



Thermodynamic Equilibria of Animals with Environment

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THERMODYNAMIC EQUILIBRIA OF ANIMALS WITH ENVIRONMENT¹

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INTRODUCTION

All processes of life, all physiological events, do work and expend energy. A continuing supply of energy is necessary for an animal to live. One of the primary means by which the environment influences animals is through the exchange of energy. If the animal takes in more energy than it gives out it will get warmer, overheat and perish. If the animal loses more energy than it gains it will cool and not survive. An animal may warm or cool for a limited period of time, but on the average, over an extended period of time, an animal must be in energy balance with its environment. The mobility of most animals permits them to seek the environment most compatible with their physiological requirements for energy. The factors of the environment which are primarily responsible for energy flow to an animal are several, e.g. radiation (sunlight, skylight, and radiant heat), air temperature, wind, and humidity. There are other environmental factors, such as the gravitational, electrical, or magnetic fields, which might determine energy flow between animals and environment but may be ignored as generally not significant to the energy budget of an animal. The microclimate around an animal is thought of as a four dimensional space in which the four independent variables—radiation, wind, air temperature, and humidity—are acting simultaneously and are each time dependent.

The exchange of energy between an animal and its environment affects the body temperature of the animal. The body temperature is considered here as a dependent variable. The rate of moisture loss by the animal is in part determined by environmental

conditions and in part by the animal's physiology. The metabolic rate, although primarily a physiological property of the animal involving chemical energy, may also depend somewhat on environmental conditions. Hence, in working with relations between an animal and its environment, one is confronted with two or more dependent variables of the animal and four or more independent variables of the environment. Generally, the problem of interaction between an animal and its environment can be no simpler than this six or seven dimensional space. These variables of body temperature, rate of moisture loss, metabolic heat, radiation, air temperature, wind, and humidity must be written in a self-consistent framework or else there is no basis for comparison. This self-consistent framework is energy. There is no other relation than energy which connects the environmental factors with the animal response. All energy flow quantities used in this article are expressed in calories/cm² of animal surface/minute.

The outermost surface of skin, fur, or feathers of an animal is the transducing surface across which the environment interacts with the internal physiology. The streams of energy flowing to and from this surface are shown in Fig. 1. There may be direct sunlight, S , scattered skylight, s , and reflected light, $r(S + s)$. There always is infrared thermal radiation emitted by the soil, rock, and vegetation surfaces of the environment, R_g , and from the atmosphere, R_a . The animal will lose energy by radiation from its surface according to the radiation law, $\epsilon\sigma T_r^4$, where ϵ is the emissivity of the skin, fur, or feather surface, σ is the Stefan-Boltzmann constant, and T_r is the surface temperature of the radiating outermost surface. The actual physical surface from which this radiation occurs is often very irregular and complex, varying up and down with the structure of the fur,

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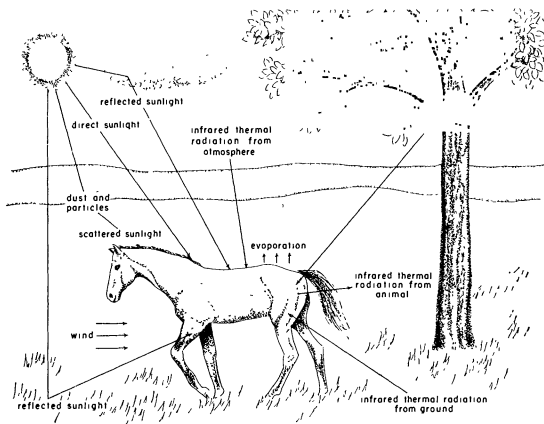


FIG. 1. Streams of energy between an animal and the environment.

feathers, or skin. The wind may blow with a speed, V , expressed in cm sec^{-1} . If the air temperature, T_a , is cooler than the surface temperature, T_r , of the animal, then energy is lost from the animal to the air by convection. The term convection includes conduction in the boundary layer of air next to the animal surface and mass movement of air beyond the adhering boundary layer. If the air is warmer than the animal surface temperature, then convection will add heat to the animal. When there is no wind movement, convection still occurs in the form of free convection set up by the temperature differential between the animal surface and the air. In addition to convection heat may be exchanged by direct conduction if the animal is in contact with a substrate at a different temperature.

Energy is lost vaporizing water within the respiratory tract and expelling it from the animal. The amount of water lost in grams per unit time when multiplied by the latent heat of vaporization of water at the appropriate temperature (580 calories per gram at 30°C), gives the rate of water loss in energy units of cal sec^{-1} or cal min^{-1} . The respiratory moisture loss is E_{ex} and moisture lost by sweating is E_{sw} . All quantities are expressed finally in terms of unit surface area as $\text{cal cm}^{-2} \text{min}^{-1}$. In addition to the streams of energy described above, energy is lost by defecation and urination. This is usually a small part of the total energy flow.

The model formulated here is simple. The animal is treated for conceptual purposes as a series of concentric cylinders. We know that an animal is not, in fact, simply concentric cylinders, but has appendages and irregular shapes. Yet a great deal is understood concerning the energy budget of an animal from a simple model to which complications can be added later.

The analysis given here is for steady state situations. However, much of the time an animal is in a transient energy state as it moves about in the en-

vironment. Yet while in transient states the energy budget for the animal must average within the environmental limits permitted by the steady state requirements for survival. An animal may search for food in an environment which is intolerable to it as a steady state situation, providing it is in this environment for a small period of time compared to the body time constant of the animal.

The purpose of this study is to put on a quantitative basis the interaction between animals and environment. From this our intention was four-fold; to establish the relative importance of each environmental factor and animal property to the animal energy budget; to assess the allowable errors in measurement of these factors and properties; to predict with reasonable accuracy the surface and core temperatures for any animal in any specified environment; and, knowing the physiological requirements and physical properties of the animal, to predict the limits of the climatic habitat it must occupy to survive.

The difficulty of dealing with and describing the effects of the environment on organisms has been realized for a long time (Gagge 1936; Winslow, Herrington, & Gagge 1937; and Riemerschmid 1943). In some instances careful experiments have been performed to establish some of the relations of the environment to the heat load on organisms (Digby 1955; Church 1960 a, b; Birkebak 1966; Bartlett & Gates 1967; and Norris 1967) but it is impractical to examine experimentally all the possible combinations of radiation, air temperature, wind velocity, animal size or dimension, feather or fur thickness, metabolic rate, and evaporative water loss. Moreover, one would have little insight into the relative importance of each of the environmental and animal parameters in a given situation until the full experiment was completed. There are considerable experimental difficulties in trying to simulate accurately many natural environments in which animals exist. In addition, the allowable errors in the measurements of environmental quantities and animal properties have not been evaluated in the context of all the variables acting simultaneously. For example, how precisely must we know the conductivity of fat or flesh? Does the same thickness of fur confer equal advantages to animals of different dimensions? Because of the need to try to understand why and how the environments of this planet interact with its animals, we have devised an elementary mathematical model of environment-animal energy exchange based on the physics of heat transfer and the known physical and physiological properties of animals. The predictive power of such a model is enormous, as is demonstrated here.

THE ENERGY BUDGET

The total surface of an animal in a steady state situation must have a net energy flow of zero. The sources of energy flow between an animal and the

environment are metabolism, moisture loss or gain, radiation, convection, and conduction. The energy budget of an animal is written in the following form:

$$\begin{aligned} \text{Energy In} &= \text{Energy Out} \\ M + Q_{\text{abs}} &= \varepsilon \sigma T_r^4 + h_c(T_r - T_a) + E_{\text{ex}} + \\ &\quad E_{\text{sw}} \pm C \pm W \quad (1) \end{aligned}$$

where M is the metabolic rate, Q_{abs} is the amount of radiation absorbed by the animal surface, h_c is the convection coefficient, C is heat conducted to the substrate, W is work done, and the other quantities have been identified in the text. Most of these terms are very complex in themselves and are described in more detail below. All terms in the equation are expressed in $\text{cal cm}^{-2} \text{ min}^{-1}$. For each new set of given conditions each of the terms in Eqn. (1) has a particular value and the surface temperature T_r of the animal adjusts so as to balance the energy budget. If anyone term changes in value, the surface temperature will readjust to a new equilibrium value. All quantities vary with time and may change simultaneously.

Metabolic rates for specific animals were taken from the literature. In most cases the values published are in $\text{cc O}_2(\text{g-hr})^{-1}$. To convert them to cal min^{-1} , an assumption was made about the type of food each specific animal was consuming; e.g. shrews were assumed to be metabolizing protein only. The caloric energy released when one cc of O_2 is consumed depends upon whether protein, fat, or carbohydrate is being oxidized. The metabolic heat released is known (Prosser & Brown, 1961) for protein, 4.5 $\text{cal} (\text{cc of O}_2)^{-1}$; fat, 4.8 $\text{cal} (\text{cc of O}_2)^{-1}$; and carbohydrate, 5.05 $\text{cal} (\text{cc of O}_2)^{-1}$. In order to convert metabolic rate from $\text{cc O}_2(\text{g-hr})^{-1}$ to cal min^{-1} , the literature value was multiplied by the weight of the animal, then by the caloric equivalent of the food typically consumed, then by a unit conversion to convert hours to minutes.

Surface area was computed by procedures described by Birkebak (1966). For animals smaller than 10 cm in diameter possessing small appendages, their appendage surface area was neglected. Appendage surface areas for larger limbs were determined using a mean diameter of each limb segment and its length. Total surface area was divided into the metabolic rate in cal min^{-1} to get heat production per unit area.

The metabolic rate of an animal is governed by genetic limitations to its physiology and by particular environmental conditions. The metabolic rate may be nearly constant or it may vary over a considerable range of values. All animals will lose water by breathing and some animals will sweat or salivate. The rates of water loss by various means and under various conditions must be known to understand the energy budget of an animal.

An animal receives in the natural habitat several streams of radiation including direct sunlight, sky-

light, reflected sunlight and thermal radiation. These radiations, R_i , are of various intensities and spectral compositions and come from many sources and directions. The animal surface presents various areas, A_i , to the different incident fluxes of radiation. The animal surface absorbs the various incident fluxes with mean absorptivities, \bar{a}_i . The amount of radiation absorbed, Q_{abs} , by an animal whose total surface area is A , is given by:

$$\begin{aligned} A Q_{\text{abs}} &= \sum_{i=1}^n \bar{a}_i A_i R_i \\ &= \bar{a}_1 A_1 S + \bar{a}_2 A_2 s + \bar{a}_3 A_3 r(S + s) + \\ &\quad \bar{a}_4 A_4 R_g + \bar{a}_5 A_5 R_a \quad (2) \end{aligned}$$

where r is the reflectivity of the underlying surface to sunlight and skylight. It is, of course, possible that several of the a_i 's are equal and perhaps some of the A_i 's equal one another, but in general they are different. The mean absorptivities to the various streams of incident radiation represent the coupling between the animal surface and the radiation field. If the animal is black to all wavelengths of incident radiation, the coupling of the animal surface temperature and the animal energy budget to the incident radiation is strong. If the animal is white to all wavelengths of radiation, then its surface temperature is decoupled from the incident radiation. Values of the absorptivities for different animals are given later in this paper.

Because the radiation from each source has a unique spectral quality at any given moment in time, the mean absorptivity, \bar{a}_i , of the animal surface to each incident flux of radiation is different. The spectral quality of the radiation from various sources is shown in Fig. 2 and the spectral absorptivities for various selected animals are given in Fig. 3. The mean value of the absorptivity of an animal surface to incident monochromatic radiation, λR_i , at each wavelength, λ , is given by:

$$\bar{a}_i = \frac{\int_{\lambda} a_{\lambda} R_i d\lambda}{R_i d\lambda} \quad (3)$$

where λa is the monochromatic absorptivity of the animal surface.

To estimate carefully the amount of radiation absorbed by an animal's total surface is generally very difficult and involves all of the complexities expressed in Eqns. (2) and (3). Yet such estimates are made reasonably well if the intensities of the streams of radiation are known and if the mean absorptivities are known. These quantities are readily measurable and when not measured are estimated fairly well.

The transfer of energy by convection is the result of a temperature difference between the animal surface temperature and the air temperature nearby. All surfaces have adhering to them a boundary layer of air which is the transition zone for the temperature gradient, for the moisture gradient, and for the dif-

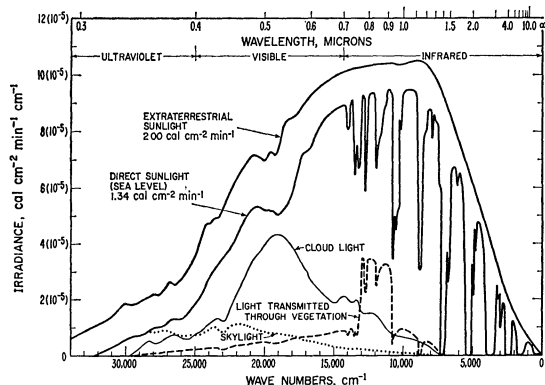


FIG. 2. The spectral distribution of extraterrestrial sunlight, direct sunlight at the Earth's surface, light from an overcast, skylight, and sunlight transmitted through the vegetation canopy.

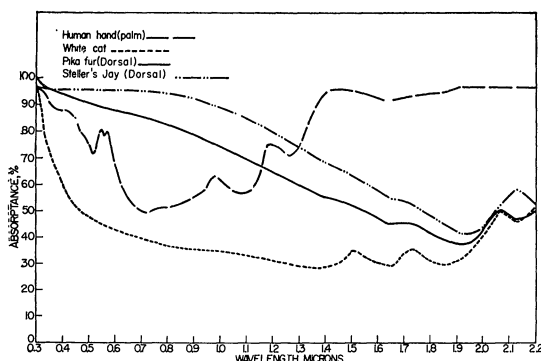


FIG. 3. Spectral absorbance of human hand, white cat, Pika (dorsal), and Steller's Jay (dorsal) as a function of wavelength.

fusion of gases between the animal surface and the free air. The thickness of the boundary layer is approximately proportional to the two-thirds root of the dimension (diameter) of the animal and depends upon the roughness, shape, and orientation of the surface. Experiments have shown the thickness of the boundary layer of cylinders to vary inversely with the one-third root of the wind speed. Heat is conducted from the animal surface across the boundary layer until free air movement beyond the layer carries the heat away by convection. Since the thicker the boundary layer the less the convection, the convection coefficient is inversely proportional to the boundary layer thickness. The convection coefficient is given by:

$$h_c = k \frac{V^{1/3}}{D^{2/3}} \quad (4)$$

where V is the wind speed in cm sec^{-1} , D is the diameter of the animal's body in cm and k is a constant which has units such that h_c is in $\text{cal cm}^{-2} \text{min}^{-1}$

$^{\circ}\text{C}^{-1}$. For a smooth cylinder with axis perpendicular to the direction of the wind flow, $k = 6.17 \times 10^{-3}$ (Gates, 1962). Strictly speaking, k should be evaluated experimentally for each animal, but throughout this work the cylinder value is used.

HEAT TRANSFER WITHIN THE ANIMAL

Heat is conducted from the surface of the animal inward to the body core if the surface temperature, T_s , is greater than the body temperature, T_b . Heat is conducted outward to the surface if the core temperature is greater than the surface temperature. A schematic diagram of the concentric cylinder model used for the analysis presented here is shown in Fig. 4. There is an inner core where the metabolic energy, M , is generated at a temperature, T_b , and from which respiratory moisture loss expels energy, E_{ex} , from the

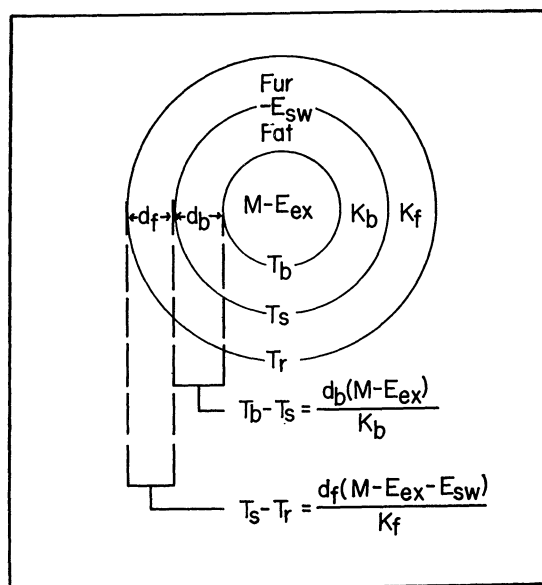


FIG. 4. Concentric cylinder model of animal for heat transfer analysis. M = metabolism, E_{ex} = respiratory moisture loss, E_{sw} = moisture loss by sweating, T_b = body temperature, T_s = skin temperature, T_r = radiant surface temperature, K_b = conductivity of fat, K_f = conductivity of fur or feathers, d_b = thickness of fat, and d_f = thickness of fur or feathers.

body cavity. This central core is surrounded by a fatty layer of thickness, d_b , and conductivity, K_b . The fatty layer terminates at the skin at temperature, T_s . The skin may or may not be surrounded by fur or feathers. If it is, then the fur or feathers are represented by another concentric cylinder of thickness, d_f , and conductivity, K_f . During steady state conditions, the energy crossing each concentric cylindrical surface must be the same.

The net amount of energy generated within the body is $(M - E_{ex})$. This amount of energy must

be conducted through the fatty layer, across which there is a temperature difference ($T_b - T_s$). Hence,

$$M - E_{ex} = \frac{K_b}{d_b} (T_b - T_s) \quad (5)$$

At the skin surface an amount of energy, E_{sw} , is lost to sweating or evaporation of moisture. The amount of energy conducted through the layer of fur or feathers, across which there is a temperature differential ($T_s - T_r$), must be the same energy conducted across the fat, ($M - E_{ex}$), less the energy lost by sweating:

$$M - E_{ex} - E_{sw} = \frac{K_f}{d_f} (T_s - T_r) \quad (6)$$

The total temperature difference between the internal body temperature, T_b , and the external radiating surface temperature, T_r , is:

$$\begin{aligned} T_b - T_r &= (T_b - T_s) + (T_s - T_r) \\ &= \frac{d_b}{K_b} (M - E_{ex}) + \frac{d_f}{K_f} (M - E_{ex} - E_{sw}) \end{aligned} \quad (7)$$

Eqn. (7) defines the ability of any animal to maintain a given temperature differential between inside and outside in terms of the following basic properties: fat, fur, or feather thicknesses and conductivities; metabolic rate; and moisture loss by breathing and sweating. The conductivity of fat is generally five to eight times greater than the conductivity for fur or feathers. Hence, for fur bearing animals and for birds, the fatty tissue adds little in the way of insulation. But for animals without fur or feathers, the fat layer must provide all of the insulation.

For animals without fur or feathers, Eqn. (7) reduces to the following when the radiating surface becomes the skin surface at temperature T_s :

$$T_b - T_s = \frac{d_b}{K_b} (M - E_{ex}) \quad (8)$$

The energy budget of the skin surface for an animal without fur or feathers is the same as represented in Eqn. (1) except with T_s replacing T_r .

The ability of an animal to support a given temperature differential is represented in Figs. 5 and 6. Here, all combinations of values known for M , E_{sw} , E_{ex} , d_b , and d_f are considered to determine the maximum and minimum values for $(T_b - T_s)$ and $(T_s - T_r)$. The conductivity of fat with total (hypothetical) vasoconstriction is not variable and the conductivity of fur or feathers can change with compactness and with moisture content. However, the conductivity of fat and fur was assumed to be constant. The thicknesses d_b and d_f were varied when necessary to take account of heat transport by the circulatory system. For the results presented here it was our desire to calculate the outer limits for an animal's tolerance.

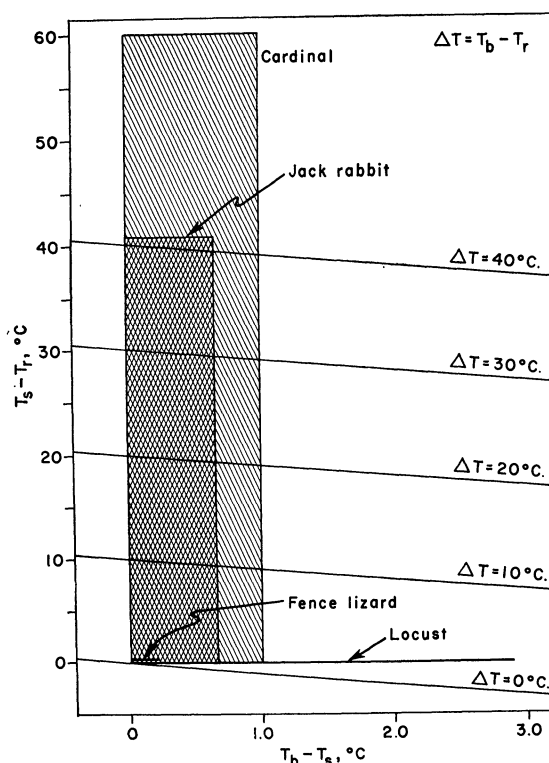


FIG. 5. Temperature differential between body and radiant surface temperature for animals. Abscissa is temperature difference across the body fat. Ordinate is temperature difference across the fur or feather layer.

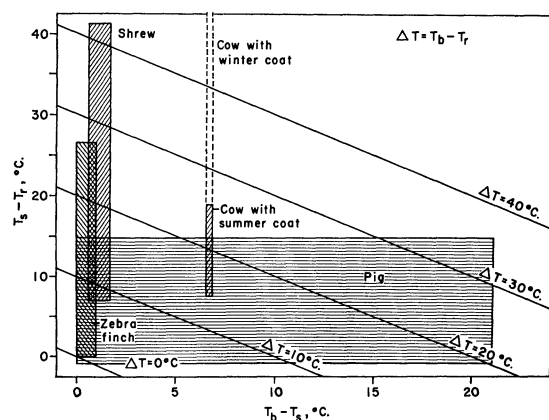


FIG. 6. Temperature differential between body and radiant surface temperature for animals. Abscissa is temperature difference across the body fat. Ordinate is temperature difference across the fur or feather layer.

To do this we would use the maximum thickness of fat or assumed conductivity of fur or feathers to be the conductivity of air at the maximum thickness of fur or feathers. The conductivity of fat used was $0.0294 \text{ cal cm}^{-1} \text{ min}^{-1} \text{ }^\circ\text{C}^{-1}$ (Hatfield & Pugh, 1951) and the conductivity of air was $0.0036 \text{ cal cm}^{-1} \text{ min}^{-1}$

$^{\circ}\text{C}^{-1}$ (Gates, 1962). The error allowable for d_b or d_f depends on the particular animal. The affect of an error on a particular calculation can be determined only with reference to the climate space diagram for each animal.

The vertical axis of Figs. 5 and 6 represents the temperature differential which the animal can maintain between skin and free air across fur or feathers and the adhering boundary layer of air. The horizontal axis represents the temperature differential which the animal can maintain between the body cavity and the skin across the layer of fat. The fine lines shown in Figs. 5 and 6 represent the sum of the values of the axes or the total temperature difference ($T_b - T_r$). These two figures show the enormous range of values of ($T_b - T_r$) or ($T_b - T_s$) for various animals. The values of the parameters used for the calculations are given in Table 1.

ENERGY EXCHANGE FOR ANIMAL SURFACE

The energy exchange for an animal surface is given by Eqn. (1). Substituting into Eqn. (1) the convection coefficient expressed by Eqn. (4), one gets the following:

$$M + Q_{\text{abs}} = \epsilon \sigma T_r^4 + k(V^{1/3}/D^{2/3})(T_r - T_a) + E_{\text{ex}} + E_{\text{sw}} \pm C \pm W \quad (9)$$

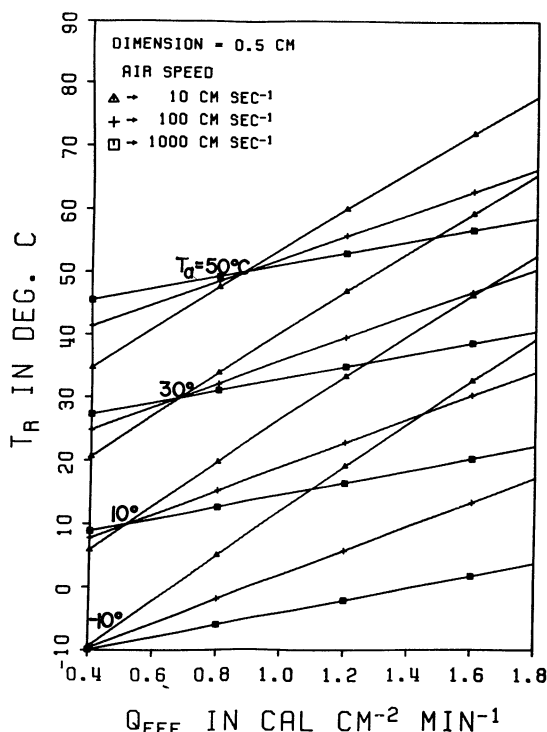


FIG. 7. Relations between radiant surface temperature of a small animal of diameter 0.5 cm as a function of $Q_{\text{eff}} = M + Q_{\text{abs}} - E_{\text{ex}} - E_{\text{sw}}$ where M = metabolic rate, Q_{abs} = radiation absorbed by animal surface, E_{ex} = respiratory moisture loss rate, and E_{sw} = sweating moisture loss rate. T_a = air temperature.

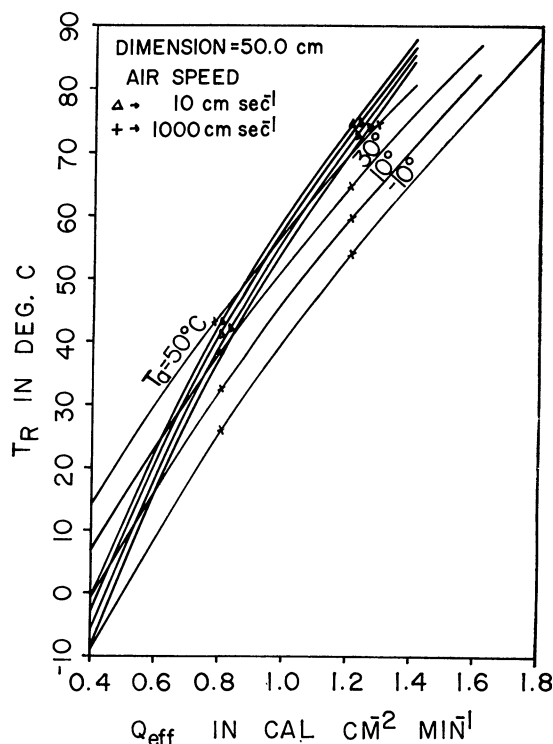


FIG. 8. Relations between radiant surface temperature of a large animal of diameter 50 cm as a function of $Q_{\text{eff}} = M + Q_{\text{abs}} - E_{\text{ex}} - E_{\text{sw}}$ where M = metabolic rate, Q_{abs} = radiation absorbed by animal surface, E_{ex} = respiratory moisture loss rate, and E_{sw} = sweating moisture loss rate. T_a = air temperature.

The work done by the animal is considered zero for the calculations given here. The influence of the environmental variables, air temperature, radiation, and wind speed on the radiant surface temperature of the animal is seen from Eqn. (9). It is desired to visualize the relation between the radiant surface temperature, T_r , and the independent variables of T_a , M , Q_{abs} , E_{ex} , E_{sw} , C , and D . Obviously some simplification must be made. For this purpose Q_{eff} , the net effective energy available for reradiation and convection, is defined as:

$$Q_{\text{eff}} = M + Q_{\text{abs}} - E_{\text{ex}} - E_{\text{sw}} \quad (10)$$

Hence:

$$Q_{\text{eff}} = \epsilon \sigma T_r^4 + k(V^{1/3}/D^{2/3})(T_r - T_a) \quad (11)$$

where the conductance term is considered negligible. It is always easy to put the conductance term in when needed. It is now necessary to understand the dependence of T_r on Q_{eff} , T_a , V , and D .

The relation between T_r and Q_{eff} is shown in Figs. 7 and 8 for an animal of diameter 0.5 cm and 50.0 cm respectively at air temperatures of -10 , 10 , 30 , and 50°C . In Fig. 7, wind speeds of 10 , 100 , and $1,000$ cm sec^{-1} are given, while in Fig. 8, only 10 and $10,000$ cm sec^{-1} are shown. The lines at different wind speeds must intersect at the point where $T_r = T_a$.

The relation between T_r and Q_{eff} is always steeper at low wind speeds than at high wind speeds and steeper for a large dimension than for a small dimension. The reason for this is that T_r is more tightly coupled to the air temperature by convection

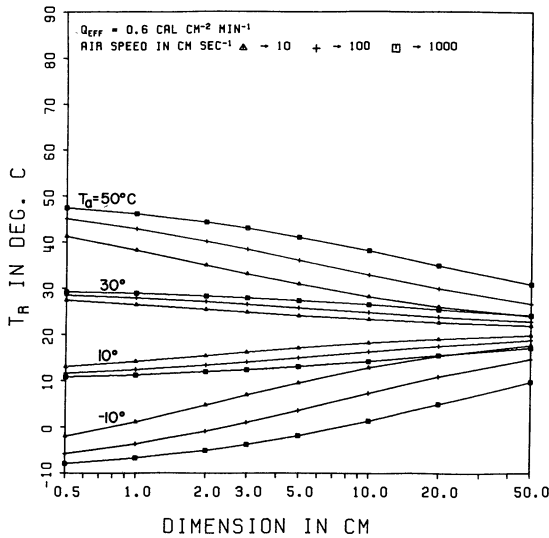


FIG. 9. Relations between radiant surface temperatures of animals as a function of animal diameter for given air temperature, T_a , and $Q_{eff} = M + Q_{abs} - E_{ex} - E_{sw} = 0.6 \text{ cal cm}^{-2} \text{ min}^{-1}$ where M = metabolic rate, Q_{abs} = radiation absorbed by animal surface, E_{ex} = respiratory moisture loss rate, and E_{sw} = sweating moisture loss rate.

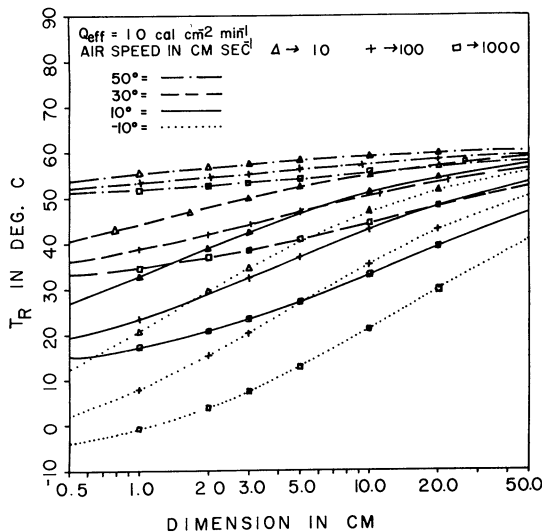


FIG. 10. Relations between radiant surface temperatures of animals as a function of animal diameter for indicated air temperatures and $Q_{eff} = M + Q_{abs} - E_{ex} - E_{sw} = 1.0 \text{ cal cm}^{-2} \text{ min}^{-1}$ where M = metabolic rate, Q_{abs} = radiation absorbed by animal surface, E_{ex} = respiratory moisture loss rate, and E_{sw} = sweating moisture loss rate.

when the wind speed is higher or when the dimension is smaller, or both.

The relation between T_r and the diameter of the animal is shown in Figs. 9 and 10 at a Q_{eff} of 0.6 and $1.0 \text{ cal cm}^{-2} \text{ min}^{-1}$ respectively for wind speeds of 10, 100, and $1,000 \text{ cm sec}^{-1}$ and air temperatures of $-10, 10, 30$, and 50°C . The curves for the three wind speeds converge at each air temperature for small dimension because of convection, but for large dimension, where convection has little influence, all curves for all wind speeds and air temperatures converge at the value of T_r corresponding to the blackbody temperature of the Q_{eff} . Hence, when Q_{eff} is $0.6 \text{ cal cm}^{-2} \text{ min}^{-1}$, the curves converge to 20°C and when Q_{eff} is $1.0 \text{ cal cm}^{-2} \text{ min}^{-1}$, they converge to 60°C at large dimensions. These numbers simply mean that the animal has net energy supplied by radiation absorbed plus metabolic heat less energy consumed in evaporative water loss equivalent to the energy supplied by a blackbody at these temperatures. At a fixed air temperature of 30°C and wind speed of 100 cm sec^{-1} , the relation between T_r , dimension, and Q_{eff} is shown in Fig. 11. Similar plots can be made at any other air temperature.

RADIATION ABSORBED

The average radiation absorbed as a function of the air temperature was calculated for a cylinder with specific absorptivity to sunlight. The irradiation of a cylinder can represent reasonably well the average irradiation of an animal. The purpose here is to get generalized approximations to the average

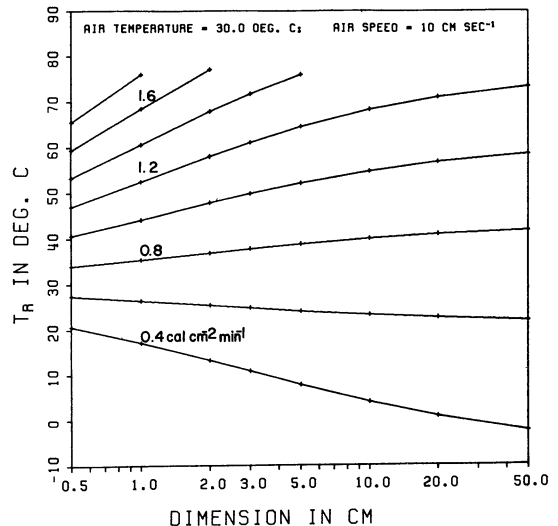


FIG. 11. Relations between radiant surface temperatures of animals as a function of animal diameters for various values of $Q_{eff} = M + Q_{abs} - E_{ex} - E_{sw}$ where M = metabolic rate, Q_{abs} = radiation absorbed by animal surface, E_{ex} = respiratory moisture loss rate, and E_{sw} = sweating moisture loss rate.

amount of radiation absorbed under various circumstances. The sun is a point source of radiation, the skylight is scattered light from the upper hemisphere, reflected light is from the lower hemisphere, and thermal radiation emitted by the ground surface is from the lower hemisphere, and thermal radiation emitted by the sky comes from the upper hemisphere. To get the average radiation from the sun on the upward facing half of the cylinder, one must make the following calculation:

$$\bar{S} = \frac{2Sf_o \int_0^{\pi/2} \cos\vartheta \, d\vartheta}{\pi} = \frac{2S}{\pi} \quad (12)$$

where S is the incident stream of direct sunlight and ϑ is the angle between the radial direction of an element on the surface of the cylinder and the direction of the sun. The integral is over a 90° quadrant of the cylinder and the two in the numerator gives the radiation on two quadrants or upper half cylinder. The extended sources of radiation, such as the skylight and the thermal radiation from ground and atmosphere, irradiate the cylinder fairly uniformly. The lower half of the cylinder may receive some reflected light, $r(S + s)$, which averages somewhere between what a diffuse reflecting surface would give and what a specular reflecting surface would produce. The absorptivity to sunlight and skylight of various animals may vary from as low as 0.2 to nearly 1.0, but the absorptivity to infrared thermal radiation is almost always between 0.95 and 1.0. For the purpose of these calculations, which necessarily must be approximate, the absorptivities to sunlight, skylight, and reflected light are assumed to be the same and equal to a and the absorptivities to thermal radiation equal to 1.0. On this basis, the following calculations were made to give the average radiation absorbed by the cylinder.

$$\bar{Q}_{abs} = \frac{a(2/\pi)S + as + ar(S + s) + R_a + R_g}{2} \quad (13)$$

The amount of direct sunlight changes with the air temperature for the following reasons. Warm air temperatures generally imply summer conditions or tropical conditions; but either of these is true when the sun is high in the sky at small zenith angle during midday. For these conditions, the amount of sunlight reaching the surface is generally high. When very low air temperatures exist, it generally implies winter conditions and the sun is low in the sky at midday. The amount of sunlight incident at the earth's surface is low for these low temperature conditions. Exceptions to this situation include the low temperatures of high mountain regions of low and middle latitudes in the summer when the direct sunlight is intense. These exceptional cases can be easily worked out separately. On this basis, an estimate was made of \bar{Q}_{abs} as generally related to air

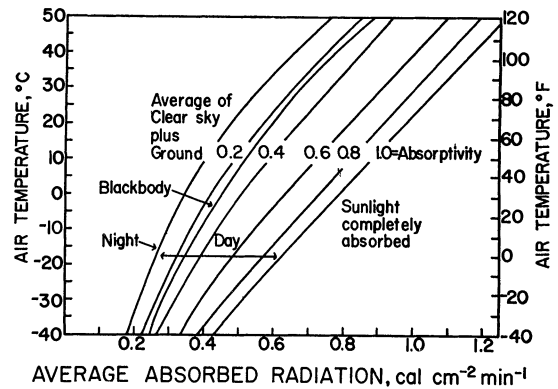


FIG. 12. Relations between the air temperature and the amount of radiation absorbed by a cylinder of various absorptivities to direct, scattered, and reflected sunlight. The absorptivity to the infrared thermal radiation from atmosphere and ground is unity. The intensity of radiation from a blackbody at the air temperature is shown. At night all radiation incident is longwave infrared. The ground radiates as a blackbody near to air temperature, but the clear sky radiates as a graybody at a much lower temperature than the air. Hence, the average radiation on a cylinder at night receiving radiation from ground and sky is less than the blackbody radiation at the air temperature.

temperature for values of absorptivity from 0.2 to 1.0. The results of this calculation are given in Fig. 12. If the absorptivity to sunlight is 0 or there is no sunlight, e.g. night-time conditions, then only thermal radiation from the ground and sky is incident on the cylinder and the average radiation absorbed is midway in value between the two fluxes. This situation is shown by the line in Fig. 12 marked "clear sky plus ground." The flux of atmospheric radiation as a function of the air temperature was estimated from Swinbank's (1963) observations and empirical formula. The thermal radiation from the ground was estimated by assuming the ground surface temperature to be near to the air temperature. This is considered a reasonable approximation, although the ground surface may be warmer or cooler than the air, depending upon various circumstances. Also shown in Fig. 12 is the line representing radiation from a blackbody at the air temperature.

CLIMATE SPACE

One of the ultimate goals for the energy budget analysis of animals is to predict the climate space which any given animal must occupy in order to survive. An animal may actually occupy a more restrictive climate space than predicted here for other reasons such as territorial limits, food supply, etc.; but an animal cannot occupy a larger climate space than that permitted by his properties. The appropriate climate space is identified by means of the analysis presented in the previous sections. The climate space is the four dimensional space which the

animal can endure, formed of radiation, air temperature, wind and humidity, each acting simultaneously. It is the combination of these variables which will make the energy budget of the animal compatible with its body temperature requirements. The relations between T_r and the external environmental factors have been demonstrated as well as the relations between the internal physiological characteristics of the animal, including the animal's body temperature, and the radiant surface temperature, T_r . If one knows the body temperature and the extreme values it can have for survival, the metabolic rate, the water loss, the absorptivity, the diameter, and the thickness of fat and of fur or feathers, one can determine the simultaneous set of values of climate factors for survival of the animal. First, Eqn. (7) is solved for T_r and then Eqn. (9) is solved for the various combinations of Q_{abs} , T_a , and V for a given dimension. The humidity is not included in the calculations presented here. Allowance is made for the fact that an animal can vary its metabolic rate, water loss rate, fur or fat thickness and insulation, body temperature and sometimes absorptivity to radiation by means of color change. One must know these properties for an animal and what variation to expect for extreme conditions. Usually this information is difficult to obtain and often one or more values are missing from the information available for a particular animal.

The relations which must exist among the climate variables to give a certain body temperature or range of body temperatures for a specific animal with specific properties are now described. The relations could extend over all temperature, radiation, and wind values but are limited in the figures to the extremes of air temperature, radiation, and wind normally encountered by the animal.

Desert Iguana

The relatively large, white desert iguana, *Dipsosaurus dorsalis*, has been extensively studied and values of its properties are readily available. This animal will tolerate a maximum body temperature of 46°C (Norris, 1953). For the calculations presented here, a maximum body temperature of 45°C is used. The minimum body temperature which the animal will tolerate, according to experience by the senior author, is 3°C. A *Dipsosaurus* of 50.8 grams had a surface area of 174.8 cm² (Norris, 1967). For our calculations, we used an animal weighing 67 grams with a surface area of 180 cm². The metabolic rates used here are from Dawson & Bartholomew (1958) and the evaporative water loss from Templeton (1960). The fat thickness used is taken to be skin thickness and was measured by the authors. The diameter of the desert iguana is typically about 1.5 cm. Spectral absorptivity measurements of *Dipsosaurus* were made by Porter (1967) and by Norris (1967). The average absorptivity of the surface of a dark colored *Dipsosaurus* is about 0.8 and of a light colored lizard, 0.6.

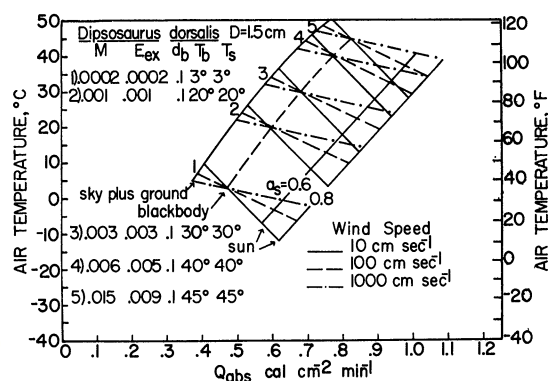


FIG. 13. Climate diagram for *Dipsosaurus dorsalis* showing relations between air temperature, radiation absorbed and wind speed for constant body and radiant surface temperatures at actual values of metabolic and water loss rates.

The climate space diagram for *Dipsosaurus dorsalis* is shown in Fig. 13. The data used for the various parameters are listed in the figure. A small poikilotherm like a lizard has relatively little physiological control of body temperature. The minimum tolerated body temperature of 3°C is given for minimum metabolic rate and minimum water loss according to the lines marked (1). These lines would indicate that in still air this lizard could not survive a night-time air temperature of less than 10°C if it were exposed to the clear night sky and not less than 5°C if in a wind of 1,000 cm sec⁻¹. A blackbody cavity, e.g. a burrow, would have to be at 3°C or greater for the lizard to survive. It is likely that this is lower than he could withstand for extended periods of time. In full sun in still air, the lizard could not survive air temperatures less than -12°C if dark, nor -7°C if light colored. In a wind of 1,000 cm sec⁻¹ in sunshine, it could not withstand less than -2°C if dark, nor 0°C if light. The maximum lethal limits are between 28°C and 33°C air temperatures in full sunshine in still air for dark and light colored animals respectively, are about 40°C in wind of 1,000 cm sec⁻¹. Normally a lizard near the ground surface will not encounter a wind of this magnitude because of the great wind sheer near the surface. At night, the *Dipsosaurus*, when exposed to clear sky, could sustain air temperatures between 47 and 51°C. However, air temperatures of this magnitude do not occur at night. *Dipsosaurus* in the shade is an environment approximating a blackbody cavity. The maximum shade temperature is equal to the maximum body temperature of 45°C.

The smaller the animal the more nearly horizontal are the lines in the climate space diagram since the convection coefficient is large and the animal surface temperature is coupled tightly to the air temperature. From the climate space diagram one can predict the environmental conditions which force the

desert iguana to move to a more favorable situation. If the desert iguana is in still air in full sun and the air temperature goes above 30°C, he must go into partial shade in order to endure the conditions. If the air temperature at the ground surface in the vicinity of the desert iguana goes above 45°C in the shade, he will need to seek a burrow at a cooler temperature. *Dipsosaurus* may prefer a behavioral limit, such as the set of lines No. (4), rather than the maximum lethal limit as set by lines No. (5) (Fig. 12). In this instance, the desert iguana will seek cooler habitats when the air temperature exceeds 40°C in the shade. The behavioral limits may be well within the lethal limits set by the climate space diagram.

Masked Shrew

The smallest of mammals are the shrews, which are sometimes characterized by high metabolic rates and the necessity to search for food incessantly. *Sorex cinereus*, the masked shrew, is distributed throughout the northern United States, Canada, and Alaska. The metabolic rates, fur thickness, and body temperatures are taken from the work of Morrison, Ryser, & Dawe (1959). Minimum body temperature tolerated is about 37.5°C and maximum body temperature 41°C. The surface area of an extended shrew, for which the calculations here were made, was 20.6 cm², and of a curled up shrew, 13.6 cm². Surface areas were based on the work of Morrison and Teitz (1957). The absorptivity for the shrew was measured by us to be 0.8. The climate space diagram for *Sorex cinereus* is shown in Fig. 14. The most striking feature of the climate space diagram is its demonstration of the low maximum temperature limit for the shrew. Since the shrew lives on the ground surface amidst leaf litter and in burrows, it is rarely subjected to any significant amount of wind. Water loss from the shrew has not been measured and values used here are assumed. The set of curves marked (2) and (3)

are for metabolic rate and moisture losses near the thermal neutral zone. In still air, curve (3) would show that in blackbody conditions the shrew could not withstand an air temperature greater than 24°C. If the shrew is exposed to the cold night sky, it can withstand an air temperature of up to 31°C in still air. In full sunlight with still air, the shrew cannot endure an air temperature greater than 6°C for extended periods of time. Morrison, Ryser, & Dawe (1959) did not measure moisture loss, but measured metabolic rates, body temperatures, and air temperatures. We assumed $T_r = T_a$ in curves (3) and (4) to compute water loss in order to make our calculated body temperatures agree with those of Morrison, Ryser, and Dawe (1959) for the metabolic rates and chamber temperatures they used. If the set of lines, No. (4), are valid, then a shrew in still air could sustain blackbody temperatures not to exceed 27°C. It is very doubtful that *Sorex cinereus* can withstand this temperature for any sustained length of time, since this requires dumping a substantial amount of water. It is more likely that the real temperature maximum for this shrew is between 20 and 24.5°C, as given by curves (2) and (3) for still air.

The low temperature limit shown for *Sorex cinereus* is based on its maximum metabolic rate of 0.496 cal cm⁻² min⁻¹, maximum fur thickness, no moisture loss (which is unreal, although it could be very low), minimum body temperature 37.5°C, and minimum surface area of a curled animal. This would indicate a blackbody temperature lower limit of -41°C. In sunshine, the shrew could go to a slightly lower temperature. It is very doubtful that a shrew can actually maintain itself under these conditions very long and more likely that the minimum air temperature is perhaps -10 to -20°C. The shrew spends the winter under snow and when snow cover is not available would need to spend very cold periods beneath leaf litter or in the soil.

Zebra Finch

The Zebra finch is a small seed-eating bird from Australia which has been imported to other countries of the world as pets. The Zebra finch is an easy experimental bird for which good physiological data exist. The majority of the data are from Cade (1964), who gives body size, weight, metabolic rates, and water loss. Further metabolic rates are given by Hamilton & Heppner (1967). Body temperatures, feather thickness, and fat thickness as well as weight (11.5 grams), surface area (31.4 cm²), diameter (2.5 cm), and absorptivities were obtained by us. The birds are naturally nearly white and have an absorptivity between 0.21 and 0.27. When dyed black, their absorptivity is 0.59.

The climate space diagram for the Zebra finch is shown in Fig. 15. The bird is small and does not have very thick feather covering. The result is that the white Zebra finch cannot survive very low air temperatures in still air where the limit in the sun

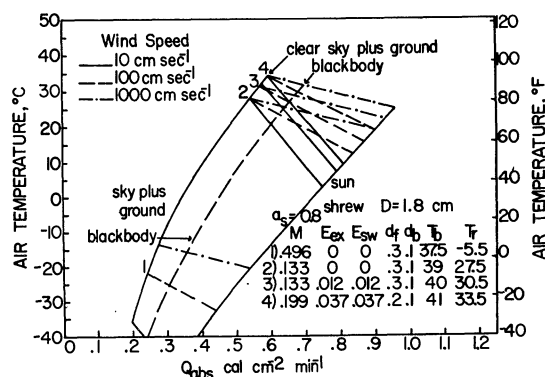


FIG. 14. Climate diagram for a Shrew showing relations between air temperature, radiation absorbed, and wind speed for constant body and radiant surface temperatures at actual values of metabolic and water loss rates.

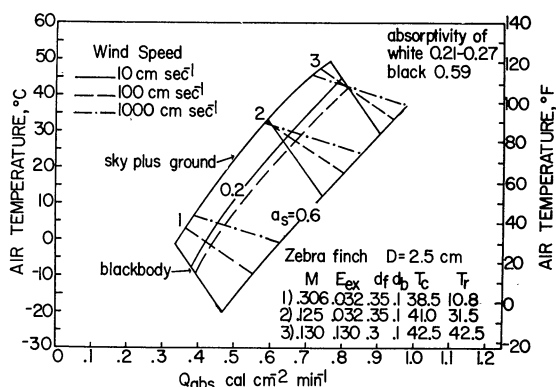


Fig. 15. Climate diagram for a Zebra Finch showing relations between air temperature, radiation absorbed, and wind speed for constant body and radiant surface temperatures at actual values of metabolic and water loss rates.

is about -10°C , but in the shade about -7.5°C . The lower limit for the black Zebra finch in the full sunlight is -20°C for still air. Obviously, the bird could not fly at these air temperatures and survive. When flying or in wind, these birds would not withstand air temperatures less than about 0 to 3°C in full sunlight, nor less than about 7°C at night. The white Zebra finch can withstand relatively high air temperatures in full sunlight, up to 42.5°C , but the black-dyed Zebra finch could only withstand 30°C in still air.

Kentucky Cardinal

The Kentucky cardinal, *Richmondia cardinalis*, a brilliantly colored red bird with a top notch, has in recent years extended its range westward and north-eastward from its original range in the southern United States and Mexico. All metabolic and water loss rates, body temperatures, and weights for the cardinal are from Dawson (1958). The dimensions ($D = 5$ cm) and surface area (110 cm²) are from Birkebæk (1966) and from our own work. The thickness of feathers and fat are from Birkebæk (1966) and from our own measurements. The absorptivity of 0.8 was measured by us with the spectrophotometer.

The climate space diagram for the cardinal is shown in Fig. 16. Many interesting things can be understood by studying this diagram carefully. At the high temperature limit the cardinal would not withstand full sunlight in still air for extended periods of time at an air temperature exceeding 20°C , but in wind of 100 cm sec⁻¹ could withstand up to 26°C and at $1,000$ cm sec⁻¹, up to 31°C . A cardinal will perch in a tree top singing where there is generally some air movement when air temperatures are moderate, but must fly into the shade when air temperatures become high. The cardinal can withstand very high air temperatures (up to 50°C in still air) at night when exposed to clear sky. With wind of $1,000$ cm sec⁻¹, the warmest night-time air temperature for

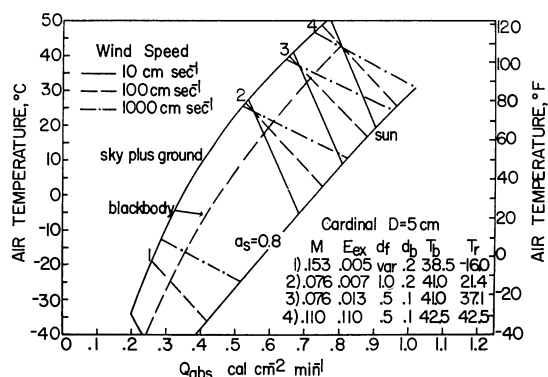


Fig. 16. Climate diagram for a Cardinal showing relations between air temperature, radiation absorbed, and wind speed for constant body and radiant surface temperatures at actual values of metabolic and water loss rates.

the cardinal is about 46.5°C . The evaporative water loss given for the lines No. (4) is not from Dawson, but was calculated by us to be the water loss which must occur for the bird to withstand an air temperature of 42.5°C .

At the low temperature limit, the cardinal can increase its metabolic rate, decrease its water loss, fluff out its feathers to increase insulation, and perhaps tuck its bill under its wing, which would further reduce surface area and minimize water loss. According to our calculations based on the best data available, the cardinal could withstand very low temperatures in still air. Since the lowest temperatures for most habitats occur about 0600 on winter days, it is apparent that the cardinal will not have sunshine available at this time and will be in a blackbody habitat or one of lower radiation flux. The lower limit for a cardinal with blackbody conditions would be about -40°C in still air and -16°C in wind of $1,000$ cm sec⁻¹. As is true with the other animals, we do not feel very certain about the precision of the lower limits for the climate space of the cardinal, but it may be a reasonable estimate. The uncertainty has to do with the amount and quality of the insulation. The lower limits indicated here seem to be compatible with the known climate conditions within the winter range of the cardinal.

The behavior of the cardinal for the thermal neutral range is shown by the set of lines No. (2) and (3). Other examples of thermal neutral conditions of metabolism, water loss rate, and thermal insulation (thickness of fat or feathers) could be given but they will be between those shown here. It is seen from Fig. 16 that the cardinal in sunshine during thermal neutral body conditions generally must have cool or moderate temperatures. If the cardinal is not in full sun but is outside on an overcast day, he can withstand moderate to warm temperatures without becoming stressed thermally. When exposed to the

full sun, the cardinal can endure 15°C warmer temperatures with a wind of $1,000\text{ cm sec}^{-1}$ than when in relatively still air (10 cm sec^{-1}) and remain in a thermal neutral condition. However, when exposed to an environment which is approximately a blackbody at the air temperature, a wind of $1,000\text{ cm sec}^{-1}$ permits the cardinal to be in only slightly warmer air than when in still air for the same metabolic rate and water loss rate.

Sheep

The sheep, *Ovis aries*, is an animal with unusual thermal insulation given by its thick covering of fleece. Sheep at the St. Louis stockyards were measured to give an average diameter of 25 cm unshorn, a surface area of 1.06 m^2 and a mean weight of 69.6 Kg . Metabolic rates were obtained from Joyce & Blaxter (1964) and from Brockway, McDonald & Pullar (1965). It was known from the work of Slee (1966) that a shorn sheep in a cold room could withstand a fairly low temperature. A metabolic rate was computed for the known values of T_b , T_s , and d_f for the coldest temperatures encountered by the sheep in Slee's work. The metabolic rate obtained was compared favorably with values given by Joyce & Blaxter (1964) and by Brockway, McDonald & Pullar (1965). Water loss rates are from Brockway, McDonald & Pullar (1965). The thickness of fur was taken from Slee (1966) for the intermediate case and reasonable estimates of the thickness were made for the extreme cases. The fat thickness used was based on the average of measurements made on slaughtered sheep at the St. Louis stockyards. The body temperature for the upper limit was 41.7°C , as given by Lee & Robinson (1941) and for the minimum and thermal neutral conditions given as 39.5°C by Joyce & Blaxter (1964). The absorptivity of fresh fleece from the stockyards as measured with our spectrophotometer was 0.7 .

The climate space diagram for the sheep is given

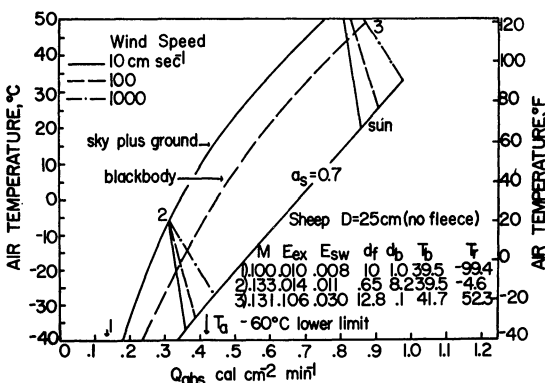


FIG. 17. Climate diagram for a Sheep showing relations between air temperature, radiation absorbed, and wind speed for constant body and radiant surface temperatures at actual values of metabolic and water loss rates.

in Fig. 17. Because of the larger body size of the sheep, the amount of heat transferred by convection is small, the sheep temperature is decoupled from the air temperature, and the lines in the climate space diagram become steeper than for smaller animals. Consider for a moment the upper limit for a sheep. In still air a sheep in full sun cannot endure for long an air temperature above about 20°C or with a small amount of air movement (100 cm sec^{-1}) above about 24°C . If temperatures are substantially greater than these values, sheep are to be found in partial shade out of the full solar irradiation. A sheep may endure blackbody conditions to air temperatures as high as 44 to 49°C ; and if the animals can stand in the shade of a tree or a cliff and radiate to a clear cold sky, they can endure air temperatures of 55°C or greater. The sheep tended by the Navajo Indians in the arid southwest no doubt take advantage of the latter situation and should be found to behave in precisely this way. Sheep which are being grazed high in the mountains may be in the full sun during midday, but usually there is some wind and the air temperature is not much above 25°C . Because of the steepness of the limiting lines, a small reduction in the flux of incident radiation will make an enormous difference in the maximum air temperature which can be endured. The lower limit which can be tolerated by sheep is very low indeed and indicates that sheep may endure almost any degree of cold and wind, providing they have a thick coat of fleece and sufficient food to maintain their metabolic rate.

Pig

The domesticated pig, *Sus scrofa*, is a medium sized animal with considerable body fat and relatively little fur covering. The body dimensions for a pig were obtained by measurements of adult pigs at the St. Louis stockyards. The mean diameter is taken as 36 cm , surface area 1.36 m^2 , and body weight 102.8 Kg . The thicknesses of fat and hair covering were averages of measurements made at the stockyards. The metabolic rates, water loss rates, and body temperatures were obtained from Mount's chapter in Hafez (1968). Lee & Robinson (1941) give a maximum body temperature of 41°C . The absorptivity of the pig was measured with the spectrophotometer to be 0.59 for a white pig and 0.79 for a black pig. Kelly, Bond, & Heitman (1954) measured the spectral reflectance of white, red, and black pigs. They found the white pig to absorb 49% of incident solar radiation, the red about 75% , and the black about 93% . Their measurements did not cover the full spectrum of solar radiation, but only from 0.4 to 1.0μ . High reflectance of near infrared wavelengths beyond their range of measurements would reduce the average absorptivity to solar radiation and bring their measurements more in line with ours.

The climate space diagram is shown in Fig. 18.

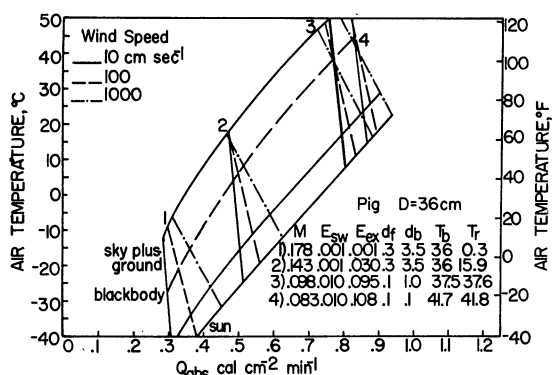


FIG. 18. Climate diagram for a Pig showing relations between air temperature, radiation absorbed, and wind speed for constant body and radiant surface temperatures at actual values of metabolic and water loss rates.

The lines are steep because of the relatively large body size. The diagram would indicate that a pig should not be in full sun when the air temperature is above about 23°C with wind of 100 cm sec⁻¹. A pig could endure partial shade at air temperatures of 35°C, full shade up to 40°C, and air temperatures as high as 45° to 50°C only if he is fully shaded from the sun but radiating to the cold sky as well. Kelly, Bond, & Heitman (1954) clearly recognized the advantage of constructing animal shelters which would shade the animals from the sun but let them also exchange radiation with the cold north sky. These investigators state that "beef cattle of European breeds cannot usually live without shade in the summers of the Imperial Valley of California." They found that swine at an "environmental" temperature of 38°C were losing energy, primarily through evaporation of water. This is consistent with our calculations.

Differences in fur color are expected to make notable differences in the limiting climate conditions for the animals when exposed to full sun. The climate space diagram would indicate the black pig would find it difficult to endure full sun when the air temperature was above about 10°C, the red pig above about 15°C, and the white pig above about 25°C when there is little air movement. Pigs enjoy wallows and the opportunity they provide for losing heat by conduction and evaporation.

Pigs lose heat rapidly during severe winter conditions because of their lack of fur insulation. Thus at extremely low air temperatures and during severe winter conditions pigs must have shelter. In still air with blackbody conditions, pigs can withstand an air temperature of -27°C and in wind of 1,000 cm sec⁻¹, only down to -15°C.

Jack Rabbit

The jack rabbit, *Lepus californicus*, is an animal of western America which lives in extreme environ-

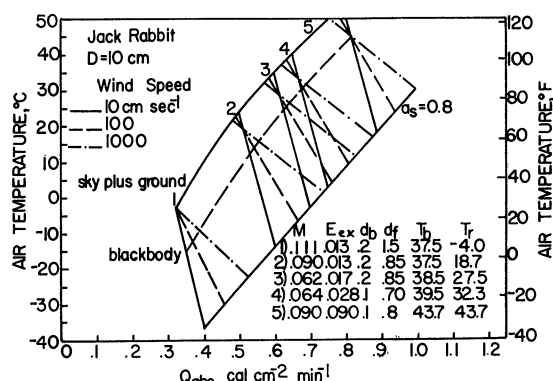


FIG. 19. Climate diagram for a Jack Rabbit showing relations between air temperature, radiation absorbed, and wind speed for constant body and radiant surface temperatures at actual values of metabolic and water loss rates.

ments. Most of the metabolic data, water loss information, surface area of 1740 cm², weight of 2.3 Kg, and body temperatures are derived from Schmidt-Nielsen, et al. (1965). The body diameter of 10 cm was estimated from general information available concerning the jack rabbit. Schmidt-Nielsen, et al. (1965) give the maximum body temperature as 43.7°C and the minimum as 37.5°C. The absorptance of the fur was not measured, but assumed to be approximately 0.8.

The climate space diagram for the jack rabbit is shown in Fig. 19. In still air the jack rabbit will not be in full sun at air temperatures above 20°C except during transient conditions. If there is strong air movement, 1,000 cm sec⁻¹, the jack rabbit may not be in full sun in steady state at air temperatures above 30°C. The jack rabbit, which is predominantly nocturnal, could endure night temperatures as high as 45 to 50°C. During very hot days, e.g. days with T_a = 40°C, the jack rabbit must be in deep shade and may rest in a position whereby it could cool radiatively to the cold north sky. In any event, the jack rabbit will not be found in full sun during hot days for extended periods of time.

The jack rabbit may endure down to -15°C with considerable cover, which protects it from radiative loss to the sky. In sunshine in the winter this rabbit may sustain temperatures as low as -35°C, if there is very little wind. In strong wind they are limited to air temperatures above -20°C.

Hypothetical Animals

It is of great interest to understand the climatic limitations associated with an animal with any specified properties. The analytical method permits us to explore the entire continuum of properties and climate limitations for poikilotherms and homeotherms.

The first example to be considered here is a lizard, a poikilotherm, whose metabolic rate and evaporative water loss are considered so small as to be essentially

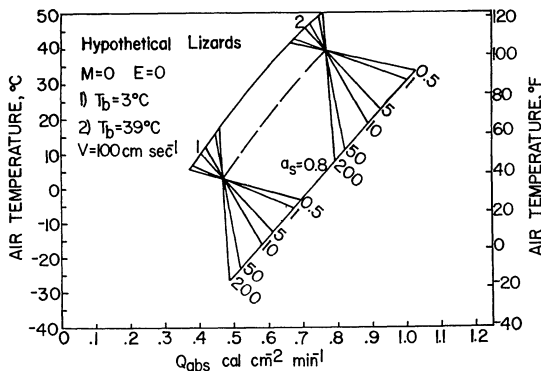


Fig. 20. Climate diagram for hypothetical lizards of varying body size from 0.5 to 200 cm showing relations between air temperature and radiation absorbed at constant wind speed of 100 cm sec⁻¹.

zero. When this is true, thermal insulation does not affect the body temperature for steady state conditions and Heath's (1964) beer can analogy is essentially correct. Fig. 20 shows the climate space for air flow of 100 cm sec⁻¹ for lizards of various dimensions, assuming a maximum body temperature of 39°C and a minimum body temperature of 3°C. This diagram would indicate that a small lizard can withstand a higher air temperature limit than can a large lizard when in full sunlight. This is the result of the small lizard's losing heat more rapidly by convection than the large lizard. The large lizard will endure a lower air temperature in full sunlight than will a small lizard for a given body temperature. When considering actual habitats, one must use the air temperature at the level of the lizard body in the immediate vicinity of the body. If the lizard crawls into a burrow or under a fallen tree, this habitat approximates a blackbody at the temperature of the burrow or space around the lizard. Our discussion of steady state climate space does not take into account transient states which are often governing animal behavior. We can only say that the lizard in transient states must average out within its steady state requirements.

The lizard may spend the night in a habitat which approximates blackbody conditions for which the absolute minimum environmental temperature is 3°C and the maximum environmental temperature is 39°C. If the lizard is exposed to the clear night sky, then the air temperature must be warmer than 3°C in order that the lizard body temperature not drop below 3°C. On the other hand, for conditions of maximum body temperature the air temperature may exceed 39°C if the lizard is exposed to the clear night sky. Normally a lizard would not encounter such a condition.

The large lizard, because of his greater heat capacity, has a body temperature which responds more slowly to changes in environmental conditions than

does the small lizard. If he is already warm, the large lizard can spend more time in cold air moving around seeking a position in the sun in order to bask.

One can conclude from Fig. 20 that a large lizard can sustain a large change of air temperature but a relatively narrow change of radiation absorbed when maintaining a constant body temperature. On the other hand, a small lizard can maintain its body temperature constant with a large change of radiation absorbed if the air temperature changes by a small amount only. For either a small or a large lizard, an increase in radiation absorbed requires a decrease of air temperature for a constant body temperature. For a given air temperature, a large lizard in sunshine will always have a warmer body temperature than a small lizard.

The results of calculations leading to the above Fig. 20 apply directly to behavioral observations by the senior author of small lizards in the deserts of southern California. Fairly early in the morning when the ground is still cold and there is little wind, many small lizards, e.g. *Uta stansburiana*, the side-blotched lizard, climb onto rocks to warm up. Why don't they stay on the ground to absorb the sun's rays? From Fig. 20 it is now quantitatively evident why they should climb onto rocks. They are tightly coupled convectively to the air temperature and radiation does not have as strong an effect on them as it does on large animals. By climbing up on a rock and turning their back or side to the sun, they not only maximize the amount of radiant energy absorbed but perhaps more importantly they get above the coldest layer of air at the soil surface (Gates, 1962). The rock has its own boundary layer, too, which on the sunny side of the rock will be near the surface temperature of the rock and will in part insulate the lizard from colder air provided there is little wind.

As the desert warms up and the wind begins to blow, the rock and the air layer around it now become cooler than the substrate with its boundary layer of hot air. In the heat of the day the senior author has frequently observed lizards, e.g. *Callisaurus draconoides*, the zebra-tailed lizard, on top of rocks on the side opposite the sun with their bodies pointing at the sun. Besides minimizing the radiation intercepted from the sun, they have placed themselves in the best possible convective environment. Not only are the animals up in cooler air, but in a higher wind speed regime (Gates, 1962). Fig. 20 shows us that a small drop in air temperature is exceedingly important to a lizard with a small characteristic dimension.

The potential climate relations for homeotherms is explored by means of several diagrams, since a homeotherm may or may not have fur or feather insulation and of course may be of various sizes and have varying metabolic rates. Fig. 21 displays the climate space for a small homeotherm ($D = 5$ cm) without fur or feathers whose body temperature is fixed

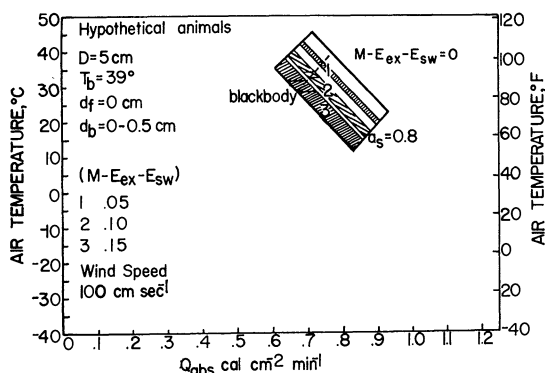


FIG. 21. Climate diagram for hypothetical small homeotherm with no fur or fat insulation showing relations between air temperature and radiation absorbed for a constant wind speed of 100 cm sec⁻¹. Three values of $M - E_{ex} - E_{sw}$ are given in cal cm⁻² min⁻¹. Each crosshatched area is bounded by lines for minimum and maximum amount of fat.

at 39°C and has variable amounts of fat and variable quantities of metabolic rate minus moisture loss rate. The diagram is calculated for a gentle breeze of 100 cm sec⁻¹. The uppermost boundary for Fig. 21 and the next three figures is for a condition $M - E_{ex} - E_{sw} = 0$. Each of the shaded areas represents climate relations necessary to maintain body temperature at 39°C for varying amounts of $(M - E_{ex} - E_{sw})$. It is notable that a small homeotherm with no fur or feather insulation has enormous difficulty maintaining its body temperature nearly constant. Put another way, the climate to which a small homeotherm is restricted is very narrow for survival. The hypothetical homeotherm illustrated in Fig. 21 would not survive a night-time environmental or blackbody temperature less than about 28°C. The small homeotherm without insulation must have a very high metabolic rate in order to survive temperate or cool conditions.

The allowable error in the values of d_b can be indicated from Fig. 21. If the maximum net metabolic rate ($M - E_{ex} - E_{sw}$) is 0.05 cal cm⁻² min⁻¹ an error in measurement of d_b of 0.5 cm is not a serious error compared to the same error in d_b for an animal with a net metabolic rate of 0.15 cal cm⁻² min⁻¹ where the affect is 3 times as serious.

The climate space for a large homeotherm without fur or feather insulation and body temperature of 39°C is shown in Fig. 22. The lines of constant surface temperature for constant body temperature are now very much steeper than for the small animal. The large homeotherm without fur or feather insulation can withstand a blackbody temperature as low as 13°C and maintain a fixed body temperature of 39°C when $M - E_{ex} - E_{sw} = 0.20$ cal cm⁻² min⁻¹. It is easy for the reader to visualize what the climate space will do if a fixed body temperature of 32°C is

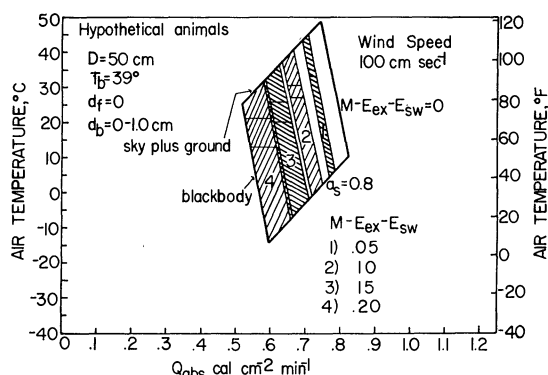


FIG. 22. Climate diagram for hypothetical large homeotherm with no fur or fat insulation showing relations between air temperature and radiation absorbed for a constant wind speed of 100 cm sec⁻¹. Three values of $M - E_{ex} - E_{sw}$ are given in cal cm⁻² min⁻¹. Each cross-hatched area is bounded by lines for minimum and maximum amount of fat.

required rather than 39°C by noting that the intersection of the dashed blackbody line with the upper boundary line marked $(M - E_{ex} - E_{sw} = 0)$ is the body temperature of the animal. If one cuts out an overlay of the climate space parallelogram and slides it downward to the left along the blackbody line until the intersection is at the new body temperature, say 32°C, one can see the new climate requirements of air temperature and radiation absorbed. Hence, if 32°C is the body temperature required rather than 39°C, the suggested procedure will show that the lowest blackbody temperature compatible for survival, if $M - E_{ex} - E_{sw} = 0.20$ cal cm⁻² min⁻¹, is now 6°C. The decrease in minimum air temperature for survival is the same amount as the decrease in required body temperature. Fig. 22 illustrates once again how very difficult it is for a homeotherm without fur or feathers to survive large variations of climate. The fine horizontal lines seen clearly in Fig. 22 and less clearly in Fig. 21 are limits of the air temperature as prescribed by compatible day and night maximum air temperatures. Rarely will a night-time air temperature maximum exceed a daytime temperature maximum, although we know it occasionally does happen for strong advective conditions. In other words, if the daytime temperatures with much sunlight available are very cold, the night-time temperature is not likely to be very warm. The animal may go from cold daytime air temperatures to warm night-time conditions by moving into a burrow or under a log. The parallelogram between two fine horizontal lines within a given crosshatched zone is the region of compatible climate conditions encountered in the air above ground day and night.

The climate space for a small homeotherm with fur or feather insulation and a body temperature of 39°C is shown in Fig. 23. By comparing this figure

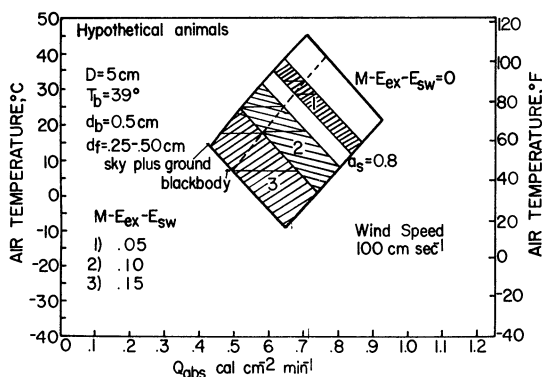


FIG. 23. Climate diagram for hypothetical small homeotherm with fur or feather insulation showing relations between air temperature and radiation absorbed for a constant wind speed of 100 cm sec⁻¹. Three values of $M - E_{ex} - E_{sw}$ are given in cal cm⁻² min⁻¹. Each cross-hatched area is bounded by lines for minimum and maximum amount of fur or feathers.

with Fig. 21, the significant importance of fur and feather insulation for a homeotherm is seen immediately. The well insulated homeotherm can withstand much lower temperatures for the same values of $(M - E_{ex} - E_{sw})$ than can the homeotherm without good insulation.

The climate space for a large homeotherm with fur or feather insulation and a body temperature of 39°C is shown in Fig. 24. Here the use of a good thickness of fur or feather insulation permits the large homeotherm to maintain its body temperature at 39°C when the air temperature becomes quite low. Comparing Figs. 21 and 22, and also 23 and 24, one notices how much steeper are the constant surface temperature lines for constant body temperature for the large homeotherm than for the small homeotherm. The large animal cannot withstand as high an air temperature in full sunshine at the temperature maximum as can the small animal and the small animal requires more radiation or a higher metabolic rate at low air temperatures for survival than does the large animal.

SUMMARY

Any organism must be in thermodynamic equilibrium when averaged over a reasonable length of time in order to survive. Environmental factors affecting the exchange of energy between an organism and the environment are sunlight, skylight, reflected light, thermal radiation, air temperature, air movement, and water vapor pressure of the air. Animal properties which affect the exchange of energy are metabolic rate, moisture loss rate, conductance of fat, fur, or feathers, absorptivity to radiation, and body size, shape, and orientation. The mechanisms affecting energy exchange are radiation, convection, conduction, and evaporation.

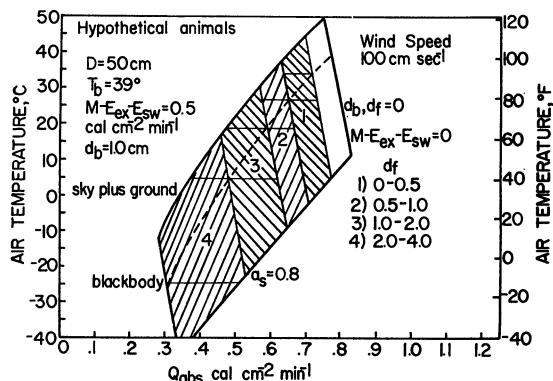


FIG. 24. Climate diagram for hypothetical large homeotherm with fur or feather insulation showing relations between air temperature and radiation absorbed for a constant wind speed of 100 cm sec⁻¹. Three values of $M - E_{ex} - E_{sw}$ are given in cal cm⁻² min⁻¹. Each cross-hatched area is bounded by lines for minimum and maximum amount of fur or feathers.

A mathematical model for the energy budgets of animals is derived based on simple concentric cylinder approximations to body geometry. From the physiological requirements for a certain body temperature or temperature range, the simultaneous values of radiation, air temperature, and wind speed are derived in order that the animal is in energy balance. The three dimensional space of radiation absorbed, wind speed, and air temperature is referred to as the climate space which the animal must occupy in order to survive. Climate spaces for the following animals are derived: desert iguana, masked shrew, zebra finch, cardinal, jack rabbit, pig, and sheep. In addition, the climate spaces for families of hypothetical poikilotherms and homeotherms are derived.

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TABLE 1. Values of parameters

Parameters used for calculations. M, E_{ex} , and E_{sw} in cal cm⁻² min⁻¹, d_b , d_f in cm, and ΔT_f and ΔT_b in °C.

	M		E_{ex}		E_{sw}		d_b		d_f		ΔT_f		ΔT_b	
	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min
Shrew.....	0.496	0.199	0	0.037	0	0.037	0.1	0.1	0.3	0.2	41.3	6.9	1.7	0.6
Cow														
Summer.....	0.149	0.149	0.013	0.006	0.083	0.008	1.4	1.4	0.5	0.5	18.8	7.4	6.8	6.5
Winter.....	0.149	0.149	0.013	0.006	0.083	0.008	1.4	1.4	2.7	2.7	101.0	39.8	6.8	6.5
Pig.....	0.178	0.083	0.001	0.108	0.001	0.010	3.5	0.1	0.3	0.1	14.7	-1.0	21.0	-0.1
Zebra Finch.....	0.306	0.130	0.032	0.130	0	0	0.1	0.1	0.35	0.30	26.6	0	0.9	0
Locust.....	0.86	0.0001	0.020	0	0	0	0.1	—	—	—	—	—	2.9	0
Cardinal.....	0.153	0.110	0.005	0.110	0	0	0.2	0.1	1.5	0.5	61.7	0	1.0	0
Jack Rabbit.....	0.111	0.090	0.013	0.090	0	0	0.2	0.1	1.5	0.8	40.8	0	0.7	0
Fence Lizard.....	0.01	—	0.003	—	—	—	0.1	—	—	—	—	—	0.5	—

TABLE 2. Wind tunnel experiments.

	Char-acteristic Dimension (cm)	Air Temperature (°C)	Wind Speed (cm/sec)	Q_{abs} (cal/cm ² -min)	Mean Absorptivity	Zenith Angle (deg.)	T_f Calculated (°C)	T_f Measured (°C)
Siberian Snow Leopard (<i>Panthera uncia</i>).....	23.0	27.5	259	1.45	0.78	90	61.7	58
Gray Fox (<i>Urocyon cinereo argenteus</i>).....	13.5	27.8	269	1.10	0.66	90	53.9	53
Glaucous-Winged Gull (<i>Larus glaucescens</i>).....	3.0	28.0	268	0.81	0.48	20	33.4	34
Starling (<i>Sturnus vulgaris</i>).....	4.6	27.8	268	1.29	0.85	90	54.0	56
Cardinal (<i>Richmondia cardinalis</i>).....	4.6	27.5	268	0.97	0.76	32	40.9	42
Eastern Meadowlark (<i>Sturnella magna</i>).....	5.7	27.2	268	1.07	0.78	45	46.3	50
Bobwhite (<i>Colinus virginianus</i>).....	6.4	27.2	268	1.12	0.78	55	49.4	48

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APPENDIX I—WIND TUNNEL EXPERIMENTS

The convection coefficient, h_c , used in the energy budget equation was the engineering value for smooth cylinders (Gates, 1962). Most animals, however, are furred or feathered. To evaluate the error inherent in using a convection coefficient for smooth cylinders and applying it to feathered and furred cylinders, we compared measured and predicted surface temperatures of stuffed animals in a wind tunnel. Surface temperatures were measured with a Barnes portable radiometer (Gates, 1968). To predict surface temperature, the Q_{abs} had to be determined.

Spectral absorption as a function of wavelength of the animal's surface was determined from reflectance measurements made by a Beckman DK-2A spectro-reflectometer. Energy as a function of wavelength from overhead floodlamps was determined from manufacturers' specifications. Beer's Law (Porter, 1967) was used to determine the energy available to the animal after it passed through the plexiglas. Absorption coefficients of plexiglas were determined using plexiglas transmission data from the DK-2A spectro-reflectometer (Porter, 1967). The monochromatic energy available at the animal's surface times the monochromatic absorption of the surface was integrated over the whole spectrum by a high speed digital computer. The energy absorbed (by a plane normal to the incident light) times the cosine of the zenith angle, where the zenith angle is the angle from the vertical, gives the actual amount of radiation absorbed. The temperature of the plexiglas sheet between the lights and the animals was measured with the portable radiometer pointed up at the plexiglas from the position of the animal's back. By using the radiometer to view temperatures in the hemisphere viewed by the back of the animal, the infrared energy striking the back of the animal can be determined. Wind speed was measured with a Hastings wind meter at the level of the back and about 3 cm upwind of the back. Air temperature was measured with a small thermocouple in the same location. The characteristic dimension was taken across the body at the point of measurement. The fur or feathers were not depressed except to insure that good contact was occurring with the calipers. A ruler was used for the very large animals.

The energy budget equation was solved for T_r , assuming a convection coefficient for a smooth cylinder at right angles to the wind. The actual surface temperature of the animals was measured with the radiometer. Table 2 lists the animals studied and the data which were used in the energy budget predictions. The animals were oriented normal to the wind. Agreement between calculated and measured surface temperatures was generally good.

The predicted surface temperatures of a stuffed whooping crane chick and a stuffed ostrich chick were very different from measured values. These differences were due to convection coefficients which differ from the values for a smooth cylinder. To reduce the error in Q_{abs} and to solve the energy budget equation for approximate convection coefficients for the oddly shaped bodies of the chicks, a large radiant tunnel was installed at the end of the wind tunnel. Q_{abs} in the tunnel consisted only of longwave infrared radiation which is nearly perfectly absorbed. The h_c 's for the whooping crane chick and the ostrich chick were determined using a non-linear regression program on a high speed digital computer. The data for the program came from ten experiments on each of the birds in the radiant tunnel.