Man and Animals in Hot Environments

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Preface

This book is an introduction to the physiological reactions of man and animals to hot environments. It is intended for those who already have some knowledge of physiology. The aim has been to bridge the gap between general texts on physiology and advanced books on environmental physiology that deal with the specific problems of particular regions or individual species. Advanced works of this kind are referred to in the text and given in the bibliography.

The bibliography is extensive, but in spite of the formidable literature we are still ignorant of many aspects of thermal physiology, and the species that have been studied in detail are only a small proportion of those that may usefully receive attention. Physiologists have often seemed to assume that all animals are similar to man, dogs, cats, and rats, but these species have been chosen for study on the basis of convenience and not because they are representative of animals as a whole. There is another basis on which the selection of species for study can be made, however, and that is their usefulness to man. Man is of obvious interest to himself and has been given a separate chapter, but in the chapters on animals emphasis has been placed, when possible, on those species that have been domesticated and on which man depends for food and labor.

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Contents

CHAPTER 1

The Thermal Environment

Hot, Thermally Neutral, and Cold Environments

The deep body temperature of homeothermic animals is maintained within fairly narrow limits by elaborate thermoregulatory mechanisms. These rely on a large number of graded physiological, morpohological, and behavioral responses, which in turn depend on the thermal nature of the environment. The thermal characteristics of the environment are essentially air temperature, radiant temperatures (infrared and solar radiation), rate of air movement, humidity, wetting by precipitation or otherwise, and in certain cases the nature of the floor. These thermal characteristics determine the levels of heat exchange between animal and environment (Chapters 2 and 3).

The term "heat exchange" implies either heat loss from the animal to the environment or heat gain by the animal. In the cold, animals lose heat through channels that depend on a temperature gradient, that is, by radiation, convection, and conduction. These channels are often termed "sensible" because the loss of heat through them is a form of energy transfer that can be detected by the senses. Under hot conditions animals tend to gain heat through these channels and can lose heat to the environment only by evaporation either from the body surface (by sweating or by the evaporation of water other than sweat) or by panting (Chapters 3 and 4). In the cold, the primary problem for animals is conserving the heat they produce, an end achieved by insulative and behavioral adaptations. Under hot conditions, in contrast, the problem is one of heat dissipation by physiological and behavioral means (Chapters 4, 5, and 7). Between cold and hot lies an intermediate range in which animals find little difficulty in maintaining body temperature. This zone varies with species and the age and adaptation of the animal, and is related to the zone of thermal neutrality (Chapters 2 and 3) in which the rate of heat production is at a minimum.

Below a certain air temperature an increase in the rate of oxygen consumption occurs in homeothermic animals. This air temperature, which must be determined under given conditions as discussed below, is termed the "critical temperature." Below this point the environmental conditions can be described as "cold" because the animal must increase its metabolism in order to maintain thermal equilibrium. Immediately above the critical temperature there is a range of temperature over which oxygen consumption does not change. However, at some still higher air temperature the animal's body temperature begins to increase because heat cannot be lost fast enough. As a consequence of this increase in the temperature of the tissues, and because chemical reactions proceed faster at higher temperatures, oxygen consumption increases. The oxygen consumption curve for a hypothetical mammal is shown in Fig. 1–1.

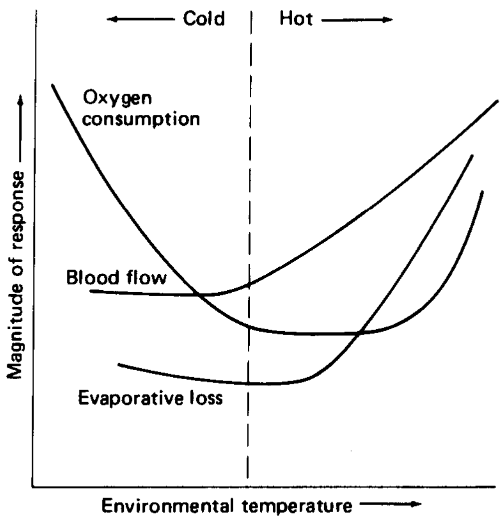

Fig. 1–1. Oxygen consumption curve for a hypothetical homeotherm. The terms "hot" and "cold" can be defined in terms of the animal's physiological responses to its environmental temperature.

The rate at which heat is lost through radiation, convection, and conduction can be modified by changes in the rate at which blood flows through the skin (Chapter 5). Variations in the rate of peripheral blood flow alter the tissue insulation between the core and the skin surface and the skin temperature. Below the critical temperature the rate of peripheral blood flow is very small. If the rate of peripheral blood flow is measured as the air temperature is increased (Fig. 1–1), both the flow and the skin temperature begin to increase near the critical temperature and heat loss is facilitated.

Below the critical temperature the loss of water by evaporation from the skin is small. As the environmental temperature rises above the critical level evaporative heat loss is increased (Chapter 4). As the temperature rises still further, sensible heat loss declines toward zero and the evaporative channel becomes the only effective route for heat loss.

In the idealized diagram of Fig. 1–1 there is a range of temperature over which oxygen consumption and evaporative heat loss remain at a minimum and only peripheral blood flow changes. Within this range of environmental conditions, thermal equilibrium can be maintained with a minimum expenditure of raw materials in the form of food and water, indicating a zone of minimal material demand. Some authors have recently suggested that the definition of thermal neutrality be restricted to this zone (Mount, 1974); the older definition of the term refers to the zone in which oxygen consumption is minimal. However, in some instances this wider zone can include temperatures at which sweating or panting occurs and that may therefore be considered as too hot for a strictly "neutral" zone. This matter is given further attention in Chapter 3.

It is most important to appreciate that in Fig. 1–1 environmental temperature has been represented as simply the air temperature as measured with a dry bulb thermometer. There is no indication that air movement, radiant temperature, or humidity are involved. If, however, the critical temperature is determined as air temperature in environments with different wind speeds, for example, the critical temperature is higher under more windy conditions than in still air. This is because convective heat transfer for a given air temperature is greater in a wind than in still air. Similarly, if the critical temperature is determined at constant air temperature but under different conditions of radiant heating, it is found that when the radiant temperature is high the critical temperature is reduced. To avoid this confusion it is usual to have the air movement as low as possible and to specify the critical temperature in an environment with the radiant temperature the same as the air temperature. The exact conditions should in any event be stated.

Even when the climatic conditions have been fixed, however, other factors in the environment can influence the critical air temperature; for example, the provision of straw bedding lowers the critical temperature because it enables the animal to increase the amount of external insulation. Two or more animals together can modify the effects of a fall in ambient temperature by huddling, and even a single animal can alter the surface area of its body available for radiant, convective, and conductive heat transfer simply by changing its posture.

There are several additional factors that can influence the effect of a given environment on an animal's physiological responses to temperature. Animals on a high level of food intake have a lower critical temperature than those on a low level (Chapter 3). Metabolism may be influenced by the animal's previous thermal history: the resting metabolism of an animal that has been exposed to heat for some days is lower than that of a control animal exposed to the cold. Prolonged exposure to a particular set of conditions also influences the endocrine system (Chapter 6). Seasonal changes often occur in the amount of external insulation so that the critical temperature is lower in the winter than in the summer. Such animals as mice that have been raised from birth in a hot environment grow longer tails and so have a greater surface area available for heat exchange. A further complication is that all measurements should be made under steady-state conditions, that is, when body temperature is not changing. If this condition is not met, then account must be taken of the heat that has been stored in the body or lost. In practice, the condition can only be met over short periods because body temperature tends to fluctuate rhythmically over a 24-hour period.

This combination of effects means that it is very difficult to make strict comparisons between animals even of the same species. What is a warm environment for one animal may be a cold one for another. This is certainly true for members of the same species but of different age, for example, newborn and mature pigs. Among species the differences may be very great indeed. The arctic fox in winter has a critical temperature below −30°C, whereas the laboratory rat's critical temperature is about +28°C. As a result a room at 10°C is "warm" for the fox and "cold" for the rat.

The reaction of animals and man to hot environments is discussed in Chapters 9 and 10. These discussions are limited, for the most part, to the climatic aspects of the environment, but it must be appreciated that both animals and man live in microenvironments that may be quite different from the surrounding macroenvironments. Man, especially, modifies his surroundings and may create a hot environment, such as a boiler room, in a temperate climate or he may, like the Eskimo, use clothes with a high insulation and so contrive to live in a subtropical microenvironment although the air temperature is below zero.

Development of Climatic Physiology

To a large extent the development and understanding of climatic physiology depended on progress in the physical sciences. As Mendelsohn's historical survey (1964) showed, the heat generated by animals has intrigued man since early times. However, until the development of measuring instruments an understanding of the problems involved was not possible. For example, the idea that the heart was the seat of an innate burning heat was held for hundreds of years before the temperature in the heart of an animal was measured with a mercury-in-glass thermometer in the seventeenth century. There still remained a confusion over the distinction between temperature and quantity of heat, a confusion (it might be added) that has sometimes occurred even today.

Some idea of early investigations in climatic physiology can be gained from reading two papers by Blagden (1774, 1775), which must be among the first written on the effects of a hot environment on man and animals. These reports include a much-quoted reference to experiments in which it was demonstrated that a man or a dog could survive in a hot room for the length of time it took a piece of meat exposed to the same environment to be cooked. Some extracts of the first paper are reproduced below (by permission of The Royal Society), but the originals are worth reading in full, both for the style and for the content.

> Experiments and Observations
> in an Heated Room
> By Charles Blagden, M.D., F.R.S.
> Redde Feb 16 1774
>
> About the middle of January several gentlemen and myself received an invitation from Dr. George Fordyce, to observe the effects of air heated to a much higher degree than it was formerly thought any living creature could bear. We all rejoiced at the opportunity of being convinced, by our own experience, of the wonderful power with which the animal body is endued, of resisting an heat vastly greater than its own temperature; and our curiosity was not a little excited to observe the circumstances attending this remarkable power.

The second paper was read more than a year later and involved temperatures up to 260°F. The use of the terms "temperature" and "heat" in these papers suggests very strongly that at this time the distinction of meaning between them was not fully appreciated; for example, "Many repeated trials in successively higher degrees of heat, gave still more remarkable proofs of our resisting power" and again "pure water was heated to 140°F of the thermometer, whilst that with the wax had acquired an heat of 152°F," or "the actual heat of my body, tried under my tongue, and by applying closely the thermometer to my skin, was 98°F, about a degree higher than its ordinary temperature."

From other passages it is clear that a number of key observations have been made in these studies. For example, Blagden suffers more effect from the first exposure than from those reported in the second study, and he records that the first experiments have been made in the evening after a heavy meal. He also comments that the heat is more readily endured when the air is still and suggests that this is because air in contact with the body is cooled. In other words, he appreciates the effects of a boundary layer of air. In a footnote there is an interesting observation on evaporative cooling in amphibia.

> I applied a thermometer, in a hot summmer day, to the belly of a frog, and found the quicksilver sink several degrees: a rude experiment indeed, but serving to confirm the general fact, that the living body possesses a power of resisting the communication of heat.

However, it is not very clear whether Blagden fully appreciates the effects of evaporation because he seems to have believed that man's ability to withstand temperatures above body temperature is not entirely due to the vaporization of water.

In the following chapters the present state of knowledge about the reactions of man and animals to hot environments will be examined.

CHAPTER 2

Heat Exchange between Animal and Environment

Metabolic Heat and Its Dissipation

As a result of its metabolic activity, an animal produces heat. The rate at which heat is produced bears a direct relation to the metabolic rate measured as oxygen consumption. For this reason the two rates are often considered as relating to the same quantity and as being interchangeable, provided the animal is not doing external work. Although "metabolic rate" and "heat production" may have the same meaning, they are not necessarily of the same magnitude as heat loss. The rate of heat loss from an animal is determined by the rate of heat production and the rate at which heat is being lost from or stored in the body as the result of changes in the temperatures of its parts:

$$M = H + S \qquad (2\text{–}1)$$

where M = rate of heat production, or metabolic rate
H = rate of heat loss
S = rate of change of stored heat

M is always positive because it represents a collection of reactions of net exothermic value. S may be positive or negative; it is positive when the mean body temperature is rising and heat is being stored in the body and it is negative when the mean body temperature is falling. H is much more commonly positive than negative because the animal's net requirement is the dissipation of metabolic heat production. However, H can be negative, as for example in the rewarming following hypothermia or under conditions that induce hyperthermia, when there is a large positive storage rate derived from environmental heating. Under these conditions the environment acts as a heat source and not as a heat sink for the animal's metabolic heat. H is given by:

$$H = H_R + H_C + H_D + H_E \qquad (2\text{–}2)$$

where H_R = radiant heat loss
H_C = conductive heat loss
H_D = conductive heat loss
H_E = evaporative heat loss

H_R, H_C, and H_D may individually or collectively be positive (net heat loss from the animal, with the environment as a heat sink) or negative (net heat gain, with the environment as a heat source), depending on the temperature relations between animal and environment. H_E is nearly always positive, although under extreme conditions there may be net condensation of water vapor on an animal placed in an environment with a dewpoint above the skin temperature.

The relation among the production, loss, and storage of heat in the organism indicates the manner in which heat from metabolic processes is dissipated. Without loss to the environment, heat can be stored temporarily in the body but this mechanism is limited by the entailed rise in body temperature. For example, if a 70-kg man has a thermal capacity of 3.47 kJ kg^{-1} °C^{-1} (Burton and Edholm, 1955), a mean rise in body temperature of 1°C absorbs $70 \times 3.47 = 242.9$ kJ, which represents approximately 35 minutes of resting heat production. Heat is stored when the organism is exposed to high environmental temperatures that change heat loss into a heat gain from the environment, so that H becomes negative. S then becomes positive, both because of metabolic heat production and because of heat gained from the environment. This situation occurs in the camel during the daytime, when it is exposed to high temperatures. The animal's body temperature rises several degrees during the day and then falls during the succeeding night.

The subject of thermal capacity and body heat content in man has been discussed by Minard (1970). The difference between heat production and heat loss represents the change in heat content. When this change is divided by the thermal capacity, the change in mean body temperature is derived. A value of 3.47 kJ kg^{-1} °C^{-1}, which has been assumed for man for some time, lies between the extremes of 1.88 for fat and 4.18 for water; the value for lean flesh has been determined as 3.47. A closer approximation to the true value may therefore be based on the fat content of the subject. A higher fat content leads to a lower specific heat and a lower fat content to a higher specific heat. In practice, however, 3.47 kJ kg^{-1} °C^{-1} is commonly used.

Body Temperature

The implication of thermoregulation in the homeotherm is that body temperature is controlled, by processes of heat production and heat loss, at a stable level that is approximately maintained in spite of fluctuations in the environment. It is, in fact, the deep body temperature that is the controlled quantity; peripheral tissue temperatures vary considerably, depending on ambient conditions. The proportion of the body at the core temperature of 37°C in man is expanded under warm conditions, with a high skin temperature, and contracted in the cold, with a low skin temperature (Fig. 2–1). More ex-

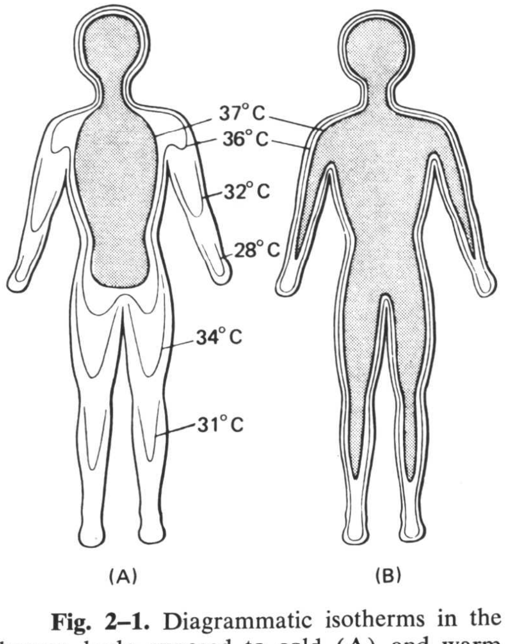

Fig. 2–1. Diagrammatic isotherms in the human body exposed to cold (A) and warm (B) conditions. The core of deep body temperature (shaded) shrinks in the cold, leaving a peripheral shell of cooler tissue (Aschoff and Wever, 1958).

treme temperature variations within the organism occur in other animals, examples being the very low foot temperature in the herring gull exposed to cold and the low skin temperature in the pig raised in a cold environment (Irving, 1964). It follows that there is no single body temperature and that the term "homeotherm" applies essentially to the maintenance of a stable core temperature. If the skin temperature is held at a given level by the animal's metabolic responses and if the metabolizing tissues are also deep in the animal, the deep body temperature varies considerably for the following reasons. If the environment becomes cooler, so that heat loss from the animal increases, the rate of heat production must increase if the skin temperature is to remain constant. Because the animal's thermal insulation between its core and periphery is finite, and although sometimes very slight is never zero, the increased rate of heat production leads to a rise in the temperature difference between core and periphery. In practice, the only situations in which surface temperature control leads to stable deep temperature control are the cases of a highly conducting, centrally heated object, such as a metal sphere containing an electric heater, and of forced convection in a fluid, as in a rapidly stirred water bath containing a heater.

Although the core temperature is stable in the sense that it does not fluctuate rapidly when the environment changes, it is not constant. It varies with time of day, activity and environmental conditions. The actual manner in which the body temperature is controlled in the homeotherm has been the subject of continuing extensive discussion and many explanations have been put forward. Accounts of the experimental evidence on which some of the hypotheses and models have been based can be found in a number of reviews (Hardy, 1961; Bligh, 1966).

Variations in temperature in different parts of the organism are associated with variations in heat storage. The practical implication of this in measuring heat loss from an animal is that heat loss is increased or decreased by changes in heat storage. The direct measurement of heat loss is therefore limited as an indication of metabolic rate. Burton (1935) has derived the mean body temperature for man as $0.65\ T_R + 0.35\ T_S$, where T_R is the rectal temperature and T_S is the mean skin temperature. He bases his calculations on 54 percent of the body volume lying within 25 mm of the body surface. Although T_S contributes only one-third of the mean body temperature, its variation is usually much greater than that of T_R.

Poikilotherm and Homeotherm

In poikilotherms, the body temperature tends to follow the environmental temperature because the resting level of heat production is very low and because there is no autonomic thermoregulatory system of the type existing in mammals and birds. This does not mean that the body temperature is always the same as the environmental temperature. The body temperature in insects rises when they become active, and this rise permits a higher level of metabolism than can occur at the lower level. This is an example of activity producing a difference between body and environmental temperatures in a poikilotherm. In certain lizards, a relatively stable body temperature can be produced by the animal moving between sun and shade. This use of environmental diversity to give a measure of thermoregulation is clearly itself environment-dependent, whereas the example of the active insect shows how a gradient can be maintained between body and environment by metabolic means.

Such poikilothermic regulations differ from those in the homeotherm both in the range of mechanisms at the animal's disposal and in the ways in which these are integrated functionally. Both the metabolic rate and the vasomotor and pilomotor effects on the rate of heat loss in the homeotherm are governed centrally. Effects of peripheral origin involve behavioral adjustments, including activity and posture. The net result in the homeotherm is the maintenance of a relatively stable deep body temperature in spite of fluctuations in environmental temperature. Stability, although limited in extent and duration, also occurs in the poikilotherm, but the built-in autonomic mechanism is absent.

The metabolic rate in the poikilotherm increases as body temperature increases, according to the van't Hoff effect, over the whole temperature range (Fuhrman and Fuhrman, 1959). The Q_{10} is the factor by which the velocity of a reaction is multiplied by a rise in temperature of 10°C and is given by the equation:

$$Q_{10} = \left(\frac{K_2}{K_1}\right)^{10/(T_2-T_1)} \qquad (2\text{–}3)$$

where K_1 and K_2 are velocity constants corresponding to temperatures T_1 and T_2. When, as often occurs, the rate of reaction is doubled by a rise of 10°C, $Q_{10} = 2$. The homeotherm, in contrast, shows a relation between its body temperature and metabolic rate only at the extremes of cold and heat, where the body temperature is falling or rising (Graham et al., 1959; Mount, 1968a). At intermediate temperatures the body temperature is maintained at a steady level by variations in metabolic rate and thermal insulation that lead to greater or lesser heat losses, depending on whether the environmental temperature is lower or higher.

The homeotherm characteristically produces considerable heat and the minimum production under warm conditions is in excess of the requirement for thermoregulation. The considerable resting heat production of the homeotherm, compared with that of the poikilotherm, can be exemplified by a comparison of rodents and lizards in the desert. The metabolic rate of the desert rodent is about seven times that of the desert iguana at an environmental temperature of 37°C, when the iguana's deep body temperature is similar to that of the rodent (Schmidt-Nielsen, 1964).

When the environmental temperature continues to rise, the metabolic rate in the homeotherm also eventually begins to rise, as does body temperature. The homeotherm is then behaving more like a poikilotherm in that its heat production is following the body temperature, which itself is following the environmental temperature. The animal is now outside the range within which it can control its body temperature, and unless it is removed to cooler conditions it dies in hyperthermia. A corresponding situation occurs when the environment is so cold that the animal's maximal metabolic response does not maintain body temperature. The metabolic rate and body temperature then decline together and the animal dies in hypothermia.

Heat Flow

The maintenance of a relatively stable core temperature in an organism exposed to a fluctuating environment presupposes some form of control of the flow of heat between the organism and its environment. It is apparent that a higher rate of heat production in a body can produce a higher body temperature. In addition, increased thermal insulation allows the temperature to rise although the rate of production of heat may remain constant. The homeotherm has control over both heat production and insulation and consequently exhibits a pattern of interrelation between heat flow, body–environment temperature difference, and thermal insulation. The modes of heat transfer between organism and environment are examined in this chapter and thermal insulation is considered in Chapter 3.

In most circumstances, the rate at which heat is lost or gained by a body is almost exactly proportional to the temperature difference between the body's surface and the environment. This relation is often described in terms of Newton's law of cooling, but this law, as it names implies, is primarily concerned with the rate of change of the temperature of the body. In an animal at equilibrium, cooling is not taking place although there is heat flow. It is therefore more appropriate to consider heat flow rather than cooling (Kleiber, 1961).

Heat flow is proportional to the temperature gradient and to the thermal conductance of the medium through which the heat is passing. This is a statement of Fourier's law, which may be expressed as:

$$H = \lambda \frac{A}{L}(T_1 - T_2) \qquad (2\text{–}4)$$

where H = rate of heat flow
A = surface area
L = thickness of medium through which heat is passing
λ = thermal conductivity of medium
$T_1 - T_2$ = temperature difference across the medium

This can be rewritten in a form corresponding to Ohm's law for the flow of electricity:

$$H = A\,\frac{(T_1 - T_2)}{R} \qquad (2\text{–}5)$$

where $R = L/\lambda$
= resistance to heat flow per unit cross-sectional area

In this instance, R can be defined as the "specific insulation," which is the insulation per unit area, a concept that can be applied to the thermal insulation between an animal's core and the environment. The reciprocal of the specific insulation is the thermal conductance, C:

$$H = AC(T_1 - T_2) \qquad (2\text{–}6)$$

The problem for the homeotherm under hot conditions is dissipating the heat it produces. The two modes of heat transfer through which heat dissipation can take place are the sensible and the evaporative. The term "sensible" is used here to indicate a mode of heat transfer that depends on a temperature gradient. It includes heat flow through radiation, convection, and conduction. Evaporative transfer, however, does not necessarily depend on a temperature gradient. It depends instead on the heat that is taken up by water when it changes from the liquid to the vapor state. Its particular significance is that loss of heat can still take place by this means even when the surroundings are at a higher temperature than the animal.

Sensible Heat Transfer

Each mode of sensible heat transfer depends primarily on the difference between the animal's surface temperature and the corresponding environmental temperature. The corresponding environmental temperatures are the mean radiant temperature, the air temperature, and the floor temperature, for radiative, convective, and conductive heat transfer, respectively. The magnitude of the heat flow through each channel also depends on additional factors, which are given in Table 2–1.

Radiation

Heat exchange by radiation in animals is conveniently considered in two parts. The first part deals with exchange when radiation from the surroundings is all "long wave," that is, emitted by surfaces at a range of temperatures extending downward from several hundred degrees centrigrade. Long-wave radiation covers a range of wavelengths that has a maximum energy per unit wavelength occurring at a wavelength λ_{max}, which de-

Table 2–1 Factors that Influence the Different Modes of Heat Transfer between Organism and Environment

Mode of transfer	Animal characteristics	Environment characteristics
Radiant	Mean radiant temperature of surface; effective radiating area; reflectivity and emissivity	Mean radiant temperature; solar radiation and reflectivity of surroundings
Convective	Surface temperature; effective convective area; radius of curvature and surface type	Air temperature; air velocity and direction
Conductive	Surface temperature; effective contact area	Floor temperature; thermal conductivity and thermal capacity of solid material
Evaporative	Surface temperature; percentage wetted area; site of evaporation relative to skin surface	Humidity; air velocity and direction

creases as the temperature increases. The relation is given by Wien's displacement law (Jakob, 1949; Monteith, 1973), which states that $\lambda_{max} = 2897/T$ μm, where T is the absolute temperature. For a skin temperature of 30°C, λ_{max} is therefore 2897/303 = 9.6 μm; for 35°C it is 9.4 μm.

The second part of radiant exchange includes the effects of shorter wavelengths; that is, solar radiation, including the visible spectrum and the ultraviolet. Figure 2–2 shows the natural division that occurs between long-wave and short-wave radiant flux in the wavelength region between 2 and 3 μm.

An important feature of long-wave radiation is that it is transmitted by very few substances which are transparent to the shorter wavelengths of the visible spectrum. A common practical example of this is the horticultural greenhouse. Although the main effect of a greenhouse is to decrease con-

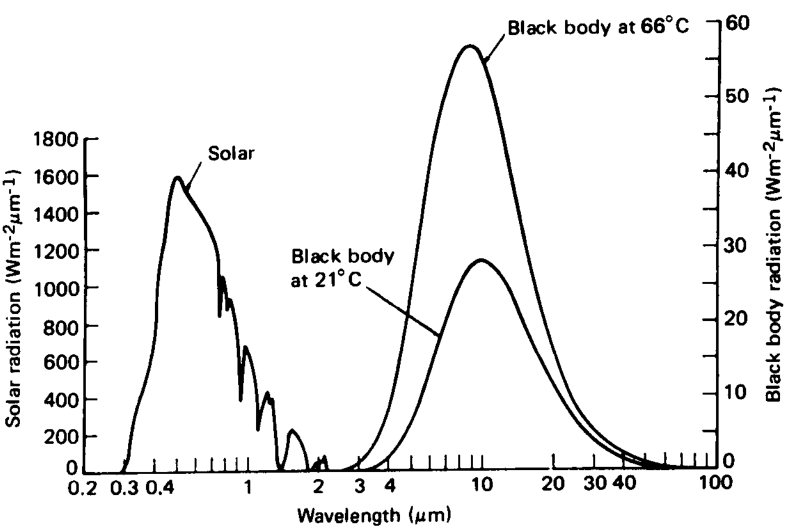

Fig. 2–2. Solar radiation at the ground for a zenith sun and radiation from black bodies at 21°C and 66°C (Bond et al., 1967, *Trans. Am. Soc. Agric. Engrs.* **10:** 622).