

A Heat Transfer Analysis of Animals: Unifying Concepts and the Application of Metabolism Chamber Data to Field Ecology

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(Received 11 December 1974, and in revised form 8 July 1975)

This paper presents a heat transfer analysis of animals which lies between detailed thermal energy budget analysis and the simplified “Newton’s Law of cooling” approach. The analysis considers the animal to be composed of two or three thermal layers. Heat transfer by conduction, convection, and thermal radiation are included separately in linearized form. Solar and thermal radiation from the environment and heat production and loss by metabolism and evaporation are included as rates. The solution for body temperature, T_b , is arranged into three parameters: (1) The *operative environmental temperature*, T_e , the effective temperature of the environment for a specific animal, combining conduction, convection, and radiation; (2) the *overall thermal conductance*, K_0 , giving the thermal insulation of the animal; (3) the *effective dry metabolic heat production*, M^* , the algebraic sum of the metabolic heat production and evaporative cooling, corrected for the partitioning of evaporative cooling between the body core and the environment.

For T_b constant, T_e and K_0 are combined into a fourth parameter, the *standard operative environmental temperature*, T_{es} . This parameter is a measure of the value of M^* required to maintain T_b constant, and allows the sensible thermal stress of different environments (e.g. a metabolism chamber and an outdoor habitat) to be compared.

The parameters T_e , K_0 , and M^* are functionally equivalent to the corresponding parameters in “Newton’s Law”. However, this should not be construed to justify the use of “Newton’s Law”, since the parameters are not measured correctly by traditional procedures. However, it is possible to make direct measurements of T_e , K_0 , T_{es} , and M^* with taxidermic models of the animal. These direct measurements allow a simplified approach to many descriptive problems in thermal physiology and ecology, while obtaining results which may be related to detailed energy budget analysis.

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1. Introduction

The complex physical and biological processes that determine the temperature of an animal in its natural habitat are an important area of study in physiological ecology. Two general theoretical approaches are commonly used to analyze heat transfer in physiology and ecology. First, many studies, beginning with Scholander, Hock, Walters, Johnson & Irving (1950) use the so-called "Newton's Law of cooling". The simplicity of the experimental procedures and the apparent simplicity of the interpretation of the parameters resulted in widespread use of "Newton's Law" to analyze data on ectotherms (e.g. Bartholomew & Tucker, 1963) and endotherms (e.g. Herreid & Kessel, 1967). However, the parameters in "Newton's Law" are incorrectly and imprecisely defined, and its simple description of the nature of heat transfer omits so many independent variables in the environment that predictive use of the results is seriously limited. Gates (1961) and Birkebak (1966) noted that procedures developed in physics and engineering must be used to analyze heat transfer between an animal and its environment to achieve a full, predictive understanding of thermal physiology and ecology. This second approach is generally called "energy budget analysis", and was foreshadowed by the "partitioned calorimetry" studies in human physiology [e.g. Winslow, Herrington & Gagge, 1936; see Kerslake (1972) for a current account]. While accurate and suitable for extensive predictive simulation studies (Porter, Mitchell, Beckman & DeWitt, 1973), energy budget studies are lengthy, complex, expensive, and require a degree of facility in analytical mathematics not commonly found in classically trained biologists. The parameters in the energy budget are indirectly related to the organism's perception of the thermal environment, and do not give immediately intuitive results. As a result, the pioneering studies of Gates (1961), Birkebak (1966), Bartlett & Gates (1967) and Porter & Gates (1969) have not been widely applied.

There is a clear need for an approach to thermal physiology and ecology which preserves the descriptive accuracy of the energy budget approach, but which has less elaborate experimental and analytic methods, and a more intuitive interpretation of the parameters.

This paper is directed toward this goal, insofar as it is attainable. My procedure is to develop a linear expression for the body temperature of an animal, based on an energy budget analysis at the level of Porter & Gates (1969). I will use lumped (averaged over the whole animal) values of temperatures and thermal conductances, and represent heat flows due to absorbed solar and thermal radiation, metabolism, and evaporation by simple constants. In addition, the non-linear processes of thermal radiation and free convection will be represented by simplified linear approximations to allow a

linear, analytic solution for body temperature. The resulting solution for body temperature is simplified by introducing the three parameters T_e , K_e , and M^* which integrate the effects of several heat transfer processes. These parameters may be measured directly on live animals in the lab, and on taxidermic models of the animal in either the laboratory or the field.

This paper will: (1) Develop the integrated parameter analysis from heat transfer theory. (2) Discuss the physical interpretation of the integrated parameters. (3) Describe methods for measuring the integrated parameters on live animals in the laboratory. (4) Describe the use of taxidermic models to measure the parameters in the field. (5) Discuss methods of relating laboratory and field measurements.

2. General Heat Transfer Analysis

(A) THE ELECTRICAL ANALOG MODEL OF HEAT FLOW

Basic principles of heat transfer analysis are the same for animals as for any other object or mechanism, and engineering texts contain extensive discussions of principles and procedures (e.g. Kreith, 1965). Gates (1961), Birkebak (1966), Kerslake (1972), and Monteith (1973) have written excellent primers for heat transfer in biological systems. Therefore, I will give only a short introduction, and refer the reader to these works for more details. Mathematical symbols are listed in Table 1 for convenient reference.

A linear, analytic solution for body temperature is needed for the development of this simplified approach to thermal biology and the associated integrated parameters. In general, a linear solution requires that the initial equations be linear in the dependent variables (animal surface and body temperatures here). Thus, the individual heat transfer processes must all be represented by constants, functions not involving dependent variables, or linear functions of the relevant animal-environment temperature difference of the form:

$$Q = K(T_1 - T_2). \quad (1)$$

Here Q denotes heat flow, T_1 and T_2 the animal and environmental temperatures, and K is the lumped thermal conductance, referred to the entire animal. Unit-area conductances or heat transfer coefficients are more commonly used in heat transfer analysis. However, it is difficult to assign a surface area to an animal, particularly so for birds and mammals which greatly increase their surface area when the plumage or pelage is erected. Thus, reference to the entire animal (or possibly body weight^{2/3}) is less ambiguous. Note that designating a coefficient as a thermal conductance only implies

TABLE 1

Mathematical symbols used

A	Total surface of the animal [equation (2)].
A_o	Effective radiating area of the animal [equation (2)].
B	Proportionality constant between K_o and K_o^m [equation (27)].
C	Heat capacitance of the animal [equation (7)].
d	Diameter of the body of the animal, excluding appendages (Table 2).
E	Total heat lost by evaporation [equation (14)].
E_b	Evaporative heat loss from the respiratory system [equation (7)].
E_r	Evaporative heat loss from the outer surface [equation (5)].
E_s	Evaporative heat loss from the skin surface of a furred animal [equation (6)].
$e_{r,f}$	Efficiency of evaporation at the outer surface of a furred animal [equation (23)].
$e_{r,n}$	Efficiency of evaporation at the outer surface of a naked animal [equation (24)].
e_s	Efficiency of evaporation at the skin surface of a furred animal [equation (22)].
G	Heat transfer coefficient to the ground [equation (7)].
H	Convective conductance, free or forced [section 2(B); equation (5)].
H_F	Free convection conductance [section 2(B)].
H_w	Forced convection conductance [section 2(B)].
\mathcal{J}	Turbulence intensity in the direction of air flow [equation (25)].
K	Thermal conductance [equation (1)].
K_f	Thermal conductance of fur or leather layer [equation (5)].
K_N	Newton's Law dry thermal conductance [equation (14)].
K_o	Overall thermal conductance [equation (10)].
K_{os}	Overall thermal conductance under standard conditions [equation (19)].
K_s	Thermal conductance of skin layer [equation (6)].
$K_{s,f}$	Thermal conductance of skin and fur/feather layers [equation (11)].
k_f	Conductivity of fur or feather layer [Table 2].
k_s	Conductivity of skin layer [Table 2].
M	Metabolic heat production [equation (7)].
M'	Oxygen consumed by metabolic processes [section 3(A)].
M^*	Effective net metabolic heat production [equation (13)].
M_s^*	Effective net metabolic heat production under standard conditions [equation (19)].
m	Superscript used to note that a parameter applies to a taxidermic model [section 4(B)].
N	Numerical correction factor used in linearizations [equation (3)].
p	Time period [equation (26)].
Q	Rate of heat flow [equation (1)].
Q_a	Absorbed thermal and solar radiation [equation (4)].
Q_e	Emitted thermal radiation [equation (2)].
Q_n	Net rate of heat transfer by all radiative processes when $T_r = \bar{T}_r$, if $N = 0$ [equation (4)].
R	Thermal radiation conductance [equation (3)].
t	Time [equation (8)].
T_a	Air temperature [section 2(B)].
T_o	Isothermal body core temperature [equation (7)].
T_e	Operative environmental temperature [equation (12)].
T_{es}	Standard operative environmental temperature [equation (21)].
T_p	Temperature of the surface under the animal [equation (7)].
T_{mc}	Temperature of a black, isothermal metabolism chamber [section 3(C)].
T_r	Temperature of the outermost surface of the animal [equation (2), section 3(A)].
\bar{T}_r	Time-average surface temperature of the animal used in the linearization of thermal radiation [equation (3)].

TABLE 1—*continued*

T_s	Skin surface temperature of an animal with fur or feathers [equation (5)].
V	Air velocity [equation (25)].
V_0	Mean air velocity [equation (26)].
x_f	Thickness of the fur layer [Table 2].
x_s	Thickness of the skin layer [Table 2].
Z	Fractional error used in Appendix B [equation (C3)].
δT	Temperature difference $T_s - T_{mc}$ [equation (C2)].
ϵ	Emissivity for thermal radiation [equation (2)].
σ	Stefan-Boltzmann constant, $5.67 \times 10^{-8} \text{ W m}^{-2} \text{ }^\circ\text{K}^{-4}$ [equation (2)].
τ	Time constant [equation (9)].

Definitions of the mathematical symbols used in this paper. The location of the definition or first use of the symbol is given in brackets after the definition. S.I. units are used throughout, with temperatures given in degrees Kelvin ($^\circ\text{K}$).

that a larger value indicates a larger heat flow for a given temperature difference, i.e. units of $\text{W}^\circ\text{K}^{-1} \text{ animal}^{-1}$. No necessary relation to the specific heat transfer process of conduction is implied. I will use S.I. units in this paper. Conversions to more commonly used units are: degrees kelvin ($^\circ\text{K}$) = $^\circ\text{C} + 273.16$; 1 watt (W) = 1 joule (J) per second (s); 1 gram calorie = 4.184 (cal_{15}) or 4.186 (ITcal) joules.

The use of lumped-parameter heat-transfer equations of the form of equation (1) makes no particular assumptions about geometry, nor does it assume that the temperature gradients in the animal or the environment are linear. The principal assumptions are: (1) The heat flow is essentially one-dimensional (i.e. from the inside of the animal to the outside, or vice versa). (2) A single temperature can represent the entire relevant part of the animal or its environment. (3) A single conductance can be assigned to the animal for a particular heat transfer process. The effect is to average each mode of heat transfer over the whole animal. Heat flow is not uniform over the whole animal, and, at any given point on the surface of the animal, the relative importance of conduction, convection, and radiation may vary considerably from the average for the whole animal. Since, in general, the integral of a product does not equal the product of the integrals of each term, this assumption can introduce errors (Kerslake, 1963). The errors are not usually large, however, and may be reduced by introducing correction factors to convert the average value of a temperature or heat transfer coefficient to an effective value giving a more accurate result. Lumped parameters have been used in nearly all energy budget analysis (Bartlett & Gates, 1967; Porter & Gates, 1969; Heller & Gates, 1971; Heller, 1971; Spotila, Soule & Gates, 1972; Moen, 1973; Smith & Miller, 1973; Porter *et al.*, 1973; Morhardt & Gates,

1974) because of the simplicity relative to distributed parameter analysis (e.g. Birkebak, 1966) and adequate accuracy. The measurement of integrated heat transfer parameters on live animals or taxidermic models, as described later in this paper [especially section 4(B)], is not affected by the lumped parameter assumption, since the animal or model integrates the distributed parameters correctly. However, the direct measurements of integrated parameters are necessarily descriptive. Thus, a numerical analysis using distributed parameters and the true, non-linear heat transfer relations is needed for predictive computer simulations, or when the precise details of the thermal significance of differences in morphology are needed in comparative or evolutionary studies.

Many transport processes besides heat flow, such as diffusion and the conduction of electricity, can be described by linear relations with the same mathematical form as equation (1), i.e. (flow) = (conductance) \times (potential difference). Thus, problems in heat transfer or diffusion are often analyzed with the aid of an equivalent electrical circuit, either directly with an analog computer, or mathematically (Kreith, 1965). The electrical analog of heat flow represents a heat transfer problem by an analogous electrical circuit. As shown in Figs 1 and 2, thermal conductances may be represented by an electrical resistor symbol, temperature by voltage, and heat flow by current flow (note that a conductance is the reciprocal of a resistance). Heat storage capacity is represented by a capacitor symbol. Heat flows not related directly to an animal-environment temperature difference and a conductance (e.g. metabolism, evaporation, solar radiation) may be represented by "black boxes" with a constant, time varying, or more complexly determined current output, as appropriate. The solution of the analogous electrical network then gives the solution of the heat transfer problem.

The basic analytical device used in electrical circuit analysis is Kirchhoff's Law. It states that the current flowing into a node (connection point in the circuit diagram) is equal to the current flowing out of the node, so that mass and energy are conserved. In heat flow analysis of animals, the nodes in the electrical circuit correspond to approximately isothermal surfaces representing interfaces between layers of the body with significantly different properties, such as the interface between the body core and the skin, or between skin and pelage.

The values of the thermal conductances used in the electrical analog model must, in general, be determined experimentally. The number of experiments required may be minimized by the use of dimensionless numbers (Reynolds, Nusselt numbers, etc.), described in detail in heat transfer texts (Kreith, 1965). In many cases, approximate values can be found by using published values for geometric objects resembling the animal under study or from calculations

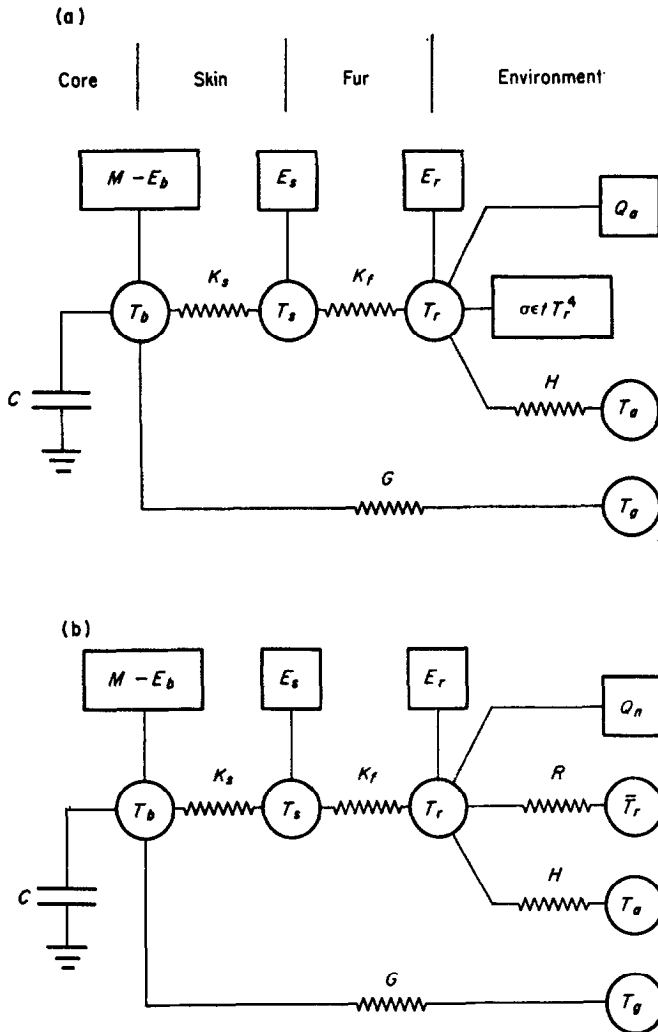


FIG. 1. (a) The basic thermal circuit representation of heat transfer in a simplified animal is shown. Thermal conductance is represented by an electrical resistance symbol, temperatures by voltages, heat storage capacity by a capacitor symbol, and heat flows by current flows. Circles are connection points or nodes, labeled with the corresponding temperature, and square boxes are heat current sources with no relation to thermal conductances. (b) The thermal circuit of a simplified animal after thermal radiation is linearized.

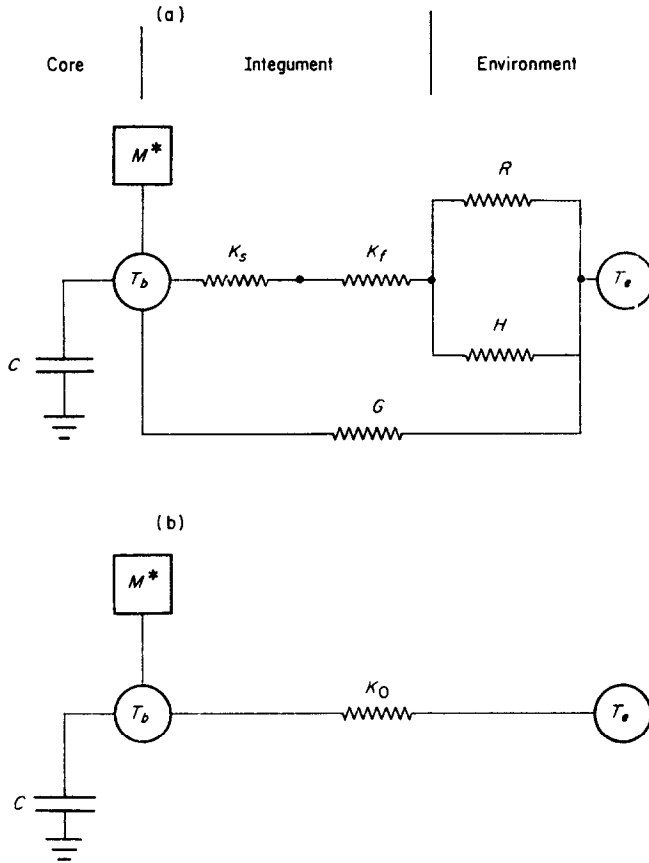


FIG. 2. (a) The reduced thermal circuit of a simplified animal using the parameters T_e and M^* . The conductance of the network connecting the nodes labeled T_b and T_e is equal to the parameter K_0 . (b) The completely reduced thermal circuit of a simplified animal using the parameters of operative environmental temperature T_e , effective net metabolic heat production M^* and overall thermal conductance K_0 . The thermal current or heat flow through K_0 is $K_0(T_b - T_e)$ and equals the sum of the flow M^* due to physiological processes and the flow $C dT_b/dt$ due to heat storage.

using general heat transfer properties of materials and the geometry of the animal and its environment. Kreith (1965), Birkebak (1966), Bartlett & Gates (1967) and Porter & Gates (1969) provide illustrations of the procedures.

(B) LINEARIZATION OF HEAT TRANSFER

Most heat transfer proceeds by processes that are essentially linear with temperature difference, as required by this analysis. However, there are two important cases where the actual heat transfer is non-linearly dependent on the surface temperature of the animal, and requires linearization. Linearization approximates the true curvilinear relationship between heat transferred and temperature with a straight line through a linearization point, such as a tangent to the curvilinear relation at a point near the center of the expected temperature range. This straight-line approximation can be used, over a limited range of temperatures or temperature differences, in place of the actual relationship. The slope of the line will then appear as a conductance in a linear relation for heat transfer. The temperature value at the linearization point appears as an imaginary environmental temperature. The value of heat transfer at the linearization point appears as a constant heat flow. This is shown in Figs 3 and 4.

The first candidate for linearization is free convection, i.e. heat transferred to still air. Heat transferred by free convection is roughly proportional to $(T_r - T_a)^{5/4}$ (Kreith, 1965), as shown in Fig. 3. The surface temperature of the animal is denoted by T_r , and T_a is air temperature. The simplest linearization point is $(T_r - T_a) = 0$, which eliminates the imaginary environmental temperature and imaginary constant heat flow, since both are equal to zero. Convective heat transfer is then equal to $H_F(T_r - T_a)$, where H_F is the linearized free convection conductance. The line used to define H_F is chosen to minimize the error in heat transferred over the range of $(T_r - T_a)$ of interest. This linearized relation can be in error by over 50% near $(T_r - T_a) = 0$. However, convective heat transfer is small in this region, and the overall effect of this error is not usually significant. When the point $(T_r - T_a)$ is not in the region of interest, a linearization about some other point may be constructed, using the tangent to the line relating $(T_r - T_a)$ and heat transferred.

Heat transfer to moving air is called forced convection, and it is essentially linear with temperature difference. Thus, the forced convection conductance, H_w , is defined so that convective heat transfer is given by $H_w(T_r - T_a)$. Since this is the same form as free convection linearized about $(T_r - T_a) = 0$, use of this linearization point allows convective heat transfer, forced or free, to be described simply by $H(T_r - T_a)$. Then H is the appropriate convective conductance for the animal and wind conditions under consideration. This

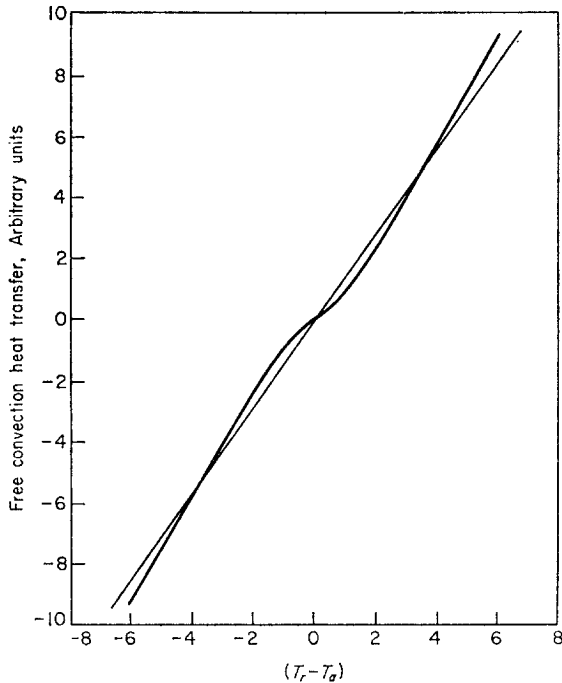


FIG. 3. The curved line shows the typical dependence of heat transferred by free convection, i.e. $\propto (T_r - T_a)^{5/4}$. The straight line is a linear approximation to the curvilinear relation for a linearization point of $(T_r - T_a) = 0$. A plot of heat transferred by free convection from an animal will have a generally similar shape, and the equation of the linear approximation line, $H_F(T_r - T_a)$, gives the approximate heat transfer. The slope of the linear approximation line is equal to H_F .

usage is slanted toward forced convection since this is the more general case in an outdoor environment, and because the elusive, unstable nature of free convection makes it a poor laboratory condition for comparative studies, as discussed in Appendix A.

Second, heat transferred by thermal radiation is proportional to T_r^4 , and must also be linearized. The rate at which heat is radiated from the outermost surface of an animal or other object is given by the Stefan-Boltzmann Law:

$$dQ_e/dA = \sigma \varepsilon T_r^4 \quad (2)$$

where dQ_e/dA is the thermal radiation emitted by a unit area of the surface, W m^{-2} , $\sigma = 5.67 \times 10^{-8} \text{ W m}^{-2} \text{ }^\circ\text{K}^{-4}$ and the emissivity of the surface is ε , $0 < \varepsilon < 1$. For most animals, $\varepsilon \cong 0.95$ (Birkebak, Birkebak & Warner, 1964). The total radiation Q_e emitted by the surface of the animal is found by

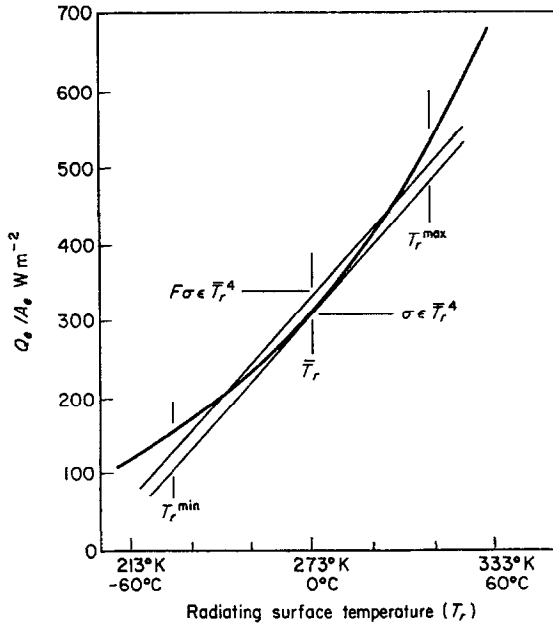


FIG. 4. The curved line plots the emitted thermal radiation per unit effective area, Q_e/A_e , of a black ($\epsilon = 1$) surface at a temperature T_r . The straight line tangent to the curve at $T_r = \bar{T}_r$ is a linear approximation to the true curvilinear relation. The slope of the line is R , and the heat transferred at the linearization point, \bar{T}_r , is $\sigma\bar{T}_r^4$. The equation of the line is then $Q_e/A_e \cong R(T_r - \bar{T}_r) + \sigma\bar{T}_r^4$. Over a range from T_r^{\min} to T_r^{\max} , the accuracy of the linear approximation may be improved, at the expense of reduced accuracy near \bar{T}_r , by multiplying $\sigma\bar{T}_r^4$ by N to raise the approximation line slightly, as shown.

multiplying $\sigma\epsilon\bar{T}_r^4$ by the effective radiating area of the animal, A_e . The effective area is less than the total surface area, A , and depends on the geometry of the animal and its environment. Halliday & Hugo (1963) describe a straightforward method of measuring A_e .

As well as emitting thermal radiation, the outer surface of the animal absorbs thermal radiation emitted by surfaces in the environment. In a simple environment, such as a metabolism chamber or other enclosure with black ($\epsilon \cong 1$) walls, the net heat transfer resulting from the emission and absorption of thermal radiation may be linearized about the average surface temperature of the animal and the enclosure (Kreith, 1965, p. 230). Linearization about the enclosure temperature is adequate for a well-designed metabolism chamber. However, it is unsatisfactory for general biological problems, since the outdoor environment lacks a well-defined radiation temperature, with the sky and bare ground differing by 50–80 °K or more on a clear day (Gates,

1968). The complexity of the outdoor environment requires that absorbed and emitted radiation be considered separately. Absorbed thermal radiation is essentially independent of T_r in an outdoor environment, and may be calculated from the geometry of the animal and environment and included in the overall heat transfer as a rate. Absorbed solar radiation is similarly independent of T_r , and may also be calculated as a heat flow rate. The combined rate of heat flow due to absorbed solar and thermal radiation is denoted by Q_a , and methods for calculating its value are described by Kreith (1965), Birkebak (1966) and Porter & Gates (1969). With this procedure, only emitted radiation involves a dependent variable and requires linearization.

The best linearization point for general environments is the mean surface temperature of the animal, \bar{T}_r , for the time period of interest. Other values may be used in some cases, such as the surface temperature of the enclosure surrounding the animal in a laboratory experiment. The linearization is diagrammed in Fig. 4. The slope of the tangent to the curve giving Q_e as a function of T_r at the point \bar{T}_r is $R = 4A_e\sigma\epsilon\bar{T}_r^3$, and is the linearized radiation heat transfer coefficient. It is found by evaluating dQ_e/dT_r at $T_r = \bar{T}_r$. The heat radiated when $T_r = \bar{T}_r$ is $A_e\sigma\epsilon\bar{T}_r^4$. The linearized approximation to the heat emitted as thermal radiation from the surface of the animal is then

$$Q_e = A_e\sigma\epsilon T_r^4 \cong R(T_r - \bar{T}_r) + NA_e\sigma\epsilon\bar{T}_r^4. \quad (3)$$

This has the expected form of a linear heat transfer rate from the surface at a temperature T_r to an imaginary environmental heat source/sink at the linearization temperature \bar{T}_r , plus a constant heat flow rate. The multiplying factor N is an optional constant slightly greater than 1 which improves the accuracy of the approximation over a fixed range. For example, the difference between the correct and linear approximation values for Q_e is less than 1% for $\bar{T}_r = 293$ °K (20 °C) over the range $9 < T_r < 32$ °C with $N = 1$, but less than 1/2% for $N = 1.005$. Similarly, the difference over a range $-3 < T_r < 50$ °C is less than 5% for $N = 1$ and 2.5% for $N = 1.025$, and over a range $-11 < T_r < 65$ °C, less than 10% for $N = 1$ and 5% for $N = 1.05$. This is diagrammed in Fig. 4.

The net heat transferred to the surface by absorbed and emitted thermal radiation and absorbed solar radiation is thus:

$$Q_a - Q_e = Q_n - R(T_r - \bar{T}_r) \quad (4)$$

where $Q_n = Q_a - NA_e\sigma\epsilon\bar{T}_r^4$.

If $N = 1$, Q_n is equal to the total net heat transfer by all radiative processes when $T_r = \bar{T}_r$. As a result of this identification and the absence of linearization error when $T_r = \bar{T}_r$, intuitive discussion and analysis is simplest when $N = 1$. I will thus assume $N = 1$ in the rest of this paper.

3. Linearized Heat Transfer in Animals

(A) THERMAL REPRESENTATION OF AN ANIMAL

Figure 1 shows the thermal circuits used to represent an animal in the subsequent analysis. The circuit has three nodes, representing: (1) The core and core-skin interface, temperature T_b . (2) The skin-external insulation (fur or feathers) interface, temperature T_s . (3) The effective external surface where radiative and convective heat exchange takes place, as defined by Clark, Cena & Monteith (1973), temperature T_e . This surface is the actual surface of a naked animal, or an effective surface lying just under the apparent surface of the plumage or pelage of an insulated animal. All of the heat storage capacity of the animal is lumped into the body core, so that the skin and external insulation has zero heat storage. This assumption is good for animals with effective fur or feather insulation, and small or large animals. However, this assumption results in some error in the calculated time course of T_b in moderate-size, naked animals, since the isothermal core does not show the significant thermal diffusion effects present in such animals.

Evaporation is expressed as a simple heat flow rate, $W \text{ animal}^{-1}$, since it is primarily determined by physiological responses, such as panting, sweating, saliva spreading, or bathing. Heat loss by evaporation is partitioned into outer surface, skin, and respiratory terms. Evaporative heat loss is equal to the mass rate of evaporation times the heat of vaporization of water, $2.4\text{--}2.6 \times 10^3 \text{ J g}^{-1}$ (Kerslake, 1972). Water which simply drips off the animal without evaporating does not appear as heat loss, and is therefore neglected. The environment does place an upper limit on evaporation which depends on the temperature of the evaporating surface and the water vapor pressure of the air, as well as the convective mass transport coefficient. For some animals, notably amphibians, these environmental factors dominate physiological factors, and a suitable relation involving evaporative surface temperatures and environmental parameters must replace the simple rates. Kreith (1965), Kerslake (1972), Monteith (1973) and Tracy (1975) discuss mass transport in more detail.

Metabolic heat production is similarly dependent on physiological factors such as activity, and will also be represented by a heat flow rate, $W \text{ animal}^{-1}$. The amount of heat M produced by the consumption of an amount of oxygen M' depends on the substrate being metabolized, and ranges from 5.50 (lipids) to 5.92 (carbohydrates) W per 1 O_2 (stp) per hr [more conventionally, 4.73 to 5.09 kcal per 1 O_2 (stp)]. Usually the animal is fasted before an experiment to restrict the constant to 5.46 to 5.58 W per 1 O_2 (stp) per hr. For some animals, notably reptiles and amphibians, metabolic heat

production is principally a function of body temperature when the animal is resting. In such cases, it may be useful to represent metabolic heat production by a suitable function of body temperature (Bakken & Gates, 1975; Bakken, 1976a).

The heat balance for the outer surface of the animal is found by summing all of the heat flows to and from the surface. Heat transfer between the surface and the air is given by the relation for forced convection or linearized free convection, $H(T_r - T_a)$. Total radiation heat transfer is given by equation (4). Evaporative heat loss is denoted by the rate E_r . Heat is transferred between the surface of the pelage and the skin surface at a rate $K_f(T_s - T_r)$. (Although I will refer to fur or pelage in this paper, the analysis applies equally to plumage and the fur-like scales found on some insects.) Heat transfer through fur is complex (Davis & Birkebak, 1974), but it may be approximated by this relation by making the pelage thermal conductance, K_f , a function of wind speed. Clark *et al.* (1973) describe an experimental procedure for measuring local values of K_f with varying air flow.

Kirchhoff's Law, applied to the node in Fig. 1(b) representing the outer surface of the animal, sums the heat flows as follows: (heat flow through pelage) + (net absorbed radiation when $T_r = \bar{T}_r$) = (heat radiated to imaginary " \bar{T}_r ") + (heat convected to air) + (heat lost by evaporation), or

$$K_f(T_s - T_r) + Q_n - R(T_r - \bar{T}_r) - H(T_r - T_a) - E_r = 0. \quad (5)$$

The equation for the heat balance of the skin-pelage interface is (heat flow from body core) = (heat flow through pelage) + (heat lost by evaporation). Applying Kirchhoff's Law to the node labeled with the skin temperature T_s ,

$$K_s(T_b - T_s) - K_f(T_s - T_r) - E_s = 0. \quad (6)$$

The effective thermal conductance of the skin and associated subcutaneous fat layer is denoted by K_s , and includes the effects of blood flow. Since the skin is a relatively small part of the total body mass, its heat capacity will be lumped with the heat capacity of the body core to simplify the analysis. Only the heat lost by evaporation at the skin-fur interface is included in E_s , since sweat or other moisture wicked to the outer surface of the pelage is included in E_r .

The equation for heat balance in the core of the animal is (heat produced by metabolism) = (heat stored) + (heat flow to skin) + (heat flow to ground) + (heat lost by evaporation). Applying Kirchhoff's Law to the node labeled T_b ,

$$(M - E_b) - C \, dT_b/dt - K_s(T_b - T_s) - G(T_b - T_g) = 0. \quad (7)$$

The rate of metabolic heat production is denoted by M . The heat capacitance

of the whole animal is lumped into the core, as described earlier, and is denoted by C . The heat capacitance is equal to the weight of the animal times the specific heat of protoplasm, $3.43 \text{ J g}^{-1} \text{ }^\circ\text{K}^{-1}$ (Bartholomew, 1972). The temperature of the ground is denoted by T_g and G is the thermal conductance between the ground and the core of the animal. The contact conductance, conductance through the tissues in contact with the ground, and the effects of blood flow are all included in G . The heat lost by evaporation from the respiratory tract is denoted by E_b .

These equations may be combined to give a single differential equation in T_b by solving the algebraic relations in equations (5) and (6) and substituting into equation (7) to eliminate T_r and T_s . The procedure outlined in Appendix B gives the following linear approximation to overall heat transfer:

$$\tau \frac{dT_b}{dt} + T_b = T_e + M^*/K_0 \tag{8}$$

where the time constant is, for constant M , E_b , E_r and E_s :

$$\tau = C/K_0. \tag{9}$$

The time constant is an important parameter when the body temperature varies, and is equal to the time required for $(1 - 1/e) \cong 63\%$ of the T_b response to a sudden change in the thermal environment or in a physiological parameter to occur. The overall thermal conductance of the animal is:

$$K_0 = \frac{(K_{sf} + G)(H + R) + GK_{sf}}{K_{sf} + H + R}. \tag{10}$$

The thermal conductance of the skin and fur layers combined, K_{sf} , is found by adding their individual thermal conductances in series:

$$K_{sf} = K_s K_f / (K_s + K_f). \tag{11}$$

The temperature of the environment, as seen by the animal, is

$$T_e = \frac{K_{sf}(HT_a + RT_r + Q_n + GT_g) + GT_g(H + R)}{(K_{sf} + G)(H + R) + GK_{sf}} \tag{12}$$

and will be called the operative environmental temperature. The effective net metabolic heat production M^* is essentially the dry metabolic heat production, with correction factors applied to E_s and E_r to account for the partitioning of the heat loss between the body core and the environment:

$$M^* = M - E_b - E_s \left[\frac{1 + \frac{H + R}{K_f}}{1 + \frac{H + R}{K_{sf}}} \right] - E_r \left[\frac{1}{1 + \frac{H + R}{K_{sf}}} \right]. \tag{13}$$

The effect of the algebraic manipulations and the linearization of thermal radiation has been to replace the complex thermal circuit of Fig. 1(a) with the simplified thermal circuit representation of the animal and its environment shown in Fig. 2(a). The total conductance of the network connecting T_b and T_e is equal to K_0 , as may be easily verified. The environment is now represented by a single temperature T_e rather than the complex assortment of temperatures in Fig. 1(b). Since the network in Fig. 2(a) can be replaced by a single conductor with a thermal conductance K_0 , as shown in Fig. 2(b), the thermal aspects of the animal are essentially represented by a thermal analog of the electrical $R-C$ circuit. The circuit is driven by the time-varying thermal potential T_e and thermal current source M^* .

The expressions for K_0 , T_e , and M^* of animals without pelage or without conduction to the substrate can be found from equations (10) to (13) by taking the appropriate limiting cases. For an animal without pelage, take the limit as $K_f \rightarrow \infty$. Then $K_{sf} \rightarrow K_s$ and the coefficient of the E_s term in equation (13) becomes identical to the coefficient of the E_r term, reflecting the lack of any distinction between E_s and E_r in the absence of pelage. Evaporation from the skin surface of a naked animal should be denoted by E_r , since the skin is now the outer surface, and is described by equation (5) rather than equation (6). Similarly, the parameters for an animal with negligible conduction to the substrate are found by taking the limits of equations (10) to (13) as $G \rightarrow 0$.

An important feature of equation (8) and the associated parameters is the economy of expression. The animal and its thermal environment can be described by the time course of only two independent variables, T_e and K_0 . This is a considerable reduction in complexity over the specification of the time course of K_s , K_f , H , G , T_a , T_b , and Q_n . The complexity resulting from the independent specification of each component in the heat transfer process is a considerable impediment to understanding of thermal physiology and ecology. Simplified descriptions using diagrams such as the climate space (Porter & Gates, 1969) or integrated parameters similar to T_e and K_0 (Kerslake, 1972) often give a better understanding. One use of the results in equations (8)–(13) is simply to give a convenient synopsis of the effective temperature of the environment, T_e , and the effective insulation of the animal, K_0 , in a detailed energy budget study.

Some care should be used in handling \bar{T}_r to get the best possible accuracy in the computed values of T_e and K_0 . The linearized expression for emitted thermal radiation of equation (3) is absolutely correct only when $\bar{T}_r = T_r$. Thus, it is desirable to choose \bar{T}_r as accurately as possible. One approach would be to select average values of H , T_a , etc. for the interval of interest. These values then can be used in a Newton's method solution of equations (5)–(7) with the original T_r^4 expression for thermal radiation retained. The

resulting average value of T_r may then be used as \bar{T}_r in calculating running values of T_e and K_0 . For greater accuracy, a continuous solution for T_r may be done using the instantaneous values of H , T_a , etc. in a Runge-Kutta or similar numeric solution of the same equations. The instantaneous values of all parameters may then be used to calculate exact running values of T_e and K_0 .

The utility of the T_e and K_0 parameters extends well beyond their use to summarize complex data. The following sections describing the interpretations of the parameters will show that they can be measured directly on live animals or models of the animals. For many studies, this allows the complexity of a detailed energy budget analysis to be bypassed. These direct measurements also can be of considerable value in detailed energy budget studies.

(B) RELATION TO "NEWTON'S LAW"

The form of equation (8) is formally equivalent to "Newton's Law of cooling". It follows that the parameters defined in equations (10), (12), and (13) are precise definitions of the corresponding parameters in "Newton's Law". The correspondence may be shown more clearly by writing the two most commonly used forms of "Newton's Law".

Animals which rely primarily on internal metabolic heat production or evaporative cooling (endotherms) are usually considered as having a constant body temperature. Then the net heat flow to or from the environment is equal to internal heat production or loss, and

$$M - E = K_N (T_b - T_a) \quad (14)$$

where $E = E_b + E_r + E_s$. The corresponding form of equation (8) is found by setting $dT_b/dT = 0$:

$$M^* = K_0(T_b - T_e). \quad (15)$$

Animals which rely primarily on external heat sources and sinks for thermoregulation (ectotherms) are assumed to have zero metabolism and evaporation. Then the net heat flow between the animal and its environment comes entirely from heat stored in the body. The corresponding form of "Newton's Law" is:

$$dT_b/dt = \frac{-K_N}{C} (T_b - T_a). \quad (16)$$

This is the equation describing Newton's (1701) original experiment, and is the only form which can properly be called "Newton's Law" (Kleiber, 1961, 1972a, 1973, 1974; Tracy, 1973; Bakken & Gates, 1974a, b). The form of equation (8) corresponding to equation (16) is found by making the same

assumption of negligible net metabolism and evaporation, so that $M^* = 0$:

$$dT_b/dt = \frac{-1}{\tau} (T_b - T_e). \quad (17)$$

Comparison of equations (14) and (15) and of (16) and (17) shows that "Newton's Law" and the linear approximation to overall heat transfer given in this paper are equivalent if $T_e = T_a$, $K_N = K_0$, and $M^* = M - E$. These equivalencies are true under special conditions, but may not be freely assumed. The special conditions are discussed together with the interpretation and measurements of T_e , K_0 , and M^* in the following sections.

The general expression of equation (8) gives a better description of real animals than either "Newton's Law" [equations (14) and (16)] or the special cases of equation (8) given by equations (15) and (17). It is generally recognized that animals cannot be neatly categorized as endotherms or ectotherms (Bartholomew, 1972). Thus, the simplifying assumptions used in equations (14)–(17) are often invalid, and these equations cannot be used to analyze experimental data. Birds and mammals use external heat sources and allow body temperature to vary with time (Schmidt-Nielsen, 1964), so that corrections for heat storage may be required. Reptiles and amphibians can have significant metabolism and evaporation (Vinegar, Hutchison & Dowling, 1970; Thorson, 1955). Bartholomew & Tucker (1963) noted that corrections for metabolic heat production were needed to analyze cooling curve data. Bakken & Gates (1975) and Bakken (1976a) have described improved procedures based on equation (8) for analyzing cooling curve data in the presence of metabolic heat production.

(C) OPERATIVE ENVIRONMENTAL TEMPERATURE

The term "environmental temperature" appears in almost every recent paper in thermal physiological ecology. It may denote almost any reading taken with a thermometer in the vicinity of the plant or animal studied, although air temperature is most often used. The preceding section comparing equation (8) with Newton's Law indicates that the operative environmental temperature, T_e , is a precise definition of this elusive concept. Operative environmental temperature is a generalization of the "operative temperature" stress index developed by Winslow, Herrington & Gage (1937). Historically, operative temperature has been interpreted as the temperature of an isothermal, blackbody cavity equivalent to the actual non-uniform environment (Gonzalez, Nishi & Gage, 1974). Morhardt & Gates (1974) related operative temperature to the climate space diagram of Porter & Gates (1969), with the same interpretation. Bakken & Gates (1975) generalized the concept to

include conduction to the substrate, and called the generalized form "operative environmental temperature". They gave the additional interpretation of T_e as the temperature of a model of the animal duplicating all external conductive, convective, and radiative properties of the animal, but with no metabolism or evaporation, when in thermodynamic equilibrium with its environment.

Appendix C outlines the equivalence of T_e and the temperature T_{mc} of a metabolism chamber with black ($\epsilon \cong 1$) walls and air and wall temperatures equal. Special care must be used in the construction of an enclosure to be used as a metabolism chamber if it is to have a constant, well defined operative environmental temperature for any animal or other object. The design requirements are discussed in detail in section 4(A). The non-linearity of thermal radiation [equation (2)] results in a slight difference between T_{mc} and T_e if T_{mc} and T_r differ. The discrepancy between T_e and T_{mc} is proportional to the difference between T_r and T_{mc} . The error analysis in Appendix C shows that T_e and T_{mc} will usually be equal to within 1 °C for $|T_r - T_{mc}| = 20$ °C, and proportionately less for smaller $|T_r - T_{mc}|$ differences. By equation (8), heat flow is proportional to $|T_b - T_e|$. The error in heat flow or K_0 measurements resulting from the assumption that $T_{mc} = T_e$ is thus less than 5%. The exact value of the error depends on the insulative value of the integument of the animal, which determines the relation of $|T_r - T_e|$ to $|T_b - T_e|$. For a bird or mammal, most of the thermal resistance [c. 75% for a 100 cm s⁻¹ wind (Tracy, 1972)] is across the plumage or pelage. Then $|T_b - T_e|$ is around four times $|T_r - T_e|$. The corresponding error in estimated heat flow or K_0 is then typically only a little more than 1%. For uninsulated animals such as reptiles, the integument has negligible insulative value (Porter *et al.*, 1973) and the error may approach 5%.

The alternate interpretation of Bakken & Gates (1975) of operative environmental temperature as the body temperature of the animal when $dT_b/dt = M^* = 0$ follows from equation (8):

$$0 + T_b = T_e + 0 \quad (18)$$

which reduces immediately to $T_b = T_e$. Operative environmental temperature is thus just the null hypothesis—the temperature that the animal would have with no physiological thermoregulation. Animals with $M^* = 0$ do not exist, although many lizards come close to this condition when inactive. However, a taxidermic model of the animal, constructed to duplicate the external convective and radiative properties of the animal, exactly satisfies the requirement that $M^* = 0$. This immediately suggests the use of such a model as an instrument to measure T_e . Taxidermic models have been suggested (Parry, 1951; Heath, 1964) or used (Lewis, 1963; Boyer, 1965; Markel, 1971) as a

way of measuring the effective temperature of the environment, but without much analysis. The construction and use of taxidermic models to measure T_e and other integrated parameters is discussed in detail in section 4(B).

The important practical feature of the operative environmental temperature of a general environment is its dependence on the size, shape, and absorptivity of the animal or object. If this were not the case, the equilibrium temperature of any object used as a temperature sensor would correctly measure the effective temperature of the environment, and energy budget analysis would not be necessary. It is occasionally possible for an object with little resemblance to the animal under study to have essentially the same operative environmental temperature. For example, a blackened copper toilet float (Vernon, 1932) has nearly the same operative temperature as a human due to a similar relation between convection and radiation (Kerslake, 1972). Such objects are more convenient to use as a T_e sensor than a taxidermic model of a large animal. However, they must be designed carefully using a full energy budget analysis of both the animal and the proposed sensor. This effects no saving in effort over an energy budget analysis. In contrast, a taxidermic model of one of the small (less than 5 kg or so) animals most commonly studied in physiological ecology is acceptable as an instrument. Since the model duplicates the size, shape, absorptivity, emissivity, and substrate contact area of the live animal, it will have the same T_e as the live animal. Thus, a model may be used to measure T_e with confidence without first undertaking a detailed energy budget analysis. The principal uncertainty in the measurement is again due to the non-linearity of thermal radiation. As noted earlier, the linearization of thermal radiation, and thus the values of R and Q_n are exact only if $\bar{T}_r = T_r$. Thus, whenever the surface temperatures of the animal and the model differ, the values of T_e operating on the animal and the model will also differ. The calculation of the magnitude of the error proceeds essentially identically to the calculation in Appendix C. The same estimates of the errors in T_e and heat flow result. The error in T_e will be about 5% of the difference in surface temperature between the animal and the model, and the effect on heat flow will be around 1-5%.

Operative environmental temperature is not a satisfactory temperature in a thermodynamic sense. It does have the dimensions of temperature, as may be verified by analyzing the units in equation (12), and it apparently satisfies the usual thermodynamic definition of temperature (Zemansky, 1957):

“The temperature of a system is a property that determines whether or not a system is in thermal equilibrium with other systems.”

Considering the environment as one system and the animal as the other, first note that the systems are not in thermal equilibrium as long as $M^* \neq 0$.

Thus, the relevant system for comparison is the taxidermic model. As discussed earlier, the temperature of the model is $T_b = T_e$ when it is in thermal equilibrium with the environment, so that T_e is necessarily the temperature of the environment *for that animal*. The problem rather lies in the zeroth law of thermodynamics (Zemansky, 1957):

“Two systems in thermal equilibrium with a third are in thermal equilibrium with each other.”

Two models of different animals in thermal equilibrium with the same microclimate will, in general, have different $T_b = T_e$ values and will thus not be in thermal equilibrium with each other. Therefore, T_e is not a completely satisfactory temperature in a thermodynamic sense. However, the economy effected in notation and instrumentation in the study of an animal by the use of the T_e parameter, plus the fact that T_e satisfies the requirements of a temperature as far as the specific animal is concerned, makes it a useful concept for many biological studies.

(D) OVERALL THERMAL CONDUCTANCE

Equation (8) shows that the overall thermal conductance determines the sensible heat flow between an animal and its environment for a given body-environment temperature difference. The important role of thermal conductance in thermal physiology and ecology has been known for some time (Scholander *et al.*, 1950). Many studies in thermal physiology and ecology have measured the thermal conductance of various animals on the basis of the “Newton’s Law” equations (14) and (16), and have assumed that K_N is a constant of the animal (e.g. Scholander *et al.*, 1950; Herreid & Kessel, 1967). However, the overall thermal conductance must be measured with respect to T_e rather than T_a , as can be seen by examining equations (14)–(17). Equation (10) shows that K_0 is not a constant of the animal, since the convective conductance, H (Kreith, 1965) and the fur conductance, K_f (Moote, 1955; Davis & Birkebak, 1974) both depend on wind speed. Further, the conductance to the substrate, G , depends on the nature of the substrate (Spray & May, 1972, provide an example). Winslow *et al.* (1937) developed an “operative heat exchange coefficient” essentially equivalent to K_0 , and noted the dependence on wind speed. Like operative temperature (Winslow *et al.*, 1937), the operative heat exchange coefficient only includes the effects of convection and radiation. Tracy (1972) examined the thermal conductance of an animal exchanging heat with an isothermal environment by convection and radiation, and showed that it varied significantly with wind speed. Bakken & Gates (1975) generalized the operative heat exchange coefficient

to include conduction to the ground, and called this generalized form "overall thermal conductance".

The overall thermal conductance of an animal may be measured with the traditional laboratory experiments, provided that T_e is used for the environmental temperature, and that the dependence on wind speed and the nature of the substrate under the animal is kept in mind. The overall thermal conductance of endothermic animals may be determined by measuring metabolism and evaporation at different wind speeds and operative environmental temperatures. In most cases [see section 3(F)] $M^* \cong M - E$, so that K_0 may be determined at each wind speed and operative environmental temperature with equations (8) or (15), depending on the constancy of T_b during the measurement. The overall thermal conductance of ectothermic animals may be measured with the traditional cooling curve experiment. The effects of metabolism on the measurement of K_0 (Bartholomew & Tucker, 1963; Bakken & Gates, 1975) may be eliminated by the procedure described by Bakken (1976a) and some knowledge of the dependence of metabolism and evaporation on T_b .

Measurement of K_0 in the field is a more difficult problem. The only available method of measuring metabolism and water loss in free animals is the doubly-labeled water technique (Lifson & Lee, 1961; Lifson & McClintock, 1966). It lacks the needed time resolution, and is very expensive. Thus, K_0 must either be calculated from the fundamental heat transfer parameters or be measured directly with an electrically heated taxidermic model. Models may be used effectively to measure K_0 for relatively small reptiles and amphibians, since Porter *et al.* (1973) have shown that the integument conductance, K_{sf} , has a negligible effect on K_0 . The procedures are described in section 4(B). Birds and mammals present a more difficult problem, since the fur or feathers are the major factor determining K_0 (Tracy, 1972). A taxidermic model of the animal cannot duplicate the ability of the animal to erect its plumage or pelage, and thus cannot reliably measure the same K_0 that the live animal would experience. Computed values of K_0 are also based on measurements made on models (Bartlett & Gates, 1967; Heller, 1971; Walthen *et al.*, 1971; Porter *et al.*, 1973) and can have the same problem. The failure of the model of a bird or mammal to duplicate the K_0 of the animal can be partly bypassed by measuring an index developed in the following section in place of K_0 . As discussed in section 4(B), this parameter can be measured with the less restrictive assumption that the K_0 of the model is proportional (rather than identical) to the K_0 of the animal.

Like T_e , K_0 is dependent on the surface temperature of the animal as a result of the non-linear nature of thermal radiation. Thus, a value of K_0 measured on an animal or taxidermic model of an animal at one surface temperature

will not be correct for otherwise identical conditions if the surface temperature is different. Further, if a value of \bar{T}_r significantly different from T_r is used to calculate K_0 , the calculation will be in error.

The magnitude of the change in K_0 due to a change in T_r , or the error in a calculation of K_0 with $\bar{T}_r \neq T_r$, depends on the relation of R to the other conductances determining K_0 . For a furred animal, the thermal conductance of the fur is the primary limit on heat transfer (Tracy, 1972). A T_r change or $|T_r - \bar{T}_r|$ difference of 20 °K changes R by 23 %, but K_0 for the vasoconstricted, furred animal described in Table 2 changes by only 1–2 % at a wind speed of 100 cm s⁻¹ and 3–5 % at 10 cm s⁻¹. At the other extreme, the K_0 of the naked, vasodilated animal changes by 4–10 % at 100 cm s⁻¹ and 9–17 % at 10 cm s⁻¹. Note that, as long as the T_r of a model or the \bar{T}_r used in a calculation lies between T_b and T_e , the errors in K_0 and T_e due to the non-linearity of emitted thermal radiation have opposite effects on heat flow. Thus, the error in total heat flow due to the non-linearity of radiation is usually less than the error in either T_e or K_0 . Some examples will be given in section 4(B).

(E) THERMAL STRESS AND STANDARD OPERATIVE ENVIRONMENTAL TEMPERATURE

Despite the complications resulting from the inter-relation of the animal and its environment, it is useful to have a simple stress index which will allow different environments to be compared in a consistent manner with a single number. This is possible principally for endotherms, where stress may be defined as the metabolism and evaporation required for thermoregulation. Such an index would allow metabolism chamber data on an animal and microclimate measurements of a habitat to be combined to give ecologically meaningful estimates of physiological stress on and the food and water requirements of the animal in that habitat. The preceding section clearly indicates that the stress index must be based on *both* operative environmental temperature *and* the overall thermal conductance, and it must reflect equivalent sensible (conductive-convective-radiative) heat transfer to and from the animal.

Such a stress index, which I will call the *standard operative environmental temperature*, denoted T_{es} , combines T_e with a standard K_0 . It may be defined with reference to a standard reference metabolism chamber with black walls, air and wall temperatures equal, a fixed laminar air flow fast enough ($\cong 100$ cm-s⁻¹) to ensure repeatable velocity measurements and forced convection conditions, and a standard substrate. The first two conditions set the temperature of the metabolism chamber equal to the operative environmental temperature in the chamber, as described in section 3(c) and Appendix A. The last two conditions fix K_0 for a given animal. The standard operative

TABLE 2

Rough estimates of the evaporation efficiencies given by equations (22)–(24) for various sizes of “animals” with and without pelage, and under heat or cold stress. The “animal” is a cylinder with an outside diameter d . The effective thickness of the skin and subcutaneous fat layer is $x_s = 0.01 d^{0.6}$ and the effective thickness of the pelage layer is $x_f = 0.02 d^{0.6}$. These thickness relations follow Kleiber’s generalization (1969, 1972b) that the thickness of skin and/or fur layers increases as weight^{1/5} ($\propto d^{3/5}$). The thermal conductivity k_s of the skin-fat layer is taken to be $0.204 \text{ W m}^{-1} \text{ }^\circ\text{K}^{-1}$ when vasoconstricted (Chato, 1966). Blood flow from vasodilation increases the conductivity of human skin 3–5x (Chato, 1966). Assuming the lower value, $k_s = 0.612 \text{ W m}^{-1} \text{ }^\circ\text{K}^{-1}$ for vasodilated skin. The thermal conductivity of dry fur is taken equal to the conductivity of air, $k_f = 0.0257 \text{ W m}^{-1} \text{ }^\circ\text{K}^{-1}$ (Birkebak, 1966; Porter & Gates, 1969). Moderately wet fur ($\sim 7\%$ by volume, fur moderately plastered down) has a conductivity of 150% that of dry fur (Birkebak, 1966) and this is assumed in the heat stressed condition, so that $k_f = 0.0385 \text{ W m}^{-1} \text{ }^\circ\text{K}^{-1}$. A mean surface temperature of $\bar{T}_r = 300 \text{ }^\circ\text{K}$ is assumed, so that $R/A_e = 6.12 \text{ W m}^{-2} \text{ }^\circ\text{K}^{-1}$. These assumptions result in an overall heat transfer coefficient at $V_0 = 10 \text{ cm s}^{-1}$ about 20% greater than the regression given for mammals by Kleiber (1972b), based on data from Herreid & Kessel (1967). The coefficients of the allometric relations for skin and pelage layer were selected for simplicity and to give a larger overall heat transfer coefficient, since the data in Herreid & Kessel (1967) was generally taken under free convection conditions, which gives very low overall heat transfer coefficients. The assumptions used in this table are very general approximations to the real animals, and care should be used in applying the results to specific animals.

Diameter of animal (cm)	Heat stress, vasodilated				Cold stress, vasoconstricted			
	Wet fur ϵ_{rf}		Naked ϵ_{rn}		Dry fur ϵ_s		Naked ϵ_{rn}	
	$V_0 = 10$	$V_0 = 100$	$V_0 = 10$	$V_0 = 100$	$V_0 = 10$	$V_0 = 100$	$V_0 = 10$	$V_0 = 100$
2	0.58	0.40	0.98	0.96	0.97	0.96	0.94	0.88
5	0.51	0.36	0.97	0.95	0.97	0.96	0.92	0.86
10	0.44	0.31	0.96	0.94	0.96	0.95	0.90	0.83
20	0.37	0.26	0.95	0.92	0.96	0.95	0.86	0.79
50	0.27	0.20	0.93	0.89	0.95	0.95	0.80	0.73

environmental temperature of a complex environment, T_{es} , is then defined as equal to the temperature of a standard reference metabolism chamber in which an animal with a given, constant body temperature requires the same effective net metabolic heat production, M^* , to maintain T_b as it does in the complex environment. The sensible heat exchange for a given T_b is also the same in both environments.

The relation between the temperature of the standard reference metabolism chamber and the general, complex environment may be found by using equation (15). The net metabolic heat production required to maintain T_b in the standard reference metabolism chamber at a temperature T_{es} is:

$$M_s^* = K_{0s}(T_b - T_{es}) \quad (19)$$

where K_{0s} is the overall thermal conductance of the animal under the standard conditions. The net metabolic heat production required in a general environment of operative environmental temperature T_e is:

$$M^* = K_0(T_b - T_e) \quad (20)$$

where K_0 is the overall thermal conductance of the animal in the general environment. The standard operative environmental temperature of the general environment is just the temperature of the standard metabolism chamber requiring the same M^* as the general environment, and is found by equating M_s^* and M^* and solving equations (19) and (20) simultaneously for T_{es} :

$$T_{es} = (K_0/K_{0s})T_e + [1 - (K_0/K_{0s})]T_b. \quad (21)$$

The standard operative environmental temperature, T_{es} , is essentially equivalent to the standard operative temperature developed as a stress index by Gagge (1940) and Gagge & Hardy (1967). Standard operative temperature, like operative temperature (Winslow *et al.*, 1937), only includes convective and radiative heat transfer.

There are two problems in applying the preceding development of T_{es} to animals. These result from the dependence of T_{es} on temperature and the omission of the ambient water vapor pressure from the analysis.

First, the simultaneous solution of equations (19) and (20) to obtain the expression for T_{es} in equation (21) assumed that T_b was constant when the conditions were equivalent. Animals may not always have the same body temperature under equivalent conditions, which can result in an error in the second term in equation (21). This is not a serious problem for good homeotherms. Heterotherms must be approached with some knowledge of the variation of T_b with time and environment. It is very difficult to use standard operative environmental temperature meaningfully for ectotherms, since T_b is not well-defined.

Second, it has been assumed that M^* was directly related to the metabolism and evaporative water loss of the animal. In fact, many possible combinations of M , E_b , E_r , and E_s in equation (13) give the same value of M^* . For example, M may be elevated above the standard level by activity, and some of the increased heat production dissipated by increased evaporation to give the same M^* . The comparison of the thermal stress of different environments need only be based on standard resting conditions. However, even standard metabolic conditions do not guarantee a unique relation of M^* to M , E_b , E_r , and E_s . The magnitude of the evaporative terms at thermoneutral or cold stressed conditions will be determined by the water vapor pressure, and these variations will be compensated by changes in M . Under heat stressed conditions many animals increase evaporation by panting. The physical effort of panting increases metabolic heat production. Additional evaporation is needed to counteract this increased heat production. The water vapor pressure strongly affects the amount of cooling for a given amount of physical effort. Thus, the metabolism and evaporation required for thermoregulation in otherwise thermally equivalent environments is affected by water vapor pressure (Adolph, 1949; Lasiewski, Acosta & Bernstein, 1966). Since the effect of water vapor pressure has not been explicitly included in the analysis, it must be specified in addition to T_{es} . Then, rather than appearing as an environmental parameter, vapor pressure appears as a limit on the evaporative cooling of the animal. It is possible to incorporate the water vapor pressure of the environment into similar stress indices (Gonzalez *et al.*, 1974). However, the direct measurement of these indices with models is difficult or impossible. Thus, they are limited to being used as calculated stress indices summarizing the thermal environment.

Another potential problem with the assumption that M^* directly reflects thermoregulatory metabolism and evaporation requirements is that evaporation from the respiratory tract, skin surface, and pelage surface are not strictly identical in the amount of heat removed from the body core by a given amount of evaporation. This is shown by the coefficients of E_s and E_r in equation (13). Since these coefficients are partly dependent on environmental conditions due to the presence of the H , G , and K_{sf} terms, a change in otherwise equivalent conditions could alter the effectiveness of E_s or E_r in cooling the body core. The discussion in the next section shows that this is a significant concern only when the pelage of the animal is wet.

(F) EFFECTIVE NET METABOLIC HEAT PRODUCTION

The effective net metabolic heat production M^* is the net thermal effect of the metabolic processes and evaporative water loss of the animal. Metabolism and evaporation have long been measured in the study of thermal physiology,

and experimental procedures are well developed (Depocas & Hart, 1957; Lasiewski *et al.*, 1966). A potential problem in the application of the results of these measurements arises from the difference in the heat removed from the body core by a given amount of evaporation, noted in the preceding section. The lack of equivalence is shown in equation (13), where the E_b , E_s , and E_r terms are multiplied by different coefficients involving parameters related to environmental conditions. These coefficients express the fact that the heat required to vaporize water on the skin or pelage surface of the animal comes from both the body core and the environment. The coefficients may be regarded as giving the efficiency of evaporation at a particular site, defined as: (efficiency of evaporation) = (heat of vaporization supplied by core)/(total heat of vaporization supplied by both core and environment). The efficiency is unity if all of the heat of vaporization is used to cool the core, and decreases when some of the heat of vaporization cools the environment. Note that this is not the same as the efficiency of water use, since the analysis neglects water lost to the animal by simply dropping off without evaporating [see section 3(A)].

An assessment of the efficiency of water use by an animal for evaporative cooling must consider all water loss, since the usual thermoregulatory responses of sweating, saliva or urine spreading, and even panting often result in some water loss by dripping. Consideration of the efficiency of evaporation is rather of utility in determining the need for separate determination of E_b , E_s , and E_r in place of the straightforward measurement of $E = E_b + E_s + E_r$. For the lumped measurement of E to be valid, either E_s and E_r must be negligible, or their coefficients must be near unity. The considerable experimental difficulty involved in separate measurement of E_b , E_s , and E_r makes a general estimate of the values of the efficiencies of evaporation useful.

The coefficient of E_b is unity, reflecting the action of E_b directly at the body core. [This is not strictly true in a more detailed model (Seymour, 1972).]

Since $K_{sf} < K_f$, the denominator of the coefficient of E_s is larger than the numerator, and the efficiency of evaporation from the skin surface,

$$\mathcal{E}_s = \frac{1 + \frac{H+R}{K_f}}{1 + \frac{H+R}{K_{sf}}} \quad (22)$$

is less than 1. However, since $K_f \ll K_s$ for an animal with effective pelage, $K_f \cong K_{sf}$, and the efficiency of cutaneous evaporative cooling, \mathcal{E}_s , is nearly unity and largely independent of H and R . Effective pelage restricts the mass transport of water vapor, and the amount of cooling possible is small. Heavy

sweating wets the fur and results in a large value of E_r . The vapor pressure gradient across the fur is also greatly reduced, so that E_s becomes negligible.

The efficiency of evaporative cooling at the outer surface of the animal is:

$$\mathcal{E}_{rf} = \frac{1}{1 + \frac{H+R}{K_{sf}}} \quad (23)$$

The efficiency of fur surface evaporation, \mathcal{E}_{rf} , is less than \mathcal{E}_s since the denominators are the same, but the numerator of the expression for \mathcal{E}_s is always greater than 1. The efficiency of fur surface evaporation is rather poor, since K_{sf} is almost always less than half of $H+R$ (Tracy, 1973). The efficiency can then be less than 67%. The value of E is thus almost always a poor indicator of total evaporative cooling in an animal with wet fur. This poor coupling of evaporative cooling to the body core contributes to the poor efficiency and effectiveness of water use in sweating and saliva spreading. This is reflected in the common observation that sheep, with their heavy wool coat, sweat very little compared with more thinly furred cattle (Yeates, 1967), and that desert rodents rarely resort to saliva spreading, commonly seen in laboratory mice and some other non-desert rodents under heat stress (Hart, 1971).

For a naked animal, the surface evaporation efficiency, \mathcal{E}_{rn} , is

$$\mathcal{E}_{rn} = \frac{1}{1 + \frac{H+R}{K_s}} \quad (24)$$

Since K_s is typically large relative to $H+R$ for small animals (Porter *et al.*, 1973), particularly since the skin is normally vasodilated when sweating, \mathcal{E}_{rn} usually exceeds 0.8.

Table 2 presents some evaluations of the evaporation efficiencies given by equations (22)–(24), using general data on the properties of biological materials given by Birkebak (1966), Chato (1966), Kreith (1965) and Porter & Gates (1969). The following conclusions may be drawn about using $(M-E)$ in place of M^* :

(1) Skin evaporation, E_s , may be safely lumped into E in animals with effective pelage, since the efficiency \mathcal{E}_s is usually greater than 0.95. If the fur is dry, $(M-E)$ may be used in place of M^* .

(2) Pelage surface evaporation, E_r , may not be lumped into E in animals with wet pelage, since the efficiency is low ($\mathcal{E}_{rf} = 0.20-0.58$). Significant E_r in animals with pelage will cause inaccuracies in assuming that $(M-E)$ is equal to M^* .

(3) Surface evaporation from naked animals, $E_s = E_r$, may be lumped into E in most cases, but care is required. Since E_r is usually significant only when the animal is heat stressed, and therefore the animal is probably vasodilated, the higher skin heat transfer coefficient will often apply. Then $\delta_{r,m} = 0.89-0.98$, so that E_r and E_b may be lumped, and $(M - E)$ used for M^* .

(4) Caution should be exercised in applying these results to animals with pelage, but also having appreciable areas of the body thinly insulated and well-supplied with sweat glands or otherwise moist (ventral-pelvic regions of some mammals, or the mucosa around the eyes, nose, and mouth) where equation (24) may be more applicable than equations (22) or (23). A distributed parameter analysis may be required in these cases.

The preceding observations show that the assumption that $M^* = (M - E)$ is inaccurate principally when an animal has wet fur or feathers. This may occur in aquatic animals, animals under heat stress that respond by sweating heavily or spreading saliva, or after unusual immersions (Moen, 1967; Lentz & Hart, 1961). Under thermoneutral or cold stress conditions, E_s and E_r are small relative to M and E_b , so that the overall error in assuming $M^* = (M - E)$ is quite small.

4. Application to Experimental Studies

(A) SUGGESTIONS FOR METABOLISM CHAMBER DESIGN

Measurements of the metabolic and evaporative water loss rate and overall thermal conductance of the live animal are needed for both a detailed energy budget analysis and the integrated parameter approach described in this paper. The metabolism chamber used for these measurements must have a well-defined temperature, preferably equal to T_e , and stable wind conditions so that K_0 may be determined under standardized, repeatable conditions. The traditional respirometer enclosure fails to satisfy either requirement. First, chambers are often constructed with metallic walls (e.g. Scholander *et al.*, 1950). Bare metal has an emissivity of $\epsilon = 0.05-0.60$, so that the radiation temperature of a small enclosure is partly determined by the temperature of the animal. The operative environmental temperature of the enclosure thus is poorly defined, and may differ significantly from air or wall temperature. Porter (1969) noted that this metallic wall effect could significantly affect metabolism measurements in cold stressed animals. A layer of flat black ($\epsilon > 0.95$) paint easily eliminates this problem. However, it does not guarantee a well-defined T_e , since free or nearly free convection conditions normally obtain. In addition to being unsuitable for determining the overall thermal conductance of the animal, as described in Appendix A, the rate of

heat transfer from the wall of the chamber to the air is low. As a result, air and wall temperature differences of $|T_a - T_w| = 5^\circ\text{K}$ can easily exist during measurements on cold stressed endotherms (Morhardt & Gates, 1974). While corrections such as that used by Morhardt & Gates (1974) or measurements of T_e with a model are possible, a better solution is to increase the rate of convection from the chamber walls. This could be done by placing a fan in the chamber to stir the air. It would then be meaningful to assign a temperature $T_{mc} = T_w = T_a$ to the chamber. The operative environmental temperature of the chamber will equal T_{mc} for any animal in the chamber, with a small error resulting from the non-linearity of thermal radiation, as described in Appendix C. The difference between T_e and T_{mc} is reduced by stirring the air in the chamber. Table 3 shows the decrease in the $|T_e - T_{mc}|$ difference due to increasing the effective wind speed from 10 to 100 cm s^{-1} . Simple stirring, however, is not satisfactory for determining K_0 . The air flow would be complex and unstable, so that H and thus K_0 would depend on the design of the chamber and the precise location of the animal within the chamber. Consequently, it would be difficult to duplicate results in different laboratories (Kerslake, 1972).

Repeatable laboratory measurements of M , E , and K_0 on live animals thus require unconventional metabolism chamber design. The chamber walls must be black at thermal wavelengths. The air must be in motion, so that air temperature will essentially equal wall temperature. These conditions define the metabolism chamber temperature, T_{mc} , and ensure that it will be essentially equal to T_e for any animal in the chamber. Further, it must have smooth, unidirectional air flow at a sufficient velocity to ensure stable, repeatable conditions for measuring K_0 . The wind velocity must be greater than about 80 cm s^{-1} to allow consistent velocity measurements in different laboratories (Gagge & Hardy, 1967). Turbulence in the incident air flow must be avoided, since it causes an increase in convective heat transfer which can be greater than 50% (Kreith, 1965; Pearman, Weaver & Tanner, 1972). The increase is roughly proportional to turbulence intensity, and is greatest at low frequencies (less than 100 Hz). Turbulence in wind-tunnel type enclosures can be minimized by the use of flow straightening honeycomb and diffusers, as described in texts on wind tunnel design (e.g. Pope & Harper, 1966). Unfortunately, a well-designed closed-circuit wind tunnel has a very large total volume relative to the test area, which complicates the measurement of oxygen consumption and evaporative water loss. Modifications reducing the volume of the tunnel result in increased turbulence. Also, the animal must be contained in the test section, and the required screens increase turbulence and produce non-uniformities of 5–10% in large scale flow due to non-uniformities in the screen weave. Thus, it will usually be necessary to measure the

TABLE 3

Errors due to the non-linearity of thermal radiation in $(T_r - T_e)$, K_0 , and Q due to a 20 °K difference between: (1) T_r and \bar{T}_r in a calculation. (2) T_r and T_{mc} in a standard metabolism chamber [see section 4(A)]. (3) T_r and T_r^m when a model is used to measure T_e and K_0 [see section 4(B)]. Errors other than those due to the non-linearity of thermal radiation which affect measurements made with taxidermic models are not included. Calculations are done for the hypothetical animal used in Table 2. The calculation assumes $T_r = 300$ °K and \bar{T}_r , T_{mc} or $T_r^m = 280$ °K, with body temperature adjusted to give this condition. A 20 °K difference is difficult to attain with a well-insulated animal. The body temperatures assumed in the calculations for the furred, vasoconstricted animal are excessively high as a result, and realistic errors will be much smaller. Note that the radiation errors in T_e and K_0 partially cancel in determining the total sensible net heat transfer by all processes, Q .

Diameter of animal (cm)	$\Delta(T_r - T_e)/^\circ\text{K}, \%$		$\Delta K_0/^\circ\text{K}, \%$		$\Delta Q/^\circ\text{K}, \%$	
	$V = 10$	$V = 100$	$V = 10$	$V = 100$	$V = 10$	$V = 100$
Furred						
2	-4.2	-2.0	4.3	1.2	2.2	0.6
5	-5.4	-2.9	4.7	1.6	2.4	0.8
10	-6.2	-3.5	4.7	1.7	2.5	0.9
20	-6.9	-4.2	4.3	1.6	2.3	0.9
50	-7.7	-5.0	3.4	1.4	2.0	0.8
Naked						
2	-4.2	-2.0	8.8	4.0	4.3	1.9
5	-5.4	-2.9	11.4	5.7	5.6	2.8
10	-6.2	-3.5	13.3	7.0	6.6	3.4
20	-6.9	-4.2	14.9	8.2	7.4	4.0
50	-7.7	-5.0	16.6	9.6	8.2	4.7

velocity distribution and turbulence over the cross-section of the working area and adjust the size and arrangement of diffusers to obtain good flow conditions. This is particularly necessary when partial diffusers are used to shape the flow profile to match the logarithmic profile seen outdoors (Monteith, 1973; Rosenberg, 1974). This wind profile matching improves the accuracy of measurements on animals on the surface of the ground (Pope & Harper, 1966).

The measurement of velocity distributions and turbulence requires a hot-wire anemometer. Hinze (1959) describes standard procedures. These instruments sense velocity with a sensor about 5 mm long, and have a time response of less than 1 ms. The turbulence intensity in the direction of flow,

\mathcal{J} , is found using the relation:

$$\mathcal{J} = \frac{\text{rms fluctuations}}{\text{mean velocity}} = \frac{1}{V_0} \left\{ \frac{1}{p} \int_0^p [V(t) - V_0]^2 dt \right\}^{1/2} \quad (25)$$

where

$$V_0 = \frac{1}{p} \int_0^p V(t) dt. \quad (26)$$

Here, p is the time period of interest, V_0 is the average air velocity, and $V(t)$ is the instantaneous air velocity.

Various wind-tunnel metabolism chamber designs are possible. Cena & McLaren (1970) describe a fairly conventional single-return tunnel, with a large volume and good flow characteristics. Gessaman (1972) describes an annular-return design with a small volume which can be constructed easily. Bakken (1976*a*) describes a small-volume, double-return design. The optimum design depends on the nature of the animal to be studied, the type of study, and available resources.

Metabolic rate, evaporative water loss, and overall thermal conductance can be measured at different wind speeds and values of $T_{mc} = T_e$ by using standard methods (Depocas & Hart, 1957; Lasiewski *et al.*, 1966). The overall thermal conductance of endotherms can be determined by using measurements of T_b , $T_{mc} = T_e$, M , and E in equation (8) or (15), as appropriate. Cooling curve determinations of K_0 for ectotherms may be made using the analysis based on equation (8) described by Bakken (1976*b*).

A wind tunnel metabolism chamber also serves as the standard reference metabolism chamber used to define standard operative environmental temperature in section 3(ε). The application of results from different studies is aided by the use of a standard set of conditions. I tentatively suggest defining $T_{es} = T_{mc}$ at a wind velocity of 100 cm s^{-1} and a turbulence intensity of 5–7%. These conditions are easily obtained even in small-volume wind tunnel metabolism chambers.

(B) USE OF TAXIDERMIC MODELS TO MAKE INTEGRATED MEASUREMENTS OF THE THERMAL ENVIRONMENT

(i) Applications

Values of T_e , K_0 , and T_{es} may be calculated from the primary heat transfer parameters measured in general energy budget studies (e.g. Birkebak, 1966; Bartlett & Gates, 1967; Spotila *et al.*, 1972; Moen, 1973; Porter *et al.*, 1973; Smith & Miller, 1973; Morhardt & Gates, 1974). Such calculated values are a useful summary of a complex environment. Also, T_e , K_0 , and M^* can be measured in laboratory experiments on live animals, so that calculated values

based on environmental data are a straightforward way of relating laboratory data to the field.

However, direct measurements of T_e , K_0 , and T_{es} with taxidermic models of the animal under study make more effective use of the simplicity of the linear approximation to overall heat transfer. The sound theoretical basis for the use of models of the animal as probes to measure the thermal environment is an important practical result of this analysis. Models of the animal under study have been suggested (Parry, 1951; Heath, 1964) or used (Lewis, 1963; Boyer, 1965; Markel, 1971) as a means of measuring the effective temperature of the environment. With the exception of a recent study by Thorkelson & Maxwell (1974), the suggestion or use of models has been accompanied by little heat transfer analysis.

Direct measurements of the integrated parameters with taxidermic models is most useful for animals weighing less than 5 kg, since models of larger animals are unwieldy. There are two principal applications for the direct measurement of integrated parameters with models: (1) They provide a simplified approach to obtaining descriptive data on the thermal environment as perceived by the animal for studies in behavior and physiology. Because the model duplicates the external heat transfer properties of the animal with fair accuracy, it acts as a reliable analog computer summing the different heat flows to and from the animal, and includes the effects of non-uniform distribution of the heat flows. Direct measurements of T_e , K_0 , and T_{es} thus bypass much of the experimental and mathematical complexity of a full energy budget study. Since T_e , K_0 , and T_{es} are well-defined in terms of a detailed energy budget study, the results of studies using integrated measurements may be used with confidence of the relation of the observed physiological and behavioral responses to thermal factors. (2) Direct measurements of T_e , K_0 , and T_{es} with models probes the thermal environment at the same size scale as the animal itself. Variations in the thermal environment are of considerable significance in behavior and ecology. For example, horned lizards need to learn the details of their thermal environment for optimum behavioral thermoregulation (Heath, 1965). The small-scale variations in the operative environmental temperature of a small animal such as a lizard on the surface of the ground are substantial. Bakken & Gates (1975) noted 5 to 10 °K variations in T_e due to microtopography and orientation, and up to 24 °K due to shading. In a simple environment, such as the desert flats studied by Porter *et al.* (1973), wind speed and air temperatures may be extrapolated to points near the surface using known micrometeorological relations (Rosenberg, 1974). In more complex environments, rocks and vegetation produce complex variations in wind direction, velocity, and turbulence (see Moen, 1973, Fig. 5.10). They also produce a complex visible and thermal radiation

field. In such habitats, a site of thermoregulatory importance to the animal may be smaller than the space occupied by a complete set of micrometeorological instruments, and complex enough to make extrapolation from nearby measurements uncertain. A taxidermic model of the animal may be used to make reliable integrated measurements in almost any area accessible to the live animal. This facilitates small-scale studies which are otherwise difficult or impossible. Measurements with models are virtually essential when the environment is so intimate that the presence of the animal significantly alters wind flow or warms the environment with lost body heat. Such modifications of the immediate environment can be an important factor in ecology, for example by extending the winter range of small birds which roost at night in dense evergreens (W. R. Dawson, private communication). A heated taxidermic model, placed in sheltered areas used by the live animal, simulates the effect of the animal in ameliorating its environment, and can be used to measure T_{es} directly.

Predictive computer simulation studies such as Porter *et al.* (1973) require separation of the physically distinct heat transfer processes acting on the animal. T_e , K_0 , and T_{es} convolute several heat transfer processes. Thus, direct measurements of these parameters with models are not, in themselves, sufficient data for such studies, although they can provide valuable additional information.

(ii) Construction of models

One source of uncertainty in the accuracy of direct measurements using taxidermic models is how well the model duplicates the actual animal. This problem is common to most energy budget studies, since models are used to measure the conductance of the integument and the convective and radiative conductances of the animal (Morrison & Tietz, 1957; Bartlett & Gates, 1967; Heller, 1971; Walthen *et al.*, 1971; Porter *et al.*, 1973). Models used to make direct measurements of T_e , K_0 , and T_{es} must principally duplicate the convective and radiative heat exchange of the animal, and the insulation of any fur or feathers. Convective heat transfer presents no problem, since the size and shape of the live animal is precisely duplicated. The absorption and emission of radiation are also easily duplicated, with some possible problems for animals which can alter their color greatly. The principal uncertainty is in the duplication of K_{sf} . The model cannot simulate the effect of vasoconstriction and vasodilation on K_s , nor can it simulate the effects of changes in the erection of fur or feathers in live animals, although the degree of erection of the insulation can be varied considerably on different models of birds and mammals. The effects of these and other errors will be discussed along with the methods for measuring T_e , K_0 , and T_{es} .

Models used to measure T_e , K_0 , and T_{es} should be constructed on a metal body core to simulate the high rate of internal heat transfer by blood flow. This gives accurate surface temperature distributions and allows the measurement of an isothermal body core temperature, T_b^m . (I will use a superscript "m" to indicate parameters for the models, which may or may not be identical with those of a live animal at the same location.) For most studies, it is desirable to have the model track rapid changes in the thermal environment. The time constant, τ^m , should thus be as short as possible. This should be done by making the heat capacitance of the model, C^m , as small as possible [see equation (9)]. Bakken & Gates (1975) describe an electroforming technique which gives thin-shell copper models with C^m less than 10% of the heat capacitance of the animal. For studies where the time response of the live animal is to be simulated, the heat capacitance of the animal must be duplicated. Since the model duplicates the volume of the animal, the metal used in the core must duplicate the heat capacity per unit volume of the animal, not the heat capacity per unit weight. Tissue has a whole body average of $2.9\text{--}3.3 \text{ J cm}^{-3} \text{ }^\circ\text{K}^{-1}$, which is matched by various brass and bronze alloys. Bartlett & Gates (1967) and Porter *et al.* (1973) describe the procedures for making such casts of animals.

Care should be taken to duplicate the natural posture(s) of the animal in the cast, since posture and orientation affect most of the heat transfer parameters, and thus T_e , K_0 , and T_{es} . Casts can be made of live ectotherms without injury to the animal (Porter *et al.*, 1973; Bakken & Gates, 1975) and give far more lifelike results than dead animals. Birds and mammals generally must be killed and skinned to make a cast for the core. The body can be arranged in a lifelike posture and frozen in position with dry ice to allow casting, as described by Morrison & Tietz (1957) and Bakken & Buttemer (1976).

The model is completed by duplicating the external heat transfer properties of the animal. The model of a naked animal should be painted to duplicate the absorptivity of solar radiation. Virtually all animals and flat paints are effectively black ($\epsilon > 0.95$) at thermal wavelengths. Models of animals with fur or feathers should be covered with the skin of the animal. The skin should be carefully cemented to the metal core to eliminate air pockets that would produce a spurious increase in K_{sf} . Alpha cyanoacrylate adhesives bond wet skin to metal effectively.

(iii) Operative environmental temperature

Operative environmental temperature, T_e , is measured by placing the model at the point of interest and measuring T_b^m . This will then, by the equivalence of $T_b^m = T_e$ noted in section 3(c), give a value of T_e for that animal and

orientation averaged for $1-2 \tau^m$. This is adequate time resolution of the thermal environment, since a thin-shell copper model of a small animal can have a time constant of less than a minute (Bakken & Gates, 1975). A solid cast will give a longer averaging period, if desired.

Some differences between T_e and T_e^m are possible. One possible error results from the dependence of T_e on K_{sf} , seen in equation (12). The model cannot duplicate the effects of piloerection or cutaneous blood flow, so that K_0^m and K_0 may differ, resulting in a difference between T_e^m and T_e . Fortunately, the dependence is very weak. It disappears when $K_{sf} \gg G$, which is a correct assumption unless the animal has a large part of its venter in contact with the ground. Another error occurs if the surface temperature of the animal and the model differ. First, there will be an error due to the non-linearity of thermal radiation. The effect is essentially as discussed for surface-metabolism chamber temperature differences in sections 4(A), 3(C), and Appendix C. Table 3 gives some numerical examples for two effective wind speeds. The error is small—around 5% of the $(T_r^m - T_r)$ difference. Second, there can be an error in the convective conductance if free convection obtains, since H_f is proportional to $(T_r - T_a)^{1/4}$. A third potential source of error is a mismatch in the absorptivity of solar radiation. A change in color from white ($\sim 25\%$ solar absorption) to black (98% solar absorption) can change the T_e of a small animal by 12 °K or more (Bakken & Gates, 1975). Thus, the absorptivity of the paint used on a model of a naked animal should be closely matched to the absorptivity of the animal, so that $Q_a^m = Q_a$. Some reptiles and amphibians can alter their absorptivity, which complicates matters. The effect is often small, but it may be necessary to use two models bracketing the absorptivity of the animal. In sum, models will give good measurements of T_e unless the animal can substantially alter its absorptivity, or unless free convection obtains and $T_r^m \neq T_r$.

(iv) Overall thermal conductance

The overall thermal conductance of an animal with a given posture and orientation can also be measured by placing a model at the point of interest. The measurement is more difficult, and requires the model to have an internal electric heater. Three procedures may be used to measure K_0^m : (1) The heater may be switched on and off at intervals of $5-7 \tau^m$, which allows the model to reach steady-state by the end of each interval. The value of T_b^m at the end of the heater off cycle gives T_e . At the end of the heater on cycle, equation (15) gives $T_b^m = T_e^m + M^{*m}/K_0^m$. By assuming that conditions were essentially constant, K_0 can be computed from the two equilibrium values of T_b^m and heater power, M^{*m} . Time resolution is poor since $10 \tau^m$ is required for each

measurement. It is unlikely that conditions will be constant for this period, even for a model with low heat capacity, so that the determination is not very accurate. (2) Much faster time response is possible by using two models, one heated and one unheated, to measure T_e^m and heated T_b^m simultaneously. Measurement of heater power allows K_0 to be calculated as before. The time resolution is gained at the expense of spatial resolution. The need for two locations with equivalent T_e 's restricts this method to relatively uniform areas. The orientation of the models must be identical, and the equivalence of T_e in the two locations checked periodically by comparing T_b^m for the two models with the heater off. (3) A third method allows K_0^m and T_e^m to be determined simultaneously with a single model. A determination requires only $1 \tau^m$, and measurements can be made at intervals of 2–3 τ^m . The procedure is essentially a cooling-curve experiment on the model. The heater in a single model is switched on and off at intervals of 1–2 τ^m , and T_b^m is measured during the heater off cycle as a function of time. The time constant τ^m and T_e can be determined simultaneously with the numerical analysis routine described by Bakken (1976a). Then K_0^m can be calculated as $K_0^m = \tau^m / C^m$. The heat capacitance of the model, C^m , can be measured directly or computed from the weights and published specific heats of the materials used in the model. The cooling curve analysis will indicate when significant changes in conditions occur during the measurement, so that these data may be eliminated. The principal disadvantage of this method is the large quantity of data to be handled.

There are two principal sources of error in measurements of K_0 with models in field studies: First, there will be errors in heat transfer by radiation and free convection when the surface temperature of the model and animal differ, as described earlier for measurements of T_e and in section 3(D). Table 3 gives some numerical examples of the error in K_0 due to the radiation effect. The radiation errors in T_e and K_0 tend to cancel in determining the total heat flow from the animal. Second, the model cannot duplicate the suite of thermoregulatory vasomotor and piloerective responses available to the live animal. As a result, K_s^m and K_f^m will not always equal K_s and K_f even for a carefully constructed model, so that K_0^m and K_0 can differ. The effect is small for naked animals such as reptiles and amphibians, since K_s has little effect on K_0 (Porter *et al.*, 1973). For animals with fur or feathers, $K_{s,f}$ is the major factor determining K_0 (Tracy, 1973), and there can be substantial differences between K_0^m and K_0 .

The uncertainties associated with animals with fur or feathers limits direct measurements of K_0 using models to the study of naked animals, which are predominantly ectothermic. Since both K_0 and T_e must be specified to determine the heat flow from an animal, direct measurements of these two

parameters separately are useful principally in the study of ectothermic animals. Fortunately, insulated endotherms can be studied by using standard operative environmental temperature, T_{es} , which can be measured with the less restrictive assumption that $K_0^m \propto K_0$.

(v) *Standard operative environmental temperature*

Standard operative environmental temperature, T_{es} , was defined in section 3(E) as the temperature of a standard reference metabolism chamber which imposed the same requirement for thermoregulatory M^* as the general environment. It is essentially a specification of M^* needed by the animal to maintain T_b . One way to measure M^* would be to place a model equipped with an electric heater in the environment, and regulate the power supplied to the heater to maintain $M_b^m = T_b$. The power supplied to the heater, M^{*m} , can be measured easily. However, K_0^m may not generally be assumed equal to K_0 because of the problems in duplicating changes in piloerection and vasomotor response noted earlier. Thus, it can not be assumed that $M^{*m} = M^*$, as has been done in some studies using heated taxidermic models (Thorkelson & Maxwell, 1974). However, it is reasonable to assume that the animal vasoconstricts, vasodilates, and piloerects in a consistent way at a given level of thermal stress (i.e. of T_{es}). Since a model constructed to duplicate the approximate properties of the animal will be affected by changes in wind and radiation in essentially the same way as the live animal, it is reasonable to assume that there will be a proportionality between K_0^m and K_0 at any given T_{es} , so that

$$K_0^m = B(T_{es})K_0 \quad (27)$$

where $B(T_{es})$ is the proportionality between K_0^m and K_0 as a function of thermal stress, T_{es} . As noted earlier, T_e is independent of K_{sf} when $K_{sf} \gg G$. Even for well insulated animals, this assumption is true because only the feet are normally in contact with the ground, giving a small contact area. Heat exchange with the ground is often further reduced by counter-current heat exchange in the limbs (Scholander & Krog, 1957). Then $T_e^m = T_e$, and T_{es} will be approximately the same for the animal and the model:

$$T_{es}^m \cong [B(T_{es})K_0/B(T_{es})K_{0s}]T_e + [1 - B(T_{es})K_0/B(T_{es})K_{0s}] = T_{es}. \quad (28)$$

Thus, measurements of K_0^m and T_e made in the environment with a model can be used to find a standard operative environmental temperature which is nearly the same for both the model and the live animal. The live animal may then be placed in the standard reference metabolism chamber at the values of $T_{es} = T_{mc}$ determined with the model, and the value of M^* needed by the animal at the point measured with the model determined. The individual values of M and E that the animal would have had can be determined by

measuring the water vapor pressure along with T_{es} . Then that vapor pressure can be duplicated in the reference chamber when M and E are measured on the live animal. [Note that it is not correct to duplicate relative humidity. Relative humidity is a strong function of air temperature, which can vary considerably at a given T_{es} . Vapor pressure is the actual factor determining evaporation (Kerlake, 1972; Monteith, 1973). Wind speed can also influence evaporation from a naked animal, but has little influence on evaporation from an animal with dry insulation.]

It is not necessary to measure T_e^m and K_0^m separately and then compute T_{es} from equation (21) or (28). Standard operative environmental temperature was defined so as to uniquely determine the M^* needed to maintain a given body temperature. Thus, there is a direct one-to-one relation between T_{es}^m and M^{*m} . The relation can be readily measured by placing the model in a standard metabolism chamber, regulating T_b^m at the value maintained by the animal, and measuring M^{*m} as a function of T_{es} . A graph can then be constructed relating M^{*m} to T_{es} . A similar graph can be constructed relating T_{es} and M^* for the live animal. Since both graphs have the same parameter, T_{es} , for one axis, they may be combined into a single graph relating M^{*m} and M^* . Similar graphs can be constructed relating M^{*m} to M and E at various humidities.

Essentially continuous records of T_{es} can be made by constructing the model on a thin-shell electroformed copper body with embedded resistance wire as a heater. Bakken & Buttemer (1976) describe the construction procedures. The heater can be supplied by a proportional controller set at the body temperature of the animal. The heater power can be measured continuously by measuring the current supplied to the model. Constantan heater wire will have a constant resistance at all power loads, so that $M^{*m} = (\text{current})^2 (\text{heater resistance})$. Since T_b^m is held nearly constant, the response of the model to changes in conditions is far more rapid than the time constant of the model, τ^m . This is essentially the principle used to achieve fast response in constant-temperature hot-wire anemometers (Hinze, 1959).

The measurement of T_{es} is not subject to most of the errors discussed for the measurement of T_e and K_0 . Since the model is heated to the T_b of the animal, the surface temperatures of the animal and the model will be nearly equal. The errors due to the non-linearity of thermal radiation and free convection are thus negligible. Since virtually all homeotherms are covered with fur or feathers, the radiative and convective properties of the model will be identical to the animal. The only source of error is the assumption that the animal and the model will respond similarly to changes in wind, solar radiation, and temperature so that $K_0^m = B(T_{es})K_0$. As long as the model is constructed with approximately the same degree of erection of the fur or

feathers that the animal would have, the assumption is undoubtedly fairly accurate. However, the assumption is likely to fail if the animal and the model differ greatly. It may well be desirable to have two or three models with different degrees of erection of the insulation for use over different temperature ranges. The actual errors in the use of models to determine T_{es} must be studied experimentally in the laboratory. This work is in progress, and preliminary results will be reported elsewhere (Bakken & Buttemer, 1976).

5. Summation

It is possible to formulate a simple, linear representation of heat transfer between an animal and its environment by using lumped parameters and a linearized expression for thermal radiation. This relation, the linear approximation to overall heat transfer, is similar in its mathematical form to "Newton's Law", but the parameters are quite different.

The first parameter is the effective temperature of the environment, called the operative environmental temperature, T_e , which combines heat transfer to the air, ground, can surrounding surfaces, and the absorbed solar radiation. It equals the temperature of an inanimate object, such as a taxidermic model, in thermal equilibrium with the environment. A suitably constructed model using a thin-shell metal core can respond to changes in the environment with a time constant of less than a minute. It may thus be used as a probe to measure nearly instantaneous values of T_e at the point in the habitat occupied by the model. The small size of the model allows it to be used to probe the variations in the thermal environment at the size scale experienced by a small animal.

T_e can often differ from T_a by 24 °K, and vary by 5–10 °K simply due to changes in microtopography and the orientation of the animal. These variations can be significant factors in thermoregulatory behavior. Measurements of T_e with a model are not subject to the distributed parameter assumption used in the analysis, since the model integrates the spatial environment in the same way as the animal. However, if the surface temperatures of the animal and the model differ, there will be an error in T_e measured by the model of about 5% of the difference in surface temperatures.

Although the operative environmental temperature of an environment is generally different for different animals, it is possible to construct a laboratory environmental chamber so that the temperature of the chamber, T_{mc} , is essentially equal to T_e for any animal inside. The requirements are that the surfaces of the chamber be black ($\varepsilon \cong 1$) and that the air in the chamber be vigorously stirred, so that the wall and air temperatures of the chamber are

identical, and thus equal to T_e . Radiation, other than the thermal radiation from the walls of the chamber, must be essentially zero.

The second parameter is the overall thermal conductance K_0 . It can be measured in the laboratory, using a live animal, provided that the third parameter, the effective net metabolic heat production M^* , can be measured accurately. Unless the animal has wet pelage, or is naked and strongly vasoconstricted, the assumption that M^* equals the dry metabolic heat production ($M - E$) is adequately accurate. Then K_0 can be determined from equation (8) by measuring T_b , M , and E in a metabolism chamber properly constructed to give a well-defined T_e . The outdoor environment presents more of a problem. A taxidermic model of the animal cannot duplicate the full suite of vasomotor and piloerective responses present in a live animal, and thus can be used to give only an approximate indication of the effect of an environment on K_0 , unless the thermal conductance of the animal's integument is much greater than the heat transfer coefficients to the environment, as is approximately true for small lizards and amphibians.

It may be possible to estimate K_0 , T_e , and thus the M^* required for an animal to maintain T_b constant in an outdoor habitat by using a heated taxidermic model and a standard metabolism chamber. This standard metabolism chamber must maintain air and wall temperatures equal to define T_e . In addition, it must provide a reasonably smooth, unidirectional air flow to fix the K_0 of an animal in the chamber. Then the standard operative environmental temperature of an outdoor environment, T_{es} , is defined as the temperature (T_e) of a standard metabolism chamber in which an animal requires the same M^* to maintain a given body temperature as would be required to maintain the same T_b in the outdoor environment. The heater power required to maintain a given T_b^m in a taxidermic model at a point in a natural habitat can be used to measure the T_{es} of the habitat for that model. If it can be assumed that the taxidermic model is sufficiently similar to the live animal that the K_0 of the model has a constant proportionality to the K_0 of the animals for all wind and radiation conditions, the value of T_{es} determined by the model is approximately equal to the T_{es} experienced by a live animal in the same location at the same time. Now the standard metabolism chamber is designed so that T_e , and thus T_{es} , is the same for any animal or object inside. Thus, the actual M^* required by a live animal to maintain T_b in an environment can be measured by placing the animal in a standard metabolism chamber at the values of T_{es}^m measured by a model.

The linear approximation to overall heat transfer and the associated integrated parameters are complementary to the conventional energy budget approach. Because the integrated parameters T_e , K_0 , and T_{es} confound the actual physical heat transfer processes, their utility is limited to descriptive

problems. Similarly, direct measurements of the integrated parameters alone do not suffice as a data base for predictive computer simulation studies. Like other analyses that use lumped parameters and an isothermal body core, this analysis cannot be used to study the effect of variations in thermal loads over the surface of the animal, or the effect of heat transfer within the body core. However, the linear approximation to overall heat transfer has many uses in descriptive studies and as an adjunct to full energy budget studies.

Because the integrated parameters T_e , K_0 , and T_{es} are known as functions of the individual heat transfer parameters, they may be computed from the more general data as a summary of the thermal environment through time. For the same reason, measurements of physiology and behavior made with reference to the integrated parameters may be used in more general energy budget studies. Since T_e , K_0 , and M^* are essentially the parameters measured in laboratory metabolism studies, an integrated thermal stress parameter such as the standard operative environmental temperature is a particularly direct way to relate laboratory data to field measurements of environmental parameters. Direct measurements of T_e , K_0 , and T_{es} made with taxidermic models may be used to validate computer simulations of animal-environment interactions. Taxidermic models also may be used to measure T_e , K_0 , and T_{es} in confined spaces or areas very near the ground which are inaccessible to conventional instruments. Models also can aid the study of the effect of the animal in conditioning its immediate environment by warming it with lost body heat and by restricting air movement. In many behavioral and physiological studies where the details of the thermal environment play a secondary, descriptive role, direct measurements using taxidermic models greatly simplify the experimental and mathematical work needed while providing valid descriptive data.

This work has been supported by Atomic Energy Commission Grant AT(11-1)-2164 and National Science Foundation Grant GB 40980. I wish to express my deep appreciation to Dr David M. Gates for his support and encouragement of this work, which was done in his laboratory. William A. Buttemer, William R. Dawson, David M. Gates, and James R. Spotila read the manuscript and offered many valuable suggestions. Special thanks go to my wife Laura for typing, reading, and commenting on the manuscript.

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APPENDIX A

In principle, free convection could be chosen as the standard metabolism chamber condition. This has the attraction that free convection obtains in most metabolism and thermal conductance studies to date. Thus, a free convection standard would allow existing data and simple equipment to be

used. However, there are several objections to free convection. First, heat transfer to the air in the chamber from the walls is slow. The heat lost from a small endotherm in the chamber can easily raise air temperature 5 °K above wall temperature (Morhardt & Gates, 1973). The effective temperature of the chamber will lie somewhere between air and wall temperature, and is thus poorly known. Second, free convection conductances H_F are approximately proportional to $(T_r - T_a)^{-1/4}$ (Kreith, 1965, p. 336–338), so that a change from 5 to 10 °K in $(T_r - T_a)$ results in a 19% change in H_F . Free convection can be linearized, as discussed in section 2(B), but the results are not entirely satisfactory. Also, true free convection is an elusive condition, since any stray air movement will have a strong effect on H_F and result in considerable scatter in experimental data (Ede, 1967, p. 119) which might be assigned to "biological variability". Stray air currents are necessarily present if oxygen consumption is measured, since the air in the chamber must be mixed to allow accurate data reduction (Depocas & Hart, 1957). The low rates of air movement usually used to mix air in metabolism chambers often results in the undesirable combined free and forced convection condition described earlier.

A third reason to avoid free convection conditions is that the conductance of the fur is then determined mainly by its thickness, and not its quality. Appreciable wind in the chamber allows the effect of penetration of wind into the pelage (Davis & Birkebak, 1974; Lentz & Hart, 1960; Moote, 1955) to be studied. This allows a better estimate of the actual insulative value of the pelage.

APPENDIX B

Derivation of the Parameters K_0 , T_e , and M^* .

The procedure is as follows. First, solve equation (5) for T_r :

$$T_r = \frac{K_f T_s + R\bar{T}_r + HT_a + Q_n - E_r}{K_f + R + H} \quad (\text{B1})$$

The right member of equation (B1) may be substituted for T_r in equation (6). Then equation (6) may be solved for T_s :

$$T_s = \frac{(K_s T_b - E_s)(K_f + R + H) + K_f(R\bar{T}_r + HT_a + Q_n - E_r)}{(K_s + K_f)(H + R) + K_s K_f} \quad (\text{B2})$$

Now, equation (B2) may be used to eliminate T_s in equation (7). To form the desired parameters and equation (8), first divide through by the T_b coefficient. Then group all purely environmental heat flows ($R\bar{T}_r$, GT_g , HT_a , Q_n) into one term representing the effect of the environment on T_b , and all physiological heat flows (M , E_b , E_s , E_r) into another term representing the effect of physiological processes on T_b . Then equation (7) assumes the form:

$$\begin{aligned}
 -C \left[\frac{(K_s + K_f)(H+R) + K_s K_f}{[K_s K_f + G(K_s + K_f)][H+R] + GK_s K_f} \right] \frac{dT_b}{dt} - T_b \\
 + \left[\frac{K_s K_f (HT_a + R\bar{T}_r + GT_g + Q_n) + GT_g (K_s + K_f)(H+R)}{[K_s K_f + G(K_s + K_f)][H+R] + GK_s K_f} \right] \\
 + \left[\frac{(M - E_b)[(K_s + K_f)(H+R) + K_s K_f] - E_s K_s (K_f + R + H) - E_r K_s K_f}{[K_s K_f + G(K_s + K_f)][H+R] + GK_s K_f} \right] = 0. \quad (B3)
 \end{aligned}$$

Inspection of equation (B3) shows that K_s and K_f appear only as $K_s K_f$ or $(K_s + K_f)$. Now thermal conductances may be combined in series and parallel by applying the corresponding rules for electrical conductances. Parallel conductances K_1 and K_2 have a total conductance $(K_1 + K_2)$, and series conductances have a total conductance of $1/(1/K_1 + 1/K_2) = K_1 K_2 / (K_1 + K_2)$. Since K_s and K_f are series conductances, the combined conductance K_{sf} , given by equation (11), is a reasonable parameter to introduce by dividing the numerator and denominator of each group of terms by $(K_s + K_f)$. The first term in brackets is then seen to be identical to $(1/K_0)$ in equation (10), and the second bracketed term is just T_e as given in equation (12). The last bracketed term appears as

$$\begin{aligned}
 (M - E_b) \frac{1}{K_0} - E_s \left[\frac{\frac{K_{sf}}{K_f} (K_f + R + H)}{(K_{sf} + G)(H+R) + GK_{sf}} \right] \\
 - E_r \left[\frac{K_{sf}}{(K_{sf} + G)(H+R) + GK_{sf}} \right]. \quad (B4)
 \end{aligned}$$

By multiplying and dividing by $(H+R+K_{sf})$, this assumes the form

$$\frac{M^*}{K_0} = \frac{1}{K_0} \left[M - E_b - E_s \left(\frac{K_{sf}(K_f + R + H)}{K_f(K_{sf} + R + H)} \right) - E_r \left(\frac{K_{sf}}{(K_{sf} + R + H)} \right) \right]. \quad (B5)$$

This is reduced to M^* as given by equation (13) by rearranging the E_s coefficient and dividing the numerator and denominator of the E_r coefficient by K_{sf} .

APPENDIX C

Equivalence of T_e and the Temperature of a Black, Isothermal Enclosure

The equivalence of T_e and the temperature of a black, isothermal metabolism chamber, T_{mc} , can be demonstrated by first rearranging equation (12) as follows:

$$T_e = \frac{K_{sf}(HT_a + R\bar{T}_r + Q_n) + GT_g(H + R) + K_{sf}GT_g}{(K_{sf} + G)(H + R) + GK_{sf}} \quad (C1)$$

Now for a black object in a black, isothermal chamber, $Q_n = (T_{mc}^4 - \bar{T}_r^4)$, and is exactly zero if $\bar{T}_r = T_{mc}$. This occurs if $\bar{T}_r = T_{mc}$ was initially used in the linearization of equation (2) or if a taxidermic model in thermal equilibrium is considered, which has $T_r = T_{mc}$ since $M^*/K_0 = 0$. Since the metabolism chamber and the animal are assumed to be black ($\epsilon \cong 1$) and isothermal $T_a = T_g = T_{mc}$, and equation (B6) immediately reduces to $T_e = T_{mc}$.

In the general case of a live animal or a taxidermic model not in thermal equilibrium, $T_r \neq T_{mc}$, and $T_e \neq T_{mc}$ because of the non-linear nature of thermal radiation. If thermal radiation were linear with temperature difference, the net radiation transfer when $T_r = \bar{T}_r$, Q_n , would be $R(T_{mc} - \bar{T}_r)$. Then $R\bar{T}_r + Q_n = RT_{mc}$, and it would immediately follow that $T_e = T_{mc}$ for a black, isothermal chamber and any surface temperature T_r . The actual difference between T_e and T_{mc} due to the non-linearity of thermal radiation can be found by letting $T_r = \bar{T}_r = T_{mc} + \delta T$. Then, by expanding in binomial series form and using equations (3) and (4):

$$\begin{aligned} R\bar{T}_r + Q_n &= R(T_{mc} + \delta T) + A_e \sigma T_{mc}^4 - A_e \sigma (T_{mc} + \delta T)^4 \\ &= RT_{mc} + A_e \sigma [4\delta T(T_{mc}^3 + 3T_{mc}^2 \delta T + 3T_{mc} \delta T^2 + \delta T^3) + T_{mc}^4 \\ &\quad - (T_{mc}^4 + 4T_{mc}^3 \delta T + 6T_{mc}^2 \delta T^2 + 4T_{mc} \delta T^3 + \delta T^4)]. \end{aligned}$$

Collecting terms,

$$R\bar{T}_r + Q_n = RT_{mc} + A_e \sigma [6T_{mc}^2 \delta T^2 + 8T_{mc} \delta T^3 + 3\delta T^4]. \quad (C2)$$

The error term is the rightmost term above. Some simplification is desirable in order to estimate the numerical significance of the effect of the non-linearity of the Stefan-Boltzmann Law. First noting that $T_{mc} \gg \delta T$, we may neglect the terms in δT^3 and δT^4 . The approximate fractional error in replacing $(R\bar{T}_r + Q_n)$ by RT_{mc} is then found by dividing the error term by RT_{mc} :

$$Z = \frac{6T_{mc}^2 \delta T^2}{4(T_{mc} + \delta T)^3 T_{mc}} \cong 1.5 \left(\frac{\delta T}{T_{mc}} \right)^2 \quad (C3)$$

For $T_{mc} = 300^\circ\text{K}$ and $\delta T = 20^\circ\text{K}$, $Z = 0.0067$ or less than 1%. The effect

on T_e can be estimated by substituting $RT_{mc}(1+Z)$ for $R\bar{T}_r + Q_n$ in equation (C1). With $T_a = T_g = T_{mc}$,

$$T_e \cong \left(\frac{K_{sf}[H+R(1+Z)] + G(H+R) + GK_{sf}}{K_{sf}(H+R) + G(H+R) + GK_{sf}} \right) T_{mc}. \quad (C4)$$

Clearly, the error is unimportant if $G > K_{sf}$. However, G is often very small due to vasoconstriction and countercurrent heat exchange in the appendages as well as very small substrate contact area. Thus, for a conservative estimate, it is best to assume $G \cong 0$. Then

$$T_e \cong \frac{H+R(1+Z)}{H+R} T_{mc}. \quad (C5)$$

The difference between T_e and T_{mc} is minimized by having $H > R$. As an estimate, the value of H for a cylinder may be used. Kreith (1965, p. 411) gives a relation for H which gives a range of H/A_e of $1.38-22.6 \text{ W}\cdot\text{m}^{-2}\cdot\text{K}^{-1}$ for diameters of $0.02-0.5 \text{ m}$ and wind velocities of $0.1-1 \text{ m}\cdot\text{s}^{-1}$. At $300 \text{ }^\circ\text{K}$, $R/A_e = 6.01 \text{ W}\cdot\text{m}^{-2}\cdot\text{K}^{-1}$ for $\varepsilon = 0.98$, which lies within the range of values of H/A_e . The smaller values of H/A_e are for the low wind velocities and larger animals. As a general estimate for most experiments on small animals, $H \cong R$ may be assumed, so that

$$T_e \cong \left(1 + \frac{Z}{2} \right) T_{mc}. \quad (C6)$$

For $T_{mc} = 300 \text{ }^\circ\text{K}$, $\delta T = 20 \text{ }^\circ\text{K}$, $T_e - T_{mc} \cong 1 \text{ }^\circ\text{K}$, and will not exceed $2 \text{ }^\circ\text{K}$ even if $H/A_e = 0$.