A Companion to ANIMAL PHYSIOLOGY

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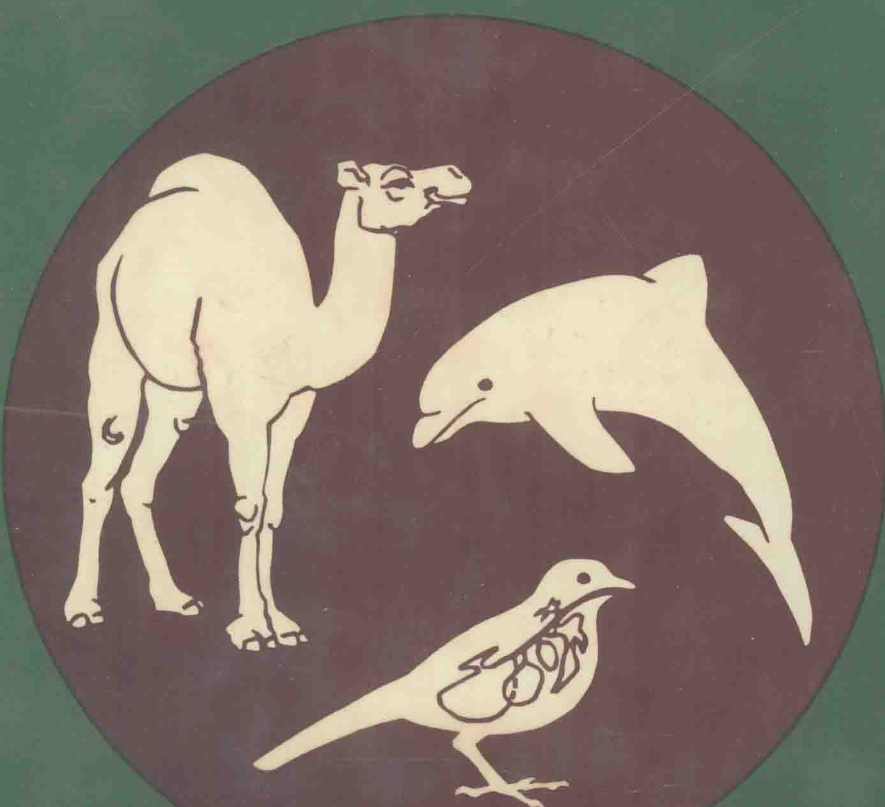

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ANIMAL PHYSIOLOGY

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About this book

A companion to animal physiology is designed as a supplement to Knut Schmidt-Nielsen's *Animal physiology* text. It attempts to provide students and professional biologists with the opportunity to pursue some of the topics introduced in *Animal physiology*. It brings together a series of papers prepared to honor Knut Schmidt-Nielsen on the occasion of his sixty-fifth birthday. The papers were presented at the Fifth International Conference on Comparative Physiology, Comparative Physiology: Perspectives, a Satellite Symposium of the XXVIII International Physiological Congress. The conference was held in Sandbjerg, Denmark, in July 1980 and was sponsored by the Interunion Commission on Comparative Physiology, representing the International Unions of Biological Sciences, Physiological Sciences, and Pure and Applied Biophysics. It brought together a group of scientists who have made important contributions to different areas in comparative physiology, and asked them to provide a perspective on what they thought was interesting and important in their particular areas.

Vikings have always sensed discovery and discovered with sensitivity. Knut Schmidt-Nielsen, a modern-day Viking of science, and his wife, Margareta, are flanked by two members of the Danish Philharmonic at the symposium banquet celebrating his birthday. The ancient Viking horns, lurs, provided the music for the banquet.

About Knut Schmidt-Nielsen

Knut Schmidt-Nielsen was born in Trondheim, Norway, in 1915. His early schooling took place in Norway. He studied under August Krogh and obtained his Doctor of Philosophy degree under Kaj Linderstrøm-Lang at the Carlsberg Laboratories in Denmark.

Knut Schmidt-Nielsen's books and his research reveal his curiosity, enthusiasm, and originality as a scientist. He enjoys physiology and is able to convey this enjoyment in his books and papers. He and his collaborators have helped us understand how animals survive in deserts; discovered salt glands in birds and reptiles; unraveled the mysteries of the bird lung; and shown that countercurrent exchanges can be organized temporally as well as spatially. He has written not only about what we know, but about what we do not as yet understand. His books and his research have stimulated students and professional biologists to try to find the answers to how animals work, and perhaps this is why Knut Schmidt-Nielsen has had such an enormous impact on comparative physiology.

Contents

PART ONE

Oxygen

Overview

Part One considers the exchange of the respiratory gases.

In Chapter 1 Peter Scheid develops a simple model of respiratory exchange. The model is used to define and evaluate the gas exchange at the respiratory surface. It compares the efficiency of three mechanisms that vertebrates use for bringing oxygen in contact with the respiratory surfaces: the countercurrent mechanism of fish gills, the crosscurrent mechanism of bird lungs, and the pool mechanism of the mammalian lung.

In Chapter 2 the pressure gradients and conductances for oxygen and carbon dioxide (defined in Scheid's model) are analyzed by Pierre Dejours to examine whether humans can climb Mount Everest without supplemental oxygen. He extends the analysis to birds, and concludes that it is the greater gas-exchange efficiency of their lungs that enables them to fly over Mount Everest.

In Chapter 3 Ewald Weibel extends the model for oxygen transport to include the pathway from the lung to the mitochondria of muscles. He divides the pathway into a number of steps and proposes that the structural design of each step is quantitatively matched. Allometry and morphometric analysis of structure are used as tools to test this hypothesis.

In Chapter 4 Johannes Piiper develops a theoretical model to evaluate the extent to which diffusion limits the exchange of O_2 and CO_2 in vertebrate respiratory organs. The model predicts a strong diffusion limitation for O_2 across amphibian skin, an intermediate limitation across fish gills, and a weak limitation across the human lung.

In Chapter 5 Peter Lutz discusses some unusual ways in which vertebrates increase the capacity of blood for carrying oxygen during exercise. He also discusses vertebrate mechanisms for the effective use of oxygen stores in the lungs during breath holds and/or dives.

In Chapter 6 Donald Jackson discusses the problems for CO_2 elimination and acid–base regulation posed by the variable temperature of ectothermic vertebrates. He describes the physiological mechanisms used by a number of ectotherms for solving these problems.

In Chapter 7 Kjell Johansen asks whether the incomplete separation between pulmonary and systemic circulation found in air-breathing fish, in amphibians, and in reptiles is advantageous. Available data reveal clear advantages in retaining an incomplete separation between pulmonary and systemic circuits in these animals.

1 A model for comparing gas-exchange systems in vertebrates

PETER SCHEID

Like all animals with aerobic metabolism, vertebrates obtain the necessary O_2 from their environment, which can be water or air. External gas exchange is aided by specialized organs – gills for water breathing in fish and some amphibians and lungs for air breathing in reptiles, birds, and mammals. Skin may aid gills and lungs as a gas-exchange organ, and in some amphibian species it represents the only route for gas exchange (see Chapter 4). In this chapter a model is developed that defines the parameters involved in gas exchange. The model is then used to compare three of the most highly structured vertebrate gas-exchange organs: gills in fish, parabronchial lungs in birds, and alveolar lungs in mammals. Most of the other gas-exchange systems can be viewed as various steps in the transition between these types and are thus more complex mixtures of the basic types.

General model for gas-exchange organs

Schema

A general schema for a gas-exchange model is depicted in Figure 1.1 (Piiper and Scheid, 1975, 1977). Medium (air or water) and blood enter the system, in which they reach an intimate contact for gases to be exchanged, separated by a tissue barrier. Whereas both medium and blood act as vehicles to convectively transport respiratory gases to the site of gas exchange, diffusion is the sole mechanism by which these gases are transferred from medium to blood or from blood to medium.

Basic parameters

For a quantitative treatment of gas exchange, a number of basic parameters must be known (see Figure 1.1). These are listed below, with typical units given in parentheses:

1. Gas-exchange rate, $\dot{M}$ (mmol · min^{-1})
2. Flow rates of medium and blood, $\dot{V}_m$, $\dot{V}_b$ (liter · min^{-1})
3. Capacitance coefficients in medium and blood, β_m, β_b (mmol · liter^{-1} · Torr^{-1}) (see below)

4. Partial pressures of the gas under consideration, in the inflowing medium (P_i) and blood (P_v) and in the outflowing medium (P_e) and blood (P_a) (Torr)
5. Diffusive conductance of the blood–medium barrier, G_{diff} (mmol · min^{-1} · $Torr^{-1}$). G_{diff} is often referred to as the diffusing capacity of the barrier, D (see below)

Basic overall equations

In order to arrive at simple equations for gas exchange, the following assumptions will be made; their validity will be discussed later:

1. The gas-exchange system is in steady state; that is, all variables are constant in time.
2. The β_m and β_b are constant over the partial pressure range considered.
3. No concentration gradients exist inside the gas-exchange system in the direction perpendicular to the medium–blood barrier.

The mass balance provides some simple links between the basic parameters:

$$\dot{M} = \dot{V}_m \cdot \beta_m \cdot (P_i - P_e) = \dot{V}_b \cdot \beta_b \cdot (P_a - P_v) \tag{1}$$

FIGURE 1.1 General schema for gas-exchange systems in vertebrates. The figure shows the various basic parameters (defined in the text) that determine gas-exchange function. No commitment is made, however, as to the specific arrangement of medium flow to blood flow at the site of gas exchange. This specific arrangement is the basis for differences among the various types of gas-exchange organ in vertebrates and is determined entirely by the structure of the system.