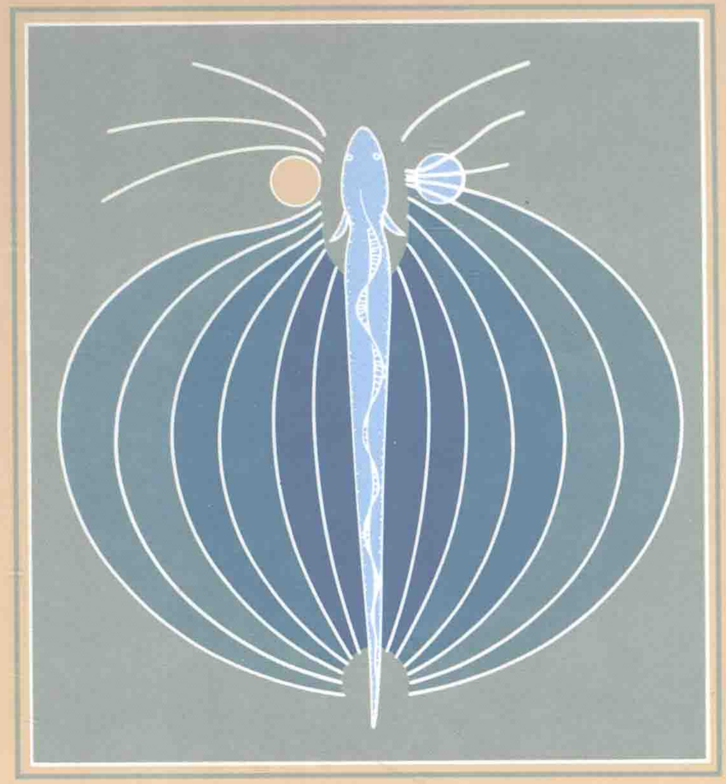

ANIMAL PHYSIOLOGY

SECOND EDITION

RICHARD W. HILL / GORDON A. WYSE

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SECOND EDITION

RICHARD W. HILL

Michigan State University

GORDON A. WYSE

University of Massachusetts at Amherst

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To
David and Christine
and to
Mary

PREFACE

Our goal in this textbook is to provide a comprehensive introduction to comparative animal physiology at a level suitable for upper-division undergraduate and beginning graduate students. Our emphasis is deliberately conceptual, for we believe that the acquisition of proper conceptual frames of reference should be the primary objective of introductory study. We develop physiological concepts from fundamental principles of chemistry, biology, and physics; and we attempt throughout to step back from the welter of available biological detail to identify patterns of significance and importance.

We have tried to make this book equally suitable for a course in comparative physiology, animal physiology, or physiological ecology. Toward this goal, we have tried to balance the general and the comparative perspectives in physiology in a way that will enlighten students rather than mislead them with overgeneralizations or burden them with exceptions. We have employed the perspectives of comparative physiology—evolutionary, adaptational, and environmental—where it is practical and desirable to do so. We consider these perspectives to be important and valuable. Nevertheless, we have not found it practical or advantageous to maintain a uniformly comparative or ecological perspective for all topics. Thus, topics such as salt and water balance receive a more ecological and comparative treatment than do others such as neural transmission. We consider this balance between general and comparative viewpoints to be essential to our goal of providing a text of manageable size, which presents the perspective of comparative physiology without requiring a prerequisite course in general physiology.

We have chosen to emphasize the ecological relations of animals because in nature it is on an ecological stage that the physiological play is acted out. We have also emphasized evolutionary perspectives in recognition of the importance of history in determining the form and functional properties of modern species. Because comparative physiology draws its greatest strength as a discipline from broad study of the differences and similarities among animals, we have treated the entire animal kingdom, with the exception only of the protists and metazoan parasites. We believe that this broad scope provides a much more satisfactory approach than a treatment limited to only vertebrates or some other circumscribed phyletic assemblage. We have attempted to provide sufficient background information on anatomy and natural history for readers to appreciate the physiology of groups that may be otherwise unfamiliar. The intimate interrelations between morphology and function are repeatedly emphasized.

NEW TO THIS EDITION

Some will recognize that this text is the descendant of an earlier work by one of us (R.W.H.). In comparison to the previous book, this one is extensively rewritten, expanded, and reorganized. The greatest change is that we have added chapters on nervous and sensory functions, muscle and other effectors, and endocrines. Along with this enlarged scope, we have expanded coverage of control mechanisms throughout. We have also greatly expanded the introductory material (Chapters 1 and 2) to include discussions of control theory, homeostasis, the autonomic nervous system, biochemical control mechanisms, and the concept of evolutionary adaptation. We have divided this introductory material into two chapters with different overriding objectives. The material in Chapter 1 is a necessary introduction for all students. On the other hand, the various concepts of physiological regulation in Chapter 2 are more complex and could profitably be mastered either at the start of a course or later. We have tried to structure Chapter 2 so as to give instructors considerable flexibility in assigning its parts for reading.

Other chapters that are descended from the first edition of this book have been extensively rewritten, updated, and expanded in content. In the present book, for example, the physiology of hearts and pacemakers is discussed in detail; the principles of intracellular volume regulation in euryhaline animals are reviewed; the phenomenon of uncoupling of oxidative phosphorylation is discussed; the interpretive value of renal clearance studies is described; all information on renal tubular function is updated based on the explosion of data from microperfusion studies; passive models of mammalian urine concentration are discussed; the concept of the oxygen cascade is presented as an organizing principle for the treatment of oxygen delivery; the discussion of biophysical modeling of thermal relations has been expanded; and the material on water and salt relations of terrestrial animals has been synthesized by recognizing physiological (rather than merely taxonomic) groupings. A concerted effort has been made throughout to give increased prominence to synthetic principles and organizing concepts. Furthermore, the number of figures and tables has been substantially increased. Inevitably, expansions in some places require constrictions elsewhere. At first, we had intended to increase the number of chapters on special physiological problems, but we found that a decrease was necessary. We felt it important to retain at least one chapter in which an integrated approach to a physiological problem could be pursued in depth, and we chose diving as the subject, in part because it provides an instructive example of how inquisitiveness and new data can lead to a new world view (Chapter 15). Altitude physiology is now covered in the form of boxes within the chapters on oxygen delivery (Chapters 12 and 13). Biological rhythms are treated in Chapter 2.

ACKNOWLEDGMENTS

Where once people bemoaned the passage of an era when one or two individuals could together claim reasonable mastery of all of biology, the growth of knowledge has now reached a point where maintaining mastery of just a single subdiscipline—such as physiology—is a challenge. We are acutely aware of the magnitude of the challenge and here express our regret for any errors we have made and our plea that readers bring errors or other shortcomings to our attention. So that communications can be properly directed, we mention that Chapters 1–15 and 21 are mostly the work of Hill, whereas Chapters 16–20 and the material on endocrine biochemistry and invertebrate endocrinology in Chapter 21 are principally by Wyse.

The quality of the manuscript has been significantly improved by the comments and help of a number of biologists who have critically read part or all of it. Among them are Albert F. Bennett, University of California at Irvine; Eric Bittman, University of Massachusetts; Ronald L. Calabrese, Harvard University; Donald P. Christian, University of Minnesota, Duluth; Douglas A. Eagles, Georgetown University; Franz Engelman, University of California at Los Angeles; Robert E. Gatten, Jr., University of North Carolina, Greensboro; Richard J. Hoffman, Iowa State University; Theodore M. Hollis, The Pennsylvania State University; James L. Larimer, University of Texas, Austin; Leo E. Lipetz, The Ohio State University; L. M. Passano, University of Wisconsin, Madison; Henry D. Prange, Indiana University; Gregory Snyder, University of Colorado, Boulder; Donald H. Whitmore, University of Texas, Arlington; Leah H. Williams, West Virginia University. We also have profited immeasurably from our routine interactions with colleagues over the years. The contributions of those colleagues are often difficult to trace to their end effect on our thinking, and composing a list of all the individuals who have been influential and helpful would be a challenge. We wish to thank them all, however, and in the process acknowledge our awareness that this book is very much a product of the world community of comparative biologists. Where halftones appear in the text, we have nearly always received the generous cooperation of fellow scientists in obtaining original prints of the illustrations. We thank those individuals and all who have given us permission to use data or illustrations from their work. In particular, we thank the following men and women who have helped us obtain or have made available unpublished halftone illustrations: Bernd Heinrich, Dave Hinds, Michael Hlastala, Daniel Luchtel, Keith R. Porter, Frank L. Powell, Jane K. Townsend, and Walter S. Tyler. Kjell Johansen, whose data are featured prominently in several chapters, not only provided illustrative material but offered repeated encouragement over the years; his recent death is a source of sadness. Much of Hill's writing was done at the Marine Biological Laboratory in Woods Hole. Acknowledgment is made to the Laboratory and also to John W. H. Dacey (Woods Hole Oceanographic Institution), who was always eager to help in many ways. We also express our gratitude to Claudia M. Wilson, Thomas R. Farrell, and the staff of Harper & Row, without whose sympathetic editorial counsel and assistance this project could not have been completed. Finally, we thank our wives, Susan and Mary, for their steadfast support, and perhaps even more we thank our children, who have undoubtedly not always comprehended why we were off at the office so much, for their affection and forbearance.

Richard W. Hill
Gordon A. Wyse

NOTE TO THE STUDENT

We hope you will read the preface, which describes our goals and perspectives in this text. Our highest hope is that you will share the sense of excitement that we have felt in studying the grand patterns of animal function. If we have helped you in that quest, our efforts to create a readable and informative book will have been rewarded.

Writing a textbook involves a constant tension between the desire to recognize all available knowledge and the need to highlight general patterns that emerge from the background of detail. Inevitably, the identification of patterns entails the circumvention of some detail, the running roughshod over some data painstakingly gathered. The question for an author is always how to strike the proper balance. Too little attention to detail leads to abstractions so crude as to bear little resemblance to real nature. Yet, as one pundit has put it, the compression of too many details into the space available can create a black hole rather than a supernova. Another concern is that science is always changing; whole worldviews can be replaced with others. One of the finest of intellectual challenges is to preserve the capacity to make the intellectual leap from one worldview to another when justified by evidence. That is a lifelong challenge for you, as it is for us. We trust that the following pages do not reflect too many failures on our part in those respects.

We want to discuss here three additional issues we have confronted as authors. The first is the matter of giving references to our sources.

The knowledge described in this book is the product of decades of study by thousands of investigators. Scientists announce new knowledge by means of research reports in the scientific journals. In the formal scientific literature, when an author makes reference to a piece of such reported knowledge, it is customary to provide a citation to the journal and article in which the knowledge is documented; the author thus provides authority for the information and enables readers to "check out" the original research report for themselves. We debated whether we should do the same in this book. Our decision was that the text would become too cluttered if we provided a citation for every piece of knowledge, and we could devise no satisfactory formula for referencing some pieces of knowledge but not others. Thus, you will not find citations in the running text of our book. What we have done is to give you an ample reading list at the end of each chapter, and we have been certain to include in each list some individual research reports (idiosyncratically selected) as well as books and review articles. Should you wish to pursue a topic that you have learned about in this book, you will usually be able to find leads into the literature on the topic by using the reference lists we have provided. Sometimes, the lists deliberately include articles that express viewpoints at odds with our own presentation in this text. Two details concerning the reference lists are important. We have placed an asterisk (*) next to certain of the readings in each chapter that we believe would be especially worthwhile for your first explorations beyond this book. Also, we have clustered together in Appendix A at the end of the book some references that apply to a diversity of chapters. As a group, these references are extremely important, and most chapter reading lists include a reminder that you should consult Appendix A to find them.

Another topic we debated was whether to include a glossary. Because glossaries typically provide little more than verbatim quotes of definitions found in the text proper, we decided to omit a glossary and provide special directions to the definitions in the text. If you need a definition of a word or concept, turn to the page listed in bold type under that word or concept in the index. This system has the advantage that you will usually find explanatory material on the same page as you will find the definition.

The final matter we want to discuss is a conundrum: the question of what units of measure to use. There has been of late a concerted effort to adopt a single system of units in physiology. This system, called the Système International (SI, for short), recognizes seven base units of measure; all other units are to be derived from these seven. For instance, the base units of mass, length, and time are the kilogram (kg), meter (m), and second (s), respectively; the derived unit for energy is then the $m^2 \cdot kg/s^2$, which is known as a joule (J), and the derived unit for pressure is the $kg/(m \cdot s^2)$, which is called a pascal (Pa). In principle, we support the exclusive adoption of SI units; there is little to recommend having two, three, or four different units of measure for one parameter. Nonetheless, we believe also that there are legitimate practical concerns that must be weighed against the application of principle in a book of this sort. Most important, readers must be prepared to function with units that are in common usage, and those are not always the SI units; we believe we would do little to advance understanding by expressing blood pressures in kilopascals when the truth remains that for the immediate future at least, most of you who come to use such pressures in your work will be confronted with instruments calibrated in millimeters of mercury (mm Hg) or torr. Thus, for each parameter, we have chosen to emphasize units that are in reasonably common usage. If a unit is not part of the SI, we point that out and note its relation to the appropriate SI unit. Appendix B summarizes the SI units and their relations to traditional units. The following reference provides details on the SI: C. H. Page and P. Vigoureux, *The International System of Units*. National Bureau of Standards Special Publication 330, U.S. Government Printing Office, Washington, DC, 1974.

Richard Hill
Gordon A. Wyse

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chapter 1

Organism, Environment, and Adaptation

Physiology is the study of the function of organisms. In this text, our primary objective is to develop the basic concepts of animal physiology as presently understood. Our approach is *comparative*. That is, while we give substantial emphasis to mammals, we compare and contrast how functions are carried out in other vertebrates and invertebrates as well.

One advantage of the comparative approach to animal physiology is that it aids comprehension of our own functional attributes. By examining how particular functions are carried out by various animal groups that are built on diverse plans and occupy diverse environments, we gain a perspective on mammalian function that could not be obtained by looking at mammals alone. Indeed, advances in understanding of mammalian physiology in the past have often depended on studies of other organisms. The functional attributes of nerve fibers and vertebrate kidney tubules, for example, were first uncovered through investigations of squids and frogs, because the relevant tissues of the latter organisms are more amenable to study than those of mammals.

Another advantage of the comparative approach is that it permits patterns of physiological evolution to be identified. Comprehension of those patterns is often crucial to analyzing the adaptive value of physiological features (p. 5).

The comparative approach also has the inherent virtue of expanding physiological knowledge to include the full range of animals. An understanding of the functional attributes of fish, bees, and squids is of its own intrinsic interest to those who aspire to comprehend the natural world.

As we embark on our study of physiology, it is important that we focus at the outset on the concepts of organism and environment and on the process—adaptation—by which organisms have become matched to their environments. These are the concerns of this first chapter.

THE ORGANIZED AND DYNAMIC STATE OF BODY CONSTITUENTS

We are accustomed to seeing the world macroscopically, but this view is incomplete. Suppose for a moment that we could reduce our scale of vision to the atomic–molecular level and gaze at a woodland or pond. We would see atoms and molecules everywhere. In particular, here and there we would see self-sustaining physicochemical systems of high organization. Organization within these systems would be reflected both in the presence of large, complex molecules and in a patterned orientation of those molecules relative to one another. The organization of the systems would persist through time. These self-sustaining organized systems are what at a macroscopic level we call organisms.

We would see atoms and molecules moving into and out of each organized system. Some atoms and molecules would have a rapid passage; they would enter at a particular point, follow a particular path through the organized system, and exit at another particular point. These atoms and molecules would be undergoing ingestion and egestion. More importantly, we would see other atoms and molecules entering and exiting the *structure* of the organized system. They would be incorporated into or removed from the *organization itself*. In human beings, for example, iron atoms from foods are incorporated into hemoglobin in red blood cells, and later some of the atoms are excreted when the blood cells are broken down; the average longevity of a human red blood cell is only about 4 months. Calcium atoms enter the skeleton and later are withdrawn. As shown by the seminal investigations of Rudolf Schoenheimer and his colleagues in the 1930s, body fats and proteins are continually broken down and resynthesized at substantial rates. The resynthesis is carried out in part using molecules newly acquired from the environment, such as fatty acids and amino acids from foods. Human adults typically resynthesize about 3 percent of their body protein each day.

From this view of the world, we gain a number of important insights. (1) The material constituents of animals are in a state of dynamic exchange with the environment. In this regard, animals differ from objects such as telephones, which may be highly organized at an atomic–molecular level but do not exchange material with the outside world (except through surface wear). (2) Because atoms and molecules can change between being part of an organism and being part of its environment, it is not always easy to say where environment stops and organism begins. Consider, for example, a carbon atom in a piece of bread. When the bread is sitting on your table, the carbon atom is clearly part of your environment. Most of you would likely agree that it is still part of the environment when it is in your small intestine. But is it part of the environment or is it part of you when it is being transported in your bloodstream? And how should it be categorized when it has been absorbed by some cell? If finally the carbon atom becomes built into your own protein, we would firmly say that it is part of you. We recognize from this exercise that the material "boundaries" between an organism and its environment are not sharp. (3) A further and most important consequence of the exchange of atoms between organism and environment is that an organism is not a discrete material entity. Suppose you were to mark every atom in an adult animal's body at one point in time. If you then reexamined the animal 2 years later, many of the marked atoms would be gone, having been replaced with new, unmarked atoms taken in from the outside world. Thus, the precise material construction of an organism—unlike that of an inanimate object—does not persist through time. What then does persist? The *organization*. Part of the essential nature of organisms is that they are self-sustaining organizations.

The creation and maintenance of organization require not only material constituents but also energy (Chapter 3). Indeed, the acquisition and use of energy have loomed as major factors in animal evolution and are important themes of this book.

ORGANISM AND ENVIRONMENT

The environment is the theater in which the animal must function successfully. Physiological features that are appropriate in some environments may be woefully inappropriate in others. Thus, an accurate interpretation of an animal's physiology is dependent on detailed knowledge of the environment it occupies.

The ***environment*** of an animal is comprised of all the chemical, physical, and biotic components of its surroundings. As pointed out by the great physiologist Claude Bernard over a century ago, organism and environment are defined in terms of each other. Only by saying what "organism" is can we say what "environment" is. Consider, for example, a parasite inside a human being. From our usual perspective, the human is "organism," but from the perspective of the parasite, the human is "environment." All organisms, in fact, are part of the environment of other organisms.

An organism and its environment strongly interact with each other, further blurring the boundary between the two. All organisms are obviously influenced by aspects of their environment, such as temperature, light, and pollutants. Less obviously, the environment can be affected by the organism. Consider, for instance, a mouse in a small cavity in a tree. In winter, the mouse warms the cavity to temperatures above those in the outside world. Then the mouse responds physiologically to the elevated temperatures in the cavity. Clearly, mice are able to modify the thermal parameter of their own environment. In like manner, fish may deplete the water of oxygen and then must cope with low "environmental" oxygen levels.

We tend to divide the environment conceptually into different aspects or factors, a practice with advantages and disadvantages. The factors traditionally recognized have included temperature, humidity, light, wind, pH, salt concentration, oxygen concentration, food supply, competition, and predation. This factorial approach makes it easier for us to appreciate and analyze the multidimensional complexity of the environment, but it presents two dangers. First, we must recognize that some factors are more easily quantified than others. Temperature, for example, can be measured accurately and inexpensively. Light can be measured accurately but only with a more expensive instrument. Food supply can be quantified only approximately and with great difficulty. There is a temptation to study that which we can measure readily. The danger is that we may overemphasize the importance to animals of the factors we can easily quantify and underemphasize factors that we find more difficult to assess.

A second danger is that we may fail to take into account the *interaction* of environmental factors. Factors do not operate in isolation. Instead, the effect of any one factor may well depend on the simultaneous influence of others. Among carp, for example, the lowest tolerable environmental oxygen concentration depends on temperature. At 30°C, the carp require at least 1.3 mg of oxygen per liter of water, but about 0.8 mg O_2/L is sufficient at 1°C. Lowering the temperature decreases the metabolic rates of the fish, permitting them to survive in the face of lower oxygen levels. Interactions among factors can become very intricate, especially as the number of factors involved is increased. In turn, experiments to elucidate these interactions can become too complex to be practical. The danger is that simplifications introduced into experiments for the sake of practicality may cause us to overlook important interactive effects.

Microclimates

One important concern in evaluating animal environments is that we humans are relatively large organisms, and as we walk about, most of our sense organs are located several feet above the ground. Our conception of the climate and other conditions in an area may therefore bear little relation to the actual conditions experienced by many other animals. George Bartholomew, one of the founders of the modern ecological approach to comparative physiology, has expressed this important point especially well:

> Most vertebrates are much less than a hundredth of the size of man and his domestic animals, and the universe of these small creatures is one of cracks and crevices, holes in logs, dense underbrush, tunnels and nests—a world where distances are measured in yards rather than miles and where the difference between sunshine and shadow may be the difference between life and death. Climate in the usual sense of the word is, therefore, little more than a crude index to the physical conditions in which most terrestrial animals live.*

The actual climate in which a species lives is termed its ***ecoclimate*** or ***microclimate***. Three examples will serve to illustrate the kind of essential information that is gained in studies of microclimatology. Figure 1.1 depicts temperature and humidity conditions in a habitat occupied by *Ligia oceanica*, a semiterrestrial marine isopod crustacean. Note that the entire width of the habitat depicted would fit well within the length of a human footprint. And yet the climate is far from uniform. On the slope to the left, the isopod experiences a hot substrate (34°C), cool air (20°C), direct sunlight, breezes, and a relatively low humidity (70 percent). Just a few centimeters away, at the base of the layer of pebbles, it finds moist, dark, and uniformly warm stillness.

Figure 1.2 shows the annual maximal and minimal temperatures at various depths below the ground surface in portions of the Arizona desert. The annual temperature excursion in the air at 1 m above the ground is about 40°C. The excursion on the desert surface is twice as great. The surface heats up more than the air during the daytime because of absorption of solar radiation, and it cools below air temperature at night because of radiative loss of heat to the cold sky (see Chapter 6). In the soil, the total annual temperature excursion becomes rapidly smaller with increasing depth. Small rodents in their burrows find temperatures far below those on the surface during summer and much above those on the surface during winter. Although we humans think of deserts as hot places, the greatest thermal stress for nocturnal rodents may well be winter cold. The animals are in their burrows during the heat of the day in summer but in some cases venture out during the cold of night in winter.

*From G. A. Bartholomew, *Symposia of the Society for Experimental Biology*, No. 18, pp. 7–29. Academic, New York, 1964.

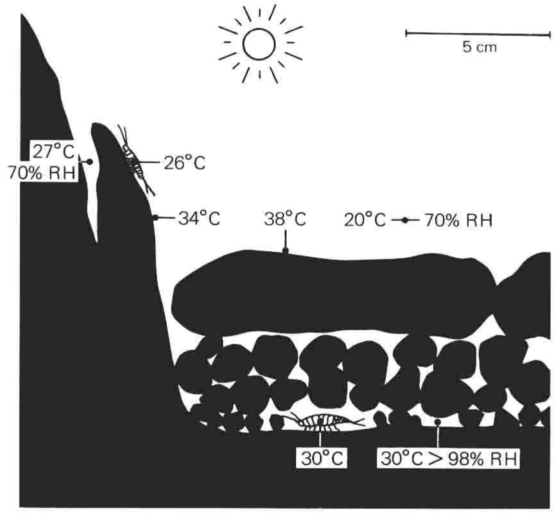

Figure 1.1 Diagrammatic section of the base of a red sandstone cliff and pebbles inhabited by *Ligia oceanica*, showing microclimatic temperatures and relative humidities (RH) and body temperatures of the animals. [From E. B. Edney, *J. Exp. Biol.* **30**:331–349 (1953).]

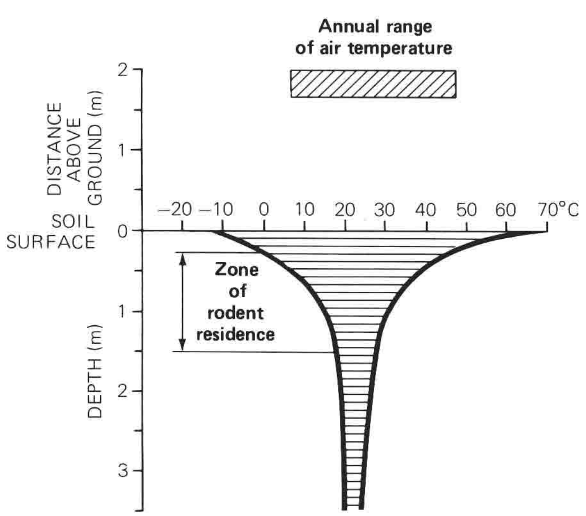

Figure 1.2 Annual range of temperatures in the soil of the Arizona desert near Tucson. Curve to the left depicts minimal temperatures recorded over the year; curve to the right depicts maximal temperatures recorded. The annual range of temperatures in the air is also shown. [From X. Misonne, *Mem. Inst. R. Sci. Natur. Belg., 2me Ser.* **59**:1–157 (1959).]

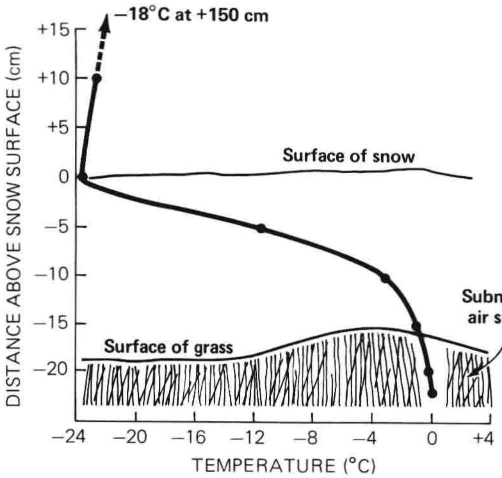

Figure 1.3 Temperature at points above, in, and under a 20-cm-thick snow cover in Sweden on 5 March, 1962, at 4 A.M. Various factors lead to development of a subnivean air space among the grass, between the ground and lower edge of the snow cover. It is postulated that small mammals can move about relatively freely in this air space. [After C.-C. Coulianos and A. G. Johnels, *Ark. Zool.* **15**:363–370 (1963).]

Finally, in Figure 1.3, we see that in cold northern regions, animals moving about under snow may find temperatures 20°C higher than in the air above.

Other Challenges to Understanding Animal Environments

The need to describe physical conditions in secluded places is only one of the hurdles that may be faced in describing the environments of animals. Another need is to understand the *behavior* of the animals sufficiently to know how they partition their time among the various microclimates available to them. Developing this behavioral understanding may be a major challenge if the species is small or secretive. Consider, for example, the difficulty of determining the lengths of time spent in various microclimates among the rocks by the isopods in Figure 1.1.

Just as our human experience of climate may bear little relation to the experience of other species, so also our sensory perceptions may be a poor guide to the perceptions of other species. This is another concern in understanding the relations of animals to their surroundings. We know, for example, that honeybees and certain other insects probably see flowers differently than we do because their eyes can sense reflected ultraviolet light to which we are blind. We also know that some birds can navigate using magnetic fields of which we are unaware. In these and other respects, we must be alert to the possibility that the sensory universe in which other animals live may be unlike our own.

ADAPTATION

From time immemorial, people have recognized that the properties of animals are often well matched to the environments they occupy. Animals living fully exposed to the heat of deserts often have exceptional capabilities of dealing with heat, for example; and ones exposed to arctic cold are often particularly well suited to the challenge. Several theories have been proposed to explain the match between animals and their environments. Evolution by natural selection is the one favored by most biologists today.

One way that people express the match between animals and environments is by saying that the properties of the animals are "adapted" to the conditions under which they live. This idea of "adaptation" is a central concept in animal physiology (as in most biological disciplines), and it bears some scrutiny not only because it is important but also because it is easily misused. Exactly what is meant by adaptation? And how might we determine whether a characteristic of an animal is in fact adaptive? There has been a call of late for increased rigor in answering these questions. One reason for the call is that all too often biologists in the past have seemed willing to assume, in essence, that every product of biological evolution is necessarily adaptive. Based on this assumption, the literature has become filled with impromptu rationalizations designed to explain the adaptive utility of each and every animal feature. To the extent that adaptation is simply assumed, it loses force as a scientific concept. There is a movement underway to establish an empirical science of adaptation. The function of such a science would be to provide definitions and standards whereby claims of adaptation could be evaluated by use of evidence rather than simple assertion.

To say that "an animal is adapted to its environment" is likely to mean little more than that the animal can survive and reproduce there. As already suggested, the really challenging question concerns not whether whole animals are adapted but whether particular animal characteristics are adaptive.

Suppose that a particular attribute of a species can exist in two genetically controlled states, *A* and *B*. For instance, let us consider as an attribute the affinity of the hemoglobin in red blood cells for oxygen, with state *A* being a relatively high affinity and state *B* being relatively low. Suppose now that there is a population of animals containing appreciable numbers of individuals with each type of hemoglobin. If individuals with type *A* enjoy a greater probability of surviving and reproducing successfully than ones with type *B*, then—by this very fact—the genes inducing state *A* will tend to increase in frequency in the population from one generation to the next (and those inducing state *B* will decrease). It could happen that after many years, virtually all individuals born into the population would be of type *A*. You will recognize this as the process of natural selection. If we were to come upon the population during the later phases of its evolutionary history and find it populated almost exclusively by individuals of type *A*, and if we were to know that state *A* had come to this position of prominence through the process of natu-