

CHAPTER 4

Group Selection

THIS BOOK is a rejoinder to those who have questioned the adequacy of the traditional model of natural selection to explain evolutionary adaptation. The topics considered in the preceding chapters relate mainly to the adequacy of this model in the realms of physiological, ecological, and developmental mechanisms, matters of primary concern to individual organisms. At the individual level the adequacy of the selection of alternative alleles has been challenged to only a limited degree. Many more doubts on the importance of such selection have been voiced in relation to the phenomena of interactions among individuals. Many biologists have implied, and a moderate number have explicitly maintained, that groups of interacting individuals may be adaptively organized in such a way that individual interests are compromised by a functional subordination to group interests.

It is universally conceded by those who have seriously concerned themselves with this problem (e.g., Allee *et al.*, 1949; Haldane, 1932; Lewontin, 1958B, 1962; Slobodkin, 1954; Wynne-Edwards, 1962; Wright, 1945) that such group-related adaptations must be attributed to the natural selection of alternative *groups* of individuals and that the natural selection of alternative alleles within populations will be opposed to this development. I am in entire agreement with the reasoning behind this conclusion. Only by a theory of between-group selection could we

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achieve a scientific explanation of group-related adaptations. However, I would question one of the premises on which the reasoning is based. Chapters 5 to 8 will be primarily a defense of the thesis that group-related adaptations do not, in fact, exist. A *group* in this discussion should be understood to mean something other than a family and to be composed of individuals that need not be closely related.

The present chapter examines the logical structure of the theory of selection between groups, but first I wish to consider an apparent exception to the rule that the natural selection of individuals cannot produce group-related adaptations. This exception may be found in animals that live in stable social groups and have the intelligence and other mental qualities necessary to form a system of personal friendships and animosities that transcend the limits of family relationship. Human society would be impossible without the ability of each of us to know, individually, a variety of neighbors. We learn that Mr. X is a noble gentleman and that Mr. Y is a scoundrel. A moment of reflection should convince anyone that these relationships may have much to do with evolutionary success. Primitive man lived in a world in which stable interactions of personalities were very much a part of his ecological environment. He had to adjust to this set of ecological factors as well as to any other. If he was socially acceptable, some of his neighbors might bring food to himself and his family when he was temporarily incapacitated by disease or injury. In time of dearth, a stronger neighbor might rob our primitive man of food, but the neighbor would be more likely to rob a detestable primitive Mr. Y and his troublesome family. Conversely, when

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a poor Mr. X is sick our primitive man will, if he can, provide for him. Mr. X's warm heart will know the emotion of gratitude and, since he recognizes his benefactor and remembers the help provided, will probably reciprocate some day. A number of people, including Darwin (1896, Chap. 5), have recognized the importance of this factor in human evolution. Darwin speaks of it as the "lowly motive" of helping others in the hope of future repayment. I see no reason why a conscious motive need be involved. It is necessary that help provided to others be occasionally reciprocated if it is to be favored by natural selection. It is not necessary that either the giver or the receiver be aware of this.

Simply stated, an individual who maximizes his friendships and minimizes his antagonisms will have an evolutionary advantage, and selection should favor those characters that promote the optimization of personal relationships. I imagine that this evolutionary factor has increased man's capacity for altruism and compassion and has tempered his ethically less acceptable heritage of sexual and predatory aggressiveness. There is theoretically no limit to the extent and complexity of group-related behavior that this factor could produce, and the immediate goal of such behavior would always be the well-being of some other individual, often genetically unrelated. Ultimately, however, this would not be an adaptation for group benefit. It would be developed by the differential survival of individuals and would be designed for the perpetuation of the genes of the individual providing the benefit to another. It would involve only such immediate self-sacrifice for which the probability of later repayment would be sufficient

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justification. The natural selection of alternative alleles can foster the production of individuals willing to sacrifice their lives for their offspring, but never for mere friends.

The prerequisites for the operation of this evolutionary factor are such as to confine it to a minor fraction of the Earth's biota. Many animals form dominance hierarchies, but these are not sufficient to produce an evolutionary advantage in mutual aid. A consistent interaction pattern between hens in a barnyard is adequately explained without postulating emotional bonds between individuals. One hen reacts to another on the basis of the social releasers that are displayed, and if individual recognition is operative, it merely adjusts the behavior towards another individual according to the immediate results of past interactions. There is no reason to believe that a hen can harbor grudges against or feel friendship toward another hen. Certainly the repayment of favors would be out of the question.

A competition for social goodwill cannot fail to have been a factor in human evolution, and I would expect that it would operate in many of the other primates. Altman (1962) described the formation of semipermanent coalitions between individuals within bands of wild rhesus monkeys and cited similar examples from other primates. Members of such coalitions helped each other in conflicts and indulged in other kinds of mutual aid. Surely an individual that had a better than average ability to form such coalitions would have an evolutionary advantage over its competitors. Perhaps this evolutionary factor might operate in the evolution of porpoises. This seems to be the most likely explanation for the very solicitous

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behavior that they sometimes show toward each other (Sliper, 1962, pp. 193-197). I would be reluctant, however, to recognize this factor in any group but the mammalia, and I would imagine it to be confined to a minority of this group. For the overwhelming mass of the Earth's biota, friendship and hate are not parts of the ecological environment, and the only way for socially beneficial self-sacrifice to evolve is through the biased survival and extinction of populations, not by selective gene substitution within populations.

To MINIMIZE recurrent semantic difficulties, I will formally distinguish two kinds of natural selection. The natural selection of alternative alleles in a Mendelian population will henceforth be called *genic selection*. The natural selection of more inclusive entities will be called *group selection*, a term introduced by Wynne-Edwards (1962). *Intrademic* and *interdemic*, and other terms with the same prefixes, have been used to make the same distinction. It has been my experience, however, that the repeated use in the same discussion of "inter" and "intra" for specifically contrasted concepts is a certain cause of confusion, unless a reader exerts an inconvenient amount of attention to spelling, or a speaker indulges in highly theatrical pronunciation.

The definitions of other useful terms, and the conceptual relations between the various creative evolutionary factors and the production of adaptation are indicated in Figure 1. Genic selection should be assumed to imply the current conception of natural selection often termed *neo-Darwinian*. An *organic adaptation* would be a mechanism designed to promote

Evolutionary Process

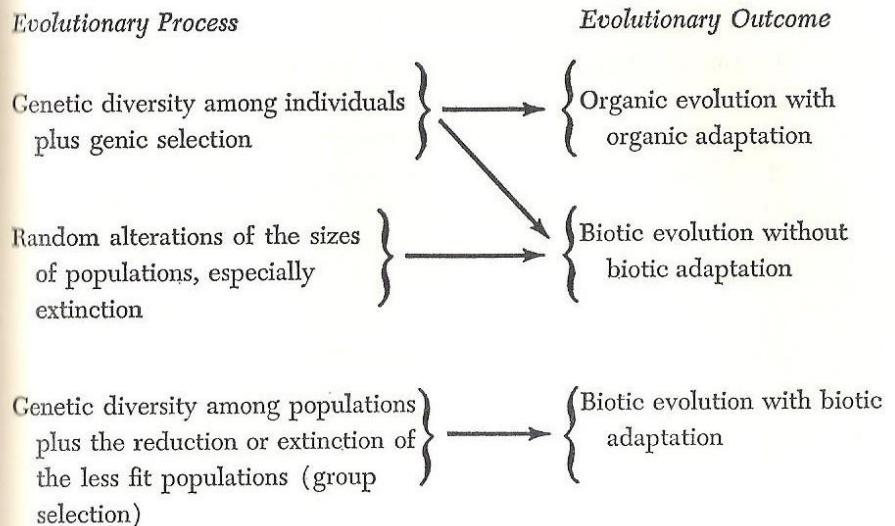


FIGURE 1. Summary comparison of organic and biotic evolution, and of organic and biotic adaptation.

the success of an individual organism, as measured by the extent to which it contributes genes to later generations of the population of which it is a member. It has the individual's *inclusive fitness* (Hamilton, 1964A) as its goal. Biotic evolution is any change in a biota. It can be brought about by an evolutionary change in one or more of the constituent populations, or merely by a change in their relative numbers. A *biotic adaptation* is a mechanism designed to promote the success of a biota, as measured by the lapse of time to extinction. The biota considered would have to be restricted in scope so as to allow comparison with other biotas. It could be a single biome, or community, or taxonomic group, or, most often, a single population. A change in the fish-fauna of a lake would be considered biotic evolution. It could come about through some change in the characters of one or more of the constituent populations or through a change

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in the relative numbers of the populations. Either would result in a changed fish-fauna, and such a change would be biotic evolution. A biotic adaptation could be a mechanism for the survival of such a group as the fish-fauna of a lake, or of any included population, or of a whole species that lives in that lake and elsewhere.

I believe that it is useful to make a formal distinction between biotic and organic evolution, and that certain fallacies can be avoided by keeping the distinction in mind. It should be clear that, in general, the fossil record can be a direct source of information on organic evolution only when changes in single populations can be followed through a continuous sequence of strata. Ordinarily the record tells us only that the biota at time t' was different from that at time t and that it must have changed from one state to the other during the interval. An unfortunate tendency is to forget this and to assume that the biotic change must be ascribed to appropriate organic change. The horse-fauna of the Eocene, for instance, was composed of smaller animals than that of the Pliocene. From this observation, it is tempting to conclude that, at least most of the time and on the average, a larger than mean size was an advantage to an individual horse in its reproductive competition with the rest of its population. So the component populations of the Tertiary horse-fauna are presumed to have been evolving larger size most of the time and on the average. It is conceivable, however, that precisely the opposite is true. It may be that at any given moment during the Tertiary, most of the horse populations were evolving a smaller size. To account for the trend towards larger size it is merely necessary to

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make the additional assumption that group selection favored such a tendency. Thus, while only a minority of the populations may have been evolving a larger size, it could have been this minority that gave rise to most of the populations of a million years later. Figure 2 shows how the same observations on the fossil record can be rationalized on two entirely different bases. The unwarranted assumption of organic evolution as an explanation for biotic evolution dates

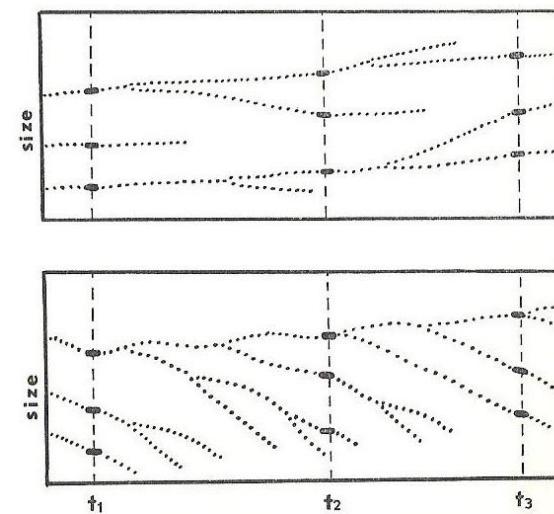


FIGURE 2. Alternative ways of interpreting the same observations of the fossil record. Average sizes in hypothetical horse species at three different times are indicated by boldface marks on the vertical time-scale at times t_1 , t_2 , and t_3 . Upper and lower diagrams show the same observations. In the upper, hypothetical phylogenies explain the observations as the result of the organic evolution of increased size and of occasional chance extinction. In the lower, the hypothetical phylogenies indicate the organic evolution mainly of decreased size, but with effective counteraction by group selection so that the biota evolves a larger average size.

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at least from Darwin. In *The Origin of Species* he dealt with a problem that he termed "advance in organization." He interpreted the fossil record as indicating that the biota has evolved progressively "higher" forms from the Cambrian to Recent, clearly a change in the biota. His explanation, however, is put largely in terms of the advantage that an individual might have over his neighbors by virtue of a larger brain, greater histological complexity, etc. Darwin's reasoning here is analogous to that of someone who would expect that if the organic evolution of horses proceeded toward larger size during the Tertiary, most equine mutations during this interval must have caused larger size in the affected individuals. I suspect that most biologists would tend toward the opposite view, and expect that random changes in the germ plasm would be more likely to curtail growth than to augment it. Organic evolution would normally run counter to the direction of mutation pressure. There is a formally similar relation between organic evolution and group selection. Organic evolution provides genetically different populations, the raw material on which group selection acts. There is no necessity for supposing that the two forces would normally be in precisely the same direction. It is conceivable that at any given moment since the Cambrian, the majority of organisms were evolving along lines that Darwin would consider retrogression, degeneration, or narrow specialization, and that only a minority were progressing. If the continued survival of populations were sufficiently biased in favor of this minority, however, the biota as a whole might show "progress" from one geologic period to the next. I expect that the fossil record is actually of little use in

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evaluating the relative potency of genic and group selection.

In another respect the analogy between mutation and organic evolution as sources of diversity may be misleading. Mutations occur at random and are usually destructive of any adaptation, whereas organic evolution is largely concerned with the production or at least the maintenance of organic adaptation. Any biota will show a system of adaptations. If there is no group selection, i.e., if extinction is purely by chance, the adaptations shown will be a random sample of those produced by genic selection. If group selection does operate, even weakly, the adaptations shown will be a biased sample of those produced by genic selection. Even with such bias in the kinds of adaptations actually represented, we would still recognize genic selection as the process that actually produced them. We could say that the adaptations were produced by group selection only if it was so strong that it constantly curtailed organic evolution in all but certain favored directions and was thus able, by its own influence, to accumulate the function of organic adaptations and the production of the additional details of complex adaptations. This distinction between the production of a biota with a certain set of adaptations of a biota will be emphasized again in a number of contexts.

IN DISCUSSING the adaptations and the general fitness of an individual organism we can often make value judgments with some confidence. We may be familiar enough with the physiology and ecology of the organism to state an opinion on how fit it is, relative to other organisms in the same population. We can be

especially confident of our opinion when the organism shows some gross impairment of what we know to be an important mechanism. A horse with a broken leg has a very low fitness compared with most of the uninjured members of its herd. It might happen that soon after such an unfavorable estimate of its fitness, all but two of the herd-mates of our injured horse wander into a steep-walled canyon where they are trapped and killed by a fire. It might turn out that, by chance, the two that escaped are a son and a daughter of the individual with the broken leg. This would make this horse extraordinarily successful but would not invalidate our adverse judgment of its fitness. We could still insist that it was of very low fitness but also very lucky. Fitness is not related to genetic survival in any deterministic fashion. Chance is also an important factor. We cannot measure fitness by evolutionary success on an individual basis. It should be judged in individuals by the extent and effectiveness of design for survival. We can judge any horse with a broken leg to be of quite low fitness, because such an injury is a grave impairment of its adaptive design. Only if such judgments conflict with the facts of evolutionary success and failure in a significant majority of cases would we be proved wrong. Such judgments are undoubtedly right most of the time. For a horse population we can surely say that individuals characterized by fleetness, disease resistance, sensory acuity, and fertility are more fit than those that are less fleet, less resistant, etc. The science of equine physiology has advanced enough so that we have a detailed understanding and appreciation of the horse's design for survival and can have no reasonable doubt of the importance and effectiveness of that design.

Ideally we should approach the subject of biotic adaptation in the same way. Unfortunately we do not have a comparable understanding of the physiology and ecology of populations and more inclusive groups. Can we describe any biotically adaptive mechanisms of a population of horses? Would we be able to recognize an impairment of any such mechanism as confidently as we would recognize a fracture as an individual impairment? Such questions will be left primarily for later chapters. At this point I wish merely to point out that if it were not for the obvious existence of organic adaptations and of their taxonomic diversity, there would be no need for the theory of genic selection. Similarly, unless there are such things as biotic adaptations, there is no need for the theory of group selection.

If we cannot adequately detect and measure design for success, perhaps we can measure the less interesting but necessarily correlated factor of success itself. It is certainly possible, under the proper conditions, to measure the evolutionary success of an individual organism. We need merely count its descendants of two or three generations later and compare this count with the mean of its contemporaries' descendants. More often than not, a highly successful organism would have been of above average fitness. We could determine what characters contribute most to fitness by noting those that are most strongly correlated with success. For populations this method would be more difficult, because a much longer time would be necessary. There is more hope, perhaps, for meaningful answers to the question, "How well is the population now succeeding?" than for the question, "How well will it have succeeded a thousand

years from now?" When we see an adult animal or plant that we judge to be healthy and vigorous, and that we know has produced healthy offspring, we regard it as being currently successful. Might there not be comparable indications of health and vigor in a population on the basis of which we might say that it is currently successful and therefore probably fit? This seems to be the most frequent approach to the problem of assaying the presence of biotic adaptation in Mendelian populations.

A commonly assumed measure of population success and well-being is simply the number of individuals. This parameter may sometimes be satisfying and useful, e.g., in comparisons of genetically different fruit-fly populations in identical environments (Carson, 1961). In its crude form, however, I doubt that many people would find this definition consistently acceptable. Is a fox population less successful than the more numerous rabbits on which it feeds? The use of mere number as an indication of adaptation can be made more generally valid by the introduction of various "adjustments." Mass, rather than number, may be used for species of different sized individuals; or comparisons may be limited to ecologically equivalent types, to equal areas, to similar stages in the life cycle, etc. Even then, however, there will be many instances of comparisons that will rank one population as better adapted than another but in so doing will do violence to an intuitive judgment of population fitness. Are the diatom populations of the North Atlantic better adapted than those of Lake Geneva? They are larger populations at any season and they are denser at most. There is no way of knowing just

where to stop in compiling a list of adjustments and correction factors.

A possible alternative is to use as a measure of success, not population size, but its current rate of change in size (Fisher's *Malthusian parameter*), as was done by Odum and Allee (1956), Kimura (1958), and Barker (1963). A population that is increasing rapidly would be considered more successful than one that is stationary in size or decreasing. Here again there are situations in which the approach would not agree with what we feel we should really mean by population well-being. By this criterion the diatom populations of both the North Atlantic and Lake Geneva would be alternatively at a much higher and a much lower level of adaptation than the human population. A number of treatments of the problem (e.g., Pimentel, 1961; Brereton, 1962A; Wynne-Edwards, 1962) have assumed, in fact, that there are times when a reduction in number is adaptive. This conclusion is implied by the use of the term *regulation* in the sense of adaptive control of population size, a matter taken up in Chapter 8. Brown (1958) maintained that the best-adapted populations show, not stability, but wide fluctuations in number, which make it possible for the species to expand into new habitats.

Lewontin (1958B) suggested that population fitness be measured by ecological versatility. Thus if one population can survive in only one of two environments and another population can survive in both, he would regard the second as better adapted. Here again the suggestion seems reasonable at first but breaks down in any number of actual situations. If we were to recognize three general habitats, the

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terrestrial, the freshwater, and the marine, the populations of certain euryhaline or amphibious animals would have to be considered better adapted than the great majority of the birds and mammals. Many bacteria would be better adapted than any angiosperm, and so on. Judgments based on habitat versatility would depend as much on the classification of habitats as on the properties of populations.

The basic problem, which Lewontin clearly recognized, is the very common one of the easily measured variables' not being the theoretically important ones. The important factor is the degree of assurance, especially that provided by biotic adaptations, for long-term population survival. Thoday (1953, 1958) proposed this as the definition of population fitness, but did not suggest any simple formula for its objective measurement. The attainment of such population fitness is often implied as an important element in evolutionary progress (see pp. 49-54). In practice, estimates of current population success (itself a crude estimate of fitness, or design for success) are based on readily measurable demographic variables that must be very imperfectly correlated with long-term survival and extinction. It may be true that the set, "large population," has a lower rate of extinction within 10,000 years than the set, "small population." In the same way increasing populations can be given more favorable prognoses than diminishing populations. I am sure that most biologists would agree, however, that such characteristics form an extremely unreliable basis for predicting long-term survival and extinction.

My own preference is for numerical stability, regardless of absolute numbers, as a measure of current

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population success. This measure is assumed to be the most relevant by Pimentel (1961), Brereton (1962A and B), Dunbar (1960), and Wynne-Edwards (1962). Whatever advantages this measure possesses may be partly offset by its being somewhat more difficult to assess than either absolute size or momentary rate of change in size. Stability can be assessed by the amplitude of fluctuation about a long-term mean. A population with a very low amplitude of fluctuation would be considered more successful than one that has large ups and downs. It is the downs that are important. A population that does not, over a long interval of time, drop below one-half of its long-term mean would presumably be in a healthier state than one that frequently drops below one-third of its long-term mean. The important consideration is the likelihood of dropping to zero, and I presume that this is more likely for the relatively more variable population, regardless of its absolute numbers. The cause of such stability is supposed by Brereton (1962A) and Wynne-Edwards (1962) to be due in most cases to the presence of biotic adaptations. Some restriction would have to be placed on the way in which fluctuations are measured. Those that are a part of the normal life cycle should not be included. Comparisons should be made between means of entire cycles or of similar points (e.g., minima) of successive cycles.

All of the various criteria mentioned above have been assumed by different authors to be reliable measures of group success and to be the obvious goals of biotic adaptations. So all must be borne in mind in the ensuing chapters where these supposed

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adaptations are discussed. In this chapter the treatment of biotic adaptation will be confined to the theory of its genesis, and will indicate that there is no firm reason to expect group selection to be an important creative factor.

First of all, it is essential, before proceeding further with the discussion, that the reader firmly grasp the general meaning of biotic adaptation. He must be able to make a conceptual distinction between a population of adapted insects and an adapted population of insects. The fact that an insect population survives through a succession of generations is not evidence for the existence of biotic adaptation. The survival of the population may be merely an incidental consequence of the organic adaptations by which each insect attempts to survive and reproduce itself. The survival of the population depends on these individual efforts. To determine whether this survival is the proper function or merely an incidental by-product of the individual effort must be decided by a critical examination of the reproductive processes. We must decide: Do these processes show an effective design for maximizing the number of descendants of the individual, or do they show an effective design for maximizing the number, rate of growth, or numerical stability of the population or larger system? Any feature of the system that promotes group survival and cannot be explained as an organic adaptation can be called a biotic adaptation. If the population has such adaptations it can be called an adapted population. If it does not, if its continued survival is merely incidental to the operation of organic adaptations, it is merely a population of adapted insects.

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LIKE the theory of genic selection, the theory of group selection is logically a tautology and there can be no sane doubt about the reality of the process. Rational criticism must center on the importance of the process and on its adequacy in explaining the phenomena attributed to it. An important tenet of evolutionary theory is that natural selection can produce significant cumulative change only if selection coefficients are high relative to the rates of change of the selected entity. Since genic selection coefficients are high relative to mutation rates, it is logically possible for the natural selection of alternative alleles to have important cumulative effects. It was pointed out on pp. 22-23 that there can be no effective selection of somata. They have limited life spans and (often) zero biotic potential. The same considerations apply to populations of somata. I also pointed out that genotypes have limited lives and fail to reproduce themselves (they are destroyed by meiosis and recombination), except where clonal reproduction is possible. This is equally true of populations of genotypes. All of the genotypes of fruit-fly populations now living will have ceased to exist in a few weeks. Within a population, only the gene is stable enough to be effectively selected. Likewise in selection among populations, only populations of genes (gene pools) seem to qualify with respect to the necessary stability. Even gene pools will not always qualify. If populations are evolving rapidly and have a low rate of extinction and replacement, the rate of endogenous change might be too great for group selection to have any cumulative effect. This argument precisely parallels that which indicates that mutation rates must

be low relative to selection coefficients for genic selection to be effective.

If a group of adequately stable populations is available, group selection can theoretically produce biotic adaptations, for the same reason that genic selection can produce organic adaptations. Consider again the evolution of size among Tertiary horses. Suppose that at one time there was a genus of two species, one that averaged 100 kilograms when full grown and another that averaged 150 kilograms. Assume that genic selection in both species favored a smaller size so that a million years later the larger of the two averaged only 130 kilograms and the smaller had become extinct, but had lost 20 kilograms before it did so. In this case we could say that the genus evolved an increased size, even though both of the included species evolved a decreased size. If the extinction of the smaller species is not just a chance event but is attributable to its smaller size, we might refer to large size as a biotic adaptation of a simple sort. However, it is the origin of complex adaptations, for which the concept of functional design would be applicable, that is the important consideration.

If alternative gene pools are not themselves stable, it is still conceivable that group selection could operate among more or less constant rates of change. A system of relatively stable rates of change in the gene frequencies of a population might be called an evolutionary trajectory. It could be described as a vector in n -dimensional space, with n being the number of relevant gene frequencies. In a given sequence of a few generations a gene pool may be undergoing certain kinds of change at a certain rate. This is only one of an infinite number of other evolutionary trajec-

tories that might conceivably be followed. Some trajectories may be more likely to lead to extinction than others, and group selection will then operate by allowing different kinds of evolutionary change to continue for different average lengths of time. There is paleontological evidence that certain kinds of evolutionary change may continue for appreciable lengths of time on a geological scale. Some of the supposed examples disappear as the evidence accumulates and shows that actual courses of evolution are more complex than they may have seemed at first. Other examples are apparently real and are attributed by Simpson (1944, 1953) to continuous genic selection in certain directions, a process he terms "orthoselection."

Wright (1945) proposed that group selection would be especially effective in a species that was divided up into many small populations that were almost but not quite isolated from each other. Most of the evolutionary change in such a species would be in accordance with genic selection coefficients, but the populations are supposed to be small enough so that genes would occasionally be fixed by drift in spite of adverse selection within a population. Some of the genes so fixed might benefit the population as a whole even though they were of competitive disadvantage within the population. A group so favored would increase in size (regarded as a benefit in Wright's discussion) and send out an augmented number of emigrants to neighboring populations. These migrants would partly or wholly counteract the adverse selection of the gene in neighboring populations and give them repeated opportunity for the chance fixation of the gene. The oft-repeated opera-

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tion of this process eventually would produce complex adaptations of group benefit, but of competitive disadvantage to an individual. According to this theory, selection not only can act on preexisting variation, but also can help to produce the variation on which it acts, by repeatedly introducing the favored gene into different populations.

Wright formally derived this model in a review of a book by G. G. Simpson. Later, Simpson (1953, pp. 123; 164-165) briefly criticized Wright's theory by pointing out that it leaves too much to a rather improbable concatenation of the population parameters of size, number, degree of isolation, and the balance of genic and group selection coefficients. The populations have to be small enough for genetic drift to be important, but not so small that they are in danger of extinction, and they have to be big enough for certain gene substitutions to be more important than chance factors in determining size and rate of emigration. The unaugmented rates of immigration must be too small to reestablish the biotically undesirable gene after it is lost by drift. The populations must be numerous enough for the postulated process to work at a variety of loci, and each of the populations must be within the necessary size range. Lastly, the balance of these various factors must persist long enough for an appreciable amount of evolutionary change to take place. At the moment, I can see no hope of achieving any reliable estimate of how frequently the necessary conditions have been realized, but surely the frequency of such combinations of circumstances must be relatively low and the combinations quite temporary when they do occur. Simpson also expressed doubts on the reality of the biotic adaptations that Wright's theory was proposed to explain.

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A number of writers have since postulated a role for the selection of alternative populations within a species in the production of various supposed "altruistic" adaptations. Most of these references, however, have completely ignored the problem that Wright took such pains to resolve. They have ignored the problem of how whole populations can acquire the necessary genes in high frequency in the first place. Unless some do and some do not, there is no set of alternatives for group selection to act upon. Wright was certainly aware, as some later workers apparently were not, that even a minute selective disadvantage to a gene in a population of moderate size can cause an almost deterministic reduction of the gene to a negligible frequency. This is why he explicitly limited the application of his model to those species that are subdivided into many small local populations with only occasional migrants between them. Others have postulated such group selection as an evolutionary factor in species that manifestly do not have the requisite population structures. Wynne-Edwards (1962), for example, postulated the origin of biotic adaptations of individual disadvantage, by selection among populations of smelts, in which even a single spawning aggregation may consist of tens of thousands of individuals. He envisioned the same process for marine invertebrates that may exist as breeding adults by the million per square mile and have larval stages that may be dispersed many miles from their points of origin.

A POSSIBLE escape from the necessity of relying on drift in small populations to fix the genes that might contribute to biotic adaptation, is to assume that such genes are not uniformly disadvantageous in competi-

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tive individual relationships. If such a gene were, for some reason, individually advantageous in one out of ten populations, group selection could work by making the descendants of that population the sole representatives of the species a million years later. However, this process also loses plausibility on close examination. Low rates of endogenous change relative to selection coefficients are a necessary precondition for any effective selection. The necessary stability is the general rule for genes. While gene pools or evolutionary trajectories can persist little altered through a long period of extinction and replacement of populations, there is no indication that this is the general rule. Hence the effectiveness of group selection is open to question at the axiomatic level for almost any group of organisms. The possibility of effective group selection can be dismissed for any species that consists, as many do, of a single population. Similarly the group selection of alternative species cannot direct the evolution of a monotypic genus, and so on.

Even in groups in which all of the necessary conditions for group selection might be demonstrated, there is no assurance that these conditions will continue to prevail. Just as the evolution of even the simplest organic adaptation requires the operation of selection at many loci for many generations, so also would the production of biotic adaptation require the selective substitution of many groups. This is a major theoretical difficulty. Consider how rapid is the turnover of generations in even the slowest breeding organisms, compared to the rate at which populations replace each other. The genesis of biotic adaptation must for this reason be orders of magnitude slower

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than that of organic adaptation. Genic selection may take the form of the replacement of one allele by another at the rate of 0.01 per generation, to choose an unusually high figure. Would the same force of group selection mean that a certain population would be 0.01 larger, or be growing 0.01 faster, or be 0.01 less likely to become extinct in a certain number of generations, or have a 0.01 greater emigration rate than another population? No matter which meaning we assign, it is clear that what would be a powerful selective force at the genic level would be trivial at the group level. For group selection to be as strong as genic selection, its selection coefficients would have to be much greater to compensate for the low rate of extinction and replacement of populations.

The rapid turnover of generations is one of the crucial factors that makes genic selection such a powerful force. Another is the large absolute number of individuals in even relatively small populations, and this brings us to another major difficulty in group selection, especially at the species level. A species of a hundred different populations, sufficiently isolated to develop appreciable genetic differences, would be exceptional in most groups of organisms. Such a complexly subdivided group, however, might be in the same position with respect to a bias of 0.01 in the extinction and replacement of groups, as a population of 50 diploid individuals with genic selection coefficients that differ by 0.01. In the population of 50 we would recognize genetic drift, a chance factor, as much more important than selection as an evolutionary force. Numbers of populations in a species, or of taxa in higher categories, are usually so small that chance would be much more important in deter-

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mining group survival than would even relatively marked genetic differences among the groups. By analogy with the conclusions of population genetics, group selection would be an important creative force only where there were at least some hundreds of populations in the group under consideration.

Obviously the comments above are not intended to be a logically adequate evaluation of group selection. Analogies with the conclusions on genic selection are only analogies, not rigorously reasoned connections. I would suggest, however, that they provide a reasonable basis for skepticism about the effectiveness of this evolutionary force. The opposite tendency is frequently evident. A biologist may note that, logically and empirically, the evolutionary process is capable of producing adaptations of great complexity. He then assumes that these adaptations must include not only the organic but also the biotic, usually discussed in such terms as "for the good of the species." A good example is provided by Montagu (1952), who summarized the modern theory of natural selection and in so doing presented an essentially accurate picture of selective gene substitution by the differential reproductive survival of individuals. Then in the same work he states, "We begin to understand then, that evolution itself is a process which favors cooperating rather than disoperating groups and that 'fitness' is a function of the group as a whole rather than separate individuals." This kind of evolution and fitness is attributed to the previously described natural selection of individuals. Such an extrapolation from conclusions based on analyses of the possibilities of selective gene substitutions *in* populations to the production of biotic adaptations *of* populations is

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entirely unjustified. Lewontin (1961) has pointed out that population genetics as it is known today relates to genetic processes in populations, not of populations.

LEWONTIN (1962; Lewontin and Dunn, 1960) has produced what seems to me to be the only convincing evidence for the operation of group selection. There is a series of alleles symbolized by *t* in house-mouse populations that produces a marked distortion of the segregation ratio of sperm. As much as 95 per cent of the sperm of a heterozygous male may bear such a gene, and only 5 per cent bear the wild-type allele. This marked selective advantage is opposed by other adverse effects in the homozygotes, either an embryonic lethality or male sterility. Such characters as lethality, sterility, and measurable segregation ratios furnish an excellent opportunity for calculating the effect of selection as a function of gene frequency in hypothetical populations. Such calculations, based on a deterministic model of selection, indicate that these alleles should have certain equilibrium frequencies in the populations in which they occur. Studies of wild populations, however, consistently give frequencies below the calculated values. Lewontin concludes that the deficiency must be ascribed to some force in opposition to genic selection, and that group selection is the likely force. He showed that by substituting a stochastic model of natural selection, so as to allow for a certain rate of fixation of one or another allele in family groups and small local populations, he could account for the observed low frequencies of the *t*-alleles.

It should be emphasized that this example relates

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to genes characterized by lethality or sterility and extremely marked segregation distortions. Selection of such genes is of the maximum possible intensity. Important changes in frequency can occur in a very few generations as a result of genic selection, and no long-term isolation is necessary. Populations so altered would then be subject to unusually intense group selection. A population in which a segregation distorter reaches a high frequency will rapidly become extinct. A small population that has such a gene in low frequency can lose it by drift and thereafter replace those that have died out. Only one locus is involved. One cannot argue from this example that group selection would be effective in producing a complex adaptation involving closely adjusted gene frequencies at a large number of loci. Group selection in this example cannot maintain very low frequencies of the biotically deleterious gene in a population because even a single heterozygous male immigrant can rapidly "poison" the gene pool. The most important question about the selection of these genes is why they should produce such extreme effects. The segregation distortion makes the genes extremely difficult to keep at low frequency by either genic or group selection. Why has there not been an effective selection of modifiers that would reduce this distortion? Why also has there not been effective selection for modifiers that would abolish the lethality and sterility. The *t*-alleles certainly must constitute an important part of the genetic environment of every other gene in the population. One would certainly expect the other genes to become adapted to their presence.

Segregation distortion is something of a novelty in

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natural populations. I would be inclined to attribute the low frequency of such effects to the adjustment of each gene to its genetic environment. When distorter genes appear they would be expected to replace their alleles unless they produced, like the *t*-alleles, drastic reductions in fitness at some stage of development. When such deleterious effects are mild, the population would probably survive and would gradually incorporate modifiers that would reduce the deleterious effects. In other words, the other genes would adjust to their new genetic environment. It is entirely possible, however, that populations and perhaps entire species could be rendered extinct by the introduction of such genes as the *t*-alleles of mice. Such an event would illustrate the production, by genic selection, of characters that are highly unfavorable to the survival of the species. The gene in question would produce a high phenotypic fitness in the gamete stage. It might have a low effect on some other stage. The selection coefficient would be determined by the mean of these two effects relative to those of alternative alleles, regardless of the effect on population survival. I wonder if anyone has thought of controlling the mouse population of an area by flooding it with *t*-carriers.

I AM entirely willing to concede that the kinds of adaptations evolved by a population, for instance segregation distortion, might influence its chance for continued survival. I question only the effectiveness of this extinction-bias in the production and maintenance of any adaptive mechanisms worthy of the name. This is not the same as denying that extinction can be an important factor in biotic evolution. The

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conclusion is inescapable that extinction has been extremely important in producing the Earth's biota as we know it today. Probably only on the order of a dozen Devonian vertebrates have left any Recent descendants. If it had happened that some of these dozen had not survived, I am sure that the composition of today's biota would be profoundly different.

Another example of the importance of extinction can be taken from human evolution. The modern races and various extinct hominids derive from a lineage that diverged from the other Anthropoidea a million or perhaps several million years ago. There must have been a stage in which man's ancestors were congeneric with, but specifically distinct from, the ancestors of the modern anthropoid apes. At this time there were probably several and perhaps many other species in this genus. All but about four, however, became extinct. One that happened to survive produced the gibbons, another the orang, another the gorilla and chimpanzee, and another produced the hominids. These were only four (or perhaps three or five) of an unknown number of contemporary Pliocene alternatives. Suppose that the number had been one less, with man's ancestor being assigned to the group that became extinct! We have no idea how many narrow escapes from extinction man's lineage may have experienced. There would have been nothing extraordinary about his extinction; on the contrary, this is the statistically most likely development. The extinction of this lineage would, however, have provided the world today with a strikingly different biota. This one ape, which must have had a somewhat greater than average tendency toward bipedal locomotion and, according to recent views, a tendency

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towards predatory pack behavior, was transferred by evolution from an ordinary animal, with an ordinary existence, to a cultural chain reaction. The production and maintenance of such tributary adaptations as an enlarged brain, manual dexterity, the arched foot, etc. was brought about by the gradual shifting of gene frequencies at each genetic locus in response to changes in the genetic, somatic, and ecological environments. It was this process that fashioned a man from a beast. The fashioning was not accomplished by the survival of one animal type and the extinction of others.

I would concede that such matters of extinction and survival are extremely important in biotic evolution. Of the systems of adaptations produced by organic evolution during any given million years, only a small proportion will still be present several million years later. The surviving lines will be a somewhat biased sample of those actually produced by genic selection, biased in favor of one type of adaptive organization over another, but survival will always be largely a matter of historical accident. It may be that some people would not even recognize such chance extinction as important in biotic evolution. Ecologic determinists might attribute more of a role to the niche factor; man occupies an ecologic niche, and if one ancestral ape had failed to fill it, another would have. This sort of thinking probably has some validity, but surely historical contingency must also be an important factor in evolution. The Earth itself is a unique historical phenomenon, and many unique geological and biological events must have had a profound effect on the nature of the world's biota.

There is another example that should be consid-

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ered, because it has been used to illustrate a contrary point of view. The extinction of the dinosaurs may have been a necessary precondition to the production of such mammalian types as elephants and bears. This extinction, however, was not the creative force that designed the locomotor and trophic specializations of these mammals. That force can be recognized in genic selection in the mammalian populations. There are analogies in human affairs. In World War II there was a rubber shortage due to the curtailment of imports of natural rubber. Scientists and engineers were thereby stimulated to develop suitable substitutes, and today we have a host of their inventions, some of which are superior to natural rubber for many uses. Necessity may have been the mother of invention, but she was not the inventor. I would liken the curtailment of imports, surely not a creative process, to the extinction of the dinosaurs, and the efforts of the scientists and engineers, which certainly were creative, to the selection of alternative alleles within the mammalian populations. In this attitude I ally myself with Simpson (1944) and against Wright (1945), who argued that the extinction of the dinosaurs, since it may have aided the adaptive radiation of the mammals, should be regarded as a creative process.

GROUP selection is the only conceivable force that could produce biotic adaptation. It was necessary, therefore, in this discussion of biotic adaptation to examine the nature of group selection and to attempt some preliminary evaluation of its power. The issue, however, cannot be resolved on the basis of hypothetical examples and appeals to intuitive judgments

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as to what seems likely or unlikely. A direct assessment of the importance of group selection would have to be based on an accurate knowledge of rates of genetic change, due to different causes, within populations; rates of proliferation and extinction of populations and larger groups; relative and absolute rates of migration and interbreeding; relative and absolute values of the coefficients of genic and group selection; etc. We would need such information for a large and unbiased sample of present and past taxa. Obviously this ideal will not be met, and some indirect method of evaluation will be necessary. The only method that I can conceive of as being reliable is an examination of the adaptations of animals and plants to determine the nature of the goals for which they are designed. The details of the strategy being employed will furnish indications of the purpose of its employment. I can conceive of only two ultimate purposes as being indicated, genic survival and group survival. All other kinds of survival, such as that of individual somata, will be of the nature of tactics employed in the grand strategy, and such tactics will be employed only when they do, in fact, contribute to the realization of a more general goal.

The basic issue then is whether organisms, by and large, are using strategies for genic survival alone, or for both genic and group survival. If both, then which seems to be the predominant consideration? If there are many adaptations of obvious group benefit which cannot be explained on the basis of genic selection, it must be conceded that group selection has been operative and important. If there are no such adaptations, we must conclude that group selection has not been important, and that only genic

selection—natural selection in its most austere form—need be recognized as the creative force in evolution. We must always bear in mind that group selection and biotic adaptation are more onerous principles than genic selection and organic adaptation. They should only be invoked when the simpler explanation is clearly inadequate. Our search must be specifically directed at finding adaptations that promote group survival but are clearly neutral or detrimental to individual reproductive survival in within-group competition. The criteria for the recognition of these biotic adaptations are essentially the same as those for organic adaptations. The system in question should produce group benefit in an economical and efficient way and involve enough potentially independent elements that mere chance will not suffice as an explanation for the beneficial effect.

Chapters 5 to 8 are a review of what are apparently regarded as the more likely examples of biotic adaptation. I will discuss these various examples in an attempt to evaluate their reality and thereby assess the importance of group selection as a creative evolutionary force that supplements genic selection.

Adaptations of the Genetic System

THE MACHINERY of sexual reproduction in higher animals and plants is unmistakably an evolved adaptation. It is complex, remarkably uniform, and clearly directed at the goal of producing, with the genes of two parental individuals, offspring of diverse genotypes. How the production of diverse rather than uniform offspring contributes to the ultimate goal of reproductive survival may not be immediately obvious, but the precision of the machinery can only be explained on the basis of selection for efficiency in the production of offspring with the parental genes but not the parental genotypes.

There are some troublesome terminological problems confronting anyone discussing sexual reproduction. The definition used here is implied above. Reproduction is sexual if it produces offspring with new combinations of the parental genes, and does so by means of machinery designed to produce that result. Mutations in asexual clones may ultimately produce genetically diverse descendants, but mutations, as will be argued below, are never by design. So mutation is not a mechanism of sexual reproduction. In the ensuing discussion, a Mendelian population is to be thought of as a group of organisms which, by virtue of at least occasional sexuality, possesses a common gene pool. A narrower category would be a strictly sexual population which, like man, reproduces only by sexual means.