

## CHAPTER 9

### The Scientific Study of Adaptation

THE PRECEDING discussions have portrayed a certain view of natural selection and advocated this view as the only acceptable theory of the genesis of adaptation. Natural selection arises from a reproductive competition among the individuals, and ultimately among the genes, in a Mendelian population. A gene is selected on one basis only, its average effectiveness in producing individuals able to maximize the gene's representation in future generations. The actual events in this process are endlessly complex, and the resulting adaptations exceedingly diverse, but the essential features are everywhere the same.

The significance of a Mendelian population is that it is a major part of the environment in which selection takes place. The population gene pool is the genetic environment of every gene. For each individual the population may be an important ecological factor in a variety of ways. It may provide some important resources, competition for other resources, and a social structure that favors the possession of specific social adaptations. The population parameters assign, to each individual, its age-related probability distributions of death, of reproduction, of specific kinds of stresses, of sex-ratios among social contacts, and of measures of spatial and ecological vagility. Such aspects of the demographic environment are factors to which organisms are precisely adapted, but this adap-

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tation is often neglected in evolutionary discussions because of the tendency to think of a population as something adapted, rather than an environment to be adapted to.

A neontological species is a group of one or more populations that have irrevocably separated from other populations as a result of the development of intrinsic barriers to genetic recombination. The species is therefore a key taxonomic and evolutionary concept but has no special significance for the study of adaptation. It is not an adapted unit and there are no mechanisms that function for the survival of the species. The only adaptations that clearly exist express themselves in genetically defined individuals and have only one ultimate goal, the maximal perpetuation of the genes responsible for the visible adaptive mechanisms, a goal equated to Hamilton's (1964A) "inclusive fitness." The significance of an individual is equal to the extent to which it realizes this goal. In other words, its significance lies entirely in its contribution to one aspect of the vital statistics of the population.

Acceptance of these conclusions means that some widely used concepts are invalid and must be abandoned. The question inevitably arises as to how such an abundance of misinterpretation has arisen. I believe that the major factor is that biologists have no logically sound and generally accepted set of principles and procedures for answering the question: "What is its function?" In practice this question is answered on the basis of a variety of criteria, some of which are of value, but their use is largely dictated by taste and intuition and their value obscured by terminological inconsistencies.

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A frequent and often useful procedure is to rely on analogies between biological adaptations and human artifice. We can thus understand a structure such as a mammalian oviduct as a mechanism for conveying an ovum and early embryo to the uterus. Other analogies help us to understand the uterus as designed for the protection and nourishment of the embryo and foetus. We may similarly recognize the whole complex of reproductive machinery of both sexes as having the goal of producing viable offspring. But why are offspring produced? Is it, as is often stated, for the perpetuation of the species? Or are they produced, as I have maintained, to maximize the representation of the parental genes in the next and subsequent generations? There can be no more important question asked about mammalian reproduction, but there is no established procedure for answering it.

Analogies between biological phenomena and human affairs can also be of value at the level of groups of individuals, but there is no simple and reliable guide to tell us where to stop. Certainly there are interesting parallels between man and animal in family organization, especially between extended multigeneration human families and the colonies of social insects. There may be interesting parallels at even higher levels. A species has a continuity beyond the lives of its individual members; so has a nation of men. A species maintains itself by the activities of its members despite destructive external influences; so does a nation. But does a species have anything at all akin to a spirit of nationalism? A New Frontier? A Five-Year Plan? Does a species have a collective will to avoid extinction or anything at all similar to such a collective interest? No modern biologist has ex-

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plicitly proposed that such factors are operative in the history of a species, but I believe that biologists are unconsciously influenced by such thinking, and that this is true of some distinguished and capable scholars.

I see no other way of interpreting Cott's (1954) statement that conspicuous colors and behavior characterize the "less valuable" members of a species; or Amadon's (1959) statement that males of polygynous birds can live dangerously because "males need not be as numerous as females." Cott's reference to the "value" of an individual is apparently not concerned with its value to itself. Amadon obviously did not refer to how numerous a particular male genotype is. Nor are these uses of the concept of value and need being discussed from the standpoint of man's economic or aesthetic interests. They are being discussed from a species point of view as if there were some kind of collective interest that must be served.

Uncritical analogy with self-conscious human organizations is probably not the whole explanation for the humanization of groups of organisms. There may also be a desire, unconscious in many and expressed by a few, to find not only an order in Nature but a moral order. In human behavior a sacrifice of self-interest and devotion to a suprapersonal cause is considered praiseworthy. If some other organisms also showed concern for group welfare and were not entirely self-seeking, these organisms, and Nature in general, would be more ethically acceptable. In most theological systems it is necessary that the creator be benevolent and that this benevolence show in his creation. If Nature is found to be malicious or morally indifferent, the creator is presumably malicious or

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indifferent. For many, peace of mind might be difficult with the acceptance of either of these conclusions, but this is hardly a basis for making decisions in biology.

There is a rather steady production of books and essays that attempt to show that Nature is, in the long run and on the average, benevolent and acceptable to some unquestionable ethical and moral point of view. By implication, she must be an appropriate guide for devising ethical systems and for judging human behavior. In some cases it would appear that "love thy neighbor" must stand or fall according to whether mutualism or parasitism is the more prevalent phenomenon. Attempts to demonstrate the benevolence of Nature often take the form of name changing. The killing of deer by mountain lions meant "nature red in tooth and claw" to a generation of "social Darwinists." To a more recent generation it has become Nature's kindness in preventing deer from becoming so numerous that they die of starvation or disease. To Darwin himself there was a poorly defined "grandeur" in such processes. The simple facts are that both predation and starvation are painful prospects for deer, and that the lion's lot is no more enviable. Perhaps biology would have been able to mature more rapidly in a culture not dominated by Judeo-Christian theology and the Romantic tradition. It might have been well served by the First Holy Truth from the Sermon at Benares: "Birth is painful, old age is painful, sickness is painful, death is painful . . ." (attributed to the Buddha by Burt, 1955).

Of the terminological problems, *organized* and *organization* are especially troublesome. When a biologist says that a system is organized, he should mean

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organized for genetic survival or for some subordinate goal that ultimately contributes to successful reproduction. For a given organism we can usually specify a particular sort of approach to the problem of survival. An *Ascaris*, for example, is organized for survival in the intestines of horses. It has adaptive mechanisms that minimize the disadvantages of such a way of life and that help it to exploit the advantages of intestinal parasitism. Each part of the animal is organized for some function tributary to the ultimate goal of the survival of its own genes.

Organization attributed to groups should be subject to the same considerations. A family group of nesting birds is clearly organized for genetic survival. One critical function, that of rapid, efficient, and precise morphogenesis, is performed by the nestlings. The adults provide the germ cells for the production of the young and then supply the heat necessary for successful development, and after that they may supply food. There may be a division of labor between the parents and this too is designed to promote genetic survival for each of the parents. The most elaborate nonhuman social organizations—in numbers of subordinate individuals and in complexity of division of labor—are those of the social insects. These animal societies show parallels to ships' crews, ball teams, and other human organizations, which have the advantage of rational planning and cultural tradition.

This basically functional nature of biological organization may seem obvious, but it is possible to overlook it, because of the shifting meanings of the term "organization." Even the most chaotically disorganized system may have a precise statistical organi-

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zation. The statistics of chaos or randomness is a basic standard for statistics in general. A parameter of any collection of entities may have a precisely specifiable arithmetic mean and other measures of central tendency, a precisely determined variance, skewness, kurtosis, and so on. The precision with which such population parameters may be maintained is not necessarily an indication of functional precision, it merely indicates a statistical constancy. The fact that a collection of organisms, whether it be a Mendelian population of insects, a herd of buffalo, or a pound of peanuts, has a precise mean size, weight, mutation rate, age distribution, etc., means that these parameters can be statistically organized. It does not mean that they are functionally organized.

Examples of groups of organisms that are functionally organized were mentioned above, but, as I argued in Chapter 7, not all groups have such organization. Each type of group must be examined separately to determine whether its characteristics make functional sense. Such an examination of a family-group of birds or of the bees in a hive unmistakably favors the recognition of a functional organization. An examination of other groups, such as a swarm of moths around a lamp or a mass of mussels on a piling, force no such conclusion. It is certainly possible that some groups have a functional organization that is too subtle to be appreciated by the conceptual and technical equipment of the observer. Considerations of parsimony, however, demand that we not recognize a functional organization unless we have definite evidence for it. We should not invoke biological principles where statistics suffices. In Chapter 8, I argued

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that most of the examples of gregariousness and other group phenomena can be explained as the statistical summation of individual adaptation and require no recognition of a functional organization of the group.

One aim of this book is to convince the reader that an understanding of the general nature of adaptation is important and that its study requires a more rigorously disciplined treatment than it ordinarily receives. Indeed, I believe that it is important enough to warrant a special branch of biology for its investigation, and in the remainder of this chapter I will suggest ideas that might aid in the development of such a special field of inquiry.

The most urgent requisite for the success of any science is that it have a name. Pittendrigh (1958) suggested that the explicit recognition of the functional organization of living systems be called *teleonomy*. This term would connote a formal relationship to Aristotelian teleology, with the important difference that teleonomy implies the material principle of natural selection in place of the Aristotelian final cause. I suggest that Pittendrigh's term be used to designate the study of adaptation.

Teleonomy would not be a branch of the study of evolution. Its first concern with a biological phenomenon would be to answer the question: "What is its function?" An initial assumption might be, in Pittendrigh's words, that "some feature of the organism—morphological, physiological, or behavioral . . . serves some proximate end (food getting, escape, etc.) that the observer believes he can discern fully by direct observation and without reference to the history of the organism." I know of no better illustration of this process of recognizing functional design

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from careful observation than that provided by Paley (1836) in an answer to the suggestion that the eye just happened to be suitable for vision:

. . . that it should have consisted [by chance], first, of a series of transparent lenses (very different, by the by, even in their substance, from the opaque materials of which the rest of the body is, in general at least, composed; and with which the whole of its surface, this single portion of it excepted, is covered) secondly of a black cloth or canvass (the only membrane of the body which is black) spread out behind these lenses so as to receive the image formed by pencils of light transmitted through them; and placed at the precise geometrical distance at which, and at which alone, a distinct image could be formed, namely, at the concurrence of the refracted rays: thirdly, of a large nerve communicating between this membrane and the brain . . . is too absurd to be made more so by any augmentation.

Any such plausible demonstration of design in relation to a goal would provide the answer to the teleonomist's prime question. His next task would be to explain why the mechanism in question is maintained as a normal characteristic of the species and not allowed to degenerate. His initial attempt would be to explain the mechanism as the inevitable consequence of the natural selection of alternative alleles in an environment described in relevant genetic, somatic, and ecological (including social and demographic) terms. As I have indicated many times, I believe that this attempt can almost always be successful, but if the attempt fails, a teleonomist may explore other

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possibilities, such as group selection or even mystical causes if he is so inclined.

Pittendrigh's assumption that the proximate end of an adaptation is something that a biologist "can discern fully by direct observation" may be too optimistic. The lateral lines of fishes and the singing of birds were directly observed for centuries without their immediate functions being fully discerned. In other cases a proximate end was discerned, but erroneously, as in the recognition of wings in the enlarged pectoral fins of a "flying" gurnard. And what is the purpose of increased melanin production in human skin exposed to sunlight? The immediately obvious answer turns out, on detailed investigation, to be at best only partly correct (Blum, 1961). More remote goals are also of teleonomic importance, but may be even more difficult to determine. Bird songs function as aids in the maintenance of territory, but what is the function of territory? A variety of alternative answers may be found in the recent literature.

How, ultimately, does one ascertain the function of a biological mechanism? In this book I have assumed, as is customary, that functional design is something that can be intuitively comprehended by an investigator and convincingly communicated to others. Although this may often be true, I suspect that progress in teleonomy will soon demand a standardization of criteria for demonstrating adaptation, and a formal terminology for its description. When this need arises, teleonomists will find many useful suggestions in the work of Sommerhoff (1950), who proposed just such a system of criteria and symbolism for dealing with adaptation. I was tempted to use Sommerhoff's system in this work, but decided that its general unfa-

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miliarity would be too great a disadvantage. Also, I believe that the system as proposed is suitable only for facultative individual responses, and will need revision for use with obligate adaptations.

Perhaps the main reason why biologists have not adopted a formal system for determining functional relationships is that many of the problems are so readily solved intuitively. We do not need weighty abstractions to help us decide that the eye is a visual mechanism. Also there are many helpful parallels between natural and artificial mechanisms, and it is so convenient as to be inevitable that parallel terminology be used. The close analogy between the lens of a camera and the lens of an eye make the term *lens* appropriate for both. From the teleonomist's point of view it is most important that these terminological transfers be made only when there is a real functional analogy between what man's reasoning (and trial and error) can produce and what natural selection can produce. One should never imply that an effect is a function unless he can show that it is produced by design and not by happenstance. The mere fact of the effect's being beneficial from one or another point of view should not be taken as evidence of adaptation. Under these rules it is entirely acceptable to conclude that a turtle leaves the sea to lay eggs, but not that a lemming enters it to commit suicide.

Parsimony demands that an effect be called a function only when chance can be ruled out as a possible explanation. In an individual organism an effect should be assumed to be the result of physical laws only, or perhaps the fortuitous effect of some unrelated adaptation, unless there is clear evidence that it is produced by mechanisms designed to produce it.

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In groups of organisms an effect should be ascribed completely, if possible, as the fortuitous summation of individual activities, unless there is evidence of coordinated teamwork for producing the effect, or mechanisms for producing group benefit by individual self-sacrifice. One should postulate adaptation at no higher a level than is necessitated by the facts.

When an organic adaptation is recognized, its explanation by genic selection can take one of several forms. It might be a fixed feature of the organism, or it might be facultative. Ordinarily the nature of the observations to be explained will leave no doubt as to which is correct, but in the absence of other indications the fixed response, being more parsimonious, is preferable. Means of quantitative characters can be adaptive in two different ways. The mean may represent a close approximation to a finite optimum, for example the osmotic pressure of tissue fluids. In other cases the optimum may be infinity or zero, and the observed values are merely the best that can be accomplished by selection in opposition to opposing forces and compromised by the demands of other adaptations. Measures of fleetness and of mutation rate were cited as approximations to infinity and zero. For an intermediate optimum an adequate explanation would be to show that a mutation causing deviations in either direction would be selected against. For optima at zero or infinity it is merely necessary to show that deviations in one direction would always be adversely selected. In this case there would be mechanisms designed to keep something as high or as low as possible, or at least above or below a certain threshold. There are probably many such adaptations. A primitive human instinct to choose the sweet-

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est available fruit normally led to the eating of the ripe and nutritious, and the avoidance of the green or rancid. The same instinct now leads many of us to consume more candy than ripe fruit. A female stickleback normally is well adapted if she submits to the most active and red-bellied of her suitors. She therefore prefers grotesquely exaggerated models to those of more normal color and proportions. Such reactions to superoptimal stimuli (Tinbergen, 1951) reflect the presence of economical adaptations wherever they would function as well as more expensive ones.

Teleonomic understanding would be aided by having a recognized hierarchy of adaptations, or at least a way of specifying the subordination of one function to another. Such a system would follow Tinbergen's hierarchical classification of instincts on the basis of the nature and generality of the purposes served. The most general category would be the adaptations that are so basic as to be found in all organisms. Every organism has mechanisms for its own nutrition. Every organism has morphogenetic adaptations, those relating to growth, differentiation, reproduction, and other aspects of the completion of the life cycle. Every organism has defense mechanisms, at least in the broad sense of devices concerned with the prevention of damage to the trophic and morphogenetic machinery. Thus contractile vacuoles, eyes, and barbed spines are all defense mechanisms.

No complete explanation of a biological phenomenon can be achieved without an inquiry into its evolutionary development, and a teleonomic analysis would not proceed far without the use of historical

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data. The analysis would disclose much that is functionally inexplicable. The inversion of the retina, the crossing of the respiratory and digestive systems, and the use of the urethra for both excretory and male reproductive functions represent errors in the organization of the human body. They have no functional explanation but can be understood as aspects of functional evolution. Historical considerations are also necessary in explaining the many functionally arbitrary limitations that are always apparent in the design of an organism: Why is man a mere biped and not a Centaur? Why do marine turtles not have gills? Why must a giraffe be limited to the same number of neck vertebrae as a mouse? Lastly, evolutionary, or at least comparative data will often furnish clues to the functional meaning of biological phenomena. Pittendrigh (1958) gave some examples in his discussion of how comparisons of the reactions of two species of insects to light and moisture aided in the understanding of the function of these reactions in both species.

The specification of a general type of ecological environment, such as the Atlantic epipelagic at 60°S, specifies something about the specific problems that must be solved by the trophic, morphogenetic, and defensive adaptations of the inhabitants. Even in such a simple and homogeneous environment, however, a wide variety of approaches to the problems of life can be met. Diatoms and whales are both adapted to the same habitat, but solve their common problems with entirely different machinery, and it is in such functionally inexplicable differences between organisms that the need for evolutionary principles becomes necessary in the study of adaptation. *Whale*

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and *diatom* refer to unique historical developments. History has decreed that the diatom be an autotroph. Its approach to life is to make the most efficient possible use of inorganic salts, carbon dioxide, water, and sunlight in the manufacture of all its necessary biochemicals, and to make the most efficient possible use of these in morphogenesis. This historical decision implies the possession of a most complex and miniaturized system of enzymatic machinery, every cog of which is of vital importance. It might be of value to a diatom to have an effective sensory and motor system of defense against herbivorous animals. Any evolutionary step in this direction, however, would have meant burdening the germ plasm with additional information that would have compromised the precision of instructions concerned with enzymatic mechanisms. Such developments have been vigorously opposed by selection, because throughout the history of the diatom, even slight impairments of the enzyme systems resulted in serious reductions in fitness. The whale's ancestry was exposed to different selection pressures. Its nutrition was dependent on the efficiency of the sensory and motor mechanisms used in the capture and ingestion of animals. The synthetic enzyme systems were so compromised by the development of efficiency in predation that the whale has lost or failed to acquire the enzymes necessary to synthesize many of the necessary biochemical building blocks for its proteins, nucleic acids and coenzymes.

It is physiologically correct to say that the whale needs to ingest certain vitamins because it is unable to synthesize them, but historically, the cause-effect relationship is the other way around. The whale was

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able to require certain vitamins because it ordinarily ingested them. Any system will degenerate to the extent to which there is a relaxation of selection pressures for its maintenance. Emerson (1960) called attention to this principle, although his interpretation of it differs from mine, and Kosswig (1947) discussed some illustrative examples.

One of the chief goals of establishing a hierarchical organization of adaptations is to distinguish between the forces that initiated the development of an adaptation and the secondary degenerations that the adaptation, once developed, permitted. I remember a particularly relevant oral discussion of the function of inquilinism among pearlfishes. These slender-bodied fishes live in the respiratory systems of sea cucumbers. They apparently emerge at night to forage, and return at dawn to their hosts. They are largely without pigment, and there is some evidence that they are harmed by exposure to daylight. The question arose: Do these fishes enter the sea cucumbers to avoid light, or do they do so to avoid predators? The feeling of the group seemed to be that if the behavior fulfills both needs, it must be regarded as having a dual function. This is a physiologically valid conclusion, but teleonomically naïve. The two needs are surely not historically coordinate. All fish are under pressure to avoid predators, but very few are damaged by exposure to light. This must have been the condition of the ancestors of the pearlfishes. The habit of entering holothurians developed as a defense against predators, and the fish became extremely specialized in behavior and physiology for exploiting the advantages of inquilinism. This required or permitted the degeneration of a number of

adaptations: the caudal fin disappeared; the eyes were reduced; and the integumentary pigments and other defenses against light were reduced in effectiveness. In this way inquilinism became a necessary part of the defense against physiological damage by light. It was not, however, as a defense against radiation that the behavior originated. The avoidance of light is a secondary need, which has arisen as a result of a degeneration of the mechanisms that ordinarily make such avoidance unnecessary.

Not all secondary needs arise by degeneration. Some are engendered as special problems to be met in the operation of a primary adaptation. If the need to avoid predators is met by taking refuge in holothurian respiratory systems, an efficient means of locating a host becomes important. A special sensory device for locating sea cucumbers would be an adaptation subordinate to inquilinism.

What would ordinarily be considered an environmental stress can become a needed resource as a result of highly effective adaptation to it. Immersion in water that is colder than the freezing point of the tissues would be a trauma for most warm-blooded animals. Large Arctic pinnipeds, however, have become so well able to maintain normal body temperatures under water at  $-2^{\circ}\text{C}$  that they can readily suffer heat prostration in what man would consider cold air. An environmental factor that would cause a dangerous chilling in most mammals has become a benefit to a walrus.

An even better example is provided by the adaptation of microorganisms to antibiotics. In extreme cases it may be found that a strain of bacteria requires an antibiotic that would result in the total

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destruction of another strain. The highly resistant bacteria apparently make obligate adjustments to the presence of the antibiotic, and when the antibiotic is not there to interact with these adjustments, the metabolism is so disrupted that normal growth cannot take place.

I believe that sleep is such a secondary requirement. In the ancestry of a species that requires sleep there may have been a population in which periodic dormancy was a facultative adaptation. It would have served to conserve energy by restricting the foraging and other vital activities to times when they could be carried out with the greatest efficiency and least danger. If nocturnal dormancy were always beneficial, however, a well-adapted facultative response system would make it a consistent and reliable feature of the life history. Adaptations that require sleep could then be added in subsequent evolutionary development, and sleep would evolve from a capacity to a requirement.

I would likewise interpret various social "needs" of animals as secondary adaptations. Allee (1940, 1951, etc.), on the basis of evidence that has subsequently been questioned (Lack, 1954A, Slobodkin, 1962), concluded that birds that breed in colonies of many pairs enjoy, as a result of the close proximity of the other individuals, a greater success in reproduction. This and other observations were taken to indicate that the need for social contacts is a basic characteristic of life and is met by gregariousness in the species noted. I would take the same observations to mean that the social species have made obligate adjustments to the presence of their fellows, and have evolved other adaptations predicated on the assump-

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tion of a certain social environment. When this environment is radically changed by the removal of the group, these adaptations may fail to function normally. I would regard it as a mistake to say that anything is a basic characteristic of life. In an organism we see only the basic characteristics of matter and the results of billions of years of adjustment to a changing environment.

I would like to nominate one more principle for initial inclusion in the science of teleonomy. This principle is that the nature of the stimuli that initiate and regulate a response may be no indication of the function of the response. This concept is certainly recognized by many biologists, but has been most clearly stated by Pittendrigh (1958). He illustrated the principle by showing that certain activities of wild populations of fruit flies are controlled by a timing mechanism regulated by visual cues from the day-night cycle of illumination. The function of the timing, however, is not an adjustment to conditions of illumination, but to changes in humidity. The sensory endowments of *Drosophila* are such that they are better able to anticipate future humidity conditions on the basis of illumination than on the basis of humidity itself. The insects adapt to an important, but poorly perceived environmental factor, humidity, by reacting to a closely correlated factor, light, that is unimportant in itself but reliably perceived. Perhaps an even better example is the timing of a plant's preparation for winter dormancy on the basis of day length. Precise observations of day length for a few days would be a better guide to what temperatures will be like two months later than would a few days of temperature observation.

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THE FORMALLY disciplined use of the theory of genic selection for problems of adaptation, as suggested in this book, should foster progress and understanding regardless of the extent to which this theory constitutes a true or adequate explanation. I am sure that by the standards of a generation hence, our current picture of evolutionary adaptation is, at best, oversimplified and naïve. It is only by the rigorous application of a theory, however, that its imperfections can be recognized and rectified. We must take the theory of natural selection in its simplest and most austere form, the differential survival of alternative alleles, and use it in an uncompromising fashion whenever a problem of adaptation arises. When such usage results in a simple and plausible explanation, the theory will thereby have demonstrated its strength. When the best such explanation is complex and not very plausible, the way is paved for a better theory.

The principle of natural selection is not, as a general rule, used by biologists in an adequately disciplined fashion. It is usually applied to problems like that of long-term morphological changes, as seen by paleontologists, or to problems of ecotypic specialization (usually climatic) and cladogenesis. These phenomena make easy demands on a theory of adaptation. Most of the conclusions on patterns of speciation would be much the same whether based on Lamarckian, nineteenth-century Darwinian, or modern genetic concepts. The fact that a modern paper on speciation in a certain genus contains such terms as mutation, gene flow, and selection, need not imply that it is conceptually much advanced beyond what Lamarck or Darwin might have written. Darwin's and even Lamarck's concepts form a perfectly ade-

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quate basis for explaining most of the phenomena of systematics.

I would certainly not suggest that any field of scientific investigation should be pursued with decreased effort, and I would urge that the field of evolutionary systematics is of high importance. Nevertheless, I maintain that such studies are not likely to lead to important advances in achieving a general understanding of evolutionary adaptation. The same conclusion was cogently advanced by Epling and Catlin (1950).

The important advances will come from quantitative studies of the phenomena of adaptation, not studies merely of the superficial ecotypic adaptation emphasized in systematics, but studies of the distribution and phylogenetic variation in the general strategies employed in the game of life. Darwin devoted a considerable amount of effort and space in his publications to such problems. Despite his statement that the origin of species is the "problem of problems" in natural history, he dealt with much besides cladogenesis and descriptive phylogeny in *The Origin of Species*. In this book and elsewhere he devoted much space to explanations for the origin and evolution of such adaptations as sexuality, intelligence, aerial flight, organs of extreme perfection, such as the vertebrate eye, those of seemingly trivial importance, such as fly-swatter tails, and the group-related adaptations of the social insects. Darwin's works show a more wholesome balance of topics than is shown by the modern evolutionary literature, with its bias for climatic adaptation and cladogenesis.

I believe that important insights can still be obtained from theoretical studies of some of the same

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questions that Darwin discussed in 1859. Similar attention should be devoted to population sex ratios; the significance of the X-Y sex determining mechanism and the seemingly arbitrary distribution of male and female heterogamety; the significance of chromosome number and linkage relations; phylogenetic variation in reproductive physiology and behavior; phylogenetic variation in life cycles in general, and the adaptive significance of paedogenesis, parthenogenesis, apomixis, metagenesis, metamorphosis, etc.; phylogenetic and ontogenetic distribution of developmental rates, especially the long juvenile stages of birds and the presence and duration of pelagic dispersal stages of sedentary marine organisms; the origin of any really outstanding characters such as human intelligence and insect societies; and the evolutionary loss of adaptations of all kinds in groups that once possessed them.

I would regard the problem of sex ratio as solved (see pp. 146-156). There is, of course, a large absolute mass of relevant literature on all the other problems mentioned. The attention devoted to them, however, is minute in comparison with the effort expended on taxonomic problems that are of no greater importance.

There may be an apt analogy between the theory of natural selection as it is today and the atomic theory of two centuries ago. The concept of matter as fundamentally particulate had been used in an undisciplined fashion at least since the days of Democritus. It was invoked, as natural selection often is today, whenever it seemed expedient to do so, but nothing was ever really demanded of the theory. Real tests, such as the prediction of temperature-volume rela-

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tionships in gases or of the weights of the products of a chemical reaction would have been impossible to formulate. The theory had to be stated in an explicit, quantitative, and uncompromising form before it was possible to recognize logical implications or to demand that there be a precise congruence between the theory and observation. The essential service was provided by Dalton, who proposed six theoretical postulates about the nature of atoms. To Dalton, atoms were always thus and so. His statements allowed no compromises and took no refuge in vagueness. Inconsistencies with observational data very soon came to light, and after two peaceful but largely fruitless millennia the concept of material atomism was seriously brought into question. The theory survived in a modified form, even though every one of Dalton's six postulates turned out to be wrong, or at least inaccurate. Dalton performed an enormous service, because his theory provided a basis for questions that could be decided by objective evidence. In this way he helped to open the door to the modern era of the science of chemistry.

Perhaps today's theory of natural selection, which is essentially that provided more than thirty years ago by Fisher, Haldane, and Wright, is somewhat like Dalton's atomic theory. It may not, in any absolute or permanent sense, represent the truth, but I am convinced that it is the light and the way.

