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Environmental Physiology III

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Environmental Physiology III

Publisher's Note

The *International Review of Physiology* remains a major force in the education of established scientists and advanced students of physiology throughout the world. It continues to present accurate, timely, and thorough reviews of key topics by distinguished authors charged with the responsibility of selecting and critically analyzing new facts and concepts important to the progress of physiology from the mass of information in their respective fields.

Following the successful format established by the earlier volumes in this series, new volumes of the *International Review of Physiology* will concentrate on current developments in neurophysiology and cardiovascular, respiratory, gastrointestinal, liver, endocrine, kidney and urinary tract, environmental, and reproductive physiology. New volumes on a given subject generally appear at two-year intervals, or according to the demand created by new developments in the field. The scope of the series is flexible, however, so that future volumes may cover areas not included earlier.

University Park Press is honored to continue publication of the *International Review of Physiology* under its sole sponsorship beginning with Volume 9. The following is a list of volumes published and currently in preparation for the series:

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- Volume 20: **ENVIRONMENTAL PHYSIOLOGY III** (D. Robertshaw)
- Volume 21: **LIVER PHYSIOLOGY** (N. B. Javitt)

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Consultant Editor's Note

The first volume of the *International Review of Physiology* appeared in 1974, and since that time this new review series has become an important part of physiological literature. One of its most important purposes is to provide a comprehensive learning source for teachers and students of physiology throughout the world.

To explain the reasons for beginning this new publishing venture, we need to repeat once again the philosophy, the goals, and the concept of the *International Review of Physiology*. This Review has the same goals as all other reviews for accuracy, timeliness, and completeness, but it also has policies that we hope and believe will add important qualities often missing in reviews, especially integration of physiological mechanisms and instructiveness. To achieve these goals, the publishing format provides for 1200 to 1500 pages per year, divided into physiological subspecialty volumes organized by experts in their respective fields. This extensive coverage allows consideration of each subject in depth. And to make the review as timely as possible, a new volume in each area of physiology is normally published every two years. In addition, occasional volumes will be published at appropriate times on such topics as the liver, the eye, and other physiological subspecialty areas that might not warrant a new volume every two years.

To help in achieving the goals of the *International Review of Physiology*, special editorial policies have been established. A simple but firm request is made to each author that he utilize his expertise and his judgment to sift from the mass of publications those new facts and concepts that are important to the progress of physiology; that he make a conscious effort not to write a review consisting of an annotated list of references; and that the important material that he does choose be presented in thoughtful and logical exposition, complete enough to convey full understanding as well as being woven into context with previously established physiological principles. Hopefully, these processes will bring to the reader a series of treatises that he will use not merely as a reference but also as an exercise in refreshing and modernizing his whole store of physiological knowledge.

Arthur C. Guyton

Preface

If scientists are to retain the sympathetic and fiscal support of the lay public then it is important that they be able to demonstrate that the direction of their research can be adjusted to meet current needs and concerns of society. In so far as a physiologist is a scientist so must he also be seen to accept that he has social responsibilities in his research. The chapters in this review are meant to reflect the role that environmental physiology is playing in attempting a) to understand the physiological responses of man and animals to ever-changing environmental conditions, b) to provide a sound scientific base for medicine, and c) to appreciate mechanisms of survival in different surroundings. Environmental physiology therefore has a very broad base that extends into many other branches of physiology. No longer is environmental physiology synonymous with temperature regulation; rather, it relates to the environment in its broadest context. The avid use of fossil fuels has created pollution problems that affect the physiology and health of all living creatures, including man. A chapter is included therefore on the physiological effects of elevated atmospheric levels of carbon monoxide, one of the more important atmospheric pollutants. The recognition that the supply of fossil fuels is finite has led to an awareness of the need for energy conservation. In the design and heating of buildings for man and animals it is necessary to know not only the transfer of heat through the walls of the structure but also the physics of heat transfer through clothing and animal coats. Authors from Poland and England have reviewed present knowledge in this field.

The role of fever in combating infectious disease has not been fully understood, and some new evidence that has accumulated in recent years is reviewed here. This evidence indicates that fever may be an important and possibly essential response that allows the host to overcome the infection. In that fever represents an elevated but controlled body temperature, and so also during exercise is body temperature maintained at a higher level, it has been speculated that both situations may have some common underlying basic mechanism.

The ability to withstand cold by the generation of internal heat is reviewed by an Australian author. A great deal of research in Australia has been directed to understanding cold thermogenesis because of the high incidence of sheep mortality brought about by cold exposure, particularly at shearing time. This research shows how physiologists may be able to contribute to the solution of a farming problem.

Although man is more or less ubiquitous, permanent residence at high altitudes or in marine environments has presented a physiological challenge: lack of oxygen. One chapter reviews the physiological effects of altitude and another chapter is directed toward the adaptations of marine mammals for prolonged survival under hypoxic conditions, i.e., during diving.

Thus, although some seemingly unrelated areas are reviewed, reflecting the diversity of the discipline, the general theme of this volume is the contributions that the study of physiology can make to solve some of the current concerns of man's society.

Environmental Physiology III

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1

Transfer of Heat Through Animal Coats and Clothing

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When invited to contribute to this volume, the authors had recently completed a related review for a British Institute of Physics journal. The different readerships dictate different emphasis, and since completion of the earlier review a good deal of fresh material has become available. The units employed here are also different, in part, from those used previously. However, since a majority of factual material is common, a substantial proportion of the present review is closely based on that which appeared in *Physics in Medicine and Biology* (1).

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LIST OF SYMBOLS AND UNITS

The symbols used in this review and their units are as follows:

C , convective heat flux (W m^{-2})

E , evaporation rate ($\text{G m}^{-2} \text{s}^{-1}$)

H_d , sensible heat flux (W m^{-2})

I , thermal resistance, when in $\text{m}^2 \text{K W}^{-1}$

K , skin surface heat load (W m^{-2})

M , net metabolic heat flux (W m^{-2})

R_n , net radiation (W m^{-2})

T , temperature ($^{\circ}\text{C}$ or K)

X , thickness (m)

c_p , constant pressure specific heat ($\text{J g}^{-1} \text{K}^{-1}$)

d , diameter (m or cm)

k , thermal conductivity ($\text{W m}^{-1} \text{K}^{-1}$)

l , coat thickness (m or cm)

p , effective hair area per unit of coat depth (cm^{-1})

r , with subscript, transfer resistances in s cm^{-1} ; e.g., for water vapor, r_w , and for heat, r_h

u , wind speed (m s^{-1})

λ , latent heat vaporization of water (J g^{-1})

ρ , density (g m^{-3})

σ , the Stefan-Boltzmann constant = $56.7 \times 10^{-9} \text{ W m}^{-2} \text{K}^{-4}$

χ , concentration of water vapor in air (g m^{-3})

i_m , water vapor permeability index

Gr , Grashof number

Le , Lewis number

Nu , Nusselt number

Sh , Sherwood number

Other symbols and subscripts are as in text.

Environmental physiologists have devoted many years of study to the mechanisms of homeothermy, which enable mammals and birds to maintain an essentially constant body core temperature. The majority of research work in this field has been concentrated on the physiology of the control of body temperature, including a great deal of detailed study of biochemical processes. However, the mandatory requirement for effective homeothermy is not possession of a thermostat, but possession of adequate insulation. Despite the fact that the physics of heat transfer through animal insulators, including clothing, is not mathematically complex, it has until recently received less attention than a number of the secondary subcutaneous mechanisms concerned in homeostasis. In a previous review in this series Mitchell (2), who has himself contributed to key papers in this field, including one of the few *in vivo* measurements of clothing insulation (3), remarked that our understanding of the physical processes of heat transfer through mammalian coats, although still imperfect, has improved greatly in recent years, but that clothing is still poorly understood. Mitchell's conclusions are still valid. In addition, reasonably quantitative studies of avian coats can still be counted on the fingers of one hand.

The aim of this chapter is to review current knowledge of the physics of animal insulators, and to describe how their structure controls the processes of energy exchange between the skin surface and the ambient environment (1). Improved knowledge of the physical barrier to heat loss is surely essential for better understanding of homeothermy.

A layer of air, trapped by a fibrous coat, provides the major part of body insulation for all except a few of the larger terrestrial mammals, the cetaceans, and other aquatic mammals. In this chapter we do not consider subcutaneous (tissue) insulation in any detail, since, not only is it possessed by all homeotherms, whether or not they have a coat above the skin, but it is also demonstrable in poikilotherms. For example, cold-blooded animals over the size range from bumble bees (4) to fully grown crocodiles (Bell, personal communication) are able to thermoregulate quite effectively by the control of tissue insulation. The response of the body to environmental demands is obviously both very flexible and precise (5); for example, the body core temperature of most homeotherms can be maintained constant to a few tenths of a degree Celsius when the metabolic rate is constant. However, unless the subject is contained within a calorimeter, it is impossible to estimate total heat loss with comparable precision. Currently it is only possible to measure the insulation of clothing or animal coat specimens to about $\pm 10\%$, even on a calibrated flux plate. *In vivo* the values may be reduced to less than a half of those on a flux plate, and the errors of insulation estimation are greatly increased even on a realistic manikin. Because of these uncertainties the physical theories of heat transfer that are presented in this chapter have been selected according to the logical Principle of Ockham's Razor; i.e., where alternatives exist, the simplest rational theorem that fits the facts has been selected. Overcomplexity in the formulation of theories of heat transfer

through animal coats is not only unnecessary, but can inhibit communication between the different specialists involved in this multidisciplinary subject. It is a disease particularly prevalent in some of the engineering literature, where the use of sophisticated mathematics has sometimes borne little relation to physiological reality.

The problems of clothing military personnel for a wide variety of severe climates during the 1939-1945 war, from the tropics to the arctic and from submarines to the new environments of high-flying airplanes, prompted scientific studies of clothing (6-8). Subsequently, studies of the clothing requirements for men in severe environments have been continued, relevant to, for example, the arctic explorer, the military aircraft pilot, and the diver. The air-conditioning of buildings has also increased interest in human comfort in everyday environments and its relationship to clothing and work (9-12). The development of synthetic fibers has also resulted in much research on the structure and properties of textiles, but this has its own special literature, which is outside the scope of the present review.

Studies of the properties of animal coats have had two stimuli. First, the increasing intensification of animal production in the postwar period and emphasis on its efficiency have led to research on the relationships between the metabolism of farm animals and their environments, including the effects of coat insulation (13, 14). Second, the stimulus for the parallel approach to wild animals, which originated from the same period, has been the desire to understand the thermal and physiological limits that determine the ecological ranges and population densities of wild species of homeotherms (15-17).

ENERGY BALANCE AND INSULATION

The principal function of the coats of homeothermic animals and the clothing of man is the regulation of thermal energy exchange between the body and its environment. Homeothermy is maintained only at the cost of unceasing metabolism, the heat component of which must be dissipated. Thus, the problem of the homeotherm is not so much the conservation of heat as the regulation of dissipation to equal production. Since the ratio between the rate of heat production at rest and that during maximum exercise is usually of the order of 1:10, a variety of solutions may be necessary even for a single species in one environment. Insulating coats play a major role in the regulation of heat dissipation.

Application of the First Law of Thermodynamics to steady heat transfer at the surface of the body gives

$$M = R_n + C + \lambda E \quad (1)$$

where all terms are expressed as watts per square meter of body surface. Because we are interested in external insulation, we have eliminated the

respiratory heat fluxes by defining M as the net metabolic heat flux that must be dissipated from the body surface; R_n , C , and λE represent losses of heat by radiation, convection, and evaporation, respectively. λ is the latent heat of vaporization of water and E is the evaporation rate per unit of area. Equation 1 is an approximation, since terms that are usually minor, such as conduction to the ground and the energy required to warm food and water to body temperature, have been neglected. The application of the energy balance equation to homeotherms is discussed in detail by Gates (16), Monteith (18), Mitchell (5), Monteith and Mount (14), Gates and Schmerl (19), and for man in particular by Sibbons (20) and Monteith et al. (21), and in a number of other texts.

The sensible heat flux, $R_n + C$, must pass through the coat thermal resistance, I , and depends on the temperature difference across the insulating layer. Evaporative heat transfer may, to a first approximation, be considered to be driven separately through the coat by the gradient of water vapor concentration, against a diffusive resistance, r_v . Hence,

$$M = \frac{(T_s - T_c)}{I} + \frac{\lambda(\chi_s - \chi_a)}{r_v} \quad (2)$$

where T_s and T_c are the temperatures of the skin below the coat and of the coat surface, respectively, and I has units of $\text{m}^2 \text{K W}^{-1}$. In the evaporative term, χ_s and χ_a are the concentrations of water vapor at the skin surface and in the air outside the coat, respectively, in units of g m^{-3} . If λ is in units of J g^{-1} , then r_v , the resistance to vapor transfer, has units of the reciprocal of velocity, s m^{-1} (18, 22, 23). Where the thickness, l , of a coat can be accurately defined, something which is rarely easy, the resistance, r_v , may ideally be derived from first principles, since it is related to the diffusivity for water vapor, D , by

$$r_v = l/D \quad (3)$$

The insulation, I , may be related to the effective thermal conductivity of the coat, k , by the similar relation

$$I = l/k \quad (4)$$

We may use the similarity between heat and mass transfer to show the equivalence between r_v and I . When the Sherwood number and Nusselt number, the dimensionless mass transfer and heat transfer coefficients, are equal, then the Lewis Relation (24) states that the coefficient of mass transfer ($h_m = r_v^{-1}$) is equal to the convective heat transfer coefficient ($H_c = I^{-1}$) divided by the volumetric specific heat of the medium. Hence,

$$h_m = \frac{h_c}{\rho c_p} \quad \text{or} \quad I = \frac{r_v}{\rho c_p} \quad (5)$$

Where sensible heat transfer is not by convection alone, the same form may be used, but r_v must be replaced by a resistance to heat transfer, r_h , in the same units. The sensible heat flux, H_d , may, therefore, be expressed as

$$H_d = \frac{(T_s - T_c)}{I} = \frac{\rho c_p (T_s - T_c)}{r_h} \quad (6)$$

where the product, ρc_p , of the density (ρ) and the specific heat (c_p) is the volumetric specific heat of the medium. The choice of the value for this constant is somewhat arbitrary in this system. Cena and Clark (25, 26) have recently pointed out that, for heat transfer in air, selection of the value for STP ($1,298 \text{ J m}^{-3} \text{ K}^{-1}$) has the advantage of giving a whole number conversion, of $2 \text{ s cm}^{-1} = 1 \text{ clo}$, between resistances in seconds per centimeter and the empirical *clo* unit of clothing insulation, still employed in much of the literature. Because of the advantages of using the same system of units for both heat and mass transfer resistances, values of insulation are presented in both $\text{m}^2 \text{ K W}^{-1}$ and s cm^{-1} (the preferred submultiple) in this chapter. Those who still think in *clo* need simply to divide the figures in seconds per centimeter by two. Table 1 presents representative values of thermal resistance in all three units.

In order to estimate the heat loss from an animal, we must consider the internal insulation and that provided by the air layer outside the coat in addition to that of the coat itself. If we define r_s as the skin and tissue resistance and r_a as the air resistance, then r_s can typically take values between about 0.3 and 1 s cm^{-1} for large animals, whereas r_a has a maximum value of around 1 s cm^{-1} (27). Depending on the circumstances we must, therefore, add to the resistances in Table 1 a value between 0.3 and 2 s cm^{-1} if we wish to estimate the conductance of the three resistances in series, $h = \rho c_p (r_s + r_h + r_a)^{-1}$. For example, a man wearing the standard clothing used in the

Table 1. Typical thermal resistances or insulations in $\text{m}^2 \text{ K W}^{-1}$, the empirical *clo* unit, and the alternative based on the Lewis Relation

Coat	Thermal resistance		
	$\text{m}^2 \text{ K W}^{-1}$	<i>clo</i>	s cm^{-1}
Best bed, sleeping bag, or nest	1.55	10	20
Warmest practical arctic clothing; coats of large arctic mammals	0.77	5	10
Heavy clothing for outdoors in winter; coats of temperate climate animals	0.31	2	4
Normal clothing; coats of small animals	0.155	1	2
Light summer and hot climate clothing	0.077	0.5	1
Shorts and singlet, for exercise	0.037	0.3	0.6
Still dry air (per cm)	0.4	2.6	5.2

definition by Gagge et al. (28) of the clo , $r_h = 2 \text{ s cm}^{-1}$, may have a low tissue resistance (about 0.3 s cm^{-1}) and be in an environment with low air movement ($r_a \approx 1 \text{ s cm}^{-1}$). The total resistance to heat loss is, therefore, 3.3 s cm^{-1} and the conductance is $h = 1298 \div 330 = 3.94 \text{ W m}^{-2} \text{ K}^{-1}$. At the standard metabolic rate of 58 W m^{-2} the man should, therefore, be comfortable in an environment 15°K below body temperature, i.e., 22°C , which is near enough to Gagge et al.'s figure of 21°C for the present purposes.

Water vapor is unfortunately usually measured in units of partial pressure (e) rather than concentration. The appropriate S.I. form is the kiloPascal (kPa), although meteorologists insist on persisting with the millibar, disguised as the hectoPascal (hPa). The conversion to the units of concentration employed in Equation 2, which may be derived from first principle, via the Gas Laws, is

$$\chi = \frac{2170}{T} e \quad (7)$$

where T is the absolute temperature in K. Expressed in vapor pressure units of kPa, the conductance (h_e) for evaporative heat transfer is, therefore,

$$h_e = \frac{2170\lambda}{T r_v} \quad (8)$$

which gives for 3 s cm^{-1} resistance (of the order of that for normal clothing and the external air layer in series) $h_e \approx 60 \text{ W m}^{-2} \text{ kPa}$ at normal temperatures.

METABOLIC HEAT PRODUCTION

Environmental physiologists will be familiar with the classical picture of the responses of the metabolic heat production of homeotherms to their thermal environment. However, we need to present the "metabolic diagram" (Figure 1) in order to show how insulation determines both the energy costs of homeothermy and the lethal limits of the range of environments that an animal may tolerate. If, for simplicity, the environment of an animal is represented by a single environmental temperature, T , a typical graph of metabolic heat production and loss against T will resemble Figure 1.

Most homeotherms show a limited range of temperatures, between the lines C and D on Figure 1, in which their metabolism is a minimum and no effort is required for thermoregulation (29). The width of this zone may vary from tens of degrees in large animals to a few degrees in small neonate animals. It depends on both the size of the animal and its insulation, as well as on other variables, such as food intake. The insulation or thermal resistance of the coat acts in series with the external insulation of the air. For the purposes of measurement and modeling, the flow of heat through the in-

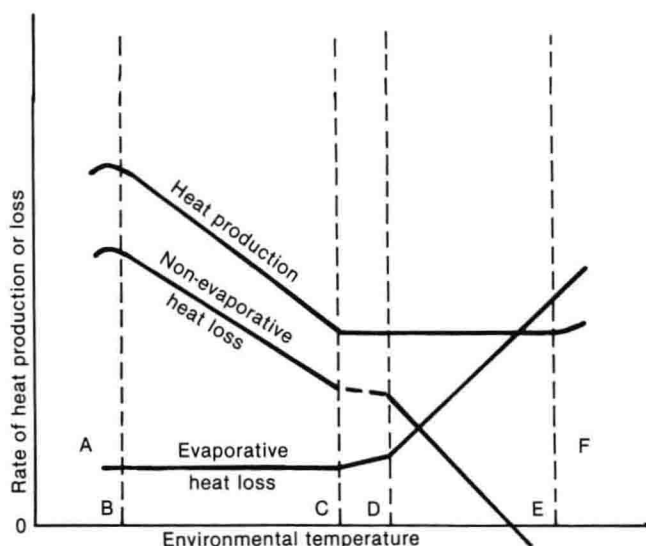


Figure 1. Diagram of relationships between heat production, evaporative and nonevaporative heat loss, and deep-body temperature in a homeothermic animal. A, zone of hypothermia; B, temperature of summit metabolism and incipient hypothermia; C, critical temperature; D, temperature of marked increase in evaporative loss; E, temperature of incipient hyperthermal rise; F, zone of hyperthermia; CD, zone of least thermoregulatory effort; CE, zone of minimum metabolism; BE, thermoregulatory range. The zones are as defined by Mount (29). Reproduced by permission.

sulation can be described by using a simple resistance analogue (Figure 2). In the analogue (27), I_c is the coat resistance, I_a the external resistance, and I_r a "resistance" for radiative energy transfer. In the simplest case, when the air and radiant environmental temperatures are equal, we may define a single external resistance $I_a = I_a I_r / (I_a + I_r)$.

Newton's Law of Cooling is often assumed to apply to homeothermic animals. However, Fourier's Law of Heat Loss, which states that the rate of sensible heat exchange between a body and its surroundings is proportional to their temperature difference, is more appropriate. Indeed, neither applies within the zone of "least thermoregulatory effort" (29) where animals control their heat loss by changing body insulation. However, at a lower critical temperature, T' (C in Figure 1), the sensible heat transfer through the coat becomes equal to the net metabolism at the minimum rate, M . This temperature is determined largely by coat insulation. At the lower critical temperature, T' , neglecting evaporation,

$$M = (T' - T) / (I_c + I_e) \quad (9)$$

Because in most coated animals and man I_c is usually substantially greater than I_e , the lower critical temperature is determined principally by