

F O U R T H E D I T I O N

ECKERT

# ANIMAL PHYSIOLOGY

MECHANISMS AND ADAPTATIONS



RANDALL • BURGGREN • FRENCH

FOURTH EDITION

ECKERT  
**ANIMAL  
PHYSIOLOGY**

MECHANISMS AND ADAPTATIONS



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For our families, and, of course,  
for Roger

## ABOUT THE AUTHORS

### DAVID RANDALL

A prominent fish physiologist and a leading expert in respiratory and circulatory physiology, David Randall collaborated with the late Roger Eckert on the earlier editions of *Animal Physiology* and continues his contribution in the fourth. A faculty member at the University of British Columbia in Vancouver, Canada, since 1963, and full professor since 1973, Randall was appointed Associate Dean of Graduate Studies in 1990. Elected a fellow of the Royal Society of Canada in 1981, Randall has been both a Guggenheim and a Killam fellow, and was awarded the prestigious Fry Medal for research contributions to zoology by the Canadian Society of Zoology in 1993. In 1995, he received the Award of Excellence from the American Fisheries Society for

contributions to the field of fish physiology. A frequent symposium lecturer on fish physiology and other subjects, most recently in Brazil, France, Germany, Italy, the People's Republic of China, Russia, and the United States. He has worked with both the World Health Organization and the United States Environmental Protection Agency in developing ammonia criteria. Widely published as author and co-author in leading journals, Randall is co-editor of the noted series *Fish Physiology* (Academic Press), of which 15 volumes are in print. Volume 16, subtitled "Deep-Sea Fish," will appear in 1997. Along with his other duties, Randall co-teaches third year courses in vertebrate physiology and environmental physiology. His research interests concern the interactions between gas and ion exchange across fish gills.

### WARREN BURGGREN

Warren Burggren has taught in physiology for 23 years, and has been a professor of biological sciences at the University of Nevada at Las Vegas since 1992. Courses he has taught at UNLV and at the University of Massachusetts, where he was Professor of Zoology from 1987 through 1991, include Human Anatomy and Physiology, Bioenergetics, Introductory Zoology, and Comparative Physiology. Burggren's research interest include developmental physiology, comparative animal physiology, and environmental and ecological physiology. In particular, his research focuses on the ontogeny of respiratory and cardiovascular systems, and how the systems that regu-

late them change over the course of development. Burggren has been actively involved in symposia, seminars, and formal extramural research/training activities in many countries. A co-author of *The Evolution of Air Breathing in Vertebrates* (Cambridge University Press, 1981), Burggren has been a frequent contributor since 1980 to edited collections of physiology, including Prosser's *Comparative Animal Physiology, Fourth Edition* (Wiley-Liss, 1991). Burggren co-edited *Environmental Physiology of the Amphibia* (University of Chicago Press, 1992), and more recently co-edited *Development of Cardiovascular Systems; Molecules to Organisms* (Cambridge University Press, 1997).

### KATHLEEN FRENCH

A neurobiologist at the University of California at San Diego since 1985, Kathleen French has for 10 years taught upper division courses in embryology, mammalian physiology for premedical students, and cellular neurobiology. In addition, at UCSD, French participates in a training program to instruct science teaching assistants in the techniques and philosophy of teaching. She also serves on the faculty of the Neuroscience and Behavior Course at the Marine Biological Laboratories in Woods Hole, Massachusetts, an intensive course designed primarily for graduate students and post-doctoral fellows. French brings her expertise in—and love of—teaching to her

role as co-author of the current edition of *Animal Physiology*, along with a lifelong interest in the nervous systems of organisms from a broad range of phyla. As an Associate Project Scientist at UCSD, French's research focuses on the control of neuronal development, a topic that she has studied in various invertebrate species. Her current research concerns the cellular events that control differentiation of identified neurons in the medicinal leech, with an emphasis on the cellular physiology of embryonic neurons and the effects of cell-cell contacts. She has been the author and co-author of numerous published research and review articles in journals including the *Journal of Neuroscience* and *Journal of Neurophysiology*.

# PREFACE

It is nearly ten years since the third edition of *Animal Physiology* first appeared, written by Roger Eckert with the help of David Randall. Roger died in 1986 while revising the third edition, which was completed by George Augustine and David Randall. That book formed the basis for the fourth edition, which is fittingly referred to as *Eckert Animal Physiology*. Although this new edition has been extensively revised and redesigned, the approach that so successfully characterized earlier editions has been maintained: the use of comparative examples to illustrate general principles, often supported by experimental data. In addition, we have emphasized the principle of homeostasis, and we have updated the molecular and cellular coverage. Retained in this edition is the comprehensive coverage of tissues, organs, and organ systems. Cellular and molecular topics are integrated early in the book so that common threads are developed to explain and compare the interactions between regulated physiological systems that produce coordinated responses to environmental change in a wide variety of animal groups. The basic principles and mechanisms of animal physiology and the adaptations of animals that enable them to exist in so many different environments form the central theme of this book.

The diversity and adaptations of the several million species that make up the animal kingdom provide endless fascination and delight to those who love nature. Not the least of this pleasure derives from a consideration of how the bodies of animals function. At first it might appear that with so many kinds of animals adapted to such a variety of lifestyles and environments, the task of understanding and appreciating the physiology of animals would be overwhelming. Fortunately (for scientist and student alike), the concepts and principles that provide a basis for understanding animal function are relatively few, for evolution has been conservative as well as inventive.

A beginning course in physiology is a challenge for both teacher and student because of the interdisciplinary nature of the subject, which integrates chemistry, physics, and

biology. Most students are eager to come to grips with the subject and get on with the more exciting levels of modern scientific insight. For this reason, *Eckert Animal Physiology* has been organized to present the essential background material in a way that allows students to review it on their own and go on quickly to consider animal function and to understand its experimental elucidation.

*Eckert Animal Physiology* develops the major concepts in a simple and direct manner, stressing principles and mechanisms over the compilation of information and illustrating the functional strategies of animals that have evolved within the bounds of chemical and physical possibility. Common principles and patterns, rather than exceptions, are emphasized. Examples are selected from the broad spectrum of animal life, consciously illustrating similarities between organisms; for example, similar compounds are associated with reproduction in both humans and yeast. Thus, the more esoteric and peripheral details receives only passing attention, or none at all, so as not to distract from central ideas. We use the device of a narrative, describing experiments, to provide a feeling for methods of investigation while presenting information.

## ORGANIZATION OF THE BOOK


For the first time, the chapters are organized into three parts, which we feel will promote an understanding of animals as integrated systems at every level of organization. Each part is introduced by an opening statement that gives students an overview of the material to follow. Part I contains four chapters and is concerned with the central principles of physiology. Part II (Chapters 5–11) deals with physiological processes, while Part III (Chapters 12–16) discusses how these basic processes are integrated in animals living in a variety of environments. All 16 chapters have been extensively reworked and reorganized to stay abreast of new scientific developments.



## NEW TO THIS EDITION

- A new chapter on methodology (Chapter 2) in Part I, in which some of the latest molecular techniques are discussed and illustrated, along with traditional methods.
- This emphasis on molecular coverage continues throughout the book; Chapters 5, 6, and 7, for example, are updated with recent insights into the cellular and molecular underpinnings of membrane excitation, synaptic transmission, and sensory transduction.
- Part II features a new chapter (Chapter 8, Glands: Mechanisms and Costs of Secretion), which brings together information on an important, but frequently neglected, effector system.
- In Part II, Chapter 11 (Behavior: Initiation, Patterns, and Control) preserves and expands the descriptions of vertebrate and invertebrate nervous systems found in previous editions, presenting an up-to-date view of systems neurobiology, one of the fastest-growing areas of neurobiology. Several concepts from neuroethology, which bridges the gap between the pure study of behavior and the study of cellular function in the nervous system, are introduced, along with examples of important recent neuroethological studies.
- The role of the nervous system in maintaining homeostasis through the modulation of all systems has been incorporated into Part III, which further advances the integrated approach of the book.
- There is an increased emphasis throughout the book on environmental adaptations, and specific examples of environmental adaptation (such as water balance in elephant seals in Chapter 14) illustrate the general principles of comparative physiology.
- Some of the new topics introduced in the fourth edition include a section on the immune response in Chapter 12 (Circulation), and a section on biorhythms in Chapter 13 (Using Energy: Meeting Environmental Challenges).

legends. For the first time, full color drawings have been added, creating a high quality visual program to further motivate students.

- Spotlights provide in-depth information about the experiments and individuals associated with important advances in the subject matter, the derivation of some equations, or simply historical background on a topic under discussion.
- Thought questions within chapter text (look for the ) encourage problem-based learning and stimulate discussion on various aspects of the material presented.

The text narrative includes effective, integrated examples to support principles; while presenting information, it provides consistent thematic coverage and a feeling for methods of investigation. References to the literature within the body of the text and in figure legends are made unobtrusively, but with sufficient frequency that students can become aware of the role of scientists and their literature as a subject is developed. Further pedagogical aids include key terms that are explained and appear in boldface type at their first mention in the text, and that are formally defined in a useful, comprehensive glossary. End of chapter materials include a summary, which provides the student with a quick review of important points covered in the chapter, review questions, and an annotated list of suggested further readings. Students will find the following resources at the back of the book: appendixes that provide information on units, equations, and formulas; the glossary; and a bibliography that includes the full citations of all references cited in the chapters. Our goal has been to produce a balanced, up-to-date treatment of animal function that is characterized by its clarity of exposition. We hope that readers will find *Eckert Animal Physiology* valuable, and we welcome your constructive criticism and suggestions.

September 1996

DAVID RANDALL  
WARREN BURGGREN  
KATHLEEN FRENCH

## PEDAGOGY

- The ideas developed in the text are illuminated and augmented by liberal use of illustrations and figure

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DAVID RANDALL  
WARREN BURGREN  
KATHLEEN FRENCH



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# PART I

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## PRINCIPLES OF PHYSIOLOGY

Animal physiology is the study of how living animals function. Both the cheetah racing after a gazelle and the rattlesnake striking at a desert rat coordinate specialized anatomical features and physiological processes to capture their prey and, in turn, to evade predators and prolong life. The arctic fox on the cover of this book possesses a luxurious coat of fur, as well as finely tuned physiological mechanisms, to protect it from the bitter cold of its environment. Even animals living in an apparently ideal environment, with benign temperatures year round, ample food sources, and regular day/night cycles, face challenges, which include the pressures of sharing a habitat with members of their own, and with other, species. Meeting the demands of survival has resulted in numerous evolutionary variations on the basic theme of life, and the environments in which life expresses itself are equally varied. As a result, animal physiologists have a vast array of animals and environments available in which to investigate how animals work. (There is now some indication that life may have existed on Mars, so the environments open

to physiological study may not be limited to Earth.) Even so, the broad range of philosophical and technological approaches in the study of animal physiology rest on a relatively small number of fundamental concepts, which are presented in Part I of this book. These concepts are essential for understanding the physiological processes that underlie the behavior of predators like the cheetah and the rattlesnake and the evolution of physiological control mechanisms that allow animals—such as the desert rat and the arctic fox—to maintain internal body conditions that enable them to survive, even in very hostile environments.

Chapter 1 explores the central themes in animal physiology, including the close relationship between structure and function, the processes of adaptation and acclimation, and the concepts of homeostasis and its maintenance by feedback control systems. In science, all knowledge is based on experiments; consequently, in Chapter 2 we discuss the nature of experimentation and the various perspectives animal physiologists adopt in designing hypotheses and test-

ing them. We briefly describe many of the major experimental methods that are currently used by physiologists, including new and rapidly evolving molecular techniques.

From the beginning, physiology has been grounded in physics and chemistry, and Chapter 3 reviews basic physical and chemical principles that underlie the physiological mechanisms discussed in the rest of the book. This chapter focuses particularly on the processes of metabolism, the biochemical reactions that are the basis for all physiological processes. The membranes that surround cells and their internal organelles provide an important example of how physical and chemical mechanisms combine in living

cells to produce biological processes. In Chapter 4 we investigate the nature of cell membranes. We pay specific attention in this chapter to how the outer membrane of a cell helps to stabilize its internal environment. Active transport of materials across cell membranes is discussed in detail, because this process is crucial for numerous physiological processes as diverse as conduction of nerve impulses, regulation of body fluids, and uptake of nutrients, all discussed in later sections. How fundamental biochemical, molecular, and cellular processes are combined to produce the integrated regulation of physiological systems throughout an animal's body is discussed in Parts II and III of the book.