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CHAPTER 2

Natural Selection, Adaptation, and Progress

One of the strengths of scientific inquiry is that it can progress with any mixture of empiricism, intuition, and formal theory that suits the convenience of the investigator. Many sciences develop for a time as exercises in description and empirical generalization. Only later do they acquire reasoned connections within themselves and with other branches of knowledge. Many things were scientifically known of human anatomy and the motions of the planets before they were scientifically explained.

The study of adaptation seems to show the opposite mode of development. It has already had its Newtonian synthesis, but its Galileo and Kepler have not yet appeared. The "Newtonian synthesis" is the genetical theory of natural selection, a logical unification of Mendelism and Darwinism that was accomplished by Fisher, Haldane, and Wright more than thirty years ago. For all its formal elegance, however, this theory has provided very limited guidance in the work of biologists. Ordinarily it does little more than to give a vague aura of validity to conclusions on adaptive evolution and to enable a biologist to refer to goal-directed activities without descending into teleology. The inherent strength of the theory is restricted by the paucity of generalizations, analogous to Kepler's laws, that can serve on the one hand as summaries of large masses of observations and, on the other hand, as logical deductions from the theory.

The deficiency of course is not absolute. The kind of generalization I have in mind is well illustrated by Lack's conclusion on the selection of fecundity in animals that feed their young (discussed on pp. 161-162) and Fisher's conclusion on population sex ratios (see pp. 146-156). With perhaps another hundred such insights we could have a unified science of adaptation.

The current lack of such unification has some unfortunate consequences. One is that a biologist can make any evolutionary speculation seem scientifically acceptable merely by adorning his arguments with the forms and symbols of the theory of natural selection. Thus we have biologists recognizing, in the name of natural selection, mutation, isolation, etc., adaptations designed to meet the demands of geologically future events. This fallacy commonly occurs in the guise of provisions for "evolutionary plasticity." Other biologists speak of natural selection as ensuring that an individual or a population will have all the adaptations that are *necessary* for its survival and imply that adaptations are never expected to be more or less than *adequate* to ensure survival. Such powers might appropriately be attributed to a prescient Providence, but certainly not to natural selection, as this process is commonly described.

Another tendency that survives, despite its lack of a theoretical justification, is a belief in a deterministic succession of evolutionary stages. Simpson's book of 1944 can be taken to symbolize the end of orthogenetic interpretations of paleontological data, but long-term evolutionary determinism is still detectable in some discussions of *progress* in evolution. Huxley (1953, 1954), for example, argued that evolutionary progress was inevitable and proceeded by a series of advances to new levels until all possible levels but one had been achieved: ". . . by the Pliocene only one path of progress remained open—that which led to man" (1954, p. 11). Huxley admits that the details of the process of progressing to higher levels would have been unpredictable at any one point in geological time, but says, "On the other hand, once we can look back on the facts we realize that it could have happened in no other way" (1953, p. 128). The force that drives and guides evolutionary progress is said to be natural selection. This argument is an excellent example of how one can abide by the outward forms of the theory but violate its spirit.

I doubt that many biologists subscribe to the view of evolution as a deterministic progression towards man, but there is widespread belief in some form of aesthetically acceptable progress as an inevitable outcome of organic evolution. In this chapter I will discuss some of the limitations of the process of natural selection and their bearing on some common suppositions, such as the inevitability of progress. The stress on limitations does not indicate any doubt on my part as to the importance of natural selection. Within its limited range of activity, it has a potency that may still be generally underestimated by the majority of biologists. There is a very illuminating discussion by Muller (1948) on this point.

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 his 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. Chapter 3 will deal more fully with the connections between a gene and its phenotype and external environment. Chapter 4 will consider more inclusive systems than the gene as objects of natural selection.

A thorough grasp of the concept of a gene's mean phenotypic effect on fitness is essential to an understanding of natural selection. If individuals bearing gene *A* replace themselves by reproduction to a greater extent than those with gene *A'*, and if the population is so large that we can rule out chance as the explanation, the individuals with *A* would be, as a group, more fit than those with *A'*. The difference in their total fitness would be measured by the extent of replacement of one by the other. By definition of mean, the mean effect on individual fitness of A would be favorable and of A' unfavorable. This maximization of mean individual fitness is the most reliable phenotypic effect of selection at the genic level, but even here there are complications and exceptions. For example, a gene might be favorably selected, not because its phenotypic expression favors an individual's reproduction, but because it favors the reproduction of close relatives of that individual. This complication is considered on pp. 195-197. Wright (1949) and Hamilton (1964A) have provided generally applicable theoretical discussions of the relationship of selection to individual fitness.

Natural selection commonly produces fitness in the vernacular sense. We ordinarily expect it to favor mechanisms leading to an increase in health and comfort and a decrease in danger to life and limb, but the theoretically important kind of fitness is that which promotes ultimate reproductive survival. Reproduction always requires some sacrifice of resources and some jeopardy of physiological well-being, and such sacrifices may be favorably selected, even though they may reduce fitness in the vernacular sense of the term.

We ordinarily expect selection to produce only "favorable" characters, but here again there are exceptions. In the effects of a gene there may be influences on more than one character. A given gene substitution may have one favorable effect and another unfavorable one in the same individual, often, but not necessarily, in different parts of the life cycle. The same gene may produce mainly favorable effects in one individual but mainly unfavorable effects in an-

other, because of differences in environment or genetic background. If the mean effect is favorable, the gene will increase in frequency, and so will all its effects, both positive and negative. There are many relevant examples. An embryonic lethality is a character that has been produced in certain mouse populations by natural selection. The gene that causes this condition is favorably selected, up to an appreciable frequency, because of a favorable effect, "meiotic drive" in the male gamete stage (Lewontin and Dunn, 1960). Senescence, certain kinds of "normal" sterility (see Chapters 7 and 8), and various hereditary diseases are other examples of unfavorable characters that owe their prevalence to natural selection. In all such examples, the favorable selection of the genetic basis for such deleterious effects must be ascribed to other effects of the same genes. Favorable selection of a gene is inevitable if it has a favorable mean effect compared to the available alternatives of the moment.

Another frequent outcome of natural selection is the promotion of the long-term survival of the population. One example, the maintenance of fleetness in deer, was cited in the first chapter, and many similar examples could be given. Here again, however, there are exceptions. The constant maximization of mean fitness in some populations might bring about an increasing ecological specialization, and this might mean reduced numbers, restricted range, and vulnerability to changed conditions. Haldane (1932) mentioned flower specialization for very efficient pollination by a taxonomically small group of insects as an example of such vulnerability to extinction caused by natural selection. Haldane also mentioned the production of elaborate weapons or of conspicuous ornamentation and display, which might be favored in competition for mates, as factors that decrease population fitness by the wasteful use of resources and the damage and vulnerability to predators caused by sexual conflict. Probably most evolutionary increases in body size cause a decrease in numbers, and this might contribute to extinction. An excellent example of decrease in numbers brought about by natural selection is the evolution of the slave-making instinct in certain groups of ants (Emerson, 1960).

In discussions of the role of adaptation in the survival of populations one often finds statements to the effect that selection caused certain developments because they were necessary. It is often difficult to distinguish semantic and conceptual difficulties, but I believe that there are common conceptual fallacies such as might be illustrated by this statement:

> The white coat of the polar bear is *necessary* for the stalking of game in the snowy regions in which it lives. The whiteness was favored by selection because darker individuals were unable to survive.

I would correct this argument by substituting *advantageous* for *necessary* in the first sentence, and by adding the words *as well* to the end of the second. Ecological or physiological necessity is not an evolutionary factor, and the development of an adaptation is no evidence that it was necessary to the survival of the species. We might indulge at this point in the fanciful act of rendering all present polar bears and their descendants a bright pink. We can now be sure

that the species will not henceforth survive *as well.* Its numbers will suddenly decline and its geographic and ecological range rapidly contract, but we cannot be sure that this decrease will proceed all the way to extinction. Each polar bear, after meeting unaccustomed frustration in its hunting, will adapt by hunting for longer periods of time. Some may learn that they can hunt more successfully at night than by day. These and other adjustments might enable the species to continue in those regions where pinkness is, for one reason or another, less of a handicap than in others. Needless to say, there are many obviously necessary adaptations. If, instead of depriving the bear of its whiteness we deprived it of its lungs, it would immediately become extinct. Such examples, however, do not invalidate the conclusion that the mere presence of an adaptation is no argument for its necessity, either for the individual or the population. It is evidence only that during the evolutionary development of the adaptation the genes that augmented its development survived *at a greater rate* than those that did not. Usually, but not always, the presence of an adaptation causes the species to be more numerous and widespread than it would be without it. Nicholson (1956, 1960) has discussed this relationship of natural selection to population density and has concluded that improved adaptation would often have but slight effect on numbers, because even slight increases might greatly intensify the density-governed reactions that normally check population growth. Nicholson is the leading champion of the belief that population densities in nature represent stable equilibria.

The converse argument also holds. The fact that a certain adaptation is necessary to the survival of a species has no bearing on its likelihood of evolving. We can say of every group of organisms that is now extinct that whatever adaptations were necessary for its survival were not, in fact, evolved. This does not demonstrate that there were no tendencies in the necessary direction; it merely means that these tendencies, if there, were not adequate. However, there is no necessity for believing that they were there. The imminence of extinction does not evoke emergency measures on the part of a population. I can imagine that a sonar system would be an advantage in the nocturnal navigation of owls, just as it is for bats. I presume also that many populations of owls have become extinct and that some of these might have survived if provided with even a slight additional advantage, such as a rudimentary sonar system. Would we be more likely to see the beginnings of such a system, or of any other adaptive mechanism, in a small population declining towards extinction than in a large and expanding one? I doubt that any ornithologist would be willing to devote much time looking into such a possibility. I assume that the failure of owls to evolve sonar results from their lack of some necessary preadaptations in all their populations, regardless of size. The lack of sonar is no evidence that it is not necessary for continued existence. Perhaps a post-Recent adaptive radiation of bats will make it necessary for all owls to have an effective sonar system. If so, they will simply join the pterodactyls and hosts of other organisms that lacked necessary adaptations.

The possibility that populations can take special steps in response to the threat of imminent extinction

is often implied in elementary biology texts in discussions of adaptive radiation or of the continued survival of ancient types. Certain species, we are told, were able to avoid extinction by seeking marginal habitats, thereby escaping competition from more progressive forms. The avoidance of extinction might well be a result of specialization for niches in which competition is minimal, but it cannot, historically, have been a cause of evolutionary change. Only in an endlessly recurring cycle, as is shown by the succession of generations in a population, can one class of events be both the cause and the effect of another. A mouse can retreat to a hole to avoid being killed by a cat, but a population cannot retreat to a marginal habitat to avoid being killed off by competition. Such a development can only be a secondary effect of the differences in the genetic survival of individuals in the evolving population.