of the more favoured types would be balanced by the continual extinction of lines less fitted to survive, so that, just as, looking backward, we could trace the ancestry of the whole group back to a single individual progenitor, so, looking forward at any stage, we can foresee the time when the whole group then living will be the descendants of one particular individual of the existing population. If we consider the prospect of a beneficial mutation occurring at any instant, ultimately prevailing throughout the whole group, and so leading to evolutionary progress, it is clear that its prospect of doing so will depend upon its chance of falling, out of the whole population, upon the one individual whose descendants are destined ultimately to survive. At first sight this chance appears to be extremely small; but we must take account of the fact that in so far as the mutation is beneficial, its occurrence will increase the prospect of the individual, in which it occurs, proving ultimately victorious. In the limiting case in which the benefit derived from the new mutation tends to zero the chance of success is evidently only one in as many individuals as there are in the competing group. If on the other hand the benefit is appreciable, the chance of success will certainly be greater than this by an amount which now depends on the amount of heritable diversity in the group, and on the prospect of the occurrence of other beneficial mutations, before the replacement of the original population by the improved type has been completed. If the total rate of mutations is so small that the usual condition of the group is one of genetic uniformity, any advantageous mutation may be expected to prevail, provided it survives the chances of accidental death during the initial period in which it is represented by only one or few individuals. These chances, which are effectively the same with asexual or with sexual reproduction, have been considered in an earlier chapter (IV).

The evolutionary progress of an asexual group thus presents the dilemma that it can only utilize all those beneficial mutations which occur, and survive the dangers of the initial period, if the rate of occurrence of mutations is so low that the population of competing organisms is normally in a state of genetic uniformity, and in such a state evolutionary progress will necessarily be almost at a standstill: whereas if on the contrary the mutation rates, both of beneficial and of deleterious mutations, are high enough to maintain any considerable genetic diversity, it will only be the best adapted genotypes which can become the ancestors of future generations, and the beneficial mutations which occur will have only the minutest chance of not appearing in types of organisms so inferior to some of their competitors, that their offspring will certainly be supplanted by those of the latter. Between these two extremes there will doubtless be an optimum degree of mutability, dependent on the proportion of beneficial to deleterious mutations, and therefore on the aptitude of the group to its place in nature; but it is not difficult to see that the rate of progress, supposing that the optimum mutability were established, would still be very inferior to that of a sexual organism placed in the same circumstances.

The argument developed above as to the rate of evolutionary progress of a group of asexual organisms may be applied to the evolutionary progress in any one particular locus, in a species of sexual organisms, if we suppose that changes of several different kinds may take place in an homologous set of genes. The comparative rates of progress of sexual and asexual groups occupying the same place in nature, and at the moment equally adapted to that place, are therefore dependent upon the number of different loci in the sexual species, the genes in which are freely interchangeable in the course of descent. From what is known of the higher animals this number must be at least several thousands; but even a sexual organism with only two genes would apparently possess a manifest advantage over its asexual competitor, not necessarily from any physiological benefit derived from sexual union, but from an approximate doubling of the rate with which it could respond to Natural Selection. On this view, although asexual reproduction might be largely or even exclusively adopted by particular species of sexual groups, the only groups in which we should expect sexual reproduction never to have been developed, would be those, if such exist, of so simple a character that their genetic constitution consisted of a single gene.

The nature of species

From genetic studies in the higher organisms it may be inferred, that whereas genetic diversity may exist, perhaps in hundreds of different loci, yet in the great majority of loci the normal condition is one of genetic uniformity. Unless this were so the concept of the wild type gene would be an indefinite one. Cases are indeed known, as in the agouti locus in mice, in which more than one kind of wild gene have been found, these being both dominant to their other non-lethal allelomorphs; but numerous as are the loci in which such genetic diversity must exist, we have some reason to suppose that they form a very small minority of all the loci, and that the great majority exhibit, within the species, substantially that complete uniformity, which has been shown to be necessary, if full advantage is to be taken of the chances of favourable mutations. In many loci the whole of the existing genes in the species must be the lineal descendants of a single favourable mutation.

The intimate manner in which the whole body of individuals of a single species are bound together by sexual reproduction has been lost sight of by some writers. Apart from the intervention of geographical barriers so recently that the races separated are not yet regarded as specifically distinct, the ancestry of each single individual, if carried back only for a hundred generations, must embrace practically all of the earlier period who have contributed appreciably to the ancestry of the present population. If we carry the survey back for 200, 1,000, or 10,000 generations, which are relatively short periods in the history of most species, it is evident that the community of ancestry must be even more complete. The genetical identity in the majority of loci, which underlies the genetic variability presented by most species, seems to supply the systematist with the true basis of his concepts of specific identity or diversity. In his *Contributions to the Study of Variation,* W. Bateson frequently hints at an argument, which evidently influenced him profoundly, to the effect that the discontinuity to be observed between different species must have owed its origin to discontinuities occurring in the evolution of each. His argument, so far as it can be traced from a work, which owed its influence to the acuteness less of its reasoning than of its sarcasm, would seem to be correct for purely asexual organisms, for in these it is possible to regard each individual, and not merely each specific type, as the last member of a series, the continuity or discontinuity of which might be judged by the differences which occur between parent and offspring; and so to argue that these provide an explanation of the diversity of distinct strains. In sexual organisms this argument breaks down, for each individual is not the final member of a single series, but of converging lines of descent which ramify comparatively rapidly throughout the entire specific group. The variations which exist within a species are like the differences in colour between different threads which have crossed and recrossed each other a thousand times in the weaving a single uniform fabric.

The effective identity of the remote ancestry of all existing members of a single sexual species may be seen in another way, which in particular cases should be capable of some quantitative refinement. Of the heritable variance in any character in each generation a portion is due to the hereditary differences in their parents, while the remainder, including nearly all differences between whole brothers and sisters, is due to genetic segregation. These portions are not very unequal; the correlations observed in human statistics show that segregation must account for a little more than two-fifths, and the hereditary differences of the parents for nearly three-fifths of the whole. These hereditary differences are in their turn, if we go back a second generation, due partly to segregation and partly to hereditary differences in the grandparents. As we look farther and farther back, the proportion of the existing variance ascribable to differences of ancestry becomes rapidly smaller and smaller; taking the fraction due to segregation as only $\frac{2}{5}$ in each generation, the fraction due to differences of ancestry 10 generations back is only about one part in 160 while at 30 generations it is less than one in four millions. It is only the geographical and other barriers to sexual intercourse between different races, factors admittedly similar to those which condition the development of incipient species as geographical races, which prevent the whole of mankind from having had, apart from the last thousand years, a practically identical ancestry. The ancestry of members of the same nation can differ little beyond the last 500 years; at 2,000 years the only differences that would seem to remain would be those between distinct ethnographic races; these, or at least some of the elements of these, may indeed be extremely ancient; but this could only be the case if for long ages the diffusion of blood between the separated groups was almost non-existent.

Fission of species

The close genetic ties which bind species together into single bodies bring into relief the problem of their fission—a problem which involves complexities akin to those that arise in the discussion of the fission of the heavenly bodies, for the attempt to trace the course of events through intermediate states of instability, seems to require in both cases a more detailed knowledge than does the study of stable states. In many cases without doubt the establishment of complete or almost complete geographical isolation has at once settled the line of fission; the two separated moieties thereafter evolving as separate species, in almost complete independence, in somewhat different habitats, until such time as the morphological differences between them entitle them to 'specific rank'. It would, however, be contrary to the weightiest opinions to postulate that specific differentiation had always been brought about by geographic isolation almost complete in degree. In many cases it may safely be asserted that no geographic isolation at all can be postulated, although this view should not be taken as asserting that the habitat of any species is so uniformly favourable, both to the maintenance of population, and to migration, that no 'lines of weakness' exist, which, if fission is in any case imminent, will determine the most probable geographic lines of division. It is, of course, characteristic of unstable states that minimal causes can at such times produce disproportionate effects; in discussing the possibility of the fission of species without geographic isolation, it will therefore be sufficient if we can give a clear idea of the nature of the causes which condition genetic instability.

Any environmental heterogeneity which requires special adaptations, which are either irreconcileable or difficult to reconcile, will exert upon the cohesive power of the species a certain stress. This stress will be least when closely related individuals are exposed to the environmental differences, and vanishes absolutely if every individual has an equal chance of encountering either of two contrasted environmental situations, or each of a graded series of such situations. It is greatest when associated with circumstances unfavourable to sexual union, of which the most conspicuous is geographical distance, though others, such as earliness or lateness in seasonal reproduction, may in many cases be important. I do not know any such circumstance, which, in the genetical situation produced, differs essentially from geographical distance, in terms of which, therefore, it is convenient to develop the theory.

We may consider the case of a species subjected to different conditions of survival and reproduction at opposite ends of its geographical range. Certain of the genes which exist as alternatives will be favoured at one extreme, and will tend there to increase, while at the other extreme they will be disadvantageous and tend to diminish in frequency, the intermediate region being divisible into a series of zones in which the advantage increases, from a negative value at one extreme, through zero at a region in which the selective advantage is exactly balanced, to a certain positive advantage at the other extreme. A condition of genetic equilibrium is therefore only established if the increase in frequency in the favourable region and the decrease in frequency in the unfavourable region, not only balance each other quantitatively, but are each equal to the rate at which genes diffuse by migration and sexual union, from the one region to the other. This rate must itself be determined, apart from migratory or sedentary habits of the species, by the length of each zone across which diffusion occurs, by the density of population along it, and finally by the gradient in the frequency ratio between the gene and its allelomorph as we pass across it. So long as a sufficient gradient can be maintained, accompanied by an active diffusion of germinal material, so long the local varieties, although, possibly, distinct differences between them may be detected, will have no tendency to increase these differences in respect of the frequency of the genes in which they differ, and will be connected by all grades of intermediate types of population.

The longer such an equilibrium is maintained the more numerous will the genetic differences between the types inhabiting extreme regions tend to become, for the situation allows of the extinction of neither the gene favoured locally nor its allelomorph favoured elsewhere, and all new mutations appearing in the intermediate zone which are advantageous at one extreme but disadvantageous at the other will have a chance of being added to the factors in which they differ. In addition to those genes which are selected differentially by the contrasted environments, we must moreover add those, the selective advantage or disadvantage of which is conditioned by the genotype in which they occur, and which will therefore possess differential survival value, owing not directly to the contrast in environments, but indirectly to the genotypic contrast which these environments induce. The process so far sketched contains no novel features, it allows of the differentiation of local races under natural selection, and shows that this differentiation must, if the conditions of diffusion are constant, be progressive. It involves no tendency to break the stream of diffusion, or consequently to diminish in degree the unity of ancestry which the species possesses. It is analogous to the stretching of a material body under stress, not to its rupture.

There are, however, some groups of heritable variations which will influence diffusion. In the case we are considering in which the cause of isolation is geographical distance, the instincts governing the movements of migration, or the means adopted for dispersal or fixation, will influence the frequency with which the descendants of an organism, originating in one region, find themselves surrounded by the environment prevailing in another. The constant elimination in each extreme region of the genes which diffuse to it from the other, must involve incidentally the elimination of those types of individuals which are most apt so to diffuse. If it is admitted that an aquatic organism adapted to a low level of salinity will acquire, under Natural Selection, instincts of migration, or means of dispersal, which minimize its chances of being carried out to sea, it will be seen that selection of the same nature must act gradually and progressively to minimize the diffusion of germ plasm between regions requiring different specialized aptitudes. The effect of such a progressive diminution in the tendency to diffusion will be progressively to steepen the gradient of gene frequency at the places where it is highest, until a line of distinction is produced, across which there is a relatively sharp contrast in the genetic composition of the species. Diffusion across this line is now more than ever disadvantageous, and its progressive diminution, while leaving possibly for long a zone of individuals of intermediate type, will allow the two main bodies of the species to evolve almost in complete independence.

In cases in which the cause of genetic isolation is not merely geographical distance, but a diversity among different members of the species in their habitats or life history, in connexion with which different genetic modifications are advantageous; the isolation will of course not be increased by the differential modification of the instincts of migration, or the means of dispersal; but by whatever type of hereditary modification will minimize the tendency for germinal elements, appropriate to one form of life, to be diffused among individuals living the other form, and among them consequently eliminated.

The power of the means of dispersal alone, without the necessity for selective discrimination in either region, is excellently illustrated by the theory, due to Ray Lankester, which satisfactorily accounts for the diminution or loss of functional eyes by the inhabitants of dark caverns. Ray Lankester pointed out that the possession of the visual apparatus is not merely useless to such animals but, by favouring their migration towards sources of light, will constantly eliminate them from the body of cave inhabitants, equally effectively whether they survive or perish in their new environment. Those which remain therefore to breed in the cavern are liable to selection in each generation for their insensibility to visual stimuli. It should be noted that with such very restricted habitats migrational selection of this sort might attain to very high intensity and in consequence produce correspondingly rapid evolutionary effects.

Sexual preference

A means of genetic isolation which is of special importance in that it is applicable equally to geographical and to other cases is one, which for want of a better term, we may consider under the heading of reproductive or sexual preference.

The success of an organism in leaving a numerous posterity is not measured only by the number of its surviving offspring, but also by the quality or probable success of these offspring. It is therefore a matter of importance which particular individual of those available is to be their other parent. With the higher animals means of discrimination exist in the inspection of the possible mate, for in large groups the sense organs are certainly sufficiently well developed to discriminate individual differences. It is possible therefore that the emotional reactions aroused by different individuals of the opposite sex will, as in man, be not all alike, and at the least that individuals of either sex will be less easily induced to pair with some partners than with others. With plants an analogous means of discrimination seems to exist in the differential growth rate of different kinds of pollen in penetrating the same style.

An excellent summary of recently established facts in this field has been given by D. F. Jones (*Selective Fertilization*, University of Chicago, 1928). Cases are known in maize in which discrimination is exercised against pollen bearing certain deleterious mutant factors, and in one case in *Oenothera* against ovules bearing a certain lethal factor. In these reactions both the genotype of the mother plant and that of the pollen are exposed to selection, and it is this that serves to explain the remarkable fact established by Jones' own observations with maize, that pollen applied in mixtures is on the whole less effective the greater the genetic diversity between the seed parents and the pollen parent. Such a generalized tendency towards homogamy, which is perhaps especially manifest in maize owing to the enormous number of recessive defects, which by continued cross pollination have accumulated in that plant, would, however, be far less effective in promoting the fission of species than would the selection of discriminative tendencies specially directed towards that end, such as must occur, as will be explained more fully below, in a group constantly invaded by the diffusion of unfavourable genes.

In general the conditions upon which discrimination, when possible, can usefully be exercised seem to be (i) that the acceptance of one mate precludes the effective acceptance of alternative mates, and (ii) that the rejection of an offer will be followed by other offers, either certainly, or with such high probability, that the risk of their non-occurrence shall be smaller than the probable advantage to be gained by the choice of a mate. The first condition is satisfied by the females of most species, and in a considerable number of cases by the males also. In other cases, while it would be a serious error for the male to pursue an already fertilized female, it would seem that any opportunity of effective mating could be taken with advantage. The second condition is most evidently satisfied when members of the selected sex are in a considerable majority at the time of mating.

The grossest blunder in sexual preference, which we can conceive of an animal making, would be to mate with a species different from its own and with which the hybrids are either infertile or, through the mixture of instincts and other attributes appropriate to different courses of life, at so serious a disadvantage as to leave no descendants. In the higher animals both sexes seem to be congenitally adapted to avoid this blunder and from the comparative rarity of natural hybridization among plants, save in certain genera where specific distinctness may have broken down through maladaptation in this very respect, we may infer the normal prevalence of mechanisms effective in minimizing the probability of impregnation by foreign pollen. It is therefore to be inferred that in the higher animals the nervous system is congenitally so constructed, that the responses normal to an association with a mate of its own species are, in fact, usually inhibited by the differences which it observes in the appearance or behaviour of a member of another species. Exactly what differences in the sensory stimuli determine this difference in response it is of course impossible to say, but it is no conjecture that a discriminative mechanism exists, variations in which will be capable of giving rise to a similar discrimination within its own species, should such discrimination become at any time advantageous.

A typical situation in which such discrimination will possess a definite advantage to members of both sexes must arise whenever a species occupying a continuous range is in process of fission into two daughter species, differentially adapted to different parts of that range; for in either of the extreme parts certain relatively disadvantageous characters will constantly appear in a certain fixed proportion of the individuals in each generation, by reason of the diffusion of the genes responsible for them from other parts of the range. The individuals so characterized will be definitely less well adapted to the situation in which they find themselves than their competitors; and in so far as they are recognizably so, owing, for example, to differences in tint, their presence will give rise to a selective process favouring a sexual preference of the group in which they live. Individuals in each region most readily attracted to or excited by mates of the type there favoured, in contrast to possible mates of the opposite type, will, in fact, be the better represented in future generations, and both the discrimination and the preference will thereby be enhanced. It appears certainly possible that an evolution of sexual preference due to this cause would establish an effective isolation between two differentiated parts of a species, even when geographical and other factors were least favourable to such separation.

Sexual selection

The theory put forward by Darwin to account for the evolution of secondary sexual characters involves two rather distinct principles. In one group of cases, common among mammals, the males, especially when polygamous, do battle for the possession of the females. That the selection of sires so established is competent to account for the evolution, both of special weapons such as antlers, and of great pugnacity in the breeding season, there are, I believe, few who doubt, especially since the investigation of the influence of the sex hormones has shown how genetic modifications of the whole species can be made to manifest themselves in one sex only, and has thereby removed the only difficulty which might have been felt with respect to Darwin's theory.

For the second class of cases, for which the amazing development of the plumage in male pheasants may be taken as typical, Darwin put forward the bold hypothesis that these extraordinary developments are due to the cumulative action of sexual preference exerted by the females at the time of mating. The two classes of cases were grouped together by Darwin as having in common the important element of competition, involving opportunities for mutual interference and obstruction, the competition being confined to members of a single sex. To some other naturalists the distinction between the two types has seemed more important than this common element, especially the fact that the second type of explanation involves the will or choice of the female. A. R. Wallace accepted without hesitation the influence of mutual combats of the males in the evolution of sex-limited weapons, but rejected altogether the element of female choice in the evolution of sex-limited ornaments.

It has been pointed out in Chapter II that a detailed knowledge of the action of Natural Selection would require an accurate evaluation of the rates of death and reproduction of the species at all ages, and of the effects of all the possible genetic substitutions upon these rates. The distinction between one kind of selection and another would seem to require information in one respect infinitely more detailed, for we should require to know not the gross rates of death and reproduction only, but the nature and frequency of all the bionomic situations in which these events occur. The classification of causes of death required by law is sufficiently complex, and would require very extensive medical knowledge if full justice were to be done to it in every case. Even qualified medical men, however, are not required to specify the sociological causes of birth. In pointing out the immense complexity of the problem of discriminating to which possible means of selection a known evolutionary change is to be ascribed, or of allotting to several different means their share in producing the effect, I should not like to be taken to be throwing doubt on the value of such distinctions as can be made among the different bionomic situations in which selection can be effected. The morphological phenomena may be so striking, the life-history and instincts may have been so fully studied in the native habitat, that a mind fully stored with all the analogies within its field of study may be led to perceive that one explanation only, out of those which are offered, carries with it a convincing weight of evidence. Every case must, I conceive, be so studied and judged upon by persons acquainted with the details of the case, and even so in the vast majority of cases the evidence will be too scanty to be decisive. It would accord ill with the scope of this book (and with the pretensions of its author) to attempt such a decision in any particular case. There does seem room, however, for a more accurate examination of the validity of the various types of argument which have been used, and which must be used if any interpretation at all is to be put upon the evidence, than seems hitherto to have been attempted.

It is certain that some will feel that such an abstract form of treatment does injury to the interest of the subject. On the other hand I am confident that many engaged in the actual work of observation and classification would welcome any serious attempt to establish impartial principles of interpretation. The need is greatest in a subject, in which generalizations embodying large numbers of observational facts are of such high value, that in controversy mere citations of fresh facts seem sometimes to be invested with a logical force, which they do not really possess; it is possible thus for even the fairest minded of men, when thoroughly convinced of the correctness of his own interpretation, in which conviction he may be fully justified, to use in its support arguments which, had he been in real doubt, he could scarcely have employed. To take but a single instance of a most innocent lapse of logic in discussions of sexual selection; it was pointed out by Wallace that very many species which are conspicuously or brilliantly coloured, and in which the females are coloured either exactly like the males, or, when differently coloured are equally conspicuous, either nest in concealed situations such as holes in the ground or in trees, or build a domed or covered nest so as completely to conceal the sitting bird. In this concealment Wallace perceived an explanation of the lack of protective coloration in the female. To the objection, which seems to have originated with the Duke of Argyll, that a large domed nest is more conspicuous to an enemy than a smaller open nest, Wallace replied that as a matter of fact they do protect from attack, for hawks or crows do not pluck such nests to pieces. Darwin, on the other hand, believed that there was much truth in the Duke of Argyll's remark, especially in respect to all tree-haunting carnivorous animals. It will be noticed that neither controversialist seems to perceive that the issue is not concerned with the advantages or disadvantages of covered nests, or that, however disadvantageous these nests may be supposed to be, they nevertheless do fulfil the conditions required by Wallace of precluding the selection during brooding of protective colours in the female, by the action of predators to which brooding females might otherwise have been visible.

A much more serious error, which has not been without echoes in biological opinion, was made by Wallace in arguing that the effect of selection in the adult is diminished by a large mortality at earlier stages (*Darwinism*, p. 296).

> In butterflies the weeding out by natural selection takes place to an enormous extent in the egg, larva, and pupa states; and perhaps not more than one in a hundred of the eggs laid produces a perfect insect which lives to breed. Here, then, the impotence of female selection, if it exists, must be complete; for, unless the most brilliantly coloured males are those which produce the best protected eggs, larvae, and pupae, and unless the particular eggs, larvae, and pupae, which are able to survive, are those which produce the most brilliantly coloured butterflies, any choice the female might make must be completely swamped. If, on the other hand, there *is* this correlation between colour development and perfect adaptation at all stages, then this development will necessarily proceed by the agency of natural selection and the general laws which determine the production of colour and of ornamental appendages.

It should be observed that if one mature form has an advantage over another, represented by a greater expectation of offspring, this advantage is in no way diminished by the incidence of mortality in the immature stages of development, provided there is no association between mature and immature characters. The immature mortality might be a thousandfold greater, as indeed it is if we take account of the mortality of gametes, without exerting the slightest influence upon the efficacy of the selection of the mature form. Moreover, Wallace himself attached great importance to other selective effects exerted upon mature butterflies as is shown by his treatment of protective resemblance on page 207 of the same work. It cannot therefore have been the cogency of the argument he uses which determined Wallace's opinion, but rather the firmness of his conviction that the aesthetic faculties were a part of the 'spiritual nature' conferred upon mankind alone by a supernatural act, which supplies an explanation of the looseness of his argument.

The two fundamental conditions which must be fulfilled if an evolutionary change is to be ascribed to sexual selection are (i) the existence of sexual preference at least in one sex, and (ii) bionomic conditions in which such preference shall confer a reproductive advantage. In cases where the two conditions can be satisfied, the existence of special structures, which on morphological grounds may be judged to be efficacious as ornaments, but to serve no other useful purpose, combined with ecological evidence that the structures are at their fullest development in the mating season, and are then paraded conspicuously, provides evidence of the same kind as, in other cases, is deemed conclusive as to the evolutionary significance of bodily structures.

With respect to sexual preference, the direct evidence of its existence in animals other than man is, and perhaps always will be, meagre. The extreme oddity of the preferences reported of individual birds in captivity suggests that their mentality is sometimes deranged, at least in respect of sexual preference, by the artificial conditions, and show no more that an effective nervous mechanism does in fact exist, which responds differently to different suitors. The only point of value, which it would seem might be determined by such observations, is the extent to which different hen birds concur in their preferences among the cocks. Since, I suppose, only one choice could be confidently observed in each season, such a test could only be applied with sufficient numbers to polygamous birds; among these, however, it should be possible to demonstrate it with certainty, if an order of preference exists.

The strongest argument adduced by Darwin in respect to birds in the wild state must certainly be given now a different interpretation. He gives numerous cases in which when one of a pair of birds is shot its place is found almost immediately to be taken by another of the same sex, whether male or female. He concludes that, surprising as it may seem, many birds of both sexes remain unpaired, and also—and here only we part company with him—this, because they cannot find a mate to please them. If this were the true explanation it would indicate sexual preferences so powerful as to inhibit mating altogether in a considerable proportion of birds, and such intensity of preference could scarcely be maintained in a species unless the advantage to the prospects of the progeny due to the possibility of gaining a very superior mate were larger than the certain loss of an entire breeding season. As will be seen, it is difficult to assign in most cases a rational basis for so great an advantage. On the other hand the researches of H. E. Howard upon *Territory in Bird Life* provide a very simple and adequate explanation of the fact observed. On this view the birds which remain unmated do so because they are not in possession of a breeding territory where they can nest unmolested, but are ready to mate at once with a widow or widower left in possession of this coveted property. I do not know, however, how much evidence there is for asserting that it is always the widowed bird and a new mate, rather than a new pair, which is found in possession of the vacant territory. The adoption of existing young suggests that sometimes at least it is the former.

If instead of regarding the existence of sexual preference as a basic fact to be established only by direct observation, we consider that the tastes of organisms, like their organs and faculties, must be regarded as the products of evolutionary change, governed by the relative advantage which such tastes may confer, it appears, as has been shown in a previous section, that occasions may be not infrequent when a sexual preference of a particular kind may confer a selective advantage, and therefore become established in the species. Whenever appreciable differences exist in a species, which are in fact correlated with selective advantage, there will be a tendency to select also those individuals of the opposite sex which most clearly discriminate the difference to be observed, and which most decidedly prefer the more advantageous type. Sexual preference originating in this way may or may not confer any direct advantage upon the individuals selected, and so hasten the effect of the Natural Selection in progress. It may therefore be far more widespread than the occurrence of striking secondary sexual characters.

Certain remarkable consequences do, however, follow if some sexual preferences of this kind, determined, for example, by a plumage character, are developed in a species in which the preferences of one sex, in particular the female, have a great influence on the number of offspring left by individual males. In such cases the modification of the plumage character in the cock proceeds under two selective influences (i) an initial advantage not due to sexual preference, which advantage may be quite inconsiderable in magnitude, and (ii) an additional advantage conferred by female preference, which will be proportional to the intensity of this preference. The intensity of preference will itself be increased by selection so long as the sons of hens exercising the preference most decidedly have any advantage over the sons of other hens, whether this be due to the first or to the second cause. The importance of this situation lies in the fact that the further development of the plumage character will still proceed, by reason of the advantage gained in sexual selection, even after it has passed the point in development at which its advantage in Natural Selection has ceased. The selective agencies other than sexual preference may be opposed to further development, and yet the further development will proceed, so long as the disadvantage is more than counterbalanced by the advantage in sexual selection. Moreover, as long as there is a net advantage in favour of further plumage development, there will also be a net advantage in favour of giving to it a more decided preference.

The two characteristics affected by such a process, namely plumage development in the male, and sexual preference for such developments in the female, must thus advance together, and so long as the process is unchecked by severe counterselection, will advance with ever-increasing speed. In the total absence of such checks, it is easy to see that the speed of development will be proportional to the development already attained, which will therefore increase with time exponentially, or in geometric progression. There is thus in any bionomic situation, in which sexual selection is capable of conferring a great reproductive advantage, the potentiality of a runaway process, which, however small the beginnings from which it arose, must, unless checked, produce great effects, and in the later stages with great rapidity.

Such a process must soon run against some check. Two such are obvious. If carried far enough, it is evident that sufficiently severe counterselection in favour of less ornamented males will be encountered to balance the advantage of sexual preference; at this point both plumage elaboration and the increase in female preference will be brought to a standstill, and a condition of relative stability will be attained. It will be more effective still if the disadvantage to the males of their sexual ornaments so diminishes their numbers surviving to the breeding season, relative to the females, as to cut at the root of the process, by diminishing the reproductive advantage to be conferred by female preference. It is important to notice that the condition of relative stability brought about by these or other means, will be of far longer duration than the process in which the ornaments are evolved. In most existing species the runaway process must have been already checked, and we should expect that the more extraordinary developments of sexual plumage were not due like most characters to a long and even course of evolutionary progress, but to sudden spurts of change. The theory does not enable us to predict the outcome of such an episode, but points to a great advantage being conferred by sexual preference as its underlying condition.

Exactly in what way the males which most effectually attract the attention and interest of the females gain thereby a reproductive advantage is a much more difficult question, since polygamy is not nearly so widespread as sex-limited ornaments, and the theory of sexual selection therefore requires that some reproductive advantage should be conferred also in certain monogamous birds. Darwin's theory on this point is exceedingly subtle. He supposes in effect that there is a positive correlation in the females between the earliness with which they are ready to breed, and the numbers of offspring they rear, variations in both these variates being associated, as Darwin suggests, with a higher nutritional condition. Whether this is so in fact it is difficult to say, but it should be noted that the dates of the breeding phenomena of a species could only be stabilized if birds congenitally prone to breed early did not for this reason produce more offspring. The correlation required by Darwin's theory must be due solely to non-hereditary causes, such as chance variations of nutrition might supply. Whether or not there is such a correlation, it would seem no easy matter to demonstrate.

There does seem, however, to be one advantage enjoyed by the males mated earliest in any one district, and which therefore might be conferred by sexual preference; namely, that due to mortality during the breeding season. The death rates of animals are often surprisingly high, and a death rate of only one per cent. per week would give a considerable advantage to the earlier mated males, even if the chances of survival of his offspring were unfavourably affected by his death.

A second circumstance in which sexual preference must afford some reproductive advantage is in the remating of birds widowed during the breeding season: it appears certain that an abundance of unmated birds are usually at hand to take advantage of such a situation, and the choice among these gives to those preferred a reproductive advantage, equally in the case of both sexes. To judge, however, of the relative efficacy of the different possible situations in which sexual preference may confer a reproductive advantage, detailed ecological knowledge is required.

The possibility should perhaps be borne in mind in such studies that the most finely adorned males gain some reproductive advantage without the intervention of female preference, in a manner analogous to that in which advantage is conferred by special weapons. The establishment of territorial rights involves frequent disputes, but these are by no means all mortal combats; the most numerous, and from our point of view, therefore, the most important cases are those in which there is no fight at all, and in which the intruding male is so strongly impressed or intimidated by the appearance of his antagonist as not to risk the damage of a conflict. As a propagandist the cock behaves as though he knew that it was as advantageous to impress the males as the females of his species, and a sprightly bearing with fine feathers and triumphant song are quite as well adapted for war-propaganda as for courtship.

The selective action here considered combines the characteristics of the two classes to which Darwin applied the term sexual selection, namely the evolution of special weapons by combats between rival males, and the evolution of adornments which attract or excite the female. An appearance of strength and pugnacity is analogous to the possession of these qualities in producing the same effect: but the effect is produced in a different way, and in particular, as in the case of attractive ornaments, by the emotional reaction of other members of the species. It involves in fact closely similar mental problems to those raised by the existence of sexual preference. One difference should be noted; in the case of attractive ornaments the evolutionary effect upon the female is to fit her to appreciate more and more highly the display offered, while the evolutionary reaction of war paint upon those whom it is intended to impress should be to make them less and less receptive to all impressions save those arising from genuine prowess. Male ornaments acquired in this way might be striking, but could scarcely ever become extravagant.

Sex limitation of modifications

A difficulty which was regarded rather seriously during the development of the theory of sexual selection is implicit in the limitations of many of the structures ascribable to sex-limited selection, to the particular sex on which the selection acts. The difficulty lay in how far selection acting on only one sex ought to be expected to affect the characters of both sexes, and whether a mutation originally affecting the development of both sexes could be confined to one sex only, by counterselection on the other sex.

Of the large mutational changes chiefly available for genetic study the great majority manifest themselves equally in the two sexes; in an important minority the effect is either unequal in the two sexes or strictly limited to one sex. In birds and mammals a clearly understood mechanism of sexual differentiation lies in the internal secretions of the gonads, which are sexually differentiated, and possibly in a sexual differentiation of other internal secretions. It is a natural inference that a proportion of the mutations which occur affecting any given structure will be, from the first, sex limited in their appearance, and, if they produce their effect only in conjunction with the internal secretions of the sexual glands of one sex, their appearance will be delayed to the adult stage like the other signs of sexual maturity. This proportion may be as low as that observed in the genetic mutations, and indeed the only reason for thinking that it may be higher is that these somewhat violent changes may perhaps be expected to be produced by deviations occurring at an early stage of development, while the slighter changes to which progress by Natural Selection must chiefly be due may more frequently be initiated at later developmental stages.

Whatever the frequency, however, of sex limitation, it may fairly be inferred that selection acting upon one sex only, would, in the complete absence of counter-selection in the other sex, lead to an evolutionary modification not very unequal in the two sexes. Well-marked sexual differentiation must on this view be ascribed to a condition in which the selective agencies acting on the two sexes oppose each others influence. On the view that both sexes are in most species highly adapted to their place in nature, this situation will be readily brought about by the selection of modifications in one sex only, for these, in so far as they are not sex-limited, will be accompanied by changes in the opposite sex, which, on the assumption of high adaptation, will generally be disadvantageous and therefore opposed by selective agencies. Without the assumption of high adaptation, opposition between the actions of selection on the two sexes must be fortuitous and rare, and it is by no means clear how the widespread occurrence of sex-limited modification can on this view be explained.

Since the whole body of genetic evidence seems to favour, and even to require, the view that organisms are in general extremely closely adapted to their situations, we need only consider the consequences of this view. Selection applied to particular qualities in one sex only will then tend, in the first instance, to modify this sex slightly more than the other. The opposite sex will only be modified so far as to bring into play agencies exerting selection, in the opposite direction, and with equal intensity. The advantage of protective coloration, stressed by Wallace, is of obvious importance in this connexion. From this point, which must be reached relatively rapidly, onwards, the selective advantage of a mutation in respect of the selective activity under consideration, will not depend at all upon the average of its effects in the two sexes, but only upon the difference between these effects. If it enhances the sexual contrast and makes the two sexes less alike, it will be favoured by selection, and will have therefore a definite probability of contributing its quotum towards the building up of sexual differentiation. If on the contrary its effect would have been to render the sexes more alike, it will be rejected by the selection in progress. In this, the more prolonged evolutionary phase, it should be noted that any effect which the new mutations may have upon both sexes equally, or, in fact, the average of their effects upon the two sexes, will be immediately neutralized by a change of frequency in those factors which, without being sex limited, influence the development of the organ in question.

Besides the mutations, the effects of which are conditioned by the sexual secretions, an important class of mutations are those which influence the nature of these secretions themselves: for in the condition of sexually opposed selections, any modification of these secretions, which, without impairing their normal action, enhances or increases the range of their developmental effects will thus afford a further means of increasing sexual differentiation. In this way it is by no means a supposition to be excluded as impossible that a character at first manifested equally by the two sexes should, by the action of natural selection, later become sex-limited in its appearance.

Natural Selection and the sex-ratio

The problem of the influence of Natural Selection on the sex-ratio may be most exactly examined by the aid of the concept of reproductive value developed in Chapter II. As is well known, Darwin expressly reserved this problem for the future as being too intricate to admit of any immediate solution. (*Descent of Man*, p. 399).

> In no case, as far as we can see, would an inherited tendency to produce both sexes in equal numbers or to produce one sex in excess, be a direct advantage or disadvantage to certain individuals more than to others; for instance, an individual with a tendency to produce more males than females would not succeed better in the battle for life than an individual with an opposite tendency: and therefore a tendency of this kind could not be gained through natural selection. Nevertheless, there are certain animals (for instance, fishes and cirripedes) in which two or more males appear to be necessary for the fertilization of the female: and the males accordingly largely preponderate, but it is by no means obvious how this male-producing tendency could have been acquired. I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous to the species, it would follow from natural selection, but I now see that the whole problem is so intricate that it is safer to leave its solution for the future.

In organisms of all kinds the young are launched upon their careers endowed with a certain amount of biological capital derived from their parents. This varies enormously in amount in different species, but, in all, there has been, before the offspring is able to lead an independent existence, a certain expenditure of nutriment in addition, almost universally, to some expenditure of time or activity, which the parents are induced by their instincts to make for the advantage of their young. Let us consider the reproductive value of these offspring at the moment when this parental expenditure on their behalf has just ceased. If we consider the aggregate of an entire generation of such offspring it is clear that the total reproductive value of the males in this group is exactly equal to the total value of all the females, because each sex must supply half the ancestry of all future generations of the species. From this it follows that the sex ratio will so adjust itself, under the influence of Natural Selection, that the total parental expenditure incurred in respect of children of each sex, shall be equal; for if this were not so and the total expenditure incurred in producing males, for instance, were less than the total expenditure incurred in producing females, then since the total reproductive value of the males is equal to that of the females, it would follow that those parents, the innate tendencies of which caused them to produce males in excess, would, for the same expenditure, produce a greater amount of reproductive value; and in consequence would be the progenitors of a larger fraction of future generations than would parents having a congenital bias towards the production of females.

Selection would thus raise the sex-ratio until the expenditure upon males became equal to that upon females. If, for example, as in man, the males suffered a heavier mortality during the period of parental expenditure, this would cause them to be more expensive to produce, for, for every hundred males successfully produced expenditure has been incurred, not only for these during their whole period of dependence but for a certain number of others who have perished prematurely before incurring the full complement of expenditure. The average expenditure is therefore greater for each boy reared, but less for each boy born, than it is for girls at the corresponding stages, and we may therefore infer that the condition toward which Natural Selection will tend will be one in which boys are the more numerous at birth, but become less numerous, owing to their higher death rate, before the end of the period of parental expenditure. The actual sex-ratio in man seems to fulfil these conditions somewhat closely, especially if we make allowance for the large recent diminution in the deaths of infants and children; and since this adjustment is brought about by a somewhat large inequality in the sex ratio at conception, for which no *a priori* reason can be given, it is difficult to avoid the conclusion that the sex-ratio has really been adjusted by these means.

The sex-ratio at the end of the period of expenditure thus depends upon differential mortality during that period, and if there are any such differences, upon the differential demands which the young of such species make during their period of dependency; it will not be influenced by differential mortality during a self-supporting period; the relative numbers of the sexes attaining maturity may thus be influenced without compensation, by differential mortality during the period intervening between the period of dependence and the attainment of maturity. Any great differential mortality in this period will, however, tend to be checked by Natural Selection, owing to the fact that the total reproductive value of either sex, being, during this period, equal to that of the other, whichever is the scarcer, will be the more valuable, and consequently a more intense selection will be exerted in favour of all modifications tending towards its preservation. The numbers attaining sexual maturity may thus become unequal if sexual differentiation in form or habits is for other reasons advantageous, but any great and persistent inequality between the sexes at maturity should be found to be accompanied by sexual differentiation, having a very decided bionomic value.

Summary

A consequence of sexual reproduction which seems to be of fundamental importance to evolutionary theory is that advantageous changes in different structural elements of the germ plasm can be taken advantage of independently; whereas with asexual organisms either the genetic uniformity of the whole group must be such that evolutionary progress is greatly retarded, or if there is considerable genetic diversity, many beneficial changes will be lost through occurring in individuals destined to leave no ultimate descendants in the species. In consequence an organism sexually reproduced can respond so much more rapidly to whatever selection is in action, that if placed in competition on equal terms with an asexual organism similar in all other respects, the latter would certainly be replaced by the former.

In order to take full advantage of the possible occurrence of advantageous mutations, mutation rates must be generally so low that in the great majority of loci the homologous genes throughout a single species are almost completely identical, and this is the condition which we appear to find in the higher organisms. With sexual reproduction species are not arbitrary taxonomic units such as they would be with asexual reproduction only, but are bound together by sharing a very complete community of ancestry, if we look back only a hundred generations. The bulk of intraspecific variance apart from the differences between geographic races, in which some degree of isolation has taken effect, must be ascribed to segregation during comparatively few generations in the immediate past.

Selection acting differently on different parts of a species, whether or not these parts are distinguished geographically, will induce distinctions between them in the frequency with which different genes or gene combinations occur, with out necessarily impairing the unity of the species. An element of instability will, however, be introduced in such cases, by genetic modifications affecting the frequency of germinal interchange between the parts; and this, under sufficiently intense selection, will lead to the fission of species, even in the absence of geographical or other barriers to intercourse.

An important means of fission, particularly applicable to the higher animals, lies in the possibility of differential sexual response to differently characterised suitors. Circumstances favourable to the fission of species into parts adapted to different habitats will also be favourable to the development both of discrimination and of sexual preference.

The main postulate of Darwin's theory of sexual selection, namely the exercise of sexual preference, will thus tend to be satisfied by the effects of previous selection. We may infer that the rudiments of an aesthetic faculty so developed thus pervade entire classes, whether or not this faculty is in fact afforded opportunities of inducing evolutionary change. In species so situated that the reproductive success of one sex depends greatly upon winning the favour of the other, as appears evidently to be the case with many polygamous birds, sexual selection will itself act by increasing the intensity of the preference to which it is due, with the consequence that both the feature preferred and the intensity of preference will be augmented together with ever-increasing velocity, causing a great and rapid evolution of certain conspicuous characteristics, until the process can be arrested by the direct or indirect effects of Natural Selection.

Consideration of the mechanism of sex-limited hormones, by which the secondary sexual characteristics of mammals and birds are largely controlled, shows that sexual differentiation may be increased or diminished by the action of Natural Selection, either through the occurrence of mutations sex-limited in effect, or through a modification of the hormone mechanism. It is thus not impossible that a mutant form, at first manifested equally by both sexes, should later, under the action of selection, become confined to one sex only. The question of the ratio of the sexes at maturity has not the same importance for sexual selection as was formerly thought, at least in species in which the number of breeding pairs is limited by the allocation of territory. It is shown that the action of Natural Selection will tend to equalize the parental expenditure devoted to the production of the two sexes; at the same time an understanding of the situations created by territory will probably reveal more than one way in which sexual preference gives an effective advantage in reproduction.