

# Principles of Animal Physiology

Christopher D. Moyes Patricia M. Schulte

Third Edition



Principles of

# Animal Physiology

THIRD EDITION

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# Brief Contents

## Part One

Introduction to  
Physiology 2



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### CHAPTER 1

Introduction to Physiological  
Principles 2

### CHAPTER 2

Physiological Evolution of  
Animals 20

### CHAPTER 3

Chemistry, Biochemistry,  
and Cell Physiology 38

## Part Two

The Cellular Basis of  
Animal Physiology 98

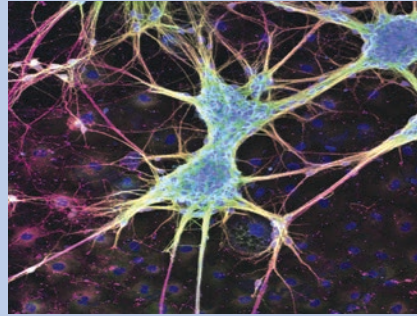


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### CHAPTER 4

Cell Signaling and Endocrine  
Regulation 98

### CHAPTER 5

Neuron Structure and  
Function 154

### CHAPTER 6

Cellular Movement and  
Muscles 208

## Part Three

Integrating Physiological  
Systems 256



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### CHAPTER 7

Sensory Systems 256

### CHAPTER 8

Functional Organization of  
Nervous Systems 310

### CHAPTER 9

Circulatory Systems 356

### CHAPTER 10

Immune Systems 414

### CHAPTER 11

Respiratory Systems 442

### CHAPTER 12

Locomotion 498

### CHAPTER 13

Ion and Water Balance 542

### CHAPTER 14

Digestion and Energy  
Metabolism 592

### CHAPTER 15

Thermal Physiology 634

### CHAPTER 16

Reproductive Physiology 668

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Chris Moyes received his Ph.D. in Zoology from the University of British Columbia in the area of comparative muscle physiology. After postdoctoral fellowships in molecular physiology at the U.S. National Institutes of Health and Simon Fraser University, he took

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

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

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



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

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

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

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

## Dedication

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

# Contents

Preface xix

Acknowledgments xxxiii

## PART ONE INTRODUCTION TO PHYSIOLOGY 2



### CHAPTER 1

## Introduction to Physiological Principles 2

### OVERVIEW 4

### UNIFYING THEMES IN PHYSIOLOGY 5

#### Integration in Physiology 5

Animal physiologists study phenomena at multiple levels of organization 6

Animal physiologists address basic and applied questions 7

#### Physics and Chemistry: The Basis of Physiology 7

The laws of diffusion help to explain the evolution of animal form and function 7

Mechanical theory helps us understand how organisms work 8

Electrical potentials are a fundamental physiological currency 9

Temperature affects physiological processes 9

Biochemical and physiological patterns are influenced by body size 9

#### Form, Function, and Evolution 11

Form and function are the products of evolution 11

Animals have many traits in common 12

What is adaptation? 12

Not all differences are evolutionary adaptations 13

Phenotypes may be homologous or analogous 14

#### Regulation and Homeostasis 15

Animals can be physiological conformers or regulators 15

Homeostasis is the maintenance of internal constancy 15

Feedback loops control physiological pathways 16

Negative feedback loops maintain homeostasis 17

Positive feedback loops cause explosive responses 17

Acclimation and acclimatization result in reversible phenotypic changes 17

Animals can also irreversibly alter their phenotype 17

Summary 18 • Review Questions 19 • Synthesis Questions 19



### CHAPTER 2

## Physiological Evolution of Animals 20

### INTRODUCTION 21

### ANIMAL EVOLUTION AND PHYSIOLOGY 22

#### Multicellularity and the Invention of Tissues 23

Placozoans and sponges lack discrete tissues 24

Cnidarians possess true tissues 24

Bilaterians are triploblastic with some degree of cephalization 25

Protostomes and deuterostomes differ in the embryonic origins of the mouth and anus 25

A coelom forms by enterocoely or schizocoely 25

Platyhelminthes include parasitic and free-living worms 26

Mollusks possess a calcareous shell 27

Annelids have segmented bodies 27

Arthropods show metamerism and tagmatization 27

Deuterostomes include echinoderms and chordates 28

#### Vertebrates 28

Different agnathan ancestors gave rise to modern agnathans and fish 28

Cartilaginous fish evolved from placoderms 29

Several groups of bony fish evolved in the Devonian period 29

Sarcopterygians gave rise to tetrapods 31

Amphibians must return to water to breed 31

Reptiles and their ancestors have dominated land for 300 million years 31

Mammals evolved from therapsid reptiles 32

Birds are modern reptiles 32

### EVOLUTIONARY CONSERVATION AND CONVERGENCE IN ANIMAL PHYSIOLOGY 32

#### Molecular Innovations 33

The myosin gene family divergence underlies much of animal diversity 33

$\text{Na}^+/\text{K}^+$  ATPase is essential for ion homeostasis and excitable tissues 33

The appearance of collagen coincided with tissue formation 35

Hormones extended the range of cell-to-cell signaling 35

#### Integrative Processes 36

The evolution of complexity was accompanied by an increase in cephalization 36

Terrestriality arose in multiple lineages 36  
 Metabolic pathways are broadly conserved, though metabolic rate varies widely 36  
 Summary 37 • Review Questions 37 • Synthesis Questions 37



## CHAPTER 3

# Chemistry, Biochemistry, and Cell Physiology 38

### OVERVIEW 39

### CHEMISTRY 39

#### Energy 39

Food webs transfer energy 40  
 Energy is stored in electrochemical gradients 41  
 Chemical energy is transferred in chemical reactions 42  
 Covalent bonds involve shared electrons 42  
 Weak bonds control macromolecular structure 43  
 Weak bonds are sensitive to temperature 44  
 Reaction rates are influenced by temperature 44

#### Properties of Water 45

The properties of water are unique 45  
 Solubility determines how much solute can dissolve in water 46  
 Solutes influence the physical properties of water 46  
 Solutes move through water by diffusion 46  
 Solutes in biological systems impose osmotic pressure 47  
 Differences in osmolarity can alter cell volume 48  
 Acids and bases alter the pH of water 49  
 Both pH and temperature affect the ionization of biological molecules 50  
 Buffers limit changes in pH 50

### BIOCHEMISTRY 51

#### Enzymes 52

All chemical reactions are governed by the laws of thermodynamics 52  
 Enzymes accelerate reactions by reducing the reaction activation energy 53  
 Enzyme kinetics describe enzymatic properties 53  
 The physicochemical environment alters enzyme kinetics 55  
 Allosteric and covalent regulation control enzymatic rates 56  
 Enzymes convert nutrients to reducing energy 57  
 ATP is a carrier of free energy 57

#### Proteins 58

Proteins are polymers of amino acids 58  
 Proteins are folded into three-dimensional shapes 59  
 Molecular chaperones help proteins fold 60

#### Carbohydrates 60

Animals use monosaccharides for energy and biosynthesis 60  
 Complex carbohydrates perform many functional and structural roles 61

Gluconeogenesis builds glucose from noncarbohydrate precursors 62  
 Glycolysis is a low-efficiency, high-velocity pathway 63  
 Terminal dehydrogenases oxidize NADH under anaerobic conditions 65

### Lipids 66

Fatty acids are long aliphatic chains produced from acetyl CoA 66  
 Fatty acids are oxidized in mitochondrial  $\beta$ -oxidation 67  
 Fatty acids can be converted to ketone bodies 68  
 Triglyceride is the major form of lipid storage 68  
 Phospholipids predominate in biological membranes 69  
 Steroids share a multiple ring structure 70

### Mitochondrial Metabolism 71

The TCA cycle uses acetyl CoA to generate reducing equivalents 71  
 The ETS generates a proton gradient, heat, and reactive oxygen species 72  
 The  $F_1F_0$  ATPase uses the proton motive force to generate ATP 73  
 Creatine phosphokinase enhances energy stores and transfer 74

### Integration of Pathways of Energy Metabolism 74

Oxygen and ATP control the balance between glycolysis and oxidative phosphorylation 75  
 Physical properties of fuels influence fuel selection 75  
 Fuel selection can be calculated from the respiratory quotient 75  
 Energetic intermediates regulate the balance between anabolism and catabolism 76  
 Metabolic rate is the sum of all chemical reactions 76

### CELL PHYSIOLOGY 77

#### Membrane Structure and Transport 77

The lipid profile affects membrane properties 77  
 Lipid membranes are heterogeneous 77  
 Environmental stress can alter membrane fluidity 78  
 Membranes possess integral and peripheral proteins 78  
 Many molecules must move across cellular membranes 78  
 Membrane proteins can facilitate the diffusion of impermeant molecules 79  
 Active transporters use energy to pump molecules against gradients 80  
 The movement of charged molecules depends on the electrochemical gradient 81  
 The Nernst equation allows calculation of the equilibrium potential 82  
 Cells maintain a resting membrane potential 82  
 The  $Na^+/K^+$  ATPase establishes concentration gradients 82  
 The membrane potential represents a balance between equilibrium potentials 82  
 The Goldman equation can be used to calculate membrane potential 83  
 Changes in membrane permeability alter membrane potential 83

#### Cellular Organization 84

Mitochondria are the powerhouse of the cell 84  
 The cytoskeleton controls cell shape and directs intracellular movement 85

The endoplasmic reticulum and Golgi apparatus mediate vesicular traffic 85

The extracellular matrix mediates interactions between cells 86

Most tissues are composed of multiple cell types 88

Epithelial tissues share four specialized properties that affect solute movements 88

Solutes move across epithelial tissues by paracellular and transcellular transport 89

**Physiological Genetics and Genomics** 90

Nucleic acids are polymers of nucleotides 90

DNA is a double-stranded  $\alpha$ -helix packaged into chromosomes 90

DNA is organized into genomes 91

Transcriptional control acts at gene regulatory regions 91

RNA degradation influences RNA levels 92

Global changes in translation control many pathways 93

Cells rapidly reduce protein levels through protein degradation 93

Protein variants arise through gene duplications and rearrangements 93

Ancient genome duplications contribute to physiological diversity 95

Summary 96 • Review Questions 96 • Synthesis Questions 97

• Quantitative Questions 97

## PART TWO THE CELLULAR BASIS OF ANIMAL PHYSIOLOGY 98



### CHAPTER 4

## Cell Signaling and Endocrine Regulation 98

### OVERVIEW 99

### THE BIOCHEMICAL BASIS OF CELL SIGNALING 101

#### General Features of Cell Signaling 101

Indirect signaling systems form a continuum 102

The structure of the messenger determines the type of signaling mechanism 103

#### Peptide Messengers 104

Peptide messengers are released by exocytosis 104

Peptide messengers dissolve in extracellular fluids 105

Peptides bind to transmembrane receptors 105

#### Steroid Messengers 106

Steroids bind to carrier proteins 107

#### ■ BOX 4.1 CHALLENGES TO HOMEOSTASIS Endocrine Disruptors 108

Steroids bind to intracellular receptors 109

#### Biogenic Amines 109

Thyroid hormones diffuse across the membrane 110

Thyroid hormones are hydrophobic messengers 110

#### Other Classes of Messenger 111

Eicosanoids are lipid messengers 111

There are three known gaseous chemical messengers 111

Purines can act as neurotransmitters and paracrines 112

#### Communication of the Signal to the Target Cell 112

Ligand-receptor interactions are specific 113

Receptor type determines the cellular response 113

Receptors have several domains 113

A ligand may bind to more than one receptor 114

Ligand-receptor binding obeys the law of mass action 114

Receptor number can vary 114

Receptor affinity for a ligand can vary 115

Ligand signaling must be inactivated 115

#### ■ BOX 4.2 MATH IN PHYSIOLOGY Ligand-Receptor Interactions 116

### SIGNAL TRANSDUCTION PATHWAYS 118

#### Intracellular Receptors 119

#### Ligand-Gated Ion Channels 121

#### Signal Transduction via Receptor-Enzymes 121

Receptor guanylate cyclases generate cyclic GMP 122

Receptor tyrosine kinases signal through Ras proteins 123

Receptor serine/threonine kinases directly activate phosphorylation cascades 124

#### Signal Transduction via G Protein-Coupled Receptors 124

G protein-coupled receptors are extremely diverse 125

G proteins can act through  $\text{Ca}^{2+}$ -calmodulin 126

G proteins can interact with amplifier enzymes 126

Amplifier enzymes alter the concentration of second messengers 126

Guanylate cyclase generates cGMP 127

Phospholipase C generates phosphatidylinositol 127

Cyclic AMP was the first second messenger discovered 128

Signal transduction pathways can interact 130

### INTRODUCTION TO ENDOCRINE SYSTEMS 130

#### Characteristics of Endocrine Systems 130

Hormone levels are regulated by feedback loops 133



- The actions of insulin illustrate the principle of negative feedback 133
- The actions of oxytocin illustrate the principle of positive feedback 133
- Feedback loops can be complex 134
- Pituitary hormones provide examples of several types of feedback loops 135
- Neurohormones from the posterior pituitary are involved in first-order feedback loops 135
- The hypothalamus regulates the secretion of anterior pituitary hormones 135
- Prolactin is an anterior pituitary hormone involved in a second-order feedback loop 136
- Many anterior pituitary hormones participate in third-order pathways 136
- A single hormone can be regulated by multiple types of feedback pathways 137
- Antagonistic hormone pairs provide precise regulation 138
- Hormones can demonstrate additivity and synergism 139
- Hormone levels are influenced by both synthesis and removal 140
- Endocrine pathologies occur when hormone levels are dysregulated 140
- The responsiveness of the target cell can vary 140

■ **BOX 4.3 APPLICATIONS**

- Cell-To-Cell Communication and Diabetes Mellitus 141

- The nervous and endocrine systems interact in the stress response 142
- The hypothalamo-pituitary axis is involved in the stress response 143

**Evolution of Endocrine Systems** 144

- Endocrine systems vary in complexity among animal phyla 144
- Hyperglycemic hormones are an example of an invertebrate neurohormone 144
- The major steroid hormones differ between vertebrates and arthropods 145
- Arthropods also use other terpenoids as hormones 146
- The structure and function of many hormones is highly conserved in vertebrates 146
- Some hormonal pathways have evolved via gene duplication 147
- Some hormones have acquired new functions during vertebrate evolution 147
- Some hormone pathways are reduced in humans 148
- The structure of endocrine glands varies among the vertebrates 148
- The structure of the pituitary differs among vertebrates 149
- The neurohormones of the posterior pituitary vary among vertebrates 149

- Summary 151 • Review Questions 152 • Synthesis Questions 152
- Quantitative Questions 153



**CHAPTER 5**

**Neuron Structure and Function** 154

**OVERVIEW** 155

**SIGNALING IN A VERTEBRATE MOTOR NEURON** 157

**Electrical Signals in Neurons** 157

- Ionic concentration gradients and permeability establish membrane potential 157
- The Nernst equation can be used to calculate the equilibrium potential of an ion 158
- The Goldman equation is used to calculate the membrane potential 159
- The  $\text{Na}^+/\text{K}^+$  ATPase maintains the membrane potential 159

■ **BOX 5.1 MATH IN PHYSIOLOGY**

- Using the Nernst and Goldman Equations 160

- Changes in membrane permeability cause electrical signals 160
- Ion channel function can be studied using the voltage clamp 162

**Signals in the Dendrites and Cell Body** 162

- Graded potentials vary in magnitude 162
- Graded potentials are short-distance signals 163
- Graded potentials can trigger action potentials at the axon hillock 164
- Graded potentials can be integrated across time and space 165

**Signals in the Axon** 166

- Voltage-gated channels generate the action potential 167
- Voltage-gated  $\text{Na}^+$  channels open at the threshold potential 167
- A positive feedback loop drives the depolarization phase 168
- Voltage-gated  $\text{Na}^+$  channels have two gates 168
- Voltage-gated  $\text{K}^+$  channels open slowly 169

■ **BOX 5.2 APPLICATIONS**

- Voltage-Gated  $\text{Na}^+$  Channel Blockers 170

- Both  $\text{Na}^+$  and  $\text{K}^+$  shape the action potential 171
- Action potentials transmit signals across long distances 172
- Vertebrate motor neurons are myelinated 174
- Axons conduct action potentials unidirectionally 174
- Action potential frequency carries information 176

**Signals Across the Synapse** 176

- Intracellular  $\text{Ca}^{2+}$  regulates neurotransmitter release 176
- Action potential frequency influences neurotransmitter release 177
- Acetylcholine is the primary neurotransmitter at the vertebrate neuromuscular junction 178
- Signaling is terminated by acetylcholinesterase 178
- Postsynaptic cells express specific receptors 179
- Neurotransmitter amount and receptor activity influence signal strength 179

**DIVERSITY OF NEURAL SIGNALING** 180

**Structural Diversity of Neurons** 180

- Neurons can be classified based on their function 180

Neurons can be classified based on their structure 180  
 Neurons are associated with glial cells 182

### Diversity of Signal Conduction 184

Voltage-gated ion channels are encoded by multiple genes 184  
 Voltage-gated  $\text{Ca}^{2+}$  channels can also be involved in action potentials 185  
 Conduction speed varies among axons 185  
 The cable properties of the axon influence current flow 185

- BOX 5.3 **CHALLENGES TO HOMEOSTASIS**  
 RNA Editing of Potassium Channels as an Adaptation to Cold Environments 186

Intracellular and membrane resistance influence conduction speed 188

Membrane capacitance influences the speed of conduction 189

Giant axons have high conduction speed 191  
 Myelinated neurons evolved in the vertebrates 192  
 Myelination increases conduction speed 193

### Diversity of Synaptic Transmission 194

Electrical and chemical synapses play different roles 194  
 Chemical synapses have diverse structures 195  
 There are many types of neurotransmitters 196  
 Neurotransmitters can be excitatory or inhibitory 198  
 Neurotransmitter receptors can be ionotropic or metabotropic 198  
 Acetylcholine receptors can be ionotropic or metabotropic 198  
 The biogenic amines play diverse physiological roles 199  
 Neurons can synthesize more than one kind of neurotransmitter 201  
 Neurotransmitter release varies depending on physiological state 201

### Evolution of Neural Signaling 203

Many organisms use electrical signaling 203  
 Action potentials in nonmetazoans involve  $\text{Ca}^{2+}$  204  
 Animals have unique voltage-gated  $\text{Na}^{+}$  channels 204  
 Neurotransmitters evolved from ancient signaling molecules 204

Summary 205 • Review Questions 205 • Synthesis Questions 206  
 • Quantitative Questions 207



## CHAPTER 6

# Cellular Movement and Muscles 208

### OVERVIEW 209

### CYTOSKELETON AND MOTOR PROTEINS 210

#### Microtubules 210

Tubulin is composed of  $\alpha$ -tubulin and  $\beta$ -tubulin 212  
 Microtubules show dynamic instability 213  
 Microtubule polarity determines the direction of movement 214

#### ■ BOX 6.1 **APPLICATIONS**

Pharmaceutical Uses of Microtubule Disruptors 215

Kinesin and dynein move along microtubules 215  
 Cilia and flagella are composed of microtubules 216

#### Microfilaments 217

Microfilaments are polymers of actin 217  
 Actin polymerization can generate movement 218  
 Actin uses myosin as a motor protein 218  
 The sliding filament model describes actino-myosin activity 219  
 Myosin activity is influenced by unitary displacement and duty cycle 222

### MUSCLE 223

#### General Features of Striated Muscles 223

Muscle cells possess thick and thin filaments 224  
 Striated muscle thick and thin filaments are arranged into sarcomeres 224  
 Myosin II has a unique duty cycle and unitary displacement 226  
 Sarcomeric organization determines contractile properties of the muscle cell 226  
 Actino-myosin activity is activated by  $\text{Ca}^{2+}$  228  
 Thick filaments also influence contractile properties 229  
 Muscle contraction can generate force 230  
 Cardiac and skeletal muscle cells differ in some structural properties 231

#### ■ BOX 6.2 **MATH IN PHYSIOLOGY**

Factors Affecting Force, Work, and Power 232

#### Excitation in Vertebrate Skeletal and Cardiac Muscles 234

Striated muscles are all activated by an action potential 234  
 Striated muscles differ in the time course of the action potential 235  
 Cardiac and skeletal muscles differ in refractory periods 236  
 Skeletal muscle excitation is triggered by neurotransmitters 237  
 T-tubules enhance action potential penetration into the myocyte 238  
 Cardiac muscle cells are stimulated by other muscle cells 238

#### Excitation-Contraction Coupling in Striated Muscles 239

Depolarization leads to an increase in cytoplasmic  $[\text{Ca}^{2+}]$  239  
 DHPR activation induces  $\text{Ca}^{2+}$  release from the SR 240  
 Relaxation follows removal of  $\text{Ca}^{2+}$  from the cytoplasm 241  
 Many factors contribute to differences in properties of striated muscles 242

### DIVERSITY IN MUSCLE STRUCTURE AND FUNCTION 243

#### Smooth Muscle 243

- BOX 6.3 **CHALLENGES TO HOMEOSTASIS**  
 Remodeling Muscle in Response to Changing Conditions 244

Smooth muscle lacks organized sarcomeres 244  
 Smooth muscle contraction is regulated by both thick and thin filament proteins 246  
 Latch cross-bridges maintain smooth muscle contraction for long periods 247

**Invertebrate Muscles** 248  
 Many invertebrates possess obliquely striated muscle 248  
 Invertebrate muscles contract in response to graded excitatory postsynaptic potentials 249  
 Asynchronous insect flight muscles do not use  $\text{Ca}^{2+}$  transients 249  
 Mollusk catch muscles maintain contraction for long periods 251

**Specialized Muscles and Transdifferentiated Muscle** 252  
 Sonic muscles produce rapid contractions but generate less force 252  
 Heater organs and electric organs are modified muscles 253  
[Summary 254](#) • [Review Questions 254](#) • [Synthesis Questions 255](#)  
 • [Quantitative Questions 255](#)

**PART THREE INTEGRATING PHYSIOLOGICAL SYSTEMS** 256



**CHAPTER 7**  
**Sensory Systems** 256

**OVERVIEW** 257

**GENERAL PROPERTIES OF SENSORY RECEPTION** 257

**Classification of Sensory Receptors** 259  
 Receptors can be classified based on stimulus location or modality 259  
 Receptors may detect more than one stimulus modality 260  
**Stimulus Encoding in Sensory Systems** 260  
 Sensory pathways encode stimulus modality 260  
 Receptive fields provide information about stimulus location 261  
 Sensory receptors have a dynamic range 261  
 There is a trade-off between dynamic range and discrimination 262  
 Range fractionation increases sensory discrimination 262  
 Sense organs can have a very large dynamic range 263  
 Many receptors encode signals logarithmically 263  
 Tonic and phasic receptors encode stimulus duration 264

**CHEMORECEPTION** 265

**The Olfactory System** 265  
 The vertebrate olfactory system can distinguish thousands of odorants 265  
 Odorant receptors are G protein coupled 265  
 An alternative chemosensory system detects pheromones 267  
 Invertebrate olfactory mechanisms differ from those in vertebrates 268

- **BOX 7.1 APPLICATIONS**  
 Using Pheromones to Alter Behavior 269

**The Gustatory System** 270  
 Taste buds are vertebrate gustatory receptors 270  
 Vertebrate taste receptors use diverse signal transduction mechanisms 270

Coding differs between the olfactory and gustatory systems 272  
 Taste reception differs between vertebrates and invertebrates 272  
 Nociceptors detect noxious chemical stimuli 273

**MECHANORECEPTION** 273

**Touch and Pressure Receptors** 274  
 Vertebrate tactile receptors are widely dispersed 274  
 Vertebrate proprioceptors monitor body position 275  
 Insects have several types of tactile and proprioceptors 275  
**Equilibrium and Hearing** 276  
 Statocysts are the organ of equilibrium for invertebrates 276  
 Insects use a variety of organs for hearing 276  
 Vertebrate organs of hearing and equilibrium contain hair cells 277  
 Tip links are critical for mechanosensory transduction 280  
 Hair cells are found in the lateral line and ears of fish 280  
 Vertebrate ears function in hearing and equilibrium 280  
 The vestibular apparatus is the organ of equilibrium in vertebrates 280  
 The inner ear detects sounds 282  
 In terrestrial vertebrates, hearing involves the inner, middle, and outer ears 284

Cetaceans have highly modified ears 285  
 The inner ear of mammals has specializations for sound detection 286  
 Outer hair cells amplify sounds 286  
 The ears can detect sound location 287

**PHOTORECEPTION** 287

**Photoreceptors** 287  
 The structure of photoreceptor cells differs among animals 287  
 Mammals have two types of photoreceptor cells 288  
 Chromophores allow photoreceptors to absorb light 290  
 The mechanisms of phototransduction differ among organisms 291

**The Structure and Function of Eyes** 291  
 There are two major types of compound eyes in arthropods 293  
 Structurally diverse eyes share underlying molecular similarity 294

The structure of the vertebrate eye relates to its function 294  
 The lens focuses light on the retina 295  
 Vertebrate retinas have multiple layers 295  
 Information from rods and cones is processed differently 296  
 Signal processing in the retina enhances contrast 297  
 The brain processes the visual signal 298  
 Color vision requires multiple types of photoreceptors 300  
 Color vision evolved secondarily in primates 301  
 Some photoreceptors are not involved in vision 302

### Other Sensory Modalities 302

Thermoreceptors detect temperature 302

- BOX 7.2 **CHALLENGES TO HOMEOSTASIS**  
 Circadian Rhythms in the Modern World 303

Electroreceptors detect electrical fields 304  
 Magnetoreceptors detect magnetic fields 305

- BOX 7.3 **MATH IN PHYSIOLOGY**  
 Communication in Weakly Electric Fish 306

Summary 308 • Review Questions 308 • Synthesis Questions 309  
 • Quantitative Questions 309



## CHAPTER 8

# Functional Organization of Nervous Systems 310

### OVERVIEW 311

### ORGANIZATION AND EVOLUTION OF NERVOUS SYSTEMS 312

#### Evolution of Nervous Systems 312

Sponges lack a nervous system 313  
 Cnidarian nerve nets allow complex behaviors 314  
 Nervous system complexity varies among flatworms 315  
 Nematodes and annelids show substantial cephalization 315

### THE ARTHROPOD NERVOUS SYSTEM CONTAINS SEGMENTAL GANGLIA 315

Cephalopods have the largest and most complex brains among invertebrates 316  
 The echinoderms lack an obvious brain 316  
 Vertebrates have a hollow dorsal nerve cord 317

### THE CNS OF VERTEBRATES 317

#### Anatomy of the Vertebrate CNS 317

The vertebrate CNS is encased in cartilage or bone 317  
 The meninges surround the CNS 317  
 The CNS is physiologically separated from the rest of the body 318  
 The CNS contains gray and white matter 319  
 The spinal cord mediates information flow between the brain and body 319

#### The Vertebrate Brain 319

Vertebrate brains have three main regions 320

Brain size varies among vertebrates 321

- BOX 8.1 **MATH IN PHYSIOLOGY**  
 Brain Size and Brain Complexity 322

The relative sizes of brain regions vary among vertebrates 324  
 The hindbrain supports basic functions 325  
 The midbrain is greatly reduced in mammals 325  
 The forebrain controls complex processes 325  
 The corpus callosum allows communication between hemispheres 325  
 The hypothalamus maintains homeostasis 327  
 The limbic system influences emotions 327  
 The thalamus acts as a relay station 328  
 The cortex integrates and interprets information 328  
 The cortex exhibits topographic organization 330  
 Mirror neurons fire in response to observed behaviors 330

### THE PERIPHERAL NERVOUS SYSTEM OF VERTEBRATES 331

#### The Autonomic Nervous System 331

The sympathetic and parasympathetic branches act together to maintain homeostasis 332  
 The anatomy of the sympathetic and parasympathetic branches differs 333  
 The neurotransmitters of the sympathetic and parasympathetic systems differ 334  
 Some effectors receive only sympathetic innervation 335  
 The central nervous system regulates the autonomic nervous system 336  
 The enteric nervous system regulates the gut 337

#### Somatic Motor Pathways 337

### INTEGRATIVE FUNCTIONS OF NERVOUS SYSTEMS 337

#### Coordination of Behavior 338

Reflex arcs control many involuntary behaviors 338  
 Pattern generators initiate rhythmic behaviors 339  
 Pattern generators govern swimming behavior in the leech 339  
 Pattern generators and reflexes are involved in tetrapod locomotion 340  
 The brain coordinates voluntary movements 341  
 Communication is a complex behavior 341

- BOX 8.2 **CHALLENGES TO HOMEOSTASIS**  
 Ocean Acidification Affects Fish Behavior by Disturbing Brain Homeostasis 342

#### Learning and Memory 344

Invertebrates show simple learning and memory 344  
 The hippocampus is important for memory formation in mammals 346

- BOX 8.3 **APPLICATIONS**  
 Functional Magnetic Resonance Imaging and Brain Plasticity 347

#### Regulation and Homeostasis 349

Multiple brain regions send inputs to the hypothalamus 349  
 The hypothalamus helps maintain ion and water balance 349  
 The hypothalamus regulates body temperature 349



- The hypothalamus regulates food intake 349
- The hypothalamus is involved in the stress response 349
- The hypothalamus regulates circadian rhythms 350
- The hypothalamus regulates sleep-wake cycles 351
- Sleep is divided into phases 353

Summary 354 • Review Questions 354 • Synthesis Questions 355  
 • Quantitative Questions 355



## **CHAPTER 9**

# Circulatory Systems 356

### **OVERVIEW** 357

### **UNITY AND DIVERSITY OF CIRCULATORY SYSTEMS** 358

#### **General Characteristics of Circulatory Systems** 358

- Circulatory systems use diverse pumping structures 358
- Circulatory systems can be open or closed 359
- Circulatory systems pump several types of fluids 360
- Blood and hemolymph contain proteins 361
- Blood and hemolymph contain cells 361
- Vertebrate blood has three main components 361

#### **Circulatory Plans of the Major Animal Phyla** 362

- Most annelids have closed circulatory systems 363
- Most mollusks have open circulatory systems 363
- Arthropod circulatory systems vary in complexity 363
- Crustacean hearts are both suction and pressure pumps 364
- Insects have simple open circulatory systems 365
- Chordates have both open and closed circulatory systems 366
- Closed circulatory systems evolved multiple times in animals 366

#### **The Circulatory Plan of Vertebrates** 367

- Vertebrate blood vessels have complex walls 368
- Wall thickness varies among blood vessels 368
- Blood vessels undergo angiogenesis 370
- Low oxygen levels can promote angiogenesis 370
- Vertebrate circulatory systems contain one or more pumps in series 371
- Mammals and birds have completely separated pulmonary and systemic circuits 371
- Many tetrapods have incompletely separated pulmonary and systemic circuits 372

#### **The Physics of Circulatory Systems** 372

- The radius of a tube affects its resistance 373
- The resistance of a vessel determines the flow 373

■ **BOX 9.1 MATH IN PHYSIOLOGY**  
 Poiseuille's Equation 374

- Velocity of flow is determined by pressure and cross-sectional area 375
- Pressure exerts a force on the walls of blood vessels 375

## **STRUCTURE AND FUNCTION OF VERTEBRATE HEARTS** 376

### **Heart Anatomy** 376

- The myocardium can be spongy or compact 377
- Fish heart chambers are arranged in series 378
- Amphibian hearts have three chambers 379
- Most reptiles have five heart chambers 379
- Crocodylians have completely divided ventricles 380
- Birds and mammals have four heart chambers 381
- Cardiac anatomy is related to respiratory mode 382
- Cardiac anatomy changes during development 383

### **The Cardiac Cycle** 384

- Fish hearts contract in series 384
- The mammalian cardiac cycle is similar to that of fish 384
- Some vertebrate hearts fill actively 385
- The right and left ventricles develop different pressures 385

### **Control of Cardiac Contraction** 386

- Pacemaker cells initiate the heartbeat 387
- The nervous and endocrine systems can modulate heart rate 387
- Pacemaker depolarizations can spread via gap junctions 389
- Cardiac action potentials have an extended depolarization phase 389
- Conducting pathways spread the depolarization across the heart 390
- The integrated electrical activity of the heart can be detected with the EKG 390
- The heart functions as an integrated organ 391
- Cardiac output is the product of heart rate and stroke volume 391
- The nervous and endocrine systems can modulate stroke volume 391

■ **BOX 9.2 APPLICATIONS**

Using the EKG to Diagnose Heart Conditions 392

End-diastolic volume modulates stroke volume 394

## **REGULATION OF CIRCULATORY FUNCTION** 395

### **Regulation of Flow** 396

- The arterioles control blood distribution 396
- Myogenic autoregulation maintains blood flow 396
- Metabolic activity and paracrine signals influence blood flow 397
- The nervous and endocrine systems regulate arteriolar diameter 398

### **Regulation of Blood Pressure** 399

- The arteries dampen pressure fluctuations 399
- Mean arterial pressure is determined by systolic and diastolic pressures 400
- The skeletal muscle and respiratory pumps aid venous return to the heart 400
- The veins act as a volume reservoir 401
- Peripheral resistance influences pressure 401
- The baroreceptor reflex is the primary means of regulating MAP 402
- The kidneys also play a role in maintaining blood volume and MAP 403

■ **BOX 9.3 CHALLENGES TO HOMEOSTASIS**

Hypertension 404

Blood pressure can force fluid out of the capillaries 404

The lymphatic system returns filtered fluids to the circulatory system 406

Changes in body position can alter blood pressure and flow 407

Changes in body position can cause orthostatic hypotension 408

Very tall animals must have specialized circulatory systems 408

**The Circulatory System During Exercise** 410

The cardiovascular control center of the brain regulates the circulatory system 410

Cardiac output increases during exercise 410

Patterns of blood flow change during exercise 411

Blood pressure changes only slightly during exercise 411

Higher brain centers are also involved 411

Summary 412 • Review Questions 412 • Synthesis Questions 412

• Quantitative Questions 413



**CHAPTER 10**

**Immune Systems** 414

**OVERVIEW** 415

**INNATE IMMUNITY** 418

**Recognition of Pathogens** 418

Pattern-recognition receptors detect pathogen-associated molecular patterns 418

Toll-like receptors activate immune responses 419

**Phagocytic Cells** 420

Phagocytic cells engulf and digest foreign cells 420

Opsonins promote phagocytosis 421

Complement molecules promote other immune processes 422

**Executing Pathogens in the Innate Immune System** 423

Granulocytes and natural killer cells secrete cytotoxic compounds 423

Antimicrobial peptides can be secreted by many cell types in all multicellular organisms 423

Inflammation is an early response to pathogens and tissue damage 423

**ADAPTIVE IMMUNITY OF VERTEBRATES** 425

■ **BOX 10.1 APPLICATIONS**

Transgenic Mosquitoes 426

**Humoral Immunity** 426

Antibodies are composed of variable and constant regions 427

Diversity in immunoglobulins arises through gene recombination 428

Antibody classes differ in the C regions 429

Complement molecules interact with immunoglobulins 430

**Cell-Mediated Immunity** 430

Antigen-presenting cells display fragments of pathogens on the cell surface 431

T cells recognize MHC; antigen complexes presented on the surface of other immune cells 432

B cells produce antibodies 433

■ **BOX 10.2 MATH IN PHYSIOLOGY**

Elevating Antibody Titer 434

Immune cells move via the lymph 434

Lymphocytes mature in lymph nodes 435

**Integration with Other Physiological Systems** 435

Allergic responses are stimulated by mast cells 435

Increases in body temperature impede pathogen replication 436

The GI tract has immunological defenses 436

■ **BOX 10.3 CHALLENGES TO HOMEOSTASIS**

The Immune System and Thermoregulation 438

Some species can transfer immunity to offspring 438

Steroid hormone levels affect the immune system 439

Summary 441 • Review Questions 441 • Synthesis Questions 441

• Quantitative Questions 441



**CHAPTER 11**

**Respiratory Systems** 442

**OVERVIEW** 443

**RESPIRATORY STRATEGIES** 444

**The Physics of Respiratory Systems** 444

Gases exert a pressure 445

Henry's law describes how gases dissolve in liquids 445

Gases diffuse at different rates 446

Fluids flow from areas of high to low pressure 447

Resistance opposes flow 447

**Types of Respiratory Systems** 448

Very thin animals can rely on diffusion alone for gas exchange 449

Most animals use one of three major respiratory strategies 449

Gas-exchange surfaces are often ventilated 450

Perfusion of the respiratory surface affects gas exchange 450

**VENTILATION AND GAS EXCHANGE** 452

**Ventilation and Gas Exchange in Water** 453

Most mollusks ventilate their gills using cilia 453

Crustacean gills are located on the appendages 454

Echinoderms have diverse respiratory structures 454

Feeding lampreys ventilate their gills tidally 455

Elasmobranchs use a buccal pump for ventilation 455

Teleost fishes use a buccal-opercular pump for ventilation 456

Fish gills are arranged for countercurrent flow 458

**Ventilation and Gas Exchange in Air** 458

Arthropods use a variety of mechanisms for aerial gas exchange 459

Tracheal systems are inefficient in water 460  
 Some aquatic insects breathe through siphons 460  
 Some aquatic insects carry bubbles of air 461  
 Many insects actively ventilate the tracheae 461  
 Air breathing has evolved multiple times in vertebrates 462  
 Amphibians ventilate their lungs using a buccal force pump 463  
 Reptiles ventilate their lungs using a suction pump 465  
 Birds unidirectionally ventilate their lungs 466  
 The alveoli are the site of gas exchange in mammals 467  
 Mammals ventilate their lungs tidally 468  
 The work required for ventilation depends on lung compliance and resistance 469  
 Surfactants increase lung compliance 469  
 Airway resistance affects the work required to breathe 470  
 Aspiration-based pulmonary systems have substantial dead space 470  
 Pulmonary function tests measure lung function and volumes 470

■ **BOX 11.1 APPLICATIONS**  
 Treating Respiratory Distress Syndrome in Premature Infants 471

Ventilation-perfusion matching is important for gas exchange 472

**GAS TRANSPORT TO THE TISSUES** 473

**Oxygen Transport** 473

There are three main types of respiratory pigments 473

- **BOX 11.2 MATH IN PHYSIOLOGY**  
 Pulmonary Function Tests 474

Respiratory pigments have characteristic oxygen equilibrium curves 476  
 The shapes of oxygen equilibrium curves differ 478  
 Blood pH and  $P_{CO_2}$  can affect oxygen affinity 478  
 Root-effect hemoglobins help to deliver oxygen to the swim bladder 479  
 The rete mirabile maintains the low pH and high  $P_{O_2}$  at the gas gland 480  
 The Root effect may also assist in delivering oxygen to systemic tissues 481  
 Temperature affects oxygen affinity 481  
 Organic modulators can affect oxygen affinity 482

**Carbon Dioxide Transport** 482

The carbon dioxide equilibrium curve quantifies carbon dioxide transport 482  
 Blood oxygenation affects  $CO_2$  transport 483  
 Vertebrate red blood cells play a role in  $CO_2$  transport 483  
 The respiratory system can regulate blood pH 484

**REGULATION OF VERTEBRATE RESPIRATORY SYSTEMS** 486

**Regulation of Ventilation** 486

Chemosensory input influences ventilation 487  
 Other factors regulate breathing 488

**Environmental Hypoxia** 488

Fish respond to hypoxia in many ways 488

Air breathers can experience high-altitude hypoxia 488  
 High altitude can cause pathological responses in lowland animals 490  
 Some human populations have colonized high altitudes 490  
 High-altitude mammals have various adaptations to function well in hypoxia 490  
 Birds have a greater tolerance of high-altitude hypoxia than do mammals 490  
 Metabolic suppression is a common response to hypoxia 491

**Diving** 491

Anaerobic metabolism takes over at the aerobic dive limit 491

- **BOX 11.3 CHALLENGES TO HOMEOSTASIS**  
 Adaptations to High Altitude in Bar-Headed Geese 492

Diving animals have increased body oxygen stores 494  
 Nitrogen narcosis is a problem at depth 494  
 Decompression sickness can occur on ascent 495  
 Marine mammals decrease oxygen demand during a dive 495  
 Diving animals have modified responses to  $CO_2$  495

Summary 496 • Review Questions 496 • Synthesis Questions 496  
 • Quantitative Questions 497



**CHAPTER 12**

**Locomotion** 498

**OVERVIEW** 499

**LOCOMOTOR SYSTEMS** 499

**Muscle Fiber Types** 500

Many invertebrates use simple circular and longitudinal muscles to move 500  
 Fish have anatomically separated muscle fiber types 502  
 The pattern of locomotor muscle contraction is controlled by motor neurons 503  
 Tetrapods have a multiplicity of fiber types 504  
 Locomotor muscles are organized into locomotor modules and functional groups 505

**Energy Metabolism** 506

Glycolysis and mitochondria support different types of locomotion 507  
 Mitochondrial content influences muscle aerobic capacity 507  
 Muscle must recover from high-intensity activity 508  
 Metabolic transitions accompany prolonged exercise 508  
 Hormones control fuel oxidation in muscle 509

**Perfusion and Oxygen Delivery to Muscle** 511

Capillary networks bring oxygen to vertebrate muscle fibers 511

- **BOX 12.1 APPLICATIONS**  
 Exercise and Type 2 Diabetes Mellitus 512

Vasoactive agents regulate blood vessel diameter 512

Myoglobin aids in oxygen delivery and utilization 513

Locomotor physiology is maximized in animal athletes 514

### **Skeletal Systems** 515

Hard skeletons are made from cellular secretions 515

- **BOX 12.2 CHALLENGES TO HOMEOSTASIS**  
Migration 516

Vertebrate skeletons are composed of mineralized calcium 516

Skeletal components act as mechanical levers 518

Skeletons can store elastic energy 519

Work loops determine if a muscle is working as motor, brake, or strut 521

## **MOVING IN THE ENVIRONMENT** 522

### **Gravity and Buoyancy** 522

Body composition influences buoyant density 523

Lipid accumulations aid buoyancy in zooplankton and chondrichthians 523

Gas bladders aid buoyancy in bony fish 523

### **Fluid Mechanics** 524

Reynolds numbers determine turbulent or laminar flow 525

The relative importance of viscous and inertial effects determine Re 526

Streamlining reduces drag 526

### **Aerodynamics and Hydrodynamics** 527

Aerofoils and hydrofoils generate lift 527

Soaring uses lift from natural air currents to overcome gravity 528

True flight arose at least four times 529

Fluid movements can generate propulsion 530

Fin and wing shapes influence fluid movements 531

### **Terrestrial Life** 532

Aquatic animals invaded the land several times 532

Metamorphosis remodels anatomy and physiology for terrestrial locomotion 533

Flightless birds evolved in the absence of terrestrial predators 533

Animals of similar geometry should be able to jump to the same heights 534

Terrestrial animals require strong bones and postural musculature 534

### **Energetics of Movement** 535

Energy demands of movement can be expressed as total costs or mass-specific costs 535

- **BOX 12.3 MATH IN PHYSIOLOGY**  
COT in Cod 536

Animals change style of movement to alter the costs of locomotion 537

Environment determines energetic costs 537

Body size affects costs of locomotion 538

[Summary 540](#) • [Review Questions 540](#) • [Synthesis Questions 541](#)

• [Quantitative Questions 541](#)



## **CHAPTER 13**

# **Ion and Water Balance** 542

### **OVERVIEW** 543

### **IONIC AND OSMOTIC REGULATION** 544

#### **Strategies for Ionic and Osmotic Regulation** 545

Animals may be regulators or conformers 545

The environment provides water in many forms 546

Solute can be classified as perturbing, compatible, or counteracting 547

#### **Evolution, Environment, and Osmoregulation** 548

Marine invertebrates are osmoconformers 548

Most ancient fish are osmoconformers 549

Bony fish are ionoregulators and osmoregulators 549

Some fish move between freshwater and seawater 550

Terrestriality evolved multiple times in animals 550

The integument is an osmotic barrier 551

Desert animals have water-conserving adaptations 553

- **BOX 13.1 CHALLENGES TO HOMEOSTASIS**  
Life Without Water 554

#### **Nitrogen Excretion** 555

Ammonia is produced in amino acid metabolism 555

Ammonia can be excreted across epithelial tissues 556

Birds, reptiles, and insects excrete uric acid 556

Urea is produced in the ornithine-urea cycle 557

Each nitrogenous waste strategy has inherent costs 558

The mode of nitrogen excretion can change with development or environment 558

Cartilaginous fish produce urea as an osmolyte 559

### **THE KIDNEY** 559

#### **Kidney Structure and Function** 560

The nephron is the functional unit of the kidney 561

The kidney performs four main processes 562

Filtration occurs at the glomerulus 562

Glomerular filtration pressure is affected by hydrostatic pressure and oncotic pressure 563

- **BOX 13.2 MATH IN PHYSIOLOGY**  
Calculating Glomerular Filtration Rate (GFR) and Renal Clearance 564

The kidney can maintain GFR across a range of blood pressures 565

The primary urine is modified by reabsorption and secretion 567

Cellular properties differ among regions of the tubule 568

The proximal tubule reabsorbs salts and organic metabolites 569

The loop of Henle mediates sequential uptake of water, then salt 570

The distal tubule mediates  $K^+$  secretion,  $NaCl$  reabsorption, and hormone-sensitive water recovery 571

The collecting duct regulates ion and water flux 571

The loop of Henle creates a countercurrent multiplier 572

Vasopressin alters the permeability of the collecting duct 573



Recycling of urea helps to establish the osmotic gradient in the medulla 574

The vasa recta maintains the medullary osmotic gradient via a countercurrent exchanger 574

Micturition is regulated by reflex and higher pathways 575

### Roles of the Kidney in Homeostasis 575

Aldosterone regulates sodium and potassium balance 575

The renin-angiotensin-aldosterone pathway regulates blood pressure 575

Natriuretic peptides also play a role in sodium balance 576

The respiratory system and excretory system contribute to acid-base balance 576

### Water Intake and Excretion 577

Hypothalamic factors regulate thirst 577

The excretory system interacts with the cardiovascular system to regulate blood pressure 578

### Evolutionary Variation in the Structure and Function of Excretory Systems 580

Invertebrates have primitive kidneys called nephridia 580

Insects use Malpighian tubules and the hindgut for ion and water regulation 581

Chondrichthian kidneys produce hypoosmotic urine and retain urea 582

The role of the fish kidney differs in freshwater and seawater 583

The amphibian kidney changes in metamorphosis 583

Terrestrial animals have kidneys that help conserve water 584

Fish gills transport ions into and out of the water 584

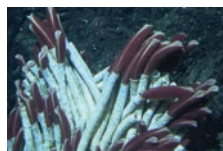
Digestive epithelia mediate ion and water transfers 586

Reptiles and birds possess salt glands 586

#### ■ BOX 13.3 APPLICATIONS Conservation Physiology of Salmon 587

Elasmobranch rectal glands excrete  $\text{Na}^+$  and  $\text{Cl}^-$ , while retaining urea 588

Summary 590 • Review Questions 590 • Synthesis Questions 590  
• Quantitative Questions 591



## CHAPTER 14 Digestion and Energy Metabolism 592

### OVERVIEW 593

### THE NATURE AND ACQUISITION OF NUTRIENTS 594

#### Nutrients 594

Diets provide energy for activity, growth, maintenance, and reproduction 594

Vitamins and minerals participate in catalysis 595

Inadequate supply of essential amino acids compromises growth 596

Animals require linoleic and linolenic acid in the diet 597

Digestion of specific nutrients requires specific enzymes 597

Many animals incorporate symbiotic organisms into their digestive physiology 597

Enterosymbionts play multiple roles in digestive physiology 598

### Finding and Consuming Food 598

Animals sense food using chemical, electrical, and thermal cues 598

#### ■ BOX 14.1 APPLICATIONS The Human Microbiome 599

Simple animals digest food within phagocytic vesicles 600

Feeding structures are matched to diet 600

Bird beaks are composed of keratinized tissue 601

Mammals have bony teeth 602

### DIGESTION AND ASSIMILATION 603

#### Digestive Systems 603

Gut complexity is linked to the appearance of the coelom 605

The digestive systems of complex animals maximize surface area 605

Specialized compartments increase the efficiency of digestion 607

Salivary glands secrete water and digestive enzymes 608

The stomach secretes acid and mucus 608

The intestine is where most nutrients are hydrolyzed and absorbed 609

#### Assimilation 611

Carbohydrates are hydrolyzed in the lumen and transported by multiple carriers 611

Proteins are broken down into amino acids by proteases and peptidases 612

Lipids are transported in many forms 613

### DIGESTION AND METABOLISM 615

#### Regulating Digestive Systems in Individuals 615

Hormones control the desire to feed 615

Hormones and neurotransmitters control gastrointestinal secretions 617

Retention time affects the efficiency of nutrient uptake 618

Gut motility is regulated by nerves and hormones that act on smooth muscle 618

#### Metabolic Transitions 619

#### ■ BOX 14.2 MATH IN PHYSIOLOGY Gut Reactor Theory 620

Nutrient stores are regulated between meals 622

#### ■ BOX 14.3 CHALLENGES TO HOMEOSTASIS Obesity 624

Prolonged food deprivation can trigger a starvation response 626

Pythons may rebuild the digestive tract for each meal 627

#### Evolutionary Variation in Metabolic Rate 628

Metabolic rate can be measured by direct or indirect calorimetry 628

Field metabolic rate relies upon doubly labeled water 629

Maximal sustained MR is about five times greater than RMR 629

Body size influences metabolic rate 629  
 Body temperature affects metabolic rate 630  
 The metabolic theory of ecology links animal metabolism to ecological relationships 630

Summary 631 • Review Questions 632 • Synthesis Questions 632  
 • Quantitative Questions 632



## CHAPTER 15

### Thermal Physiology 634

**OVERVIEW** 635

#### HEAT EXCHANGE AND THERMAL STRATEGIES 636

##### Controlling Heat Fluxes 636

Water has a higher thermal conductivity than air 637  
 Convective heat exchange depends on fluid movements 638  
 Radiant energy warms some animals 638  
 Evaporation induces heat losses 639  
 Ratio of surface area to volume affects heat flux 639  
 Insulation reduces thermal exchange 640

##### Thermal Strategies 640

Poikilotherms and homeotherms differ in the stability of  $T_B$  641  
 Ectotherms and endotherms differ in the source of body thermal energy 641  
 Heterotherms exhibit temporal or regional endothermy 641  
 Animals have a characteristic degree of thermotolerance 642  
 Temperature affects metabolic scope 644  
 The evolution of thermal tolerance has complex origins 644

#### COPING WITH A CHANGING BODY TEMPERATURE 645

##### Macromolecular Structure and Metabolism 645

Animals can remodel membrane fluidity 645

- BOX 15.1 **APPLICATIONS**  
 Thermal Tolerance and Conservation Biology of Atlantic Cod 646

Animals remodel membranes to maintain near-constant fluidity 647

Temperature changes enzyme kinetics 648  
 Evolution may lead to changes in enzyme kinetics 649  
 Ectotherms can remodel tissues in response to long-term changes in temperature 649

- BOX 15.2 **MATH IN PHYSIOLOGY**  
 Evaluating Thermal Effects on Physiological Processes Using  $Q_{10}$  and Arrhenius Plots 650

##### Life at High and Low Body Temperatures 650

Some enzymes display cold adaptation 651  
 Stress proteins are induced at thermal extremes 652  
 Ice nucleators control ice crystal growth in freeze-tolerant animals 653  
 Antifreeze proteins can prevent intracellular ice formation 654

## MAINTAINING A CONSTANT BODY

### TEMPERATURE 655

#### Thermogenesis 656

Shivering thermogenesis results from unsynchronized muscle contractions 656

Some insects use metabolic futile cycles to warm flight muscle 657

Membrane leakiness enhances thermogenesis 657

Thermogenin enhances mitochondrial proton leak 658

- BOX 15.3 **CHALLENGES TO HOMEOSTASIS**  
 Evolution and Development of Thermogenin 659

#### Regulating Body Temperature 660

A central thermostat integrates central and peripheral thermosensory information 660

Piloerection reduces heat losses 661

Changes in blood flow affect thermal exchange 661

Counter-current exchangers in the vasculature help retain heat 662

Sweating reduces body temperature by evaporative cooling 663

Panting increases heat loss across the respiratory surface 663

Relaxed endothermy results in hypometabolic states 664

Summary 666 • Review Questions 666 • Synthesis Questions 666  
 • Quantitative Questions 667



## CHAPTER 16

### Reproductive Physiology 668

**OVERVIEW** 669

#### REPRODUCTION 670

#### REPRODUCTIVE ENDOCRINOLOGY 671

##### Reproductive Hormones 671

Vertebrates rely on progesterone, androgens, and estrogens 671

Gonadotropins control steroid hormone levels 672

JH and 20HE control development and reproductive physiology of arthropods 672

- BOX 16.1 **APPLICATIONS**  
 Pesticides Targeting Insect-Specific Hormonal Pathways 674

##### Sex Determination 674

Clonal reproduction is asexual 675

Parthenogenesis is a short-circuit of sexual reproduction 675

Animals may be simultaneous or serial hermaphrodites 675

Sex is determined in some species by environmental conditions 676

#### GAMETOGENESIS AND FERTILIZATION 677

##### Gametogenesis 677

Ova are produced within follicles of somatic tissue 677

The yolk provides building blocks and metabolic precursors 678

Insect eggs are surrounded by a chorion 679  
Egg structure differs in aquatic and terrestrial  
vertebrates 680  
Spermatogenesis requires production of motile  
gametes 680  
Leydig cells and Sertoli cells control spermatogenesis 681  
Reproductive hormones interact with other hormones 682

### Mating, Fertilization, and Embryonic

#### Development 682

- BOX 16.2 **CHALLENGES TO HOMEOSTASIS**  
Reproduction and Stress 683

Mating is under physiological control 684  
Male copulatory organs increase the efficiency of sperm  
transfer 684  
Erection is controlled by vascular changes in the penis 685  
Sperm alter activity in response to chemokinetic and chemotaxic  
molecules 686  
Females use sperm storage to ensure uninterrupted  
reproduction 686  
Individual sperm can compete for the opportunity to fertilize  
the egg 686  
Some animals delay embryonic development 686  
Postfertilization development relies on maternal factors 687  
Amniotes produce four extraembryonic membranes early  
in development 687

Glossary 700

Animal Index 723

Subject Index 729

## REGULATING REPRODUCTION AND DEVELOPMENT IN MAMMALS 688

### Coordinating the Ovarian and Uterine Cycles 688

Hormones control the ovarian and uterine cycles 688  
The follicular phase of ovulation is driven by FSH 689  
Ovulation and the luteal phase follow an LH surge 689  
The endometrial cycle parallels the ovulatory cycle 691  
A placenta forms after a fertilized ovum implants in the uterine  
wall 691  
Maternal changes in physiology accompany pregnancy 692  
Contractions of uterine smooth muscle induce parturition 693

### Postnatal Growth and Development 693

Prolactin also controls parental care of offspring 693  
Milk is a secretory product of mammary glands 694  
Mammary gland secretions include two novel products, casein  
and lactose 695

- BOX 16.3 **MATH IN PHYSIOLOGY**  
Scaling of Milk Production 696

Milk energy output influences infant growth rate 697  
Early postnatal development requires remodeling of each  
physiological system 698

Summary 698 • Review Questions 699 • Synthesis Questions 699  
• Quantitative Question 699

# Preface

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

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

## KEY THEMES

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

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

- Physiology integrates across levels of biological organization from molecules to populations.

- Physiological processes are based in the laws of chemistry and physics.
- Physiological diversity among animals is the result of evolutionary processes.
- Physiological processes are homeostatically regulated.

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

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

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

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

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



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

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

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

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

## NEW FOR THE 3rd EDITION

For the 3rd Edition, we expanded the pedagogical features throughout the text to facilitate students' learning. New

for the 3rd Edition, you will find the following in each chapter:

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

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

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

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

### Chapter 1, Introduction to Physiological Principles

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

### Chapter 2, Physiological Evolution of Animals

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

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

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

and thermal effects, clearing up ambiguity about these topics.

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

#### **Chapter 4, Cell Signaling and Endocrine Regulation**

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

#### **Chapter 5, Neuron Structure and Function**

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

#### **Chapter 6, Cellular Movement and Muscles**

- New Figures to illustrate topics including (1) skeletal muscle structure, explaining how all of the muscles fit together; (2) the impact of arrangement (series versus parallel) on muscle structure; and (3) muscle fiber mosaics.
- An expanded feature on force and work, which consolidates the force/work/power material in a single location.
- New and revised Figures that help distinguish between muscle fiber types, expanding the discussion of smooth muscle.

- A reorganization of the discussion of EC coupling that more clearly distinguishes between cardiac and skeletal muscle.
- A new feature on muscle remodeling in exercise, combining the themes of structural changes and cellular regulation.

#### **Chapter 7, Sensory Systems**

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

#### **Chapter 8, Functional Organization of Nervous Systems**

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

#### **Chapter 9, Circulatory Systems**

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

### Chapter 10, Immune Systems

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

### Chapter 11, Respiratory Systems

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

### Chapter 12, Locomotion

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

### Chapter 13, Ion and Water Balance

- An expanded discussion of osmotic strategies used by animals, highlighting the important transitions that arose in the context of animal evolution.
- A reorganized section on kidney function and regulation, focusing on the four main homeostatic functions: ion balance, osmotic balance, pH balance, and blood pressure regulation.
- A new feature that delves into the quantitative analysis of renal clearance, including an explicit discussion of the concept of a “virtual volume.”

- A new feature, “Conservation Physiology of Salmon,” highlighting recent work showing how ionoregulatory physiology influences the survival of animals in nature.

### Chapter 14, Digestion and Energy Metabolism

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

### Chapter 15, Thermal Physiology

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

### Chapter 16, Reproductive Physiology

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

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

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# Supplements

## COMPANION WEBSITE

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

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Principles of

Animal Physiology

THIRD EDITION

## CHAPTER

## 1

Introduction to  
Physiological  
Principles

## Learning Objectives

After reading this chapter,  
you should be able to:

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



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

Photo source: Frogkick/Fotolia.

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

tidepools, desiccation can be an important challenge, especially on sunny days in exposed areas of the habitat. All of these environmental changes are physically challenging for animals, and animals that live in the intertidal zone have physiological specializations that help them cope with their harsh environment.

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

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

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

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

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



## OVERVIEW

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

Physiology is a central discipline in biology linking the underlying molecular and cellular mechanisms to characteristics of whole organisms such as performance and fitness (Figure 1.2). The physiological properties of an animal are aspects of the animal’s **phenotype**, which includes all of the observable traits of an organism at all levels of biological organization, from the biochemistry of the cell to the anatomy, physiology, and behavior of the animal. Physiological

traits, like other characteristics of animals, are determined in large part by the **genes** of the genome—the **genotype**—but are also influenced by the way the genes are regulated, particularly in response to external conditions. Thus, both the genotype of an organism and its environment interact through development to produce the phenotype of the adult organism.

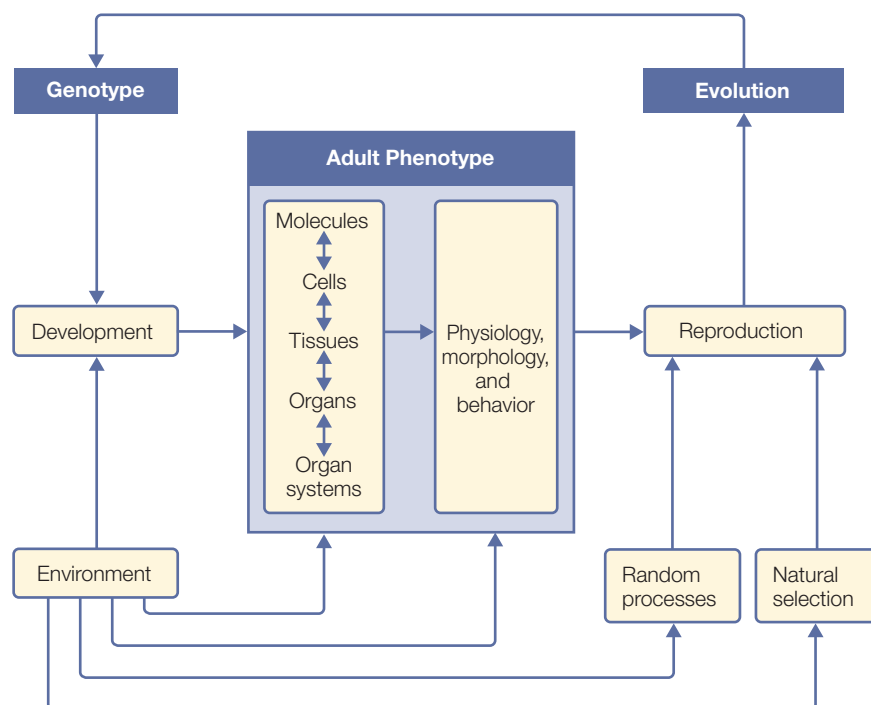
Physiologists must be able to understand how processes occurring at the molecular, cellular, tissue, organ, and organ system levels of organization interact to influence the physiological phenotype. Each physiological process is a product of the activities of complex tissues, organs, and systems that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

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

**FIGURE 1.2** Physiology is a central discipline in biology

**Morphology**, physiology, and behavior are key components of the phenotype of an adult organism. These phenotypes are the result of interactions between the genotype and the environment acting on processes at all levels of biological organization. Variation in

morphology, physiology, and behavior can influence performance and reproductive success. Thus, physiology has implications for evolutionary change in the genotype of a population over time.



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

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

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

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

## UNIFYING THEMES IN PHYSIOLOGY

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

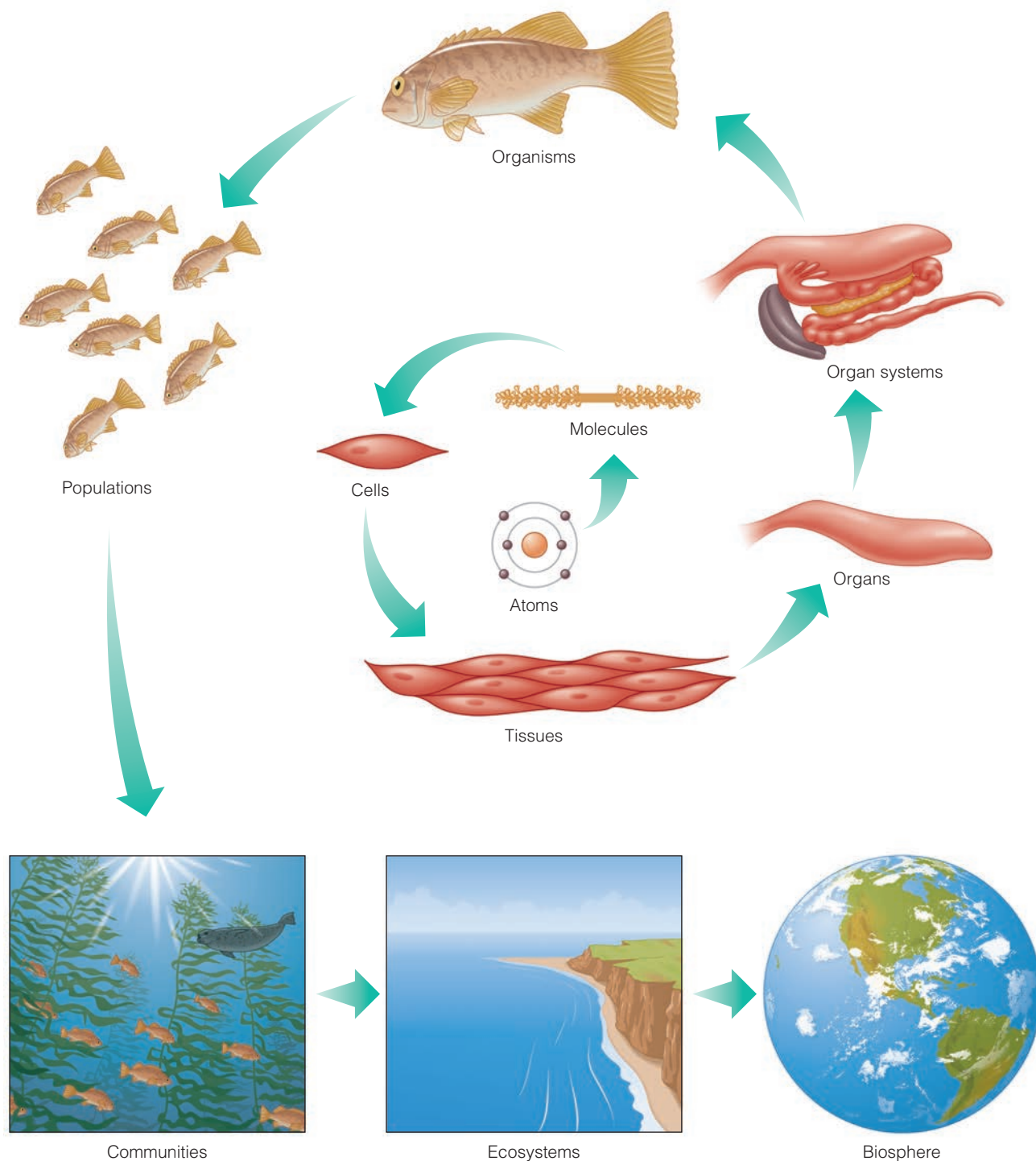
### Integration in Physiology

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

**Table 1.1 Unifying themes in animal physiology**

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

**FIGURE 1.3** Levels of biological organization



**Animal physiologists study phenomena at multiple levels of organization**

Although animal physiology is characterized by its focus on how individual organisms function, physiologists usually consider multiple levels of organization as they strive to understand how animals work. Often a physiologist

interested in a process at one level of organization also studies its function at a lower level. For example, someone studying how a salmon can live in salt water during part of its life and freshwater during another part might study the patterns of changes in ion levels in the blood and also study the cellular mechanisms in the gills that control

those processes. This approach, known as **reductionism**, assumes that we can learn about a system by studying the function of its parts.

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

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

### Animal physiologists address basic and applied questions

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

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

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

also requires substantial knowledge of animal physiology to help develop optimal rearing practices to maintain health and promote the growth of farm animals.

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

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

### CONCEPT CHECK

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

## Physics and Chemistry: The Basis of Physiology

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

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

The process of diffusion affects almost every physiological process, so understanding the physical laws that govern



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

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

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

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

In addition, we can demonstrate from considering Brownian motion, or the random movement of particles in a solution, that the time needed for a particle to diffuse across

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

### Mechanical theory helps us understand how organisms work

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

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

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

### Electrical potentials are a fundamental physiological currency

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

### Temperature affects physiological processes

Because physiological processes have their basis in physical and chemical laws, they are profoundly affected by temperature. The rate of most chemical reactions increases as temperature increases. Increasing the temperature increases the energy of molecules and causes an increase in the number of collisions between molecules in a closed system. Most reactions involve the breakage or formation of chemical bonds, which can occur only if molecules are close to each other. So the more molecular collisions occur, the faster the rate of a chemical reaction. However, at high temperatures many of the intermolecular interactions that stabilize proteins begin to break down and protein function declines. Because most biochemical reactions involve

proteins as **catalysts**, when these catalysts break down, the rate of the reaction falls. The effects of temperature on molecular events combine to influence the way animals interact with environmental temperature. Thus, temperature has a profound effect on processes at all levels of biological organization.

### Biochemical and physiological patterns are influenced by body size

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

**FIGURE 1.4** A cat skeleton and an elephant skeleton, drawn at the same size

Note the proportionally thicker limb bones of the elephant.

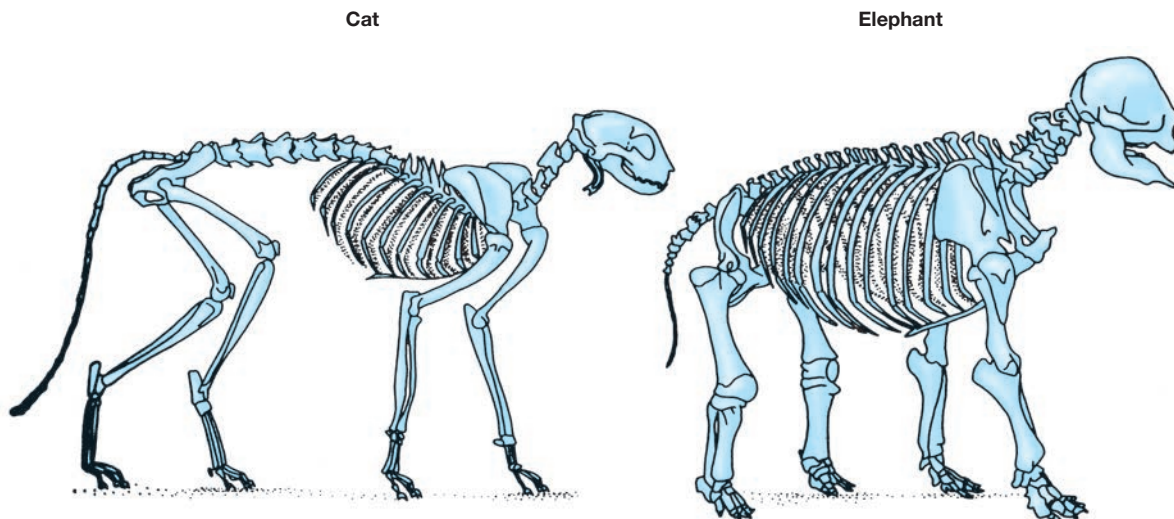


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