# Principles of Animal Physiology

THIRD EDITION

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# Brief Contents

# About the Authors

**Christopher D. Moyes, Ph.D.**
Queen's University

Chris Moyes received his Ph.D. in Zoology from the University of British Columbia in the area of comparative muscle physiology. After postdoctoral fellowships in molecular physiology at the U.S. National Institutes of Health and Simon Fraser University, he took a position at Queen's University, where he is a Full Professor in the Department of Biology, and Department Head (2013–2015). He teaches a spectrum of courses in animal physiology, comparative biochemistry, and cell biology. Using a wide range of comparative and traditional models, his research addresses questions in molecular physiology and metabolic biochemistry. One major theme of his research is the study of the evolutionary and developmental origins of variation in muscle structure and function. Another major area of his research is the response of animals to environmental stress. In all of his research he emphasizes the integration of physiological processes, from molecular to organismal levels.

Dr. Moyes is a recipient of the Ontario Premier's Research Excellence Award. He is a member of the American Physiological Society and the Canadian Society of Zoologists and has served on research grant panels for the Natural Science and Engineering Research Council of Canada and the U.S. National Science Foundation. He is also Editor-in-Chief of *Comparative Biochemistry and Physiology B Biochemistry*.

He has published more than 100 peer-reviewed papers, including contributions to four books.

More of his research is detailed on his homepage at http://post.queensu.ca/~cdm2/.

**Patricia M. Schulte, Ph.D.**
University of British Columbia

Trish Schulte received her Ph.D. in Biological Sciences from Stanford University in the area of evolutionary physiology. After graduating, she took a position as an assistant professor in the Department of Biology at the University of Waterloo, and then moved to the Department of Zoology at the University of British Columbia in Vancouver where she is currently a Full Professor.

Research in her laboratory focuses on the mechanisms that fish use to respond to environmental stressors such as high temperature, hypoxia, and altered salinity. She is particularly interested in understanding how genetic variation among individuals contributes to variation in their stress response across multiple levels of biological organization, and assessing the consequences of this variation for performance and fitness in variable environments. Dr. Schulte's research group also conducts applied research in fisheries, aquaculture, and aquatic toxicology. She has published over 100 peer-reviewed papers, including contributions to several books.

Dr. Schulte was the President of the Canadian Society of Zoologists (2007–2008), and is a member of the Society for Integrative and Comparative Biology, The Society for Experimental Biology, and the American Physiological Society. She was the co-editor in chief of the journal *Physiological and Biochemical Zoology* (2009–2014), and is a member of the editorial board of the journal *Comparative Biochemistry and Physiology*.

Dr. Schulte has taught physiology courses at multiple levels, including introductory physiology, comparative physiology, and human physiology. She is a recipient of a several teaching awards, including the UBC Science Undergraduate Society Award for Excellence in Teaching and the Faculty of Science Achievement Award for Teaching. She is currently the departmental director for Life Sciences for the Carl Wieman Science Education Initiative at UBC, which is dedicated to promoting the use of evidence-based approaches to science education for undergraduates.

You can learn more about her research and teaching activities on her homepage at http://www.zoology.ubc.ca/person/pschulte.

**Dedication**

*Thanks to our families, friends, colleagues, and students for their influence and support during the development of this textbook. We dedicate this textbook to the memory of Peter Hochachka, an inspiration to comparative physiologists and valued mentor to both of us.*

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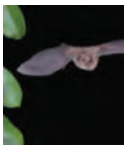

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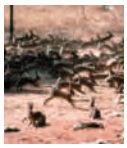



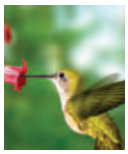

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# Preface

The 21st century is an incredibly exciting time to be a biologist. Animal biologists now have access to data from a range of complete animal genomes covering a broad spectrum of the diversity of animals. At the time of writing this preface, complete genomes already exist for several hundred species of invertebrates and over two hundred species of vertebrates; in the next few years, we expect that genome sequences will be available for thousands of species of animals. But the fundamental questions about how the genes in these genomes work together to allow animals to perform their diverse physiological functions and to go about their daily lives are still largely unanswered. Animal physiologists are at the forefront of integrating this new genome sequence information into a functional and evolutionary framework as part of their efforts to understand how animals work. Our goal in writing this textbook is to convey a sense of this excitement to students who are approaching the study of animal physiology for the first time.

One of the challenges that students face when they approach their first course in physiology is the great breadth and diversity of the subject matter. Physiology is among the most integrative of the life sciences, drawing on ideas from chemistry, physics, mathematics, molecular biology, and cell biology for its conceptual underpinnings. In addition, to fully appreciate the physiological diversity of animals, students must have a working knowledge of environmental biology, ecology, systematics, and evolutionary biology. We have written this book to give students a well-organized and engaging treatment of the fundamental principles of animal physiology. Throughout the book, we integrate concepts from all levels of biological organization to explore the nature of diversity in biological molecules, cells, physiological systems, and whole animals. We hope that this approach will spark the interest of all students, whatever their background preparation.

## KEY THEMES

Students are sometimes so focused on remembering the "facts" of physiology that they are unable to place these facts into a well-developed conceptual framework. To help students get past this difficult barrier, we organized this book around several key themes and fundamental principles that are highlighted in each chapter and strove to present this material in an accessible fashion that engages student learning.

**A Focus on Unifying Principles.** In Chapter 1, we introduce four unifying themes in animal physiology:

- Physiology integrates across levels of biological organization from molecules to populations.
- Physiological processes are based in the laws of chemistry and physics.
- Physiological diversity among animals is the result of evolutionary processes.
- Physiological processes are homeostatically regulated.

Every chapter revisits these key themes, providing a unifying thread that ties together our concept of animal physiology.

**Orientation Around Learning.** To promote comprehension, each chapter begins with ***Learning Objectives*** that connect directly with the headings in the chapter and with the Review Questions at the end of the chapter. To assist with the integration of material across chapters, many chapters feature a new ***Looking Back*** section that identifies the critical background material found in earlier chapters.

**An Emphasis on Animal Diversity and Evolution.** We are strongly committed to the importance of teaching about the physiological diversity of animals, because we feel that this diversity is a fundamental property of the natural world. We also believe that books focusing only on humans can cause students to form the erroneous impression that physiological processes in humans are typical of those in all animals, and thus we provide diverse examples in their evolutionary context. As a result, we include extensive discussion of physiological processes in both vertebrates and invertebrates throughout the book and attempt to interweave evolutionary thinking into these discussions. Our new Chapter 2 discusses the major events in the evolution of animals, with a focus on the evolution of physiologically significant traits and how they contributed to the evolutionary diversification of the major animal groups.

**Attention to the Integrative Nature of Animal Physiology.** Throughout the book, we emphasize the integrative nature of physiology in a number of ways. Each chapter begins with an opening essay that provides a short, engaging vignette that places the system under discussion into its environmental or evolutionary framework. Together, these features help to build student understanding of how physiological systems interrelate and depend on each other.

**Integration of Physiology with Cell and Molecular Biology.** We divided this book into three main sections. In Part One, we provide an overview of the basic principles of animal physiology, identifying the common themes in the discipline and emphasizing the role of evolution in animal diversity.

In Part Two, we discuss the cellular basis of animal physiology. The goal of Part Two is to provide students with a general context for understanding animal physiology and to show how, at a cellular level, animals are both similar to and different from other organisms. We hope that this treatment will help students begin to see how the somewhat abstract processes that they study in other courses have direct relevance to the understanding of animal physiology.

Providing a strong foundation in cellular and molecular physiology is critical for students because our understanding of animal physiology has changed dramatically in the last 10 years due to advances in fields such as genomics, transcriptomics, proteomics, and cell biology, and a solid understanding of these disciplines is central to the modern concept of physiology.

In Part Three, we discuss how cells and tissues interact to form the integrative physiological systems of animals. We consider each of the major physiological systems in turn, building on the twin themes of conservation and diversity to address the question: How do different animals use fundamentally similar building blocks to construct unique physiological systems to meet the challenges imposed by the environment? Throughout the third part of this book, we integrated the discussion of the cellular and molecular processes that underpin physiological processes, at a depth that will encourage students to understand the relevance of these disciplines to animal physiology.

**Integrated Treatment of Endocrine Regulation.** The treatment of endocrine systems is one unique element in the book's organization. Rather than relegating these systems to a single isolated chapter, we discuss endocrinology in Part Two in the context of the various means of cellular signaling and communication, and then integrate the presentation of its various physiological roles throughout the chapters in Part Two. We find that students better understand how hormones control systems once they have been introduced to all the diverse ways in which cells send and receive signals. By establishing the foundation of cellular control early in the text, we are able to discuss the impact of specific hormones and glands in the context of each physiological system, increasing the integrative nature of the discussion. This approach places the endocrine system in its appropriate evolutionary framework—as one of several means of intercellular communication that are available to multicellular organisms—and clearly demonstrates how communication and coordination are critical for the functioning of essentially every organ system.

## NEW FOR THE 3rd EDITION

For the 3rd Edition, we expanded the pedagogical features throughout the text to facilitate students' learning. New for the 3rd Edition, you will find the following in each chapter:

- A short and engaging chapter-opening essay that introduces an animal or scenario that epitomizes the importance of the physiological system discussed in the chapter.
- Learning Objectives that organize ideas into major themes for students.
- Looking Back sections that direct students to specific material earlier in the text.
- More succinct chapter summaries that focus on the major points.

From Chapter 4 onward, each chapter showcases these feature boxes:

- **Math in Physiology** takes a quantitative approach to physiological principles.
- **Challenges to Homeostasis** discusses how animals respond to physiological challenges.
- **Applications** addresses how physiology can be used or studied to solve real-world problems.

In addition, we revised the narrative and the figures extensively with the goal of helping students to master some of the most difficult concepts in physiology. The highlights of these changes in the 3rd Edition include:

### Chapter 1, Introduction to Physiological Principles

- A new opening feature on Porcelain crabs to emphasize environmental physiology and the applications of physiology to conservation biology.
- A new focus on exploring the unifying themes that tie together both the basic and applied aspects of the discipline of animal physiology.
- An expanded discussion of the relationship between form and function, the concepts of homology and analogy, and scaling as a unifying principle in physiology, including several new Figures

### Chapter 2, Physiological Evolution of Animals

- **New to the 3rd Edition!** This chapter provides a survey of animal diversity, focusing on the origins of physiological traits and the significance of phylogenies.
- This chapter introduces the critical events in animal evolution and the role of environment in the selective process.

### Chapter 3, Chemistry, Biochemisty, and Cell Physiology

- A more refined discussion of energetics, including an explanation of chemical energy transfers, bonds, solubility,

and thermal effects, clearing up ambiguity about these topics.

- A reorganized and expanded discussion of metabolic rate determinants, collecting information from disparate 2nd Edition chapters into a single section.
- A more complete discussion of the membrane potential/Nernst equation/Goldman equation, with this important information in the body of the chapter, rather than in a boxed feature.
- A discussion of tissue types and the roles and regulation of epithelial tissues, including transport and transporters.

### Chapter 4, Cell Signaling and Endocrine Regulation

- A substantial reorganization of the second half of the chapter to provide a more focused discussion of the fundamental shared principles of endocrine regulation, using selected examples from vertebrates to illustrate these principles.
- An expanded section discussing endocrine systems and how they evolved, including a new Figure showing the major endocrine glands of mammals.
- A new section on the evolution of the vertebrate pituitary gland.

### Chapter 5, Neuron Structure and Function

- A more comprehensive explanation of the Nernst and Goldman equations, including a new Figure and boxed feature.
- A revised discussion of saltatory conduction, including a new Figure.
- An expanded discussion of molecular events at the synapse.
- An updated discussion of the evolution of neurons that reflects the recent cloning of bacterial voltage-gated $Na^+$ channels.

### Chapter 6, Cellular Movement and Muscles

- New Figures to illustrate topics including (1) skeletal muscle structure, explaining how all of the muscles fit together; (2) the impact of arrangement (series versus parallel) on muscle structure; and (3) muscle fiber mosaics.
- An expanded feature on force and work, which consolidates the force/work/power material in a single location.
- New and revised Figures that help distinguish between muscle fiber types, expanding the discussion of smooth muscle.
- A reorganization of the discussion of EC coupling that more clearly distinguishes between cardiac and skeletal muscle.
- A new feature on muscle remodeling in exercise, combining the themes of structural changes and cellular regulation.

### Chapter 7, Sensory Systems

- New sections on topics including nociception, hearing in whales and dolphins, and the photoreceptors involved in circadian rhythms.
- A new boxed feature on using pheromones to alter behavior.
- An expanded discussion of electroreception, including a new Figure.
- An updated discussion of magnetoreception.

### Chapter 8, Functional Organization of Nervous Systems

- An expanded treatment of the organization and evolution of nervous systems.
- Increased coverage of the general anatomy of the central nervous system, with more information about the spinal cord.
- New boxed features examining (1) the scaling of brain size, neuron number, and behavioral complexity; (2) how ocean acidification affects fish behavior by disturbing brain homeostasis; and (3) functional magnetic resonance imaging and brain plasticity.
- New sections on the corpus callosum, mirror neurons, and language acquisition in birds.
- An expanded discussion of the enteric nervous system.
- A new section focusing on the role of the hypothalamus in regulating bodily functions such as circadian rhythms and sleep-wake cycles.

### Chapter 9, Circulatory Systems

- New discussions of orthostatic hypotension and space flight, physiology of dinosaur circulatory systems, the development of the human heart, and the coevolution of circulatory and respiratory systems.
- Revised and clarified discussion of the evolution of the lymphatic system, amphibian circulatory systems, ion channels and pacemaker currents, and the cardiovascular physiology of giraffes.
- A new boxed feature dealing with the use of EKG technology to diagnose heart conditions.
- New Figures to illustrate the evolution of vertebrate circulatory systems and cardiac anatomy, the development of the mammalian heart, and the effect of elevated blood pressure on risk of cardiovascular disease.

### Chapter 10, Immune Systems

- **New** to the 3rd Edition! This chapter discusses comparative immunology, with a focus on evolutionary diversity of the innate and adaptive immune systems.
- It includes discussion of the molecular mechanisms that organisms use to detect foreign molecules and the roles of the various immune cells, particularly B cells and T cells.
- The addition of a chapter on immunology provides context for the interaction between immunity and other physiological processes, particularly the circulatory, thermal, and digestive systems.

### Chapter 11, Respiratory Systems

- A new discussion of the potential for unidirectional ventilation in crocodile lungs.
- A revised discussion of Root effect hemoglobins, emphasizing recent research suggesting a role for these hemoglobins in delivery of oxygen to systemic tissues in fish.
- A new section on the evolution of myoglobin in diving mammals.
- New boxed features dealing with (1) the treatment of respiratory distress syndrome in premature infants, (2) pulmonary function tests, and (3) adaptations to high altitude in bar-headed geese.

### Chapter 12, Locomotion

- An expanded discussion of the importance of animal athletes as models for understanding physiological evolution.
- New features on type II diabetes and migration.
- An expanded discussion of the regulation of homeostasis in muscle.
- A new feature on the cost of transport and a revised discussion of work loops that deconstruct positive and negative work to help students understand the biophysical basis of locomotion.

### Chapter 13, Ion and Water Balance

- An expanded discussion of osmotic strategies used by animals, highlighting the important transitions that arose in the context of animal evolution.
- A reorganized section on kidney function and regulation, focusing on the four main homeostatic functions: ion balance, osmotic balance, pH balance, and blood pressure regulation.
- A new feature that delves into the quantitative analysis of renal clearance, including an explicit discussion of the concept of a "virtual volume."
- A new feature, "Conservation Physiology of Salmon," highlighting recent work showing how ionoregulatory physiology influences the survival of animals in nature.

### Chapter 14, Digestion and Energy Metabolism

- A change in the scope of the chapter to also include energy metabolism and its regulation.
- A reorganization of the section on regulation of digestion to discuss processes along a linear timeline.
- A new *Applications* feature focusing on the gut microbiome, with appropriate cross-referencing to the new Immune Systems chapter.
- A new feature focusing on obesity as a homeostatic challenge.
- A more consistent treatment of the many hormones that regulate digestion and metabolic rate.

### Chapter 15, Thermal Physiology

- An expanded discussion of thermal biology to better consider physiological ecology, including a new Applications feature on thermal tolerance and conservation biology of Atlantic cod, an expanded discussion of the impact of temperature on metabolism, and new material on thermal effects on aerobic scope and the OCLTT hypothesis.
- Revised discussion of the evolution of uncoupling proteins, including introduction of a **Challenges to Homeostasis** feature on the evolution and development of thermogenin and brown adipose tissue.
- Revised treatment of the ectotherm/endotherm, poikilotherm/homeotherm distinctions, with a revised Figure.
- A new summary Figure on the diversity in futile cycles.
- A modified discussion of Arrhenius plots to include more student-driven calculations as part of a Math in Physiology feature.

### Chapter 16, Reproductive Physiology

- A new feature on pesticides targeting insect-specific pathways addresses how pesticides can be used to target insect development and reproduction.
- A Math in Physiology feature combines the concepts of allometry with the constraints on milk production.

We hope that you enjoy using this textbook. Please feel free to contact us at the email addresses below if you have any comments or suggestions on how we could make this book an even better tool to help you learn or teach animal physiology.

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# Supplements

## COMPANION WEBSITE

This student resource features answers to the Review Questions and Concept Checks that appear in the text, chapter-specific quizzes, links to physiology labs and other relevant websites, an interactive glossary, and more. Please visit www.pearsoncanada.ca/animalphysiology.

## COMPUTERIZED TEST BANK

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# Acknowledgments

Preparing the 3rd Edition of our textbook required a team of dedicated people to bring it to fruition. The Pearson Canada team conducted the extensive research needed to identify the strengths and weaknesses of our 2nd Edition. They also helped us revise the chapters, developing the manuscript into the finished product. A team of three editors managed the three-year revision process. Maurice Esses, Lise Dupont, and Lisa Rahn managed to keep us on track, successfully maintaining the delicate balance between motivation and persistence. It is impossible to imagine how the 3rd Edition could have been completed without their support.

The 3rd Edition continues to benefit from the work done by the developmental team in place for the 1st and 2nd Editions, notably Catherine Murphy, the developmental editor, Laura Southworth, our art development editor, and Susan Malloy and Marie Beaugureau, our project editors at Benjamin Cummings.

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## REVIEWERS

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