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Heat-Transfer Analysis of Animals: Some Implications for Field Ecology, Physiology, and Evolution

GEORGE S. BAKKEN AND DAVID M. GATES

Introduction

Mathematical modeling studies in science are not an end in themselves, but rather a tool. The fundamental purpose of mathematical analysis is to provide generalized, intellectually tractable insight into the operation and interaction of the complex factors involved in the physical and biological process under study. Two often contradictory requirements must be met. First, the model must include all relevant factors, with sufficient detail to give predictive precision for validation and practical applications of the analysis. Second, the analysis must be simple enough to be intellectually tractable and give a clearer subjective understanding than the raw data and knowledge of the individual processes involved. The second requirement implies that the model be constructed so that it is analytically soluble. For the complex nonlinear processes in biology, this is seldom possible without sacrificing precision. This is certainly true in thermal analysis of animals.

The best procedure in such a case is to proceed by a series solution that gives successive approximations to the real situation. The first-order approximation can be designed to carry the principal factors and have an analytic solution to fulfill the second requirement. Higher-order terms in the series and numerical solutions may then be used to give predictive precision when required.

In the past, mathematical analyses of heat transfer and temperature regulation in animals have fallen into two classes. First, most physiologists and physiological ecologists use "Newton's law of cooling." This gross oversimplification of the heat-transfer process states only that the heat transfer between an object and its environment is linearly proportional to a constant and a temperature difference. Neither the constant (Tracy, 1972) nor the temperature difference is well defined in the natural environment, and thus Newton's law provides no insight into the actual processes and interactions of heat transfer in animals. At the other extreme are the

very detailed studies of heat transfer and temperature distribution in the human body, with emphasis on control processes and mechanisms. The symposium edited by Hardy *et al.* (1970) surveys recent work. Precise models of this sort are specific for the particular animal and usually require computer evaluation. Such a model, although precise, provides little more general insight into the principles and biological implications of thermoregulation than direct empirical experimentation on the animal.

We have followed an intermediate approach, pioneered in ecology by the work of Porter and Gates (1969), wherein the contributions to the total thermal budget of the animal are separated by mode (conduction, convection, radiation, metabolism, etc.) but averaged over the whole animal or "lumped." The use of lumped parameters assumes the mathematically false relation

$$\int f(x) \cdot g(x) dx = \left[\int f(x) dx \right] \cdot \left[\int g(x) dx \right] \quad (1)$$

However, the relation is usually approximately correct and may be further corrected by introducing factors that convert the actual average of a parameter to an effective value which gives more nearly correct results. This procedure is well developed in the treatment of radiation (Kreith, 1965, pp. 217-234) with shape factors. During the remainder of this discussion of lumped parameters, we shall assume any such factor to be included so that all symbols represent effective rather than true average values. This is not to suggest that a distributed-parameter analysis may not be necessary for some studies. However, this lumped-parameter analysis is quite adequate for investigating large-scale trends in comparative physiological ecology and evolution.

Our general intent here is to outline the formalism that we have developed for the lumped-parameter model of the thermal energy budget of an animal, including the time-dependent effects of heat storage by the heat capacity of body tissues and body-temperature-dependent metabolic heat production. We shall discuss a few of the more interesting implications of the theory for simplified field instrumentation for studies of thermal ecology and time-dependent thermoregulatory behavior, and some general implications for the evolutionary history of thermoregulation. We shall not develop the theory in detail, but instead will present the results and qualitative arguments for the biological interpretations.

The Model: Description and Steady-State Solution

General Description

Heat transfer is a complex process, involving a number of mechanisms that operate simultaneously. The underlying physics of these mechanisms is well known except for the more complex cases of convective heat transfer. The reader is re-

ferred to a good general introduction to heat-transfer theory, such as Kreith (1965), for the essential principles of heat transfer. The application of heat-transfer theory to animals is complex because of the unusual properties of biological materials, especially fur (Davis and Birkebak, 1974). Good introductions to the application of heat-transfer theory to animals can be found in Birkebak (1966), Porter and Gates (1969), and Tracy (1972).

We have used the electrical analog representation of heat flow in the development of the model (Kreith, 1965, pp. 18–20). Essentially, this assumes that heat flow is linear, at least for a modest range of temperature differences. Then heat flow follows approximately the general relation: flow = (potential difference)/resistance. Thus heat flow may be regarded as equivalent to a current flowing in an electrical circuit, temperature difference as equivalent to voltage difference, and thermal resistance or conductance equivalent to an electrical resistor. Consequently, a thermal circuit can be represented by the same symbols as an electrical circuit, as shown in Figs. 16.1 and 16.2. The basic analytic device used in the development is Kirchhoff's law, which states that the energy flowing into a node (T_x) in a circuit diagram is equal to the energy flowing out of the node (i.e., conservation of energy). In heat-flow analysis, nodes correspond to isothermal (or nearly so) surfaces of the body, particularly the interfaces between the core and the skin, skin and pelage, and pelage and the environment. In a distributed-parameter model the surface elements are infinitesimal and strictly isothermal, whereas in the lumped-parameter model the surfaces are only approximately so. Figure 16.1 shows representative thermal circuits for various classes of animals. These models lump all heat capacity in an isothermal core. This is a reasonable assumption for animals with effective pelage and very large animals but results in errors in moderate-size, uninsulated animals, where thermal diffusion can be significant. (Colbert *et al.*, 1946, show an example of this in the delayed thermal rise and death of a small *Alligator mississippiensis*.)

The simplest nontrivial circuit, Fig. 16.1a, will serve to illustrate the development of the model. Kirchhoff's law applied to the surface node, (T_r), assumes the form (heat leaving surface) = (heat flowing to surface), or

$$H(T_r - T_a) + \sigma\epsilon T_r^4 + E_r = K(T_b - T_r) + Q_a \quad (2)$$

where K = conductivity from the surface element at temperature T_r to the body core at temperature T_b

H = convection coefficient

T_a = air temperature

Thermal radiation from the surface to the environment is given by the $\sigma\epsilon T_r^4$ term, where the Stefan-Boltzmann constant $\sigma = 8.12 \times 10^{-11} \text{ cal cm}^{-2} \text{ }^\circ\text{K}^{-4} \text{ min}^{-1}$, and the emissivity ϵ ranges from 0 to 1, with biological materials typically 0.95–0.99. Evaporative cooling at the surface is denoted by E_r and total absorbed radiation by Q_a . The sign convention regards metabolic heat production and heat flow from the core to the environment as positive.

A second equation results from applying Kirchhoff's law to the T_b node which

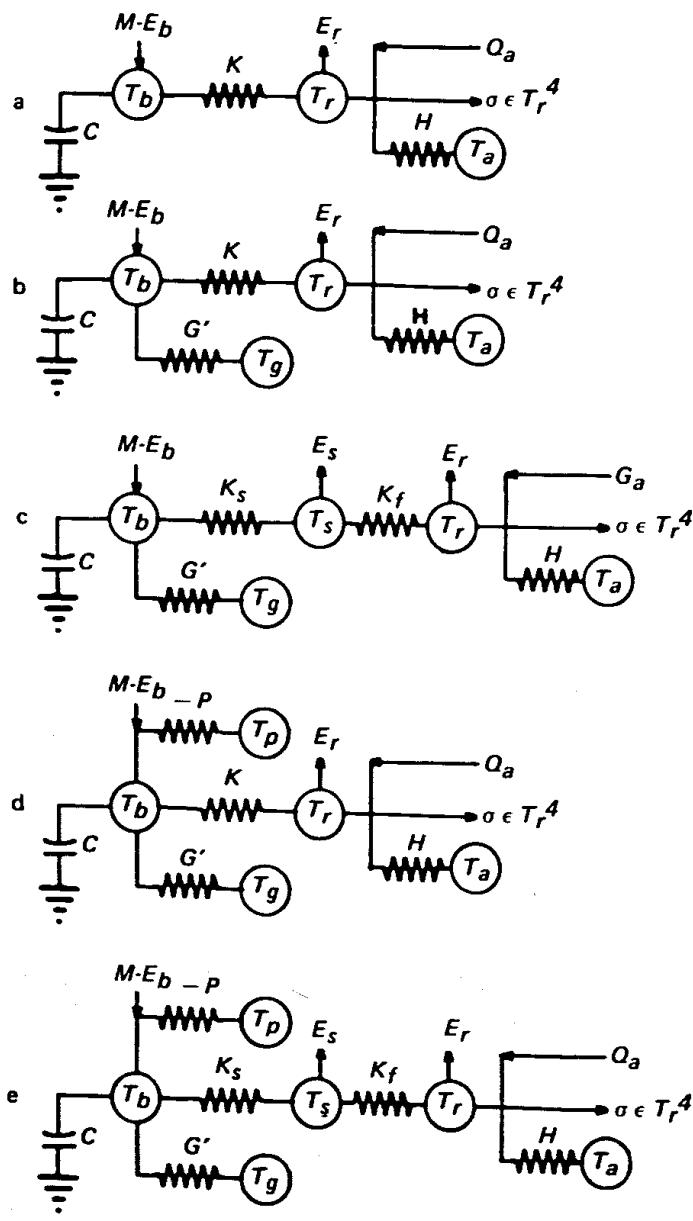


Fig. 16.1. Thermal circuit diagrams for the electrical analog representation of various classes of animals. The connection points or nodes represent parts of the animal or environment with a well-defined temperature such as the body core (T_b) or the ground temperature (T_g). Each node is labeled with the thermal potential or temperature of the corresponding part of the animal or the environment. The resistor symbols represent the thermal conductance between the parts of the animal or environment represented by the nodes connected by the resistance symbol. The capacitor symbol represents the heat capacity of the body of the animal. Simple arrows indicate simple thermal currents or heat flow which are not directly related to a temperature or thermal conductance. Diagram a represents a naked animal with negligible conduction to the ground. Diagram b represents a naked animal with significant conduction to the ground. Diagram c represents an animal with both pelage and significant conduction to the ground. In diagrams a-c, metabolism and evaporative water loss are assumed constant. In diagrams d and e, metabolism and respiratory evaporation are assumed to be linearly dependent on body temperature in the neighborhood of some body temperature $T_b = T_p$, so $(M - E_b) \rightarrow (M - E_b)_p + P(T_b - T_p)$. As explained in the text, this is equivalent to placing an imaginary conductance $-P$, connecting the body core with an environmental heat source/sink at a temperature T_p , as shown.

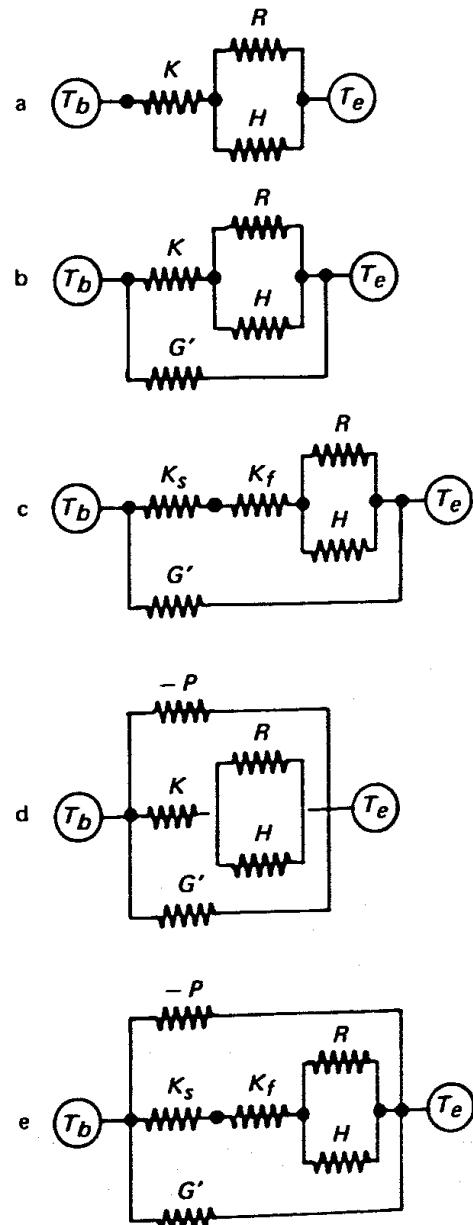


Fig. 16.2. Equivalent circuits for the same classes of animals as in Fig. 16.1. The air, ground, radiant, and surface temperatures have been formed into an equivalent environmental temperature T_e , called the "operative environmental temperature." The thermal resistances between the parts of the animal and between the animal and the environment have been formed into an equivalent circuit of thermal resistance I , equivalent to the insulation parameter measured in metabolism chamber experiments. The net metabolic heat production ($M - E_b$) is the thermal current flowing through this circuit. Surface and skin water loss E_r and E_s see somewhat different equivalent circuits and equivalent temperatures, and must be suitably combined with $(M - E_b)I$ to give the temperature difference between the body core and the operative environmental temperature, $T_\Delta = T_b - T_e$, as described in the text.

corresponds to the isothermal core of the animal. This has the form (heat stored) + (heat flowing out) = (net heat production) or

$$C \frac{dT_b}{dt} + K(T_b - T_r) = M - E_b \quad (3)$$

where C = heat capacity of the body

M = rate of metabolic heat production

E_b = rate of heat loss due to respiratory evaporation

dT_b/dt = rate of change of T_b with time

For the moment net metabolic heat production ($M - E_b$) will be assumed constant and independent of T_b and T_a . All coefficients, including E_r , E_b , M , and Q_a , are referred to a unit surface area in the lumped-parameter analysis. A convenient choice of units is to express temperature in degrees Kelvin ($^{\circ}\text{K} = ^{\circ}\text{C} + 273.16$); K , H , and other heat-transfer coefficients in $\text{cal cm}^{-2} \text{K}^{-1} \text{min}^{-1}$; heat capacity C in $\text{cal cm}^{-2} \text{K}^{-1}$; and physiological terms such as M and the various E 's in $\text{cal cm}^{-2} \text{min}^{-1}$.

Although Eqs. 2 and 3 can be solved simultaneously as they stand, the T_r^4 radiation term introduces excessive complexity. To facilitate a solution, we have chosen to linearize the radiation term by expanding it about a mean surface temperature \bar{T}_r and dropping higher-order terms. Then

$$\sigma\epsilon T_r^4 = (4\sigma\epsilon\bar{T}_r^3)T_r - 3\sigma\epsilon\bar{T}_r^4 \quad (4)$$

This linearization differs from the usual procedure used in engineering and is dictated by the lack of a well-defined radiant temperature in the natural environment. It is convenient to denote the linearized radiation coefficient $4\sigma\epsilon\bar{T}_r^3$ by R and form a term $Q_n = (Q_a + 3\sigma\epsilon\bar{T}_r^4)$. The error term in the linearization of radiation is about $6\sigma\epsilon\bar{T}_r^2(T_r - \bar{T}_r)$, which limits the range of validity to $(T_r - \bar{T}_r) < 10$ to 30°C , depending on the overall significance of the thermal radiation term. Then Eq. 2 has the form

$$H(T_r - T_a) + RT_r + E_r = K(T_b - T_r) + Q_n \quad (2a)$$

Steady-State Solution

The steady-state solution of Eqs. 2a and 3 corresponds to the model analyzed by Porter and Gates (1969) and is useful in developing the notation and some ideas for instrumentation. Solving Eqs. 2a and 3 with $dT_b/dt = 0$ for T_b by eliminating T_r gives

$$T_b = (M - E_b) \frac{K + H + R}{K(H + R)} - E_r \frac{1}{H + R} + \frac{HT_a + Q_n}{H + R} \quad (5)$$

To simplify notation, we may define a quantity I equivalent to the insulation parameter of Scholander *et al.* (1950):

$$I = \frac{K + H + R}{K(H + R)} \quad (6)$$

This is a thermal resistance (units $\text{cm}^2 \text{ }^\circ\text{K min cal}^{-1}$). Further, we may define an "operative environmental temperature" T_e :

$$T_e = \frac{HT_a + Q_n}{H + R} \quad (7)$$

T_e may be identified as the temperature of an inanimate object of zero heat capacity with the same size, shape, and radiative properties as the animal and exposed to the same microclimate. It is also equivalent to the temperature of a blackbody cavity producing the same thermal load on the animal as the actual nonblackbody microclimate, and therefore may be regarded as the true environmental temperature seen by that animal. Finally, we may define a "physiological offset temperature" T_Δ to represent the amount an animal may offset T_b from T_e by utilizing metabolism, evaporation, and insulation.

$$T_\Delta = (M - E_b)I - E_r \left(\frac{1}{H + R} \right) \quad (8)$$

With these definitions the heat flow from the animal can be represented by the equivalent circuits given in Fig. 16.2. I is the equivalent resistance of the network connecting T_b and T_e in Fig. 16.2. The expression for body temperature becomes

$$T_b = T_e + T_\Delta \quad (9)$$

The quantities I and T_e are equivalent to the operative heat-exchange coefficient, I_o , and the operative temperature, T_o , concepts used in the human physiology literature (Herrington *et al.*, 1937; Kerslake, 1972, p. 66). The parameters in I and I_o , T_e and T_o , are identical for Eqs. 6 and 7, but the insulation and the operative environmental temperature for the more general thermal circuits of Fig. 16.1 are not equivalent to I_o and T_o .

In general an animal has conduction to the ground and may have external pelage. To incorporate this in the model, K must be broken into two parts, K_s for the skin and K_f for the pelage. Similarly, evaporation takes place from both the skin and the pelage surface, denoted by E_s and E_r , respectively. Conduction to the ground acts independently from other heat-loss mechanisms and is denoted by a separate coefficient G' transmitting heat to the ground at a temperature T_g . The final circuit is shown in Fig. 16.1c. Applying Kirchhoff's law to the nodes at the core, skin-fur interface, and fur surface gives three simultaneous equations with a solution identical to that of Eq. 9. However, I , T_e , and T_Δ are now defined as follows:

$$K_{sf} = \frac{K_s K_f}{K_s + K_f} \quad (10)$$

$$I = \frac{K_{sf} + H + R}{(K_{sf} + G')(H + R) + K_{sf}G'} \quad (11)$$

$$T_e = \frac{K_{sf}(HT_a + Q_n) + G'T_g(K_{sf} + H + R)}{(K_{sf} + G')(H + R) + K_{sf}G'} \quad (12)$$

$$T_\Delta = (M - E_b)I - E_s \frac{K_{sf} + [K_s/(K_s + K_f)](H + R)}{(K_{sf} + G')(H + R) + K_{sf}G'} \quad (13)$$

$$- E_r \frac{K_{sf}}{(K_{sf} + G')(H + R) + K_{sf}G'} \quad (13)$$

Net metabolic heat production $M - E_b$ is again assumed constant and independent of T_b . Equation 12 is a more general form of the operative environmental temperature than Eq. 7, and the difference from the operative-temperature concept of human physiology is clear.

Notice that if E_s and E_r are assumed to be zero, Eq. 13 is formally equivalent to Newton's law of cooling:

$$T_\Delta = T_b - T_e = I(M - E_b) \quad (13a)$$

The errors inherent in analyzing physiological data with Newton's law are quite clear from a brief consideration of Eqs. 11 and 12. The insulation of an animal is often considered a property of the animal. However, Eq. 11 shows that I is a function of the convection coefficient, which depends in part on the wind velocity of the environment, and the conduction coefficient to the substrate G' , which will depend on the posture of the animal and the properties of the substrate, particularly the conductivity and the heat capacity. Conversely, the temperature of the environment is not the air temperature or the enclosure temperature, but depends on all the thermal properties of the environment and properties of the animal, such as K_{sf} , and size, shape, and posture, which strongly affect the values of G' and H . Thus we have the interesting situation in which the supposed property of the animal, I , is determined in part by the environment (as noted by Tracy, 1972), and the temperature of the environment, T_e , is determined by the properties of the animal. This should be a sufficient warning against the use of oversimplified analysis and should clearly indicate that heat transfer in animals shows the strong interactions between the animal and its environment so characteristic of all ecological problems.

Applications in Instrumentation

A frequent criticism of more detailed studies of heat transfer in animals is that the resulting model is too complex to be used in field studies of thermal ecology, where the primary interest is biology, not heat transfer. This criticism has some merit, and consequently we have tried to cast the result of our model in more general terms. The $T_b = T_e + T_\Delta$ formulation is a result. We have also tried to develop simple instrumentation that would be less expensive, complex, and heavy than the usual micrometeorological instruments but yet give results with general validity which are of use in more specialized studies. In particular, some method of making an integrated reading of the thermal stress on the animal, ideally the operative environmental temperature T_e , is needed to replace the largely meaningless "black-bulb thermometer" reading commonly used as an overall heat-stress index.

The identification of T_e as the "true" environmental temperature and its equivalence to the temperature of an inanimate model of the animal suggests that it would be useful to measure T_e directly with a cast of the animal as a " T_e thermometer." This measurement is similar to the use of the Vernon (1932) globe thermometer, which is designed (Kerslake, 1972, pp. 67-72) to approximate the

response of a human by adjusting H and R to give the same value of T_e (as in Eq. 7) as a human. This instrument and its dubious progeny, the black-bulb thermometer, are of limited use since they only approximate the actual values of H and R and completely omit some factors (primarily G') in Eq. 12. Most of these limitations are eliminated if an object that exactly duplicates the animal except for metabolism and water loss is used as a thermometer and placed in the same position in the environment as the animal under study. The exact method of construction will depend on the study to be conducted. Most commonly it will be desirable to have a rapid response so that the operative environmental temperature may be monitored continuously. This requires a low heat capacity, which can be best achieved by using a thin metal cast, painted to duplicate the radiative properties of the animal or covered by the integument of the animal using taxidermy techniques. A technique for making thin shell metal casts of reptiles and amphibians is discussed in the Appendix to this chapter. Alternatively, it may be desirable to duplicate the time response of the animal so that the heat capacity of the animal must be duplicated. It must be remembered that the heat capacity of the *whole* animal must be duplicated, and this requires that the heat capacity per unit volume, not per unit weight, be duplicated. Tissue has a whole-animal average of approximately 0.7–0.8, and this range is duplicated by various brass and bronze alloys which could be used to make a solid cast. Also, the hollow cast could be filled with a suitable composite material, with the composition adjusted to match the heat capacity of the animal.

The primary utility for a cast as a T_e thermometer is in the study of small reptiles and amphibians. Lizards control their body temperature closely (Cowles, 1940; Cowles and Bogert, 1944; Heath, 1964, 1965, 1968) by behavioral means—that is, by adjusting their position and posture in the environment so that the time-average value of T_e falls inside the preferred range of body temperatures. Minor variation in shade, skin color, substrate, exposure to the sky, wind velocity, and temperature strongly influence T_e for a small animal near the ground. The distance scale is much too small to allow normal micrometeorological instrumentation. Under these conditions, several T_e thermometers placed at various locations in the environment would provide a “map” of operative environmental temperatures available to the lizard. This map would greatly facilitate behavioral studies.

To demonstrate the range of operative environmental temperatures present in an apparently homogeneous environment, a number of T_e thermometers were constructed in the form of thin-walled metal cylinders with a 4:1 length-to-diameter ratio. Diameters ranged from 0.64 to 15.5 cm. The site was a sparsely vegetated sand spit on the shore of Douglas Lake, Cheboygan County, Michigan, near The University of Michigan's Biological Station's Alfred M. Stockard Lakeside Laboratory. This site provided good exposure to solar radiation and wind during most of the day.

Typical results are shown in Table 16.1. One series of cylinders was placed on 0.64-cm square balsa wood blocks so that they were 2–3 mm above the sand substrate. Another series was hung 20 and 90 cm above the substrate by cotton thread. All were in an area roughly 1 by 2 m and most were within an area $\frac{1}{2}$ by 1 m. The shaded cylinder was placed on leaf and twig litter under a low (0.5-m-high) bush that provided broken shade. Within this area, light gray 1.6-cm-diameter cylinders

Table 16.1 Operative Environmental Temperatures of Cylinders of Various Diameters, Colors, and Orientations in a Sandy Area Exposed to Full Sun and Wind^a

Cylinder	Diameter (cm)	Position	Exposure	Height (cm)	Color	T_e (°C)
1	1.6	ESE-WNW	Sun	0.3	White	37.5
2	1.6	ESE-WNW	Sun	0.3	Black	50.0
3	1.6	ESE-WNW	Sun	0.3	Gray	45.5
4	1.6	NNE-SSW	Sun	0.3	Gray	46.0
5	1.6	Vertical	Sun	0.3	Gray	41.0
6	1.6	ESE-WNW	Sun	20.0	Gray	39.5
7	1.6	ESE-WNW	Sun	90.0	Gray	36.0
8	1.6	ESE-WNW	Shade	1.0	Gray	28.3
9	0.64	ESE-WNW	Sun	0.3	Gray	41.5
10	1.6	ESE-WNW	Sun	0.3	Gray	45.5
11	2.86	ESE-WNW	Sun	0.3	Gray	45.5
12	3.81	ESE-WNW	Sun	0.3	Gray	47.5
13	15.50	ESE-WNW	Sun	1.0	Gray	47.0

^a A small shrub 0.5 m high provided broken shade for cylinder 8. All cylinders were in an area of 1 × 2 m. Microclimate parameters for this area were: $T_{air} = 26^\circ\text{C}$; $T_{ground} = 38.5^\circ\text{C}$; wind at 20 cm, 67 cm s^{-1} ; wind at 90 cm, 310 cm s^{-1} ; solar radiation in an 0.3- to 3-μ band, $1.3 \text{ cal cm}^{-2} \text{ min}^{-1}$. August 17, 1972, 14:15 to 14:16. Douglas Lake Cheboygan County, Michigan.

placed at the surface could experience an operative environmental temperature range from 28 to 46°C .

To validate the concept further, we have constructed thin shell casts of the common western fence lizard, *Sceloporus occidentalis*, by the method described in the Appendix. Since the net metabolic heat production is very small, the temperature of the lizard should approximate T_e under equilibrium conditions. Comparisons of the lizard with the cast are given in Fig. 16.3.

The use of this technique with small endotherms is less straightforward since the high internal heat production will increase \bar{T}_r and alter R and Q_n . In this case a model must be constructed with a heater and covered by the integument of the animal; the model attached to a temperature controller set to T_b . If the heat capacity C is known, I may be determined from a cooling curve (see the next section). Then measuring the heater power ($M - E_b$) allows T_Δ to be measured and T_e thus to be determined from Eq. 9. Of course, heater power is equivalent to metabolic rate and thus is a direct index of environmental stress. However, determination of T_e gives a more intuitive result since temperature is an intensive parameter, whereas heater power or metabolism is an extensive parameter that is hard to use comparatively.

We wish to emphasize here that animals larger than the space occupied by a complete set of micrometeorological instruments are best studied directly; the diseconomy of substituting a brass moose for proper instruments is fairly clear.

The general concept of a thin metal cast as meteorological instrumentation and the development of the necessary technology suggest another important application. Convective heat transfer is one of the primary modes of heat loss in smaller

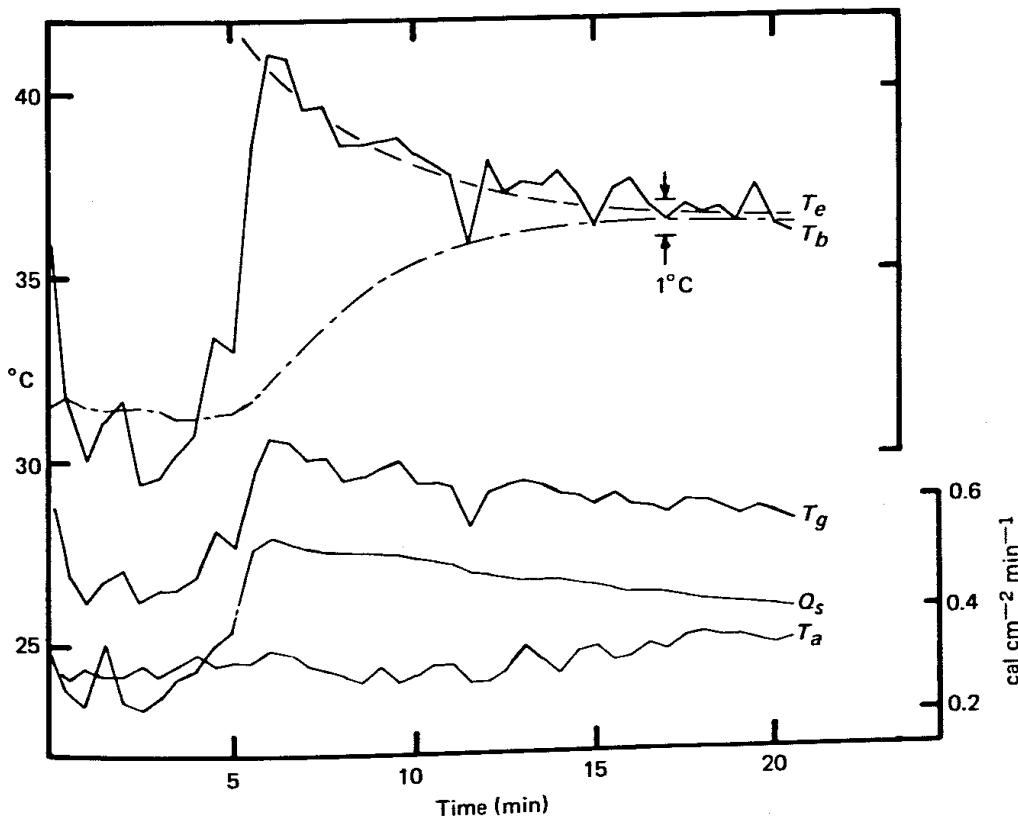


Fig. 16.3. Comparison of the body temperature T_b of a 9-g lizard (*Sceloporus occidentalis*) with the operative environmental temperature T_e measured by a fast-response thin metal cast of another lizard of the same size and species. To ensure uniform microclimate conditions, the animals were placed on a flat styrofoam substrate ($G' \approx 0$). Note the rapid response of the hollow cast, which has a time constant of less than 1 min, with 90 percent response in less than 2 min. Note also that when the cast and the lizard are in thermal equilibrium (arrow), T_e and T_b agree within $\pm 1^\circ\text{C}$. This good agreement is due to a good match between the absorptivity of the cast and the lizard. This match is partly fortuitous, since the lizard can, like most lizards, actively vary its absorptivity. Other lines in the figure are the air temperature T_a , the styrofoam surface temperature T_g , and the incident solar radiation (Eppley pyranometer) Q_s .

animals, and knowledge of the convection coefficient of an animal in different air-flow conditions in the natural habitat is essential. However, the air flow in outdoor conditions is complex and ill defined, with large-scale velocity variations (gusts) and small-scale microturbulence from vegetation and other irregularities. Consequently, convection coefficients typically show 50 percent turbulent enhancement and poor (± 50 percent) correlation with air velocity when measured outdoors (Pearman *et al.*, 1972). A further problem for smaller animals is that the wind velocity and air temperature near the ground follow a logarithmic profile and thus vary over the animal.

This situation complicates the usual procedure for developing correlations between laboratory data and field conditions. The usual procedure for applying

convection coefficient data is to express the data in terms of dimensionless units, called the Reynolds number (Re), Nusselt number (Nu), and Prandtl number (Pr). A full description of the use and interpretation of the dimensionless quantities is given in most heat-transfer texts (e.g., Kreith, 1965). Very briefly, and with great oversimplification, the Prandtl number is a constant of the fluid, the Reynolds number is a dimensionless velocity, and the Nusselt number is a dimensionless convection coefficient. They are related as follows:

$$Nu = Re^n Pr^m$$

so a plot of Nu versus Re can be used to find the convection coefficient for objects of any size in any wind velocity as long as the objects are of similar shape and similarly oriented to air flow and the air flow has the same general character with respect to velocity profiles and turbulence.

Because of these complexities, the usual procedure of calculating the convection coefficient from Reynolds number–Nusselt number plots made using wind-tunnel data and field measurements of wind velocity becomes complex. Extensive measurements of the mean wind velocity, gusts, and small-scale microturbulence to within a few millimeters of the surface would be required to determine the convection coefficient accurately. In most cases this effort would not be justified by the improvement in the accuracy of the convection coefficient determination, particularly since the variability in all the relevant parameters under field conditions is great. However, the environment often shows consistencies in the level of gustiness, turbulence, wind direction, and velocity in relation to the surface topography, and the consequences for the convection coefficient could well be biologically significant. Also, the general problem of the details of convection in the outdoor environment is of considerable intrinsic interest.

For example, Porter *et al.* (1973) have shown how the lizard *Dipsosaurus dorsalis* exploits the air-velocity profile by climbing higher in bushes to obtain greater convective cooling as the day becomes progressively hotter toward noon. It would be interesting to know if variations in turbulence level may be exploited similarly.

A phenomenon that needs further investigation is the effect of size on the convection coefficient of animals near the ground. For free-stream conditions, it is well known that the convection coefficient decreases approximately as the square root of the diameter of the object. However, at or near the surface of the ground the velocity profile must also be considered. A large object near the surface of the ground will extend farther above the surface and thus into the higher-velocity region of the profile. Thus a large object experiences a higher average air velocity than a smaller object. Since the convection coefficient increases roughly as the square root of the air velocity, this will increase the convection coefficient of the larger object relative to the smaller, opposing the free-stream tendency of the convection coefficient to decrease with size. The net effect is for the convective heat loss of small and large animals to differ by less than might be expected. Table 16.2 shows the consequences for T_e .

This effect also suggests that essentially upright or long-legged animals would

Table 16.2 Equilibrium Temperatures of Gray Cylinders Outdoors over a Sandy Substrate at The University of Michigan's Biological Station at Douglas Lake, Cheboygan County, Michigan

Diameter (cm)	Surface Level ^a T_e ($^{\circ}$ C)	Above Surface ^b T_e ($^{\circ}$ C)
0.64	33.0	30.5
1.59	36.5	34.0
2.86	37.0	35.0
3.81	37.0	36.25
15.5	36.75	39.0

^a Surface level (3 mm): solar radiation 1.0 ly, air temperature 22° C, wind $100\text{--}150 \text{ cm s}^{-1}$.

^b 90 cm above surface: solar radiation 0.8 ly, air temperature 27.5° C, wind $40\text{--}80 \text{ cm s}^{-1}$.

Note that the temperatures of the cylinders, equal to the operative environmental temperatures T_e for the cylinders, are well separated 90 cm above the ground by the decrease in the convection coefficient with increasing diameters. However, at the surface the cylinders are in a velocity gradient and the larger cylinders experience a higher average wind velocity, counteracting the decrease in convection coefficient with size. The result is that the operative environmental temperature is essentially the same for all the cylinders except for the smallest (0.64 cm), even though the meteorological conditions (higher radiation, higher wind speed, and larger difference between cylinder and air temperature) would be expected to give a larger differential in T_e . This effect is also partly due to the lower wind velocity and hence reduced convection coefficients at the surface, so that the significance of thermal radiation, which is the same for all size cylinders, is relatively greater.

have a substantial convective advantage over animals of similar size that have horizontal posture or short legs.

The effort required for a fundamental study of the convection coefficient in a turbulent flow showing a logarithmic profile cannot be justified for general field studies where the fundamental interest is biology rather than heat transfer. A simpler means of determining the convection coefficient with good accuracy is required. We suggest that the best procedure for most thermal ecology studies of small animals near the surface is not to develop Reynolds number-Nusselt number correlations in the wind tunnel and then determine the field convection coefficient by measuring wind velocity and using the Re-Nu correlation. Instead, the convection coefficient would be determined directly by using a pair of gold-plated, polished, metal casts, one heated and the other unheated, as a field convection coefficient meter. The procedure is identical to the use of the heated-bulb-thermometer anemometer.

The procedure is to place the casts on a substrate of low thermal conductivity, such as styrofoam, so that G is essentially zero. Then the insulation I is given by Eq. 6. Since the emissivity of polished gold is low ($\epsilon = 0.05\text{--}0.02$), the radiative-heat-transfer coefficient $R = 4\sigma\epsilon\bar{T}_r^3$ will be around $4 \times 10^{-4} \text{ cal cm}^{-2} \text{ s}^{-1} \text{ }^{\circ}\text{C}^{-1}$ compared with $H = 5 \text{ to } 10 \times 10^{-3} \text{ cal cm}^{-2} \text{ s}^{-1} \text{ }^{\circ}\text{C}^{-1}$ for cylinders 2–10 cm in diameter in laminar flow of 10 cm s^{-1} . Thus, even for low air velocities, R may be assumed zero as a first approximation, in which case I becomes

$$\lim_{R \ll H} I = \lim_{R \ll H} \frac{(K + H + R)}{K(H + R)} = \frac{K + H}{KH} \quad (14)$$

Since the cast is made of metal, K is very large and $K + H \approx K$. Thus

$$\lim_{K \gg H} I = \lim_{K \gg H} \frac{K + H}{KH} = \frac{K}{KH} = \frac{1}{H} \quad (15)$$

The heated cast is equivalent to an animal with metabolism so that, since E_b and E_r are zero for the polished gold cast, Eq. 13a gives for the cast

$$T_b^{\text{cast}} = T_e^{\text{cast}} + \frac{M^{\text{cast}}}{H} \quad (16)$$

where M^{cast} is just the power dissipated in the heater. Since T_e^{cast} is just the temperature of the unheated gold-plated cast (as discussed for the " T_e " thermometer

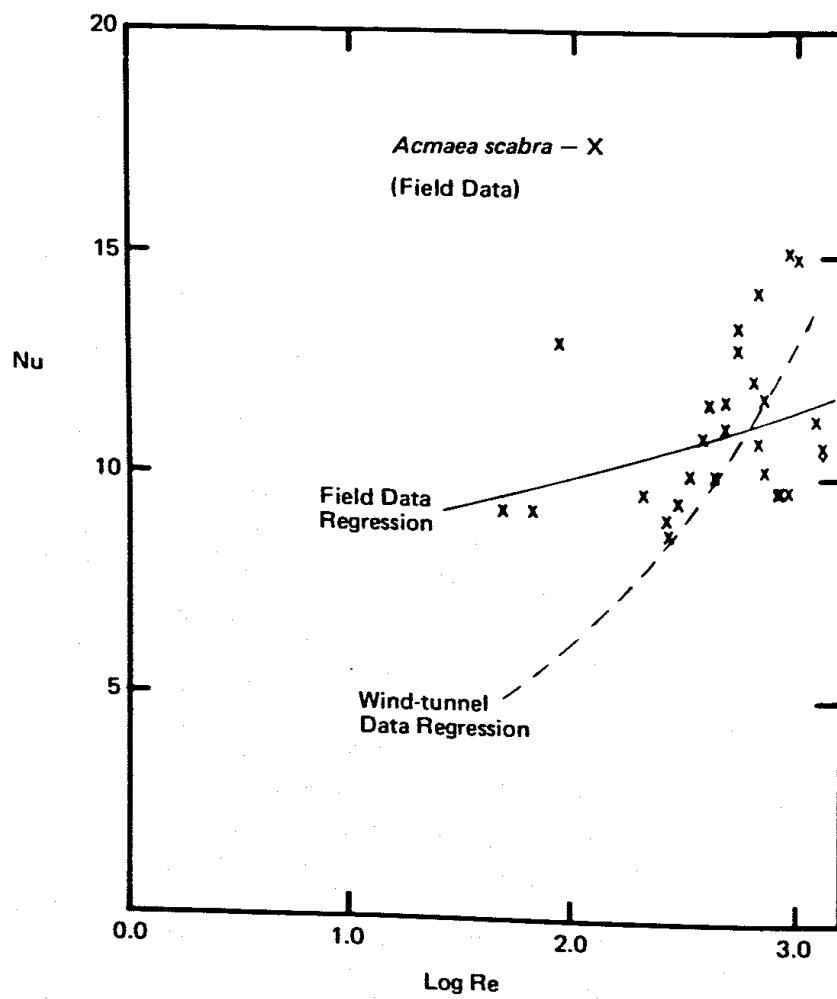


Fig. 16.4. Plot of the Reynolds number Re (a dimensionless wind velocity) versus the Nusselt number Nu (a dimensionless convection coefficient) for a gold-plated cast of the intertidal limpet *Acmaea scabra* (Gastropoda). Re is determined for the height of the shell and the wind velocity measured 2 cm above the substrate and extrapolated to measurements at 5 and 10 cm above the substrate. Note that, owing to turbulent, unstable air flow, the actual Nusselt number differs significantly from the value that would be calculated using wind-tunnel data and the Re value measured in the field.

application of the painted hollow-metal cast), all the parameters in Eq. 16 are known, and, to a first approximation,

$$H = \frac{T_{\text{hot cast}} - T_{\text{cold cast}}}{M^{\text{cast}}} \quad (17)$$

Accurate determinations will require corrections for the small errors (around 10 percent or less) that result from residual conduction and radiation. Because the corrections are small, they need not be known with great precision.

The heater in the heated gold-plated cast may be operated in either the constant-current ($M_{\text{heater}} = \text{constant}$) or constant-temperature ($T_b^{\text{cast}} = T_{\text{hot cast}} = \text{constant}$) mode. The constant-current mode requires less equipment but gives a slow response, since an appreciable amount of time is required to dissipate the heat stored in the cast. Response time can be reduced by using a thin metal cast, as described in the Appendix. More rapid response is attainable with the constant-temperature mode, but a temperature-control unit must be used and the heater power suitably monitored.

To test the utility of this approach, we constructed gold-plated silver casts of the intertidal limpets *Acmaea scabra* and *Acmaea digitalis* (Gastropoda) with heaters and thermocouples for S. E. Johnson's study (Chapter 31, this volume). Figure 16.4 shows data that Johnson obtained in the field. The site was a protected cove on the Hopkins Marine Station grounds which had very turbulent and unpredictable wind flow with 90–180° fluctuations in wind direction and comparable velocity fluctuations. There is little correlation between the wind velocity at the apex of the shell and the convection coefficient (Reynolds number and Nusselt number do not correlate), although the data are not inconsistent with wind-tunnel results (dashed line). This is a feature of the environment and not the technique, since the Reynolds–Nusselt number plot in Fig. 16.5, using data that Johnson took in a wind tunnel with a cast replica of the rock surface for the wind-tunnel floor, shows good results. The instruments and methods used were otherwise identical for both sets of data.

Figures 16.4 and 16.5 clearly show that, had the convection coefficient been determined from wind-velocity measurements and the wind-tunnel Re–Nu plot (Fig. 16.5), the convection coefficient would frequently have been 40 or 50 percent in error from the actual field convection coefficient (Fig. 16.4). Although some additional effort is required to construct the casts, the equipment is as easy to use as a conventional heated thermometer anemometer.

The Model: Time-Dependent Solutions

Abrupt Change in Microclimate

We defined the parameters T_e , T_Δ , and I for both furred and naked animals with and without conduction to the ground in Eqs. 5–7 and 10–13. The application of Kirchhoff's law to any of the thermal circuits in Fig. 16.1 results in two or three

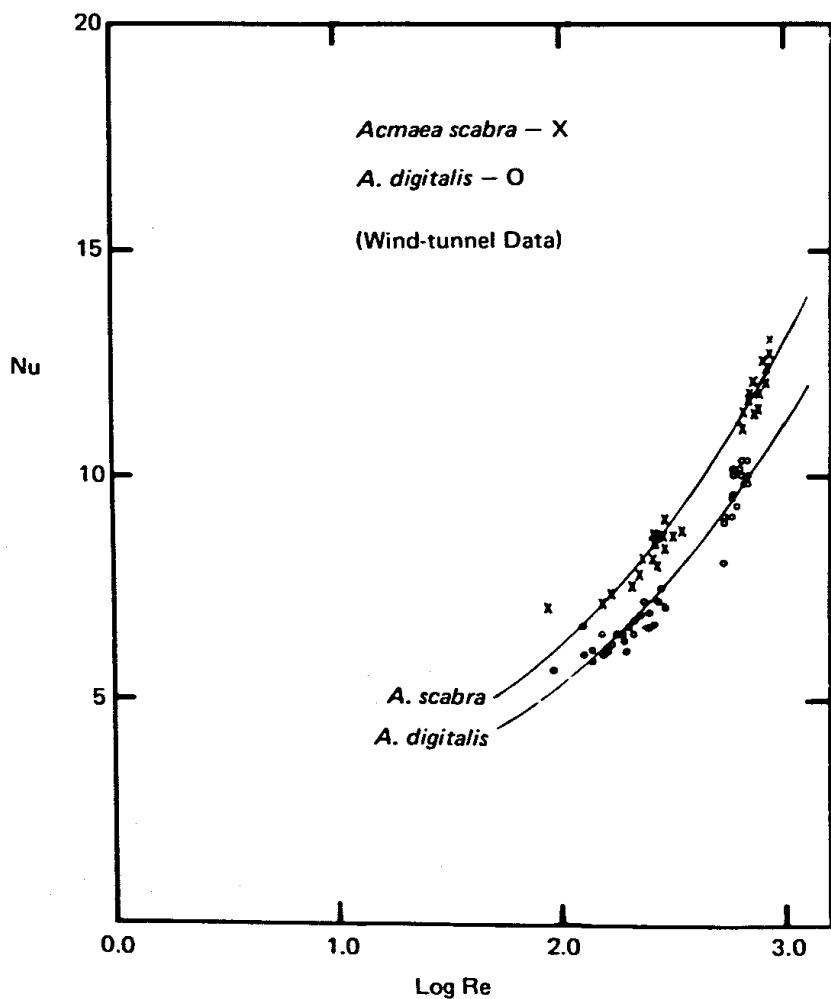


Fig. 16.5. Plot of Reynolds number–Nusselt number data taken from gold-plated casts of the shell of two species of intertidal limpets (Gastropoda). Note that Nu and Re correlate well under stable wind-tunnel conditions. A plaster replica of the natural rock substrate was used as the floor of the wind tunnel to duplicate the natural level of turbulence in the air flow at the surface. The Reynolds number was determined as in Fig. 16.4.

simultaneous equations equivalent to Eqs. 2a and 3 for circuit 1A. All but one of the equations are strictly algebraic, and thus the set may be reduced to a single ordinary differential equation. The proper definition of T_e , T_Δ , and I for each case represented by the various circuits in Fig. 16.1 allows the resulting differential equation to be written in the same form for all cases:

$$\frac{dT_b(t)}{dt} + \frac{T_b(t)}{IC} = \frac{T_e + T_\Delta}{IC} \quad (18)$$

Equation 18 may be solved by expressing T_e and T_Δ as time-dependent functions that describe the environment and the animal's physiological response.

The most useful solution is obtained for the case where an animal of body temperature $T_b = T_e + T_\Delta$ moves into a new microclimate ($T_e \rightarrow T'_e$) and changes

its physiological state ($T_\Delta \rightarrow T'_\Delta$) and allows its body temperature to vary with time [$T_b \rightarrow T_b(t)$] until a new equilibrium temperature $T'_b = T'_e + T'_\Delta$ is reached as $t \rightarrow \infty$. This corresponds to shuttling behavior in an ectotherm or a heating-cooling-curve experiment on an ectotherm. The situation is equivalent to a resistor-capacitor discharge in electronics and would be expected to show a simple exponential decay. This is indeed the case, as applying the boundary conditions $T_b(t=0) = T_e + T_\Delta$ and $T_b(t \rightarrow \infty) = T'_e + T'_\Delta$ gives the solution

$$T_b(t) = (T'_e + T'_\Delta) + [(T_e + T_\Delta) - (T'_e + T'_\Delta)]e^{-t/\tau} \quad (19)$$

where the time constant $\tau = IC$. The time constant is the simplest (in a mathematical sense) description of the response of a system showing exponential behavior, and is numerically the time required for $(1 - 1/e) \cong 63$ percent of the total change to occur.

Shuttling Between Two Microclimates

This time-dependent solution is applicable to shuttling behavior, where an animal has access to two microclimates with corresponding activity states. In the hotter microclimate, the equilibrium body temperature is denoted $T'^h_b = T'_e^h + T'_\Delta^h$, and in the colder microclimate, the equilibrium body temperature is denoted $T'^c_b = T'_e^c + T'_\Delta^c$. The animal has a range of preferred body temperatures with upper and lower set points for thermal responses. We may denote the upper set point by T_b^h and the lower set point by T_b^c , and assume that both values lie between T'^h_b and T'^c_b . As a first approximation to real behavior, we may assume that the behavior is purely thermoregulatory with minimum activity. Then the animal will remain in the colder microclimate until $T_b(t) = T_b^c$ and then move into the warmer microclimate. When $T_b(t) = T_b^h$, the animal will return to the cooler microclimate, completing the cycle. This behavior is diagrammed in Fig. 16.6.

This type of behavior may be approached analytically by using Eq. 19 to compute the body temperature as a function of time in each microclimate or the total time that can be spent in each microclimate as a function of the set points and the microclimate parameters. Equation 19 may be rewritten in the form

$$T_b(t) = T_b^h + (T_b^c - T_b^h)e^{-t/\tau_h} \quad (19a)$$

for the animal in the warmer microclimate. The elapsed time when $T_b(t) = T_b^h$ and the animal returns to the cooler microclimate is

$$t_h = -\tau_h \ln \frac{T_b^h - T_b^c}{T_b^c - T_b^h} \quad (20)$$

A similar calculation may be done to find the time spent in the cool microclimate, with the result

$$t_c = -\tau_c \ln \left(\frac{T_b^c - T_b^h}{T_b^h - T_b^c} \right) \quad (20a)$$

In practice the animal will not be concerned solely with thermoregulation, and other considerations will result in behavior that is less regular. Cabanac and

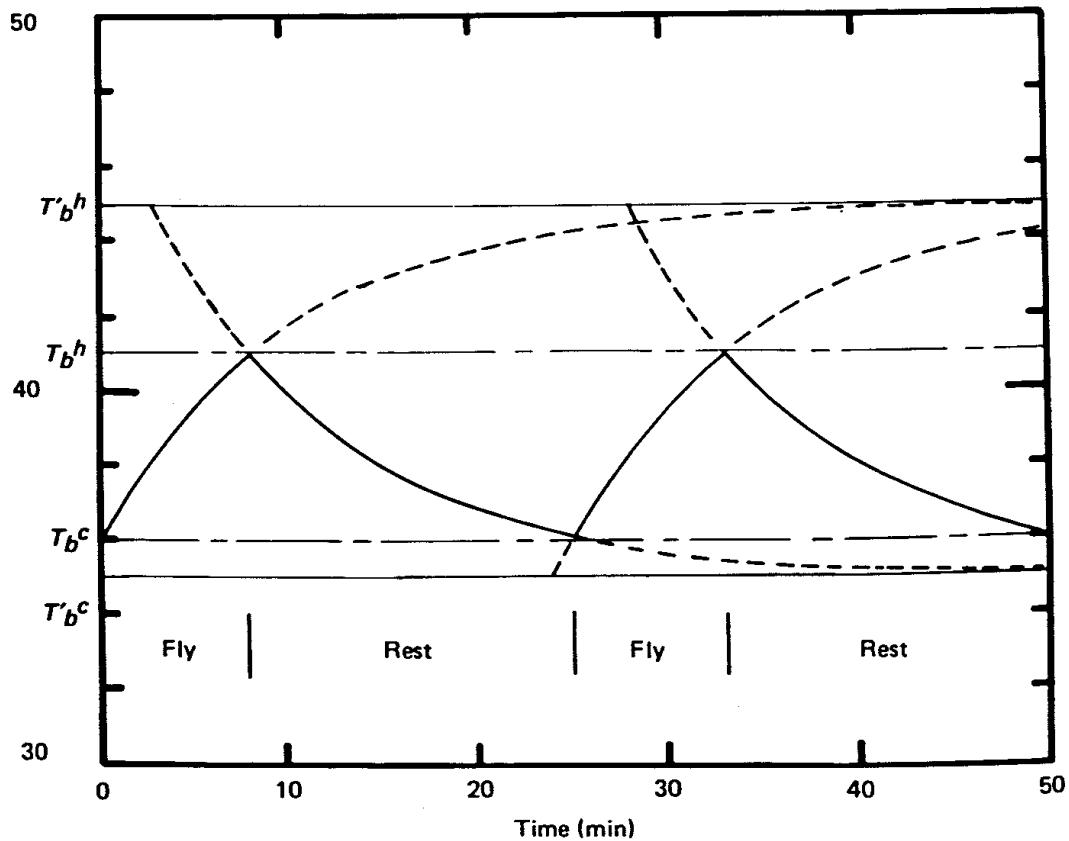


Fig. 16.6. Plot of body temperature T_b against time for idealized shuttling behavior. The upper and lower set points for body temperature are T_b^h and T_b^c . The equilibrium body temperature in the hot environment is T_b^{h*} and, in the cold environment, T_b^{c*} . The legend indicates the activity state for a hummingbird shuttling in response to hot conditions as described in the text.

Hammel (1971, Fig. 1) and Hammel *et al.* (1967, Fig. 1) show laboratory shuttling behavior in the lizard *Tiliqua scincoides*.

The most obvious condition besides thermoregulation that would influence the behavior of a shuttling animal is the presence of a food resource in either a hot or cold microclimate. The animal might then be concerned with maximizing the time available in whichever microclimate contained the food resource. To study this case, a duty cycle \mathcal{D} may be defined which gives the percentage of total active time that may be spent in the food-containing microclimate as a function of the microclimate and physiological parameters. For the case with the resource in the warm environment,

$$\mathcal{D}_h = \frac{\Delta t_h}{\Delta t_h + \Delta t_c} \quad (21)$$

and for the food resource in the cold environment,

$$\mathcal{D}_c = \frac{\Delta t_c}{\Delta t_h + \Delta t_c} \quad (21a)$$

Since the time spent in each part of the environment and the duty cycle depends on the choice of T_b^h and T_b^c , a wide range of strategies is possible. The duty cycle for the time spent in the hotter environment is a maximum for T_b^c just slightly less than T_b^h , but the duration of each excursion approaches zero. Since food-gathering efficiency often increases with the length of each excursion, optimizing strategies exist for maximum foraging per unit time under any given set of T_b^h , T_b^c , T_b^{sh} , and T_b^{sc} . These strategies may well be employed by lizards, turtles, and other animals, so this sort of analysis is of considerable utility in understanding the details of shuttling behavior and its effect on foraging.

The study of shuttling behavior by thermal modeling is not restricted to the study of ectotherms. Many endotherms show a labile body temperature and use it to facilitate excursions into conditions that cannot be tolerated for an extended period of time. For a large animal such as a camel, the "shuttling excursion" can even be all day (Schmidt-Nielsen, 1964).

In some cases a detailed study of the thermal energy budget, including behavioral aspects such as shuttling, is required to answer such ecological questions as that which relates to the nature of the limiting factor on an organism. One possible study is suggested by a study of Stiles (1971) on the time budget of Anna's hummingbird, *Calypte anna*. Stiles noted that the percentage of total time spent flying decreased as both the air temperature and the black-bulb temperature (which roughly indicates the amount of solar radiation present) increased. The percentage of total time spent flying, in fact, was almost the same on different days with essentially the same air temperature and radiation (black-bulb temperature) conditions, although the partitioning of activities during flight was very different. On days during the breeding season a large fraction of the flight time was spent in territorial defense; during the nonbreeding season most of the flight time was devoted to feeding (Stiles, 1971, Fig. 1).

The agreement of the total percentage of the time spent flying despite rather different biological behavioral requirements suggests that the hummingbird experienced excessive heat stress due to high air temperature and radiation combined with high metabolic heat production while flying. To remain active, the hummingbird apparently used a shuttling strategy, as diagrammed in Fig. 16.6.

It is possible to use data from the literature for several species to evaluate Eqs. 19-21, and the results (see Fig. 16.6) are also consistent with this interpretation. However, attempting to interpret data from several different species of hummingbird and the microclimate significance of the temperature of a test tube of unspecified size, "painted with flat black enamel, placed in full sun and out of the wind" (Stiles, 1971), is dubious at best.

Alternatively it may be argued that nighttime temperatures, and consequently thermoregulatory demands on metabolic reserves, are covariant with daytime temperatures, and that less flight time was needed to obtain food on hot days. The difference between feeding time during the breeding and nonbreeding season could be ascribed to the more abundant food resources available during the breeding season, and the very close agreement in total flying time could be fortuitous.

Simple regression-type analysis would probably confirm both hypotheses, and thus this study illustrates a case in which a complete thermal- and food-energy-

budget analysis is required to understand the actual ecological factors influencing the behavior of an animal.

General field studies of the thermal aspects of shuttling, foraging, time budgets, and behavior are complicated by the wide range of T_e values in the environment noted earlier. It will be necessary to have a fairly complete map of the T_e values in the study area to understand this class of problems fully, and apply Eqs. 19-21 to separate thermoregulatory from other behavior. The use of casts as " T_e thermometers" is probably the only economical method of making such a map.

Metabolism and Cooling-Curve Experiments

A common experiment in the study of the physiological ecology of ectotherms is the heating-cooling-curve experiment. This experiment normally consists of equilibrating the animal at one temperature and then placing it in a hotter or colder environment and monitoring the body temperature until it reaches a new equilibrium. The curve is then evaluated using Newton's law of cooling, usually in the form

$$\frac{dT_b(t)}{dt} = -\frac{1}{IC} [T_b(t) - T_A] \quad (22)$$

where T_A is the "ambient" temperature, usually taken to be the air or wall temperature of the enclosure where the heating or cooling takes place. The usual parameter determined is the "cooling constant" or conductance $1/I$, expressed in a variety of units.

Several inaccuracies are associated with this procedure, as can be seen by writing Eq. 18 in the same form:

$$\frac{dT_b(t)}{dt} = -\frac{1}{IC} [T_b(t) - (T'_e + T'_\Delta)] \quad (22a)$$

First, as indicated by Eqs. 6 and 11, the insulation I or thermal conductance $1/I$ is not a constant of the animal but depends greatly on the variable environmental factors that determine H , R , and G' . The resulting errors are significant, as Tracy (1972) has discussed. In addition to his comments on convection (H) and radiation (R), I wish to point out that conduction to the substrate may often be the dominant mode of heat loss, so that any variation in the nature of the substrate may create serious errors. Spray and May (1972) found that the rate of heating and cooling of a turtle (*Chrysemys picta*) differed by 32 percent, depending on the clay content of the substrate. This large difference indicates that conduction to and through the substrate was a major avenue of heat transfer. However, the type, thickness, temperature, and thermal conductivity of the substrate is rarely specified in cooling-curve experiments.

Second, note that the endpoint temperature for the cooling or heating curve is not the air or surface temperature or even the operative environmental temperature, but the sum of the operative environmental temperature T'_e and the physio-

logical offset temperature T'_Δ . If the data are plotted using T_a or T'_e as the endpoint T_A , any T'_Δ resulting from metabolic heat production or evaporative water loss will produce further error in the determination of I . This correction was noted for metabolic heat production by Bartholomew and Tucker (1963), but the effect of evaporative water loss was not noted. Their method of correcting I was to take the slope of the semilog plot from the usual method of plotting $T_b - T_a$ and apply the correction to the resulting value of I . This involves the extrapolation of a curved line and is subject to inaccuracy. The proper procedure is to determine the true endpoint $T_e + T_\Delta$ by letting the animal come to thermal equilibrium and taking the resulting equilibrium body temperature as the endpoint, rather than T_A or T'_e . The semilog plot will then always give a straight line unless T'_e or T'_Δ varies during the experiment.

Thus far in the analysis we have assumed that M , E_b , and E_r are constant, with the consequence that they affect the endpoint temperature and the rate of change of body temperature dT_b/dt but, with proper data analysis, do not affect I or τ . However, the metabolic and evaporative water-loss rates normally depend on body temperature, typically in an exponential fashion. Spotila *et al.* (1973) have noted that a body-temperature-dependent metabolic rate or evaporative water-loss rates will affect I and τ . Strunk (1971) reached the same conclusion, but confused the time constant τ with the rate of change dT_b/dt and made numerous serious calculational and interpretive errors which largely invalidate his work (Bakken and Gates, 1973).

The effect is qualitatively as follows. For M , E_b , E_r , and E_s constant, T'_Δ will be constant at a fixed value determined by the heat-transfer characteristics of the animal and the environmental conditions. However, when any of the M and E parameters depend on T_b , the endpoint body temperature, $T'_b = T'_e + T'_\Delta$, will change during the heating or cooling process, and approach ($dT'_\Delta/dT_b < 0$) or recede from ($dT'_\Delta/dT_b > 0$) the body temperature as it attempts to reach equilibrium.

For example, in a heating-curve experiment, the body temperature will increase at a rate appropriate to a simple constant endpoint, $T'_b = T'_e + T'_\Delta$, with M and E 's having the values appropriate to the initial body temperature. However, for $0 < dT'_\Delta/dT_b < 1$, the endpoint temperature T'_b will steadily increase to a final equilibrium value T'^{eq}_b since T'_Δ increases with the increase of net metabolic heat production. Since the rate of change of body temperature initially will correspond to a low temperature difference, $T_b(t) - T'_b < T_b(t) - T'^{eq}_b$, it will take longer for the body temperature to come to equilibrium than if the large value of T_Δ corresponding to T'^{eq}_b were present initially. The result is that the animal will appear to have a time constant larger than IC when $\log [T_b(t) - T'^{eq}_b]$ is plotted against time.

The exact details of the behavior of T_b will depend on the rate of increase of T'_Δ with T_b , dT'_Δ/dT_b . The case just described assumes that $0 < dT'_\Delta/dT_b < 1$. If $dT'_\Delta/dT_b = 1$, the body temperature will increase at a constant rate until heat death results. If $dT'_\Delta/dT_b > 1$, T'_Δ increases faster than T_b , the body temperature will increase at an increasing rate, corresponding to explosive heat death. If $dT'_\Delta/dT_b < 0$, the body temperature will equilibrate more rapidly than for a positive or constant value of dT'_Δ/dT_b , and the time constant will appear smaller than IC .

The situation where the animal is cooling ($dT_b/dt < 0$) may be similarly analyzed, with the same result: $dT'_\Delta/dT_b > 0$ increases τ and $dT'_\Delta/dT_b < 0$ decreases τ .

In general, the dependence of T_Δ on T_b will be exponential. An analytic solution is possible for this case, but it is much simpler and more instructive to consider the case where the net metabolic heat production ($M - E_b$) is linearly dependent on T_b while E_s and E_r remain constants. For this case we take some body temperature $T_b = T_p$ as a linearization point and form the T_b dependence of ($M - E_b$) as follows:

$$M - E_b = (M - E_b)_p + P(T_b - T_p) \quad (23)$$

where $(M - E_b)_p$ is the value of $(M - E_b)$ at $T_b = T_p$, and $P = d(M - E_b)/dT_b$.

The term $P(T_b - T_p)$ has the same mathematical form as the conductive and convective heat-transfer terms in the equations that result from applying Kirchhoff's law to the circuits in Fig. 16.1a-c. Thus the variable metabolism term $P(T_b - T_p)$ may be regarded as placing a fictitious negative conductance $-P$ (a negative conductance is equivalent to an amplifier), connecting T_b with a heat source of temperature T_p , as diagrammed in Fig. 16.1d and e. A real conductance of this sort would be expected to change the insulation and thus the time constant, so the mathematically equivalent metabolic heat production dependent on body temperature would be expected to do the same.

For the most general case where the animal has pelage, Kirchhoff's law may be applied to the diagram in Fig. 16.1e to give three equations, which may be solved simultaneously as before. The solution may be arranged as in Eqs. 9 and 19, but the parameters, T_e , T_Δ , and I assume apparent values that differ from the body-temperature-independent-metabolism cases in Eqs. 11-13. These apparent values will be denoted by a superscripted a . The apparent insulation is

$$I^a = \frac{K_{sf} + H + R}{(K_{sf} + G' - P)(H + R) + K_{sf}(G' - P)} = \frac{I}{1 - IP} \quad (24)$$

where I is as given by Eq. 11. Further,

$$T_e^a = \frac{K_{sf}(HT_a + Q_n) + G'T_g(K_{sf} + H + R)}{(K_{sf} + G' - P)(H + R) + K_{sf}(G' - P)} = \frac{T_e}{1 - IP} \quad (25)$$

$$\begin{aligned} T_\Delta^a &= [(M - E_b)_p - PT_p]I^a - E_s \frac{K_{sf} + [K_s/(K_s + K_f)](H + R)}{(K_{sf} + G' - P)(H + R) + K_{sf}(G' - P)} \\ &\quad - E_r \frac{K_{sf}}{(K_{sf} + G' - P)(H + R) + K_{sf}(G' - P)} \\ &= \frac{(T_\Delta)_p}{1 - IP} - PT_p I^a \end{aligned} \quad (26)$$

Here $(T_\Delta)_p$ is T_Δ evaluated at $T_b = T_p$.

From Eq. 24 we can clearly see that when $(M - E_b)$ increases as T_b increases (i.e., $P > 0$), I^a will be increased, increasing $\tau^a = I^a C$, as was argued qualitatively. For $M - E_b$ decreasing as T_b increases, $P < 0$ and I^a and τ^a are reduced. Explosive

body-temperature rise and heat death occur when I^a , and thus τ^a , become negative, so the exponent in Eq. 19 becomes positive. This occurs when

$$P \geq \frac{(K_{sf} + G')(H + R) + K_{sf}G'}{K_{sf} + H + R} = \frac{1}{I} \quad (27)$$

For a nonfurred animal, K_{sf} in Eq. 10 reduces to the skin conductivity K_s . Since K_s is much greater than K_f or K_{sf} , a much larger positive P is required to produce explosive heat death than for a furred animal. Thus an animal insulated with pelage is much more sensitive to the effects of a metabolic rate dependent on body temperature than a naked animal, a fact that is of general importance to the evolution of endothermy as well as its simple application to explosive heat death.

The values of the parameters were earlier indicated to be apparent rather than actual values. The situation can be clarified by considering an animal with body-temperature-dependent net metabolic heat production in thermal equilibrium with $T_b = T_b^{eq}$. Then the net metabolic heat production is indistinguishable from that of an animal with a constant net metabolic heat production $(M - E_b)^{eq} = (M - E_b)_p + P(T_b^{eq} - T_p)$. Since the metabolic rate is constant, Eqs. 11–13 apply, with Eq. 13 having the form

$$\begin{aligned} T_b^{eq} &= [(M - E_b)_p + P(T_b^{eq} - T_p)]I - E_s \frac{K_{sf} + [K_s/(K_s + K_f)](H + R)}{(K_{sf} + G')(H + R) + K_{sf}G'} \\ &\quad - E_r \frac{K_{sf}}{(K_{sf} + G')(H + R) + K_{sf}G'} \end{aligned} \quad (13b)$$

Then the equilibrium body temperature is

$$T_b^{eq} = T_e + T_\Delta^{eq} \quad (28a)$$

$$= T_b^a + T_\Delta^a \quad (28b)$$

where Eq. 28a uses the terms in Eqs. 11, 12, and 13, and Eq. 28b uses the terms in Eqs. 24–26. The two expressions for T_b^{eq} may be shown to be formally identical by solving Eq. 28a, which contains T_b^{eq} on both the right and left sides of the equal sign, for T_b^{eq} . The resulting expression is identical with Eq. 28b. Thus there is no conflict between the solutions in the steady-state case. However, the measured values of the parameters τ and I will differ depending on whether the measurement is made by a steady-state method (Eq. 13a) or cooling-curve analysis.

The problem presented by the apparent values of T_Δ^a , T_e^a , and I^a may be simplified somewhat and the effect of body-temperature-dependent net metabolic heat production clarified with the aid of the discussion above, which shows the identity of the body-temperature-dependent and constant $M - E_b$. Recall that the time-dependent solution for a sudden change of environment and activity level was equivalent to Eq. 19 and, in the present case,

$$T_b(t) = (T_e^a + T_\Delta^a) + [(T_e^a + T_\Delta^a) - (T_e^a + T_\Delta^a)]e^{-t/\tau^a} \quad (19b)$$

where $\tau^a = I^a C$. Since both the initial and the final conditions represent thermal equilibrium, net metabolic heat production is constant in both T_Δ and T'_Δ . Then the equivalent expressions of Eqs. 28a and 28b may be used to rewrite Eq. 19a as

$$T_b(t) = (T_e^a + T_\Delta^{eq}) + [(T_e^a + T_\Delta^{eq}) - (T_e^a + T_\Delta^{eq})]e^{-t/\tau^a}$$

or

$$T_b(t) = T'_b^{eq} + (T_b^{eq} - T'_b^{eq})e^{-t/\tau^a} \quad (19c)$$

The cooling curve of an animal with net metabolic heat production dependent on body temperature, when plotted with respect to the final equilibrium body temperature T'_b^{eq} as suggested for the constant-metabolism case, gives just a straight line in the usual semilog plot. However, the slope of the line corresponds to the apparent time constant τ^a . The apparent insulation $I^a = I/1 - IP$ thus will differ from the values measured by a cooling-curve experiment on a dead, non-evaporating animal or determined by a steady-state measurement of metabolic rate versus metabolism chamber temperature on a live animal. The effect of body-temperature-dependent net metabolic heat production may be summarized as follows:

1. The equilibrium body temperature T_b^{eq} for a given set of conditions will be a function of the relation of the net metabolic heat-production temperature coefficient P to the various thermal conductivities for the various heat loss pathways, as given by Eq. 28b.
2. The metabolism coefficient P acts as a negative conductance or amplifier of body-temperature variations for $P > 0$. $P > 0$ implies that net metabolic heat production increases with a T_b increase.
3. The net effect of $P > 0$ is to decrease the denominator of Eqs. 24–26 and thus to increase the apparent insulation I^a , time constant τ^a , and the total amount of change in T'_Δ resulting from a given change in environmental conditions $T_e \rightarrow T'_e$. The combined increase in the total temperature change and in the time constant will increase the time required for the animal to come to a new equilibrium body temperature in response to a change in environmental conditions.
4. The conditions for explosive heat death, where T_b increases at an increasing rate, corresponds to the time constant becoming negative. This occurs when $P > 1/I$.
5. The effects of body-temperature-dependent metabolic heat production are augmented by small values of K_{sf} and G' , that is, in a well-insulated animal. This requires a well-insulated animal such as a bird or mammal to maintain $M - E_b$ essentially constant by adjusting evaporative water loss to offset M . (In a more complete analysis it can be shown that cutaneous water loss E_s and E_r can be used as well as E_b , but the analysis is greatly complicated.)

Metabolism, Cooling Curves, and the Evolution of Thermoregulation

The question of the evolution of thermoregulation has been one of considerable interest, and has resulted in a great deal of speculation and argument. However, most of the thermoregulatory organs involve soft tissues that are rarely preserved in the fossil record. Consequently, the majority of hypotheses for the mode of evolution of thermoregulation by endothermic means have rested on analogy with highly evolved living forms. This procedure is fraught with considerable hazard,

since, unlike the laws of physics, chemistry, and most processes of geology, uniformitarianism cannot always be assumed with respect to the physiology of animals. This is a consequence of the applicability of uniformitarianism to some of the fundamental aspects of biology, specifically genetics, selection, and the continued process of evolution.

Generally we wish to suggest that a more profitable approach might be based on principles where uniformitarianism may be assumed more safely. Thus we would base speculation about the evolution of endothermy on the physics of heat transfer, biochemical processes, and general physiological processes that need not be considered specific to one phyletic line. This necessarily involves model building and analysis, and the thermal-energy-budget theory such as we have outlined here is immediately applicable. The particular power of the model-building approach is that it need not be restricted to consideration of organisms with living prototypes, but allows consideration of hypothetical animals that possess morphological structures and combinations of properties not present in existing forms.

The proper execution of a study of this nature requires the careful analysis of the various processes of heat transfer and the physiology of thermoregulation as seen in living forms that possess features to be included in the model animal. It requires careful synthesis of the hypothetical animals to be investigated. Here we can sketch only the simplest sort of analysis of this type, but we think it gives some interesting insights into some pathways of evolution of endothermy, differing somewhat from present speculation.

The dynamics of cooling and the results of cooling-curve studies have often been related to the evolution of endothermy. Generally the concept has been that the initial steps toward homeothermy occurred to prolong the time that an animal could spend at its preferred body temperature for activity or digestion (Bartholomew and Tucker, 1963). The ability to control the rate of heat gain and loss would allow an animal with, for example, a high preferred body temperature to warm quickly and cool slowly, thereby increasing the time spent at the preferred body temperature. This is shown in Eqs. 19-21, where a large τ_c and a small τ_h would give a longer duty cycle in the cold environment. As noted in the preceding section, body-temperature-dependent net metabolic heat production results in effective time constants τ^a that differ significantly from the constant metabolism value $\tau = IC$. This effect should be included in any discussion of this path for the evolution of endothermy.

The usual hypothesis (Bartholomew and Tucker, 1963; Dawson and Hudson, 1970) is that a slow elevation of the basal metabolic rate resulted in an increased capacity to control the rate of change of body temperature. This was amplified by vasoconstrictive control of I and hence τ . Further evidence cited for this mode of evolution of endothermy is provided by the ontogeny of endothermy in altricial animals (principally rodents and birds), where a thermoregulatory capability is shown in metabolism chamber experiments before effective insulation develops in the form of pelage (Dawson and Hudson, 1970; Dawson and Evans, 1960). Finally, it has been suggested (Gunn, 1942; Cowles and Bogert, 1944; Cowles, 1958; Bartholomew and Tucker, 1963) that insulation in the absence of significant metabolic heat production would be maladaptive since it would slow the rate of warming

of animals with a high preferred body temperature and, especially in a cold seasonal climate, prevent the attainment of adequately high body temperature.

Although widely accepted, these arguments are by no means unassailable, even on biological grounds. First, it is not clear that the basal metabolic rate is the primary factor in homeothermy. The response of birds and mammals to cold stress includes a large component of muscular thermogenesis by shivering. The most obvious difference between birds and mammals and lower vertebrates is the presence of nonshivering thermogenesis; nevertheless, shivering thermogenesis certainly is the logical candidate as the primitive mechanism since it is available more widely and has been observed in reptiles, notably breeding pythons (Vinegar *et al.*, 1970). By far the most spectacular example of endothermy in the absence of a high basal metabolic rate is the intermittent endothermy of the flight muscles in several orders of insects, notably the sphingid moths (Heinrich, 1971).

The ontogenetic arguments based on the development of altricial birds and animals are also misleading since these animals, at the time of the onset of thermo-regulatory behavior, are normally well insulated by the nesting material provided by the parents, and typically several young form a thermal unit in the nest with a higher aggregate heat production than a single individual. Endothermy is a much more economical proposition under these conditions than when the young animals are fully exposed outside the nest in a metabolism chamber. The thermoregulatory behavior seen under metabolism conditions is probably a laboratory artifact representing an emergency reaction to unusual conditions that would very likely be ruinously expensive in metabolic cost as a routine strategy.

The argument for the maladaptive value of fur for reptiles is generally based on heliothermic desert lizards, who typically maintain a high active body temperature by behavioral means (Cowles and Bogert, 1944; Heath, 1964, 1965; Brattstrom, 1965). Operative temperatures in the preferred range of body temperatures for basking lizards, 35–42°C, exist only during the daylight hours when Q_a is large enough to produce an operative environmental temperature substantially greater than air temperature (see Eqs. 7 and 12). A short time constant is necessary to allow T_b to reach the preferred value while such operative temperatures are available. However, an animal with a lower preferred body temperature, in the 20–30°C range, would find exposure to the operative temperatures present in full sun highly stressful.

Many groups of animals with primitive characteristics show such a low preferred body temperature. Brattstrom (1965) lists the mean active body temperature of various reptile groups. Turtles have T_b around 28.4°C, but this depends on the group and can be considerably lower. Snakes have a mean T_b of 25.6°C and lizards as a whole, including nondesert groups, have a mean T_b of only 29.1°C, with the Gekkonidae, Anguidae, and Xantusidae all below 25°C. The rhynchocephalian *Sphenodon punctatum* has a very low active body temperature, somewhat below 20°C. Finally, the monotremes, which are the most primitive mammalian group, have a very low upper temperature tolerance, with thermoregulation failure at an air temperature of approximately 30°C. In particular, the platypus, *Ornithorhynchus anatinus*, suffers heat stress for a metabolism chamber temperature (roughly equal to T_e) above 25.0°C (Smyth, 1973). Most of these groups have ecological specializa-

tions that may disqualify them from being obviously better models of therapsids than heliothermic lizards. However, when considered with the low preferred body temperatures of most amphibians, it seems as reasonable to postulate a low ($20\text{--}30^{\circ}\text{C}$) body temperature for therapsids as the high ($35\text{--}40^{\circ}\text{C}$) value derived from heliothermic lizards.

With this assumption, it is more reasonable to suppose, as did Cowles (1940, 1946), that the evolution of insulating pelage preceded endothermic thermoregulation as a defense against heat stress induced by solar radiation. As a result of its large time constant, a well-insulated animal with limited net metabolic heat production would assume a mean body temperature near the daily average operative environmental temperature (Spotila *et al.*, 1973), thus escaping the stress of large daily body-temperature fluctuations. This is undoubtedly an adaptive benefit, since the selection of a constant body temperature is far more widespread than the selection of a high body temperature. This adaptation would be of particular value to a large, slow-moving animal living in an exposed habitat with little shade. In this case good body insulation giving a very long time constant would protect the animal from overheating while foraging in the direct sunlight all day.

A contemporary model would be the land tortoise *Gopherus* and the box turtle *Terrapene*. These animals often forage exposed to the sun but are rather slow moving and cannot escape to shade quickly by flight or rapid digging. Spray and May (1972) have shown that *Gopherus polyphemus* and *Terrapene carolina* use the reverse strategy in controlling their heating and cooling rates from that described earlier for lizards. Because of the problem associated with heat stress, they adjust their circulation to minimize the heating rate and maximize the cooling rate, so that they may maximize the time available for foraging in the sun. The capacity for altering the rate of heat transfer is quite as remarkable as that reported for the Galapagos marine iguana, *Amblyrhynchus cristatus* (Bartholomew and Lasiewski, 1965). *T. carolina* cooled twice as fast as it heated, whereas *A. cristatus* heated twice as fast as it cooled. *G. polyphemus* cooled about $1\frac{1}{2}$ times as fast as it heated. The insulation provided by the shell of the turtles is a significant factor in rejecting solar radiation, since it may be heated above the temperature that would injure living tissue. Not only does it add insulation to that possible by vasoconstriction, but it also allows vasoconstriction to reduce K to values that would result in surface temperatures exceeding the injury value if the tissue did not have the extra protection.

Summing up the preceding argument, we are suggesting that a proto-mammal might have evolved some form of hair as a protection against solar radiation, as suggested by Cowles (1940, 1946). The insulation evolved as a solar radiation shield would then be a preadaptation which allows a relatively minor increase in metabolic heat production to result in an adaptively significant T_{Δ} . When the animal was subjected to cold stress as well as heat stress, which would occur in a seasonal midlatitude or "temperate" climate, selection for increased metabolic heat production could act to produce a recognizably mammalian form. The increased metabolic heat production would most probably have been muscular activity since an elevated basal rate would result in heat stress under warm conditions.

One possible objection is that, under warm conditions, the metabolic heat

generated by normal locomotor activity of an insulated animal would also elevate T_b , producing heat stress. If an initially reptilian metabolism with a low overall rate and dependence on anaerobic metabolism for bursts of activity is assumed, the average rate of heat production will be low enough that evaporative cooling by panting or saliva spreading could reduce the net heat production to an essentially zero or even negative (net evaporative cooling) value. These mechanisms are well developed in many reptiles, including crocodilians, lizards, and turtles, for dealing with an external heat load. Evaporative cooling mechanisms would presumably be a necessary preadaptation to allow the animal to enter hot, high-radiation environments that would provide subsequent selection for insulation. As an example, the wool insulation in sheep, which use panting as the primary mechanism for evaporative cooling, decreases the heat load significantly in the presence of strong solar radiation (Yeats, 1967).

As we suggested earlier, the effect of body temperature on metabolic rate must be considered in connection with the evolution of endothermy. This can be illustrated by the following hypothetical animal and thermoregulatory behavior.

The animal is assumed to have evolved some form of insulation in response to strong solar radiation, as suggested by Cowles (1940, 1946). The animal is also assumed to have an essentially reptilian metabolism with a low capacity for aerobic metabolism and a consequent dependence on anaerobic metabolism for activity. The endogenous heat production that results from activity would be small and could be easily dissipated by panting and saliva spreading. During cooler conditions, the animal would not be subject to heat stress, and less evaporative cooling would be required. This would be the case during cool seasonal conditions for a large animal or cool daily conditions for a small animal.

An animal of this sort would be able to gain a selective advantage by the following strategy, which would represent an early form of endothermy. If this animal, adapted to strong solar radiation, encountered cooler conditions, the insulation would retard the rate of warming of the animal so that it would not become active until late in the day. Foraging and prey pursuit would result in the production of metabolic heat. Since the animal is in an assumed condition where only the lower part of the active body temperature range will have been obtained, it will probably not use increased evaporative cooling to offset metabolic heat production, and the body temperature will tend to remain constant or rise. The animal will be assumed to cease foraging after the end of the daylight hours as T_b falls. It will then be faced with the problem of maintaining adequate body temperature for digestion. The contemporary gecko *Gehyra variegata* models aspects of this behavior (Bustard, 1967).

This problem has been described by Cowles and Bogert (1944) for a reptile attempting to adopt nocturnal habits to escape seasonal peaks in heat stress during the day. The body temperature of a small, uninsulated animal would fall rapidly at night, and digestion would probably cease as in modern reptiles. The result could be the salmonella-type food poisoning commonly seen in reptiles maintained at excessively cool temperatures, resulting from the continued activity of microorganisms in the digestive tract. The situation would be somewhat better for the hypothetical insulated reptile. First, the larger value of the insulation I would give

a longer time constant $\tau = IC$, which would increase the time that the body temperature would be adequate for digestion. Further, since the animal would not be using evaporative cooling ($M - E_b$) and P would have positive values. The metabolic rate and heat production would be well above the standard rate, owing to digestion and assimilation. It is thus quite possible for the temperature coefficient of metabolism, P , to be significant relative to the thermal conductance of the animal, $1/I$, if the animal is somewhat insulated, as postulated. This would result in a further increase of the time constant $\tau = IC$ to $\tau^a = IC/(1 - IP)$ as discussed earlier, particularly in Eqs. 19b and 24. This further increases the time available for digestion. Because of the amplifying effect on P and I , the value of fur-like insulation on the assumed proto-endotherm is thus greater than is evident when only the effect of insulation on the simple time constant IC and the temperature difference T_Δ that can be maintained in steady state are considered. Physical activity during the digestive period would also tend to maintain body temperature at a level adequate for digestion.

Other scenarios of this sort can also be used to illustrate the amplifying effect of the temperature coefficient on insulation, which could lead to selection for increased insulation, increased aerobic metabolism, and ultimately endothermy as we know it. The scenario described is particularly attractive since it illustrates how selective forces resulting from falling seasonal temperatures would tend toward the nocturnality that has frequently been postulated for therapsid proto-mammals and early mammals (Jerison, 1971). The capacity for nocturnal foraging would open new niches closed to animals with a relatively high body-temperature requirement and without a usable heat-production and storage capacity.

A key feature of this scenario for the evolution of endothermy is the implied selection pressure for increased aerobic metabolism. If the hypothetical animal is assumed to be a predator, it is probable that the pursuit and capture of the prey would utilize anaerobic metabolism and result in an oxygen debt. The repayment of the debt would be complicated by the aerobic metabolism requirements of the elevated body temperature and digestion. This would result in selection for increased aerobic capacity.

Selection for increased aerobic capacity would be even greater in a sequel to the preceding scenario. The animal can be assumed to have improved his insulation and aerobic capacity somewhat in response to the selective pressures outlined above. The hypothetical animal could then forage nocturnally by using its insulation to retain the heat generated by locomotor activity during foraging, or by strictly heat-producing muscular contractions similar to the proto-shivering of breeding pythons. This would closely parallel the strategy used by sphinx moths to maintain muscular coordination during nocturnal foraging.

In addition to its thermoregulatory significance, an increased aerobic capacity would allow more activity which would be useful in foraging and escape from predators. This could be independently subject to positive selection and contribute to the evolution of increased aerobic capacity, or act as a preadaptation for the evolutionary processes outlined above.

An increase in basal metabolic rate to the level associated with contemporary mammals would result if it is assumed that the scope of aerobic metabolism is

limited so that an increase in active metabolism results in an increase in basal aerobic metabolism. The increase in active aerobic metabolic capacity would thus be the key to endothermy and the elevated basal metabolic rate seen in mammals and birds. W. R. Dawson (private communication) has also suggested that an increase in active aerobic metabolism led to endothermy, and this mechanism is implied in the work of Heath (1968), Bakker (1971), and McMahon (1973).

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Appendix: Construction of Hollow Metal Casts of Small Reptiles and Amphibians

The process for constructing hollow metal casts of small reptiles and amphibians is one of the variants of a process known as electroforming, a process most commonly used in preparing master molds for phonograph records, typefaces, and masters for coins and medallions. Basically, the process consists of preparing a master, usually negative, mold of conductive material or a material that may be treated to make the surface conductive. The surface is then heavily plated with copper or other suitable metal to the desired thickness and detached from the mold. Owing to the complex shape of a small animal and the difficulties inherent in plating strongly concave surfaces and assembling the resulting highly fragile separate halves of the cast, an alternative procedure commonly used in art work is preferable. The procedure is to make a positive cast of the object to be electroformed in a low-melting-point substance such as wax or a low-melting-point alloy such as Wood's alloy (melting point 70–80°C) and plating the surface to the desired thickness. This process sacrifices the fine detail possible in the negative mold process. The loss is not great because the coating may be much thinner than the desired thickness of the final cast if Wood's alloy is used, since a film of the alloy adheres to the outer electroplated layer and reinforces it after the bulk of the core has been melted out and the cast cooled. For a small (10–50 g) lizard, an electroplated copper layer of 0.04 mm is adequately rigid to withstand the process of melting out the core. The final cast is about 0.5 mm thick and thus easily handled as long as it is cooler than the melting point of the Wood's alloy. An additional advantage of Wood's alloy is that it may be cast in algin-base dental plaster, and thus live animals may be used as models. We shall now summarize the procedure.

Step 1

Prepare a molding box slightly larger than the animal. The sides should slope 10–20° from bottom to top to facilitate removal of the mold. The top and bottom should have three or four holes about 1–1.5 cm in diameter and be removable, with hooks on the sides of the box for heavy rubber bands to secure them in place when required.

The molding may be done with any of the quick-setting alginate impression materials used in dentistry. We have obtained good results with Jeltrate type I fast-set material (L. D. Caulk Co., Division of Dentsply International, Inc., Milford, Delaware 19963). The usual formulation used in dentistry does not flow easily enough; we find that a ratio of 100 ml of water to 60 ml by volume of powder, mixed for 5 s in a blender, gives better properties in this application. A blender of average size can prepare batches containing 150–300 ml of water. Larger or smaller batches do not mix well and require the simultaneous use of several blenders. Rinsing immediately after mixing a batch with cold water by blending for 20 s with the container half full greatly simplifies the following steps, since three mixes are required in quick succession.

To facilitate handling, chill or otherwise anesthetize the animal to be used as a model. While the animal is cooling, prepare a substrate layer in the molding box about 2 cm thick using the molding material. After the animal is ready and the substrate layer has set, prepare enough molding material to pour a second layer that will cover the legs, tail, and part of the back of the animal to a point just anterior to the hind legs. Proper immersion may require that the mold be tilted as shown in Fig. 16.7. Pour the molding material before immersing the animal to ensure that the ventral region will be reproduced. Immerse the animal in the molding material and force the feet and tail to the substrate layer, and allow the molding compound to set. Placing four fingertips in the material to a depth of 5–10 mm will provide "registration pins," which greatly facilitate reassembly of the mold for casting. Then the third layer is mixed and poured and the lid forced in place, with excess molding material escaping through the holes provided. The layers and position of the animal are diagrammed in Fig. 16.7. After layer 3 has

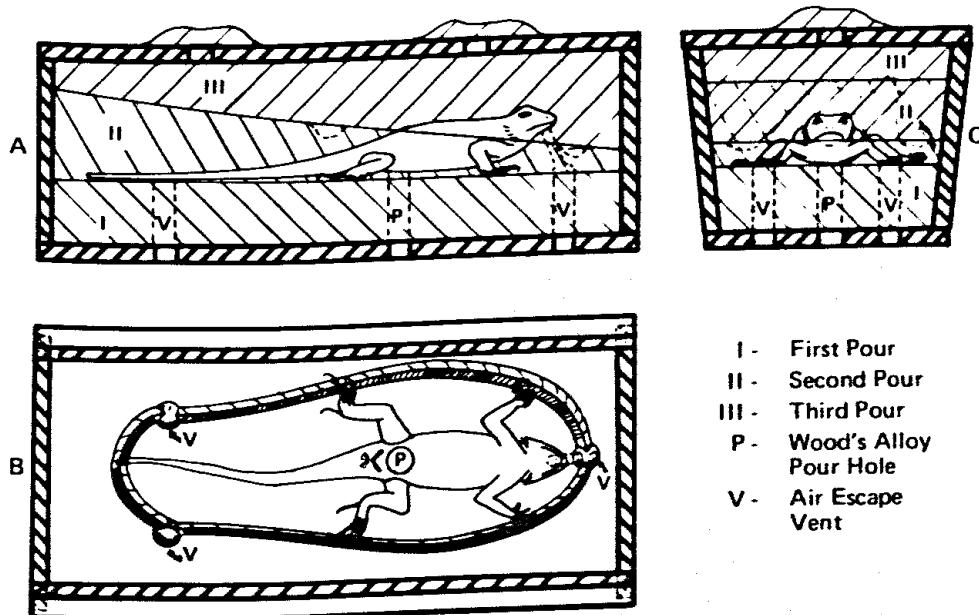


Fig. 16.7. Diagram of the molding box and arrangement of the successive layers of alginate dental investment compound for preparing a mold from a live lizard.

set, remove the lids and mold, and lift layer 3 from the posterior end until the back is exposed, and then press forward to slip the mold off the head and neck. The animal may now resume breathing. The elapsed time since immersion will vary with the speed of the investigator and the time required for the molding compound to set. The setting time is strongly dependent on the concentration of the mix and the water temperature, with quicker setting at higher concentrations of powder and higher water temperatures. Typical times will run from 2 to 6–7 min.

Separate layers 1 and 2 and locate the toes and tail on the ventral side of layer 2. Remove enough molding material from the tips of the toes to allow air to escape when the Wood's alloy is poured. Slit the mold along the ventral side of the tail and free the tail to prevent autotomy. Flex the mold and use forceps to remove the legs. The animal will usually have rewarmed by this time and will be most helpful in assisting its removal.

Step 2

Using a cork borer, make a hole through the first two layers into the ventral region of the mold to pour the alloy. Make at least two additional holes through layer 1 for vents and cut grooves in layer 2 to connect them with the toes, tip of the tail, and nose to allow air to escape during the pour as shown in Fig. 16.7. Heat the mold to 50–60°C. The best way is to boil the mold in water. Pat dry with towels and reassemble the mold in the box. A layer or two of wet paper towels under the cover will help compress the joints in the mold and minimize the amount of flash on the final cast. Melt the Wood's alloy, heat to 130–150°C, and pour slowly into the ventral opening. Immerse the mold in cold water to cool the cast to below 40°C (this usually takes about $\frac{1}{2}$ h) and remove. Trim the flash (extra metal forced into the joints in the mold and in the pour and vent holes). If the legs and tail are incomplete, the vents must be enlarged, new vents added, and/or the mold heated more before the pour. Excessive spattering during the pour or bubbles and an irregular crystalline surface on parts of the cast indicate that the alloy was too hot when poured or that it cooled too slowly. Reconstruct missing toes (it is very difficult to reproduce toes in small animals using this technique) by inserting copper wire heated with a soldering iron and coated with nonacid flux into suitably placed holes drilled in the feet and shaping to the proper length and curvature. *Caution!* Wood's alloy contains toxic heavy metals, including bismuth and cadmium, and should be melted under a hood. Gloves should be worn during trimming.

Step 3

Prepare a copper plating solution in advance. The following formulation gives good results:

Distilled water	1 liter
Copper sulfate (CuSO ₄ · 5H ₂ O)	250 g
Sulfuric acid (conc.)	75 g
Thiourea	0.005 g

Filter the prepared solution through activated carbon after preparation and before each use to remove organic impurities that cause brittle crumbly deposits. The electroplating apparatus consists of a 0 to 8-V 15-A dc power supply and a magnetic-bar stirring apparatus. Concentrations and materials are not critical. See an electroplating text such as W. Blum and G. Hogaboom (*Principles of Electroplating and Electroforming*, 3rd ed. New York: McGraw-Hill Book Company, 1949) for more details.

All traces of grease, oxide, and other nonconductive coatings must be removed from the cast by cleaning with a strong degreasing solvent such as trichloroethylene and pickling in a dilute sulfuric or hydrochloric acid solution. Just before plating, the cast should be electrocleaned in a weak acid electrolyte such as dilute sulfuric acid by connecting the cast to the negative terminal of the power supply and a stainless-steel electrode to the positive terminal. Placing the electrode and cast in the solution with about 5 to 6 V applied results in the liberation of hydrogen at the cast, which reduces any remaining oxide coating. After all trace of oxide has been removed, rinse the cast under running water and distilled water. Store in distilled water while preparing the copper plating apparatus.

Select a container large enough to immerse the cast horizontally, and cut a piece of copper sheeting with an area of twice the area of the cast to serve as the anode. The copper anode should be carefully degreased to prevent organic contamination of the plating solution and enclosed in filter paper or thoroughly washed muslin to retain the assorted bits of crud that evolve during the plating operation. Fill the beaker with plating solution, immerse the cast in the center of the container by hanging by a 20-24 AWG copper wire, and connect the cast to the negative terminal and the anode to the positive terminal of the power supply. Apply 4 to 7 V with continuous stirring until the desired thickness of plating is achieved. The exact time for a given thickness is a function of voltage and temperature. For a small lizard, 4-5 V at 30°C for 2½ h gives good results. Lumpy deposits on the nose and feet indicate that the anode is too large or the voltage too high.

Step 4

Rinse the plated cast thoroughly and neutralize any remaining acid with soap or sodium bicarbonate. Drill or grind small openings in the tip of the tail, under the nose, and in the tip of each leg. Select a beaker large enough to allow the cast to be immersed vertically, fill with water, and bring to a boil. Suspend the cast by a piece of wire and immerse vertically in the water. As the cast heats, the Wood's alloy will melt and run out the lowest opening. Gentle vertical shaking will assist in

removing the alloy, but the cast is very fragile at this point and care should be used. After the cast has cooled, the film of Wood's alloy adhering inside the copper plate will reinforce the hollow cast so that it may be handled with relative impunity. If a pure copper cast is desired, the Wood's alloy may be rubbed with powdered graphite before plating.

Step 5

The cast may now have thermocouples attached internally, the holes for draining the Wood's alloy closed, and any missing toes reconstructed by drilling small holes in the feet and inserting copper wire and fixing with Wood's alloy solder or epoxy glue. The cast may now be painted to match the solar absorptivity of the model animal and is ready for use.

In many cases it will be desirable to know the specific heat capacity of the cast to allow the measurement of the overall heat-transfer coefficient of the cast by a cooling-curve determination. The specific heat of the components differ significantly, with Cu = 0.093, Wood's alloy = 0.0352, and paint = 0.2 to 0.4 (data from C. D. Hodgman, 1962. (ed.), *Handbook of Chemistry and Physics*, 44th ed., pp. 2352, 2378, 2379, 1962, Cleaveland: Chemical Rubber Publishing Co.) so the weight of each component must be known. In this case the cast must be weighed before and after electroforming, after melting out the core, after installing the thermocouples, and after painting.

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