© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

Contents

FOREWORD ix

PREFACE (1996) xvii

PREFACE xxiii

1. INTRODUCTION 3

Evolutionary adaptation is a special and onerous concept that should not be used unnecessarily, and an effect should not be called a function unless it is clearly produced by design and not by chance. When recognized, adaptation should be attributed to no higher a level of organization than is demanded by the evidence. Natural selection is the only acceptable explanation for the genesis and maintenance of adaptation.

2. NATURAL SELECTION, ADAPTATION, AND PROGRESS 20

Natural selection can be effective only where there are certain quantitative relationships among sampling errors, selection coefficients, and rates of random change. The selection of alternative alleles in Mendelian populations meets the requirements. Other conceivable kinds of selection do not. Selection of alternative alleles works only with an immediate better-vs.-worse among individuals in a population, and the question of population survival is irrelevant. Once a certain level of complexity is evolved, selection will maintain adaptation by occasionally substituting one adaptive character for another, but this will not result in any of the kinds of cumulative progress that have been envisioned.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

CONTENTS

3. Natural Selection, Ecology, and Morphogenesis 56

The gene is selected through a complex interaction with its environment, which can usefully be considered to include several levels: the genetic, the somatic, and the ecological. The ecological has many aspects, one of which, the "demographic," is given special treatment. Age-specific birth rates and death rates are important factors in the selection of developmental rates and other aspects of life cycles. The importance of genetic assimilation as a creative factor is minimized.

4. Group Selection 92

Selection at the genic level can produce adaptive organization of individuals and family groups. Any adaptive organization of a population must be attributed to the selection of alternative populations. Reasons are advanced for doubting, *a priori*, the effectiveness of such group selection. *Organic adaptations*, which function to maximize the genetic survival of individuals, are distinguished from *biotic adaptations*, which would be designed to perpetuate a population or more inclusive group.

5. Adaptations of the Genetic System 125

Phenomena relating to the genetic system, such as dominance, diploidy, sex-determining mechanisms, and the distribution of sexual and asexual reproduction in life cycles are easily explained as short-term organic adaptations. The survival and evolution of groups are fortuitous consequences of these adaptations and of their occasional malfunctioning, as in mutation and introgression. There is no respectable evidence of mechanisms for maintaining evolutionary plasticity or of any other biotic adaptations of the genetic system.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

CONTENTS

6. Reproductive Physiology and Behavior 158

Variations in the intensity of reproductive effort, and in the manner in which it is expended, seem designed to maximize the reproductive success of the reproducing individuals. Attention is given to the evolution of fecundity, viviparity, gregarious reproduction, and differences between the sexes in reproductive behavior. These phenomena support the conclusion that the goal of an individual's reproduction is not to perpetuate the population or species, but to maximize the representation of its own germ plasm, relative to that of others in the same population.

7. Social Adaptations 193

Selection within a population can lead to cooperative relations among closely related individuals, because the benefits of cooperation would go mainly to individuals with the genetic basis of cooperation, rather than to those of alternative genetic makeup. Selection at the genic level thus explains insect societies and analogous developments in other organisms. Other apparent examples of altruism are explained as misplaced parental behavior. They represent imperfections in the mechanisms that normally regulate the timing and execution of parental behavior. Benefits to groups often arise as incidental statistical consequences of individual activities, just as harmful effects may accumulate in the same way.

8. Other Supposedly Group-Related Adaptations 221

Various supposed biotic adaptations, such as poisonous flesh, senescence, and genetically heterogeneous somata, are examined and found to be spurious or inconclusive. The regulation of population size is shown to arise from individual adaptations or purely physical principles rather than as an adaptive organization of the group.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

CONTENTS

Similar arguments are used against the concept of an adaptive organization of ecological communities or more inclusive entities.

9. The Scientific Study of Adaptation 251

For a given biological mechanism there are no established principles and procedures for answering the question, "What is its function?" Objectively determined answers to such questions would facilitate progress in many fields of biology, but they must await development of special concepts for the study of adaptation as a general principle. Teleonomy is a suitable name for this special field of study.

Literature Cited 275

Index 291

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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-

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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 regeneration, 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

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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 populations, 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

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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-

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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-

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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 general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

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.

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

Index

acorn storage, by woodpeckers, 201
adaptation, analogy with artifice, 10, 253; as approximation to optimum, zero, or infinity, 262-63; biotic, *see* biotic adaptation; criteria of, 4, 8-13, 17-19, 122-23, 145-46, 209-12, 252-61; to cyclic changes, 31, 71; vs. fortuitous effects, 8, 16-19, 139, 144-46, 209-12, 214, 247-48; functionally arbitrary limitations on, 263-64; general vs. special, 49; to geological future, *see* teleology; harmful consequences, 17-19, 27-28, 139, 211-12, 214-15; hierarchical organization of, 263, 266-69; intuitive recognition of, 9, 258-62; statistical consequences of, 17-19, 210-19. *See also* biotic adaptation, organic adaptation, organization, function and related terms.
adaptive radiation, 30-31
adequacy, irrelevance in evolution, 28-31
adult, as goal of development, 43-44
agonistic behavior, prevalence of, 193-94
aircraft engines, progress in, 50
alarm substance, 216
Allee, W. C., 18, 92, 105, 189, 194, 209, 218, 244, 247, 268
Allison, A. C., 60
Altman, S. A., 95, 205, 220
Amadon, D., 246, 254
amphibians, dependence of metamorphosis on diet, 67; imperfections of adaptation, 53; larval adaptation, 45; nuclear-cytoplasmic interaction in development, 61-62, 64; regeneration in, 85; reversed roles of sexes, 186; vocalization, 232
Andersen, F. S., 151
Anderson, E., 144, 145
Andrew, L. E., 64
angiosperms, replacement of gymnosperms, 51-52
annual fishes, 175
antibiotics, bacterial resistance to, 267-69
ants, population structure, 146. *See also* social insects
aphids, 132, 156
apogonid fishes, 180
apple, 6, 9
Arapaima, 180
archaic Recent fishes, 51
arctic ecology, 248-50
arctic fox, 249

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

INDEX

argument from design, 6
Aristotle, 258
Ascaris, 256
ascidian, 53
atomic theory, analogy with natural selection, 272-73
ATP, universality, 134
Auerbach, C., 141
autocatalysis, 5, 135
autotrophs, origin of, 248

baboons, 220
bacteria, genetic recombination among, 133, 137; quantity of DNA, 39; resistance to antibiotics, 267-68
Bardach, J. E., 165
Barker, J. S. F., 105
barnacles, cost of reproduction, 172; sessile condition of, 127
Barnes, H., 172
bass, 51, 180
Bateman, A. J., 185
bears, as predators, 16-17; evolutionary rate, 126
beechnuts, mortality rate, 164
Betta, 180
bighorn sheep, 219
biota, arctic vs. tropical, 248-50
biotic adaptation, aesthetic appeal of concept, 232-35; at community level, 246-50; criteria of, 103, 122-24, 257-58; doubts of existence, 112, 251-52; nature of, 96-98, 103-105; necessarily limited occurrence, 113; as non-parsimonious concept, 122-24; and progress, 106; and regulation of population density, 107, 234-46; relation to group selection, 96-98; mutation as, 139, 141; in penguin reproduction, 190-91; role of dominance in, 143; role of heterozygosity, 144; role of sex ratio in, 147-49; and social insects, 197-201. *See also* various examples
biotic evolution, and chance events, 121; and extinction, 119-22; vs. organic evolution, 96-101
Birch, L. C., 32
birds, absence of viviparity, 170; age of maturity, 90-91; clutch size, 161-62, 164-65; colonial nesting, 189; dominance hierarchies, 95; flight displays, 206; flocking behavior, 217; gallinaceous, 164-65; ground-living, 91, 181; life cycle, 90-91; low reproductive rates in, 181; misplaced reproductive functions, 204; mortality rates, 90-91, 172; nesting places, 91; optimum reproductive effort, 181; polyandrous, 186; rates of development, 90-91; reversed roles of sexes, 186; sexual dimorphism, 181; social relations among, 238

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

INDEX

bithorax, 72-77
Blood, D. A., 219
bluebirds, nesting requirements, 238
bluefish, 48
Blum, H. F., 38, 260
Bodmer, W. F., 154
Bonellia, 154
Bonner, J. T., 225
Bormann, F. H., 223
Borradaile, L. A., 154
bowfin, 51, 180
Boyden, A. A., 126, 128, 129, 138
Braestrup, F. W., 246
Breder, C. M., 213-16
Brereton, J. L. G., 105, 107, 232, 234, 239
Brock, V. E., 215
Brown, W. L., 49, 105
Budd, G. M., 191
Buddha, 255
budding, 126
Bullis, H. R., 215
Burkholder, P. R., 223
Burnet, F. M., 222, 230
Burtt, E. A., 255
Buzzati-Traverso, A. A., 141

caddis fly, 86-87
Cagle, F. R., 204
Cambrian, 35, 38, 42, 54, 100
canalization, 73, 75
cannibalism, 236
caribou, 219
Carlisle, D. B., 230
Carson, H. L., 104
Catcheside, D. G., 140
catfish, 165, 180
Catlin, W., 271
cause and effect, 8-9, 31, 76-78. *See also* teleology
centrachid fishes, 180
cercaria, 46
cetaceans, schooling behavior, 217; social phenomena, 95-96
chemical conditioning of medium, 209-10
chromosome inversions, 64
chromosome number, significance of, 132-33
cichlid fishes, 166, 180
cladocerans, 156. *See also* *Daphnia*
Clarke, C. A., 25
Clarke, G. L., 218
clones, mutations in, 125, selection of, 23-24
coadaptation, 59
coconuts, mortality rate, 164
cod, 165
Cole, L. C., 66, 159
colonial reproduction, 187-91
Comfort, A., 225
commensalism, 246-47
community, organization of, 18-19, 246-50
community stabilization, 249-50
competition, ecologic vs. reproductive, 32-33; relation to natural selection, 31-33
continuous variation, vs. particulate gene, 61
copepods, fecundity, 167
Correns, C., 155
cost of reproduction, and demographic environment, 171-82; optimization of,

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

165, 171-82; related to fitness, 26; related to size and age, 182
Cott, H. B., 254
crèche system, among penguins, 190-91
Crisp, D. J., 172
criteria of adaptation, *see* adaptation
Crosby, J. L., 143
crowding, psychological damage from, 243-44
Crowe, L. K., 154
Cullen, E., 190
currency of offspring, 195, 200
cypress knees, 10
cytoplasmic influences on development, 61-64

Dalton, 272-73
Daphnia, experimental populations, 237-38; parthenogenesis of, 126-27, 132
Darling, J. F., 189
Darling-effect, 189, 268
Darlington, C. D., 7, 64, 128, 140-41
darters, 179
Darwin, C. R., 3-4, 32, 83, 94, 100, 231, 270-71
deer, depletion of browse, 17-18; herding of, 206-207; reaction to predators, 16-17, 206
degenerative evolution, 77-83, 85-86, 265-66
Democritus, 272
demographic environment, and evolution of senescence, 225-28; nature of, 66, 176, 251; and rate of development, 87-91; and selection of reproductive effort, 172-82, 245-46
density as an evolutionary factor, 29
density-governed reactions, 29
determinate growth, in fishes, 177
determinism in evolution, 21-22, 49
development rate, and population density, 235-36; selection of, 87-91
Devonian fish, complexity of, 42-43
Devonian vertebrates, numbers of surviving lineages, 120
diatom, 264-65
Dickson, G. C., 25
dietary requirements, evolution of, 265-66
Dijkgraaf, V. S., 11
dinoflagellates, 229
dinosaurs, extinction of, 121-22
dioecy vs. monecy, significance of, 147
disease, transmission of, 211-12
DNA, of amphibians, 39; biochemical instructions in, 40-42; of birds, 39; efficiency of, 41-42; as evolved adaptation, 133-35; of lungfish, 39; of mammal, 39; morphogenetic instructions in, 40-42, 46-47; optimum information con-

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

tent, 38; origin of, 36, 133-35; of protists, 39, 42; quantity of, 36-42; redundancy, 36, 39, 41-42
Dobzhansky, T., 14, 59, 64, 142
dominance, evolution of, 141-44
dominance hierarchies, 95, 218
Dougherty, E. C., 128-29, 137-38
drift, *see* genetic drift
Drosophila, adaptation to diurnal cycle, 269; bithorax phenotype, 72-74; mutation rate, 141; relative fitness of populations, 104; sex ratio, 151-52
Dunbar, M. J., 107, 248-50
Dunn, L. C., 27, 117

Earth, uniqueness of, 121
earthworms, soil modification, 18-19; somites, 194-95
ecological environment, 57-58, 66-71
ecological necessity, not an evolutionary factor, 28-30
ecological niche, 22, 121, 264-65
economy of information, 41-42, 82-86
ecosystem, arctic vs. tropical, 248-50; efficiency of, 248; organization of, 18-19, 247-50
Edwards, A. W. F., 154
egg, as soma of zygote, 61-62
egg size, in fishes, 164, 167; and mortality rates, 164
eggs, selection for size and number, 161-64, 167-68
Ehrensvärd, G., 135, 136
Ehrman, L., 145
elasmobranch, egg size, 163
elephants, mutation rates, 141; rate of evolution, 226
Elton, C., 244
embiotocid fishes, viviparity, 180
Emerson, A. E., 28, 65, 159, 164, 225, 232, 239, 266
empiricism and theory in science, 20
empiricists vs. nativist, 83
environment, *see* demographic environment, ecological environment, genetic environment, social environment, somatic environment
enzymes, origin of, 135-36
Eocene, 98
epigenetic theory of development, 62, 64
Epling, C., 271
errors in plan of human body, 264
Essig, E. O., 186
ether shock, 72-75
euphausids, predation by whales, 87
evolution, degenerative, 77-83, 85-86, 265-66; deterministic stages, 134-36; reversal of, 37-38; stochastic phases, 136
evolutionary data, importance to understanding adaptation, 263-64

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

evolutionary determinism, *see* determinism in evolution
evolutionary plasticity, chapter on genetic factors in, 127-57; relation to teleology, 21; role of diploidy in, 141; role of dominance in, 143-44; role of mutation in, 12, 139; role of outcrossing in, 129-31; role of population structure in, 232
evolutionary rate, and length of generation, 226; through group selection, 114
evolutionary trajectories, selection of, 110-11, 114
extinction, chance vs. fitness, 115, 121-22; through competition, 30-31; of dinosaurs, 121-22; of ichthyosaurs, 51; importance in biotic evolution, 119-22; of mososaurs, 51; not a creative factor, 121-22; through overspecialization, 27-28; of plesiosaurs, 51; of Pliocene mammals, 51; rates of, 115, 122

facultative vs. fixed character, 77-83
family groups, reduced competition within, 202-203; selection among, 196
fecundity, facultative individual control of, 237; independence of parental care in fishes, 165; nutritional factors in, 163-64; related to mortality rate, 161-64; selection of, 161-67; of social insects, 163-64. *See also* cost of reproduction, eggs, and various organisms
femininity, selection for, 182-87
ferns, 126, 131
fiddler crabs, regeneration in, 83
Fiedler, K., 186
Filosa, M. F., 224
Final Cause, 258
Fink, B. D., 214
Fisher, J., 190
Fisher, R. A., 3, 20, 21, 25, 88, 141-43, 149, 152, 154, 157, 184, 202, 273
fishes, brain structure, 43; chromosome numbers, 133; cost of reproduction, 180-81; courtship, 178; criteria of evolutionary progress, 48; demographic environment, 177-78; with determinate growth, 177; Devonian, 50; drought resistant eggs, 175; egg size, 164, 166; fecundity, 165-68, 178, 182; frequency of spawning, 178; gregarious reproduction, 188; histological specialization, 47; hybridization in nature, 205; with indeterminate growth, 176-77; integumentary histology, 43; lateral line, 10, 260; oral incubation, 180; parental care, 165, 178-80; regeneration in, 85; reproduc-

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

tive functions in relation to demographic environment, 172-81; schooling, 212-17; sex dimorphism, 175, 178; sexual conflict, 178; size and cost of reproduction, 178; territoriality, 178; toxic, 229-30; viviparous, 166-67, 178. *See also* specific kinds
fission, 126
fitness, as currency of offspring, 158-59; of environment, 70; inclusive, 97, 194, 196, 207; of individuals, 25-26, 101-102, 158; and levels of organization, 71; of populations, *see* population fitness; relation to reproduction, 25-26, 195, 200
fitness and chance in relation to survival, 101-103, 158-59
fixed vs. facultative character, 82
flatfishes, 48
flatworms, group protection, 209-10; regeneration in, 84
fleetness, 16-17
flight displays, of birds, 206; of mammals, 206
fluke (trematode), 45-47
flying fish, 11
"flying" gurnard, 260
Ford, E. B., 25
foreign nuclei, in egg cytoplasm, 61-62
fossil record, 21-22, 98-100
Fowler, J. A., 62, 64
Frank, F., 244
Freedman, L. Z., 205
friendship and animosity as evolutionary factors, 93-96
frog, *see* amphibians
fugitive species, 155-56
function, defined, 8-9
functional adequacy, not an evolutionary factor, 28-31
functional vs. statistical organization, 210-19, 257-58

Galileo, 20
game theory, 67-70
gametophyte of fern, 126, 131
gametophyte development, determination of, 63-64
garpike, 51, 178
gene pools, selection of, *see* group selection
genes, defined, 24; potential immortality, 24; origin of, 133-35; stability of, 24, 138-41. *See also* mutation, lethal genes
general vs. special adaptation, 49
generation length and rate of evolution, 226
genetic assimilation, 4, 7, 71-83
genetic background, *see* genetic environment
genetic drift, 111-15, 146
genetic environment, and dominance, 142-43; early evolution of, 137-38; and mutation rate, 139-40; role in determining selection

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

coefficients, 26-27, 57-61, 119
genetic information, in algae, 40-41; in *Amoeba*, 40-41; in bithorax stock, 75-76; changing interpretation during development, 62-63; for fixed and facultative adaptations, 82-83; in humans, 40-42; quantity vs. precision, 41-42
genetic mosaics, 222-25
genetic recombination, in bacteria, 133, 137; restrictions on, 24, 132-33; significance of, 131-32; in viruses, 133
genetic vs. structural homology, 65
genetic variation, unexpressed, 73-75
genetically heterogeneous somata, 222-25
genic selection, analogy with atomic theory, 272-73; coefficients of, 23-25, 56-57, 65; effectiveness, 7, 8, 24-25; expected consequences, 25-34; and favorable characters, 26-27; of fecundity, 21, 161-67; fundamental importance, 159-60; inadequacy for biotic adaptation, 116; of isoalleles, 37; of lethal genes, 24; and maximization of individual fitness, 25-26; moral and aesthetic aspects, 4, 232-34, 254-55; and morphogenesis, 56; of multiple alleles, 58; nature of, 24-26, 71, 96-101; need for theory, 103; and the origin of man, 120-21; as parsimonious concept, 108, 123-24; and rate of development, 87-91; reversal of direction, 37, 39; role of demographic parameters, 66-67, 88, 250-52; and social environment, 93-96; in social insects, 195-201; of t-alleles, 117-19; two-locus model, 59
genotype, relation to phenotype, 56
genotypic vs. phenotypic stability, 64-65
gnathostomes, 51
goal, defined, 8-9
Gotto, R. V., 167
gourami, 179
gregariousness, of cetaceans, 217; of fishes, 212-17; as fortuitous statistical effect, 257-58; of mammals, 217; of non-breeding birds, 217; as protection from predators, 213-16; of sea snakes, 217; selection for, 206-207, 212-17, 268-69; of squid, 217; of wolves, 217-18
group-related adaptations, *see* biotic adaptation
group selection, assisted by genetic drift, 111-12; of body size, 110; chapter on, 92-124; coefficients of, 114, 122; in man, 14-15; nature of, 96-101, 109-10; need for theory, 4, 8, 103, 122; as non-parsimonious

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

concept, 108; quantitative inadequacy of, 110-16; of t-alleles, 117-19
guano, 13
Guhl, A. M., 218
gymnosperms, replacement by angiosperms, 51-52

Haartman, L. von, 91
haddock, 182
Hagan, H. R., 171
Haldane, J. B. S., 3, 20, 27-28, 32, 92, 142-43, 187, 195, 273
halibut, 165, 178, 182
Hall, E. R., 218
Hall, K. R. L., 220
Halstead, B. W., 229-30
Hamilton, W. D., 26, 97, 197, 199, 252
Harper, J. L., 238
helpers, among birds, 207-208
hens, social organization, 218
hermit crabs, regeneration in, 86
heterosis, 130, 144
heterozygosity, as biotic adaptation, 144; decrease in stable environment, 38
histological specialization and evolutionary progress, 47
Hodder, V. M., 182
homosexuality, prevalence of, 204-205
horses, Eocene, 98-99; fitness, 101-103; size changes in Tertiary, 98-100, 110
Hubbs, Carl L., 205
Hubbs, Clark, 167
huddling, of mice, 212
human mind, function of, 14-16
Huxley, J. S., 21-22, 49, 86, 129
hybrid inviability or sterility, 145
hybridization, as example of reproductive malfunction, 205; selection for avoidance of, 145-46
hydra, 127

immune reaction, 222
immunological evidence of genetic homogeneity, 62
inclusive fitness, 97, 194, 196, 207
indeterminate growth in fishes, 176
individuality, mechanisms for maintenance of, 222; origin of, 135-38
Inger, R. F., 231
inquilinism, 266-67
insect pollination, 27
insects, reversed roles of sexes, 186; social, *see* social insects; viviparous, 170-71
internal fertilization, as preadaptation for viviparity, 169-70
introgressive hybridization, 144-46
invertebrates, marine populations, 113; somatic fusion in, 222; toxic, 229-30
isoalleles, selection of, 37
Ives, P. T., 141

jet vs. propeller driven aircraft, 50

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

INDEX

Kelson, K. R., 218
Kendeigh, S. C., 186, 190
Kepler, 20
Kimura, M., 35-42, 81, 105, 133, 141, 143
kin selection, 26, 195-96. *See also* group selection
Klauber, L. M., 231
Knight-Jones, E. W., 222
Koford, C. B., 205
Kojima, K., 60
Kosswig, C., 266

Lack, D., 21, 162, 164, 170, 190, 220, 240, 242, 268
lactation, selection of, 159, 187-89
Lagler, K. F., 165
lamprey, reproductive effort of, 175; successfulness of, 51
larvae of marine invertebrates, 67
lemming, 244, 261
Leopold, A. C., 227
Lerner, I. M., 144
lethal genes, selection of, 117-19
Levene, H., 59
Levitan, M., 133
Lewis, D., 154-55
Lewontin, R. C., 27, 38, 60, 92, 105, 106, 117, 144
lichens, 246
Lidicker, W. Z., 240
life, criteria and definition, 5; origin of, 5, 134-36
life cycles, evolution of, 44-45, 70-71, 87-91, 131-32, 137-38; of ferns, 131; of higher plants, 131; of parasites, 132; relative complexity, 43-47; semelparous, 174-75
linkage, significance of, 132-33
Liosner, L. D., 84
liver, regeneration of, 86-87
liver fluke, 45-47
lizard tail, regeneration of, 83
Lloyd, M., 31
Lydeckker, R., 218

McClintock, B., 140
Makino, S., 133
malaria, resistance to, 60-61
Malthusian parameter as measure of fitness, 105
mammals, adaptive radiation of, 122; arctic, 267; brain structure, 43; flight display, 206; gregarious, 188-89, 206, 217-18; histological specialization, 47; homosexuality, 205; huddling, 212; integumentary histology, 43; litter size, 163; mutual aid among, 95-96, 218-19; selection for lactation, 159, 187-88; secondary sex differences, 183-84; viviparity, 170
mammary glands, contribution to fitness, 159, 187-89
man, adaptation to solar radiation, 82, 260; mental faculties, 14-16; origin of, 14-16, 120-21; primitive social environment, 93-96; racial differences, 15, 82; rate of evolution, 226; regenera-

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

tion in, 84-85; special adaptations, 121; systematic position, 49; thermoregulation, 76-77
marginal habitats, retreat of populations to, 30-31
marine invertebrates, larvae of, 90
marsupials, replacement by placental mammals, 51-52
masculinity, selection for, 182-87
Mather, K., 32
Mayr, E., 59
means, defined, 8-9
mechanism, defined, 8-9
Medawar, P. B., 158-59, 226
meiosis, origin of, 128; role in sexual reproduction, 126
meiotic drive, 27, 117-19
Melandrium, 154-55
Mendelian population, definition of, 125
Mesohippus, 47-48
mice, embryonic lethality, 27; huddling behavior, 212; t-alleles, 27, 117-19
Michie, D., 62
Miller, R. R., 165
Milne, A., 32
mimicry, 202
miracidium, 46
Mirsky, A. E., 39
misplaced reproductive functions, 194, 203-208
Modglin, F. R., 230
Montagu, M. F. A., 14, 116
morphogenesis, origin of, 135-38; role of environment in, 66-70, 72-75
Morris, D., 205
mortality rate, and selection for rate of development, 87-91; sex differences in, 150-51
mososaurs, extinction, 51
Mottram, J. C., 181
Moyse, J., 222
Muller, H. J., 9, 22
Murie, O. J., 219
Murphy, R. C., 190
mushrooms, toxic, 229-30
musk oxen, 218-19
mutation, as biotic adaptation, 12, 138-41; and direction of evolution, 100; evolutionary role, 12, 75, 138-41, 145; randomness, 37, 100-101
mutation rates, of *Drosophila*, 141; of elephants, 141; in haploid organisms, 140-41; and length of generation, 140; optimum, 139; and rate of evolution, 38, 139; relation to selection coefficients, 24-25, 57, 109-10; selection of, 138-41
mutator genes, 139-41
mutualism, evolution of, 246-47
Myers, G. S., 175

nativists vs. empiricists, 83
natural selection, and adequacy of adaptation, 21; among children, 15-16; of clones, 23-24, 109; conditions for effectiveness, 22-25; and ecological necessity, 21; and extinction,

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

27-28; of genotypes, 109; history of concept, 3-4; importance of phenotype, 23-26; ineffectual use of theory, 20-21, 270-71; limitations of process, 21-33; and maintenance of adaptation, 54; modern opposition to, 3-4, 7; nature of process, 22-34; and optics of eye, 6; and origin of life, 5; and physical laws, 7; related to reproduction, 26; of somata, 109. *See also* genic selection, group selection
Nature, Buddhist view of, 255; as guide in ethics and morals, 254-55; Judeo-Christian view, 255
necessity, irrelevance in evolution, 28-32
Needham, A. E., 84
Neotropical fauna, replacement by Holarctic, 52
nettles, 230
Newtonian synthesis in biology, 20
niche, *see* ecological niche
niche selection, 69-70
Nicholson, J. A., 29
Noble, G. K., 186
Norman, J. R., 228

O'Donald, P., 184
Odum, H. T., 105
optimum reproductive effort, theory of, 175-77
organic adaptations, within individual somata, 221-22; nature of, 96-98, 103-104; as parsimonious concept, 108. *See also* specific phenomena and organisms, biotic adaptation
organic evolution, vs. biotic evolution, 96-101
organic soup, 5, 134
organization, functional vs. statistical, 210-19, 257-58
orthogenesis, 21-22, 49
orthoselection, 111
ostrich, 91
owls, 30

Paleozoic animals, complexity of, 42
Paley, W., 259
Panama land-bridge, 52
parasite life cycles, 132
parental care, selection of, 159-61, 187-89
parent-offspring recognition, 188-91
Park, T., 31
parsimony in explaining adaptation, 4-5, 11-13, 18-19, 123-24, 261-62
parthenogenesis, asexual nature of, 126-27; effects on selection for sex ratio, 155-56
particulate gene, vs. continuous variation, 61
Patel, B., 172
Pavlovsky, O., 59
pearlfish, 266-67
penguins, gregarious reproduction, 190-91
Penny, R. L., 191
phalaropes, 186
phenotype, relation to geno-

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

type, 56; role in natural selection, 23-26
phenotypic vs. genotypic stability, 64-65
photoperiodicity, 67, 269
photosynthesis, 248
physiological necessity, irrelevance in evolution, 28-30
pike, 48
Pimentel, D., 105, 107
pipefish, 185-86
Pittendrigh, C. S., 9, 258, 260, 264, 269
placental mammals, replacement of marsupials, 51-52
plankton, oceanic, 238
plants, criteria of progress, 48, 52-53; grafting experiments, 222; hybridization in, 145-46; life cycles, 131; outcrossing, 129; population size, 238; senescence, 227-28; sex determination, 154-55; somatic fusion, 222-25; toxic, 229-30
plasmagenes, 62, 136
plasticity, evolutionary, *see* evolutionary plasticity
plesiosaurs, extinction, 51
Pliocene, 22, 98
Pliohippus, 47-48
poisonous flesh, as biotic adaptation, 228-31
polar bear, 28-29
pollination by insects, 27
population density, adaptive regulation of, 105, 107, 148-49, 152, 234-46; and cannibalism, 236; influence of improved organic adaptation, 29; level vs. precision of regulation, 239-40; nutritional control of, 235-37; in plants, 238; and rate of development, 235-36; and rate of reproduction, 236
population fitness, and extinction, 27-28, 49-50, 106, 119-20; and numerical stability, 105-107, 232-46; vs. population success, 103-104; in relation to size, 104-105; and sex ratio, 147-49; and versatility, 105-106
population size, *see* population density
populations, experimental, 235-38; misinterpretation of concept, 251; protozoan, 235
porpoises, mutual aid among, 95-96; vocalization, 10
preadaptation, 30, 169-70
pre-Cambrian, 36
precipices, instinctive fear of, 83
predation, in experimental populations, 237-38
pregnancy, cost to female mammal, 182
prephyletic evolution, 135-37
Primates, classification, 48-49; social structure, 95
primitive organisms, continued success of, 51, 53
Proconsul, 48
progress, as accumulation of information, 35-42, 46-47;

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

in aircraft, 50; Darwin's concept of, 100-101; as development of biotic adaptation, 106; in evolution, 4, 21-22, 34-55; as evolution in an arbitrary direction, 47-49; and gene substitution, 34-35; as histological specialization, 47; as improvement of adaptation, 49-54; as increasing complexity, 42-47; multiplicity of meanings, 35; origin of concept, 35; and precision of adaptation, 34, 49-54; vs. substitution of adaptations, 53-54
promiscuity, selection for, 185-87
Protopterus, 180
pseudo-pregnancy, 205
purpose, defined, 8-9

Rand, A. L., 217
rat, liver regeneration, 86-87
rates, *see* evolutionary rate, mortality rate, mutation rate, etc.
rattlesnake, 14, 231
redia, 46
regeneration, 83-87
repellents, integumentary, 228-31
reproduction, adapted to demographic environment, 245-46; adapted to social environment, 242-43; as biotic adaptation, 159-61, 165; cost of, *see* cost of reproduction; facultative adjustment of, 173-74, 237, 242-43; gregarious, 187-91; nutritional control of, 235-37; in relation to population density, 236; seasonal, 172-73, 249-50
reproductive effort, *see* cost of reproduction
reproductive functions, imperfection of control, 203-208; misplaced, 203-208
reptile, thermoregulation, 76-77
response to stimulus vs. environmental interference, 75-78
rhesus monkey, 95
Rhizodopsis, 43
Rich, W. H., 214
Richdale, L. E., 191, 220
Riffenburgh, R. H., 215
Ris, H., 39
Ritter, W. E., 190, 201
Roe, A., 205
root grafts, 223
rotifer, 47
roundworms, regeneration and wound healing, 47, 84
rubber, artificial, 122
Russell, E. S., 7, 19, 86

salmonid fishes, 51, 174-75
Salt, G., 202
Schmidt, K. P., 231
schooling, of fishes, 212-17; other animals, 217
scorpion, 230
sea cucumber, 266-67
sea snakes, gregariousness, 217
seahorse, 185-86
seals, 188-89

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

seasonal males, 156
seasonal reproduction, evolution of, 249-50
secondary adaptations, 265-69
secondary needs, 265-69
segregation distortion, selection of, 117-19
selection, of evolutionary trajectories, 110-11; genic, *see* genic selection; interdemic and intrademic, *see* group selection, genic selection, kin selection
selection coefficients, *see* genic selection, group selection
senescence, 27, 225-28
serial homology, 87
sex determination, environmental, 154-55; genetic, 146-54; in plants, 154-55
sex ratio, evolution of, 21, 146-57, 272; role in population regulation, 148-49, 152; selection for offspring, 150-53
sexes, differing reproductive roles, 182-87; reversed roles of, 185-87
sexual vs. asexual reproduction, genic selection of, 131-32
sexual conflict, wastefulness of, 27-28; in fishes, 174-75
sexual reproduction, association with environmental change, 129-32, 137, 156; definition of, 125-27; as organic adaptation, 130-31; origin of, 133-38; in plants, 126
sexual selection, 183-85
sharks, continued survival, 51; feeding on fish school, 215; rectal gland, 10; viviparity, 180
Shaw, R. F., 154
sheep, liver fluke, 45-47
Sheppard, P. M., 25, 37
sickle cell anemia, 60-61
Simpson, G. G., 9, 21, 111-13, 122
Singer, R., 14
siphonophore, 194-95
Skutch, A. F., 207
slavery, in ants, 28
sleep, as secondary need, 268
Slijper, E. J., 96
slime molds, 223-25
Slobodkin, L. B., 92, 155, 237, 268
smelt, 113
Smith, J. L. B., 230
Smith, J. M., 242
snowshoe hare, 249
Snyder, R. L., 232, 239
social Darwinism, 255
social donors, 195
social environment, 66, 242-43, 251, 268-69
social hymenoptera, genetics of, 200
social insects, absence of viviparity, 171; analogy with human organizations, 256; caste determination, 67; evolution of social organization, 197-201; fecundity, 33-34, 163-64; with multiple queens, 199-201, 146; stings of, 230-31

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

INDEX

social needs, secondary status of, 268-69
Socrates, 23
somata, genetically heterogeneous, 222-25
somatic environment, 57-58, 61-67
somatic nuclei, genetic competence of, 62-63
Sommerhoff, G., 9, 260
sonar, of bats, 30
special vs. general adaptation, 49
specialization vs. evolutionary advance, 48-50
specialization and extinction, 27-28
species, analogy with human organizations, 253-54; nature and significance of, 252
spider monkey, habitat selection, 69
Spieth, H. T., 145
sponge, 53, 127
sporocyst, 46
sporophyte, of fern, 126, 131
sporophyte development, determination of, 63-64
squid, DNA of, 39; schooling behavior, 217
Stalker, H. D., 156
Stebbins, G. L., 129
sterility, 27, 117-19, 197-99
sticklebacks, egg masses, 179; homosexuality, 205
stimulus, unreliable as guide to function, 269
stingray, 230
stolon, 126
stonefish, 230
structural vs. genetic homology, 65
sturgeon, 178
sunfish, 165
Suomalainen, E., 132
superoptimal stimuli, 262-63
survival, roles of fitness and chance, 101-103. *See also* extinction
survival by specialization, 30-31
Svärdson, G., 167
swordfish, 214
symbiosis, 246-47
syngnathid fishes, 185-86
systematics as aid to understanding adaptation, 270-71

t-alleles, 27, 117-19
tapeworm, 161
teleology, 7, 21, 128, 258
teleonomy, 258-69
termites, intestinal symbionts, 246. *See also* social insects
tern, 189
territoriality, agonistic nature of, 193-94; in birds, 240-43; function of, 240-43
territory, non-feeding, 242
theoretical biology, immaturity of, 88
theory and empiricism in science, 20
thermoregulation, man vs. reptile, 76-77
Thoday, J. M., 49-50, 106
Thompson, D. Q., 244
thread herring, 215
tinamou, 186
Tinbergen, N., 242, 263

For general queries, contact webmaster@press.princeton.edu

© Copyright, Princeton University Press. No part of this book may be distributed, posted, or reproduced in any form by digital or mechanical means without prior written permission of the publisher.

toxins, repellent function of, 228-31
trajectories, evolutionary, 110-11, 114
transduction, 137
tree shrews, 49
trematode, 45-47
Tribolium, 31
tuna, 179
turtles, juvenile sexuality, 204; marine, 261

Underwood, G., 81
urodeles, 67

Vendrelly, R., 39
venoms, defensive, 230-31; offensive, 230
vertebrate eye, functional design of, 6, 161, 259
vertebrates, Devonian, 42-43, 120
viruses, genetic recombination among, 133; as unspecialized genes, 136-37
viviparity, in fishes, 166-67, 178; immunological obstacles, 170; in insects, 170-71; mammalian, 170; selection for, 168-71
Vorontsova, M. A., 84

Waddington, C. H., 7, 39, 49, 71-83
Warburton, F. E., 81
Wardlaw, C. W., 63
warning signals, chemical, 216; visual, 206-207
wasps, parasitic, 202-203
weaverfish, 230
Weismann, A., 3, 225
Wellensiek, U., 177
whale, 87, 264-66
White, M. J. D., 64
Williams, G. C., 61, 165, 179, 195, 196, 216, 226
Wilson, E. O., 146
woodpecker, 190-91, 201-202
Wright, S., 3, 20, 26, 58, 92, 111-13, 122, 142, 143, 196, 232, 273
Wynne-Edwards, V. C., 91, 92, 96, 105, 107, 113, 181, 187, 194, 218, 232, 239, 243-46

yeast, 13

For general queries, contact webmaster@press.princeton.edu