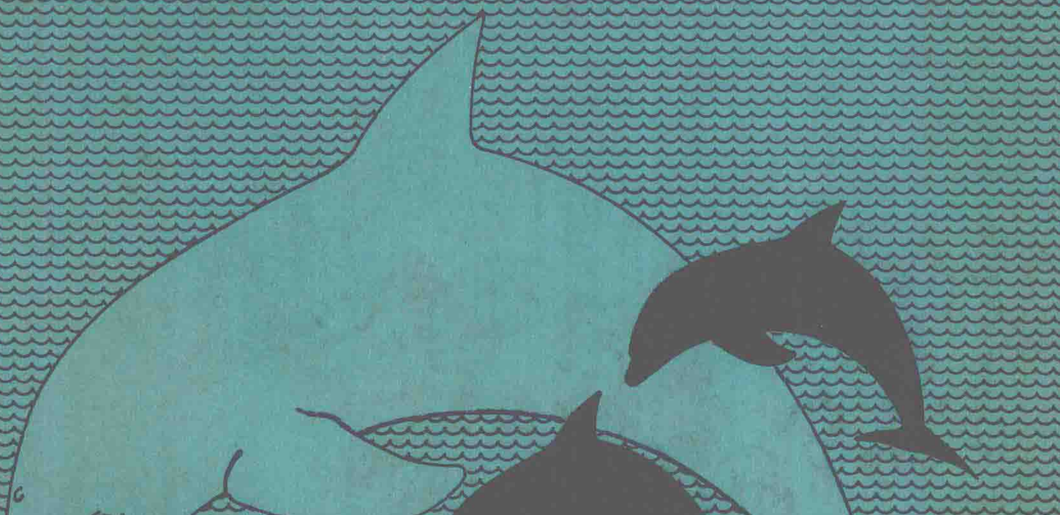
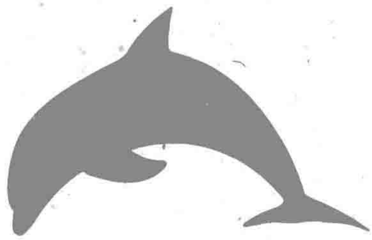
KNUT SCHMIDT-NIELSEN

ANIMAL PHYSIOLOGY
Adaptation and environment

SECOND EDITION





SECOND EDITION

ANIMAL PHYSIOLOGY: Adaptation and environment

KNUT SCHMIDT-NIELSEN

James B. Duke Professor of Physiology, Department of Zoology, Duke University

CAMBRIDGE UNIVERSITY PRESS

CAMBRIDGE LONDON NEW YORK MELBOURNE

Published by the Syndics of the Cambridge University Press
The Pitt Building, Trumpington Street, Cambridge CB2 1RP
Bentley House, 200 Euston Road, London NW1 2DB
32 East 57th Street, New York, NY 10022, USA
296 Beaconsfield Parade, Middle Park, Melbourne 3206, Australia

First published 1975
Reprinted with corrections 1975
Reprinted 1976, 1977, 1978
Second edition 1979

Printed in the United States of America
Typeset by Vail-Ballou Press, Inc., Binghamton, N.Y.
Printed and bound by The Maple Press Co., York, Pa.

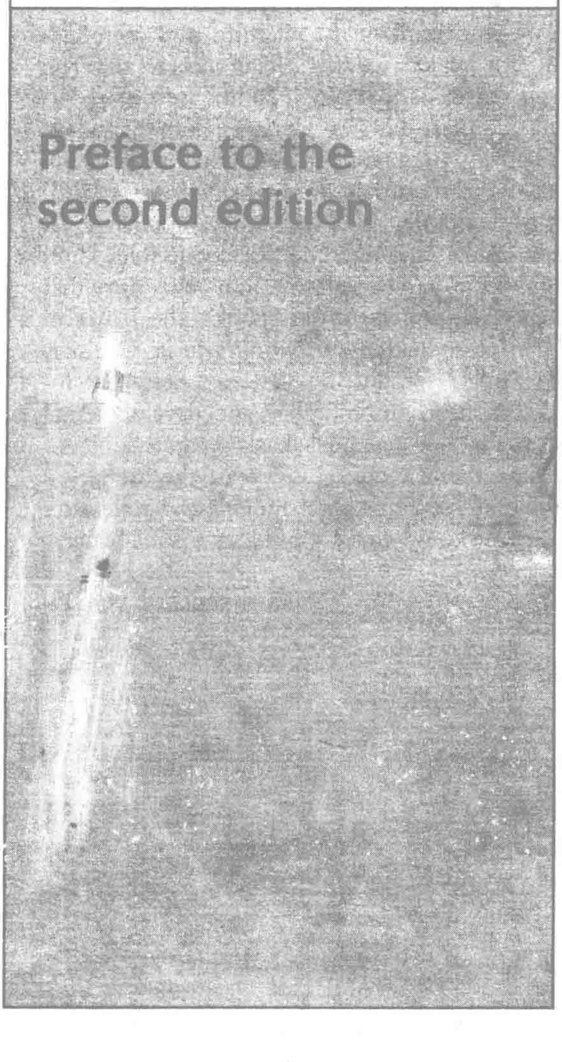
Library of Congress Cataloging in Publication Data
Schmidt-Nielsen, Knut, 1915–

Animal physiology.

Includes bibliographies and index.

1. Physiology. I. Title.
QP31.2.S363 1979 591.1 78-56822
ISBN 0 521 22178 1 hard covers
ISBN 0 521 29381 2 paperback
(First edition: ISBN 0 521 20551 4 hard covers
ISBN 0 521 29075 9 paperback)

Preface to the second edition



The reason for a second edition of a book should be to make it better. This may be done by improving existing material and by updating the information it contains, and I have tried to do both. Every chapter is revised, important new information is added, and some chapters cover their subjects in greater depth than in the first edition.

As before, I consider that the understanding of principles is more important than the mere accumulation of facts that can smother in boredom the curiosity of interested young people. I have selected new material with this in mind.

Those readers who teach physiology may wish to see a listing of changes and improvements. The respiration chapters contain new material on fish respiration, on lungless salamanders, and on the oxygen supply to birds' eggs. The chapters on blood and circulation are expanded and clarified. The chapter on food and feeding contains new material on marine waxes and their importance in the food chain, on nitrogen fixation in termites and in corals, and a substantial expansion of the discussion of noxious plant compounds and chemical defenses.

In the chapter on metabolism, new material includes discussions of the oxygen minimum layer in the ocean and of the effects of high pressure and high altitude. The treatment of problems of scaling and body size is completely revised.

The chapters on temperature and heat problems contain new material on thermal tolerance and heat death. New concepts on the biological importance of fever are discussed, and recent research on the temperature regulation of birds and bees is included. The chapters on osmoregulation and excretion have been clarified, and recent changes in our concepts of how urine is concentrated in the mammalian kidney are clearly explained.

The three chapters toward the end of the book, those on muscle, nerve, and hormones, are completely revised and much new material is added. The expanded treatment ranges from new concepts of ameboid movement and the function of flagella to the molecular events in muscle contraction. Animal locomotion and biomechanics are given a prominent place, for moving about is an important characteristic of living animals.

The material on sensory perception is updated, especially in regard to electric and magnetic stimuli and the function of the lateral line of fishes. The explanation of the nature of nerve impulses and action potentials is completely rewritten and expanded to meet current requirements.

The last chapter, on physiological integration, has also been thoroughly revised. The close connection between the central nervous system and endocrine function, which was stressed in the first edition, is clarified through discussions of exciting new developments in neuroendocrine function. Instead of an enumeration of nearly endless numbers of hormones – to be memorized by students with retentive brains – there are clear tables that outline the important principles of modern endocrinology.

As in the first edition, some essential background material that already should be known to the students is placed in appendixes, not because it is considered peripheral, but because it is so important that it must be available to those who have forgotten and need a concise restatement of basic facts.

The International System of Units (the SI system) is clearly and accurately presented in Appendix A (as it was in the first edition). In addition, the inevitable transition to the common use of SI units is helped by the side-by-side use in the text of traditional units and the corresponding SI units.

Two important fields, vitamins and reproduction, are treated very lightly or not at all. The simple reason is that much of this material is already familiar. Lists of vitamins and their deficiency symptoms are of little use; they are found in books the student has met in courses on health, home economics, and introductory biology. A deeper understanding of the metabolic roles of vitamins requires a background in biochemistry that is beyond the scope of this book. The basics of human reproduction should already be familiar, and animal reproduction is a vast field that includes so much morphology and developmental biology that it is best treated as a separate subject.

I hope that the changes increase the usefulness of the book, and that both students and colleagues will let me know what I should have done better.

KNUT SCHMIDT-NIELSEN

Contents

About this book

This book is about animals and their problems. It is not only about how things are; it is about the problems and their solutions. It is also about aspects of physiology I happen to find particularly fascinating or interesting. It is written for the student who wants to know how things work, who wants to know what animals do and how they do it.

The book deals with the familiar subjects of physiology: respiration, circulation, digestion, and so on. These subjects are treated in 13 chapters, arranged according to major environmental features: oxygen, food and energy, temperature, and water. I consider this arrangement important, for there is no way to be a good physiologist, or a good biologist for that matter, without understanding how living organisms function in their environment.

The book is elementary and the needed background is minimal. I have assumed that the student is familiar with a few simple concepts, such as are obtained in a good high school course or in introductory biology at the college level. Otherwise, there will be few demands on prerequisite knowledge. I have included in the text sufficient background information to make physiological principles understandable in terms of simple physics and chemistry. In some cases, a more rigorous treatment has been placed in an appendix (e.g., concerning solutions and osmosis). This makes it available to the student who wants to acquire a better understanding and to the teacher who wants to make such information required knowledge.

The quantity and complexity of scientific information are steadily increasing, and students are already overburdened with material to remember. Furthermore, the mere recital of facts does not increase one's understanding of general principles. I have therefore tried to present information that can provide a reasoned background for my statements or conclusions. The student will find that many problems can be understood once a few fundamental principles are familiar. I also feel that clear concepts are more important than the learning of terms, but because concepts cannot be conveyed without words, terms are necessary. However, terms should clarify and help, and must be clearly and consistently defined.

To avoid overburdening the student with information, a textbook must necessarily be selective, and many of the omissions are intentional. For example, most students will be familiar with vitamins and with the physiology of reproduction, described in terms that have become household words, and there is no need to repeat these endlessly. But mere familiarity with common household words does not automatically confer an understanding of how living organisms work. It is more important to acquire coherent concepts, consistent with available information, consistent with the rules of chemistry and physics, and consistent with what the organism needs in order to live and function in its environment.

Much of this book explores how animals can live where the environment seems to place insurmountable obstacles in their way. The book tries to compare the possible approaches and the solutions found by different animals. The study of animals with anatomical or physiological specializations can contribute much to our understanding of general principles. However, unless we look for these general principles, comparative physiology is apt to become a description of functions peculiar to uncommon animals – uncommon not because they are rare, but because they are outside our daily experience with ourselves and with well-known pets and laboratory animals such as dogs, cats, rats, and frogs. Instead, we want to put information together into general concepts that help us understand how all animals function.

The text contains literature references. These are arranged at the end of each chapter, not only to tell where I obtained some of the facts, but also to help the student satisfy his curiosity without having to search for information that often is hard to come by. The vast quantity of scientific information made it necessary to be highly selective, and opinions about the proper selection will differ.

To bring more specialized and advanced information within the reach of the reader, I have arranged a short list entitled Additional Reading at the end of each chapter, following the main list of references. These can serve as a key to further study. To spare the student from a feeling of helplessness, I have made these lists short. They include titles that vary from brief and simple essays to large, comprehensive treatises. Except for a few older works, I have restricted these lists to reasonably recent and up-to-date material.

Like most authors, I hope that friendly, and perhaps not so friendly, readers will let me know about errors I have made and what they think I should have done better.

What is physiology?

Physiology is about the functions of living organisms – how they eat, breathe, and move about, and what they do just to keep alive. To use more technical words, physiology is about food and feeding, digestion, respiration, transport of gases in the blood, circulation and function of the heart, excretion and kidney function, muscle and movements, and so on. The dead animal has the structures that carry out these functions; in the living animal the structures work. Physiology is also about how the living organism adjusts to the adversities of the environment – obtains enough water to live or avoids too much water, escapes freezing to death or dying from excessive heat, moves about to find suitable surroundings, food, and mates – and how it obtains information about the environment through its senses. Finally, physiology is about the regulation of all these functions – how they are correlated and integrated into a smooth-functioning organism.

Physiology is not only a description of function; it also asks "why?" and "how?" To understand how an animal functions, it is necessary to be familiar both with its structure and with some elementary physics and chemistry. For example, we cannot understand respiration unless we know about oxygen. Since ancient times breathing movements have been known as a sign of life or death, but the true meaning of respiration could not be understood until chemists had discovered oxygen.

The understanding of how living organisms function is helped enormously by using a comparative approach. By comparing different animals and examining how each has solved its problems of living within the constraints of the available environment, we gain insight into general principles that otherwise might remain obscure. No animal exists, or can exist, independently of an environment, and the animal that utilizes the resources of the environment must also be able to cope with the difficulties it presents. Thus, a comparative and environmental approach provides insight into physiology.

Examining how an animal copes with its environment often tends to show what is good for the animal. This may bring us uncomfortably close to explanations that suggest evidence of purpose, or teleology, and many biologists consider this scientifically improper. However, we all do tend to ask "why?" or "what good is it for the animal?" Anyway, the animal has to survive, and there is nothing improper or unscientific in finding out how and why it succeeds. If it did not arrive at solutions to the problem of survival, it would no longer be around to be studied.

This book follows an environmental approach to comparative physiology. It begins with a description of how animals obtain oxygen from the environment, whether from water or air. Next it describes the role of blood in the transport of oxygen to the tissues and how the blood is pumped around in the organism. The energy supply (food) is dealt with in a chapter on feeding and digestion, followed by a discussion of energy metabolism in general. An important environmental factor, temperature and its effects, is discussed in two chapters. Then the equally important role of water for the organism is described. One chapter deals with movements and locomotion, another with the ways an animal obtains information about its environment (senses). The last chapter of the book discusses how all these functions with the aid of the hormonal and nervous systems are controlled, correlated, and integrated into a smoothly functioning whole organism.

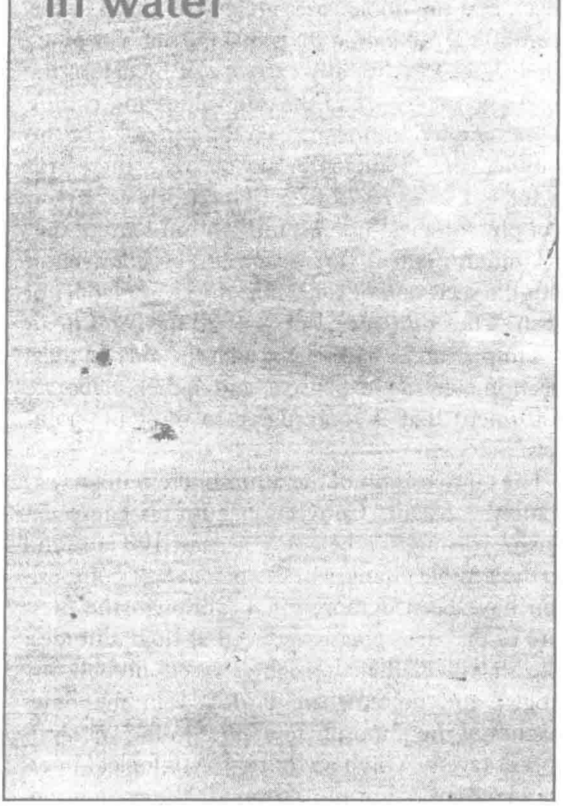
PART ONE

OXYGEN

1

CHAPTER ONE

Respiration in water



All living organisms use energy, which they must obtain from outside sources. Most plants capture the energy of sunlight and use carbon dioxide from the atmosphere to synthesize sugars and eventually all the other complex compounds that make up a plant. Animals, on the other hand, use energy from chemical compounds they obtain from plants, either directly by eating the plants or indirectly by eating other animals that in turn depend on plants. The chemical energy animals use is therefore in the end derived from the energy of solar radiation.

Most animals satisfy their energy requirements by oxidation of food materials. A small number of animals can, in the absence of oxygen, utilize chemical energy from organic compounds, but the complete oxidation of these compounds makes available roughly 10 or 20 times as much energy. Most animal food consists of three major groups of compounds: carbohydrates, fats, and proteins. The oxidation of carbohydrates and fats yields carbon dioxide and water as the only end products; the oxidation of protein yields small amounts of other end products in addition to carbon dioxide and water.

The uptake of oxygen and release of carbon dioxide constitute *respiration*, a word that applies both to the whole organism and to the processes in the cells. Animals take up oxygen from the medium they live in and give off carbon dioxide to it. Aquatic animals take up oxygen from the small amounts of this gas dissolved in water; terrestrial animals from the abundant oxygen in atmospheric air. Many small animals can take up sufficient oxygen through the general body surface, but most animals have special respiratory organs for oxygen uptake. As the cells utilize oxygen for oxidation of foodstuffs, carbon dioxide is formed and follows the opposite path, being released through the general body surface or the respiratory organs. The

water formed in the oxidation processes merely enters the general pool of water in the body and presents no special problems.

The most important and sometimes the only physical process in the movement of oxygen from the external medium to the cell is *diffusion* (i.e., movement of the gas, as a dissolved substance, from a higher to a lower concentration). The movement of carbon dioxide in the opposite direction also follows concentration gradients. The diffusion is often aided by a bulk movement (such as the circulation of blood), but this does not change the basic fact that concentration gradients provide the fundamental driving force in the movement of the respiratory gases. To understand respiration, it is therefore necessary to have a basic knowledge of the respiratory gases, their solubility, and the physics of diffusion processes.

Life presumably originated in the sea, and it is convenient to discuss aquatic respiration first and afterward deal with respiration in the air. The air-breathing animals (primarily vertebrates and insects) are among the most complex organisms; however, the largest number of animals, especially many of the less highly organized invertebrates, are aquatic. After a brief review of the respiratory gases and a bit of basic physics, this chapter deals with the problems of aquatic respiration.

GASES IN AIR AND WATER

Composition of dry atmospheric air

The physiologically most important gases are oxygen, carbon dioxide, and nitrogen. They are present in atmospheric air in the proportions shown in Table 1.1. In addition, the atmosphere contains water vapor in highly variable amounts.

What physiologists usually call nitrogen is actually a mixture of nitrogen with about 1% of the noble gases, and for accuracy these should be listed as well. However, in physiology it is customary to lump these gases with nitrogen, the main reason being that in most physiological processes, nitrogen and the noble gases are equally inert to the organism. Another reason is that the analysis of respiratory gases is usually carried out by determining oxygen and carbon dioxide values and calling the remainder "nitrogen." To the physiologist the amount of "nitrogen" in air is, therefore, 78.09 + 0.93%, or 79.02%. The nearly 1% argon is of physiological interest only in some quite special circumstances: for example, in connection with the secretion of gases into the swimbladder of a fish. The complete analysis of all the gases in an air sample can be carried out with the aid of a mass spectrometer, an expensive and rather elaborate instrument that is unavailable to most physiologists.

The composition of the atmosphere remains extremely constant. Convection currents cause extensive mixing to a height of at least 100 km, and no discernible changes in the percentage composition have been demonstrated, although the pressure of the air is greatly reduced at high altitudes. The statement that the lighter gases, notably hydrogen and helium, are enriched in the outer reaches of the atmosphere applies to the very outermost layers, which are of no physiological interest whatsoever. For our purposes, the open atmo-

TABLE 1.1 Composition of dry atmospheric air. All atmospheric air contains water vapor in highly variable amounts. The less common noble gases (helium, neon, krypton, and xenon) together make up only 0.002% of the total. [Otis 1964]

Component	%
Oxygen	20.95
Carbon dioxide	0.03
Nitrogen	78.09
Argon	0.93
Total	100.00

sphere has a constant gas composition, except for its water vapor (Spitzer 1949).

The composition of the air is maintained as a balance between the use of oxygen in oxidation processes (primarily oxidation of organic compounds to carbon dioxide) and the assimilation of carbon dioxide by plants, which in the process release oxygen.

The fear that our use of fossil fuels – oil, coal, and natural gas – may deplete the atmosphere of oxygen and add large amounts of carbon dioxide is probably unfounded. In 1910 an extremely accurate oxygen analysis showed the value of 20.948%, and during 1967 to 1970 repeated measurements gave a value of 20.946% ± 0.006. The investigators who made these very accurate analyses then calculated that if all known recoverable fossil fuel reserves were depleted, there would still be 20.8% oxygen left in the atmosphere (Machia and Hughes 1970). Physiologically this change would be of no consequence.

The slight increase in carbon dioxide caused by the combustion of all the fuel would likewise have negligible physiological effects, but this is not to say it would be harmless. Even a slight change in carbon dioxide alters the absorption of solar radiation in the atmosphere and may have an unpredictable *greenhouse effect* that over the years may drastically change climatic conditions on the earth's surface. The atmosphere is more transparent to incoming short-wave radiation than to the long-wave radiation emitted by the earth. The outgoing long-wave radiation is absorbed in the atmosphere mainly by carbon dioxide and water vapor. It is estimated that a doubling of the atmospheric carbon dioxide content would increase world temperature by 1.3 °C if atmospheric water remained constant. However, at higher temperature the atmosphere can hold more water vapor, which enhances the blanketing effect and causes further temperature rise. On the other hand, increased water vapor in the atmosphere may augment formation of clouds, which in turn reflect more of the incoming solar radiation, thus having the opposite effect. The complexity of these relationships makes predictions about the greenhouse effect of increased carbon dioxide highly uncertain (Sawyer 1972; Baes et al. 1977).

Having stressed the constancy of the atmospheric composition, we must add a few words about special cases. For example, microenvironments, such as burrows occupied by animals, have more variable air composition, with the oxygen as low as 15% or even less (Darden 1972). The carbon dioxide content is increased, but not necessarily to the same extent. However, carbon dioxide may rise to above 5%, an amount that has considerable physiological effects.

The air contained in soil – in open spaces between the soil particles – is often low in oxygen. The reason is that the soil may contain oxidizable material that can deplete the oxygen severely. Not only organic matter, but also substances such as iron sulfide, can consume oxygen until practically all free oxygen has been removed. These oxidation processes depend on temperature, humidity, and other factors, as well as on the amount of exchange with the atmosphere. Rain, for example, may block the surface porosity of the soil and at the same time provide humidity for increased oxidation, and the microatmosphere may then change drastically.

Water vapor in air

The preceding information about the percentage composition of the atmosphere referred to dry air, and we must now turn to air's water content. The pressure of water vapor over a free water surface changes with temperature (Table 1.2). At the freezing point the vapor pressure is 4.6 mm Hg