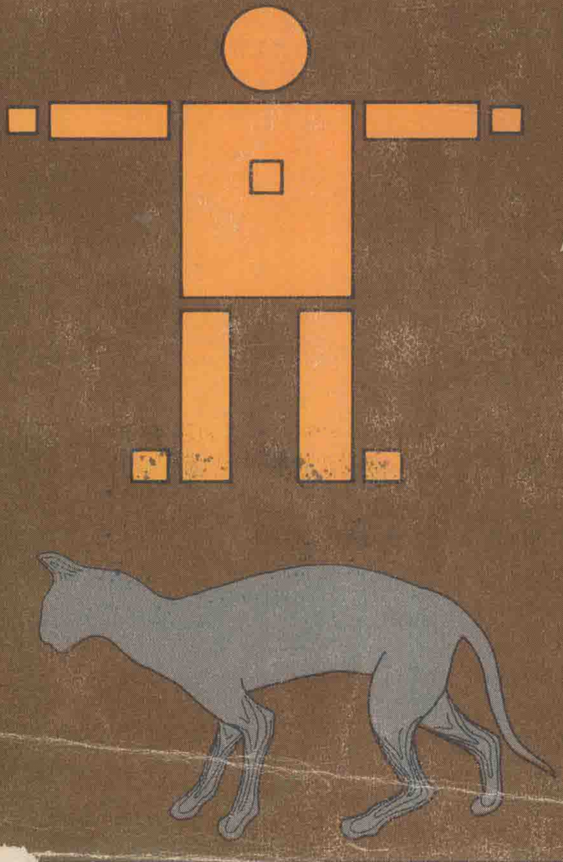
Comparative Physiology of Thermoregulation

VOLUME II

MAMMALS

Edited by G. CAUSEY WHITTOW



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Edited by G. CAUSEY WHITTOW

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Mammals

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COMPARATIVE PHYSIOLOGY OF THERMOREGULATION

Volume II

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PREFACE

The purpose of this three-volume treatise is to present separate accounts of the means by which each of the major groups of animals regulates its body temperature, heat production, and heat loss. Readers who wish to obtain information on thermoregulatory processes in different species will, it is believed, welcome this as a convenient reference work. However, it is hoped that the treatise will have more than convenience value. The juxtaposition of chapters dealing with quite different animals might tempt the investigator to read about species other than the particular one in which he is immediately interested. In so doing he might well find that the specific problem with which he is concerned is better illuminated in another species. This, of course, is the essence of comparative physiology.

The composition of Volume I was determined partly by the amount of information available on invertebrates and on vertebrates other than mammals. Most experimental work on thermoregulation has been performed on mammals, and, accordingly, this volume deals exclusively with mammalian species. Thus, a rigid distinction between homeotherms and poikilotherms, ectotherms and endotherms, and regulators and nonregulators has been avoided.

The obvious omissions in Volume II will be made good in Volume III, which, in addition, will cover some special aspects of thermoregulation. Several of the chapters in Volume III will treat thermoregulation from the point of view of physiological systems. It is believed that this approach will complement the largely taxonomic organization of the first two volumes. It is also hoped that it will lend to the work as a whole a measure of integration which could not be achieved by considerations of species or systems alone.

Once again it is a pleasure to record my gratitude to Mrs. Jane Inouye, Mrs. Hilda Copeland, and to the staff of Academic Press for their willing help in the preparation of this volume.

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Chapter 1 RODENTS*

J. S. Hart

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* This chapter is N. R. C. C. 12006.

I. Introduction

The study of temperature regulation has been pursued more intensively in the rodents than in any other group during the last 25 years, particularly during the last decade. This interest has stemmed partly from the convenience in methodology for study of animals of small body size (10^1–10^4 gm) but primarily from the great diversity in regulatory responses within the group. The latter aspect has attracted much attention from the comparative physiologists interested in hibernation, and in behavioral and physiological regulations during active states in relation to the great diversity of ecological and climatic conditions. These studies have shown that it has not been possible to understand the regulations in different species without knowledge of microclimatic conditions of their habitats and of the behavioral features of the species in question. While the characteristics of torpidity and hibernation will not be considered in this chapter, the microhabitat conditions and behavioral aspects of rodents will be analyzed, since these aspects are an important component of the total ability of a species to insulate itself from its environment.

While it may be concluded that the major interest of the zoological interpretation of temperature regulation has been in relation to the behavior of animals in nature, the rodents have been of primary interest to physiologists in the interpretation and understanding of the mechanisms of temperature regulation. Much of the work in this area has been on laboratory animals such as the white rat in which so much recent attention has been devoted to the study of responses and acclimation to cold. Much less study has been devoted to the acclimation of animals to heat.

In this chapter an attempt will be made to determine generalities common to different species and also to emphasize the species differences. The common factors include the general responses of heat production and loss in relation to body size, conductance, and fur insulation, as well as the general features of body temperature changes and thermal limits. To illustrate the theoretical aspects and definitions of some of these relationships, Fig. 1 shows some hypothetical curves of heat production at various air temperatures to illustrate tolerance and resistance limits, time changes, and acclimation.

In the left-hand section (Fig. 1) the thermal tolerance range (TOL) is defined as a zone within which no lethal effects of temperature occur after any period of time, while the zone of resistance (RES) eventually kills all the animals exposed to these temperatures. These definitions of thermal limits for heat and cold follow those of Fry (1947) as used by Hart (1957, 1961). Within the zone of tolerance there is in almost all rodents a thermoneutral range in which heat production is constant, body temperature may or may not be constant, and which is bounded on its upper and lower limits by the upper (U_c) and lower (L_c) critical temperature limits. In this diagram T_B is shown as a body temperature range which increases slightly with elevation in heat production above U_c. It is assumed that within the zone of resistance both T_B and metabolism

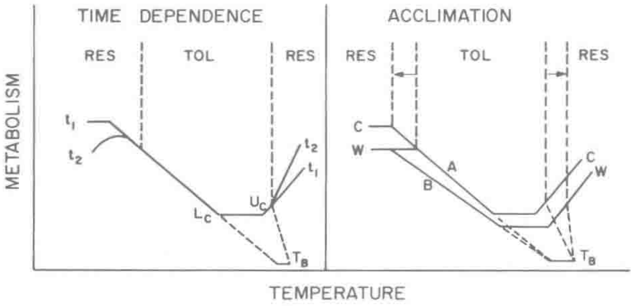

FIG. 1. Metabolic response patterns and lethal limits in relation to time of exposure and acclimation. The zone of tolerance (TOL) is a temperature range in which no lethal effects take place, and the zones of resistance (RES) are ranges in which death results after varying periods of time depending on temperature of exposure. Response patterns also change with increasing length of exposure from t_1 to t_2. Acclimation to cold shifts the tolerance and resistance zones to lower temperature by change of slope of response curve from A to B or increasing the maximal response from *W* to *C*. Acclimation to heat may shift the zones of resistance and tolerance to the right by lowering the basal metabolism and changing the heat response from *C* to *W*. T_B, body temperature; L_c, lower critical temperature; U_c, upper critical temperature.

(M)* become time dependent, ending in the death of the animal with passage of time from t_1 to t_2.

Similarly, below L_c heat production in the zone of tolerance is assumed to increase in direct proportion to the temperature differences between T_B and T_A (air temperature) according to Fourier's law of cooling (Scholander *et al.,* 1950c). Below L_c thermal conductance [defined in the literature as $M/(T_B - T_A)$] is constant, while above L_c in the thermoneutral zone it increases with constant T_B. In the zone of resistance for cold, oxygen consumption and body temperature are again time dependent. The lower the temperature, the faster T_B and M fall; therefore determination of the maximal heat production (t_1) can only be measured after a very short exposure, before M is reduced by hypothermia to t_2 after a longer exposure period (Depocas *et al.,* 1957).

In the right-hand section of Fig. 1 are shown some possible shifts with acclimation to heat or cold. As defined by Hart (1957), acclimation to cold and increase of cold resistance, as indicated by the left pointing arrow, could take place by increase of insulation (lowering of conductance) through a change in slope from A to B (insulative acclimation) without change in maximal heat production (W). Alternatively cold resistance could be increased without change in slope but with increase in capacity (C).

It will be shown that acclimation to high temperatures appears to take place in rodents by the lowering of the thermoneutral heat production. Consequently an increase in heat resistance, indicated by the right pointing arrow, could result from elevation of the U_c and lowering of the metabolism from C to W. It is also possible that acclimation to heat may produce greater resistance to hyperthermia, as suggested by the elevation of T_B.

The theory and speculation raised by these diagrams will be assessed in the forthcoming sections on temperature regulation at high and low temperatures, particularly at the thermal limits. Both comparative aspects and regulatory mechanisms will be discussed. Additional sections dealing with the effect of activity and the effect of hypoxia on thermal responses are also included. This review is intended to stress aspects of temperature regulation not considered in depth in other reviews on the subject (Hart, 1957, 1963; Hensel, 1959; Carlson, 1962, 1966; Johansen, 1962a; Morrison, 1962a; R. E. Smith and Hoijer, 1962; Gelineo, 1964; Folk, 1966; Witke (1966); Himms-Hagen (1967); R. E. Smith and Horwitz (1969) and to concentrate on the more recent studies in this area. Taxonomy of rodents has followed Ellerman (1941), Ellerman and Morrison-Scott (1951), and Hall and Kelson (1959). Terminology for symbols follows in part that proposed by Gagge *et al.* (1967).

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* Equivalent to heat production; dimensions not specified.

II. Thermal Environment of Rodents

The worldwide distribution of rodents from arctic to tropical regions of the earth and from sea level to altitudes exceeding 15,000 ft imposes a very diverse range of environmental conditions, and necessitates a great diversity of behavioral and physiological adaptations. Within these broad geographical life zones the habitat specializations of rodents, as exemplified by fossorial types which normally do not leave their underground burrows and by aquatic types such as beavers and muskrats, impose further modifications of environmental conditions with important implications for temperature regulation. In order to provide some background for an understanding of temperature regulation in rodents it is necessary to examine the actual environmental conditions of the habitat, and particularly the thermal conditions of the microclimate to which they are exposed. This includes consideration not only of the temperatures in these habitats but also other physical and ecological conditions such as snow cover, water and humidity, insolation, and protection by tunnels and vegetation. For these considerations it is convenient to discuss and contrast arctic and subarctic, temperate, and warm (mostly desert) regions separately. Although these are overlapping zones in the strict sense, the microclimatic differences are generally quite distinct.

A. Arctic and Subarctic Regions

The biological, as contrasted with the physical, delineation of the arctic and subarctic has been designated by Kimble and Good (1955) in terms of the 10°C isotherm for July and in terms of the 10°C isotherm for the four warmest months, respectively. The lower boundary of the arctic combines the boreal forest and taiga or tundra forest to form the subarctic zone (Schwartz, 1963), which corresponds well with the extent of general permafrost (Morrison, 1966). It is also a region defined in terms of day length, with extremes in energy input from summer to winter, which have both direct and indirect consequences for the energetics of rodents. In regard to the seasonal variations in light and temperature given for Alaska (Irving, 1964; Morrison, 1966), which are typical of this general region, changes in mean lower temperature from about —25°C in winter (extremes to —50°C) to 10°C in summer could not be endured by any rodent without protection. However, these regions have been successfully colonized by nine species of microtine rodents, one sciurid, and three aquatic species (Schwartz, 1963) in Siberia, and ten microtines, two aquatic rodents, and eight sciurids in North America, in addition to *Dicrostonyx* and *Zapus* (Hall and Kelson, 1959).

The insulative function of snow in providing warmer microclimates for the survival of small mammals in winter has been described mainly by Formazoff (1946) and Bashenina (1963) in Siberia, by H. M. Johnson (1951, 1957), Pruitt (1957), Weedfall (1963), and Morrison (1966) in Alaska, and also by Geiger (1950), Coulianos and Johnels (1963), and Dalenius (1963) in Europe. These authors indicate gradients through 20–30 in. of snow from —40°C or lower on the surface or ground snow interface on a cold winter day. The importance of the air space between ground and snow for small mammals is emphasized because it is in these lower layers that the smaller microtine rodents are mainly active. However, it is reported that some activity on the surface occurs at night in nocturnal *Microtus* and *Clethrionomys* at temperatures down to —20°C (H. M. Johnson, 1957). Temperatures in tunnel systems of lemmings in active subnivean feeding areas in a cold period were found to be as low as —23°C. The diurnal red squirrels were active on the surface at much lower temperatures in Alaska (Pruitt, 1958) and were commonly seen at temperatures down to —32°C (see Fig. 24).

Seasonal variations in the microclimatic temperatures under snow cover indicate habitation by rodents in the 0°C to —20°C range in winter (Pruitt, 1953, 1957; Bashenina, 1963; Bashenina and Borovskaja, 1963; Coulianos and Johnels, 1963; Weedfall, 1963) and in the 0°C to 15°C range in summer (Table I). Considerably warmer temperatures than these could presumably be attained by nests and huddling (M. S. Johnson, 1926; O. P. Pearson, 1960b; Bashenina, 1963; Stark, 1963). However, any foraging would require exposures of individual mice to the temperatures indicated. This nocturnal activity has been noted in particular before the snow depth reaches 10–20 cm. Both Formazoff (1946) and Pruitt (1957) indicate that one of the most critical periods for small rodents during cold snaps is before arrival of an adequate snow cover, which may result in considerable mortality.

The data in Fig. 2 show thermal conditions in air and in the soil at different times of the year in Alaska (Pruitt, 1957), south Michigan (Pruitt, 1959) and Arizona (Vorhies, 1945). In Alaska [and also north Michigan (Pruitt, 1953)] soil temperatures (3 in. level) were largely higher than air temperatures during winter, but fell within this range of air temperature during winter in southern Michigan and Arizona (Fig. 2). These differences are related to the insulation of the ground provided by deeper snow in the northern locations. The damping of temperature variations by soil and snow is quite marked in the deeper soil layers of the taiga (Fig. 2). However, in spite of this protection, the small mammals living in these layers and in subnivean spaces (Fig. 2) are exposed to temperatures considerably lower than in more southerly environments.