

# Brief Contents

## PART 1 PRINCIPLES OF PHYSIOLOGY



|   |  |    |
|---|--|----|
| 1 | Studying Animal Physiology                                 | 3  |
| 2 | Contemporary Experimental Methods for Exploring Physiology | 17 |
| 3 | Molecules, Energy, and Biosynthesis                        | 41 |
| 4 | Membranes, Channels, and Transport                         | 79 |

## PART 2 PHYSIOLOGICAL PROCESSES



|    |  |     |
|----|--|-----|
| 5  | The Physical Basis of Neuronal Function                          | 113 |
| 6  | Communication Along and Between Neurons                          | 155 |
| 7  | Sensing the Environment  | 215 |
| 8  | The Structural and Functional Organization of the Nervous System | 277 |
| 9  | Glands and Hormones  | 301 |
| 10 | Muscles and Animal Movement                                      | 361 |
| 11 | Behavior: Initiation, Patterns, and Control                      | 425 |

## PART 3 INTEGRATION OF PHYSIOLOGICAL SYSTEMS



|    |   |     |
|----|---|-----|
| 12 | Circulation   | 473 |
| 13 | Gas Exchange and Acid-Base Balance                          | 525 |
| 14 | Ionic and Osmotic Balance                                   | 579 |
| 15 | Acquiring Energy: Feeding, Digestion, and Metabolism        | 631 |
| 16 | Energy Expenditure: Body Size, Locomotion, and Reproduction | 667 |
| 17 | Energetic Costs of Meeting Environmental Challenges         | 699 |



# Contents



|   |           |   |           |
|---|-----------|---|-----------|
| Preface   | xv        | <b>CHAPTER 3 Molecules, Energy, and Biosynthesis</b>        | <b>41</b> |
| <b>PART 1 PRINCIPLES OF PHYSIOLOGY</b>                                      | <b>1</b>  | <b>WATER: THE UNIQUE SOLVENT</b>                            | <b>41</b> |
| <b>CHAPTER 1 Studying Animal Physiology</b>                                 | <b>3</b>  | The Water Molecule  | 41        |
| THE SUBDISCIPLINES OF ANIMAL PHYSIOLOGY                                     | 4         | Properties of Water   | 42        |
| THE HISTORY OF ANIMAL PHYSIOLOGY  | 4         | Water as a Solvent  | 42        |
| WHY STUDY ANIMAL PHYSIOLOGY?  | 5         | <b>PROPERTIES OF SOLUTIONS</b>                              | <b>44</b> |
| Scientific Curiosity  | 5         | Concentration, Colligative Properties, and Activity         | 44        |
| Commercial and Agricultural Applications                                    | 5         | Ionization of Water   | 45        |
| Insights into Human Physiology  | 5         | Acids and Bases   | 46        |
| CENTRAL THEMES IN ANIMAL PHYSIOLOGY   | 5         | The Biological Importance of pH                             | 47        |
| Structure/Function Relationships  | 6         | The Henderson-Hasselbalch Equation                          | 48        |
| Adaptation, Acclimatization, and Acclimation                                | 7         | Buffer Systems  | 48        |
| Homeostasis   | 8         | Electric Current in Aqueous Solutions                       | 49        |
| Feedback-Control Systems  | 9         | <b>Spotlight 3-1 Electrical Terminology and Conventions</b> | <b>49</b> |
| Conformity and Regulation   | 9         | Binding of Ions to Macromolecules                           | 51        |
| THE LITERATURE OF THE PHYSIOLOGICAL SCIENCES                                | 10        | <b>BIOLOGICAL MOLECULES</b>                                 | <b>52</b> |
| <b>Spotlight 1-1 The Concept of Feedback</b>                                | <b>11</b> | Lipids  | 52        |
| ANIMAL EXPERIMENTATION IN PHYSIOLOGY  | 12        | Carbohydrates   | 53        |
| <b>CHAPTER 2 Contemporary Experimental Methods for Exploring Physiology</b> | <b>17</b> | Proteins  | 54        |
| FORMULATING AND TESTING HYPOTHESES  | 17        | Nucleic Acids   | 57        |
| Animal Physiology and the August Krogh Principle                            | 18        | <b>ENERGETICS OF LIVING CELLS</b>                           | <b>59</b> |
| Experimental Design and Levels of Biological Organization                   | 18        | Energy: Concepts and Definitions                            | 59        |
| POPULAR MOLECULAR TECHNIQUES IN PHYSIOLOGY                                  | 18        | Transfer of Chemical Energy by Coupled Reactions            | 61        |
| Tracing Molecules with Radioisotopes  | 18        | ATP: Energy Source for the Cell                             | 62        |
| Visualization Techniques Using Antibodies                                   | 19        | Temperature and Reaction Rates                              | 64        |
| Genetic Engineering   | 21        | <b>ENZYMES: GENERAL PROPERTIES</b>                          | <b>65</b> |
| CELLULAR TECHNIQUES   | 24        | Enzyme Specificity and Active Sites                         | 65        |
| Uses of Microelectrodes and Micropipettes                                   | 24        | Mechanism of Catalysis by Enzymes                           | 65        |
| Microscopic Techniques  | 26        | Effects of Temperature and pH on Enzymatic Reactions        | 66        |
| Cell Culture  | 30        | Cofactors   | 66        |
| BIOCHEMICAL ANALYSIS  | 32        | Enzyme Kinetics   | 67        |
| Measuring Composition: What Is Present?                                     | 32        | Enzyme Inhibition   | 70        |
| Measuring Concentration: How Much Is Present?                               | 35        | <b>REGULATION OF METABOLIC REACTIONS</b>                    | <b>71</b> |
| EXPERIMENTS WITH ISOLATED ORGANS AND ORGAN SYSTEMS                          | 36        | Control of Enzyme Synthesis                                 | 71        |
| OBSERVING AND MEASURING ANIMAL BEHAVIOR                                     | 36        | Control of Enzyme Activity                                  | 71        |
| The Power of Behavioral Experiments   | 36        | <b>METABOLIC PRODUCTION OF ATP</b>                          | <b>72</b> |
| Methods in Behavioral Research  | 37        | Oxidation, Phosphorylation, and Energy Transfer             | 74        |
| THE IMPORTANCE OF PHYSIOLOGICAL STATE IN RESEARCH                           | 38        | <b>EFFICIENCY OF ENERGY METABOLISM</b>                      | <b>75</b> |
|   |           | <b>CHAPTER 4 Membranes, Channels, and Transport</b>         | <b>79</b> |
|   |           | <b>MEMBRANE STRUCTURE AND ORGANIZATION</b>                  | <b>79</b> |
|   |           | Membrane Composition  | 79        |
|   |           | The Fluid Mosaic Model of Membranes                         | 81        |
|   |           | Variation in Membrane Form                                  | 83        |
|   |           | <b>CROSSING THE MEMBRANE: AN OVERVIEW</b>                   | <b>83</b> |
|   |           | Diffusion   | 84        |
|   |           | Membrane Flux   | 84        |
|   |           | Osmosis   | 85        |



|   |           |
|---|-----------|
| Osmolarity and Tonicity   | 86        |
| Electrical Influences on Ion Distribution                                       | 86        |
| Donnan Equilibrium  | 87        |
| OSMOTIC PROPERTIES OF CELLS   | 88        |
| Ionic Steady State  | 88        |
| Cell Volume   | 89        |
| MECHANISMS FOR TRANSMEMBRANE MOVEMENTS  | 90        |
| Passive (Simple) Diffusion  | 91        |
| Passive Transport (Facilitated Diffusion)                                       | 92        |
| <b>Spotlight 4-1 Artificial Bilayers</b>  | <b>94</b> |
| Active Transport  | 96        |
| The Na <sup>+</sup> /K <sup>+</sup> Pump as a Model of Primary Active Transport | 96        |
| Cotransport   | 97        |
| Summary of Primary Active Transport   | 98        |
| ION GRADIENTS AS A SOURCE OF ENERGY   | 99        |
| Production of Electrical Signals  | 99        |
| Chemiosmotic Energy Transduction  | 99        |
| MEMBRANE SELECTIVITY  | 100       |
| Selectivity for Electrolytes  | 100       |
| Selectivity for Nonelectrolytes   | 101       |
| ENDOCYTOSIS AND EXOCYTOSIS  | 101       |
| Mechanisms of Endocytosis   | 102       |
| Mechanisms of Exocytosis  | 102       |
| JUNCTIONS BETWEEN CELLS   | 103       |
| Gap Junctions   | 103       |
| Tight Junctions   | 105       |
| EPITHELIAL TRANSPORT  | 105       |
| Active Salt Transport Across an Epithelium                                      | 106       |
| Transport of Water  | 108       |

## PART 2 PHYSIOLOGICAL PROCESSES



|  |            |
|--|------------|
| <b>CHAPTER 5 The Physical Basis of Neuronal Function</b>                   | <b>113</b> |
| OVERVIEW OF NEURONAL STRUCTURE, FUNCTION, AND ORGANIZATION                 | 113        |
| Transmission of Signals in a Single Neuron                                 | 115        |
| Transmission of Signals Between Neurons                                    | 115        |
| Organization of the Nervous System   | 117        |
| MEMBRANE EXCITATION  | 118        |
| Measuring Membrane Potentials  | 118        |
| <b>Spotlight 5-1 The Discovery of "Animal Electricity"</b>                 | <b>119</b> |
| Electrical Properties of Membranes   | 120        |
| The Role of Ion Channels   | 122        |
| PASSIVE ELECTRICAL PROPERTIES OF MEMBRANES                                 | 122        |
| Membrane Resistance and Conductance  | 124        |
| Membrane Capacitance   | 124        |
| <b>Spotlight 5-2 Comparing Membrane Properties of Different Cells</b>      | <b>124</b> |
| ELECTROCHEMICAL POTENTIALS   | 126        |
| The Nernst Equation: Calculating the Equilibrium Potential for Single Ions | 128        |

|  |            |
|--|------------|
| <b>Spotlight 5-3 A Quantitative Consideration of Charge Separation Across Membranes</b>                    | <b>128</b> |
| The Goldman Equation: Calculating the Steady-State Potential for Multiple Ions                             | 129        |
| THE RESTING POTENTIAL  | 131        |
| The Role of Ion Gradients and Channels   | 131        |
| The Role of Active Transport   | 13         |
| ACTION POTENTIALS  | 132        |
| General Properties of Action Potentials  | 133        |
| Ionic Basis of the Action Potential  | 135        |
| <b>Spotlight 5-4 Pioneering Studies of Action Potentials in the Squid Giant Axon</b>                       | <b>136</b> |
| THE NATURE OF ION CHANNELS   | 139        |
| <b>Spotlight 5-5 The Voltage-Clamping Method</b>   | <b>140</b> |
| Voltage-Gated Na <sup>+</sup> Channels   | 141        |
| <b>Spotlight 5-6 Patch-Clamping Techniques</b>   | <b>144</b> |
| Voltage-Gated K <sup>+</sup> Channels  | 144        |
| Absolute and Relative Refractory Periods   | 145        |
| Intracellular Ions and the Na <sup>+</sup> /K <sup>+</sup> Pump in Action Potentials                       | 146        |
| Molecular Structure of Voltage-Gated Ion Channels  | 146        |
| <b>Spotlight 5-7 Ion Channels in Novel Locations: Artificial Membranes and Cellular Expression Systems</b> | <b>148</b> |
| Other Electrically Excitable Channels  | 149        |
| <b>CHAPTER 6 Communication Along and Between Neurons</b>   | <b>155</b> |
| TRANSMISSION OF SIGNALS IN THE NERVOUS SYSTEM: AN OVERVIEW   | 155        |
| TRANSMISSION OF INFORMATION WITHIN A SINGLE NEURON   | 157        |
| Passive Spread of Electrical Signals   | 157        |
| Propagation of Action Potentials   | 159        |
| <b>Spotlight 6-1 Confirmation that Local Circuits Contribute to Action Potentials</b>                      | <b>161</b> |
| Speed of Propagation   | 162        |
| <b>Spotlight 6-2 Extracellular Signs of Impulse Conduction</b>   | <b>163</b> |
| <b>Spotlight 6-3 Axon Diameter and Conduction Velocity</b>   | <b>164</b> |
| Rapid, Saltatory Conduction in Myelinated Axons  | 165        |
| TRANSMISSION OF INFORMATION BETWEEN NEURONS  | 166        |
| Synaptic Structure and Function: Electrical Synapses   | 167        |
| Synaptic Structure and Function: Chemical Synapses   | 167        |
| Fast Chemical Synapses   | 170        |
| <b>Spotlight 6-4 Pharmacological Agents Useful in Neurophysiological Studies</b>                           | <b>173</b> |
| <b>Spotlight 6-5 Calculation of Reversal Potential</b>   | <b>177</b> |
| PRESYNAPTIC RELEASE OF NEUROTRANSMITTERS   | 181        |
| Quantal Release of Neurotransmitters   | 181        |
| Depolarization-Release Coupling  | 182        |



|  |     |   |     |
|--|-----|---|-----|
| Nonspiking Release   | 186 | <b>CHAPTER 8 The Structural and Functional Organization of the Nervous System</b>                     | 277 |
| <b>THE CHEMICAL NATURE OF NEUROTRANSMITTERS</b>                                | 186 | THE FLOW OF INFORMATION IN THE NERVOUS SYSTEM   | 277 |
| Neurotransmitters of Fast, Direct Synaptic Transmission                        | 186 | <i>Spotlight 8-1 Sensing Effectors as Housekeepers</i>  | 279 |
| Neurotransmitters of Slow, Indirect Synaptic Transmission                      | 189 | EVOLUTION OF NERVOUS SYSTEMS  | 280 |
| <b>POSTSYNAPTIC MECHANISMS</b>   | 190 | ORGANIZATION OF THE VERTEBRATE NERVOUS SYSTEM   | 284 |
| Receptors and Channels in Fast, Direct Neurotransmission                       | 190 | The Spinal Cord   | 285 |
| Receptors in Slow, Indirect Neurotransmission                                  | 194 | The Brain   | 287 |
| Neuromodulation  | 196 | The Autonomic Nervous System  | 294 |
| <b>INTEGRATION AT SYNAPSES</b>   | 198 | <b>CHAPTER 9 Glands and Hormones</b>  | 301 |
| <b>SYNAPTIC PLASTICITY</b>   | 202 | CELLULAR SECRETIONS   | 301 |
| Short-Term Homosynaptic Modulation: Facilitation, Depression, and Potentiation | 203 | <i>Spotlight 9-1 Substances with Similar Structures and Functions Secreted by Different Organisms</i> | 303 |
| Heterosynaptic Modulation  | 205 | Surface Secretions: The Cell Coat, Collagen, and Mucus  | 303 |
| Long-Term Potentiation and Depression  | 205 | Packaging and Transport of Secreted Material  | 304 |
| <i>Spotlight 6-6 Neurotransmitters and Psychoactive Drugs</i>                  | 208 | Storage of Secreted Substances  | 307 |
| <b>CHAPTER 7 Sensing the Environment</b>                                       | 215 | SECRETORY MECHANISMS  | 307 |
| <b>GENERAL PROPERTIES OF SENSORY RECEPTION</b>                                 | 216 | Glandular Secretions  | 309 |
| Properties of Receptor Cells   | 216 | Types and General Properties of Glands  | 309 |
| Common Mechanisms and Molecules of Sensory Transduction                        | 218 | <b>ENDOCRINE GLANDS</b>   | 310 |
| From Transduction to Neuronal Output   | 220 | <b>NEUROENDOCRINE SYSTEMS</b>   | 314 |
| Encoding Stimulus Intensities  | 222 | Hypothalamic Control of the Anterior Pituitary Gland  | 316 |
| Control of Sensory Sensitivity   | 225 | <i>Spotlight 9-2 Peptide Hormones</i>   | 317 |
| <b>THE CHEMICAL SENSES: TASTE AND SMELL</b>                                    | 230 | Glandular Hormones Released from the Anterior Pituitary Gland   | 317 |
| Mechanisms of Taste Reception  | 231 | Neurohormones Released from the Posterior Pituitary Gland   | 318 |
| Mechanisms of Olfactory Reception  | 234 | <b>CELLULAR MECHANISMS OF HORMONE ACTION</b>  | 320 |
| <b>MECHANORECEPTION</b>  | 238 | Lipid-Soluble Hormones and Their Receptors  | 321 |
| Insect Mechanoreceptors  | 239 | Lipid-Insoluble Hormones and Intracellular Signaling  | 321 |
| Hair Cells   | 241 | <b>PHYSIOLOGICAL EFFECTS OF HORMONES</b>  | 333 |
| Organs of Equilibrium  | 242 | Metabolic and Developmental Hormones  | 333 |
| The Vertebrate Ear   | 242 | Hormones that Regulate Water and Electrolyte Balance  | 342 |
| <i>Spotlight 7-1 Mechanics of the Basilar Membrane An Insect Ear</i>           | 246 | Reproductive Hormones   | 344 |
| <i>Spotlight 7-2 Unusually Sensitive Sensory Receptors</i>                     | 250 | Prostaglandins  | 348 |
| <b>THERMORECEPTION</b>   | 252 | <b>HORMONAL ACTION IN INVERTEBRATES</b>   | 349 |
| <b>VISION</b>  | 252 | <b>EXOCRINE GLANDS</b>  | 352 |
| Optic Mechanisms: Evolution and Function                                       | 253 | The Vertebrate Salivary Gland   | 352 |
| Compound Eyes  | 254 | Invertebrate Silk Glands  | 354 |
| <i>Spotlight 7-3 Subjective Correlates of Primary Photoresponses</i>           | 257 | <b>ENERGY COST OF GLANDULAR ACTIVITY</b>  | 356 |
| The Vertebrate Eye   | 258 | <b>CHAPTER 10 Muscles and Animal Movement</b>   | 361 |
| Photoreception: Converting Photons into Neuronal Signals                       | 262 | <b>ESSENTIALS OF SKELETAL MUSCLE</b>  |     |
| <i>Spotlight 7-4 The Electroretinogram</i>                                     | 264 | CONTRACTION   | 361 |
| <i>Spotlight 7-5 Light, Pain, and Color Vision</i>                             | 270 | Myofilament Substructure  | 364 |
| <b>LIMITATIONS ON SENSORY RECEPTION</b>  | 271 | Contraction of Sarcomeres: The Sliding-Filament Theory  | 366 |



|   |            |   |            |
|---|------------|---|------------|
| <i>Spotlight 10-1</i> The Geometry of Muscle                      | 368        | Sensory Networks  | 440        |
| Cross-Bridges and the Production of Force                         | 371        | <i>Spotlight 11-2</i> Sensory Tuning Curves   | 441        |
| <i>Spotlight 10-2</i> Motor Molecules                             | 372        | Motor Networks  | 458        |
| <i>Spotlight 10-3</i> Skinned Muscle Fibers                       | 374        | <i>Spotlight 11-3</i> Endocrine Control of Bird Song  | 466        |
| MECHANICS OF MUSCLE CONTRACTION                                   | 375        | Neuroendocrine Control of Behavior  | 467        |
| Relation Between Force and Shortening Velocity                    | 376        |   |            |
| Effect of Cross-Bridges on the Force-Velocity Relation            | 377        | <b>PART 3 INTEGRATION OF PHYSIOLOGICAL SYSTEMS</b>  | <b>471</b> |
| REGULATION OF MUSCLE CONTRACTION                                  | 379        | <b>CHAPTER 12 Circulation</b>   | <b>473</b> |
| The Role of Calcium in Cross-Bridge Attachment                    | 379        | GENERAL PLAN OF THE CIRCULATORY SYSTEM  | 473        |
| Excitation-Contraction Coupling                                   | 380        | Open Circulations   | 473        |
| The Contraction-Relaxation Cycle                                  | 387        | <i>Spotlight 12-1</i> Pressure Measurement  | 475        |
| THE TRANSIENT PRODUCTION OF FORCE                                 | 389        | Closed Circulations   | 475        |
| Series Elastic Components of Muscle                               | 390        | THE HEART   | 476        |
| The Active State  | 391        | Electrical Properties of the Heart  | 477        |
| Contractile States: Twitches and Tetanus                          | 391        | Mechanical Properties of the Heart  | 481        |
| ENERGETICS OF MUSCLE CONTRACTION                                  | 393        | <i>Spotlight 12-2</i> The Frank-Starling Mechanism  | 483        |
| ATP Consumption by the Myosin ATPase and Calcium Pumps            | 393        | Vertebrate Hearts: Comparative Functional Morphology  | 488        |
| Regeneration of ATP During Muscle Activity                        | 393        | HEMODYNAMICS  | 495        |
| FIBER TYPES IN VERTEBRATE SKELETAL MUSCLE                         | 394        | Laminar and Turbulent Flow  | 496        |
| Classification of Fiber Types                                     | 394        | Relationship Between Pressure and Flow  | 497        |
| Functional Rationale for Different Fiber Types                    | 396        | THE PERIPHERAL CIRCULATION  | 499        |
| ADAPTATION OF MUSCLES FOR VARIOUS ACTIVITIES                      | 397        | Arterial System   | 500        |
| Adaptation for Power: Jumping Frogs                               | 397        | Venous System   | 503        |
| Adaptation for Contrasting Functions: Swimming Fish               | 400        | Capillaries and the Microcirculation  | 506        |
| Adaptation for Speed: Sound Production                            | 405        | The Lymphatic System  | 510        |
| High Power and High Frequency: Insect Asynchronous Flight Muscles | 408        | CIRCULATION AND THE IMMUNE RESPONSE   | 511        |
| NEURONAL CONTROL OF MUSCLE CONTRACTION                            | 411        | REGULATION OF CIRCULATION   | 512        |
| Motor Control in Vertebrates                                      | 411        | Control of the Central Cardiovascular System  | 512        |
| Motor Control in Arthropods                                       | 413        | Control of the Microcirculation   | 516        |
| CARDIAC MUSCLE  | 414        | CARDIOVASCULAR RESPONSE TO EXTREME CONDITIONS   | 519        |
| SMOOTH MUSCLE   | 417        | Exercise  | 519        |
| Vertebrate Single-Unit and Multi-Unit Smooth Muscles              | 417        | Diving  | 520        |
| Regulation of Smooth-Muscle Contraction                           | 418        | Hemorrhage  | 522        |
| Unusual Features of Smooth-Muscle Contraction                     | 420        |   |            |
| <b>CHAPTER 11 Behavior: Initiation, Patterns, and Control</b>     | <b>425</b> | <b>CHAPTER 13 Gas Exchange and Acid-Base Balance</b>  | <b>525</b> |
| <i>Spotlight 11-1</i> Behavior in Animals Without Nervous Systems | 426        | OXYGEN AND CARBON DIOXIDE IN THE PHYSICAL ENVIRONMENT   | 525        |
| THE NEURONAL BASIS OF A SIMPLE BEHAVIOR                           | 427        | <i>Spotlight 13-1</i> Early Experiments on Gas Exchange in Animals                                | 526        |
| Simple Reflexes   | 427        | OXYGEN AND CARBON DIOXIDE IN LIVING SYSTEMS   | 526        |
| Principles of Neuronal Control                                    | 430        | <i>Spotlight 13-2</i> Effects of Human Activity on Environmental Oxygen and Carbon Dioxide Levels | 527        |
| THE STUDY OF BEHAVIOR   | 431        | <i>Spotlight 13-3</i> The Gas Laws  | 528        |
| Basic Behavioral Concepts   | 431        | OXYGEN AND CARBON DIOXIDE IN BLOOD  | 529        |
| Examples of Behavior  | 434        | Respiratory Pigments  | 529        |
| PROPERTIES OF NEURONAL CIRCUITS                                   | 439        | Oxygen Transport in Blood   | 531        |





|  |     |  |     |
|--|-----|--|-----|
| Carbon Dioxide Transport in Blood              | 534 | The Urine-Concentrating Mechanism  | 610 |
| Transfer of Gases to and from the Blood        | 535 | <b>Spotlight 14-2</b> Countercurrent Multiplier Systems                          | 611 |
| REGULATION OF BODY pH                          | 539 | Control of Water Reabsorption  | 613 |
| Hydrogen Ion Production and Excretion          | 540 | NON-MAMMALIAN VERTEBRATE KIDNEYS   | 614 |
| Hydrogen Ion Distribution Between Compartments | 541 | EXTRARENAL OSMOREGULATORY ORGANS IN  |     |
| Factors Influencing Intracellular pH           | 543 | VERTEBRATES  | 615 |
| Factors Influencing Body pH                    | 544 | Salt Glands  | 615 |
| GAS TRANSFER IN AIR: LUNGS AND OTHER           |     | Fish Gills   | 618 |
| SYSTEMS  | 545 | INVERTEBRATE OSMOREGULATORY ORGANS   | 621 |
| Functional Anatomy of the Lung                 | 545 | Filtration-Reabsorption Systems  | 621 |
| Lung Ventilation                               | 547 | Secretion-Reabsorption Systems   | 622 |
| <b>Spotlight 13-4</b> Lung Volumes             | 548 | EXCRETION OF NITROGENOUS WASTES  | 624 |
| Pulmonary Circulation                          | 550 | Ammonia-Excreting (Ammonotelic) Animals  | 625 |
| Mechanisms for Ventilation of the Lung         | 551 | Urea-Excreting (Ureotelic) Animals   | 626 |
| Pulmonary Surfactants                          | 555 | Uric Acid-Excreting (Uricotelic) Animals   | 627 |
| Heat and Water Loss Across the Lung            | 555 |  |     |
| Gas Transfer in Bird Eggs                      | 556 |  |     |
| Insect Tracheal Systems                        | 557 |  |     |
| GAS TRANSFER IN WATER: GILLS                   | 559 | <b>CHAPTER 15</b> Acquiring Energy: Feeding,<br>Digestion, and Metabolism        | 631 |
| Functional Anatomy of the Gill                 | 562 | FEEDING METHODS  | 631 |
| REGULATION OF GAS TRANSFER                     | 562 | Food Absorption Through Exterior Body Surfaces                                   | 631 |
| Ventilation-to-Perfusion Ratios                | 562 | Endocytosis  | 631 |
| Neural Regulation of Breathing                 | 564 | Filter Feeding   | 632 |
| RESPIRATORY RESPONSES TO EXTREME               |     | Fluid Feeding  | 633 |
| CONDITIONS                                     | 568 | Seizing Prey   | 634 |
| Reduced Oxygen Levels (Hypoxia)                | 568 | Herbivory and Grazing  | 637 |
| Increased Carbon Dioxide Levels (Hypercapnia)  | 570 | OVERVIEW OF ALIMENTARY SYSTEMS   | 637 |
| Diving by Air-Breathing Animals                | 570 | Headgut: Food Reception  | 640 |
| Exercise                                       | 571 | Foregut: Food Conduction, Storage, and Digestion                                 | 642 |
| SYMMORPHOSIS                                   | 572 | Midgut: Chemical Digestion and Absorption  | 643 |
| SWIMBLADDERS: OXYGEN ACCUMULATION              |     | Hindgut: Water and Ion Absorption and Defecation                                 | 646 |
| AGAINST LARGE GRADIENTS                        | 573 | Dynamics of Gut Structure and the Influence of                                   |     |
| The Rete Mirabile                              | 574 | Diet   | 647 |
| Oxygen Secretion                               | 574 | MOTILITY OF THE ALIMENTARY CANAL   | 648 |
| <b>CHAPTER 14</b> Ionic and Osmotic            | 579 | Muscular and Ciliary Motility  | 648 |
| Balance  |     | Peristalsis  | 648 |
| PROBLEMS OF OSMOREGULATION                     | 579 | Control of Motility  | 649 |
| OSMOREGULATORS AND OSMOCONFORMERS              | 582 | GASTROINTESTINAL SECRETIONS  | 651 |
| OBLIGATORY EXCHANGES OF IONS AND               |     | Exocrine Secretions of the Alimentary Canal                                      | 651 |
| WATER  | 583 | Control of Gastrointestinal Secretions   | 655 |
| Gradients Between the Animal and the           |     | <b>Spotlight 15-1</b> Behavioral Conditioning in Feeding<br>and Digestion        | 656 |
| Environment                                    | 583 | ABSORPTION   | 659 |
| Surface-to-Volume Ratio                        | 583 | Nutrient Uptake in the Intestine   | 660 |
| Permeability of the Integument                 | 583 | Transport of Nutrients in the Blood  | 661 |
| Feeding, Metabolic Factors, and Excretion      | 585 | Water and Electrolyte Balance in the Gut   | 662 |
| Water Loss via Respiration                     | 586 | NUTRITIONAL REQUIREMENTS   | 663 |
| OSMOREGULATION IN AQUEOUS AND                  |     | Nutrient Molecules   | 663 |
| TERRESTRIAL ENVIRONMENTS                       | 588 |  |     |
| Water-Breathing Animals                        | 588 | <b>CHAPTER 16</b> Energy Expenditure: Body<br>Size, Locomotion, and Reproduction | 667 |
| Air-Breathing Animals                          | 590 | THE CONCEPT OF ENERGY METABOLISM   | 667 |
| OSMOREGULATORY ORGANS                          | 593 | DESCRIBING AND MEASURING METABOLIC   |     |
| THE MAMMALIAN KIDNEY                           | 596 | RATE   | 667 |
| Anatomy of the Mammalian Kidney                | 596 | Basal and Standard Metabolic Rates   | 668 |
| Urine Production                               | 598 |  |     |
| <b>Spotlight 14-1</b> Renal Clearance          | 603 |  |     |
| Regulation of pH by the Kidney                 | 608 |  |     |



|   |            |  |     |
|---|------------|--|-----|
| The Cellular and Biochemical Components of Basal Metabolic Rate                     | 669        | DETERMINANTS OF BODY HEAT AND TEMPERATURE                          | 704 |
| Metabolic Scope   | 669        | The Physics of Heat Gain, Loss, and Storage                        | 704 |
| Direct Calorimetry: Measuring Metabolism from Heat Production                       | 670        | General Biological Mechanisms for Regulating Heat Transfer         | 706 |
| <b>Spotlight 16-1 Energy Units (or When Is a Calorie Not a Calorie?)</b>            | <b>671</b> | PHYSIOLOGICAL CLASSIFICATION USING THERMAL BIOLOGY                 | 707 |
| Indirect Calorimetry: Measuring Metabolism from Food Intake and Waste Excretion     | 671        | Homeothermy and Poikilothermy                                      | 707 |
| Radioisotopes: Measuring Metabolism by Tracking Atom Movements                      | 671        | Endothermy and Ectothermy  | 708 |
| Respirometry: Measuring Metabolism from Gas Exchange                                | 672        | Thermal Classification of Real versus Ideal Animals                | 709 |
| Respiratory Quotient  | 673        | THERMAL BIOLOGY OF ECTOTHERMS                                      | 710 |
| Energy Storage  | 674        | Ectotherms in Cold and Freezing Environments                       | 710 |
| Specific Dynamic Action   | 675        | Ectotherms in Warm and Hot Environments                            | 712 |
| BODY SIZE AND METABOLIC RATE  | 675        | Costs and Benefits of Ectothermy Relative to Endothermy            | 714 |
| Isometric and Allometric Scaling of Metabolism                                      | 675        | THERMAL BIOLOGY OF HETEROTHERMS                                    | 715 |
| Interspecific versus Intraspecific Allometry  | 679        | THERMAL BIOLOGY OF ENDOTHERMS                                      | 717 |
| ENERGETICS OF LOCOMOTION  | 681        | The Concept of the Thermal Neutral Zone                            | 718 |
| Animal Size, Velocity, and Cost of Locomotion                                       | 681        | Endothermy in Cold Environments: Producing and Retaining Body Heat | 719 |
| Physical Factors Affecting Locomotion   | 683        | Endothermy in Hot Environments: Dissipating Body Heat              | 722 |
| Aquatic, Aerial, and Terrestrial Locomotion   | 683        | NEURONAL MECHANISMS OF TEMPERATURE CONTROL                         | 725 |
| <b>Spotlight 16-2 The Reynolds Number: Implications for Large and Small Animals</b> | <b>684</b> | Thermostatic Regulation of Body Temperature                        | 725 |
| Locomotory Energetics of Ectotherms versus Endotherms                               | 688        | Thermoregulation During Activity                                   | 728 |
| BODY RHYTHMS AND ENERGETICS   | 688        | THERMOREGULATION AND SPECIALIZED METABOLIC STATES                  | 730 |
| Circadian Rhythms   | 689        | Sleep  | 730 |
| Noncircadian Endogenous Rhythms   | 690        | Torpor   | 730 |
| Biological Rhythms, Temperature Regulation, and Metabolism                          | 690        | Hibernation and Winter Sleep                                       | 731 |
| ENERGETICS OF REPRODUCTION  | 693        | Estivation   | 732 |
| Patterns of Energetic Investment in Reproduction                                    | 693        | Pyrogens and Fever   | 732 |
| The Cost of Egg and Sperm Production  | 694        | ENERGY, ENVIRONMENT, AND EVOLUTION                                 | 733 |
| Parental Care as an Energy Cost of Reproduction                                     | 695        |  |     |
| <b>CHAPTER 17 Energetic Costs of Meeting Environmental Challenges</b>               | <b>699</b> | Appendix 1: Units, Conversions, Constants, and Definitions         | A1  |
| TEMPERATURE DEPENDENCE OF METABOLIC RATE  | 699        | Appendix 2: Logs and Exponentials                                  | A2  |
| The Biochemical and Molecular Basis for Thermal Influences on Metabolism            | 699        | References Cited   | R1  |
|   |            | Glossary   | G1  |
|   |            | Index  | I1  |