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ABSTRACT

These materials were designed to be used by life science students for instruction in the application of physical theory to ecosystem operation. Most modules contain computer programs which are built around a particular application of a physical process. Several modules in the thermodynamic series considered the application of the First Law to biological systems and the heat transfer processes which govern the energy balance of organisms. This module discusses a model for which the animal's temperature is not changing with time. The concept "climate space" is used as a means for quantifying the limits of an animal's thermal environment. These limits are discussed in detail and methods for calculating these limits are described. A problem set is used to check the assumptions cf the climate space model as well as to extend it. A background in heat transfer processes is reccmmended. (Author/CS)

THE CLIMATE SPACE CONCEPT: ANALYSIS OF THE STEADY STATE HEAT ENERGY BUDGET OF ANIMALS

by

R. D. Stevenson

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PREFACE

The climate space is presented in the literature as a means of quantifying the limits of an animal's thermal environment. This module presents a more extensive discussion and shows how to calculate these limits, especially limits due to the physical environment. Ideas developed in the problem set check the assumptions of the climate space model as well as extend the use of the diagrams for predicting activity cycles. The material is aimed at general undergraduate life science students, although a background in heat transfer processes is recommended.

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INTRODUCTION

In earlier modules of the thermodynamics series, we considered the application of the First Law to biological systems (Stevenson 1977a and b) and the heat transfer processes which govern the energy balance of organisms (Stevenson 1978). The general heat budget equation for animals is

$$\Delta U = M + Q_a - Q_e - LE - C - G \qquad [1]$$

where

ΔU = change in internal energy ($W\ m^{-2}$),

M = metabolism ($W\ m^{-2}$),

Q_a = radiation absorbed ($W\ m^{-2}$),

Q_e = radiation emitted ($W\ m^{-2}$)

LE = water vapor losses ($W\ m^{-2}$),

C = convection flux ($W\ m^{-2}$),

G = conduction flux ($W\ m^{-2}$).*

Equation 1 is a complicated expression with many independent variables. Because biologists are interested in how animals modify their heat balance and why any particular behavior or physical characteristic of an animal influences this balance, they must find ways of analyzing the heat energy balance equation.

In this module we will discuss a model for which the animal's temperature is not changing with time, that is the steady state assumption that $\Delta U = 0$. Porter

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*In some of the biological literature the units of Equation 1 are $cal\ cm^{-2}\ min^{-1}$, but we have adopted the mks system here. The reader may find Appendix I, modules already referenced and Fletcher (1977) helpful in making conversions.

and Gates (1969) presented the "climate space diagram" to visually display the range of environmental conditions an organism could survive. More recently Monteith (1973) has proposed another graphical method to represent the energy balance which we will consider briefly. The works of Hatheway (1978) and Porter et al. (1973) offer alternative methods for understanding an animal's relationship to the physical environment.

THE THERMAL ENVIRONMENT: BASIS FOR THE CLIMATE SPACE

To describe the physical heat energy limits that an organism can tolerate, Porter and Gates (1969) began by examining the abiotic components of the environment. Four climatic factors -- radiation, air temperature, wind speed and humidity -- were recognized as affecting an animal's thermal balance. The authors decided that evaporative losses would be small for many organisms and could be included as maximum and minimum rates without making the losses a function of the humidity.

Tracy (1976) has, however, shown that when investigating the thermal and mass balance of wet-skinned animals such as slugs, frogs and salamanders, the water vapor concentration of the soil and the air must be known to accurately quantify these exchanges. To date the climate space concept has not been extended to include the environmental variable of water vapor concentration. Likewise, the formulation of Porter and Gates (1969) does not consider the effects of wind direction. Nor is surface temperature of the ground explicitly indicated (but see Equation 3 and Appendix II for calculation of Q_a). Radiation, air temperature and wind speed, though, which are the physical factors included in the climate space concept, are the most important abiotic variables for the thermal heat balance of most terrestrial animals.

Radiation

The most complex of the factors Porter and Gates (1969) considered is the absorbed radiation because it is composed of several shortwave and longwave components. Gates (1978) has written extensively about how to compute absorbed radiation, and we will present a short review here. In general, Q_a is the product of surface absorptivity, the surface area exposed to a particular source of radiation, and the intensity of that source. This can be written:

$$Q_a = \bar{a}_1 A_1 S + \bar{a}_2 A_2 s + \bar{a}_3 A_3 r\ (S + s) + \bar{a}_4 A_4 R_g + \bar{a}_5 A_5 R_a \qquad [2]$$

where

S is the radiation from direct sunlight $(W\ m^{-2})$,

s is the radiation from scattered sunlight $(W\ m^{-2})$,

R_g is infrared thermal radiation from the ground $(W\ m^{-2})$,

R_a is infrared thermal radiation from the atmosphere $(W\ m^{-2})$,

r is the reflectivity of the ground.

Since we wish to consider the average flux per unit surface area, the A_i's are the proportions of the total surface area exposed to each kind of radiation. The a_i's are the mean absorptivities to each kind of radiation. Roseman (1978) discusses absorption, reflection and transmission. In their original paper, Porter and Gates assumed that their animal was a cylinder. Equation 2 can then be rewritten as

$$Q_a = \frac{1}{\pi} \bar{a} S + 0.5[\bar{a} s + \bar{a} r(s + S) + R_g + R_a]. \qquad [3]$$

Here it is assumed that: 1) $A_1 = 1/\pi$; 2) scattered sunlight, reflected sunlight, reflected scattered sunlight, ground radiation, and atmospheric radiation strike half the animal (see Siegel and Howell 1972 for calculation of shape factors); 3) the mean absorptivities of the sunlight, scattered sunlight and reflected light are equal to $\bar{a}$; and 4) that the mean absorptivities of the infrared sources are 1.0.

Environmental Constraints

The climate space concept derives from the fact that there is a relation between the average incident radiation and the air temperature independent of the organism. It is generally true that warmer air temperatures occur with high radiation levels, i.e., summer or tropical conditions. Likewise colder air temperatures are usually correlated with lower radiation loadings. (Exceptions to this generalization are the high radiation levels in the mountainous regions of lower and middle latitudes during the summer when air temperatures can be low (Porter and Gates 1969).) Thus, we expect a positive correlation between the air temperature T_a and the absorbed radiation Q_a that the organism is exposed to in any given habitat. Initially, Porter and Gates considered a blackbody environment such as a cave or sheltered spot in thick vegetation. The relation between absorbed radiation and air temperature is given by the Stefan-Boltzmann Law and is plotted as the centerline in Figure 1. Next they asked what is the relationship between these two variables when an animal is exposed to a clear sky at night. Under these conditions an object will be receiving energy from the atmosphere which is at a lower temperature than the surrounding air. Gates (1978), using an empirical relationship from Swinbank (1963) for sky radiation, shows that the total radiation absorbed by the organism is

$$Q_a = \frac{\bar{a}_L(R_g + R_a)}{2} = \frac{\bar{a}_L\sigma[T_g + 273]^4 + 1.22\ \bar{a}_L\sigma[T_a + 273]^4 - 171}{2} \qquad [4]$$

where

$\bar{a}_L$ = mean absorptivity to longwave radiation,

σ = Stefan-Boltzmann's constant 5.67×10^{-8} ($W\ m^{-2}\ K^{-4}$),

T_g = ground temperature (°C),

T_a = air temperature (°C),

and the other symbols are as in Equation 2. Gates has assumed that the A_i's are one-half in each case (Siegel and Howell 1972 show how this can be derived). As before, we will let $\bar{a}_L = 1.0$. It is also convenient to approximate the ground temperature with the air temperature. In the early evening $T_g > T_a$, but several hours before sunrise the reverse is true. Equation 4 with the aforementioned assumptions is the leftmost line plotted in Figure 1. This means that if an animal were out foraging under a clear sky at night at an air temperature of 20°C, it would receive 50 $W\ m^{-2}$ less than if it were resting in a burrow.

Finally, we consider the condition when an organism is exposed to full sunlight with an absorptivity to shortwave radiation of 0.8. In this case, the radiation as a function of air temperature is given by the line to the right of the blackbody line. This line is "fuzzy" to remind us that this relationship is less well-defined than the other curves. The assumptions and calculations necessary to plot this line are discussed in Appendix II. If we now consider the difference between a blackbody and a full sunlight habitat, both at 20°C air temperature, we see that the latter would receive 300 $W\ m^{-2}$ more radiation.

The importance of Figure 1 is that we have established a region bounded by the clear sky, plus ground radiation line and the 0.8 absorptivity line that limits the combinations of Q_a and T_a found in the natural environment. This

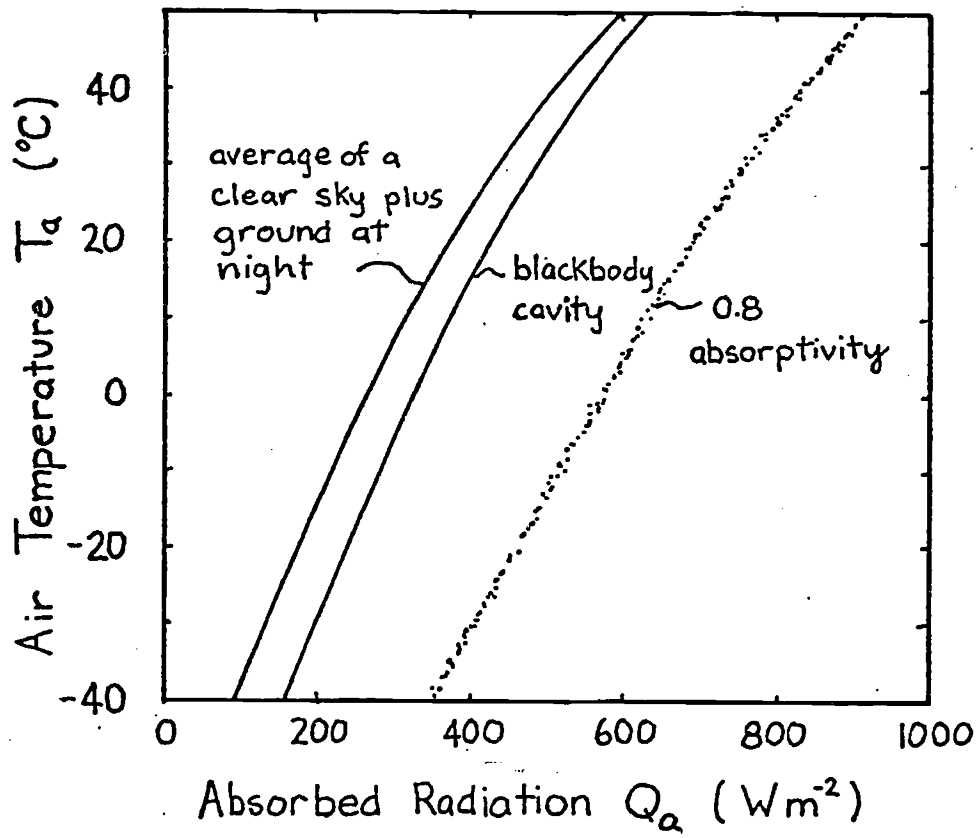

Figure 1. Relationship between the total amount of radiation flux incident on an object as a function of the air temperature. At night the object receives thermal radiation from the ground and atmosphere. In the daytime the object receives direct, reflected and scattered sunlight, in addition to the thermal radiation from the ground and atmosphere. The absorptivity to sunlight is 0.8. The right-hand boundary line is fuzzy to remind us that it is an average value. From Porter, W. P. and D. M. Gates. 1969. p. 234.

region can be divided into areas: one between the clear sky at night and blackbody line which governs the range of all nighttime conditions (S and s of Equation 2 are zero), and a second area enclosed by the blackbody and the 0.8 absorptivity lines which gives the range of most daytime conditions. The average radiation intensity can be less than blackbody levels during the day when clouds prevent the surface from receiving shortwave radiation. To see this we need to compute the absorbed radiation in the open, Q_{ao}, and compare it to that absorbed in a blackbody cavity, Q_{ac}. If solar radiation is zero ($S = s = 0$) then Equation 3 reduces to $Q_{ao} = (R_a + R_g)/2$. We assume that the surface temperature is equal to the air temperature and the temperature at the base of the clouds is less than air temperature so $R_a < R_g$ and $Q_{ao} < Q_{ac}$. In this case, the higher the clouds the cooler the radiating surface of their bases. This radiation, however, will always be greater than the radiation from a clear sky at night.

Morhardt and Gates (1974) have considered the temporal variation of Q_a and T_a more carefully. They measured T_g, T_a, R_p (= S + s on a horizontal surface), R_g and R_a hourly for a summer's day in the Colorado mountains shown as in Figure 2. These values were used to calculate Q_a for the Belding ground squirrel (*Citellus beldingi beldingi*) from an equation similar to Equation 3. In Figure 3, pairs of Q_a and T_a are plotted as a function of time. Morhardt and Gates made similar calculations for several different microhabitats. Although there were no startling conclusions about how the animal was being influenced by thermal environment, we will consider their study further in the exercises. The next step in constructing the climate space diagram is to see how the animal is influenced by radiation, air temperature, and wind speed.

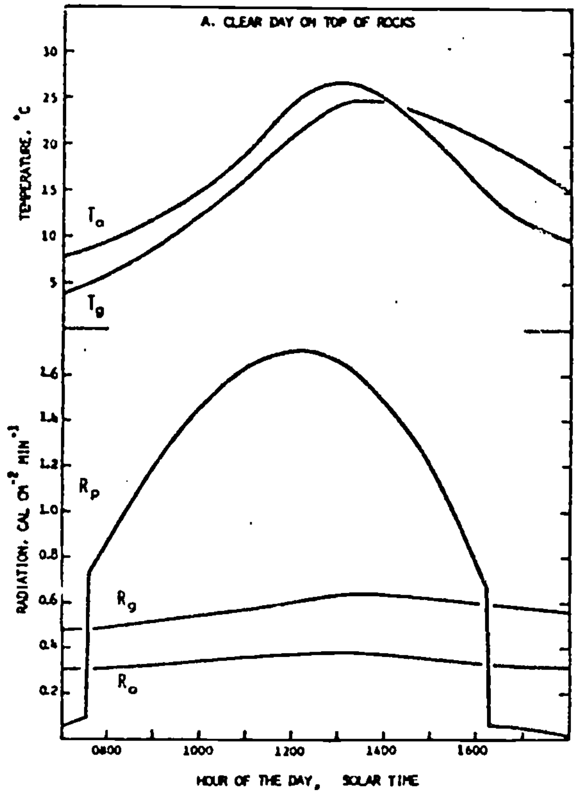

Figure 2. Daily variation in the radiant environment in different micro-habitats under different general weather conditions. The upper portion of the figure describes daily fluctuations of air temperature (T_a) and temperature of the surface of the substrate (T_g). From Morhardt, S. S. and D. M. Gates. 1974. P. 20.

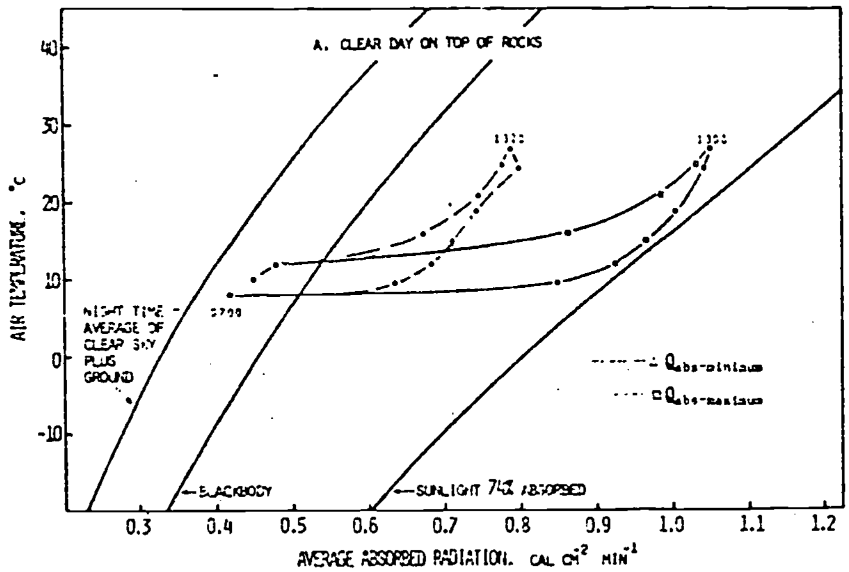

Figure 3. Climate diagram for the habitat. Data on these diagrams indicate the total amount of radiation that is absorbed by a geometrical model of a ground squirrel under conditons of air temperature and radiation shown in Figure 2. The model is oriented in two ways with respect to direct solar radiation to show how absorbed radiation differs at the same air temperature and the same time of day with differences in orientation toward the sun. The amount of radiation absorbed is greatest ($Q_{abs-maximum}$) when the long axis of the model is normal to the direction of the sun and least ($Q_{abs-minimum}$) when the hemispherical end of the model is toward the sun. All other orientations would be intermediate between these extremes. Data points are taken directly from Figure 2 at hourly or half-hourly intervals and are identified at selected points by showing the hour of the day in solar time adjacent to the points.

The line for sunlight 74% absorbed represents the maximum amount of radiation that could be absorbed by the model in direct sunlight at any air temperature. The blackbody curve indicates the intensity of radiation from a blackbody at any air temperature, and the curve labeled "night time average of clear sky plus ground" indicates the minimum energy likely to be absorbed by the model when exposed to a night sky radiating at a temperature which is cooler than the air. From Morhardt, S. S. and D. M. Gates. 1974. P. 25.

PHYSIOLOGICAL CONSTRAINTS OF THE ORGANISM

We expect two kinds of limits under steady state assumptions: one area where the environmental conditions make the organism too hot and conversely another area where it would be too cold. Furthermore, we expect an inverse relationship between air temperature and absorbed radiation because the organism must maintain an energy balance. The reader should pause here to make sure that these ideas are intuitive, as shown graphically in Figure 4. Common experience suggests that increasing the air temperature will make the environment hotter, but increasing the absorbed radiation is not as obvious. Most of us, however, are familiar with the midday heat stress common in many areas on a clear summer day. Later in the afternoon when the sun is lower in the sky Q_a will be reduced. Air temperature will also be dropping so that the transition that has occurred can be represented by the arrow labeled 2 in Figure 4. In the wintertime or early morning the reverse is true; the sun will often feel good because it provides the extra energy to move you into the acceptable region as shown with the first arrow. The exact slope and position of these limits will depend on other environmental conditions such as wind speed and characteristics of the organism such as size and insulation. One can think of the limits as the combination of physiological factors that will allow the organism to exist in that environment. For the lower limit of the energy budget calculation o an endotherm we would assume a high metabolic rate and thick insulation.

If we superimpose Figure 4 on Figure 1, the intersection or shaded region of Figure 5 is the <u>climate space</u> of the organism. It should be clear to the reader that the northwest and southeast boundaries are the results of environmental constraints while the northeast and southwest limits are the result of the

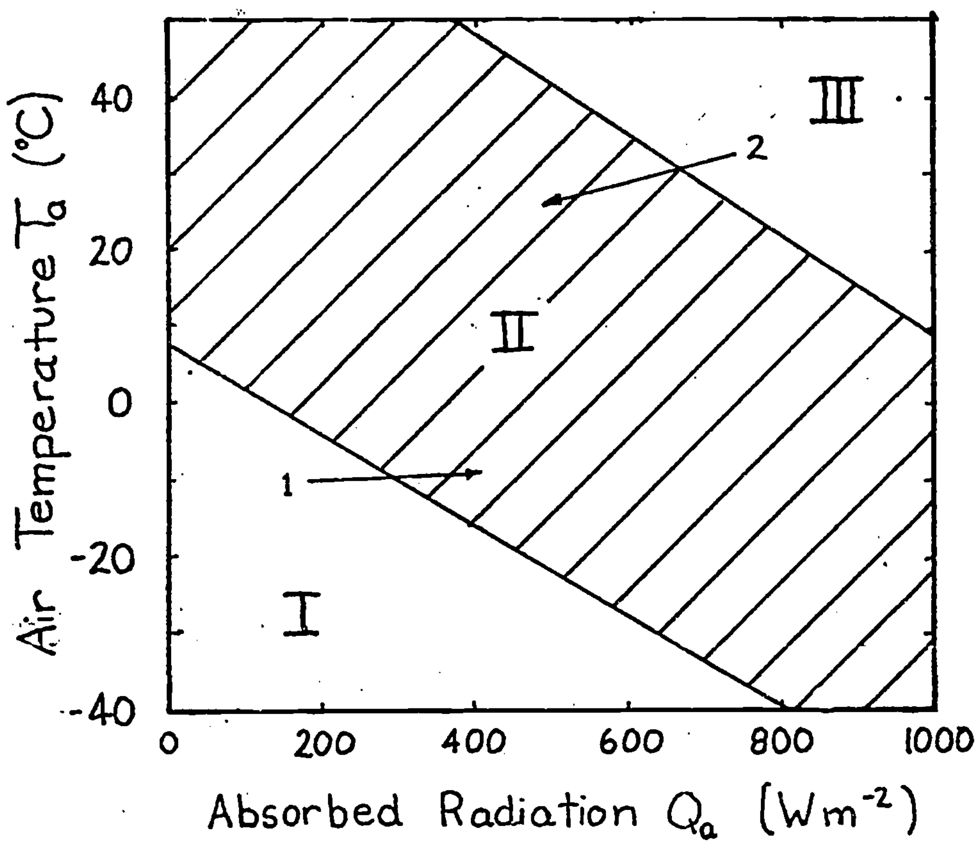

Figure 4. In Region I the animal is too cold. In Region II the animal can maintain thermal equilibrium. In Region III the animal will become overheated. Arrow 1 indicates the change in environmental conditions that takes place early in the morning. The added warmth of the sun makes the environment more "comfortable." Arrow 2 refers to the change in Q_a and T_a in the mid-afternoon on a clear summer's day.

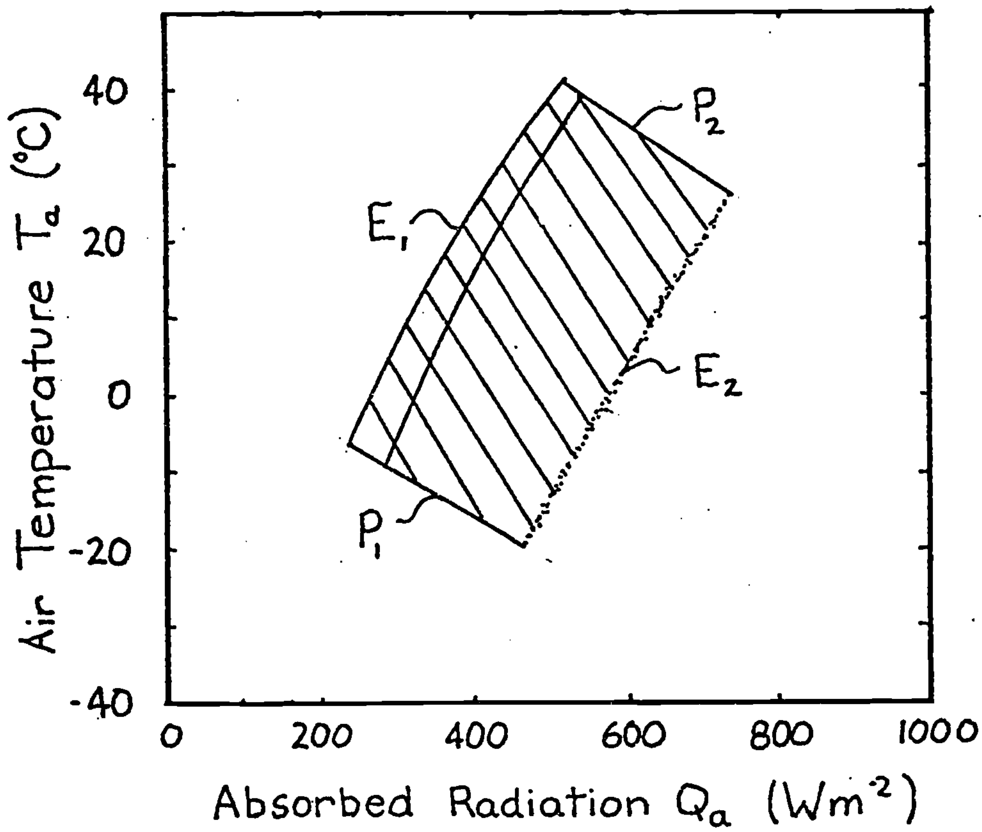

Figure 5. If we superimpose Figure 1 on Figure 4 the result is the cross-hatched region in the diagram called the climate space of the organism. The northwest (E_1) and southeast (E_2) boundaries are due to the physical environment. The southwest (P_1) and northeast (P_2) boundaries are due to the physiological limitations of the organism.

organism's need for homeostasis. The physiological limits can be calculated explicitly using the First Law of Thermodynamics. This is the task of the next section.

EXAMPLES OF THE CLIMATE SPACE

The Lizard

To write down the heat energy budget of a lizard we need only sum up the heat transfer components. Initially we consider only three of these components (absorbed radiation, reradiation and convection) because metabolism and water loss are small and they tend to cancel each other out (Porter et al. 1973). The energy entering the system must equal that which is leaving, so

$$Q_a = \varepsilon\sigma(T_s + 273)^4 + h_c(T_s - T_a) \qquad [5]$$

where

Q_a = longwave and shortwave radiation absorbed by the organism ($W\ m^{-2}$),

ε = emissivity (0.96),

σ = Stefan-Boltzmann constant $5.67\ 10^{-8}$ ($W\ m^{-2}\ K^{-4}$),

T_s = surface temperature of the lizard (°C),

T_a = air temperature (°C),

h_c = convection coefficient ($W\ m^{-2}\,{}^{\circ}C^{-1}$).

Originally Porter and Gates (1969) suggested that the convection coefficient should take the form

$$h_c = k_c V^{0.33}\ D^{-0.67} \qquad [6]$$

where

k_c = a constant 0.9274 ($W\ m^{-2}\ °C^{-1}\ (m)^{0.67} \cdot (m/s)^{-0.33}$),

V = wind speed ($m\ s^{-1}$),

D = diameter of the animal or cylinder (m).

Recently Mitchell (1976) found a spherical shape is the best overall model for convective transfer in the terrestrial environment. He used weight divided by density, which is equal to the volume, all to the one-third power as the characteristic dimension instead of the diameter. (Using laboratory measurements it is often possible to get better estimates of h_c for a particular geometry.) Generally one would calculate the Reynolds and Nusselt numbers to find the heat transfer coefficient (Kreith 1973). This procedure is outlined in the module on heat transfer processes (Stevenson 1978). With a number of assumptions which introduce only small errors, it is possible to write Mitchell's result in the same form as that of Porter and Gates (see Appendix III). We have

$$h_c = k_s V^{0.60} M_b^{-0.133} \qquad [7]$$

where

k_s = constant 17.24 ($W\ m^{-2}\ °C(m\ s^{-1})^{-0.60}(kg)^{0.133}$),

M_b = body mass (kg),

and h_c and V are as in Equation 6. We further assume that the body temperature T_b is approximately equal to the surface temperature T_s. (The error in this assumption will be checked in Problem 1.) The heat energy balance can now be written

$$Q_a = \varepsilon\sigma(T_b + 273)^4 + k_s V^{0.60} M_b^{-0.133}(T_b - T_a). \qquad [8]$$

To construct the climate space of the lizard, we need to make assumptions about the variables of Equation 8. If V, M_b and T_b are specified as constants, there is a linear relationship between Q_a and T_a. We illustrate this in Figure 6 by plotting the upper line for V = 1.0 m s^{-1}, M_b = 0.027 kg, and T_b = 39°C, and the bottom line with only T_b changed to 3°C. The shaded region in Figure 6 is the climate space of the reptile if the wind speed is the average value for the microclimate that the lizard inhabits, and if the body temperatures given are the upper and lower bounds that the animal can tolerate.

Examination of the climate space diagram allows interpretation of several of the parameters of the heat energy balance model. The boundary points of the space indicate the extreme values that the lizard is likely to encounter and still survive. The lower left-hand point of the diagram tells us that if the reptile is exposed to a clear sky at night, its body temperature will remain high enough to survive as long as the air temperature is above 7°C. The opposite corner shows that 27°C is the extreme air temperature that the lizard could endure if it were exposed to strong sunlight.

The effect of changing color is also illustrated in Figure 6. In desert environments lizards often lighten their color which lowers their mean absorptivity. For example, lowering the mean absorptivity from 0.8 to 0.6 in Figure 6 allows the lizard to increase the air temperature that it can survive from about 30°C to 32.5°C. Norris (1967) has extensively studied the effect of color change on the thermal adaptations of desert lizards.

Increased wind speed increases the relative importance of the convective term and couples the body temperature of the animal more closely to the air

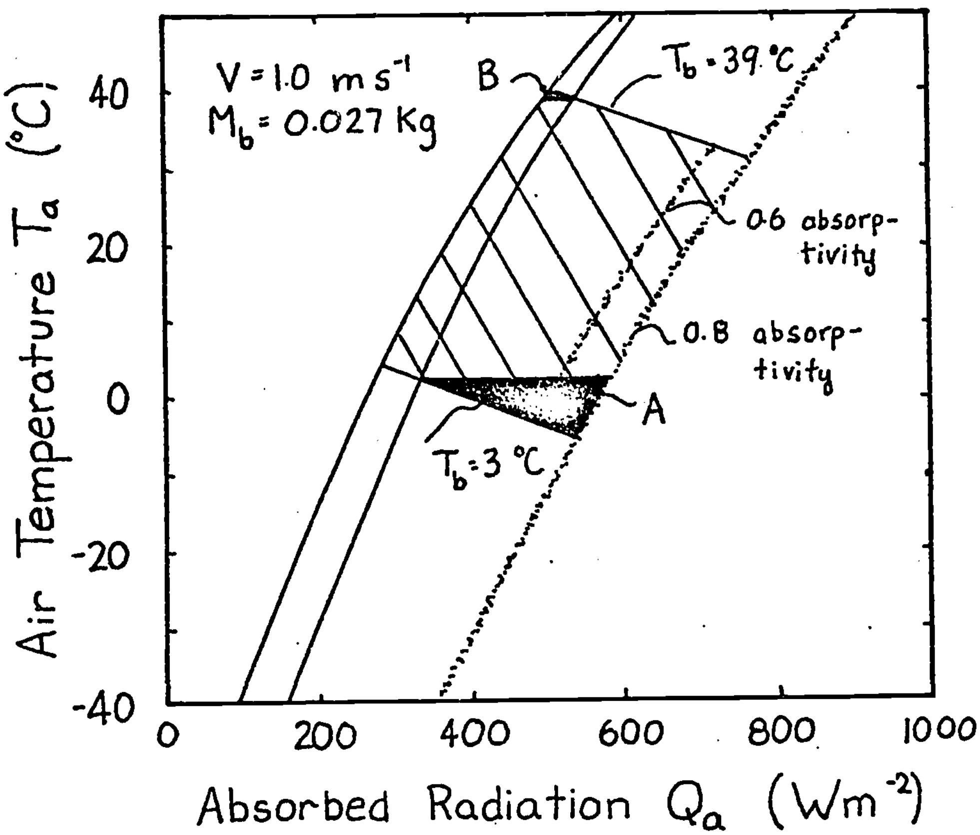

Figure 6. The hatched area is the climate space of a lizard with absorptivity to sunlight of 0.8. If the animal decreases its absorptivity to 0.6 it can increase the air temperature it can withstand from 30°C to 32.5°C. The darkened areas refer to problem 4.

temperature. Figure 7 shows the influence of wind speed on the energy balance. As the wind speed increases from 0.1 m s^{-1} to 10.0 m s^{-1} the physiological line becomes more horizontal.

We can visualize the effect of size by picking body masses of 0.001, 0.10, 10.0 and 100.0 kg to insert in Equation 8 and plotting the lines in Figure 8. As size or weight increases, the boundary layer thickens, decreasing the rate of convective exchange (a smaller component of the heat balance). This is readily seen algebraically by re-examining the convection term. We conclude that increasing size has the same effect as decreasing wind speed. It is also clear from Figure 8 that most lizards (less than 1.0 kg) are closely tied to the air temperature.

There are several observations which suggest that the thermoregulation behaviors we might predict from considering this model indeed occur. Porter and Gates (1969) observed that the small lizard (*Uta stansburiana*) (0.004 kg approximately) which is tightly coupled to the air temperature climbs rocks early in the morning. They hypothesized that this behavior was taken to avoid the cold layer of air at the ground surface. Alternatively we might ask what options are available if the lizard does not want to become too hot. From Equation 8 we see that there are at least two strategies. The animal can reduce the absorbed radiation Q_a by going to a shaded environment or it can increase its convective heat loss by climbing bushes where the wind speed is greater and T_a is lower. Descriptions of the daily activity patterns of the desert iguana (*Dipsosaurus dorsalis*) from field observations, show that both these options are used. The lizard emerges from its burrow in the morning. As T_a and Q_a increase, the animals move into the shade, then higher into the shrubs, and finally retreat

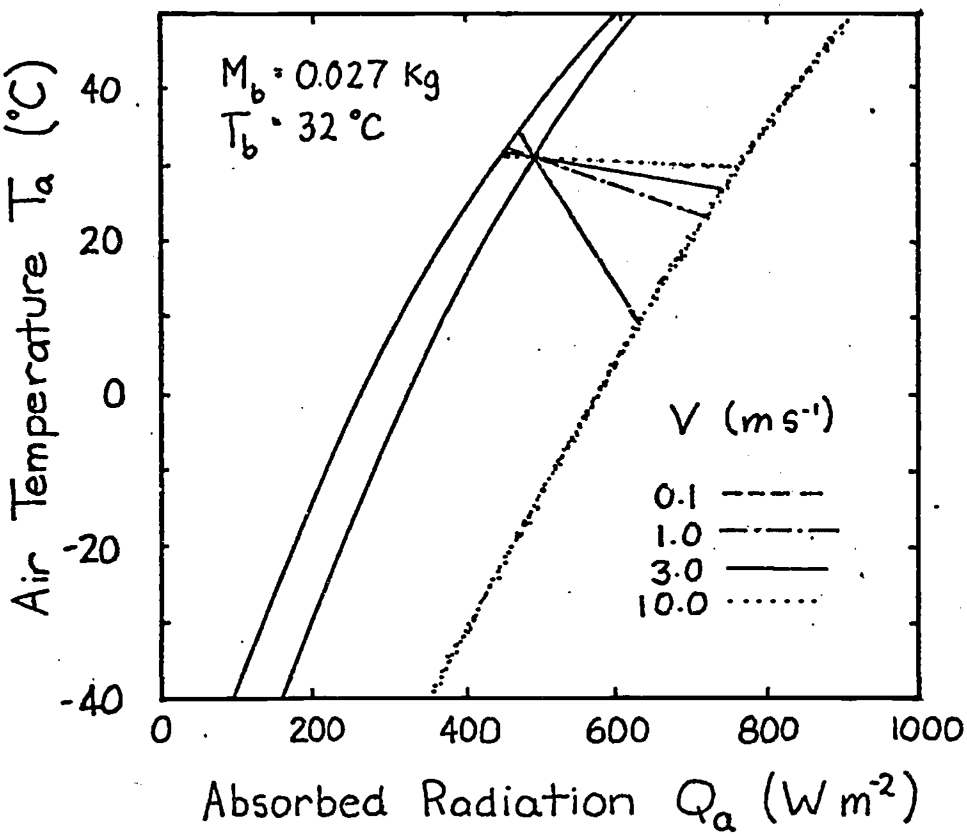

Figure 7. To investigate the effect of windspeed on the thermal balance, values of V from 0.1 to 10.0 m s^{-1} are used in equation 8.

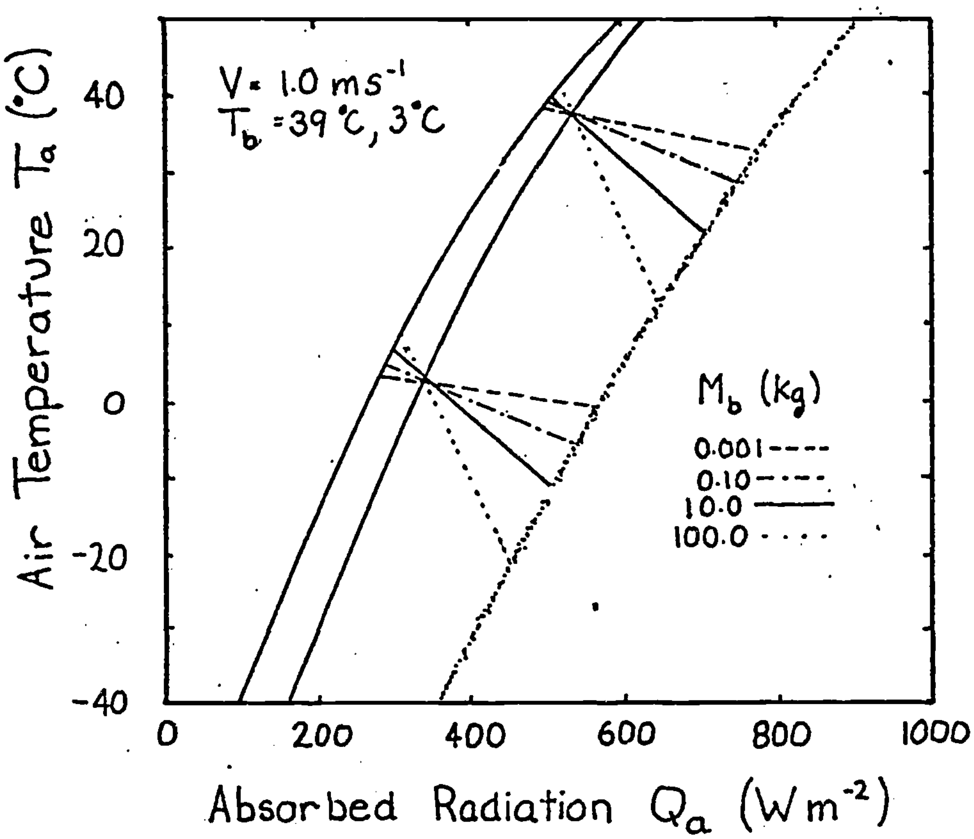

Figure 8. To illustrate the effect of size, values of weight from M_b = 0.001-100. kg were substituted into equation 8 and plotted here.

Porter et al. (1973) found good agreement between the predicted behavior from their heat transfer model and the morning activity pattern of this species.

The Cardinal

Our second and final example is the climate space diagram of the cardinal (*Richmondena cardinalis*). Several additional terms of the heat energy balance are important here. As in all homeotherms metabolism and water loss are significant sources of heat production and loss which cannot be neglected in the thermal budget. The food necessary to produce metabolic heat energy for thermoregulation is about 85% of the animal's total requirements (Bartholomew 1977). The benefits for this energetic cost probably include both the ability to process food faster and more efficiently and greater independence from the unpredictable patterns of the weather than ectotherms. The cardinal loses the majority of its water by exhaling air saturated with water vapor, although other species of birds may lose up to 50% of their water through their skin (Lasiewski et al. 1966).

The energy balance must now be written

$$M + Q_a = \varepsilon\sigma(T_r + 273)^4 + h_c(T_r - T_a) + E_{ex} \qquad [9]$$

where

M = metabolic rate ($W\ m^{-2}$),

Q_a = absorbed radiation ($W\ m^{-2}$),

ε = emissivity,

σ = Stefan-Boltzmann constant ($W\ m^{-2}\ K^{-4}$),

T_a = air temperature (°C),

h_c = convection coefficient ($W\ m^{-2}\ °C^{-1}$),

and

E_{ex} = energy flux due to respiration ($W\ m^{-2}$).

Since there are internal sources and sinks of energy production (M and E_{ex}) introduced into the equation we must consider heat transfer within the animal. Figure 9 from Porter and Gates (1969) shows a schematic view of an idealized animal in the shape of a cylinder. The isothermal core is at body temperature T_b, the skin surface is at temperature T_s, and the outer surface of the feathers (or fur) is at T_r. Water loss through the skin, E_{sw} (sweating), is included for generality. For the First Law of Thermodynamics and our steady state assumption we know that the energy crossing each boundary is the same. Beginning with the two inside circles the energy flow across the region of thickness d_b is equal to the potential (temperature difference) times the resistance (but see problem 6). Therefore,

$$M - E_{ex} = \frac{k_b}{d_b} (T_b - T_s) \qquad [10]$$

where k_b is the thermal conductivity of fat (.205 W m^{-1} °C^{-1}). By similar reasoning across the second potential we have

$$M - E_{ex} - E_{sw} = \frac{k_f}{d_f} (T_s - T_r) \qquad [11]$$

where d_f is the thickness of the fur or feathers in meters and k_f is the thermal conductivity of air (0.025 W m^{-1} °C^{-1}). The quantity of particular interest is the difference between the body temperature and the surface temperature $T_b - T_r$. We see that $T_b - T_r$ can be written as

$$T_b - T_r = (T_b - T_s) + (T_s - T_r). \qquad [12]$$

Rearranging our heat flow equations (10 and 11) and substituting into Equation 12 for $T_b - T_s$ and $T_s - T_r$ we have

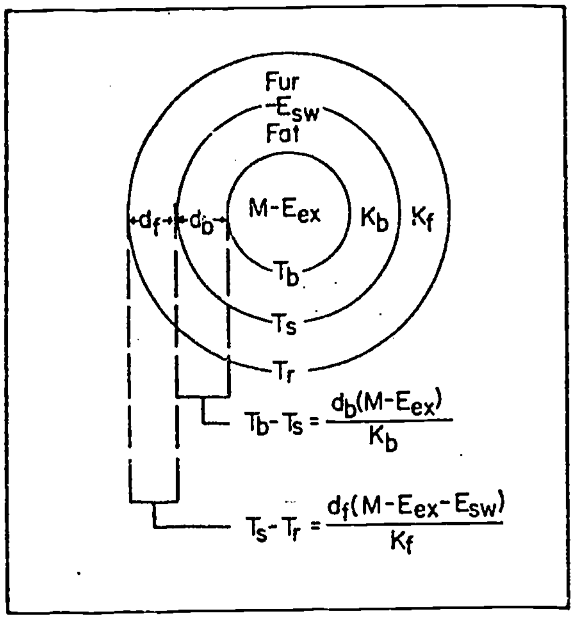

Figure 9. Concentric cylinder model of animal for heat transfer analysis. M = metabolism, E_{ex} = respiratory moisture loss, E_{sw} = moisture loss by sweating, T_b = body temperature, T_s = skin temperature, T_r = radiant surface temperature, k_b = conductivity of fat, k_f = conductivity of fur or feathers, d_b = thickness of fat, and d_f = thickness of fur or feathers. From Porter, W. P. and D. M. Gates. 1969. P. 230.

$$T_b - T_r = \frac{d_b}{k_b}(M - E_{ex}) + \frac{d_f}{k_f}(M - E_{ex} - E_{sw}). \qquad [13]$$

In the case of the cardinal E_{sw} is assumed to be zero so Equation 13 reduces to

$$T_b - T_r = (M - E_{ex})\left(\frac{d_b}{k_b} + \frac{d_f}{k_f}\right). \qquad [14]$$

Equation 14 can be used to calculate the surface temperature T_r if the other variables are specified. Once T_r is known, Equation 9 can be used to construct the climate space. Values for the parameters of Equations 9 and 14 are taken from Porter and Gates (1969) and reproduced in Table 1. These are used to construct the climate space of the cardinal in Figure 10. The numerals correspond to those in the table. Given these conditions the cardinal needs increased metabolic output and thicker insulation to withstand cold conditions. Such low levels of radiation and air temperature will occur just before sunrise during the winter. One would expect the bird to minimize its heat loss by seeking a sheltered microhabitat to avoid radiating to the atmosphere and to reduce the wind speed. Porter and Gates (1969, p. 237) add, "By tucking its bill under its wing, the cardinal will also reduce surface area and water loss." It is also interesting to examine the range of conditions for which the animal can remain in steady state if its metabolic output is at a minimum and T_b is constant. The set of lines numbered II and III illustrate these conditions. Line IV is the upper limit of stress that the cardinal can endure.

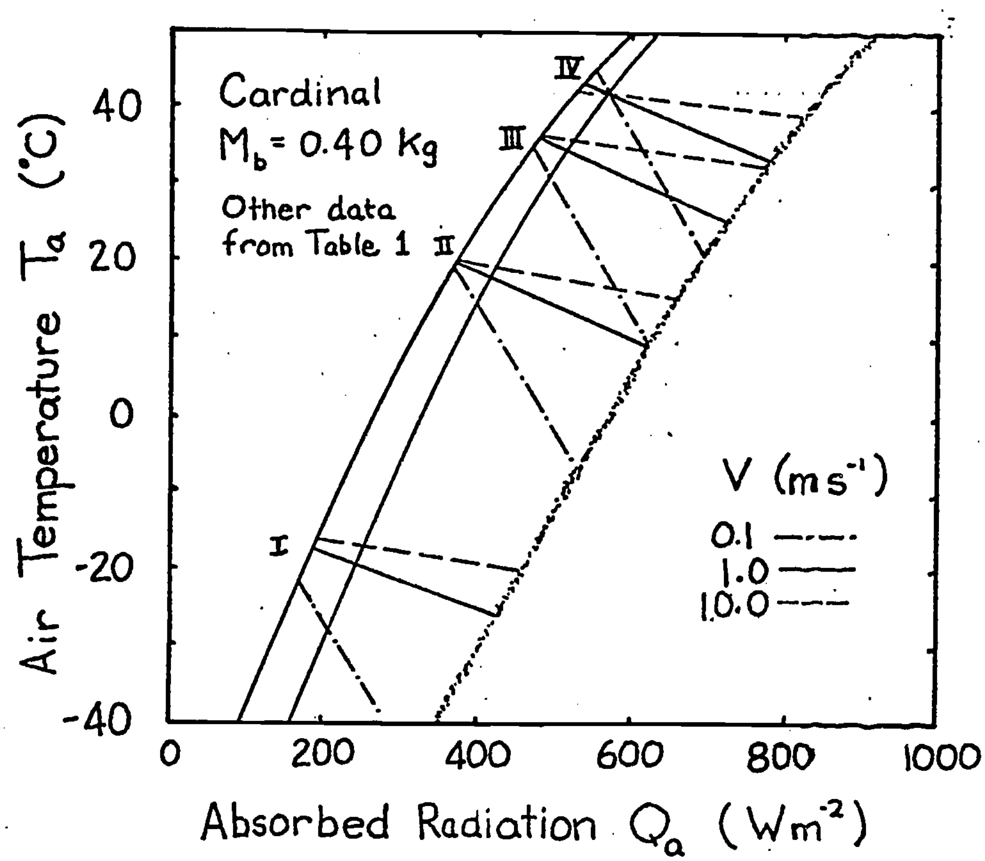

Figure 10. Climate diagram for a cardinal showing relations between air temperature, radiation absorbed, and wind speed for constant body and radiant surface temperatures at actual values of metabolic and water loss rates. From Porter, W. P. and D. M. Gates. 1969. p. 237.

Table I. Values for the climate space of the cardinal.

	M	E_{ex}	d_f	d_b	T_b	T_r
I	107	3	Var	2	38.5	-16.0
II	53	5	10	2	41.0	21.4
III	53	9	5	1	41.0	37.1
IV	77	77	5	1	42.5	42.5

M and E_{ex} in W m^{-2}, d_f and d_b in m × 10^{-3},

T_b and T_r in °C, M_b = 0.025 kg.

Monteith's Idea

In Chapter 10 of his book, Monteith (1973) presents a graphical representation of the energy balance equation which has some similarities to the climate space diagram. Instead of using absorbed radiation, he defines a quantity R_{ni} (also see Hatheway 1978) which is equal to $Q_a - (T_a + 273)^4$ to use on the abscissa. Next he derives an expression to represent the heat flow of the organism as though it were simply conducting heat to the environment

$$(M - E) = \frac{c_a p}{r_{hr}} (T_o - T_e)$$

where

M = metabolism (W m^{-2}),

E = water loss (W m^{-2}),

T_o = surface temperature (°C),

T_e = effective temperature of the environment (°C),

$\frac{c_a p}{r_{hr}}$ = equivalent conductivity (W m^{-2} °C^{-1}).

The equivalent conductivity is due to a weighing of the resistance to convection and radiation transfer. Figures 11 and 12 taken from Monteith illustrate his

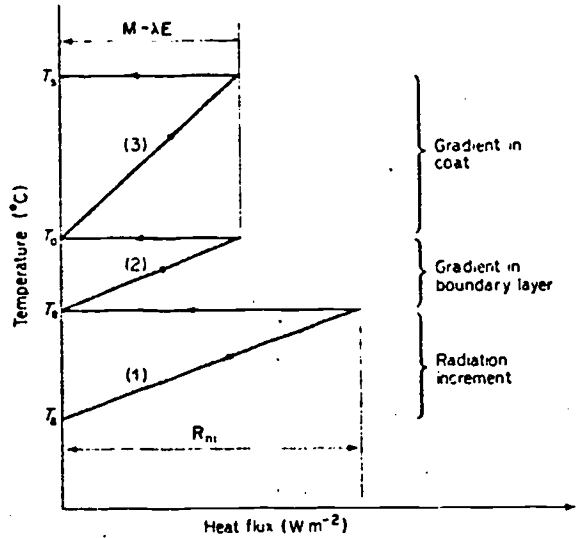

Figure 11. Main features of temperature/heat-flux diagram for dry systems. T_s is skin temperature, T_o coat surface temperature, T_e effective environment temperature, and T_a air temperature. From Monteith, J. L. 1973. P. 165.

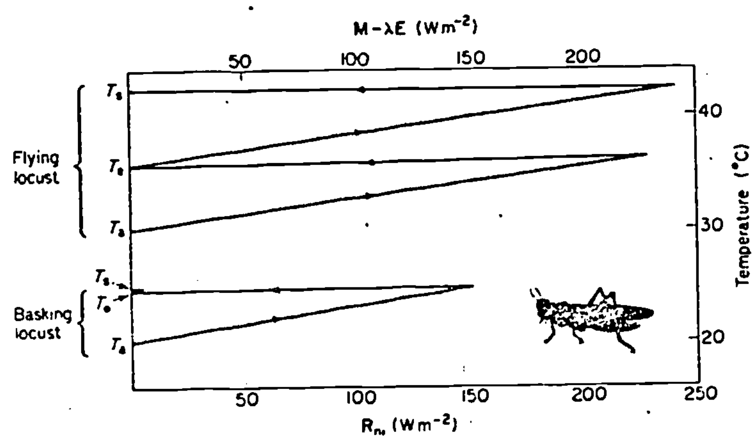

Figure 12. Temperature/heat flux diagram for locust basking (lower section of graph) and flying (upper section). From Monteith, J. L. 1973. P. 166.

method. Notice that there is a substantial metabolic contribution to the energy balance when the locust is flying and that when the insect is resting the environmental temperature is equal to the skin temperature T_s which will also equal the body temperature. Furthermore, if the environmental conditions (air temperature, wind speed, and net radiation) are given, then a range of physiological parameters (metabolism, fat thickness, fur thickness, water loss) can be found that will allow the animal to remain in thermal equilibrium. If the physiological values are known the converse problem can be solved (Monteith 1973, p. 165). The climate space concept has the advantage that it has put an outer bound on the physical environment. It may also be easier to interpret because absorbed radiation is kept separate from reradiation. Monteith's method, however, allows one to visualize the relative magnitude of each resistance element between the animal and the environment. For an example of this method see Cena and Clark (1974).

EXTENSIONS OF THE CLIMATE SPACE IDEA

The climate space concept can be extended in several ways which we will investigate in the exercises. Heller and Gates (1971) used it in a study of interspecific competition in the genus *Eutamias* (chipmunks). Spotila et al. (1973) were able to incorporate conduction when they constructed the climate space of the American alligator (*Alligator mississippiensis*). Zervanos and Hadley (1973) used these diagrams in their studies of the thermoregulation of the collared peccary (*Tayassu tajacu*). A word of caution is in order, however, concerning this representation of an animal's thermal state. We have assumed thermal equilibrium throughout. Many poikilotherms regularly try to increase their body temperature. Homeotherms also gain and then lose heat diurnally and when exercising. Schmidt-Nielsen et al. (1957) found that the camel stores and releases heat on a daily basis. More careful field measurements will have to be made before the importance of the nonequilibrium states can be ascertained.

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PROBLEMS

1. Table A provides metabolic rate, water loss, and fur and fat thicknesses for several species of animals. Using this information and Equations 10 and 11, calculate the maximum and minimum temperature differentials across the fat ($T_b - T_s$) and fur layers ($T_s - T_r$). Plot these four values placing ($T_s - T_r$) values on the abscissa. Shade the rectangle formed. Include lines of constant total differential ($T_b - T_r$).

Rank the homeotherms from the highest to lowest difference between body temperature and surface temperature. Under what environmental conditions would an animal like to make this difference large? When would the animal like to make this difference small? What other mammals do you know of besides the pig that have thick fat layers? Why might this be? How does fat compare with fur or feathers as an insulation material? What is the relative efficiency of each? Is it clear now that the assumption that $T_b \sim T_r$ for the lizard is not critical?

TABLE A

	M		E_{ex}		E_{sw}		d_b		d_f	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Shrew	396	139	26	0	26	0	1	1	3	2
Cow, summer	104	104	9	4	58	6	14	14	5	5
Cow, winter	104	104	9	4	58	6	14	14	27	27
Pig	124	58	75	1	7	1	35	1	3	1
Zebra finch	213	91	91	22	0	0	1	1	3.5	3
Locust	600	.07	14	0	0	0	1	--	--	--
Cardinal	107	77	77	3	0	0	2	1	15	5
Jack rabbit	77	63	63	9	0	0	2	1	15	8
Fence lizard	70	--	2	--	--	--	1	--	--	--

M, E_{ex}, E_{sw} in W m^{-2}, d_b, d_f in m × 10^{-3}

2. Construct the climate space of the pig, jack rabbit, and locust using the data presented below:

TABLE B (Units as in Table A)

		M	E_{sw}	E_{ex}	d_f	d_b	T_b
Pig $a_s = 0.8$, $M_b = 120$ kg	I	124	1	1	3	35	36
	II	100	1	21	3	35	36
	III	69	7	66	1	10	37.5
	IV	58	7	75	1	1	41.7
Jack rabbit $a_s = 0.8$, $M_b = 2$ kg.	I	77	0	9	15	2	37.5
	II	63	0	9	8.5	2	37.5
	III	43	0	12	8.5	2	38.5
	IV	45	0	20	7	1	39.5
	V	63	0	63	8	1	43.7
Locust $a_s = 0.8$, $M_b = 0.001$ kg	I	600	—	14	—	1	42
	II	600	—	14	—	0	20
	III	0	—	0	—	0	20
	IV	0	—	0	—	1	1

3. Spotila et al. (1973) were able to incorporate the effect of conduction. Thinking about the heat energy balance equation and assuming that the ground temperature is constant, how will the physiological limits be shifted?

4. Spotila et al. (1973) suggests that the area labeled A in the climate space of Figure 6 need not be included. Why might this be true? Are there any other areas like this? How does your answer compare with the information in Figure 3?

5. A comparison of the climate space diagrams in this module with those found in the Porter and Gates paper shows that the slopes of the lines are usually different under the same set of environmental and physiological conditions. This is because a different convection coefficient is used. Below is a table of weights and diameters for the same animals. Compute the convection coefficient in two ways: 1) using the formula that Porter and Gates (1969) provided; 2) using Mitchell's (1976) relationship, assume $V = 1.0 \text{ m s}^{-1}$. Now make the comparison in a more systematic fashion: Let V = 0.1, 0.5, 1.0,

3.0, and 10 m s^{-1} and M_b = 0.00001, 0.0001, 0.1, 10 and 1000 kg. Use the relationship between length and weight given in Appendix III to find a diameter corresponding to the weight values given. Compare the values by forming the ratio of Mitchell's h_c divided by that of Porter and Gates.

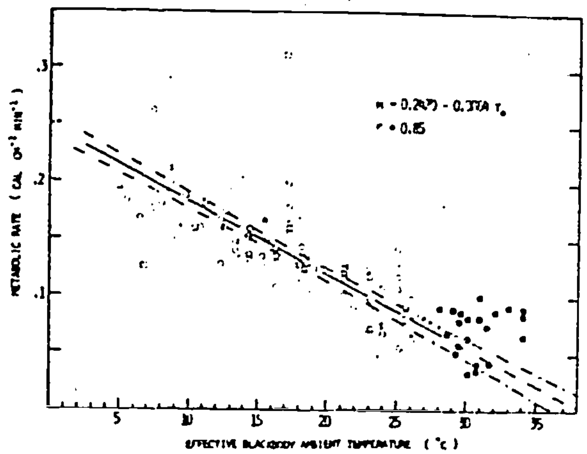
Animal	Diameter m	Body Mass kg
Sheep	.40 (fleece)	70.0
Cardinal	.050	.020
Lizard	.015	.050
Shrew	.018	.010

6. W. P. Porter (personal communication) has pointed out that Equations 10 and 11 apply to heat flow in a slab not a cylinder as shown in Figure 9. Derive the equation for heat flow through a cylinder (see Kreith 1973 or Hatheway 1977) and through a plate of the same average area under steady state conditions. When will the two formulae give approximately the same result?

Compare this with the values used in Porter and Gates (1969) tabled below. Why does this work?

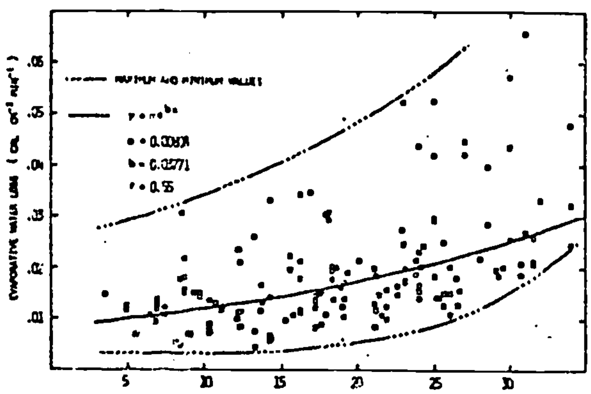
	Diameter D (cm)	Thickness of fur or feathers d_f (cm)	Thickness of fat layer d_b (cm)
Desert iguana	1.5	0.0	0.1
Shrew	1.8	0.3	0.1
Zebra finch	2.5	0.35	0.1
Cardinal	5.0	1.0	0.2
Sheep	25.0	12.8	0.1
Sheep	25.0	8.2	0.65
Pig	36.0	0.3	3.5
Jack rabbit	10.0	1.5	0.2

7. Morhardt and Gates (1973) measured both the metabolic rate and the evaporative water loss as a function of effective ambient temperature These graphs are included below (Figures 13 and 14). We know that both these physiological parameters should also depend on the radiation levels and wind speeds. Consider the metabolic chambers to be equivalent to a blackbody environment and then plot lines of constant metabolic rate and evaporative rates on the climate space diagram (let $M_b = 0.2$ kg, $V = m\ s^{-1}$). Now repeat this process on the climate space of Figure 3. What are times of environmental stress? What might be the preferred activity period of the animal? Remember that the metabolic curve is for a resting and fasting animal. How does that change your answer? Consult the original paper and investigate what other thermal microhabitats were available. Is it critical that we do not have any information about the animal in its burrow?



From Morhardt and Gates. 1974. P. 33.

Figure 13. Metabolic rates of all squirrels used in this study as a function of effective ambient temperature. Open circles represent metabolic rates of resting squirrels at effective ambient temperatures below the thermal neutral zone. Closed circles represent metabolic rates of resting squirrels at effective ambient temperatures above the lower critical temperature of 28°C. Open squares represent metabolic rates of exceptionally active squirrels, or those whose body temperature was falling below normal levels. The solid line is a least squres regression line fitted to the open circles, and the broken lines delineate the 95% confidence interval of the least squares line. The equation of the line and the correlation coefficient (r) are shown.



From Morhardt and Gates. 1974. P. 36.

Figure 14. Evaporative water loss as a function of effective temperature (corrected to 4 mg H_2O/liter air). The data collected at different relative humidities have been corrected to a constant relative humidity (vapor density = 4 mg H_2O/liter air by using Eq. (14). A logistic curve of the form $y = ae^{bx}$ is fitted to the data, and the correlation coefficient (r) is shown.

PROBLEM SOLUTIONS

1. Equation 10 is

$$M - E_{ex} = \frac{k_b}{d_b}(T_b - T_s)$$

Equation 11 is

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

$k_b = 0.205\ W\ m^{-1}\ °C^{-1}$ and $k_f = 0.025\ W\ m^{-1}\ °C^{-1}$. From this information maximum and minimum values of $(T_b - T_s)$ and $(T_s - T_r)$ can be calculated. These are tabulated below. The results are plotted on the two figures (Porter and Gates 1969, Figures 5 and 6, p. 231).

	$(T_s - T_r)$ Maximum	$(T_s - T_r)$ Minimum	$(T_b - T_s)$ Maximum	$(T_b - T_s)$ Minimum
Shrew	41.3	6.	1.7	0.6
Cow, summer	18.8	7.4	6.8	6.5
Cow, winter	101.0	39.8	6.8	6.5
Pig	14.7	1.0	21.0	0.1
Zebra finch	26.6	0	0.9	0
Locust	----	----	2.9	0
Cardinal	61.7	0	1.0	0
Jack rabbit	40.8	0	0.7	0
Fence lizard	----	----	0.5	0

	Ranking Maximum $T_b - T_r$	Total ΔT Maximum	Total ΔT Minimum	Ranking Minimum $T_b - T_r$
Shrew	3	43.5	7.5	5
Cow, summer	6	25.6	13.9	6
Cow, winter	1	107.8	46.3	7
Pig	5	35.7	1.1	4
Zebra finch	7	27.5	0	
Cardinal	2	62.7	0	
Jack rabbit	4	41.5	0	

If the environment is cold the animal will have to make this difference large to maintain T_b. It is also possible that the surface temperature will be hotter than the body temperature. Fleece on sheep can protect them from getting too hot (Hatheway 1977). Making the difference small decreases the rate of heat transfer within the body.

Many marine mammals have thick layers of fat. Fat is an economical way to store energy as well as provide insulation. It allows the animal to smooth out its form which should reduce the friction losses due to drag when swimming. Some marine mammals are covered with fur. These animals all spend time in terrestrial habitats (seals, sea lions, otter), which seems to indicate that fur is an important adaptation on land. The fur can also provide a boundary layer of air in the water which helps to cut down on heat loss. The relative efficiency of fat to air as insulation material can be computed by comparing the ratio of the conductivities. From the text we have

$$\frac{k_b}{k_f} = \frac{0.205}{0.025} = 8.2.$$

The conductivity of fat is 8.2 times greater than that of air. Therefore, to receive the same resistance to heat flow, an animal would have to have 8.2 times the thickness of fat. The lizard can only maintain a maximum 0.5 °C difference between its skin and body temperature.

2. The first step is to calculate T_r using Equation 13. This yields:

T_r °C

	I	II	III	IV	V
Pig	0.30	5.9	37.6	41.8	
Jack rabbit	-4.0	18.7	27.5	32.3	43.7
Locust	39.1	20.0	20.0	1.0	

$\varepsilon\sigma T_r^4$ values (ε = .96)

	I	II	III	IV	V
Pig	304.6	378.0	507.6	535.6	
Jack rabbit	285.9	394.9	444.7	473.8	548.6
Locust	517.8	402.0	402.0	307.5	

	Pig	Jack Rabbit	Locust
h_c, convection coefficient	9.12	15.72	43.21
M_b, mass	120 kg	2 kg	.001 kg

$h_c = 17.24 \quad V^{0.6} M_b^{-0.133}$

$V = 1.0 \text{ m s}^{-1}$

h_c will be the slope of the line so all we need to do is find one pair (Q_a, T_a) for each set of conditions given in Table B such that

$$Q_a + M = \varepsilon\sigma T_r^4 + E_{sw} + E_{ex} + h_c (T_r - T_a).$$

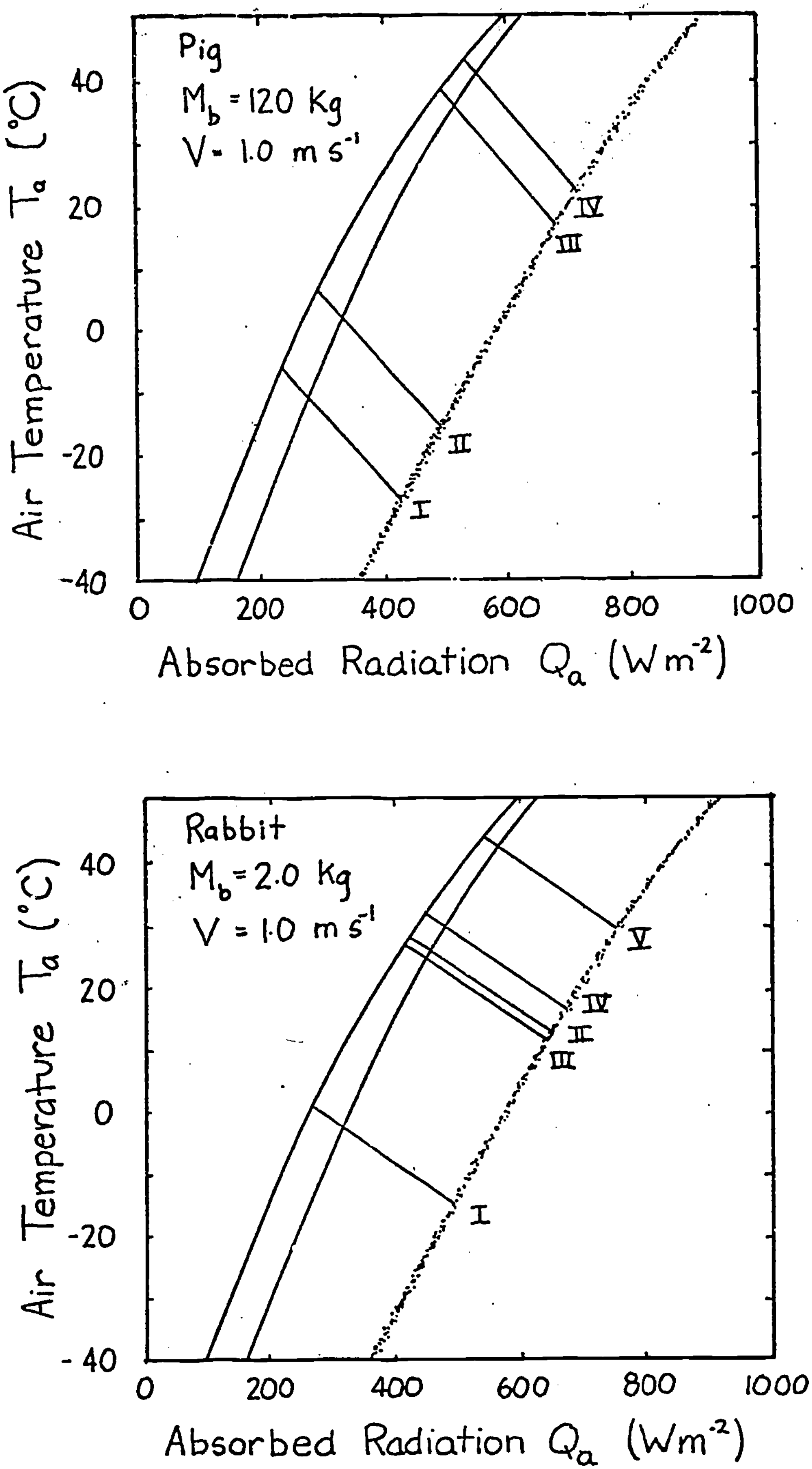
Assume $T_a = T_r$ in each case so that the convection is zero. Therefore

$$Q_a = \varepsilon\sigma T_r^4 + E_{sw} + E_{ex} - M.$$

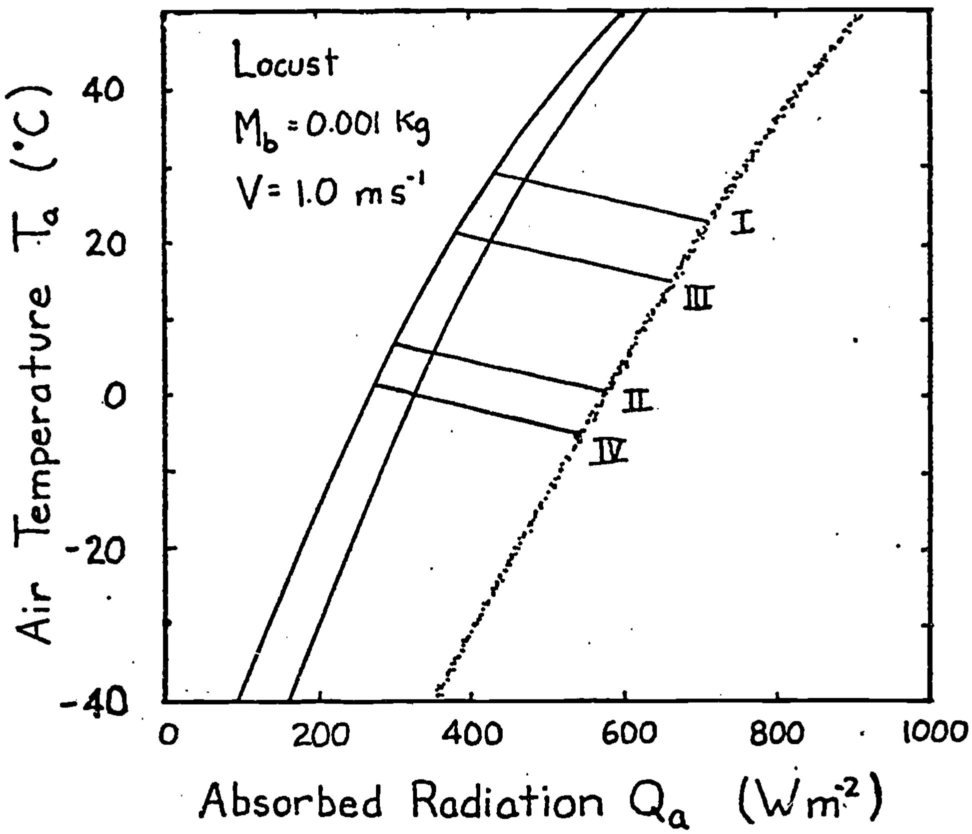
Q_a Values

	I	II	III	IV	V
Pig	183	300	512	560	
Jack rabbit	218	559	414	449	549
Locust	- 68	-184	402	307.5	

The climate space diagrams for the pig, jack rabbit and locust follow on pages 39 and 40.



Climate space diagrams for Problem 2.



Climate space diagram for Problem 2.

3. The conduction term is

$$G = \frac{k}{x}(T_r - T_g)$$

where k is the conductivity ($W\ m^{-2}\ °C^{-1}$),

T_r is the surface temperature (°C),

T_g is the ground temperature (°C),

and x is the thickness of the layer (m).

The energy balance is

$$Q_a + M = \varepsilon\sigma T_r^4 + E_{sw} + E_{ex} + h_c(T_r - T_a) + k(T_r - T_g).$$

If $T_r > T_g$, G is positive and the animal will receive more energy. This will shift the climate space to the right. If $T_g > T_r$, the opposite shift will occur.

4. Combinations of low air temperature and high radiation do not occur naturally. The coldest air temperatures will occur at night. By similar reasoning the area labeled B in Figure 6 suggests that the highest air temperatures will occur under low radiation levels. Again, this will not be true.

Figure 3 of the text shows that this is the case. Other data presented in the Morhardt and Gates paper confirm these observations. The reason is simply that the sun heats the air.

5. The two formulae needed to calculate the convection coefficients are 6 and 7.

$h_{c1} = 0.927\ V^{0.33}D^{-0.67}$ Porter and Gates

$h_{c2} = 17.24\ V^{0.60}M_b^{-0.133}$ Mitchell

	h_{c1}	h_{c2}	h_{c2}/h_{c1}
Sheep	1.712	9.78	5.7
Cardinal	6.90	29.04	4.2
Lizard	16.67	25.70	1.54
Shrew	14.76	31.85	2.2

Mitchell's h_c

V	$V^{0.33}$	.00001	0.001	0.1	1.01	10.0	160.0	M_b
		4.640	2.511	1.359	1.0	.736	.398	$M_b^{-0.1333}$
0.1	.251	20.08	10.86	5.88	4.32	3.18	1.72	
0.5	.660	52.80	28.57	15.46	11.38	8.37	4.53	
1.0	1.0	79.99	43.30	23.43	17.24	12.69	6.66	
3.0	1.933	154.63	83.68	46.29	33.32	24.53	13.26	
10.0	3.981	318.45	172.34	93.27	68.63	50.51	27.32	

Porter and Gates' h_c

V	$V^{0.333}$	.00001	0.001	0.1	1.0	10.0	1000	M_b
		.0022	.01	.0464	.10	.215	1.00	D
		59.95	21.54	7.743	4.641	2.783	1.00	$D^{-0.667}$
0.1	.464	25.80	9.27	3.33	2.00	1.20	.43	
0.5	.794	44.14	15.86	5.76	3.42	2.05	.74	
1.0	1.0	55.60	19.97	7.18	4.30	2.58	.92	
3.0	1.442	80.17	28.80	10.35	6.20	3.72	1.33	
10.0	2.154	119.75	43.03	15.47	9.27	5.56	1.99	

Let $D = L = (\frac{M_b}{\rho})^{1/3}$ from Appendix III, $\rho = 1 \times 10^3$ kg m^{-3}

then $$\frac{h_{c_2}}{h_{c_1}} = \frac{17.24\ V^{0.60}\ M_b^{-0.133}}{0.927\ V^{0.\ 3}\left[\left(\frac{M_b}{\rho}\right)^{1/3}\right]^{-2/3}} = 4.01\ V^{0.27}\ M_b^{0.089}$$

Ratio of hc_2/hc_1

V m s^{-1} \ M_b kg	.0001	.001	0.1	1.0	10.0	1000.
0.1	.801	1.17	1.77	2.16	2.65	4.00
0.5	1.20	1.80	2.71	3.33	4.08	6.12
1.0	1.41	2.17	3.26	4.04	4.92	7.46
3.0	1.93	2.91	4.38	5.37	6.59	9.97
10.0	2.66	4.01	6.03	7.40	9.08	13.75

6. The heat flow by conduction is

$$q = -kA \frac{dT}{dx} \qquad [A]$$

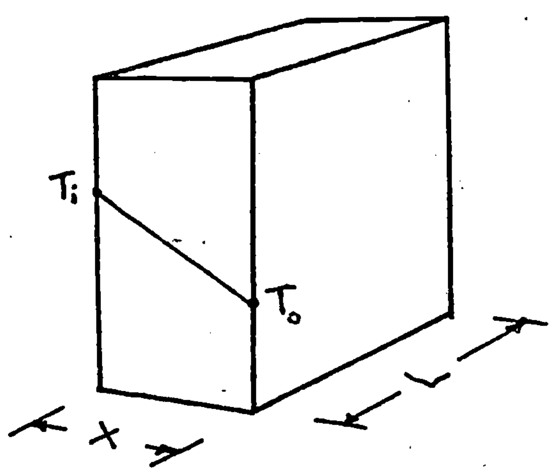
where q is heat flow (W)

k is the thermal conductivity (W m °C^{-1})

A is the area perpendicular to the heat flow (m^2)

and $\frac{dT}{dx}$ is the temperature gradient (°C m^{-1}).

For a slab under steady state conditions we can separate variables and integrate equation [A]



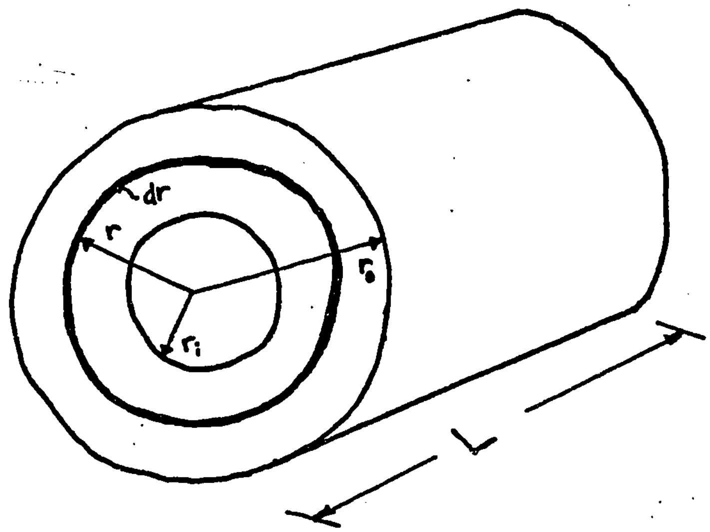
$$dT = \frac{q_s}{kA}\,dx$$

$$\int_{T_i}^{T_o} dt = -\frac{q_s}{kA}\int_0^x dx$$

$$T_o - T_i = -\frac{q_s}{kA}\,x$$

$$q_s = \frac{kA}{x}\,(T_i - T_o) \qquad [B]$$

For a cylinder we have



$$q_c = -kA\,\frac{dT}{dr}$$

$$A = 2\pi r\ L$$

$$q_c = -k\ 2\pi r\ L\ \frac{dT}{dr}$$

$$dT = -\frac{q_c}{2\pi lk}\,\frac{dr}{r}$$

$$\int_{T_i}^{T_o} dT = -\frac{q_c}{2\pi lk}\int_{r_i}^{r_o}\frac{dr}{r}$$

$$T_o - T_i = \frac{-q_c}{2\pi Lk}\,\ln\left(\frac{r_o}{r_i}\right)$$

$$q_c = \frac{2\pi lk}{\ln\left(\frac{r_o}{r_i}\right)}\,(T_i - T_o) \qquad [C]$$

Now if we assume the area of the slab is equal to $L \times 2\pi\,\frac{r_i + r_o}{2}$ and the thickness to be $r_o - r_i$ we can set the two equations [B] and [C] equal.

$$\frac{k\ L\ 2\pi\ \frac{r_i + r_o}{2}\ (T_i - T_o)}{r_o - r_i} \stackrel{?}{=} \frac{2\pi\ L\ k\ (T_i - T_o)}{\ell n\ (\frac{r_o}{r_i})}$$

Cancelling terms, we have

$$\ell n(\frac{r_o}{r_i}) \stackrel{?}{=} \frac{2(r_o - r_i)}{r_i + r_o} .$$

Therefore q_s will equal q_c if the above relationship is true. Using the data given in the problem we can compute the relative radii.

	Outside Radius (cm)	Radius to Skin (cm)	Radius to Fat Layer (cm)
Desert iguana	.75	.75	.65
Shrew	.90	.60	.50
Zebra Finch	1.25	.90	.80
Cardinal	2.5	1.5	1.3
Sheep	25.8	12.5	11.85
Sheep	20.7	12.5	11.85
Pig	18.0	17.7	14.2
Jack Rabbit	5	3.5	3.3

Checking these values we find that for the sheep when $r_o = 25.8$ and $r_i = 12.5$

then $$\frac{2(r_o - r_i)}{r_o + r_i} = .668$$ and

$$\ell n(\frac{r_o}{r_i}) = .724.$$

This is the worst case for the data which is less than a 10% difference.

You can check the error by plotting

$$\frac{\ln(\frac{r_o}{r_i}) - \frac{2(r_o - r_i)}{r_o + r_i}}{\frac{2(r_o - r_i)}{r_o + r_i}} \quad \text{vs.} \quad \frac{r_o}{r_i} .$$

The intuitive reason this works is that there is not much change in area for the different pairs of radii we have examined. It is, however, possible to show that

$$\ln(x) = 2\left[\frac{x-1}{x+1} + \frac{1}{3}\left(\frac{x-1}{x+1}\right)^3 + \frac{1}{5}\left(\frac{x-1}{x+1}\right)^5 + \ldots\right] . \qquad [D]$$

This is done by adding the series expansion for $-\ln(1 - y)$ and $\ln(1 + y)$ and then letting $y = \frac{x-1}{x+1}$. The result will give equation [D]. Using only the first term of the expansion in equation [D] with $x = \frac{r_o}{r_i}$ we get

$$\ln(\frac{r_o}{r_i}) \simeq \frac{2(r_o - r_i)}{r_o + r_i}.$$

7. On the figures the authors give equations to relate metabolic rate and evaporative water loss. These are

$$\left.\begin{array}{l} M = 0.2470 - 0.0064\ T_E,\ M(\text{cal cm}^{-2}\ \text{min}^{-1}) \\ M = 172 - 4.47\ T_E,\ M(\text{W m}^{-2}) \end{array}\right\} 5 < T_E < 27\ °C$$

$$M = 51\ \text{W m}^{-2} \qquad 27 < T_E < 35\ °C.$$

$$E = 0.00808\ e^{+0.03771\ T_E},\ E(\text{cal cm}^{-2}\ \text{min}^{-1})$$

$$E = 5.64\ e^{+0.03771 T_E},\ E(\text{W m}^{-2})$$

T_E	5	10	15	20	25	30	35
E	6.8	8.2	9.9	12.0	14.5	17.5	21.1
M	149.7	127.3	105.0	82.6	60.3	51	51

Assume an animal weight of 200 gm which = 0.2 kg.

$$\dot{h}_c = 17.24\ V^{0.6}\ M_b^{-0.1333}$$

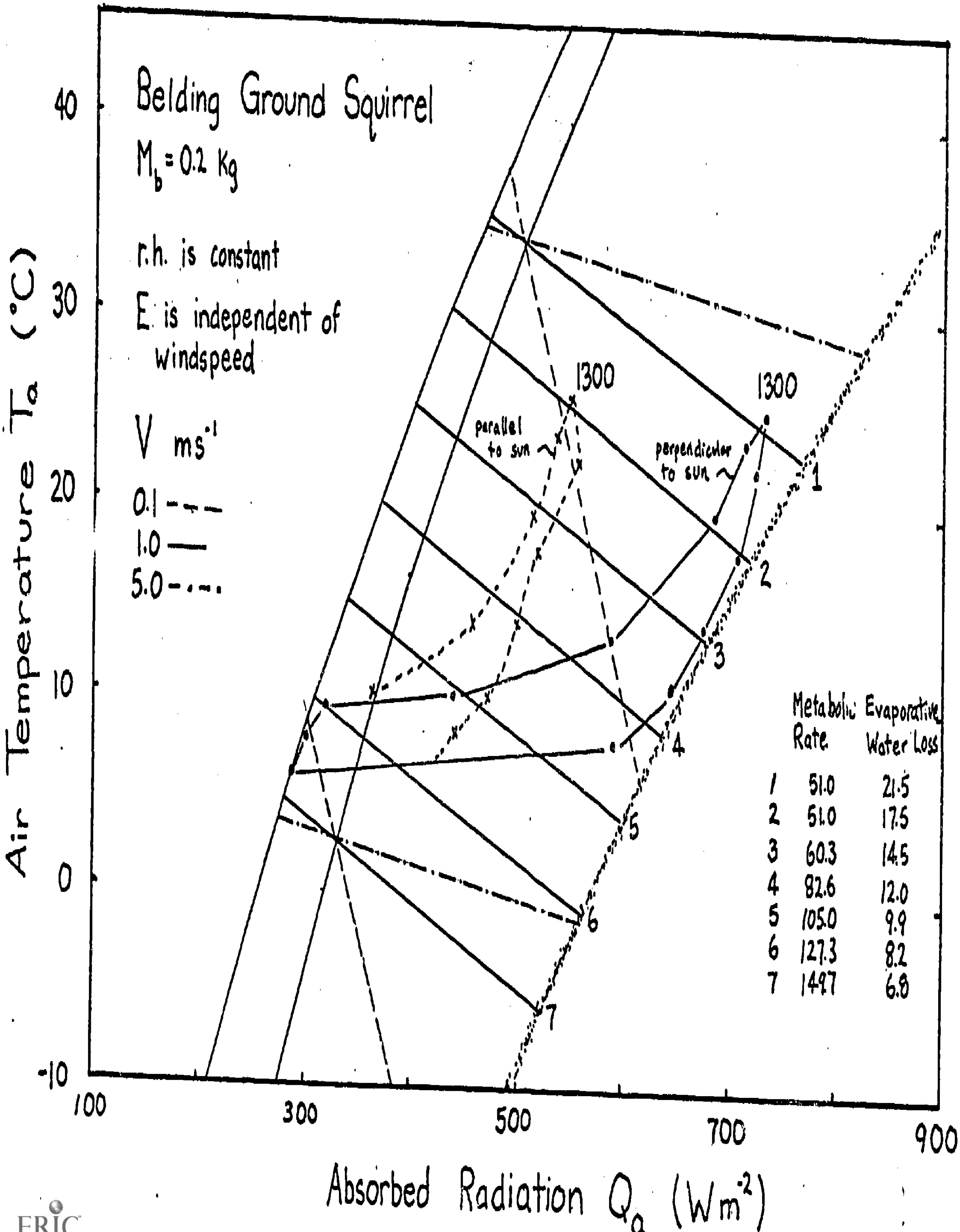
$$h_c = 5.36 \quad 21.36 \quad 56.1$$

$$\text{for } V = .01 \quad 1.0 \quad 5.0 \quad m\ s^{-1}$$

The resulting climate space diagram is given on page 48.

If the animal were simply resting outside, to reduce its metabolism to the lowest levels it should be active from 1100 to 1500 hours. The reason to go above ground, however, is for activity. Therefore, if metabolic rate increases 1.5 times, preferred activity times should shift to 800-1000 or 1500-1600 hours. It is hard to say much about water loss when the animal is active. According to the figure, if M increases to 82 W m^{-2} then E drops. But if respiration rate increases with activity then E may also increase. Morhardt and Gates considered a wide variety of above-ground habitats. A shaded environment gave much lower radiation loads during the day. If the animal orients its body parallel to the sun, this lowers Q_a also. A great deal more could have been said about the thermoregulation strategies if the thermal environment of the burrows were monitored and if microhabitat usage and body temperature as a function of time of day had been recorded. One would predict that shaded environments including the burrow would be used more in the middle of the day. To test this, one would have to make hourly observations on microhabitat usage.

The climate space diagram for Problem 7



APPENDIX I. Symbols, Units, and Dimensions

Symbol	Quantity	Unit	Dimension	S.I. equivalent
a	Absorptivity	-	-	-
$\bar{a}$	Average absorptivity to shortwave radiation	-	-	-
a, $\bar{a}_L$	Average absorptivity to longwave radiation	-	-	-
C	Convection	$W\ m^{-2}$	$MT^{-1}(HL^{-2}T^{-1})$	-
c	Specific heat of the animal	$J\ °C^{-1}$	$H\theta^{-1}$	-
$\frac{c_a p}{r_{hr}}$	This whole term has the units of a convection coefficient; c_a is the heat capacity of air, p is the density of air, $c_a p = JM^{-1}$, r_{hr} is the combined resistance to radiation and convection transfer			
°C	degrees Celsius	°C	θ	-
D	Diameter	M	L	-
d_b	Fat thickness	M	L	-
d_f	Fur or feather thickness	M	L	-
E	Water loss	$kg\ s^{-1}m^{-2}$	$MT^{-1}L^{-2}$	-
E_{ex}	Respiratory water loss	$W\ m^{-2}$	$HL^{-2}T^{-1}$	-
E_{sw}	Cutaneous water loss	$W\ m^{-2}$	$HL^{-2}T^{-1}$	-
G	Conduction	$W\ m^{-2}$	MT^{-1}	-
h_c	Convection coefficient	$W\ m^{-2}°C^{-1}$	$HL^{-2}T^{-1}\ \theta^{-1}$	-
k	Thermal conductivity of air	$W\ m^{-1}°C^{-1}$	$HL^{-1}T^{-1}$	-

Symbol	Quantity	Unit	Dimension	S.I. equivalent
k_s	Constant for convection coefficient of a sphere	$W\ m^{-2}\ °C$	$HL^{-2}\Theta^{-1}T^{-1}$	-
k_c	Constant for convection coefficient of a cylinder	$W\ m^{-2}\ °C^{-1}$	$HL^{-2}\Theta^{-1}T^{-1}$	-
k_d	Thermal conductivity of fat	$W\ m^{-1}\ °C^{-1}$	$HL^{-1}\theta^{-1}T^{-1}$	-
k_f	Thermal conductivity of fur or feathers	$W\ m^{-1}\ °C^{-1}$	$HL^{-1}\theta^{-1}T^{-1}$	-
L	Latent heat of evaporation	$J\ kg^{-1}$	L^2T^{-2}	-
L	Characteristic length	m	L	-
M	Metabolism	$W\ m^{-2}$	$HL^{-2}T^{-1}$	-
M_b	Body mass	kg	M	-
Nu	Nusselt number	-	-	-
Q_a	Absorbed radiation	$W\ m^{-2}$	$HL^{-2}T^{-1}$	-
Q_e	Emitted radiation	$W\ m^{-2}$	$HL^{-2}T^{-1}$	-
r	Reflectivity of the underlying surface	-	-	-
R_a	Atmospheric radiation (longwave)	$W\ m^{-2}$	$HL^{-2}T^{-1}$	-
R_g	Ground radiation (longwave)	$W\ m^{-2}$	$HL^{-2}T^{-1}$	-
R_p	Radiation from the sun and sky shortwave	$cal\ cm^{-2}\ min^{-1}$	$HL^{-2}T^{-1}$	$697.7\ W\ m^{-2}$
R	Reynolds number	-	-	-

APPENDIX I. Symbols, Units, and Dimensions - continued

Symbol	Quantity	Unit	Dimension	S.I. equivalent
S	Solar radiation	$W\ m^{-2}$	$HL^{-2}T^{-1}$	-
S	Sky radiation	$W\ m^{-2}$	$HL^{-2}T^{-1}$	-
t	Time	S	T	-
T_a	Air temperature	°C	Θ	-
T_e	Effective temperature	°C	Θ	-
T_g	Ground temperature	°C	Θ	-
T_o	Surface temperature	°C	Θ	-
T_r	Surface temperature	°C	Θ	-
T_s	Skin temperature	°C	Θ	-
U	Internal energy	J	ML^2T^{-2}	-
x	Length	m	L	-
δ	Boundary layer thickness	m	L	-
ε	Emissivity	-	-	-
σ	Stefan-Boltzmann constant 5.67×10^{-8}	$W\ m^{-2}\ {}^oK^{-4}$	$HL^{-2}T^{-1}\Theta^{-4}$	-
ρ	Mass density 1×10^3	$kg\ m^{-3}$	ML^{-3}	-
υ	kinematic viscosity of air	m^2S^{-1}	L^2T^{-1}	-

M = mass $H = ML^2T^{-2}$

T = time

L = length

Θ = temperature

APPENDIX II

Calculation of the Right-Hand Limit of the Climate Space

In their original paper, Porter and Gates (1969) state with regard to Equation 3, ". . . An estimate was made of $\overline{Q}_a$ as generally related to air temperature for value of absorptivity from 0.2 to 1.0." Gates (1977) shows how to calculate S and s as a function of latitude, time of year, and time of day. A representative value of 40° was chosen for latitude and then values of S, s were calculated under clear sky conditions in the late morning and afternoon. For r, a representative value of 0.15 was probably used. Curves of T_a and T_g as a function of time of day such as shown in Figure 2 were then taken from weather bureau statistics. R_a and R_g could then be calculated using the Stefan-Boltzmann law. All the numbers necessary to estimate $\overline{Q}_a$ are then available. The final step is to choose pairs of T_a and Q_a that are to be used. In Figure 3, 9:00-10:00 are hours of the day when this is true. This procedure is repeated at several latitudes and times of the year, from which the right-hand boundary can be derived.

Campbell (1977 pp. 89-92) presents simplified equations to calculate the left- and right-hand boundaries of the climate space. He includes a correction factor to average the longwave radiation from the ground and the sky for the left-hand boundary. The direct beam and diffuse shortwave radiation fluxes are simply given for the right-hand boundary. The reflected shortwave component seems to be included in the diffuse term which at 25% of the direct flux is higher than Gates (1978) gives. The absorbed shortwave radiation is then added to the left-hand boundary values. Therefore as T_a increases the shortwave component is constant using Campbell's equations but using Gates' method the shortwave flux increases.

APPENDIX III

Derivation of the Constant k_s for the Convection Coefficient

Mitchell (1976) reported that the best overall relationship between the Reynolds and Nusselt numbers is given by

$$Nu = 0.34\ Re^{0.6} \tag{1}$$

Recalling that Reynolds number Re is the ratio of interial forces to viscous forces in the fluid, we write

$$Re = \frac{VL}{\upsilon} \tag{2}$$

where

V = the fluid velocity ($m\ s^{-1}$)

L = the characteristic length (m),

and υ = the kinematic viscosity ($m^2 s^{-1}$).

The Nusselt number is a way to scale the rate of heat transfer as a function of wind velocity, size of the organism and fluid thermal diffusivity. It can also be expressed as

$$Nu = \frac{h_c L}{k} \tag{3}$$

where

h_c = heat transfer coefficient ($W\ m^{-2}\ °C^{-1}$),

L = characteristic length (m),

and k = thermal conductivity ($W\ m^{-1}\ °C^{-1}$).

Mitchell (1976) defined the characteristic length as

$$L = \left(\frac{M_b}{\rho}\right)^{1/3} \tag{4}$$

where M_b is the mass kg

ρ is the mass density $kg\ m^{-3}$.

Using these expressions we can solve for the heat transfer coefficient as a function of weight and wind velocity. Rearranging Equation 3 and substituting the Equation 1 for Nu, we have

$$h_c = \frac{k}{L}\,(0.34\ Re^{0.6}). \qquad (5)$$

We can then use Equations 2 and 4 to incorporate wind velocity and weight, respectively.

$$h_c = 0.34\,\frac{k}{L}\,(\frac{VL}{\upsilon})^{0.6}$$

$$= \frac{0.34\ k}{\upsilon^{\ 0.6}}\ V^{0.6}\ L^{-0.4}$$

$$= \frac{0.34\ \times\ k}{\upsilon^{0.6}} V^{0.6}\ (\frac{M_b}{\rho})^{-0.133}$$

$$= \frac{0.34\ \times \quad \times\ \rho^{0.133}}{\upsilon^{0.6}}\ V^{0.6}\ M_b^{\ -0.133}.$$

Letting $k_s = \frac{0.34\ \times\ k\ \times\ \rho^{0.133}}{\upsilon^{0.6}}$

if $\rho = 1 \times 10^3$ kg m^{-3} which is the density of water

$k = 2.57 \times 10^{-2}\ W\ m^{-1}\ {}^\circ K^{-1}$

at 20 °C

$\upsilon = 1.51 \times 10^{-5}\ m^2 s^{-1}$

then $k_s = 17.24.$

To see the error of assuming k and υ at 20 ° C we can compare the ratio of $\frac{k}{\upsilon^{0.6}}$.

Air temperature ° C	$\frac{k}{\upsilon^{0.6}}$
-10	20.79
20	20.07
50	19.51

The difference over the 20°C value is $\frac{1.28}{20.79}$ = 6.4 percent.