KNUT SCHMIDT-NIELS[redacted]

ANIMAL PHYSIOLOGY

Adaptation and Environment

FOURTH EDITION

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Adaptation and environment

KNUT SCHMIDT-NIELSEN

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About this book

This book is about animals and how they function in their world. First of all it is about problems and their solutions. It is also about aspects of physiology that I myself happen to find particularly interesting. The book is written for students who want to know how things work, who want 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 arranged according to major environmental features: oxygen, food and energy, temperature, and water. This arrangement is 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. There are few demands on previous knowledge, but I have assumed that the student is familiar with a few simple concepts, no more than provided by a good high school text. I have, however, included in the text sufficient background information to make physiological principles understandable in terms of simple physics and chemistry.

The quantity and complexity of scientific information today are steadily increasing, and students are already overburdened with material to remember. However, the mere recital of more facts does not signify understanding; the student needs a framework of principles on which to hang the facts. This book should help the student discover 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 technical terms. However, because concepts cannot be conveyed without words, terminology is necessary. But terms are of no use unless they are clearly and accurately defined.

Much of this book explores how animals can live in environments that seem to place insurmountable obstacles in their way. The book discusses possible approaches and solutions. Animals with anatomical and physiological specializations often 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 other humans and with well known pets and laboratory animals such as dogs, cats, rats, and frogs. What we want is to place information into general concepts that help us understand how all animals function.

The text contains references to the scientific literature. These are arranged at the end of each chapter to help interested students satisfy their curiosity without having to search for information that is often hard to come by. The vast amount of scientific information made it necessary to be highly selective, and opinions about the proper selection will differ.

To bring more advanced information within the reach of the reader, I have arranged a list of Additional Readings for each chapter, placed after the list of text references. To spare the student from a feeling of helplessness, I have made these lists short. The titles vary from brief and simple essays to large, comprehensive treatises. Except for a few classical works, these lists contain reasonably recent and up-to-date material.

Like most authors I hope that friendly and perhaps less friendly readers will let me know about errors and what I could have done better.

Preface to the fourth edition

When I started revising this book, a friend warned me against the dinosaur syndrome – when they got too big, they died out. I have therefore tried to make the book better without substantially increasing its size. I have revised existing material and have made additions where there is essential new information. However, there is no change in the general outline or the nature of the book.

A novel feature of this edition is that each chapter now begins with a brief synopsis, outlining its essential features and the fundamental principles to be discussed.

The separate Chapters 1 and 2 in the third edition, which both dealt with respiration, have been combined in one chapter. The disadvantage is that the chapter now is much longer; the advantage is more unified treatment of the principles.

New figures have been added where recent information is helpful, and some old figures have been deleted. Nearly 200 new references have been added, both as text references and for additional reading. These are chosen with emphasis on recent developments, judiciously selected from the burgeoning scientific literature but of necessity leaving much important new information unlisted.

For those who teach physiology I will mention some of the subjects where new information has been added. These include: Gas exchange in eggs, including eggs of mound-building birds and dinosaur eggs; regulation of blood flow in open circulation systems; composition of mammalian milk; recent information about deep sea rift animals and their metabolism of hydrogen sulfide from hot springs; digestion of waxes in marine communities; energy cost and economy of different gaits in horses; how biological antifreezes act; nucleating agents and freeze tolerance in vertebrates; survival of small Arctic birds in winter cold and darkness; heater organs that keep the brain and eye of swordfish warm; how the perturbing effect of urea on enzyme function in the kidney is counteracted; new ideas about Henle's loop and achievement of high urine concentrations; revised treatment of endocrine function with information about natriuretic factor, cell surface receptors, diuretic hormone in blood-sucking insects, and formation of endogenous morphine; perception of surface waves and absolute pitch in *Xenopus;* hearing in fish; electrosensitive organs in mammals; perception of infrasound for communication among elephants.

These and many other new concepts have been incorporated without making the book appreciably longer.

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APPENDIXES

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 problem 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 deeper 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. And the study of the living organism is what physiology is all about.

PART ONE

OXYGEN

CHAPTER ONE

Respiration

Why is oxygen important? It is because most animals satisfy their energy requirement by oxidation of food materials, forming carbon dioxide and water in the process.

The process of oxygen uptake and release of carbon dioxide is called *respiration*. Aquatic animals take up oxygen from the small amount of this gas dissolved in the water, terrestrial animals from the abundant oxygen in the air.

Many small animals can take up sufficient oxygen through the general body surface, but most animals need special respiratory organs for oxygen uptake. Carbon dioxide follows the opposite path, being released from the general body surface or from 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 cells is *diffusion*, a process in which a substance moves from a higher to a lower concentration. The movement of carbon dioxide in the opposite direction also follows the concentration gradients.

Diffusion may be aided by *bulk movement*, such as the movement of air in and out of the lungs, but concentration gradients remain as the fundamental driving force for moving the respiratory gases. To understand respiration it is therefore necessary to know about the respiratory gases, their solubility, and the physics of diffusion processes.

Life presumably originated in the sea, and most animals (except insects) are marine. Large-scale evolutionary adaptation to air breathing has occurred only among arthropods and vertebrates. Some snails are well adapted to terrestrial life, and a small number of other invertebrates live in various terrestrial microhabitats.

Easy access to oxygen in the atmosphere permits a high rate of metabolism and a high degree of organizational development. The greatest drawback to breathing in air is the evaporation of water.

THE ATMOSPHERE

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 atmosphere has a constant gas composition, except for its water vapor.

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.

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.

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

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 greenhouse effect

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.

This would cause extensive melting of the polar ice covers and a rise in the ocean level of 20 to 30 m or more, enough to submerge many of the world's major cities. In addition, at higher temperature the atmosphere can hold more water vapor, which enhances the blanketing effect and causes further temperature rise. However, 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 (Hansen et al. 1981; Bolin et al. 1986; Dickinson and Cicerone 1986; Ramanathan 1988).

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 (Kuhnen 1986).

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 severely deplete the oxygen. 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 the water content of air. 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 (0.61 kPa).* It increases with increasing temperature, and reaches 760 mm Hg (101.3 kPa) at 100°C. For this reason water boils at 100°C if the atmospheric pressure is 760 mm Hg. If the atmospheric pressure is lower, water boils at a lower temperature; for example, if the pressure is reduced to 17.5 mm Hg (2.34 kPa) water boils at 20°.

Any mixture of gases, such as atmospheric air, that is in equilibrium with free water contains water vapor at a pressure corresponding to the temperature, and the fraction of the air sample that is made up of water vapor therefore increases with the temperature (column 4 of Table 1.2). At 37°C, the usual body temperature of mammals, the water vapor pressure is about 47 mm Hg (6.28 kPa), and water vapor then makes up 6.2% of the air volume (see also Figure 8.10, page 323).

The lung air of humans and other air-breathing vertebrates is always saturated with water vapor at body temperature, but the outside atmospheric air usually is not. When air is saturated with water vapor, we say that the *relative humidity* (r.h.) is 100%. If the air contains less water vapor, the humidity can be expressed as a percent of the amount required for saturation at that temperature; for example, 50% relative humidity means that the air contains half the water it would contain if saturated with water vapor at that temperature.

For some purposes relative humidity is a con-

*The unit millimeters of mercury (mm Hg) is traditionally used in physiology. It is derived from the use of mercury manometers, and 1 mm Hg at 0°C is also known as 1 torr. In the International System of Units (the SI System) the pressure unit is the pascal (Pa), defined as 1 newton per square meter ($N\ m^{-2}$). Thus, 1 mm Hg = 133.3 Pa or 0.133 kPa; 1 atm or 760 mm Hg = 101.3 kPa. Further details on the use of the SI System are given in Appendix A.