Principles of Animal Physiology

Christopher D. Moyes   Patricia M. Schulte

Third Edition

Principles of Animal Physiology

THIRD EDITION

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

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

PEARSON

Toronto

VP, Cross Media & Publishing Services: Gary Bennett
Editorial Director: Claudine O'Donnell
Executive Editor: Lisa Rahn
Marketing Manager: Kimberly Teska
Program Manager: Darryl Kamo
Project Manager: Richard di Santo
Senior Developmental Editor: Lise Dupont
Production Services: Roxanne Klaas, S4Carlisle Publishing Services
Permissions Project Manager: Erica Mojzes
Photo Permissions Research: Carolyn Arcabascio, PreMediaGlobal
Text Permissions Research: Haydee Hidalgo, Electronic Publishing Services, Inc.
Art Director: Zena Denchik
Cover and Interior Designer: Anthony Leung
Cover image: GettyImages

Credits and acknowledgments for material borrowed from other sources and reproduced, with permission, in this textbook appear on the appropriate page within the text.

Library and Archives Canada Cataloguing in Publication

Moyes, Christopher D., 1960-, author
Principles of animal physiology / Christopher D. Moyes, Ph.D. (Queen's University), Patricia M. Schulte, Ph.D. (University of British Columbia). — Third edition.
Includes bibliographical references and index.
ISBN 978-0-321-83817-9 (pbk.)
1. Physiology—Textbooks. I. Schulte, Patricia M., 1965-, author II. Title.
QP31.2.M69 2014 571.1 C2014-906141-2

10 9 8 7 6 5 4 3 2 1 [WC]

PEARSON

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*.

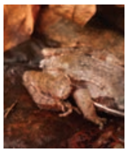
Dr. Schulte has taught physiology courses at multiple levels, including introductory physiology, comparative physiology, and human physiology. She is a recipient of a several teaching awards, including the UBC Science Undergraduate Society Award for Excellence in Teaching and the Faculty of Science Achievement 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.

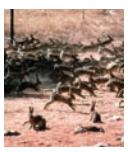
Dedication

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.

Contents



CHAPTER 3
Chemistry, Biochemistry, and Cell Physiology 38



CHAPTER 13 Ion and Water Balance 542

CHAPTER 14
Digestion and Energy Metabolism 592

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.

Chris Moyes
Queen's University
chris.moyes@queensu.ca

Trish Schulte
University of British Columbia
pschulte@zoology.ubc.ca

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

Pearson's computerized test banks allow instructors to filter and select questions to create quizzes, tests, or homework. Instructors can revise questions or add their own, and may be able to choose print or online options. These questions are also available in Microsoft Word format.

COURSESMART FOR STUDENTS

CourseSmart goes beyond traditional expectations—providing instant, online access to the required textbooks and course materials at an average savings of 60%. With instant access from any computer and the ability to search your text, you will find the content you need quickly, no matter where you are. And with online tools like highlighting and note-taking, you can save time and study efficiently. See all the benefits at www.coursesmart.com/students.

COURSESMART FOR INSTRUCTORS

CourseSmart goes beyond traditional expectations—providing instant, online access to the textbooks and course materials you need at a lower cost for students. And even as students save money, you can save time and hassle with a digital eTextbook that allows you to search for the most relevant content at the very moment you need it. Whether it's evaluating textbooks or creating lecture notes to help students with difficult concepts, CourseSmart can make life a little easier. See how when you visit www.coursesmart.com/instructors.

TECHNOLOGY SPECIALISTS

Pearson's Technology Specialists work with faculty and campus course designers to ensure that Pearson technology products, assessment tools, and online course materials are tailored to meet your specific needs. This highly qualified team is dedicated to helping schools take full advantage of a wide range of educational resources, by assisting in the integration of a variety of instructional materials and media formats. Your local Pearson Canada sales representative can provide you with more details on this service program.

PEARSON CUSTOM LIBRARY

For enrollments of at least 25 students, you can create your own textbook by choosing the chapters that best suit your own course needs. To begin building your custom text, visit www.pearsoncustomlibrary.com. You may also work with a dedicated Pearson Custom editor to create your ideal text—publishing your own original content or mixing and matching Pearson content. Contact your local Pearson Representative to get started.

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.

We would particularly like to thank various friends and colleagues who have provided input and suggestions on specific chapters. CDM would like to thank his colleagues at Queen's for their contributions to the new chapters on evolution of physiological systems (Steve Lougheed, Vicki Freisen) and comparative immunology (Bill Bendena, Virginia Walker), and to thank Doug Symes (University of Calgary) for his advice on the Cost of Transport feature. PMS would like to thank her colleagues in the comparative physiology group at UBC for their advice and support throughout this project, with particular thanks to Tony Farrell for suggestions regarding cardiac physiology, Bill Milsom for his advice on respiratory physiology, and Doug Altshuler for helpful discussions regarding ways to approach teaching neurophysiology and the nervous system.

REVIEWERS

We would also like to thank the instructors who reviewed the 3rd Edition manuscript:

Eli Asem, *Purdue University*
Adam Oliver Brown, *University of Ottawa*
Julian Christians, *Simon Fraser University*
Reyniel Cruz-Aguado, *Douglas College*
Rosa da Silva, *McMaster University*
Jeff W. Dawson, *Carleton University*
Heidi Englehardt, *University of Waterloo*
David H. Evans, *University of Florida*
Corey Flynn, *University of Calgary*
Wei Ge, *Chinese University of Hong Kong*
Kathleen Gilmour, *University of Ottawa*
Helga Guderley, *Université Laval*
Raymond P. Henry, *Auburn University*
Kelly S. Johnson, *Ohio University*
Kevin S. Kinney, *Depauw University*
Heather Koopman, *University of North Carolina at Wilmington*
Roswitha Marx, *University of Victoria*
Joanne Nash, *University of Toronto at Scarborough*
Linda Ogren, *University of California, Santa Cruz*
Robert J. Omeljaniuk, *Lakehead University*
Sushama Pavi-Denver, *University of Michigan*
Scott D. Reid, *University of British Columbia*
Gregory Schmaltz, *University of the Fraser Valley*
Jason Schreer, *State University of New York at Potsdam*
James Staples, *University of Western Ontario*
Jonathon Stillman, *San Francisco State University*
Marva Sweeney-Nixon, *University of Prince Edward Island*
Steven Swoap, *Williams College*
Keith Tierney, *University of Alberta*
Helene Volkoff, *Memorial University*
Tracy L. E. Wagner, *Washburn University*

Principles of

Animal Physiology

THIRD EDITION

CHAPTER

1 Introduction to Physiological Principles

FIGURE 1.1 **Porcelain crab (Genus *Petrolisthes*)**

Photo source: Frogkick/Fotolia.

Learning Objectives

After reading this chapter, you should be able to:

1. Describe the levels of biological organization studied by physiologists.
2. Use examples to show how the laws of chemistry and physics are relevant to understanding physiological systems.
3. Outline how evolution results in diversity of both form and function and strong links between them in animals.
4. Discuss the processes involved in physiological regulation at multiple time scales.

If you have ever been to the seashore, you will have noticed the intertidal zone—the area that is covered and uncovered by the tides each day. What you may not have realized is that the intertidal zone is one of the most challenging habitats on Earth. The cycle of tides can cause huge changes in the characteristics of the environment as the tide moves in and out. On hot days when the tide moves out, the temperature of an isolated tidepool in the high intertidal can more than double, while on cold winter days at northern latitudes the temperature can drop almost to freezing. During the day, oxygen levels may rise to several times normal due to the oxygen produced by photosynthesizing algae. At night, oxygen consumption due to respiration by the plants and animals in the tidepool can cause oxygen to drop to almost undetectable levels. These daily cycles of photosynthesis and respiration can also cause wide swings in the pH of the water, which can range from slightly acidic to very alkaline. Similarly, the salinity of a tidepool can increase on hot days as water evaporates, or decrease to nearly the salinity of freshwater on a very rainy day. For intertidal animals that live outside of tidepools, desiccation can be an important challenge, especially on sunny days in exposed areas of the habitat. All of these environmental changes are physically challenging for animals, and animals that live in the intertidal zone have physiological specializations that help them cope with their harsh environment.

Despite the challenging environmental conditions in the high intertidal zone, this zone is teeming with life. For example, Porcelain crabs—similar to the one shown in Figure 1.1—are common inhabitants of both the high intertidal and nearby subtidal zones in the rocky intertidal areas of many of the world's oceans. Animal physiologists seek to understand the mechanisms that allow species such as Porcelain crabs to survive and thrive in these highly variable conditions. The large variations in abiotic environmental parameters in high intertidal habitats are very different from the relatively constant conditions in the nearby subtidal habitats. Because subtidal habitats are always beneath the surface of the water, temperature, oxygen levels, salinity, and pH remain fairly constant both within a day and across seasons. Despite the radical differences in environmental conditions between subtidal and intertidal habitats, these habitats may be only a few meters apart in space. This feature makes the intertidal zone an intriguing place to study the physiological adaptations of the animals that live there.

Porcelain crabs are particularly useful animals for studying environmental adaptation because there are many related species that live in habitats ranging from the warm and constant conditions of the subtidal zone in the tropics to the extremely variable conditions of the high intertidal in the temperate zone. In fact, the largest genus of Porcelain crabs (genus *Petrolisthes*) contains over 100 species. By comparing the physiology of species from different habitats, it may be possible to understand the key processes that allow species to thrive in the challenging intertidal environment.

In *Petrolisthes*, there is a strong correlation between the maximum temperature of the habitat in which a species is found and the highest temperature at which the heart can beat. Species of Porcelain crabs that are found in the high intertidal in the hot tropics are able to maintain cardiac function at substantially higher temperatures than are species that are found in much cooler and more constant temperate subtidal habitats. These data suggest that the physiology of the cardiovascular system may play a role in setting the geographical distribution of Porcelain crabs.

In addition to helping to understand the present-day distribution of species such as Porcelain crabs, research in animal physiology can also help to make predictions about the likely responses of animals to environmental change. You might predict that the less hardy subtidal crabs found in the cool temperate zones would be the most likely to be vulnerable to the extreme heat waves associated with global warming, but instead the crabs that live in the hottest environments may be the species at the most risk. These high intertidal crabs are already living right at the edge of their thermal tolerance range, and they have limited ability to adjust their thermal tolerance between seasons compared with their temperate zone relatives. For these high intertidal tropical species even a small increase in extreme temperatures that they experience during a heat wave is likely to be fatal. In fact, there is already evidence suggesting that some species of Porcelain crabs have disappeared from the southern edge of their species range over the last hundred years.

The example of Porcelain crabs illustrates the important role that animal physiologists can play in addressing both fundamental biological questions as well as applied questions with practical implications. In this chapter we explore some of the unifying themes that tie together both the basic and applied aspects of the discipline of animal physiology. We return to these themes throughout this book as we explore the fascinating science of how animals work. ■

OVERVIEW

In the words of the renowned physiologist Knut Schmidt-Nielsen, animal physiology is "*the study of how animals work*." Animal physiologists study the structure and function of the various parts of an animal, and how these parts work together to allow animals to perform their normal behaviors and to respond to their environments. Almost a million different species of animals have been described by scientists, and it is estimated that as many as 7 million may currently live on Earth. Each of these species has acquired countless unique properties through **evolution**. Animal physiologists are interested in both the *causes* and the *consequences* of this great diversity.

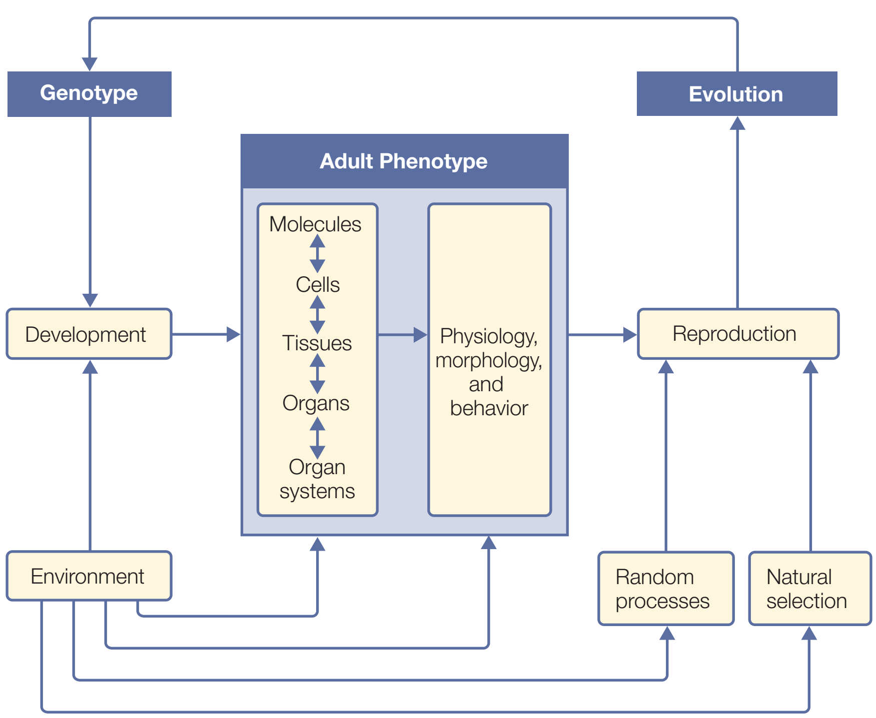
Physiology is a central discipline in biology linking the underlying molecular and cellular mechanisms to characteristics of whole organisms such as performance and fitness (Figure 1.2). The physiological properties of an animal are aspects of the animal's **phenotype**, which includes all of the observable traits of an organism at all levels of biological organization, from the biochemistry of the cell to the anatomy, physiology, and behavior of the animal. Physiological traits, like other characteristics of animals, are determined in large part by the **genes** of the genome—the **genotype**—but are also influenced by the way the genes are regulated, particularly in response to external conditions. Thus, both the genotype of an organism and its environment interact through development to produce the phenotype of the adult organism.

Physiologists must be able to understand how processes occurring at the molecular, cellular, tissue, organ, and organ system levels of organization interact to influence the physiological phenotype. Each physiological process is a product of the activities of complex tissues, organs, and systems that can arise through complex patterns of genetic regulation of countless cells. The phenotype is itself the product of processes at many levels of biological organization, including the biochemical, cellular, tissue, organ, and organ system levels. Together these processes interact to produce complex behaviors and physiological responses.

An individual genotype can have the capacity to produce more than one phenotype. Although the same genes

FIGURE 1.2 Physiology is a central discipline in biology

Morphology, physiology, and behavior are key components of the phenotype of an adult organism. These phenotypes are the result of interactions between the genotype and the environment acting on processes at all levels of biological organization. Variation in morphology, physiology, and behavior can influence performance and reproductive success. Thus, physiology has implications for evolutionary change in the genotype of a population over time.



are found in each cell, they are regulated in combinations to allow animals to develop distinct tissues.

In addition to orchestrating the normal developmental program, the genotype controls the way animals can alter their phenotype in response to physiological and environmental conditions. For example, if identical twins were raised in different places, it is possible that one twin might grow taller than the other due to differences in diet. Every individual genotype has a capacity to differ in complex, often unpredictable ways because of the way the genes respond to external conditions. Throughout this book you will encounter examples of the many ways in which organisms alter their physiological systems to respond to environmental change.

Ultimately, the phenotype (**morphology,** physiology, and behavior) of an animal influences its reproductive success. Differential survival of organisms with distinct phenotypes may result in evolutionary change in the genotype of a population over many generations. As a result, animal physiologists also consider how evolution shapes physiological phenotypes.

Evolutionary change is the ultimate cause of the enormous diversity of animal species. Despite this diversity, there are important commonalities in the physiological functioning of all animals. In this chapter we examine some of the unifying themes that are common to all of physiology. Throughout this book, we will return to these themes as we examine how animals work.

UNIFYING THEMES IN PHYSIOLOGY

Despite the great diversity of organisms on Earth, there are many commonalities within physiology—unifying themes that apply to all physiological processes. It is possible to outline the common themes in physiology in a number of ways. We have chosen to highlight four fundamental themes that we focus on throughout this book (Table 1.1).

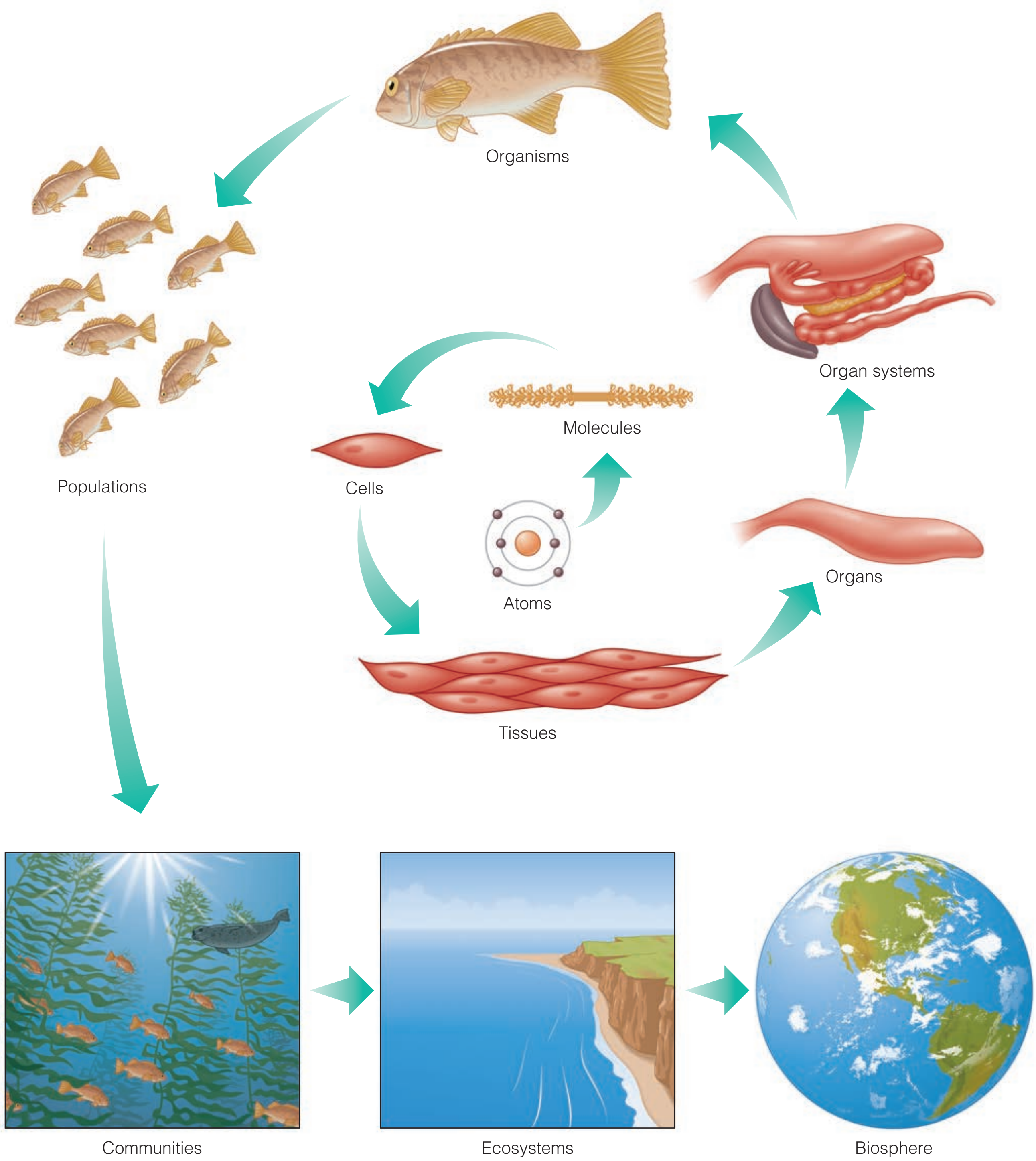
Integration in Physiology

Biologists often organize the living world by dividing it into what are termed *levels of biological organization* (Figure 1.3). Processes at each level of organization interact to produce the processes at the next level of organization. For example, atoms interact to form molecules, and molecules can be assembled into macromolecules. Macromolecules are organized into biochemical pathways and networks, and these biochemical interactions are grouped together into cells, which are the lowest level of biological organization capable of independent life. In multicellular organisms such as animals, cells are assembled into tissues, organs, and organ systems, which work together to allow the whole organism to perform its functions. Organisms interact in populations, and groups of interbreeding populations form species. Species interact to form communities, ecosystems, and ultimately the entire biosphere.

Table 1.1 Unifying themes in animal physiology

Unifying Theme	Related Ideas
Physiology is integrative.	Animal physiologists study phenomena at multiple levels of organization, from molecules to ecosystems. Animal physiologists address both basic and applied questions.
Physiological processes obey the laws of physics and chemistry.	The mechanical properties of materials influence physiological processes. Electrical laws are needed to understand the functions of membranes in all cells, including excitable cells such as neurons and muscle. Chemical laws, which govern interactions between biological molecules, help to explain the effects of temperature on physiological processes. Physical laws can be used to explain why body size affects many physiological processes.
Physiological processes are shaped by evolution.	Natural selection can cause a relationship between form and function. Differences among taxa can be adaptations as a result of evolution by natural selection, or can result from random processes. Similarity among traits can be due to homology (shared ancestry) or homoplasy (independent evolution).
Physiological processes are usually regulated.	Negative feedback loops help maintain homeostasis. Positive feedback loops generate an explosive response. Acclimation and acclimatization allow longer term, but usually reversible, adjustments to environmental change. Irreversible phenotypic adjustments can also occur during development and some can be passed across generations.

FIGURE 1.3 Levels of biological organization



Animal physiologists study phenomena at multiple levels of organization

Although animal physiology is characterized by its focus on how individual organisms function, physiologists usually consider multiple levels of organization as they strive to understand how animals work. Often a physiologist interested in a process at one level of organization also studies its function at a lower level. For example, someone studying how a salmon can live in salt water during part of its life and freshwater during another part might study the patterns of changes in ion levels in the blood and also study the cellular mechanisms in the gills that control those processes. This approach, known as **reductionism**, assumes that we can learn about a system by studying the function of its parts.

Reductionist approaches can be extremely illuminating, and have been the basis of many important biological discoveries, but ultimately many processes have characteristics that are not apparent simply by examining the component parts. This feature of complex systems is called **emergence**, which is just another way of saying that the whole is often more than the sum of its parts. The **emergent properties** of a system are properties that can be observed at one level of biological organization and that are due to the interactions of the component parts of the system. These emergent properties can be difficult to predict by studying each part in isolation. Physiologists are usually interested in emergent properties, and thus physiologists study how molecules, cells, and tissues interact to produce the complex system that is an organism.

Animal physiologists also think about how physiological processes acting in an individual organism affect the function of the organism within populations and communities. Thus, animal physiologists also are concerned about the ecological consequences of physiological processes.

Animal physiologists address basic and applied questions

Animal physiologists ask a wide range of questions that include aspects of both basic and applied biology. Basic research in animal physiology provides profound insights into how animals work and the evolutionary causes and consequences of variation in physiological processes. Animal physiologists ask questions such as: How can animals live in extreme environments? How do processes at the cellular and molecular level influence the performance of animals in the environment? Physiology also has enormous practical importance. To emphasize the practical importance of the study of animal physiology, each chapter of this book after the first three introductory chapters includes a box (Applications) that highlights an application of physiology to a real-world problem.

For example, there are important applications of physiology in conservation biology and ecology. As we saw with the Porcelain crabs that are the subject of the opening essay of this chapter, understanding the physiological functions of animals can help us predict their responses to environmental changes such as pollution, climate warming, and ocean acidification.

Another area in which animal physiology plays an important practical role is in understanding human health and disease. Medical doctors need a very strong understanding of physiology to understand and treat diseases and conditions such as heart disease, obesity, and diabetes that are very common in modern societies. Similarly, veterinary medicine relies on physiological knowledge for the treatment of diseases in animals. Agricultural production of animals for food also requires substantial knowledge of animal physiology to help develop optimal rearing practices to maintain health and promote the growth of farm animals.

Much of our medical knowledge is gained from research on animals, and thus understanding animal physiology is crucial for those involved in medical research. Such research is often performed on what are termed "**model organisms**," or species that are chosen because they have features that make them particularly suitable for specific experiments. This approach of using an animal model with features that are favorable for scientific study is known as the **August Krogh principle**: *For every biological problem there is an organism on which it can be most conveniently studied.*

Model organisms are studied by a wide community of researchers because (1) they have features that are conducive to experimentation and (2) understanding a process in the model provides insight into how the process works in other species of interest. Perhaps the most famous example of such a model system in physiology is the squid. Unlike mammals, squid have some specialized neurons that are large enough to be easily seen and readily manipulated. The use of squid as a model system was critical in the development of our understanding of how neurons work in all animals.

CONCEPT CHECK

1. How would you define physiology?
2. What is a model organism in the context of physiological research?

Physics and Chemistry: The Basis of Physiology

The integrative nature of physiology is particularly evident when we consider the role of chemistry and physics in physiology. Animals are constructed from natural materials and thus obey the same physical and chemical laws that apply to everything that we see around us. Physiologists often borrow concepts and techniques from the physical and chemical sciences, including engineering, to help them understand how animals work. As a result of this focus on chemistry and physics, physiology is a quantitative science. To emphasize the quantitative nature of physiology, each chapter of this book after the first three introductory chapters includes a box (Math in Physiology) that highlights an application of quantitative reasoning in physiology. You will also find a series of quantitative questions at the end of each chapter to help you practice these skills.

The laws of diffusion help to explain the evolution of animal form and function

The process of diffusion affects almost every physiological process, so understanding the physical laws that govern diffusion provides insights into the form, function, and physiology of animals. The eminent medical physiologist and physicist Adolf Fick developed what are now known as Fick's Laws of diffusion, which you will encounter at multiple points throughout this book. Fick's first law demonstrates that substances diffuse from areas of high concentration to areas of low concentration. This law is a special case of a much more general principle in physics and physiology: that substances move from areas of high potential energy to areas of low potential energy. This movement is a consequence of the second law of thermodynamics, which states that isolated systems spontaneously move toward a state of maximum **entropy**. This means that over time, differences in concentration, charge, temperature, or pressure will tend to equalize within a system, unless energy is added to maintain this difference.

A concentration gradient can be thought of as a source of potential energy that can be used to drive diffusion. Similarly, a voltage gradient, which represents a source of electrical potential energy, can drive the movement of charged particles. The fact that both concentration and voltage gradients can drive movements of substances is important in physiology because many important physiological processes, such as signaling in neurons and muscle cells and the active transport of materials into cells, involve the movement of charged molecules such as sodium across membranes. For these charged particles both the concentration gradient and the electrical gradient are important for determining the extent and rate of diffusion.

The same principles that apply to the diffusion of substances apply to the conduction of **heat**. Heat flows from areas of high temperature to areas of low temperature. As you will see in Chapter 15, the form and function of many animals is shaped by the need to regulate heat loss or gain. Pressure gradients also act as sources of potential energy that can move substances. Substances will move from areas of high pressure to areas of low pressure. As you will see in Chapters 9 and 11, this relationship is fundamental to understanding the functioning of the circulatory and respiratory systems in animals.

Fick's second law considers the amount of diffusion that occurs across a surface such as a cell membrane or an epithelial tissue. This law summarizes the idea that the amount of a substance that diffuses across a surface is proportional to the area of that surface and inversely proportional to the distance across which the substance must diffuse. Fick's second law is critical for understanding the form and function of epithelia such as the lungs and the gut that are involved in the exchange of substances by diffusion. These epithelia must have as large a surface area as possible and be as thin as possible to maximize the exchange of materials.

In addition, we can demonstrate from considering Brownian motion, or the random movement of particles in a solution, that the time needed for a particle to diffuse across a given distance is proportional to the square of the distance. The practical consequence of this relationship is that diffusion is rapid across short distances, but extremely slow across long distances. For example, a molecule such as sodium can diffuse across the width of a typical cell membrane (~10 nanometers) in less than 25 nanoseconds, but would take almost 30 days to diffuse across 10 centimeters and more than 15 years to diffuse across one meter (the approximate distance from the heart to the feet in an adult human) under typical physiological conditions. The limitations of diffusion across long distances help to explain why gas exchange surfaces such as lungs and gills are extremely thin, and why animals that are larger than a few millimeters in diameter must have **circulatory systems** to move substances around their bodies.

Mechanical theory helps us understand how organisms work

Each material has physical properties that are useful in some contexts but not others. It would be a mistake for an engineer to design a skyscraper from Styrofoam, or a kite of concrete. Likewise, biological materials, or biomaterials—**proteins, carbohydrates**, and **lipids**—also have characteristic physical properties that make them useful for some processes but not others. The physicochemical characteristics of these biomaterials are determined by their molecular properties. For example, the **aorta**, which is one of the largest blood vessels in a vertebrate, contains high levels of the protein collagen. This strong structural protein helps the aorta withstand the high **pressure** generated by the heart. Smaller blood vessels such as the capillaries that are not exposed to such high mechanical forces have much less collagen in their walls, which allows them to be thin to maximize the exchange of materials by diffusion.

Differences in the molecular properties of proteins may be a result of differences in the sequences of the proteins, but they can also be the result of the modification of an existing protein. The protein **keratin** provides an example of a network of proteins that can be made more rigid by the addition of bonds that cross-link multiple keratin proteins together. The keratin present in fingernails is heavily cross-linked, which helps to make it stronger and less likely to bend. The keratin in hair has fewer cross-links, which allows it to be more flexible.

In addition to mechanical properties, other engineering concepts such as flow, pressure, resistance, stress, and strain play important roles in physiology. For example, understanding how the heart pumps blood through the blood vessels has many parallels with understanding how mechanical plumbing systems work. Both physiologists and engineers must take into account factors such as pressure gradients, the power of the pump, and the resistance in the plumbing. Thus, the principles of physics that apply to engineering also apply to physiological systems.

Electrical potentials are a fundamental physiological currency

Just as we use electricity to power many of the machines we use in our daily lives, animals use electricity to power cellular activities. Cells establish a charge difference across biological membranes by moving ions and molecules to create ion and electrical gradients. All cells and many organelles within cells rely on this potential difference, or **membrane potential**, to drive processes that are needed for survival such as the movement of essential molecules across membranes. Animals also use changes in electrical potentials to send signals within and between cells, helping to coordinate the complex processes of the body. Muscle cells and neurons, two cell types that are found only in animals, use changes in membrane potential to send signals. Thus, electrical theory has played an important role in helping physiologists to understand the way that neurons and muscles work.

Temperature affects physiological processes

Because physiological processes have their basis in physical and chemical laws, they are profoundly affected by temperature. The rate of most chemical reactions increases as temperature increases. Increasing the temperature increases the energy of molecules and causes an increase in the number of collisions between molecules in a closed system. Most reactions involve the breakage or formation of chemical bonds, which can occur only if molecules are close to each other. So the more molecular collisions occur, the faster the rate of a chemical reaction. However, at high temperatures many of the intermolecular interactions that stabilize proteins begin to break down and protein function declines. Because most biochemical reactions involve proteins as **catalysts**, when these catalysts break down, the rate of the reaction falls. The effects of temperature on molecular events combine to influence the way animals interact with environmental temperature. Thus, temperature has a profound effect on processes at all levels of biological organization.

Biochemical and physiological patterns are influenced by body size

From tiny zooplankton weighing less than a milligram to blue whales weighing over 100,000 kilograms, animals vary greatly in body size, and these differences have profound effects on both the shape of an organism and on the physiological processes that allow them to perform their functions. The relationships between anatomical or physiological traits and body size are termed **scaling** relationships. When morphology or physiology change in direct proportion to body mass, the scaling relationship is said to be **isometric** (from the Greek *iso* = same, and *metric* = measure). However, it has long been known that many structures and processes do not increase proportionately with body mass. In fact, this phenomenon was first discussed by Galileo Galilei in 1638, when he described how the **bones** of larger animals are proportionately thicker than the bones of smaller animals. Figure 1.4 shows a comparison of the skeleton of a cat and an elephant, drawn at the same body size so that you can easily compare the relative thickness of the bones. Note how the bones of an elephant are much thicker than the bones of a cat. When body shape or physiology changes disproportionately as body size increases, the relationship is said to be **allometric** (from the Greek *allo* = different, and *metric* = measure).

FIGURE 1.4 A cat skeleton and an elephant skeleton, drawn at the same size
Note the proportionally thicker limb bones of the elephant.

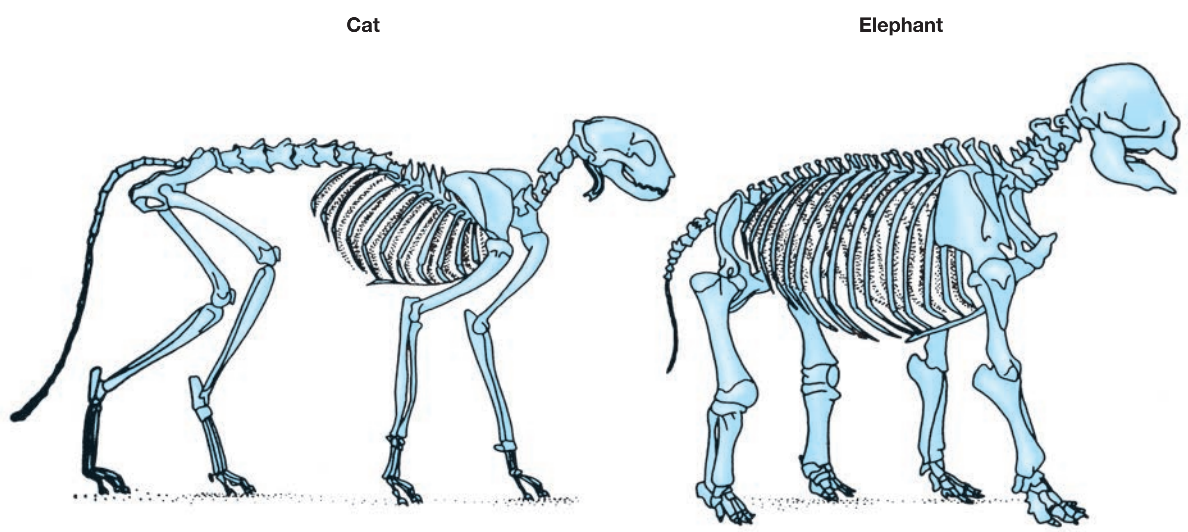


Figure source: Pough, F. Harvey; Janis, Christine M.; Heiser, John B., *Vertebrate Life*, 9th Ed" ©2013, p. 174. Reprinted and Electronically reproduced by permission of Pearson Education, Inc., Upper Saddle River, New Jersey.