Animal Physiology

FOURTH EDITION

HILL • WYSE • ANDERSON

Themes in the Study of Animal Physiology

Listed are 15 overarching themes that reappear throughout the study of animal physiology. Some of these overlap with, or even encompass, others; they are not intended to be mutually exclusive or, in all cases, equally important. An illustrative example of each theme is presented in the second column of the table. Further examples are on the pages listed in the third column (italic listing elaborates the featured example).

Theme	An Example of the Theme in Action	See Pages
The Study of Function: Animal physiology is the study of how animals function. That is, it is the study of how their cells and organs operate.	When physiologists study muscle, one of their goals is to understand how the proteins in muscle cells are able to develop mechanical forces, which are employed in locomotion, heart contraction, or other activities.	117 (Fig. 5.12) *541 (Fig. 20.5)* 623 (Fig. 23.24) 710 (Fig. 26.9)
Integration of the Sciences: Physiologists often find that they must integrate knowledge of mathematics, chemistry, or physics with knowledge of biology to answer important questions. Physiology is one of the most integrative branches of biology.	To understand how animals employ odors to orient their movements, physiologists study the *chemical* structural differences between molecules that attract or repel, and they *mathematically* describe the *physics* of how winds or water currents transport odor molecules from odor sources to the olfactory organs of animals.	7 (Fig. 1.3) 64 (Fig. 2.28) 169 (Fig. 7.3) *387* 671 (Fig. 25.2)
Emphasis on Quantitative Methods: Physiologists *quantify* the properties of animals as carefully as possible as they seek to test hypotheses or make predictions.	Starting in ancient Roman times, people thought that the dromedary camel could carry enough water in its rumen to explain its unusual ability to live without drinking. When physiologists *quantified* the amount of water in the camel rumen rather than just speaking qualitatively about it, however, they found that there was not nearly enough water in the rumen for the old idea to make sense. Negating the old idea helped lead to understanding that camels do not store water to a greater degree than other mammals. Instead, they have excellent abilities to conserve water and endure dehydration.	217 (Box 9.1) 220 (Fig. 9.7) 242–243 (Fig. 10.8) *827–828*
The Tandem Goal of Understanding Mechanism and Adaptation: When physiologists study a process, they typically emphasize a two-part goal: They try to understand both the *mechanism involved* (i.e., how the process is executed) and the *potential adaptive significance* of the process (i.e., how, if at all, it enhances evolutionary fitness).	A number of animals, including fireflies and certain fish, produce light. When physiologists study light production in such animals, they try to learn both *how* the animals make light and *why* they make it.	*6–11* 257–258 (Fig. 10.26) 465–466 760 (Fig. 28.12) 786–787 (Fig. 29.5)
The Comparative Method: To understand the adaptive significance of animal features, physiologists make extensive use of the *comparative method*, which is the examination of how particular functions are carried out by related and unrelated species living in similar and dissimilar environments.	When physiologists compare animals as distantly related as mammals and insects, they find that desert species tend consistently to have great abilities to concentrate their urine. Desert species of mammals are typically able to make urine of higher concentration than nondesert mammals, and desert insects are similarly superior to nondesert insects. These comparative observations provide evidence that the ability to make concentrated urine is an advantage—favored by natural selection—in deserts.	28 (Fig. 1.20) 119 (Fig. 5.13) 696–697 (Box 25.4) 711 (Box 26.1) *768 (Fig. 28.20)*
Phylogenetic Reconstruction: To understand the evolution of physiological properties—and thus gain perspective on the evolutionary significance of modern-day properties—physiologists employ *phylogenetic reconstructions*, in which genetic or other information on multiple species is used to reconstruct the paths of evolution.	Although body temperature is the same as water temperature in most species of fish, regardless of how big they are, certain species of fish maintain elevated temperatures in some of their tissues. From phylogenetic reconstructions, physiologists have found that the warm-tissue condition evolved on at least five independent occasions. We know, therefore, that today's fish with warm tissues do not all simply inherit the condition from a single common ancestor.	29 56–57 (Fig. 2.21) 74 (Fig. 3.5) *280 (Fig. 10.48)* 757 (Box 28.4)
The Centrality of the Environment: The specific environments in which animals have evolved and live must be considered for the functional properties of the animals to make sense.	Many specialists in high-altitude physiology argue that when lowland people travel to high altitudes, some of their typical responses are more harmful than helpful. These specialists emphasize that the human species did not evolve in high-altitude environments. Accordingly, there is no reason to *presume* that all the human responses to such environments would be beneficial.	57–58 (Fig. 2.22) 71–72 274 (Fig. 10.41) *657–658 (Box 24.5)*
Body Size: The physiological properties of related animal species typically scale in mathematically consistent ways with their body sizes. These relations are often nonproportional and thus termed *allometric*.	The metabolic rate per gram of body weight is usually higher in small-bodied species than in related large-bodied ones. Because of this relation, whenever two species of mammals of different body sizes—like mice and horses—are compared, the smaller species typically needs more food per gram of body weight than the larger one.	19 (Fig. 1.11) *177 (Fig. 7.6)* 296 (Fig. 11.11) 766–767 (Fig. 28.18)

Theme	An Example of the Theme in Action	See Pages
The Dynamic State of Body Constituents: Great quantities of many of the key constituents of the body are added and subtracted every day in many animals under many conditions. Thus the constituents of the body—far from being static—are continuously in a dynamic state of flux. This is true even though additions and subtractions are often relatively balanced, resulting in relatively constant concentrations (a phenomenon termed *homeostasis*).	Averaged over the course of an ordinary 24-h day, an adult person is likely to process more than 2 kg of adenosine triphosphate (ATP) each hour, synthesizing that amount of ATP from adenosine diphosphate (ADP) and, with only a short delay, breaking it back down to ADP. To synthesize the ATP, the person—during each hour—will use about 20 liters of oxygen (O_2) that he or she takes up from the atmosphere. During a 24-h day, the oxygen used will combine with almost 100 g (a fifth of a pound) of hydrogen atoms that have been removed from food molecules, forming about 800 milliliters of water. This water is added to the body fluids.	12–13 *189–190* 385 723–724 769 (Fig. 28.21)
Multiple Forms of Key Molecules: Animals have often evolved multiple molecular forms (sometimes called *isoforms*) of particular proteins or other sorts of molecules. Physiologists hypothesize that when two species or two tissues exhibit different molecular forms of a molecule, the forms are often specialized to function in the specific settings in which the animals live or the tissues function.	The cell membranes of all animals are composed principally of lipid molecules. Physiologists have found, however, that the membranes of all animals are not composed of chemically identical lipid molecules. Instead, multiple molecular forms of lipids are employed by different animals living under different circumstances. Cold-water fish species, for instance, construct their cell membranes using molecular forms of lipids that are less likely to harden at low temperatures than the molecular forms synthesized by warm-water species.	*38–39 (Fig. 2.3)* 250–251 (Fig. 10.19) 552–553 639 (Fig. 24.2) 656–657 (Fig. 24.20)
Phenotypic Plasticity: An individual animal is often able to change its phenotype in response to changes in the particular circumstances under which it is living (e.g., its particular environment). This ability of an individual animal to adopt two or more phenotypes despite having a fixed genotype is termed *phenotypic plasticity*.	Animals that eat only occasionally, such as pythons, often alternate between two intestinal phenotypes. When they have not had a meal for weeks, their intestinal tract is physically small, and it has poorly developed molecular mechanisms for absorbing food. After a meal, the tissues of the intestinal tract enlarge greatly, and the intestinal tract expresses well-developed absorption mechanisms.	16–18 (Fig. 1.10) 82 (Table 3.1) 94–97 *161–162 (Fig. 6.23)* 273 (Fig. 10.40) 570 (Fig. 21.5)
Interdependency of Function and Form: The *function* of a biological system typically cannot be understood without knowledge of its *structure*, and vice versa.	The kidney tubules of mammals not only produce the most concentrated urine observed in vertebrates but also differ from other vertebrate kidney tubules in that they all have distinctive hairpin shapes. Physiologists have shown that the *functional* ability to produce highly concentrated urine depends on the hairpin *structure*, which guides the urine (as it is being formed) to flow first in one direction and then in the opposite direction.	144–145 (Fig. 6.13) 268–269 (Fig. 10.35) 380 (Fig. 14.10) 670 (Fig. 25.1) *794 (Fig. 29.12)*
Applicability of the Laws of Chemistry and Physics: Animals must adhere to the laws of chemistry and physics. Sometimes chemistry and physics act as constraints, but sometimes animals gain advantages by evolving systems that capitalize on particular chemical or physical principles.	Heat transfer through air follows different physical laws when the air is still rather than moving; heat tends to move much more slowly through still air than moving air. Animals cannot change such laws of physics. They sometimes can affect which law applies to them, however, as when the ancestors of mammals evolved fur. The hairs of a furred mammal keep the layer of air next to the body relatively motionless. Heat transfer through that air is therefore slow, helping mammals retain internal heat when living in cold environments.	*238–239* 505 (Fig. 18.8) 592 (Box 22.2) 716–717
The Interdependency of Levels of Organization: An animal's *overall* functional properties depend on how its *tissues* and *organs* function, and the function of its tissues and organs depends on how its *cells* and *molecular systems* function. All these levels of organization are interdependent. An important corollary is that properties at one level of organization often cannot be fully understood without exploring other levels of organization.	When your physician strikes a tendon near your knee with a mallet, your leg straightens. For this response, electrical signals must travel along nerve cells to the spinal cord and back. The rate of travel depends in part on the *molecular* properties of ion-transporting proteins in the cell membranes of the nerve cells. It also depends in part on key *cellular* properties, such as the spacing between the sections of each nerve cell membrane that are fully exposed to the fluids bathing the cell. Molecular and cellular properties of these sorts determine the *overall* properties of the process. For instance, they determine the length of time that passes between the moment the mallet strikes and the moment your leg muscles contract.	5–6 (Figs. 1.2, 1.3) 120 (Box 5.2) 206 (Fig. 8.12) *316–318* 521 (Fig. 19.4)
The Crucial Importance of Control Mechanisms: In addition to mechanisms for reproducing, breathing, moving, and carrying out other overt functions, animals require *control* mechanisms that orchestrate the other mechanisms. The control mechanisms—so diverse that they include controls of gene expression as well as those exerted by the nervous and endocrine systems—determine the relations between inputs and outputs in physiological systems. They thereby crucially affect the functional properties of animals.	Although sheep and reindeer are born at cold times of year, newborns receive no heat from their parents and must keep warm on their own or die. They possess a process for rapid heat production. Proper control of this process requires that it be activated at birth, but not before birth when it would tend needlessly to exhaust fetal energy supplies. The control mechanism has two key properties: It activates heat production when neural thermal sensors detect cold, but its capacity to activate heat production is turned off by chemical factors secreted by the placenta. The control mechanism remains in a turned-off state until a newborn is separated from the placenta at birth. The cold environment is then able to stimulate rapid heat production.	54 (Fig. 2.19) 260–261 (Box 10.3) *293 (Fig. 11.10)* 492 (Fig. 17.18)

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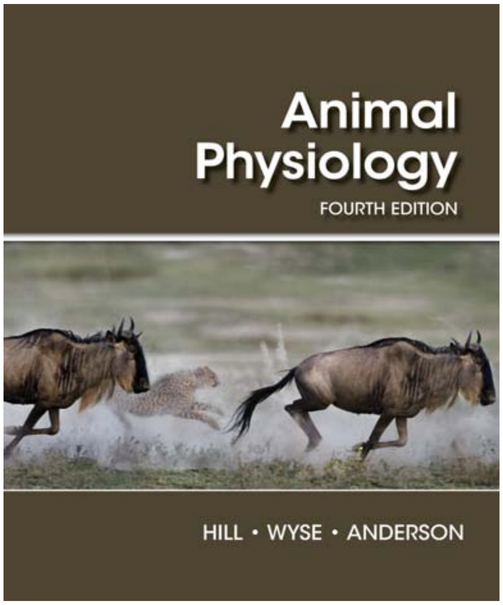

About the Cover

"Physiology in action" aptly describes this scene, photographed in the Serengeti ecosystem in Tanzania, East Africa. The cheetahs have just sprinted to make a close approach to the wildebeest antelopes they are hunting. Now exercise physiology will determine the outcome. The running speeds of the two species depend on how fast their muscle cells can produce ATP (adenosine triphosphate), the required energy source for muscular work. As soon as the cheetahs started sprinting, they started making ATP anaerobically. This source of ATP is fast and abundant, but short-lived. Thus the cheetahs will tire quickly. The wildebeests need evade them for only another minute or two to survive. Although cheetahs usually hunt by themselves, family groups like this one sometimes hunt together. Photo © Fred Ward/Corbis.

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To Sue, Dave, and Chrissie, from RWH

To Mary, from GAW

To Anita and Andy, from MA

Preface

Our most important goal in this book is to articulate the themes and overarching hypotheses of modern animal physiology. In the contemporary information era, individual facts are easier to find than ever. Themes—which collect facts into useful, coherent stories and worldviews—have always been the key challenge in textbook writing. Today that challenge is greater than ever because of the ceaseless escalation in the numbers of available facts. While recognizing this, our central goal remains the same as it was in earlier editions. We have not sought to produce an encyclopedia. Instead, we emphasize themes, worldviews, and overarching hypotheses.

Another of our key goals is to use graphics, drawings, and photographs to maximum advantage to communicate knowledge of animal physiology. Thus we have an ambitious art program. For example, as often as possible, we include drawings and photographs of animals being discussed, to ensure that readers are familiar with the subjects under discussion.

Clear, rigorous explanations of physiological concepts are a third key goal. Toward this end, we work with experienced reviewers, editors, and artists to address complex material with lucid text and revealing conceptual diagrams.

In these pages, we consistently and deliberately address animal physiology as a discipline integrated with other disciplines in biology—especially molecular biology, genetics, evolutionary biology, and ecology. We also consistently emphasize the roles of physiology throughout the life cycles of animals by discussing physiological development and by examining animal function during such important life-cycle processes as exercise, long-distance migration, seasonal rhythms, and accommodation to severe conditions (we generally omit pathology and parasitism, however). Although we give particular attention to mammals, we make a point of recognizing the other vertebrate groups and at least the arthropods and molluscs among invertebrates. We address all levels of organization that are germane, from the genome to the ecology of the animals involved.

We want to mention three specific strategies we have adopted to add interest and breadth to the book. First, we start every chapter with a vivid example of the application of the chapter's material to the lives of animals in their natural habitats. Second, we devote five entire chapters (our "At Work" chapters) to in-depth explorations of how physiologists do their work; in these chapters we break out of the usual textbook mold to discuss exciting topics—such as the diving physiology of seals and whales—with emphasis on experiments, theory maturation, integration of physiological systems, and prospects for future research. Third, we invite specialists to contribute expert Guest Boxes on emerging topics that expand the book's scope.

With our aspirations being as numerous as we have described, we have put a great deal of effort into balancing competing demands for space. The product is a complete physiology textbook that in one volume will meet the requirements of a diversity of one- or two-semester courses in animal function. Our intended audience is sophomores through beginning graduate students. To make the book accessible to as wide an audience as possible, we include both a glossary of more than 1500 terms and 11 appendices on important background concepts.

Our approach to the writing has been to work from the original scientific literature and obtain extensive peer review. Another aspect of our approach is that we have opted for the pedagogical consistency of a book written by just three principal authors. Margaret Anderson wrote Chapters 16, 20, and 21, and Gordon Wyse wrote Chapters 12–15, 18, and 19. Richard Hill wrote Chapters 1–11, 17, and 22–30. David S. Garbe, Scott A. Huettel, Matthew S. Kayser, Kenneth J. Lohmann, and Margaret McFall-Ngai wrote Guest Boxes. Matthew S. Kayser and Gordon Fain assisted with topic development in certain parts of the principal text.

The book is organized in modular fashion with the express purpose of providing instructors and students with flexibility in choosing the order in which they move through the book. The first of the six parts (modules) consists of Chapters 1 to 5, which are background chapters for the book as a whole. Most instructors will want to assign those chapters at the beginning of the course of study. Each of the subsequent five parts of the book is written to be free-standing and self-contained, so that students who have mastered the material in Part I will be well prepared to work through any of the other five parts. Two of the final five parts begin with explicitly introductory chapters that present fundamentals. All five of these parts end with "At Work" chapters. Within a part, although chapters will probably be best read in order, most chapters are themselves written to be relatively self-contained, meaning that the order of reading chapters within a part is flexible. Three additional features promote flexibility in the order of reading: the glossary, the new index, and page cross-references. Text is extensively cross-referenced both forward and backward, so that instructors and students can link material across chapters.

Throughout the book we strive to take advantage of all the assets of traditional book production to achieve a text that integrates the full range of relevant pedagogical elements to be a first-rate learning tool. Many sorts of professionals have important contributions to make for a book to be excellent. Thus many sorts of professionals have traditionally found personal fulfillment by engaging in the cooperative, synergistic production of books. The authors listed on the cover are just the tip of the iceberg. A book's art program depends on scientific illustrators. Coordination between the art and the text—a key to the success of any textbook—depends on the editorial expertise of the book's editors. An attractive science text needs to be designed and physically executed by talented people who combine scientific acumen with artistic sensibility. This book is the creative product of a team of at least a dozen people playing diverse, mutually reinforcing roles—all dedicated to providing students with a superior textbook.

We have tried to keep animals front and center. At the end of our production, as the orchestra goes silent and the klieg lights dim, we hope that animals leading their lives in their natural habitats will be the enduring image and memory left by this book—animals now better understood, but still with much to attract the curiosity of upcoming generations of biologists.

New to this Edition

We have added genomics material to most chapters to reflect the rapidly growing role of genomics and related disciplines in the modern study of animal physiology. As in all new editions, two of our central goals were to update content and enhance pedagogical effectiveness throughout. To these ends, we have reconsidered every sentence and every element of the art program. Now the total of figures and tables exceeds 750, of which over 130 are revised or new. Chapters that have received exceptional attention are: Chapter 4 (development and epigenetics), Chapter 6 (nutrition, feeding, and digestion), Chapter 10 (thermal relations), Chapter 14 (sensory processes), Chapter 17 (reproduction), Chapter 18 (animal navigation), Chapter 19 (control of movement), and Chapter 29 (kidney physiology, edited more completely to emphasize plasma regulation). The index is new and upgraded. In addition to the genomics content already mentioned, many topics have been added or substantially upgraded, including (but not limited to): bioluminescence, cardiac muscle of vertebrates, CRISPR, evolution of electric fish, gills of ram-ventilating fish, human individual variation in maximal rate of O_2 consumption, human thermoregulation, hunger and satiation, insect juvenile hormone, metabotropic sensory transduction, monarch butterfly migration, neuron population coding, ocean acidification, opah endothermy, owl auditory localization, PGC-1α roles in exercise training, physiological "personalities," python gut and cardiac genomics, voltage-gated channels, and TRP channels.

Acknowledgments

In the preparation of this edition, we were assisted in particularly memorable ways by Arnoldus Blix, Matthew Kayser, Zachary Nuttall, and David Hillis. Caroline R. Cartwright, Christina Cheng, and Nigel D. Meeks provided new photographs from their research. Special thanks also to Ewald R. Weibel, who in a sense has been a lifelong friend of this project; he contributed scanning EMs to the very first published version of this book, and for this edition he has provided a marvelous new image of human lung morphology. We also want to thank Anapaula S. Vinagre, Luciano S. de Fraga, Luiz C. R. Kucharski, and the rest of their team in Brazil, who have honored us with their enthusiasm for our book, which they have translated into Portuguese.

Our peer reviewers are particularly important to the quality of the book, although we of course accept full responsibility and at times have followed our own inclinations rather than theirs. We are thus happy to acknowledge our current peer reviewers as well as individuals who acted as reviewers for earlier editions and whose influence remains evident: Doris Audet, Brian Bagatto, Michael Baltzley, Jason Blank, Robert Bonasio, Charles E. Booth, Eldon Braun, Warren Burggren, Heather Caldwell, John Cameron, Jeffrey C. Carrier, David Coughlin, Sheldon Cooper, Daniel Costa, Emma Creaser, David Crews, Elissa Derrickson, Stephanie Gardner, Stephen Gehnrich, Steve George, Joseph Goy, Bernd Heinrich, Raymond Henry, James Hicks, Carl S. Hoegler, Richard Hoffman, Mark A. Holbrook, Jason Irwin, Steven H. Jury, William Karasov, Fred J. Karsch, Leonard Kirschner, Andor Kiss, Courtney Kurtz, Mark Kyle, Sharon Lynn, Megan M. Mahoney, Robert Malchow, Duane McPherson, Jennifer Marcinkiewicz, Ulrike Muller, Barbara Musolf, Randy Nelson, Scott Parker, Gilbert Pitts, Fernando Quintana, Matthew Rand, Beverly Roeder, Susan Safford, Malcolm Shick, Bruce Sidell, Mark Slivkoff, Paul Small, George Somero, Frank van Breukelen, John VandenBrooks, Itzick Vatnick, Curtis Walker, Zachary Weil, Alexander Werth, Eric Widmaier, and Heather Zimbler-DeLorenzo.

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Of course, no book of this scope emerges fully formed in a single edition. Thus, we also thank the following who played important roles in earlier versions of this work: Simon Alford, Kellar Autumn, Robert Barlow, Al Bennett, Eric Bittman, Jeff Blaustein, Batrice Boily, Beth Brainerd, Richard C. Brusca, Gary Burness, Bruce Byers, John Cameron, Donald Christian, Barbara Christie-Pope, Corey Cleland, Randal Cohen, Joseph Crivello, Peter Daniel, Bill Dawson, Gregory Demas, Linda Farmer, Jane Feng, Milton Fingerman, Dale Forsyth, Christopher Gillen, Kathleen Gilmour, Judy Goodenough, Edward Griff, Jacob Gunn, James Harding, Jean Hardwick, John Harley, Ian Henderson, Kay Holekamp, Charles Holliday, Henry John-Alder, Kelly Johnson, Alexander Kaiser, Reuben Kaufman, M. A. Q. Khan, William Kier, Peter King, Rosemary Knapp, Heather Koopman, Richard Lee, John Lepri, Robert Linsenmeier, Stephen Loomis, William Lutterschmidt, Steffen Madsen, Don Maynard, Grant McClelland, Kip McGilliard, Stephen McMann, Allen Mensinger, Tim Moerland, Thomas Moon, Thomas Moylan, Richard Nyhof, David O'Drobinak, Linda Ogren, Sanford Ostroy, Christine Oswald, Linda Peck, Sandra Petersen, Chuck Peterson, Richard Petriello, Nathan Pfost, Robert Rawding, Heinrich Reichert, Larry Renfro, David Richard, R. M. Robertson, Robert Roer, William Seddon, Brent Sinclair, Laura Smale, Amanda Southwood, Tony Stea, Philip Stephens, Georg Striedter, Rebekah Thomas, Heather Thompson, Irene Tieleman, Lars Tomanek, Terry Trier, Kay Ueno, Joshua Urio, Mark Wales, Winsor Watson, Leonard E. White, Susan Whittemore, Steve Wickler, Robert Winn, and Tom Zoeller.

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Thanks to our students, who have challenged us, encouraged us, taught us, and—if nothing else—listened to us over our many years of classroom teaching. Our classes with our students have been our proving ground for teaching physiology and our most fundamental source of reinforcement to take on a project of this magnitude. We are grateful to work and teach at institutions—Michigan State University, the University of Massachusetts, and Smith College—at which efforts of this sort are possible.

Special thanks to Andy Sinauer, who has helped us to think big and provided the resources to realize ambitious goals for four editions. We have all worked with many editors and publishers in our careers, and Andy is tops: an entrepreneur dedicated to putting the life of ideas on the printed page. We also extend special thanks to our editor, Laura Green, who has brought expertise and sound judgment to our work on every aspect of the book, including text, art, and pedagogy. Warm thanks, too, to Joanne Delphia, production specialist, who has completely redesigned the book for this edition; David McIntyre, photo editor; head of production Chris Small; and the others at Sinauer Associates whose talents and dedication have been indispensable. We feel privileged to have had Elizabeth Morales execute the art, which makes such a contribution to our pages. Elizabeth Pierson once again has helped with her exceptional talent as a copy editor.

We each have particular thanks to offer to the people in our personal lives whose support and patience have been indispensable. Richard Hill thanks Sue, Dave, and Chrissie, who have always been there even though the hours of writing have often meant long waits between sightings of their husband and father. Sue in particular has been a major contributor by repeatedly offering the benefits of her knowledge and judgment as a biologist. Gordon Wyse thanks Mary for her editorial talents, support, and willingness to keep planning around this long project, and Jeff, Karen, and Nancy for inspiration. Likewise, Margaret Anderson expresses gratitude to her family, especially Andy and Anita, and to her friends and students, whose boundless enthusiasm and idealism provide great inspiration.

While acknowledging the many ways others have helped, we of course accept full responsibility for the finished product and invite readers' opinions on how we could do better. Please contact us with your observations.

One of the gratifications of writing a book like this is the opportunity to participate in the raw enthusiasm of scientists for science. On countless occasions, many colleagues have performed great favors on short notice without the slightest hint of wanting pay for their professional expertise. Pure science must be one of the last redoubts of this ethic in today's professional world. We are honored to play the role of synthesizing and communicating the insights and questions that arise from the exciting search for knowledge.

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East Lansing, Michigan

Gordon A. Wyse
Amherst, Massachusetts

Margaret Anderson
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March 2016

To Our Readers

If you've ever been to a show and one of the producers stepped out on stage before the curtain went up to offer remarks about the upcoming event, you will understand the nature of these two pages. We, your authors, want to say a few words about the way we approached writing this book. We would also like to mention how we have handled several challenging issues.

One of our primary goals has been to create a book in which you will find the fascination of physiology as well as its content. Thus we start each of the 30 chapters with an intriguing example that illustrates the application of the chapter to understanding the lives of animals. Collectively, these examples highlight the many ways in which the study of physiology relates to biology at large.

Besides our desire to emphasize the fascination of physiology, we have also wanted to stress the importance of integrating knowledge across physiological disciplines—and the importance of integrating physiology with ecology, behavior, molecular biology, and other fields. We have wanted, in addition, to discuss how concepts are tested and revised during research in physiology and to focus on the cutting edges in physiological research today. To help meet these goals, we include five "At Work" chapters, which appear at the ends of five of the book's six parts. You will find that the "At Work" chapters are written in a somewhat different style than the other chapters because they give extra emphasis to the *process* of discovery. The topics of the "At Work" chapters are deliberately chosen to be intriguing and important: diving by seals and whales, animal navigation, muscle in states of use (e.g., athletic training) and disuse, mammals in the Arctic, and desert animals. Each "At Work" chapter uses concepts introduced in the chapters preceding it. We hope you will find these chapters to be something to look forward to: enjoyable to read and informative.

In the information age, with easy access to facts online, you might wonder, why should I take the course in which I am enrolled and why should I read this book? The answer in a few words is that the extraordinary quantities of information now available create extraordinary challenges for synthesis.

To explain, the more information each of us can locate, the more we need frameworks for organizing knowledge. Scientists, philosophers, and historians who comment on the practice of science are almost never of one mind. Nonetheless, they nearly universally reach one particular conclusion: In science, the mere accumulation of facts leads quite literally nowhere. The successful pursuit of scientific knowledge requires testable concepts that organize facts. Scientists create concepts that organize raw information. Then, in science, it is these concepts that we test for their accuracy and utility. A good course taught with a good textbook provides a conceptual framework into which raw information can be fitted so that it becomes part of the essential life of ideas and concepts.

We hope we have provided you not simply with a conceptual framework, but one that is "good for the future." By this we mean we have not tried merely to organize the knowledge already available. We have tried in equal measure to articulate a conceptual framework that is poised to grow and mature as new knowledge becomes available.

Just briefly we want to comment on three particular topics. First, our Box design. Boxes that start on the pages of this book often continue online. To find the web content, go to the book's website that is mentioned prominently at the end of each chapter. The part of a Box that you will read online is called a Box Extension. All the Box Extensions are fully integrated with the rest of the book in terms of concepts, terminology, and artistic conventions. Moreover, many of the Box Extensions are extensive and include informative figures. Thus, we urge that you keep reading when a Box directs you to a Box Extension.

Second, units of measure. For 40 years there has been a revolution underway focused on bringing all human endeavor into line with a single system of units called the Système International (SI). Different countries have responded differently, as have different fields of activity. Thus, if you purchase a box of cereal in much of the world, the cereal's energy value will be quoted on the box in kilojoules, but elsewhere it will be reported in kilocalories. If you go to a physician in the United States and have your blood pressure measured, you will have it reported in millimeters of mercury, but if you read a recent scientific paper on blood pressures, the pressures will be in kilopascals. The current state of transition in units of measure presents challenges for authors just as it does for you. We have tried, in our treatment of each physiological discipline, to familiarize you with the pertinent units of measure you are *most likely to encounter* (SI or not). Moreover, you will find in Appendix A an extensive discussion of the Système International and its relations to other systems of units.

The third and final specific matter on our minds is to mention our referencing system. For each chapter, there are three reference lists: (1) a brief list of particularly important or thought-provoking references at the end of the chapter, (2) a longer list of references in the section titled Additional References at the back of the book, and (3) a list of all the references cited as sources of information for figures or tables in the chapter. The final list appears in the Figure and Table Citations at the back of the book.

All three of us who wrote this book have been dedicated teachers throughout our careers. In addition, we have been fortunate to develop professional relationships and friendships with many of our students. This book is a product of that two-way interaction. In the big universities today, there are many forces at work that encourage passivity and anonymity. We urge the opposite. We encourage you to talk science as much as possible with each other and with your instructors, whether in classroom discussions, study groups, office hours, or other contexts. Active learning of this sort will contribute in a unique way to your enjoyment and mastery of the subjects you study. We have tried, deliberately, to write a book that will give you a lot to talk about.

Richard W. Hill

Gordon A. Wyse

Margaret Anderson

Media and Supplements
to accompany
Animal Physiology, Fourth Edition

For the Student
Companion Website

(sites.sinauer.com/animalphys4e)
The *Animal Physiology* Companion Website includes content that expands on the coverage in the textbook plus convenient study and review tools. The site includes the following resources:

- *Chapter Outlines* include all of the headings and subheadings from each chapter.
- *Chapter Summaries* provide quick chapter overviews.
- *Box Extensions* expand on topics introduced in the textbook and cover important additional conceptual material.
- *Online Quizzes* cover all the key material in each chapter (instructor registration required).
- *Flashcards* allow students to learn and review the many new terms introduced in the textbook.
- A complete *Glossary.*

For the Instructor
(Available to qualified adopters)
Instructor's Resource Library

The *Animal Physiology* Instructor's Resource Library includes a range of resources to help instructors in planning the course, preparing lectures and other course documents, and assessing students. The IRL includes the following resources:

Presentation Resources

- *Textbook Figures & Tables*: All of the textbook's figures (both line art and photographs) are provided as JPEG files at two sizes: high-resolution (excellent for use in PowerPoint) and low-resolution (ideal for web pages and other uses). All the artwork has been reformatted and optimized for exceptional image quality when projected in class.
- *Unlabeled Figures*: Unlabeled versions of all figures.
- PowerPoint Presentations:
  - *Figures & Tables*: Includes all the figures and tables from the chapter, making it easy to insert any figure into an existing presentation.
  - *Layered Art*: Selected key figures throughout the textbook are prepared as step-by-step and animated presentations that build the figure one piece at a time.

Answers to End-of-Chapter Questions Answers to all of the end-of-chapter Study Questions are provided as Word documents.

Test Bank Revised and updated for the Fourth Edition, the Test Bank consists of a broad range of questions covering key facts and concepts in each chapter. Both multiple-choice and short-answer questions are provided. The Test Bank also includes the Companion Website online quiz questions. All questions are ranked according to Bloom's Taxonomy and referenced to specific textbook sections.

Computerized Test Bank The entire Test Bank, including all of the online quiz questions, is provided in Blackboard's Diploma format (software included). Diploma makes it easy to assemble quizzes and exams from any combination of publisher-provided questions and instructor-created questions. In addition, quizzes and exams can be exported for import into many different course management systems, such as Blackboard and Moodle.

Online Quizzing

The Companion Website features pre-built chapter quizzes (see above) that report into an online gradebook. Adopting instructors have access to these quizzes and can choose to either assign them or let students use them for review. (Instructors must register in order for their students to be able to take the quizzes.) Instructors can add questions and create their own quizzes.

Course Management System Support

The entire Test Bank is provided in Blackboard format, for easy import into campus Blackboard systems. In addition, using the Computerized Test Bank provided in the Instructor's Resource Library, instructors can easily create and export quizzes and exams (or the entire test bank) for import into other course management systems, including Moodle, Canvas, and Desire2Learn/Brightspace.

Value Options
eBook

Animal Physiology is available as an eBook, in several different formats, including VitalSource, RedShelf, and BryteWave. The eBook can be purchased as either a 180-day rental or a permanent (non-expiring) subscription. All major mobile devices are supported. For details on the eBook platforms offered, please visit www.sinauer.com/ebooks.

Looseleaf Textbook

(ISBN 978-1-60535-594-8)
Animal Physiology is also available in a three-hole punched, looseleaf format. Students can take just the sections they need to class and can easily integrate instructor material with the text.

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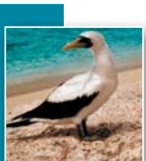

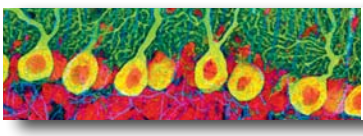

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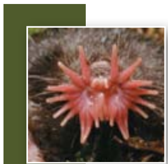

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PART I

Fundamentals of Physiology

PART I

Fundamentals of Physiology

Previous page

Bioluminescent fireflies, when contemplated, are among the animals that most vividly exemplify how the extreme endpoints of the hierarchy of life—molecules and ecology—interact and are interdependent. Having evolved unusual molecular mechanisms that permit light production, fireflies are able to communicate ecologically in unique ways. Shown is a long exposure of fireflies in early summer in Japan.

Animals and Environments

Function on the Ecological Stage

1

Long-distance migrants
Some populations of these sandpipers, which are known as red knots (*Calidris canutus*), breed in the high Arctic every summer but overwinter in southern Argentina. The birds thus migrate almost halfway around the globe twice a year. They use energy at relatively high rates not only while migrating but also during several other phases of their annual life cycle, such as their period of nesting on the cold, exposed Arctic tundra.

Animal physiology is the study of animal function—the study of "how animals work." Physiologists—the scientists who carry out this study—bring a special perspective to scenes such as birds migrating. They wonder how much energy the birds must expend to fly, where and when the birds obtain the energy, and how the birds stay oriented toward their destination so as to arrive efficiently. More broadly stated, physiologists seek to identify the functional challenges that migrating birds face, and they seek to understand the functional properties of the birds that allow them to meet the challenges.

Billions of animals migrate over the face of the planet every year, making the functional properties of migrating animals a subject of paramount importance. By definition, however, migrating animals are on the move; they do not stay in one place where they might be investigated with ease. Consequently, researchers have had to be inventive to study these animals.

Physiologists now have high-quality methods for measuring the cost of flight. Sandpipers such as those shown here are trained to fly in a wind tunnel, where their speed of flight can be controlled. While the birds fly, their rates of energy use are measured by techniques designed not to disturb them. One such technique makes use of unusual, benign isotopes of oxygen and hydrogen. These isotopes are injected into the sandpipers before they start flying, and then the rates of loss of the isotopes from the birds are measured as they fly unencumbered in the wind tunnel. From the isotope data, the birds' rates of energy use can be calculated as they fly at speeds typical of migratory flight. These rates turn out to be very high: about seven or eight times the birds' resting rates of energy use.[1] Physiologists have then combined this information with field observations on food ingestion and processing to learn how the birds obtain sufficient energy and how they manage their energy supplies to meet their flight needs during migration. One population of the sandpipers is famous for migrating every spring from southern South America to the Arctic—a distance of 15,000 km (9300 miles [mi]). In common with other populations of the same species, when these birds migrate, they alternate between extended *stopover periods*, during which they "refuel" by feeding, and *flight periods*, during which they fly nonstop for long distances—sometimes more than 5000 km (3100 mi). Based on the information available, the sandpipers fuel each long, uninterrupted flight by eating lots of clams, snails, and other food during the stopover period—often lasting 3–4 weeks—that immediately precedes the flight. By the time they take off, the birds must have enough stored energy to fuel the entire next leg of their journey because they do not eat as they fly.

During a stopover period, as the birds eat day after day, they store a great amount of energy as fat, and their body weight can increase by 50%. Physiologists have discovered, however, that the birds' adjustments during a stopover period are far more complex than simply storing fat. For part of the time, the birds' stomach and intestines are large, aiding them in processing food at a high rate. During the week before they take flight, however, several organs that they will not use during flight, including their stomach and intestines, decrease significantly in size. Other organs, such as their heart, grow larger. Overall, during that week, the body of each bird is reproportioned in ways that poise the bird to fly strongly, while reducing the amount of unnecessary weight to be carried. By investigating these phenomena, physiologists have revealed that the fascinating migrations of these birds are, in truth, far more fascinating than anyone could have imagined prior to the detailed study of function.

As you start your study of physiology, we—your authors—believe you are at the beginning of a great adventure. We feel privileged to have spent our professional lives learning how animals work, and we are eager to be your guides. If we could hop with you into a fantastic travel machine and tour Earth in the realms we are about to travel in this book, we would point out sperm whales diving an hour or more to depths of a mile or more, electric fish using modified muscles to generate 500-V shocks, just-born reindeer calves standing wet with amniotic fluid in the frigid Arctic wind, reef corals growing prolifically because algae within their tissues permit internal photosynthesis, and moths flying through cool nights with bodies as warm as those of mammals. Each of these scenes draws the interest of physiologists and continues to spark new physiological research.

[1] The method of measuring rate of energy consumption discussed here, known as the *doubly labeled water method*, is explained in greater detail on page 217.

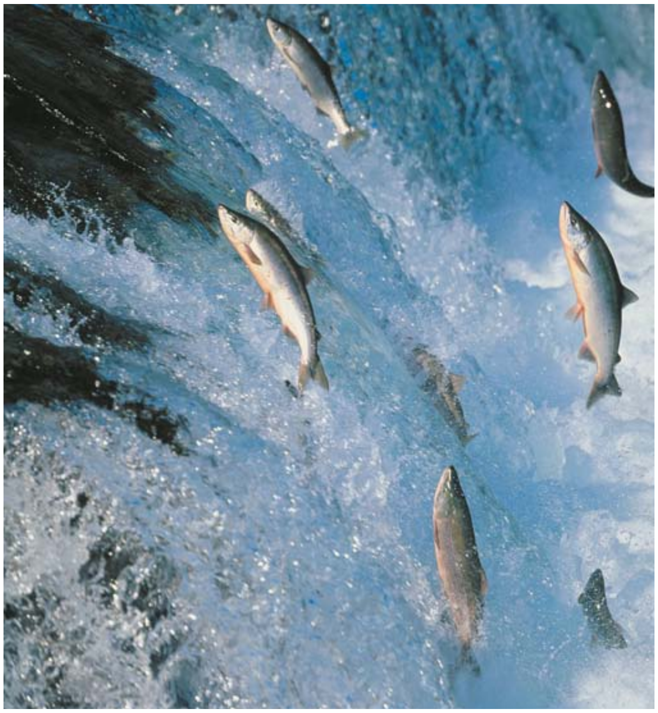


FIGURE 1.1 Pacific salmon migrating upriver to their spawning grounds Having spent several years feeding and growing in the Pacific Ocean, these fish have once again found the river in which they were conceived. Now they must power their way back to their birthplace to spawn, even though they ate their last meal at sea and will starve throughout their upriver journey. Shown are sockeye salmon (*Oncorhynchus nerka*).

The Importance of Physiology

Why is the study of animal physiology important to you and to people in general? Not the least of the reasons is the one we have already emphasized—namely, that a full understanding and appreciation of all the marvels and other phenomena of the animal world depend on an analysis of how animals work. The study of physiology draws us beyond surface impressions into the inner workings of animals, and nearly always this venture is not only a voyage of discovery, but also one of revelation.

The study of physiology also has enormous practical applications because physiology is a principal discipline in the understanding of health and disease. The analysis of many human diseases—ranging from aching joints to heart failure—depends on understanding how the "human machine" works. A physician who studies heart disease, for instance, needs to know the forces that make blood flow into the heart chambers between one heartbeat and the next. The physician also needs to know how pressures are developed to eject blood into the arteries, how the cells of the heart muscle coordinate their contractions, and how the nutrient and O_2 needs of all parts of the heart muscle are met. We discuss these and other aspects of mammalian physiology extensively in this book. Even when we turn our attention to other types of animals, our study will often have application to human questions. One reason is that nonhuman animals are often used as "models" for research that advances understanding of human physiology. Research on squids, for instance, has been indispensable for advancing knowledge of human neurophysiology because some of the nerve cells of squids are particularly large and therefore easily studied.

Physiology is as important for understanding the health and disease of nonhuman animals as it is for understanding health and disease in humans. An example is provided by studies of another group of migrating animals, the Pacific salmon—which swim up rivers to reach their spawning grounds (**FIGURE 1.1**). Physiologists have measured the costs these fish incur to swim upstream and leap waterfalls. This research has enabled better understanding of threats to their health. For instance, although each individual dam along a river might be designed to let salmon pass, a series of dams might so increase the overall cost of migration that the fish—which don't eat and live just on their stores of energy when migrating—could run out of energy before reaching their spawning grounds. With knowledge of the energetics of swimming and leaping, managers can make rational predictions of the cumulative effects of dams, rather than simply altering rivers and waiting to see what happens. The effects of water pollutants, such as heavy metals and pesticides, are other important topics in salmon physiology. Examples in other animals include studies of stress and nutrition. Careful physiological studies have solved mysterious cases of population decline by revealing that the animals were under stress or unable to find adequate amounts of acceptable foods.

In brief, physiology is one of the key disciplines for understanding

- The fundamental biology of all animals
- Human health and disease
- The health and disease of nonhuman animals of importance in human affairs

The Highly Integrative Nature of Physiology

Physiology is also important in the study of biology because *it is one of biology's most integrative disciplines*. Physiologists study all the levels of organization of the animal body. In this respect, they are much like detectives who follow leads wherever the leads take them. To understand how an organ works, for instance, information about the nervous and hormonal controls of the organ might be required, plus information about enzyme function in the organ, which might lead to studies of the activation of genes that code for enzyme synthesis. Physiology not only pursues all these levels of biological organization within individual animals but also relates this knowledge to the ecology and evolutionary biology of the animals. Students often especially enjoy their study of physiology because the discipline is so integrative, bringing together and synthesizing many concepts that otherwise can seem independent.

Suppose we observe a pheasant pursued by a fox. This scene has obvious evolutionary and ecological importance (**FIGURE 1.2A**); if the pheasant is to continue passing its genes to future generations, it must win the contest, but if it loses, the fox gets to eat. In other words, the outcome is significant at the evolutionary and ecological levels of organization. But what determines the outcome? The

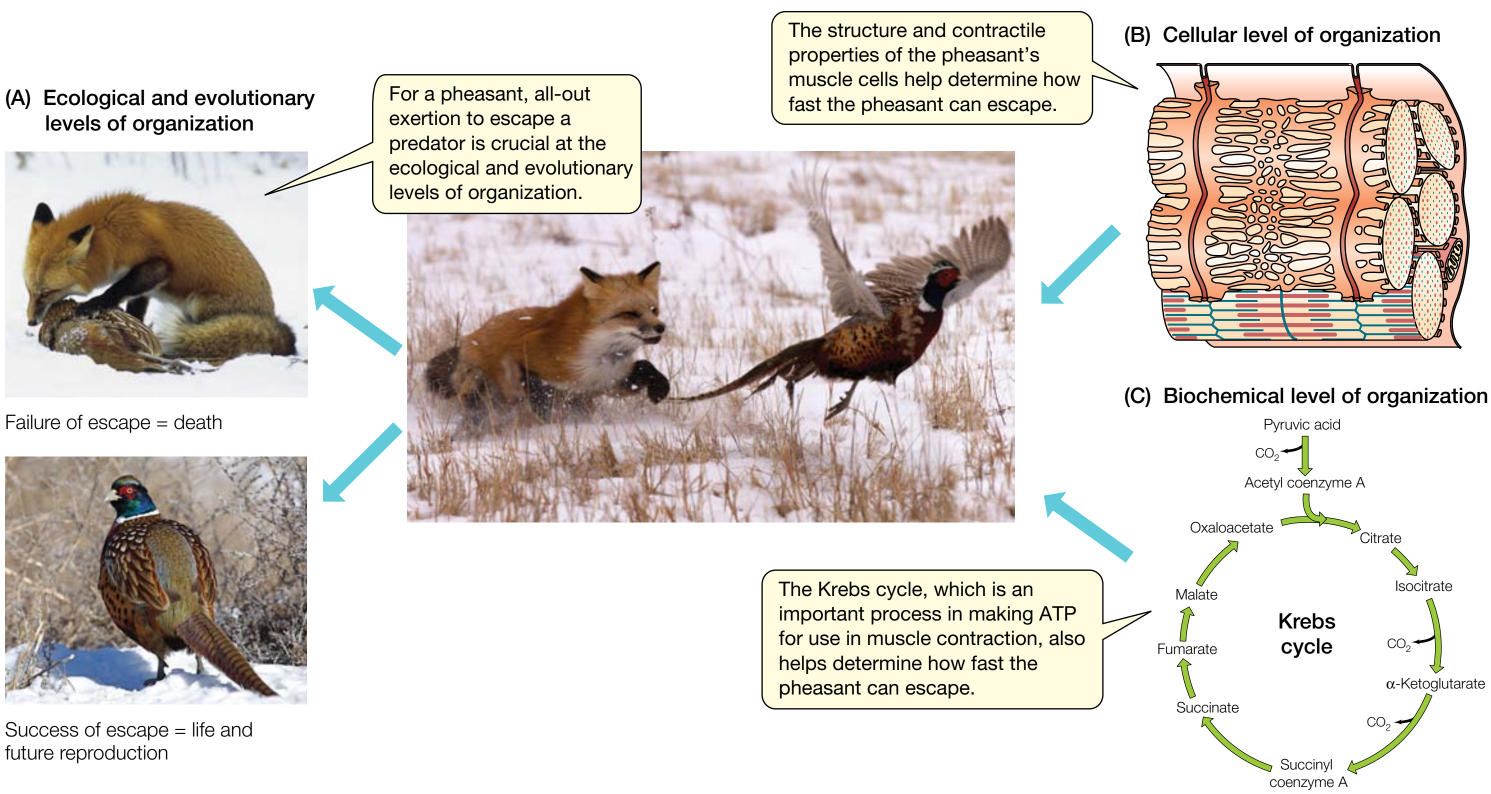


FIGURE 1.2 The study of physiology integrates knowledge at all levels of organization (A) When we see a pheasant or other animal escaping from a predator, we tend to think of the process as being entirely a matter of behavior. Actually, however, internal physiological processes such as (B) muscle contraction and (C) ATP production play key roles, because the outward behavior of the animal can be only as effective as these internal processes permit. The study of physiology considers all the relevant levels of organization, from the cellular and biochemical processes involved in running and flying to the ecological and evolutionary consequences. See Chapter 8 for more detail on ATP production and Chapter 20 for more on muscle structure and force production.

physiological properties of many of the pheasant's internal tissues play major roles. The speed at which the pheasant can escape, for example, depends on the precise ways that the pheasant's muscles work (**FIGURE 1.2B**) as they contract to produce the mechanical forces that propel the pheasant forward. The pheasant's speed also depends on its biochemical mechanisms of producing adenosine triphosphate (ATP) (**FIGURE 1.2C**), because the muscles use ATP as their source of energy for producing mechanical forces, and consequently they can work only as fast as their ATP supply permits. In a very real sense, the pheasant's success at the ecological and evolutionary levels of organization is a direct consequence of the pheasant's physiological capabilities at the cellular and biochemical levels of organization in its tissues.

To explore the highly integrative nature of the study of physiology in greater detail, let's again consider the Pacific salmon. As juveniles, these fish migrate from rivers to the open ocean. Years later, they return to the very rivers of their conception to procreate the next generation. Before a returning salmon enters freshwater, it maintains its blood more dilute than the seawater in which it swims. After it enters freshwater, however, it must maintain its blood more concentrated than the dilute freshwater now surrounding it. Another challenge the salmon faces is meeting the energy costs of its migration. Once in its natal river, a salmon no longer eats. Yet it may swim for many weeks before it reaches its spawning grounds—sometimes traveling against the river current as far as 1100 km (680 mi) and, in mountainous regions, climbing 1.2 km (0.75 mi) in altitude. During this trip, because the fish is starving, it gradually breaks down the substance of its body to supply its energy needs (e.g., needs for metabolic fuels to produce ATP); 50–70% of all tissues that can supply energy for metabolism are typically used by the time the fish reaches its destination.

As physiologists study salmon, they consider all levels of organization (**FIGURE 1.3**). As part of their background of knowledge, they recognize that the populations and species of salmon alive today not only are products of evolution but also are still evolving (see Figure 1.3A). Physiologists also recognize that the laws of chemistry and physics need to be considered (see Figure 1.3B), because animals must obey those laws—and sometimes they *exploit* them. For understanding swimming, multiple levels of organization must be considered (see Figure 1.3C). The nervous system generates coordinated nerve impulses that travel to the swimming muscles, which contract using energy drawn from ATP that is synthesized from organic food molecules that serve as metabolic fuels. The contraction of the swimming muscles then exerts biomechanical forces on the water that propel the fish forward. The investigation of swimming illustrates, too, the important general point that the study of *function* typically goes hand in hand with the study of *form*; knowledge of anatomy often sets the stage for understanding physiology, and as function is clarified, it typically helps account for anatomy. Often, the ultimate goal of a physiological study is to understand how an animal functions in its natural environment. Thus an ecological perspective is vital as well. As seen in Figure 1.3D, when an individual salmon's fluid environment changes from saltwater to freshwater, the fish alters the set of ion-transporting proteins expressed in its gills, permitting inward ion pumping in freshwater whereas ions were pumped outward in saltwater. The distance a fish swims is another important ecological consideration. Different populations of salmon travel vastly different distances. Going far upriver can provide advantages of certain kinds, such as providing pristine spawning grounds. However, this ecological factor has other consequences as well. Females that exert great effort to reach their spawning grounds, such as by swimming great distances, spawn fewer eggs because swimming diverts energy away from use in reproduction (see Figure 1.3D).

Mechanism and Origin: Physiology's Two Central Questions

Physiology seeks to answer two central questions about how animals work: (1) What is the mechanism by which a function is accomplished, and (2) how did that mechanism come to be? To understand why there are *two* questions, consider the analogous problem of how a car works. In particular, how is an engine-driven wheel made to turn?

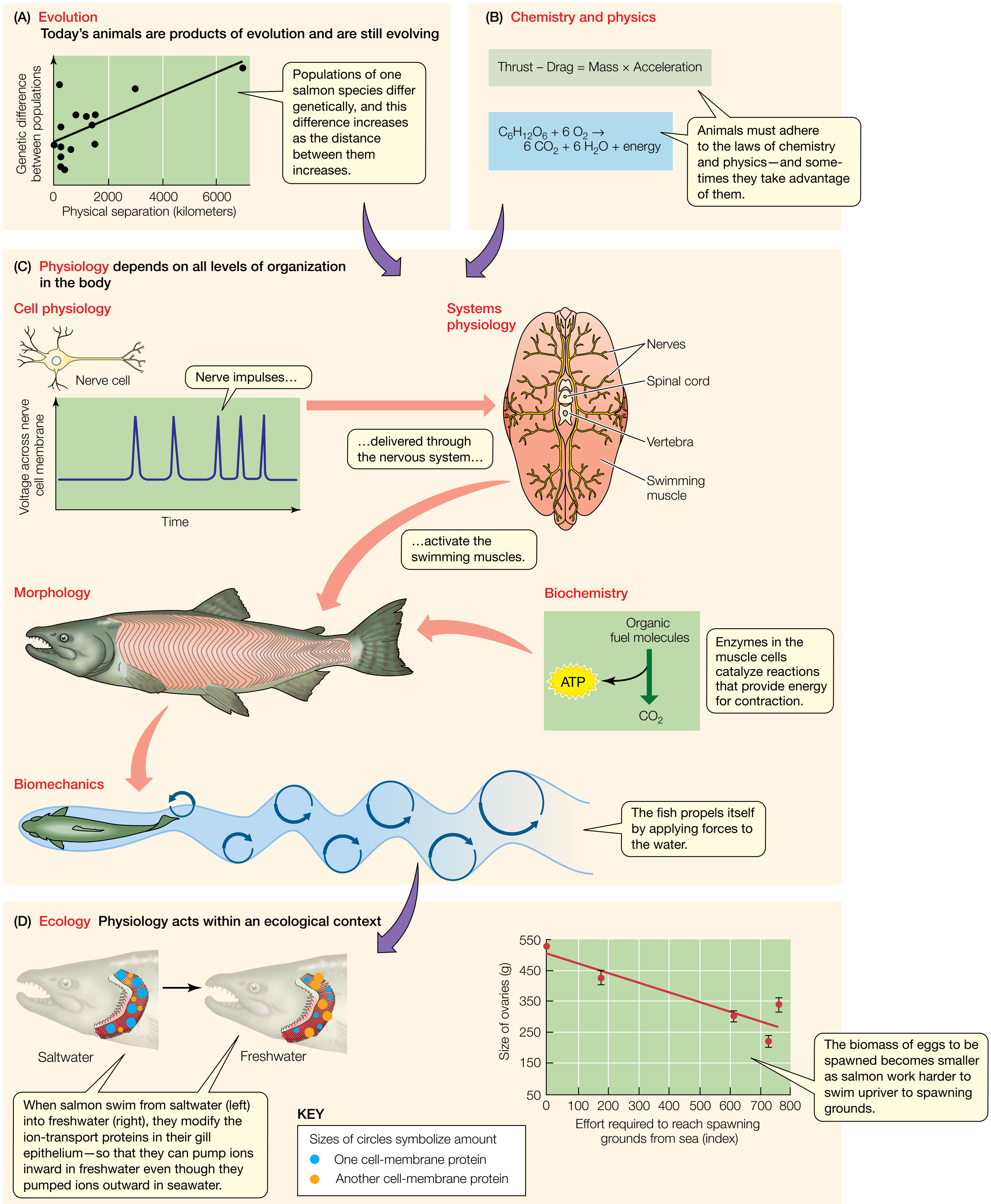
To understand this function, you could disassemble a car and experiment on its parts. You could study how the pistons inside the cylinders of the engine are made to oscillate by forces released from exploding gasoline, how the pistons and connecting rods turn the drive shaft, and so forth. From studies like these, you would learn how the car works.

At the conclusion of such studies, however, you would have only half the answer to the question of how the car works. Presuming that you have investigated a routine design of modern car, your experiments will have revealed how a routine internal combustion engine turns a wheel by way of a routine transmission. Let your mind run free, however, and you may quickly realize that there are alternative designs for a car. The engine could have been a steam engine or an electric engine, for example. Accordingly, when you ponder how a wheel turns, you see that you really face two questions: the *immediate* question of how a particular design of car makes a wheel turn, and the *ultimate* question of how that particular design came into being. Physiologists also face these two questions of *mechanism* and *origin*.

The study of mechanism: How do modern-day animals carry out their functions?

If you examine a particular car and its interacting parts to understand how it works, you are learning about the *mechanisms* of function of the car. Likewise, if you study the interacting parts of a particular animal—from organs to enzymes—to learn how it works, you are studying the animal's *mechanisms*. In physiology,

FIGURE 1.3 To develop a full understanding of salmon swimming, physiologists integrate studies at multiple levels of organization To understand the physiology of fish, physiologists consider (A) evolutionary biology, (B) the laws of chemistry and physics, and (D) ecological relations—as well as (C) body function at all levels of organization. All elements shown are for fish in a single genus, *Oncorhynchus*, the Pacific salmonid fish. In (C) the drawing in "Systems physiology" is a cross section of the body; the salmon in "Morphology" is a chinook salmon. (Graph in A—which pertains to populations of chum salmon—after Hendry et al. 2004; cross section, salmon, and biomechanics illustration in C after Videler 1993; graph in D—which pertains to sockeye salmon—after Crossin et al. 2004.) ▶



(A) Evolution
Today's animals are products of evolution and are still evolving
Genetic difference between populations
0
2000
4000
6000
Physical separation (kilometers)
Populations of one salmon species differ genetically, and this difference increases as the distance between them increases.
(B) Chemistry and physics
Thrust – Drag = Mass × Acceleration
$C_6H_{12}O_6 + 6\ O_2 \rightarrow$
$6\ CO_2 + 6\ H_2O$ + energy
Animals must adhere to the laws of chemistry and physics—and sometimes they take advantage of them.
(C) Physiology depends on all levels of organization in the body
Cell physiology
Nerve cell
Nerve impulses…
Voltage across nerve cell membrane
Time
…delivered through the nervous system…
Systems physiology
Nerves
Spinal cord
Vertebra
Swimming muscle
…activate the swimming muscles.
Morphology
Biochemistry
Organic fuel molecules
ATP
CO_2
Enzymes in the muscle cells catalyze reactions that provide energy for contraction.
Biomechanics
The fish propels itself by applying forces to the water.
(D) Ecology Physiology acts within an ecological context
Saltwater
Freshwater
When salmon swim from saltwater (left) into freshwater (right), they modify the ion-transport proteins in their gill epithelium—so that they can pump ions inward in freshwater even though they pumped ions outward in seawater.
KEY
Sizes of circles symbolize amount
One cell-membrane protein
Another cell-membrane protein
Size of ovaries (g)
550
450
350
250
150
50
0
100
200
300
400
500
600
700
800
Effort required to reach spawning grounds from sea (index)
The biomass of eggs to be spawned becomes smaller as salmon work harder to swim upriver to spawning grounds.

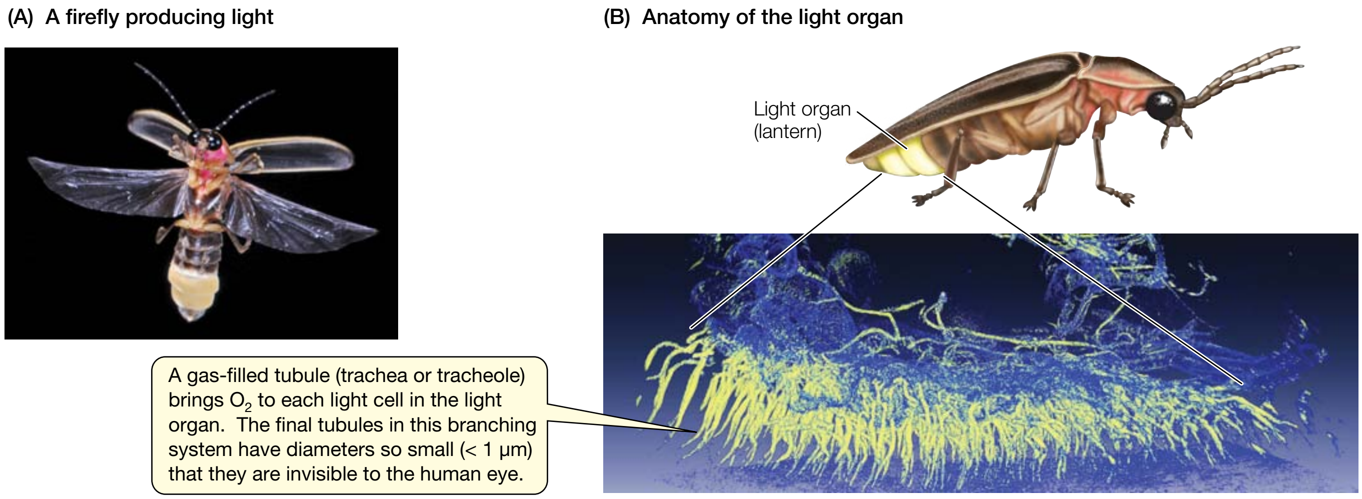


FIGURE 1.4 Light production by fireflies Fireflies are not in fact flies. Instead they are beetles. (A) Light is produced by a light organ at the posterior end of the abdomen. *Photinus pyralis*, found in the eastern and central United States, is shown here. Insects employ a system of branching gas-filled tubules to deliver oxygen (O_2) to all their cells. O_2 enters this system at pores on the surface of the insect's body. (B) A detailed image of the exceedingly fine gas-transport tubules in the light organ was finally obtained in Asian fireflies (*Luciola*) in 2014 by use of advanced X-ray methods. Each light cell in the light organ is supplied by a tiny gas-transport tubule. (Tubule image in B courtesy of École Polytechnique Fédérale de Lausanne, after Tsai et al. 2014.)

mechanism refers to the components of actual, living animals and the interactions among those components that enable the animals to perform as they do.

Curiosity about mechanism is what inspires most physiologists to study animals, and studies of mechanism dominate physiological research. Physiology, in fact, is most clearly distinguished from other biological disciplines with which it is related, such as morphology or ecology, by its central focus on the study of mechanism. A physiologist typically begins an investigation by observing a particular capability that excites curiosity or needs to be understood for practical purposes. The capability of the human visual system to distinguish red and blue is an example. Another example is the ability of certain types of nerve cells to conduct nerve impulses at speeds of over 100 meters (m) per second. Whatever the capability of interest, the typical goal of physiological research is to discover its mechanistic basis. What cells, enzymes, and other parts of the body are employed, and how are they employed, to enable the animal to perform as it does?

For a detailed example of a mechanism, let's consider light production by fireflies (**FIGURE 1.4**). Each light-producing cell in a firefly's light organ receives molecular oxygen (O_2) by way of a branching system of gas-transport tubules. O_2 enters this system from the atmosphere and is carried by the tubules to all the tissues of the insect's body (see Chapter 23). To understand how a light-producing cell emits flashes of light, let's start with the biochemistry of light production (**FIGURE 1.5A**). A chemical compound (a benzothiazol) named *firefly luciferin* first reacts with ATP to form luciferyl-AMP (*AMP*, adenosine monophosphate). Then, if O_2 can reach the luciferyl-AMP, the two react to form a chemical product in which electrons are boosted to an excited state, and when this electron-excited product returns to its ground state, it emits photons. This sequence of reactions requires a protein catalyst, an enzyme called *firefly luciferase*. A question only recently answered is how cells within the light organ are controlled so that they flash at certain times but remain dark at others. When a firefly is not producing light (**FIGURE 1.5B**), any O_2 that reaches the insect's light cells via its gas-transport tubules is intercepted (and thereby prevented from reacting with luciferyl-AMP) by mitochondria that are positioned (in each cell) between the gas-transport tubules and the sites of the luciferin reactions. The light cells produce light (**FIGURE 1.5C**) when, because of stimulation by the nervous system, the mitochondria become bathed with nitric oxide (NO).[2] The NO blocks mitochondrial use of O_2, allowing O_2 through to react with luciferyl-AMP. Facts like these form a description of the *mechanism* by which fireflies produce light.

The study of a mechanism may become so intricate that decades or centuries are required for a mechanism to be fully understood. By definition, however, the complete mechanism of any given function is present for study in the here and now. A scientist can, in principle, fully describe the mechanism of a process merely by studying existing animals in ever-finer detail.

The study of origin: Why do modern-day animals possess the mechanisms they do?

Suppose a youngster observes a firefly produce a flash of light and asks you to explain what he has seen. One way you could interpret the request is as a question about mechanism. Thus you could answer that the brain of the insect sends nerve impulses that cause the light cells to become bathed with nitric oxide, resulting in the production of excited electrons through the reaction of O_2 with luciferyl-AMP. However, the youngster who asks you to explain

[2] Interestingly, NO—the signaling molecule that controls firefly flashing—is the same molecule that initiates erection of the penis in human sexual activity (see page 490).

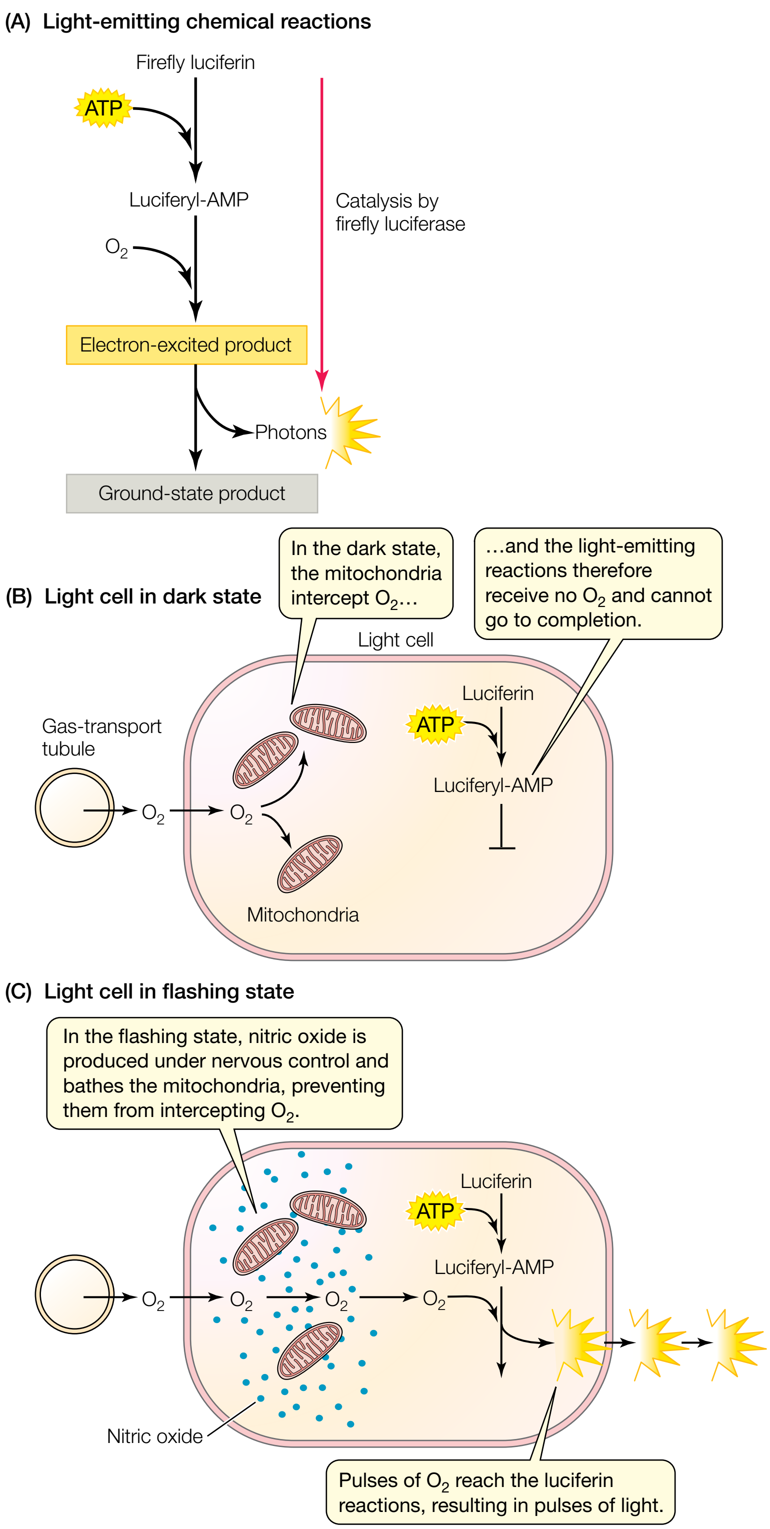


FIGURE 1.5 The mechanism of light production by fireflies (A) The chemistry of light production. (B,C) In the light cells—the cells that compose the light organ—the luciferin reactions are spatially separated from mitochondria. When a light cell is not flashing (B), the mitochondria intercept O_2. However, when a cell *is* flashing (C), O_2 gets through to the luciferin reactions. AMP = adenosine monophosphate; ATP = adenosine triphosphate.

the flashing of a firefly is probably interested in something else. The *reason* the firefly makes light is probably what is on your young friend's mind, rather than the mechanism. That is, the youngster is probably wondering *why* the firefly possesses a mechanism to make light.

For biologists, the answer lies in *evolutionary origins*. The mechanisms of modern-day animals are products of evolution, and thus the reasons for the existence of mechanisms lie in evolutionary processes. The study of evolutionary origins is a central aim of modern physiology because it promises to reveal the *significance* of mechanisms. If we can learn why evolution produced a mechanism, we will better understand what (if anything) animals gain by having the mechanism.

Because modern-day mechanisms evolved in the past, the question of origins is fundamentally historical. The origins of a mechanism, unlike the mechanism itself, cannot usually be observed directly in the here and now. Instead, origins must usually be studied indirectly, by means of inferences about the past derived from observations we can make in the present. The reliance on indirect reasoning means that evolutionary origins are rarely understood with the same certainty as mechanisms.

Natural selection is a key process of evolutionary origin

Natural selection is just one of several processes by which animals acquire traits during evolution, as we discuss later in this chapter. Natural selection, however, holds a place of special importance for biologists because, of all the modes of evolutionary change, natural selection is believed to be the principal process by which animals become fit to live in their environments.

Natural selection is the increase in frequency of genes that produce phenotypes that raise the likelihood that animals will survive and reproduce. During evolution by natural selection, such genes increase in frequency—over the course of generations—because animals with the genes are differentially successful relative to other members of their species. If we find that a physiological mechanism originated by natural selection within the prevailing environment, we can conclude that the mechanism is an asset; that is, it improves an animal's chances of survival and reproduction within the environment the animal occupies.

Adaptation is an important sister concept to natural selection. Because we discuss adaptation at length later, here we simply state that an adaptation is a physiological mechanism or other trait that is a product of evolution by natural selection. Adaptations are assets; because of the way they originated, they aid the survival and reproduction of animals living in the environment where they evolved. When we speak of the **adaptive significance** of a trait evolved by natural selection, we refer to the reason *why* the trait is an asset: that is, the reason *why* natural selection favored the evolution of the trait.

The light flashes of fireflies usually function to attract mates. The males of each species of firefly emit light flashes in a distinctive, species-specific pattern as they fly, thereby signaling their species identity to females (**FIGURE 1.6**). Using various sorts of evidence, students of fireflies infer that the firefly light-producing mechanism evolved by natural selection because light flashes can be used to