

### 3 Excerpts from *Adaptation and Natural Selection*

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I hope that this book will help to purge biology of what I regard as unnecessary distractions that impede the progress of evolutionary theory and the development of a disciplined science for analyzing adaptation. It opposes certain of the recently advocated qualifications and additions to the theory of natural selection, such as genetic assimilation, group selection and cumulative progress in adaptive evolution. It advocates a ground rule that should reduce future distractions and at the same time facilitate the recognition of really justified modifications of the theory. The ground rule—or perhaps *doctrine* would be a better term—is that adaptation is a special and onerous concept that should be used only where it is really necessary. When it must be recognized, it should be attributed to no higher a level of organization than is demanded by the evidence. In explaining adaptation, one should assume the adequacy of the simplest form of natural selection, that of alternative alleles in Mendelian populations, unless the evidence clearly shows that this theory does not suffice. . . .

Benefits to groups can arise as statistical summations of the effects of individual adaptations. When a deer successfully escapes from a bear by running away, we can attribute its success to a long ancestral period of selection for fleetness. Its fleetness is responsible for its having a *low probability* of death from bear attack. The same factor repeated again and again in the herd means not only that it is a herd of fleet deer, but also that it is a fleet herd. The group therefore has a *low rate* of mortality from bear attack. When every individual in the herd flees from a bear, the result is effective protection of the herd.

As a very general rule, with some important exceptions, the fitness of a group will be high as a result of this sort of summation of the adaptations of its members. On the other hand, such simple summations obviously cannot produce collective fitness as

high as could be achieved by an adaptive organization of the group itself. We might imagine that mortality rates from predation by bears on a herd of deer would be still lower if each individual, instead of merely running for its life when it saw a bear, would play a special role in an organized program of bear avoidance. There might be individuals with especially well-developed senses that could serve as sentinels. Especially fleet individuals could lure bears away from the rest, and so on. Such individual specialization in a collective function would justify recognizing the herd as an adaptively organized entity. Unlike individual fleetness, such group-related adaptation would require something more than the natural selection of alternative alleles as an explanation.

It may also happen that the incidental effects of individual activities, of no functional significance in themselves, can have important statistical consequences, sometimes harmful, sometimes beneficial. The depletion of browse is a harmful effect of the feeding activities of each member of a dense population of deer. If browse depletion were beneficial, I suspect that someone, sooner or later, would have spoken of the feeding behavior of deer as a mechanism for depleting browse. A statement of this sort should not be based merely on the evidence that the statistical effect of eating is beneficial; it should be based on an examination of the causal mechanisms to determine whether they cannot be adequately explained as individual adaptations for individual nourishment.

The feeding activities of earthworms would be a better example, because here the incidental statistical effects *are* beneficial, from the standpoint of the population and even of the ecological community as a whole. As the earthworm feeds, it improves the physical and chemical properties of the soil through which it moves. The contribution from each individual is negligible, but the collective contribution, cumulative over decades and centuries, gradually improves the soil as a medium for worm burrows and for the plant growth on which the earthworm's feeding ultimately depends. Should we therefore call the causal activities of the earthworm a soil-improvement mechanism? Apparently Allee (1940) believed that some such designation is warranted by the fact that soil improvement is indeed a result of the earthworm's activities. However, if we were to examine the digestive system and feeding behavior of an earthworm, I assume that we would find it adequately explained on the assumption of design for individual nutrition. The additional assumption of design for soil improvement would explain nothing that is not also explainable as a nutritional adaptation. It would be a violation of parsimony to assume both explanations when one suffices. Only if one denied that some benefits can arise by chance instead of by design, would there be a reason for postulating an adaptation behind every benefit.

On the other hand, suppose we did find some features of the feeding activities of earthworms that were inexplicable as trophic adaptations but were exactly what we should expect of a system designed for soil improvement. We would then be forced to recognize the system as a soil-modification mechanism, a conclusion that implies a

quite different level of adaptive organization from that implied by the nutritional function. As a digestive system, the gut of a worm plays a role in the adaptive organization of that worm and nothing else, but as a soil-modification system it would play a role in the adaptive organization of the whole community. This, as I will argue at length in later chapters, is a reason for rejecting soil-improvement as a purpose of the worm's activities if it is possible to do so. Various levels of adaptive organization, from the subcellular to the biospheric, might conceivably be recognized, but the principle of parsimony demands that we recognize adaptation at the level necessitated by the facts and no higher.

It is my position that adaptation need almost never be recognized at any level above that of a pair of parents and associated offspring. As I hope to show in the later chapters, this conclusion seldom has to rest on appeals to parsimony alone, but is usually supported by specific evidence.

The most important function of this book is to echo a plea made many years ago by E. S. Russell (1945) that biologists must develop an effective set of principles for dealing with the general phenomenon of biological adaptation. This matter is considered mainly in the final chapter.

The essence of the genetical theory of natural selection is a statistical bias in the relative rates of survival of alternatives (genes, individuals, etc.). The effectiveness of such bias in producing adaptation is contingent on the maintenance of certain quantitative relationships among the operative factors. One necessary condition is that the selected entity must have a high degree of permanence and a low rate of endogenous change, relative to the degree of bias (differences in selection coefficients). Permanence implies reproduction with a potential geometric increase.

Acceptance of this theory necessitates the immediate rejection of the importance of certain kinds of selection. The natural selection of phenotypes cannot in itself produce cumulative change, because phenotypes are extremely temporary manifestations. They are the result of an interaction between genotype and environment that produces what we recognize as an individual. Such an individual consists of genotypic information and information recorded since conception. Socrates consisted of the genes his parents gave him, the experiences they and this environment later provided, and a growth and development mediated by numerous meals. For all I know, he may have been very successful in the evolutionary sense of leaving numerous offspring. His phenotype, nevertheless, was utterly destroyed by the hemlock and has never since been duplicated. If the hemlock had not killed him, something else soon would have. So however natural selection may have been acting on Greek phenotypes in the fourth century B.C. it did not of itself produce any cumulative effect.

The same argument also holds for genotypes. With Socrates' death, not only did his phenotype disappear, but also his genotype. Only in species that can maintain

unlimited clonal reproduction is it theoretically possible for the selection of genotypes to be an important evolutionary factor. This possibility is not likely to be realized very often, because only rarely would individual clones persist for the immensities of time that are important in evolution. The loss of Socrates' genotype is not assuaged by any consideration of how prolifically he may have reproduced. Socrates' genes may be with us yet, but not his genotype, because meiosis and recombination destroy genotypes as surely as death.

It is only the meiotically dissociated fragments of the genotype that are transmitted in sexual reproduction, and these fragments are further fragmented by meiosis in the next generation. If there is an ultimate indivisible fragment it is, by definition, "the gene" that is treated in the abstract discussions of population genetics. Various kinds of suppression of recombination may cause a major chromosomal segment or even a whole chromosome to be transmitted entire for many generations in certain lines of descent. In such cases the segment or chromosome behaves in a way that approximates the population genetics of a single gene. In this book I use the term *gene* to mean "that which segregates and recombines with appreciable frequency." Such genes are potentially immortal, in the sense of there being no physiological limit to their survival, because of their potentially reproducing fast enough to compensate for their destruction by external agents. They also have a high degree of qualitative stability. Estimates of mutation rates range from about  $10^{-4}$  to  $10^{-10}$  per generation. The rates of selection of alternative alleles can be much higher. Selection among the progeny of individuals heterozygous for recessive lethals would eliminate half the lethal genes in one generation. Aside from lethal and markedly deleterious genes in experimental populations, there is abundant evidence (e.g., Fisher and Ford 1947; Ford 1956; Clarke, Dickson, and Sheppard 1963) for selection coefficients in nature that exceed mutation rates by one to many multiples of ten. There can be no doubt that the selective accumulation of genes can be effective. In evolutionary theory, a gene could be defined as any hereditary information for which there is a favorable or unfavorable selection bias equal to several or many times its rate of endogenous change. The prevalence of such stable entities in the heredity of populations is a measure of the importance of natural selection.

Natural selection would produce or maintain adaptation as a matter of definition. Whatever gene is favorably selected is better adapted than its unfavored alternatives. This is the reliable outcome of such selection, the prevalence of well-adapted genes. The selection of such genes of course is mediated by the phenotype, and to be favorably selected, a gene must augment phenotypic reproductive success as the arithmetic mean effect of its activity in the population in which it is selected. . . .

This [work] 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 phenomenon 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 1958, 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 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 [of *Adaptation and Natural Selection*] 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 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 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.

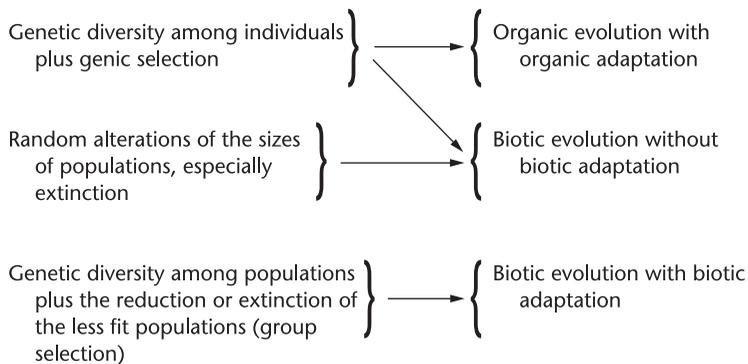
The prerequisites for the operation of this evolutionary factor are such as to confine it to a minor faction of the Earth’s biota. Many animals form dominance hierarchies, but these are not sufficient to produce an evolutionary advantage in mutual aid. A consistent interaction pattern between hens in 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 behavior that they sometimes show toward each other (Slijper 1962, pp. 193–197). I would be reluctant, however, to recog-

nize 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 prefixed, 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 3.1. 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 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 1964) 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,

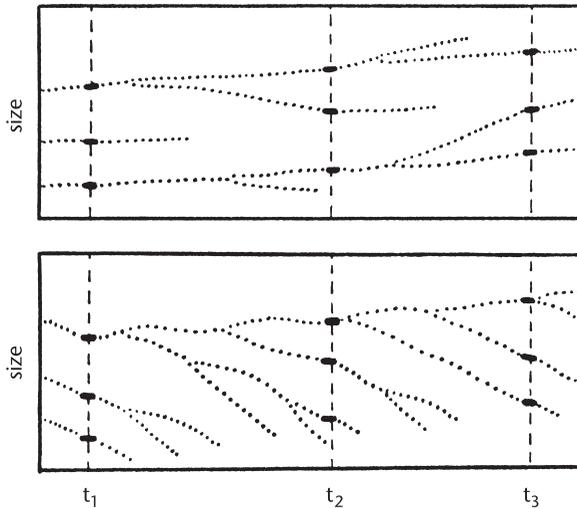


**Figure 3.1**

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

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 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 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 3.2 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 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



**Figure 3.2**

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, 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.

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 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 functional details of complex adaptations. This distinction between the production of a biota with a certain set of organic adaptations and the production of the adaptations of a biota will be emphasized again in a number of contexts.

... 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.

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 [above]

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 trajectories 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 "ortho-selection."

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 isolate 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 operation 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.

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 pop-

ulations 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 competitive 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 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 more 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 fifty diploid individuals with genic selection coefficients that differ by 0.01. In the population of fifty 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 determining 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 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 percent of the sperm of a heterozygous male may bear such a gene, and only 5 percent 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 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 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 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 Anthrozoidea 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 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 considered, 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 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.

The examples considered above all related to interactions between individuals, and the important consideration was to find a parsimonious explanation of why one individual would expend its own resources or endanger itself in an attempt to aid another. There remain a number of examples of individuals' acting, at their own expense, in a manner that benefits their conspecific neighbors in general, not specific individuals. Such activity can take place only when the animals occur in unrelated groups larger than two. The important initial problem is why animals should exist in groups of several to many individuals.

It is my belief that two basic misconceptions have seriously hampered progress in the study of animals in groups. The first misconception is the assumption that when one demonstrates that a certain biological process produces a certain benefit, one has demonstrated *the* function, or at least *a* function of the process. This is a serious error. The demonstration of a benefit is neither necessary nor sufficient in the demonstration of function, although it may sometimes provide insight not otherwise obtainable. It is both necessary and sufficient to show that the process is designed to serve the function. A relevant example is provided by Allee (1931). He observed that a certain marine flatworm, normally found in aggregated groups, can be killed by placement in a hypotonic solution. The harmfulness of such a solution is reduced when large numbers of worms, not just one or a few, are exposed to it. The effect is caused by the liberation of an unknown substance from the worms, especially dead ones, into the water. The substance is not osmotically important in itself, but somehow protects the worms against hypotonicity. Allee saw great significance in this observation, and assumed that he had demonstrated that a beneficial chemical conditioning of the environment is a function of aggregation in these worms. The fallacy of such a conclusion should be especially clear when it relates to very artificial situations like placing large numbers of worms in a small volume of brackish water. The kind of evidence that would be acceptable would be the demonstration that social cohesion increased as the water became hypotonic or underwent some other chemically harmful change; that specific integumentary secretory machinery was activated by the deleterious change; that the substance secreted not only provided protection against hypotonicity, but was an extraordinarily effective substance for this protection. One or two more links in such a chain of circumstances would provide the necessary evidence of functional design and leave no doubt that protection from hypotonicity was a function of aggregation, and not merely an effect.

The second misconception is the assumption that to explain the functional aspects of groups, one must look for group functions. An analogy with human behavior will illustrate the nature of this fallacy. Suppose a visitor from Mars, unseen, observed the social behavior of a mob of panic-stricken people rushing from a burning theatre. If he was burdened with the misconception in question he would assume that the mob must show some sort of an adaptive organization for the benefit of the group as a

whole. If he was sufficiently blinded by this assumption he might even miss the obvious conclusion that the observed behavior could result in total survival below what would have resulted from a wide variety of other conceivable types of behavior. He would be impressed by the fact that the group showed a rapid "response" to the stimulus of fire. It went rapidly from a widely dispersed distribution to the formation of dense aggregations that very effectively sealed off the exits.

Someone more conversant with human nature, however, would find the explanation not in a functioning of the group, but in the functioning of individuals. An individual finds himself in a theatre in which a dangerous fire has suddenly broken out. If he is sitting near an exit he may run for it immediately. If he is a bit farther away he sees others running for the exits and, knowing human nature, realizes that if he is to get out at all he must get out quickly; so he likewise runs for the door, and in so doing, intensifies the stimulus that will cause others to behave in the same way. This behavior is clearly adaptive from the standpoint of individual genetic survival, and the behavior of the mob is easily understood as the statistical summation of individual adaptation.

This is an extreme example of damage caused by the social consequences of adaptive behavior, but undoubtedly such effects do occur, and they may be fairly common in some species. There are numerous reports, at least at the anecdotal level, of the mass destruction of large ungulates when individuals in the van of a herd are pushed off cliffs by the press from the rear. Less spectacular examples of harm deriving from social grouping are probably of greater significance. I would imagine the most important damage from social behavior to be the spread of communicable disease.

The statistical summation of adaptive individual reactions, which I believe to underlie all group action, need not be harmful. On the contrary, it may often be beneficial, perhaps more often than not. An example of such a benefit would be the retention of warmth by close groups of mammals or birds in cold weather, but there is no more reason to assume that a herd is designed for the retention of warmth than to assume that it is designed for transmitting diseases. The huddling behavior of a mouse in cold weather is designed to minimize its own heat loss, not that of the group. In seeking warmth from its neighbors it contributes heat to the group and thereby makes the collective warmth a stronger stimulus in evoking the same response from other individuals. The panic-stricken man in the theatre contributed to the panic stimulus in a similar fashion. Both man and mouse probably aid in the spread of disease. Thus the demonstration of effects, good or bad, proves nothing. To prove adaptation one must demonstrate a functional design.

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