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Adaptation and Natural Selection.
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CHAPTER 1

Introduction

MANY of the contributions to evolutionary thought in the past century can be put in one of two opposed groups. One group emphasizes natural selection as the primary or exclusive creative force. The other minimizes the role of selection in relation to other proposed factors. R. A. Fisher (1930, 1954) showed that many of the proposed alternatives could be discounted with the acceptance of Mendelian genetics and a logical investigation of its relation to selection. Even without Mendelian genetics, Weismann (1904) effectively championed natural selection against some of its rivals of the nineteenth century. His only serious errors are traceable to his ignorance of the Mendelian gene.

The contest was decisively won by natural selection, in my opinion, when by 1932 the classic works of Fisher, Haldane, and Wright had been published. Yet even though this theory may now reign supreme, its realm still supports some opposition, perhaps more than is generally realized. Many recent discussions seem on the surface to conform to the modern Darwinian tradition, but on careful analysis they are found to imply something rather different. I believe that modern opposition, both overt and cryptic, to natural selection, still derives from the same sources that led to the now discredited theories of the nineteenth century. The opposition arises, as Darwin himself observed, not from what reason dictates but from

the limits of what the imagination can accept. It is difficult for many people to imagine that an individual's role in evolution is entirely contained in its contribution to vital statistics. It is difficult to imagine that an acceptable moral order could arise from vital statistics, and difficult to dispense with belief in a moral order in living nature. It is difficult to imagine that the blind play of the genes could produce man. Major difficulties also arise from the current absence of rigorous criteria for deciding whether a given character is adaptive, and, if so, to precisely what is it an adaptation. As I will argue at some length, adaptation is often recognized in purely fortuitous effects, and natural selection is invoked to resolve problems that do not exist. If natural selection is shown to be inadequate for the production of a given adaptation, it is a matter of basic importance to decide whether the adaptation is real.

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 organiza-

tion 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.

Evolutionary adaptation is a phenomenon of pervasive importance in biology. Its central position is emphasized in the current theory of the origin of life, which proposes that the chemical evolution of the hydrosphere produced at one stage an "organic soup" of great chemical complexity, but lifeless in its earliest stages. Among the complexities was the formation of molecules or molecular concentrations that were autocatalytic in some manner. This is a common chemical property. Even a water molecule can catalyze its own synthesis. Only rarely would a molecule be formed that would produce chance variations among its "offspring" and have such variations passed on to the next "generation," but once such a system arose, natural selection could operate, adaptations would appear, and the Earth would have a biota.

The acceptance of this account of the origin of life implies an acceptance of the key position of the concept of adaptation and at least an abstract criterion whereby life may be defined and recognized. We are dealing with life when we are forced to invoke natural selection to achieve a complete explanation of an observed system. In this sense the principles of chemistry and physics are not enough. At least the one additional postulate of natural selection and its consequence, adaptation, are needed.

This is a very special principle, uniquely biological, and must not be invoked unnecessarily. If asked to

explain the trajectory of a falling apple, given an adequate description of its mechanical properties and its initial position and velocity, we would find the principles of mechanics sufficient for a satisfying explanation. They would be as adequate for the apple as for a rock; the living state of the apple would not make this problem biological. If, however, we were asked how the apple acquired its various properties, and why it has these properties instead of others, we would need the theory of natural selection, at least by implication. Only thus could we explain why the apple has a waterproof wax on the outside, and not elsewhere, or why it contains dormant embryos and not something else. We would find that an impressive list of structural details and processes of the apple can be understood as elements of a design for an efficient role in the propagation of the tree from which it came. We attribute the origin and perfection of this design to a long period of selection for effectiveness in this particular role.

The same story could be told for every normal part or activity of every stage in the life history of every species in the biota of the Earth, past or present. For the same reason that it was once effective in the theological "argument from design," the structure of the vertebrate eye can be used as a dramatic illustration of biological adaptation and the necessity for believing that natural selection for effective vision must have operated throughout the history of the group. In principle, any other organ could be used for illustration although the adaptive design of some parts may not be as immediately convincing as that of the optics of the eye.

This book is based on the assumption that the laws

of physical science plus natural selection can furnish a complete explanation for any biological phenomenon, and that these principles can explain adaptation in general and in the abstract and any particular example of an adaptation. This is a common but not a universal belief among biologists. There are many statements in the recent literature that imply that natural selection can account for some of the superficial forms that adaptation can take, but that adaptation as a general property is something elemental and absolute in living organisms. This is what Russell (1945, p. 3) meant when he said that "directive activity" is an "irreducible characteristic of life." His position was especially clear in his treatment of re-generation, which I will consider on pp. 83-87.

A more recent attack on the adequacy of the simple form of the theory of natural selection is seen in the work of Waddington (1956, 1957, 1959), who conceded that selection is important at every level of adaptive organization, but that it is inadequate by itself and must be supplemented by "genetic assimilation." Another recent attack on the adequacy of natural selection was made by Darlington (1958), who endowed the chromosomes and genes with an evolutionary spontaneity well beyond what is contained in the traditional concept of chance mutation, and with a long-range foresight that allows preparation for the future needs of the population. I will discuss Waddington's and Darlington's work later on.

Even among those who have expressed the opinion that selection is the sole creative force in evolution, there are some inconsistent uses of the concept. With some minor qualifications to be discussed later, it can be said that there is no escape from the conclusion

that natural selection, as portrayed in elementary texts and in most of the technical contributions of population geneticists, can only produce adaptations for the genetic survival of individuals. Many biologists have recognized adaptations of a higher than individual level of organization. A few workers have explicitly dealt with this inconsistency, and have urged that the usual picture of natural selection, based on alternative alleles in population, is not enough. They postulate that selection at the level of alternative populations must also be an important source of adaptation, and that such selection must be recognized to account for adaptations that work for the benefit of groups instead of individuals. I will argue in Chapters 4 through 8 that the recognition of mechanisms for group benefit is based on misinterpretation, and that the higher levels of selection are impotent and not an appreciable factor in the production and maintenance of adaptation.

DIFFICULTIES in interpretation, especially with respect to the many supposedly group-related adaptations, may result from inappropriate criteria for distinguishing adaptations from fortuitous effects. They are also encouraged by imperfections of terminology. Any biological mechanism produces at least one effect that can properly be called its goal: vision for the eye or reproduction and dispersal for the apple. There may also be other effects, such as the apple's contribution to man's economy. In many published discussions it is not at all clear whether an author regards a particular effect as the specific function of the causal mechanism or merely as an incidental consequence. In some cases it would appear that he has

not appreciated the importance of the distinction. In this book I will adhere to a terminological convention that may help to reduce this difficulty. Whenever I believe that an effect is produced as the function of an adaptation perfected by natural selection to serve that function, I will use terms appropriate to human artifice and conscious design. The designation of something as the *means* or *mechanism* for a certain goal or function or purpose will imply that the machinery involved was fashioned by selection for the goal attributed to it. When I do not believe that such a relationship exists I will avoid such terms and use words appropriate to fortuitous relationships such as *cause* and *effect*. This is a convention in general use already, perhaps unconsciously, and its appropriateness is supported in discussions by Muller (1948), Pittendrigh (1958), Simpson (1962), and others.

Thus I would say that reproduction and dispersal are the goals or functions or purposes of apples and that the apple is a means or mechanism by which such goals are realized by apple trees. By contrast, the apple's contributions to Newtonian inspiration and the economy of Kalamazoo County are merely fortuitous effects and of no biological interest.

It is often easy, in practice, to perceive functional design intuitively, but unfortunately disputes sometimes arise as to whether certain effects are produced by design or merely as by-products of some other function. The formulation of practical definitions and sets of objective criteria will not be easy, but it is a problem of great importance and will have to be faced. An excellent beginning was made by Sommerhoff (1950), but apparently no one has built upon the foundation he provided. In this book I will rely

on informal arguments as to whether a presumed function is served with sufficient precision, economy, efficiency, etc. to rule out pure chance as an adequate explanation.

A frequently helpful but not infallible rule is to recognize adaptation in organic systems that show a clear analogy with human implements. There are convincing analogies between bird wings and airship wings, between bridge suspensions and skeletal suspensions, between the vascularization of a leaf and the water supply of a city. In all such examples, conscious human goals have an analogy in the biological goal of survival, and similar problems are often resolved by similar mechanisms. Such analogies may forcefully occur to a physiologist at the beginning of an investigation of a structure or process and provide a continuing source of fruitful hypotheses. At other times the purpose of a mechanism may not be apparent initially, and the search for the goal becomes a motivation for further study. Adaptation is assumed in such cases, not on the basis of a demonstrable appropriateness of the means to the end but on the indirect evidence of complexity and constancy. Examples are (or were) the rectal glands of sharks, cypress "knees," the lateral lines of fishes, the anting of birds, the vocalization of porpoises.

The lateral line is a good illustration. This organ is a conspicuous morphological feature of the great majority of fishes. It shows a structural constancy within taxa and a high degree of histological complexity. In all these features it is analogous to clearly adaptive and demonstrably important structures. The only missing feature, to those who first concerned themselves with this organ, was a convincing story as to

how it might make an efficient contribution to survival. Eventually painstaking morphological and physiological studies by many workers demonstrated that the lateral line is a sense organ related in basic mechanism to audition (Dijkgraaf, 1952, 1963). The fact that man does not have this sense organ himself, and had not perfected artificial receptors in any way analogous, was a handicap in the attempt to understand the organ. Its constancy and complexity, however, and the consequent conviction that it must be useful in some way, were incentives and guides in the studies that eventually elucidated the workings of an important sensory mechanism.

I have stressed the importance of the use of such concepts as biological means and ends because I want it clearly understood that I think that such a conceptual framework is the essence of the science of biology. Much of this book, however, will constitute an attack on what I consider unwarranted uses of the concept of adaptation. This biological principle should be used only as a last resort. It should not be invoked when less onerous principles, such as those of physics and chemistry or that of unspecific cause and effect, are sufficient for a complete explanation.

For an example that I assume will not be controversial, consider a flying fish that has just left the water to undertake an aerial flight. It is clear that there is a physiological necessity for it to return to the water very soon; it cannot long survive in air. It is, moreover, a matter of common observation that an aerial glide normally terminates with a return to the sea. Is this the result of a mechanism for getting the fish back into water? Certainly not; we need not

invoke the principle of adaptation here. The purely physical principle of gravitation adequately explains why the fish, having gone up, eventually comes down. The real problem is not how it manages to come down, but why it takes it so long to do so. To explain the delay in returning we would be forced to recognize a gliding mechanism of an aerodynamic perfection that must be attributed to natural selection for efficiency in gliding. Here we would be dealing with adaptation.

In this example it would be absurd to recognize an adaptation to achieve the mechanically inevitable. I believe, however, that this is essentially what is done by those who propose that gene mutation is a mechanism for ensuring evolutionary plasticity. Whatever the gene may be, it is part of the mundane world and therefore not perfect, in its self-duplication or in any other features. Its occasional alteration is physically inevitable. I will say more about this and related matters on pp. 138-141.

A frequent practice is to recognize adaptation in any recognizable benefit arising from the activities of an organism. I believe that this is an insufficient basis for postulating adaptation and that it has led to some serious errors. A benefit can be the result of chance instead of design. The decision as to the purpose of a mechanism must be based on an examination of the machinery and an argument as to the appropriateness of the means to the end. It cannot be based on value judgments of actual or probable consequences.

This can also be illustrated with an example that will probably not be controversial. Consider a fox on its way to the hen house for the first time after a heavy snowfall. It will probably encounter consider-

able difficulty in forcing its way through the obstructing material. On subsequent trips, however, it may follow the same path and have a much easier time of it, because of the furrow it made the first time. This formation of a path through the snow may result in a considerable saving of time and food energy for the fox, and such savings may be crucial for survival. Should we therefore regard the paws of a fox as a mechanism for constructing paths through snow? Clearly we should not. It is better, because it avoids the onerous biological principles of adaptation and natural selection, to regard the trail-blazing as an incidental effect of the locomotor machinery, no matter how beneficial it may be. An examination of the legs and feet of the fox forces the conclusion that they are designed for running and walking, not for the packing or removal of snow. At any rate, the concept of design for snow removal would not explain anything in the fox's appendages that is not as well or better explained by design for locomotion.

Although the construction of a path through the snow should not be considered a function of the activities that have this effect, the fox does adaptively exploit the effect by seeking the same path on successive trips to the hen house. The sensory mechanisms by which it perceives the most familiar and least obstructed routes and the motivation to follow the path of least effort are clearly adaptations.

Sometimes the important effect of an adaptation from man's point of view may not be its function. Biologically, the brewing of beer is not the function of the glycolytic enzymes of yeast. The production of guano is an important effect, for man's agricultural interests, of the digestive mechanisms of a number of

species of marine birds, but this effect is not their function. Many non-biologists think that it is for their benefit that rattles grow on rattlesnake tails.

I ASSUME that modern biologists would be nearly unanimous in agreeing that the effects mentioned above are not functions. More controversial problems of the same sort will be considered in later chapters. Perhaps one more example can be mentioned here, one that is obviously important but can only be considered rather speculatively. Do we really understand the function of man's cerebral hypertrophy? The importance of this unique character to civilized man is that it enables nearly everyone to learn at least a simple trade; it enables many of us to enjoy good literature and play a fair hand of bridge; and it enables a few to become great scientists, poets, or generals. The human mind has presumably been responsible for analogous benefits for as long as man has had a culturally based society. Despite the arguments that have been advanced (e.g., Dobzhansky and Montague, 1947; Singer, 1962), I cannot readily accept the idea that advanced mental capabilities have ever been directly favored by selection. There is no reason for believing that a genius has ever been likely to leave more children than a man of somewhat below average intelligence. It has been suggested that a tribe that produces an occasional genius for its leadership is more likely to prevail in competition with tribes that lack this intellectual resource. This may well be true in the sense that a group with highly intelligent leaders is likely to gain political supremacy over less gifted groups, but political domination need not result in genetic domination, as is

indicated by the failure of many a ruling class to maintain its numbers. Reasons for questioning the importance of selection between groups in general will be advanced in Chapter 4. Here I will merely note that the close similarity of modern races in their intellectual potentialities would argue against the effectiveness of selection between modern groups as a way of improving man's mental qualities or even of maintaining its present level. The absence of a conspicuous decline in human mentality within historical time must mean that selection has somehow continued to promote the survival of the intelligent.

I suggest that advanced mental qualities might possibly be produced as an incidental effect of selection for the ability to understand and remember simple verbal instructions early in life. We might imagine that Hans and Fritz Faustkeil are told on Monday, "Don't go near the water," and that both go wading and are spanked for it. On Tuesday they are told, "Don't play near the fire," and again they disobey and are spanked. On Wednesday they are told, "Don't tease the saber-tooth." This time Hans understands the message, and he bears firmly in mind the consequences of disobedience. He prudently avoids the saber-tooth and escapes the spanking. Poor Fritz escapes the spanking too, but for a very different reason. Even today accidental death is an important cause of mortality in early life, and parents who consistently spare the rod in other matters may be moved to violence when a child plays with electric wires or chases a ball into the street. Many of the accidental deaths of small children would probably have been avoided if the victims had understood and remembered verbal instructions and had been capable of

effectively substituting verbal symbols for real experience. This might well have been true also under primitive conditions. The resulting selection for acquiring verbal facility as early as possible might have produced, as an allometric effect on cerebral development, populations in which an occasional Leonardo might arise. This interpretation is supported by the apparent diversity of adult human mentality and by the close similarity of the sexes in intellectual endowment. A character selected for a specific adult-male function, such as the political leadership of a primitive society, would reach a high development in adult males only, and would be well standardized in this group. These arguments do not really support my interpretation very strongly, and if anyone has a better theory, I hope he will let it be known, because the problem is surely an important one. Is it not reasonable to anticipate that our understanding of the human mind would be aided greatly by knowing the purpose for which it was designed?

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 ex-

plained 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.