Principles of Animal Physiology

SECOND EDITION

James A. Wilson

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James A. Wilson OHIO UNIVERSITY

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Preface to Second Edition

Any author is pleased when a book succeeds well enough to enable a second edition to be published. My goals in writing this new edition remain the same as those described in the preface to the first edition. I have made some changes in the general organization of the text, but all the subject matter has been retained and much has been rewritten, expanded, or brought up to date (within the limits of my writing speed and publication times). The theme of regulation continues to run through this edition and is hopefully better reflected in more examples and diagrams of feedback systems and controls.

So many professors, researchers, and students have aided in the preparation of this new edition by their suggestions and comments that space does not permit me to acknowledge them all by name. However, I wish to thank all of them most sincerely for their time and trouble—without this type of input it would be impossible to produce any output.

Of course, any shortcomings or errors are entirely my own. I hope that the readers of this second edition will be as kind as those of the first and will send me their comments and criticisms.

Finally, I would like to thank the Macmillan people who have all been so helpful and patient, especially the biology editor, Woodrow Chapman, and the production supervisor, Mrs. Elaine Wetterau.

J.A.W

Preface to First Edition

This textbook was begun, as it seems many textbooks are, because of a felt need for a better source of material for the students taking a course. Although several excellent texts are available in the areas of cellular biology, general physiology, and biochemistry, it seemed to me that students at the introductory level needed a text combining discussion of the important aspects of these three areas with a consideration of higher levels of animal structure and functionplus some consideration of the comparative aspects of physiology. To meet this need, this book is entitled Principles of Animal Physiology-an indication that important ideas from all areas of physiology are presented and that the approach is a broader one than is usually found in textbooks. I tend to think of physiology as a unit, not as a series of discrete areas, and I have tried here to examine animal functioning at all levels from the molecular to the whole organism.

Any textbook requires a central theme, and in this book I have taken regulation as a major concept. In addition, I have felt it important to incorporate the similarities and differences of structure and function found in various animals—in one sense, an incorporation of data from comparative physiology.

I did not hesitate to think in terms of a lengthy book. Most available texts, in my opinion, suffer from the major defect of shortness. To present adequately the basic terms, definitions, and concepts of physiology is a lengthy undertaking. Writing a short book also necessitates a degree of

selectivity that amounts to mind reading on the part of the author as to what is going to be taught in physiology courses in many colleges and universities. Such a treatment can only drastically reduce the usefulness of a text. Nevertheless, I too have omitted some topics or given them only sketchy treatment. However, I have tried to include sufficient references to the literature so that the interested student can proceed on his own.

This book is written primarily for the interested student—not one who is necessarily majoring in physiology, but one who finds some fascination in the subject matter of physiology. My philosophy is that if a text is written in such a manner, it will also be good for any student taking a physiology course.

The main purpose of this book is to describe how physiological systems work, and such descriptions are presented primarily in physical-chemical terms. Since physiology is an experimental science, I have tried to include as much as possible on the instrumentation, methods, and approaches used in the study of different levels of animal functioning. As many data as possible are given so that the student may have some opportunity to see the sources of physiological hypotheses and theories. Naturally, space places a limit on such material but, again, references are provided discuss methods and data not completely covered in the text itself.

The book is divided into four parts, beginning with the most basic levels of structure or function in animals and progressing to the most complex. Part I is

with molecules and cell concerned organization and with the chemical and physical principles upon which biochemical reactions and energy exchanges are based. The first chapter contains a brief consideration of systems analysis, feedback regulation, adaptation, and regulation. These are extremely useful concepts to the physiologist, and they are used in all later chapters of the book. I have outlined the nature of biochemical evolution in Chapter 5. Evolution at any level is one of the most important of biological theories and especially deserves recognition in a physiology book that includes elements of comparative physiology. In Chapter 5, I have also included a listing of the names, and a rough indication of the relationships, of living animals. I find that many students taking physiology courses have either forgotten or have never been acquainted with animal names and relations. It is hoped that this listing can be used by the student to identify and relate the organisms discussed in later chapters of the book.

Part II contains the basic cellular mechanisms upon which much regulatory ability, adaptation, and responsiveness to environment are based, including a discussion of specialized cells, especially nerve and muscle cells, which exhibit such mechanisms to a high degree.

Part III on homeostasis carries regulation one step further—to the level of organized systems. The many differences that may be found among animals in the structures and functional abilities used in homeostasis are emphasized, although, as stressed in the first two parts of the book, cellular organization and functioning have many similarities in all animals.

Part IV includes elements of sensory physiology and a brief discussion of animal behavior based on selected examples. It is hoped that these examples will give an indication of how the cellular and organismal activities of the whole animal are coordinated and integrated to produce successful responses to the environment.

Each chapter has its own reference and reading list, usually a lengthy one. Although textbooks are not the place for presenting

long lists of shorter research papers, monographs and reviews by workers in various specialized fields are an aid in a bibliography that includes discussions of the research and its results. Therefore, research papers of proven significance or with important methodological details are given in the reference lists. Citations are inserted in the text in a way that creates a minimum of disruption. The citations were chosen to provide both a chronological map of physiological discoveries and also a listing of researchers associated with particular fields of study. Recognizing that some readers will not have all important sources of physiological information available to them, I have tried to provide two or more references to a given subject when possible, hoping that at least one will be available to the interested reader.

The book certainly has shortcomings, but I hope it will be of value to students, the people for whom it is written. I have not designated it as suitable for any particular level of student. Anyone with a background containing some chemistry, a little physics and mathematics, and some biology can easily learn to appreciate the physiological data. Graduate students may find it useful both for the material covered and for the references to the literature; however, it is a textbook and not an advanced treatise.

No author could be an expert in all the areas covered by this book. I have tried to present those ideas which appear most generally accepted by workers in a given area. At the same time I have not hesitated to present less well-accepted hypotheses, to give my own opinions or interpretations where necessary, and to go out on a limb when extrapolating present knowledge (or lack of it) to future work in physiology. It is hoped that the reader of this book will arrive at the conclusion that comparatively little is settled in physiology and that much remains to be done.

I gratefully acknowledge the many people who have read and criticized all or part of the manuscript. These include Professors G. S. Araki, K. S. Guthe, W. N. Holmes, T. C. Jegla, L. E. Moore, L. M. Passano, and J. Thomas. Of course, all

PREFACE TO FIRST EDITION

errors both of omission and commission are my responsibility.

I also wish to thank John and Mary Richardson for their invaluable help in the preparation of the illustrations and in the preparation of the manuscript. Nearly all of the illustrations are either new or completely redrawn and corrected. Originally I had planned to use many more electron micrographs, but it appeared that in too many cases such micrographs would be of value only to people expert in their inter-

pretation. Therefore, many morphological details are illustrated by line drawings rather than original halftones.

Last, but certainly not least, I wish to express my sincere gratitude to Mr. William D. Eastman, Executive Editor at The Macmillan Company, for his enthusiasm, his help, and especially for his patience when deadlines arrived but manuscript did not.

J.A.W.

Brief Contents

Part I Some Basic Properties of Living Systems

Chapter 1
The Nature of the Subject 3

Chapter 2
Cellular Constituents 44

Chapter 3
Cellular Organization and
Membranes 75

Chapter 4
Energy and Cellular Metabolism 121

Part II Fundamental Units of Animal Regulatory Systems

Chapter 5
Biological Membranes and Material
Transport 163

Chapter 6
Resting and Action Potentials of Excitable Cells 219

Chapter 7 Synaptic and Generator Potentials 269

Chapter 8
Contractility of Muscle and Cells 331

Chapter 9
Aspects of Nervous System
Functioning 405

Chapter 10
Endocrine and Neuroendocrine
Regulation 474

Part III Homeostasis: Regulation of the Internal Environment

Chapter 11
Circulatory Systems—Nature and
Functions 543

Chapter 12
Circulatory Systems—Types, Hearts, and Controls 594

Chapter 13
Water and Solute Regulation 645

Chapter 14
Nutrition and Body Temperature 710

Chapter 15
Animal Respiration 759

Chapter 16 Light, The Animal, and Behavior 802

Author Index 839
Subject Index 855

Detailed Contents

P	art I Some Basic roperties of Living vstems		
	Nature of the Subject 3		
1-1	Purpose and Scope of Physiology 3		
The F	ields of Physiology 4		
1-2	Morphology and Physiology 4		
1-3	Comparative Physiology and		
	Evolution 7		
1-4	Cellular and General Physiology 16		
1-5			
1-6	Other Areas of Physiology 18		
Some Resea	Concepts Underlying Physiological rch 19		
1-7	Experimentation, Mechanism, and		
	Vitalism 19		
1-8	Regulation and Adaptation 20		
1-9	Systems Analysis 23		
1-10	What Is a System? 24		
1-11	Models in Physiology 25		
1-12	The Stimulus and White and Black		
	Boxes 26		
1-13	Cybernetics, Feedback, and		
•	Regulation 29		
1-14	Components of Biological Control		
	Systems 32		
1-15	An Example of Homeostasis 33		
1-16	Instrumentation and Techniques 37		

Literature 38

References and Readings 38

	ter 2
Cellu	lar Constituents 44
2-1	General Composition of Animals 44
Water	45
2-2	The Role of Water 45
2-3	, , , , , , , , , , , , , , , , , , , ,
	Structure 46
	Thermal Properties of Water 49
2-5	The Anomalous Density of Water 50
2-6	The Dielectric Constant and
	Solubility 50
2-7	mile Contention in
	Water 51
2-8	Surface Tension and Viscosity 52
Macre	omolecules 53
2-9	Macromolecular Basis of Life 53
2-10	Amino Acids and Primary Protein
	Structure 54
	Protein Conformation 56
	Summary of Protein Linkages 61
	Primary Structure of Nucleic Acids 6
2-14	Secondary Structure of Nucleic
	Acids 64
Lipid	s and Carbohydrates 66
2-15	Structure and Functions of Lipids 66
	Carbohydrates 68
2-17	Summary 70

References and Readings 71

Cellular Organization and

Resolution 76

3-1 Purpose of the Chapter 75

3-2 Observational Methods and

Chapter 3

Membranes 75

DETAILED CONTENTS	
3-3 The Electron Microscope 763-4 Improving Contrast 773-5 Other Cellular Techniques 80	4-16 Oxidation-Reduction and Cytochromes 145
 Cellular Organization and Membranes 82 3-6 Generalized Cell Models 82 3-7 Compartmentation 82 3-8 Gross Membrane Structure 85 3-9 Evolution of Membrane Models 87 3-10 Myelin 91 3-11 Which Membrane Model Is Correct? 98 	 Control of Cellular Metabolism 150 4-17 Control of Cellular Respiration 150 4-18 Mitochondrial Compartmentation 151 4-19 Enzyme Reversibility, Duplication, and Activation 152 4-20 Feedback Inhibition and Allosteric Effects 154 4-21 Enzyme Induction and Repression 155 4-22 Summary of Metabolic Controls 156
The Extracellular Environment and Intercellular Contacts 99 3-12 The Basal Lamina 99 3-13 Collagen 99 3-14 Intercellular Contacts 102 3-15 Intercellular Junctions 103	References and Readings 157
Cellular Organelles 107 3-16 Mitochondria 107 3-17 The Endoplasmic Reticulum 108 3-18 The Lysosome Concept 109 3-19 Stimulation of Endocytosis 111 3-20 Cytofilaments, Cytotubules, and Cilia 113 3-21 The Nucleus 114 3-22 Discussion 115	Part II Fundamental Units of Animal Regulatory Systems Chapter 5 Biological Membranes and Material Transport 163 5-1 General Role and Nature of
Chapter 4 Energy and Cellular Metabolism 121 Some Principles of Thermodynamics 121. 4-1 Energy and Work 121 4-2 First Law: Conservation of Energy 123 4-3 The Second Law 124	Membranes 163 Diffusion, Osmosis, and Related Properties of Solutions 164 5-2 Simple Diffusion in Solutions 164 5-3 The Rate of Diffusion 167 5-4 Diffusion Through Membranes 168 5-5 Partition Coefficients 171 5-6 Osmosis 172
 4-4 Free Energy and Useful Work 125 4-5 Equilibria and Free Energy 126 4-6 Some Comments on Cellular Reactions 127 	 Some Terms and Units Used in Osmotic Studies 173 Other Colligative Properties 174 Ultrafiltration and Dialysis 175
The Sit Elizythe Activity 13/	Cellular Permeability and Membrane Transport 176 5-10 Fluxes and Methodology 176 5-11 Mechanisms of Material Movement 177 5-12 Erythrocytes and Arbacia Eggs 179 5-13 Cells as Osmometers 183 5-14 Distribution of Ions 183
4-13 Enzyme Nomenclature 138 Energy Metabolism 138 4-14 Metabolism and Glycolysis 138.	 5-15 The Gibbs-Donnan Equilibrium 184 5-16 Impermeable Anions 186 5-17 Active and Passive Transport in Erythrocytes 188 5-18 Energy for Active Transport 189

5-19 5-20	Donnan and Related Potentials 191 Pores and Carriers 196	6-21 6-22	Heat and Metabolism of Nerve 251 Models of Conductance Pathways 252
5-21 5-22 5-23 5-24	Water Transport 198 Active Transport of Glucose 202 Role of the Brush Border 204 Amino Acid Transport 205 The Control of Transport 205	6-23 6-24 6-25 6-26 6-27	Local Circuit Theory 255 Local Circuit Theory 255 Conduction in Myelinated Fibers 256 Voltage-Clamp Studies of Nodes 257 The Compound Action Potential 258 The Acetylcholine Hypothesis 261
	tials Across Epithelial Surfaces 206 Frog Skin Potentials 206	Refer	rences and Readings 262
	Short-Circuited Frog Skin 207 Localization of the Transport Process 208	Syna	oter 7 optic and Generator Potentials 269
5-29	Toad Bladder 210	7-1	Functions of the Dendritic Zone 269
-	ences and Readings 211	7-2	Definition of a Synapse 271 General Types of Synapses 272
Rest	oter 6 ing and Action Potentials citable Cells 219	7-4 7-5	Number and Distribution of Synaptic Endings 275 Ultrastructure of Synapses 277
	e Cell Structure and General	7-6	Chemical Versus Electrical Transmission 278
6-1 6-2 6-3 6-4 6-5 Bioel Poten 6-6 6-7 6-8 6-9 6-10 6-11 6-12	Transmission of Signals 219 The Neuron Theory 219 The Generalized Neuron 220 Axonal and Dendritic Regions 221 Sheaths of Peripheral Axons 223 ectric Potentials: Injury and Resting tials 225 Early Development of Bioelectric Concepts 225 Injury Potentials 226 The Squid Axon and Microelectrodes 227 Resting Potentials 228 The Basis of the Resting Potential 229 Electrical Characteristics of Cells 232 Note on Electrical Conventions 235 ectric Potentials: The Conducted Action tital 235 Stimulation and Recording 235	7-7 7-8 7-9 7-10 7-11 7-12 7-13 Elect Epha 7-14 7-15 7-16	Steps in Chemical Transmission 282 Steps in Chemical Transmission 282 Transmitter Release 282 Action of Transmitter on Subsynaptic Membranes 284 Drug Actions at Synapses 285 Excitatory and Inhibitory EPPs and PSPs 291 Properties of Chemically Transmitting Synapses 293 Chemical Transmitters 296 rically Transmitting Synapses and pses 299 Nature of Electrical Transmission 299 The Crayfish Giant-Motor Synapse 300 Segmental Synapses in the Crayfish and Earthworm 301 The Mauthner Cell 302
6-15 6-16 6-17	The Voltage-Clamp Method 239	Gene 7-20 7-21 7-22	Introduction 305 Classification of Receptors 305 The Pacinian Corpuscle and Crustacean
6-18 6-19 6-20	Cells 243 Perfused Axons 244	7-23 7-24 7-25	Stretch Receptor Organ 306
			xiii

DETAILED CONTENTS

Elect	ric Organs 310	8-21	The Active State 366
7-26	General Nature of Electric Organs 310	8-22	Relaxation and Relaxation Heat 368
	Mechanism of Discharge 312		
7-28	Functions of Electric Organs 314		anical Properties of Muscle 368
Macs	Cellular Contacts and Spontaneous	8-23	Muscle Responses to Single
	ntials, 314		Stimuli 368
	Introduction 314	8-24	Muscle Responses to Repeated
	Cardiac Muscle Cell Junctions 315	0 15	Stimuli 369
	Excitation and Conduction in the		The Length-Tension Curve 371 Work Load and Efficiency of Muscular
	Vertebrate Heart 317	0-20	Contraction 372
7-32	Spontaneous Potentials in Cardiac		Contraction 372
	Muscle 318	Musc	le Models and Other Contractile
7-33	Spontaneous Potentials and Excitation of		ms 375
	Smooth Muscle 320	8-27	The Glycerol-Extracted Muscle
7-34	Neuroglial Systems 321		Fiber 375
7-35	Epithelial Interconnections 322		Actomyosin Threads 376
Dafas	Manage and Bandinas 202		Slow and Fast Fibers 376
nejei	rences and Readings 323	8-30	Comments on Some Crustacean
			Muscles 377
-	pter 8	8-31	Molluscan "Catch" (Paramyosin)
Cont	tractility of Muscle and Cells 331		Muscles 378
8-1	Introduction 331		Smooth and Nonstriated Muscle 380
C			Insect Fibrillar Muscle 383
	ture and Properties of Striated Skeletal le 332		Ciliary Activity 387
			Ameboid Movement 391
	Classification of Muscles 332	8-36	Spasmonemes (or Myonemes) 393
0-3	Ultrastructure of Striated Skeletal Muscle 335	Refer	ences and Readings 393
8-4	Structure of the Sarcomere 339		
	T-filaments 341	Cha	oter 9
	• • •		octs of Nervous System
	nemistry of the Contractile Proteins 342		etioning 405
	Myosin 342		_
	Actin 344	9-1	Introduction 405
	Actomyosin 345	Some	Basic Properties of Nervous
0-Y	Tropomyosin and Troponin 346	Systei	
9-1U	Other Proteins Associated with	9-2	
	Contractility 348	-	Systems 405
The N	Techanism of Muscular Contraction 350	9-3	Structural Components of Nervous
8-11	The Sliding-Filament Model 350		Systems 407
3-12	Operation of the Cross Bridges 351	9-4	•
3-13	Alternative Models of Contraction 353	9-5	Properties of the Reflex Arc 409
3-14	Excitation-Contraction Coupling 354		•
Enora	etic and Thermal Aspects of Muscular		Vertebrate Nervous System 411
	action 357		The Spinal Cord 411
8-15	The Energy Source for	9-7	The Autonomic Nervous System 412
	Contraction 357	9-8	Mammalian Neurons 415
8-16	Phosphagens and ATP-358	9.9	Interneurons 417
3-17	Interactions of Muscle		Convergence and Occlusion 418
	Organophosphates 359	7-11	The Vertebrate Brain 419
3-18	Heat Production 361	Verte	brate Neuromuscular Controls 425
3-19	Shortening Heat 362	9-12	Components of Muscular
3-20	Activation Heat 365		Movements 425

9-13	Feedback Control of Muscular Activity- Muscle Spindles 427		Other Vertebrate Endocrine Structures 487
0.14	The Follow-up Servomechanism		The Regulation of Free Calcium 490
2-14	Theory 431	10 /	
9-15			
,	Activity—Golgi Tendon Organ 433	Inverte	brate Chemical Regulation 491
9-16	Some Vertebrate Reflexes 434	10-10	
	•		Neuroendocrine Systems 491
	tebraté Nervous Systems 437,		Crustacean Endocrine Systems 493
	The Coelenterate Nerve Net 437		Insect Endocrine Systems 494
	The Annelid Nervous System 439	10-13	
	Arthropod Nervous Systems 443		Regulation 495
9-20	Crustacean Neuromuscular Control 445		
	Control 443	Endoc	rine Systems and the Control of
Mech	anoreception and Further Nervous System	Reproc	duction and Growth 496
	oities 450		Mammalian Reproduction 496
9-21	Types of Mechanoreceptors 450		Regeneration and Metamorphosis 499
	Pain, Touch, and Temperature	10-16	Crustacean Molting 502
	Receptors 451	10-17	•
9-23	Equilibrium Receptors—		Transport 503
	Crustaceans 452		
9-24	Mechanoreceptors-Insects 454	Chrom	atophores and the Regulation of Color
9-25	Equilibrium Receptors—	Chang	es 505
	Vertebrates 455	10-18	Nature and Functions of
			Chromatophores 505
Hear	•	10-19	• •
	Insects 457	10-20	• •
	The Lateral Line of Fishes 458		Other Chromatophores 511
9-28			Crustacean Chromatophores 512
	Echolocation in Moths and Bats 462 Echolocation in Other Animals .464	10-23	Vertebrate Chromatophores 515
7-30	Echolocation in Other Animais 404		
Cont	rol of Insect Flight 465	Chemi	ical Reception and Pheromones 517
	Initiation and Maintenance of	10-24	•
	Flight 465	10-25	•
9-32	Dipteran Halteres 466		Vertebrate Chemoreception 520
9-33	Analysis of Locust Flight 466	10-27	Pheromones and Chemical
			Communications 521
Refei	rences and Readings 468	10-28	
			Coelenterates 522
Cha	pter 10		
End	ocrine and Neuroendocrine		gical Rhythms and Chronobiology 524
Reg	ulation 474		Types of Physiological Rhythms 524
10-1	Introduction 474	10-30	į ,
10-2		10-31	
10-3	* ·		Zeitgebers 526
10-4	<u>−</u>	10-32	
10-5	· · · · · · · · · · · · · · · · · · ·	40.00	Rhythms 527
		10-33	5
Verte	brate Chemical Regulation 482	10-34	
10-6	Survey of Vertebrate Endocrine	10-35	2 2
	Functions and Hormones 482	10-36	Conclusions 532
10-7	The Hypothalamus and		
	Hypophysis 482	Refer	ences and Readings 532

Part III Homeostasis: Regulation of the Internal Environment

Chapter 11 Circulatory Systems—Nature and Functions 543

Nature	of Circulatory Systems 543
	Importance of Circulatory

Systems 543

11-2 Types of Transport Systems 544

11-3 Compartmentation of Body Fluids 544

11-4 Components of Circulatory Systems 547

Hemodynamics 549

11-5 Fluid Flows 549

11-6 Viscosity 549

11-7 Hydrostatic Pressure 550

11-8 Fluid Energies 552

11-9 Blood Pressures 554

11-10 Resistance to Blood Flow 555

Blood Vessels 557

11-11 Tissues of the Vascular Wall 557

11-12 Structural Properties of Vascular Walls 559

11-13 Arteries 560

11-14 Veins 561

11-15 The Microcirculation 562

11-16 Capillary Structure 567

11-17 Capillary Functioning 570

11-18 The Lymphatic System 573

Blood 574

11-19 General Nature of Blood 574

11-20 The Hematocrit 575

11-21 Blood Volumes 576

11-22 Erythropoietin and Regulation of Erythropoiesis 577

11-23 Blood Coagulation in Mammals 579

11-24 Hemostasis in the Invertebrates 582

Blood and the Transport of Respiratory

Gases 583

11-25 Hemoglobin 583

11-26 Other Respiratory Pigments 587

11-27 Carbon Dioxide Transport 588

11-28 Acid-Base Balance 588

References and Readings 590

Chapter 12 Circulatory Systems—Types, Hearts, and Controls 594

Pumping Organs: Types and Functions 594

12-1 Introduction 594

12-2 Hydraulic Systems 595

12-3 Echinoderm Hemal and Water Vascular Systems 596

12-4 Annelids 598

12-5 Molluscs 599

12-6 Arthropods 602

12-7 Tunicates 605

12-8 Vertebrates—Fishes 605

12-9 Vertebrates—Amphibians and Reptiles 610

12-10 Vertebrates—Birds and Mammals 613

12-11 Cardiac Output 616

Electrical Activity of Hearts 619

12-12 Pacemakers and Conduction Systems 619

12-13 The Electrocardiogram 620

12-14 Cardiac Ganglia 624

12-15 The Effect of Ions on the Heart 627

12-16 Drugs and the Heart 629

Control of the Heart and Circulation 630

12-17 Starling's Law of the Heart 630

12-18 Innervation of the Mammalian Heart 631

12-19 Vasomotor Control 634

12-20 Chemical Regulation of Vasomotor Tone 635

12-21 Fluid Volumes and Arterial Pressure 636

12-22 Summary of Circulatory Controls 638

References and Readings 639

Chapter 13 Water and Solute Regulation 645

General Concepts of Osmoregulation 645

13-1 Introduction 645

13-2 Some Terms Used in Osmoregulatory Studies 646

13-3 Osmotic Environments and Animals 647

13-4 Some Methods in Osmoregulatory Studies 654

13-5 Physiological Solutions 657

	ory Organs: Methods of Study 659		ter 14
13-6	Introduction 659	Nutri	tion and Body Temperature 710
	Micropuncture Methods 660		7.4
	Stop-Flow Analysis 660	14-1	Introduction 710
13-9	Electrical Potential	Anima	l Nutrition 711
	Measurements 661		Nutritional Requirements 711
13-10			Feeding Mechanism 715
13-11			Digestion—Some Mechanical
	(GFR) 661		Aspects 716
	Renal Plasma Flow (RPF) 662	14-5	Digestion—Chemical Aspects 717
13-13	Transport Maximum T _M 662		Invertebrate Digestive Enzymes 718
			Absorption 720
Excre	ory Organs: Types and Functions 662		Symbiosis 720
13-14	The Contractile Vacuole 662		720
13-15	Coelenterates and Echinoderms 664	Calori	metry and Metabolism 721
13-16	Malpighian Tubules (Insects) 664	14-9	Calorimetric Methods 721
13-17	Protonephridia 666	14-10	The Respiratory Quotient 723
13-18	Nematodes 667	14-11	Energy Storage 724
13-19	Annelids 667		Basal and Standard Metabolism 724
13-20	Crustaceans 667	14-13	Metabolic Rate, Body Weight, and
	Molluscs 669		Surface Area 725
13-22	Structure of the Vertebrate		
	Nephron 669	Homeo	thermic Endothermic Animals 727
13-23	Glomerular Functioning 672		Heat Exchanges 727
13-24	Tubular Functioning: The		Chemical Methods of Heat Gain 72
	Countercurrent:System 675	14-10	Heat-Loss Mechanisms 732
13-25		Pathwa	ays of Thermoregulation 734
	Nephron 679	14.17	Thermoregulation 734 Thermoreceptors 734
13-26		14-18	
	Functioning 681	14-19	
13-27	Control of Fluid Volume 683		oct Fount Hypotheses 750
		Behavi	oral and Adaptive Temperature
Osmor	egulation by Animals 686	Contro	
	Lower Invertebrates 686	14-20	Introduction 738
13-29	Osmoregulation in Annelids 687		Hibernation 738
	Molluscs 688	·14-22	Invertebrate Thermal Control and
13-31	Crustaceans 689		Adaptation 739
13-32	Insects 691 ·		Aquatic Poikilotherms 741
13-33	Vertebrates—Fishes 692	14-24	The Freezing Tolerance of
13-34	Vertebrates—Amphibians and		Animals 743
	Reptiles 693		Reptiles 744
13-35	Vertebrates—Mammals and Birds 695		Amphibians 746
	•	14-27	Homeothermy in Birds and
Vitrogo	en Excretion and Storage 697	44.00	Mammals 746
3-36	Ammonia 697	14-28	Homeotherms in Cold
	Urea and the Ornithine Cycle 699	14.00	Environments 749
3-38	Uric Acid and Purine Metabolism 700	14-29	The Desert Environment 752
3-39	Other End Products of Nitrogen	Referen	ces and Readings 754
	Metabolism 700	acje:en	oces with Exemetings / 34
3-40	Some General Patterns of Nitrogen	O t -	4.5
	Excretion 702	Chapt	
•		Anima	I Respiration 759
Referei	nces and Readings 703	15-1	Introduction 759

DETAILE	D CONTENTS				
	Gas Volumes and Pressures 759	Chapter 16 Light, the Animal, and Behavior 802			
	5-3 Oxygen Diffusion and Solubility 7615-4 Standard Symbols in Respiratory Physiology 765		Mechanisms of Light Perception 802 16-1 Some Characteristics of Light 802 16-2 Animal Photoreception 802		
15-5 15-6 15-7	Some General Comments 766 Molluscs 767 Arthropods—Chelicerates and Insects 768 Arthropods—Crustaceans 771	16-3 16-4 16-5 16-6 16-7 16-8	Structure of the Vertebrate Eye 804 The Retina 805 Rod and Cone Ceils 807 Photochemistry 808 Distribution of Visual Pigments 812		
The Ma	mmalian Respiratory Systems 773 Structure 773	16-9 16-10	Processing of Visual Information 815 The Arthropod Compound Eye 817		
15-10 15-11 15-12	Viscoelasticity of Lungs and Thorax 774 Ventilation—The Mechanics 777 Ventilation—Pressure and Volume Changes 779 Respiratory Controls 781	16-11	The state of the s		
Respira	tory Mechanisms in Other		Cephalopods 825		
15-14 15-15		16-15	Bioluminescence 829		
15-17	tory-Circulatory Adaptations 790 Diving Animals 790 High-Altitude Adaptations 791	16-18	Bacterial Bioluminescence 831 Firefly Bioluminescence 831 Coelenterate Bioluminescence 832 Some Other Invertebrate Systems 833		
15-19	nd Buoyancy 793 Introduction 793	16-21	Bioluminescence in Fishes 833		
15-21	Substitution Methods for Buoyancy Control 793 Gas Floats 794	•	nces and Readings 834		
	Swim Bladders 795 ces and Readings 797		or Index 839		

Part I Some Basic Properties of Living Systems

Chapter 1 The Nature of the Subject

Glianter 2 Cellular Constituents

Charlor & Cellular Organization and Membranes

Chapter 4 Energy and Cellular Metabolism

Following a brief introduction to the history and nature of physiology, Chapter 1 discusses regulation, control, and adaptation as basic properties of all living systems. Feedback regulation and systems analysis are introduced because they provide one conceptual framework upon which physiological regulation may be placed. The idea of regulation in animals was conceived long before the development of cybernetics. However, cybernetics provides a language and the mathematics for describing rigorously any regulatory system. Chapter 1 also contains a listing of the major animal groups.

Certain classes of molecules are also basic to all living systems, and these are described in Chapter 2. Some emphasis is placed on that unique and ubiquitous molecule, water. The nature and general functions of the major classes of biological molecules are described, but much of the discussion centers on macromolecules, especially the proteins. Macromolecules are of importance because they can provide the information required by living systems for synthesis, growth, development, regulation, and adaptation. All the activities and structures discussed in later chapters depend upon the molecules described here.

The organization of molecules into cellular organelles and cell structure generally is the topic of Chapter 3. Instrumentation and methods are given consideration because at the cellular and molecular levels of biological organization instrumentation is required to analyze dimensional realms far beneath those normally perceived by human senses. Most of the discussion