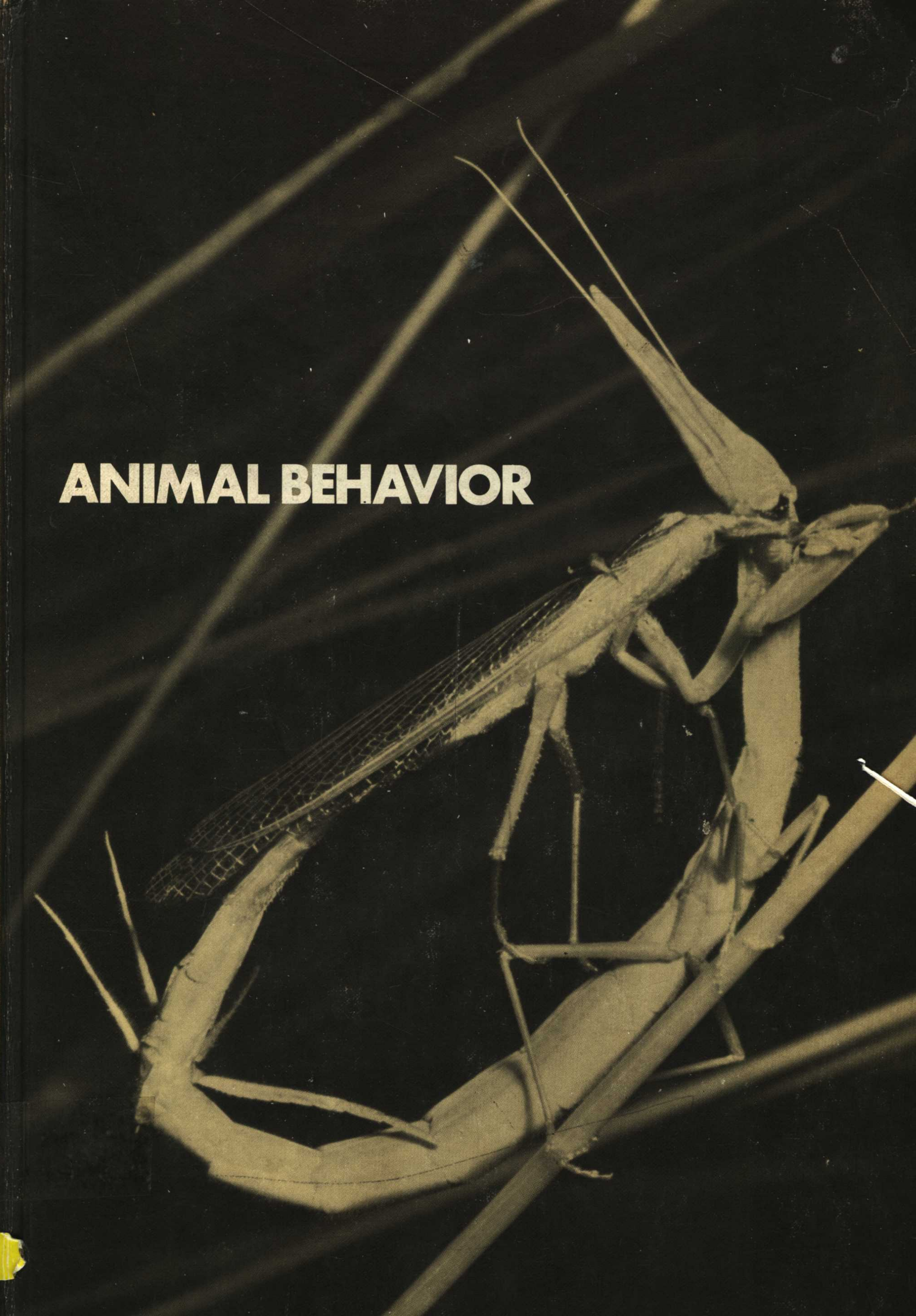
ANIMAL BEHAVIOR



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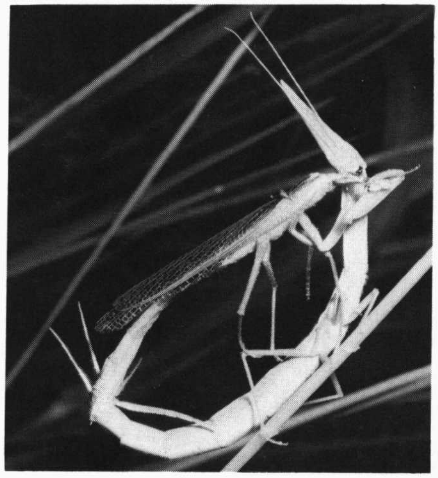

AN EVOLUTIONARY APPROACH

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To my students,
who cheerfully remind me each year
how much I have yet to learn.

ANIMAL BEHAVIOR:
An Evolutionary Approach

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THE BINDING The photograph on the binding depicts a female grass mantis consuming her mate (the winged male) during copulation in Zambia, Africa. The female has grasped the male's head and thorax with her powerful forelegs and has begun to devour the head.
Photograph by E. S. Ross.

PREFACE

I have prepared this textbook for students taking their first course in animal behavior. My objective throughout the book is to suggest how one might approach the genetics, physiology, ecology, and history of behavior from an evolutionary perspective. To the extent that my readers come to understand this approach and appreciate its usefulness in interpreting and integrating many diverse topics in animal behavior I will be satisfied. Of course, other persons would have stressed different points and, in fact, might have advanced thoroughly different arguments; although I am a somewhat partisan advocate of one viewpoint, I do not claim to have cornered the market on Truth. I sincerely encourage my readers to examine the book critically and with a willingness to challenge generalizations presented here.

I should like to discuss some features of the book that may make its use more profitable. The book is organized into three main sections: the first two chapters provide an introduction to the basic questions about animal behavior and background material on evolutionary theory; a block of twelve chapters follows which deals with answers to the fundamental questions about behavior; in the two concluding chapters an evolutionary perspective is applied to human behavior. Readers may find it useful to refer to the table of contents in the course of their reading to keep track of where they have been and where they are going in terms of the broad outline of the book. In addition, the major points of each chapter are reviewed in a concluding summary. Throughout the text scientific publications are cited by italic numbers in brackets, which refer the reader to the numbered bibliography at the end of the book—which can also serve, by the way, as a useful general listing of articles and books of possible interest to the reader. At the end of each chapter is a list of publications that I consider to be especially valuable as additional reading. Finally, because animal behavior involves doing things, I have selected as illustrations of material in the text many dramatic photographs that capture animals in behavioral acts. Although these will help you visualize animal behavior, a film is often still better, and so I have listed at the ends of chapters high-quality films that instructors may wish to use in class to complement the text.

Many people have helped me in various ways as I wrote this book, and I deeply appreciate their assistance. My undergraduate advisor, Lincoln Brower, introduced me to the rigorous, experimental study of animal behavior. In addition, he made it possible for me to spend a number of summers in Trinidad, where I had an opportunity to carry out research in a tropical setting and to sample Old Oak Rum deeply and often. My graduate advisor, Ernst Mayr, saw to it that I developed a fuller appreciation of the significance of evolutionary biology. His training profoundly influenced my interpretation of all behavioral phenomena, and I am indebted to him for his guidance. In my first teaching position at the University of Washington I was fortunate to have two colleagues who both advanced my education immeasurably. Robert Lockard and I have had many enjoyable discussions on the application of evolutionary theory to just about every conceivable aspect of behavior. His imprint on my thinking is apparent to me throughout the book. In teaching a course with Gordon Orians I again had the satisfaction of having many ideas that were new to me explained so clearly that I quickly came to believe that they were my own invention. I have borrowed many principles and techniques for organizing material on behavior from both men. Moreover, Drs. Lockard and Orians have reviewed substantial portions of my book and have made many useful suggestions for its improvement.

Other readers of sections of the manuscript who have offered important comments include Richard Alexander, Victor Denenberg, Thomas Eisner, Ernst Mayr, and Edward O. Wilson. To all these gentlemen I extend my thanks while retaining full responsibility for any errors of fact or opinion.

Naturally any textbook depends heavily on the ideas of others, and I have made an effort to cite accessible papers of authors whose work is reported here. In this context I wish to express my deep admiration for the contributions of Vincent Dethier, Konrad Lorenz, Kenneth Roeder, and Niko Tinbergen to the study of animal behavior. I offer my apologies to those scientists whose work I should have cited but which I overlooked.

Numerous colleagues have generously provided me with photographs and permission to use illustrations and quotes. Photographs appearing in the book carry the appropriate credit line for the photographer; for all other credits see p. 529. I would like to give my special thanks to the many people who have given me materials as a professional courtesy and should like to single out George Gamboa, who spent considerable time and effort to secure certain photographs that I especially wanted.

My editor, Carlton Brose, has earned my respect and gratitude for his assistance on many issues and for his attention to the seemingly endless

details that go into preparation of a book. Jill Leigh did a very competent job of typing the manuscript, with the assistance of Robert Smith, who helped with the proofreading. It also gives me pleasure to thank my parents for their help and encouragement as I developed my scientific interests. Finally, I gratefully acknowledge the many contributions my wife, Sue, and our two boys, Joey and Nicky, have made by agreeing to live with me while I wrote the book.

John Alcock

CONTENTS

ANIMAL BEHAVIOR

AN EVOLUTIONARY APPROACH

CHAPTER ONE

QUESTIONS ABOUT ANIMAL BEHAVIOR

In John Barth's book *The Sot-Weed Factor,* Henry Burlingham, tutor to Anna and Ebeneezer Cooke, is guided in the performance of his professorial duties by three principles. The first of these is of interest to us here: ". . . of the three usual motives for learning things—necessity, ambition, and curiosity—simple curiosity was the worthiest of development, it being the 'purest' . . . the most conducive to exhaustive and continuing rather than cursory or limited study, and the likeliest to render pleasant the labor of learning."

Despite years of formal education of a quite different sort than that offered by Burlingham, most of us retain at least a remnant of our native curiosity. This is certainly true of the men and women whose discoveries about behavior are described in this book. This is not to say that scientists lack the necessity to be "productive," nor are they devoid of ambition (should proof of this be required, you are encouraged to read James Watson's excellent book *The Double Helix* [*471*]). But most scientists, particularly good ones, love to learn about something. It is exciting to know enough to be able to ask a good question and then to devise a technique or an experiment that will provide a reasonable answer. I hope that these chapters on the study of behavior will provide inspiration and encouragement to those of you who wish to experience the pleasure and satisfaction of learning, simply because you are curious.

3 QUESTIONS ABOUT ANIMAL BEHAVIOR

CURIOSITY ABOUT BEHAVIOR

Anyone curious about the behavior of animals has an enormous array of potential questions to ask about any aspect of behavior that he or she observes. For example, imagine that you are wandering by a sand dune in July and come across some inch-long yellow and black wasps flying back and forth low over the surface of the dune. You approach the dune more closely, to see what they are doing. Several wasps fly up at you and buzz loudly and ominously about your head. After beating a hasty retreat you advance once again, driven by an intrinsic interest in sand wasps. The creatures buzz around again but do not sting and are soon gone. As you inspect the surface of the dune, a wasp comes burrowing straight up out of the ground, rapidly covers the exit hole with sand, and flies off. Puzzled, you wait nearby. After 10 minutes a wasp comes darting toward you low over the ground and then lands on the sand nearby. Underneath its body the wasp holds a large brown fly with its two middle legs. The front legs of the wasp energetically kick sand back under its body. In a few seconds it has opened a tunnel into the dune. It tilts its head down and its abdomen up and walks into the burrow (Figure 1). As the wasp enters the burrow, its middle legs release the fly and a hind leg pulls the unresisting insect down the tunnel. (Actually you would be an exceedingly acute observer to notice all these details the first time you watched the wasp.) After a minute or so the creature reemerges without the fly, repeats its burrow-closing behavior, and flies off into the distance.

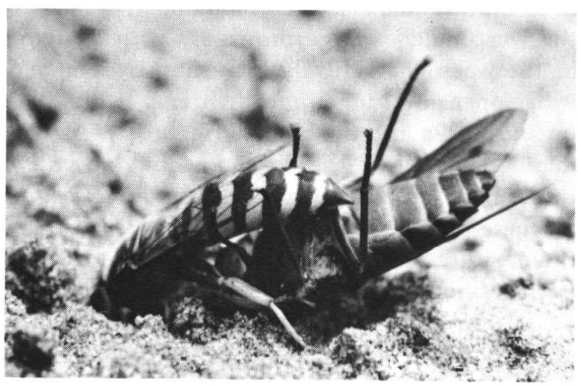
If you were suitably impressed by these events you would probably want to see them happen again. A patient observer could see the scene repeat over and over by this and other wasps entering burrows nearby. As you were watching, all sorts of questions might be running through your head. What are they doing with those flies? Why don't the flies resist being hauled into the dune on their backs? How does the wasp grab a fly in the first place? How does it manage to return repeatedly to a tiny hidden hole in a sand dune? Why does it cover up the hole each time it leaves? Why do all wasps of this type hold the fly with their middle legs only? Further reflection (it would be best if this were done in the shade somewhere) would reveal that all these questions and any others that you had invented could be categorized into two basic groups.

How Questions

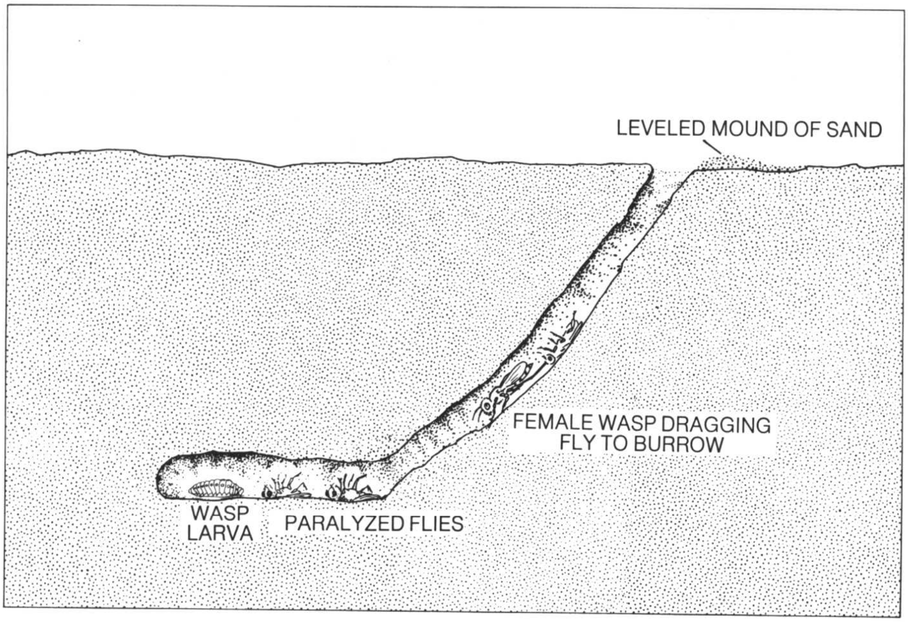
In fact, all biologically significant questions can be placed in two categories: how and why. "How questions" are questions about the mechanisms responsible for a biological event. They are concerned with the immediate or PROXIMATE cause of something. How does the wasp find and grab a fly? One answer to this question involves learning how the wasp manages to fly and maneuver in the air, how the wasp "knows" that it has found a fly when it encounters one, how the wasp uses its leg muscles to capture the fly and its stinger to paralyze it. In other words, one major group of how questions about behavior is concerned with the PHYSIOLOGICAL BASES of behavior, the mechanical causes of the activity, and the relationship among nervous system, muscles, and structures that translates into behavior.

But there is another level to how questions. How did the wasp get the kind of nervous system, muscles, and leg structures that permit it to capture flies? To answer this question it is necessary to learn something about the GENETIC and DEVELOPMENTAL BASES of behavior. One of many species of sand wasp, *Bembix pallidipicta* (Figure 1), has a special kind of nervous system capable of interpreting certain visual stimuli as objects to be captured. Hereditary genetic factors are intimately involved in the construction of that nervous system with those special abilities.

How questions about behavior require proximate answers about the immediate causal bases of that behavior. How does the sand wasp manage to capture a fly? The wasp's genetic instructions contributed to the development of a particular kind of animal with a specific kind of nervous



1
SAND WASP, Bembix pallidipicta, entering its burrow with the corpse of a large horsefly. Photograph by Howard E. Evans.



2 **UNDERGOUND BURROW of Bembix pallidipicta as seen from the side.**

system capable of detecting flies and ordering the muscles that control the wings, legs, and stinger of the wasp to do the complicated things that are the basis for capturing flies.

Why Questions

Even if you were provided with or discovered personally the answers to all imaginable how questions, you should not be completely satisfied. There are many other questions not answered by understanding the genetics and physiology of an individual animal. "Why questions" are concerned with the evolutionary or ULTIMATE reasons why an animal does something. Why does the wasp find and capture flies? On one level, an answer to this question demands an understanding of the function of the behavior in the animal's natural surroundings. The wasp captures flies "because" this copes with the ecological imperative to provide food for its offspring, a pale white grub that lives in a chamber at the end of an underground tunnel (Figure 2). The larva will eat 20–30 flies as it develops before building a sand-grain cocoon in which it will eventually metamorphose into an adult. The adult will gnaw its way up through the 10–20 inches of soil between the chamber and the surface and start the whole business over again if all goes well [*123*].

Each aspect of the wasp's behavior can be examined to determine why behaving that way may help the animal cope with ecological (environmental) demands in completing its life cycle. For example, why does the wasp close off the tunnel each time it leaves? Almost certainly this action prevents a variety of insect parasites from locating the nest, marching down the tunnel, and parasitizing the infant wasp or the prey on which it feeds. Why does the wasp hold the flies it captures upside down close to its abdomen with its middle legs only? Almost certainly this permits it to open the burrow without dropping its prey and thus exposing it to parasites, some of which follow prey-laden wasps to their nests and attempt to place a live parasitic larva on the fly [*122, 123*].

At another level of answers to why questions, the wasp behaves the way it does because of the history of the population to which it belongs. Its ancestors had varying genetic instructions that promoted a range of developmental options. Some individuals developed the kind of nervous system and structures that especially facilitated adaptive, functional behavior. That is, wasps with certain genes behaved in a manner that more effectively dealt with environmental problems (competition for food, the presence of parasites, and so on) than wasps with different genes. As a result certain individuals had more offspring that reproduced than others. Therefore, the genes of reproductively successful wasps are genes that remain in populations from generation to generation. Wasps alive today carry genetic information that in the past generally conferred a reproductive advantage on the individual that possessed it. The developmental options, and therefore the behavioral abilities, of a female *B. pallidipicta* living today are extremely limited by the historical process of evolution, a process based on differences in reproductive success (natural selection). But in return the wasp is likely to develop into a creature with a certain range of capabilities that have been relatively successful in the past and thus are likely to be useful in the present.

In summary, the two basic ULTIMATE reasons an animal does something have to do (1) with the function or ecological significance of the behavior, and (2) with the evolutionary history of the populations from which the genes of living animals are ultimately derived. In explaining behavior it is useful and necessary to make a careful distinction between proximate and ultimate causes, between how and why questions about behavior. Confusion on behavioral issues often centers on a failure to discriminate between the two [*327*]. To say, for example, that lemmings show extreme aggression at high population densities because of altered hormonal activity tells us something about a proximate reason for this but says nothing whatsoever about WHY the animal has this physiological system with its characteristic reaction to certain environmental stimuli. An evolutionary approach embraces both the study of the underlying mechanisms and the adaptive significance of behavior.

THE STUDY OF BEHAVIOR

It should be clear from this brief survey of questions about a sand wasp that the study of behavior is extremely broad-ranging, involving such diverse phenomena as the action of a gene, the structure of a nervous system, the relations of an animal to its environment, and evolutionary events lasting millions of years. Given the tentative nature of our knowledge of these things, how might one create a coherent and reasonably complete explanation of animal behavior?

There is no universally satisfying way to answer this question. However, it is the goal of the book to integrate questions and answers about behavior within the framework of evolutionary theory. Every aspect of modern biology is founded upon knowledge of the process of evolution based on Darwin's ideas about NATURAL SELECTION, as substantiated and modified by subsequent workers. Almost all biologists, whether they be geneticists, students of nervous systems (neurophysiologists), or ecologists accept the validity of evolutionary theory and its critical importance to their studies. An understanding of evolutionary principles, particularly of natural selection, is essential if one is to bring some order to the behavioral sciences [*257*].

Natural Selection

Prior to publication in 1859 of *On the Origin of Species* [*79*] a good many natural scientists believed that evolution occurred, but they did not know how it happened. Darwin's essential contribution was to provide a logical and persuasive mechanism for change—natural selection. NATURAL SELECTION IS THE DIFFERENTIAL REPRODUCTIVE SUCCESS OF INDIVIDUALS WITHIN A POPULATION THAT OCCURS BECAUSE OF GENETIC DIFFERENCES AMONG THEM. I want to stress strongly that the essence of natural selection is simply the fact that some members of a population have more progeny that live to reproduce than others. This causes changes within an interbreeding group of animals. It is the foundation of evolution. Darwin developed the concept of natural selection with the following pieces of evidence and logic, greatly condensed and summarized.

1. All living things have enormous reproductive potential. For example, were a single pair of house flies to breed in April and if all their offspring survived to reproduce and their offspring's progeny likewise survived, by August roughly 191,010,000,000,000,000,000 descendants would be living and the earth would have disappeared under a thick blanket of flies [*210*]. Creatures with much more modest numbers of children and much longer generation times are also theoretically capable of producing astronomical numbers of descendants in a relatively short period of time. Human beings are at this moment in the midst of a distressingly clear illustration of the possibility of geometric population growth [*85, 101*] (Figure 3). Darwin chose elephants to make the same point. On the assumption that elephants lived to be 100 years old and had just six offspring in the reproductive period between ages 30 and 90, a single pair would be the proud ancestors of 19,000,000 living descendants just 750 years later (if each elephant born lived to be 100 and reproduced).
2. The fact that populations tend to remain relatively stable demonstrates that most offspring die long before they reproduce (fortunately for those of us who are not fond of flies).
3. This mortality is not shared equally. There are hereditary differences among individuals that contribute to their ability to survive and reproduce. In extreme cases this is very obvious. Animals with severe congenital defects and abnormalities, such as a bird with a deformed beak or wing, almost always have a reduced reproductive capacity. The genes that underlie the production of these damaging defects are continually being removed