DIURNAL VARIATION IN MINIMAL THERMAL CONDUCTANCE OF THE WHITE-FOOTED MOUSE (*PEROMYSCUS LEUCOPUS*), THE GOLDEN HAMSTER (*MESOCRICETUS AURATUS*), AND THE EASTERN WOODRAT. (*NEOTOMA FLORIDANA*)

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This is dedicated to my wife, Marion, and our children, Kai and Tony.

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ABSTRACT

Minimal Thermal Conductance (MTC) has been used as a measure of the minimal rate of heat loss from endotherms at low ambient temperatures. An analysis of previously published data led to the suggestion of diurnal variation in MTC.

MTC may be derived as part of a lumped-parameter model describing the energy exchange of small mammals at low ambient temperatures (T_a) in a metabolism measurement chamber. This development shows that metabolism is better described as a function of the core temperature (T_c) minus the ambient temperature than as a function of Ta alone. MTC may be defined as the rate of change of metabolic rate per degree C change in (T_c-T_a, or ΔT) at $\Delta T > \Delta T_{lc}$, where ΔT_{lc} is the lower critical temperature difference.

Diurnal variation in MTC was determined for three species of rodents: Peromyscus leucopus (the white-footed mouse), Mesocricetus auratus (the golden hamster), and Neotoma floridana (the eastern woodrat). Metabolic rate, evaporative water loss, and core temperature were determined at several temperatures during the active and resting phases. In P. leucopus the steady state T_c was significantly related to the ambient temperature during resting, but not active, phase. There was little relationship between T_c and T_a in M. auratus and N. floridana.

Four different methods of estimating MTC were used. A "two-point" slope estimation method allows examination of variation in thermal conductance with T_a. There was no systematic change in thermal conductance with T_a at low T_a's, so a segmented regression procedure could be used to estimate MTC, ΔTlc, and BMR. Two other methods of calculating MTC were examined using the data for P. leucopus. Common assumptions necessary for these methods were found to be violated, causing errors in estimation of MTC. Segmented regression of MR against ΔT was determined to be the best method for measuring MTC.

In all three species both diurnal variation in MTC and variation between individuals in MTC were statistically significant. Demonstration of variation in MTC between individuals should lead to more explicit consideration of MTC as a property of individual animals. Diurnal variation in MTC was statistically significant but slight in magnitude. This differs from the suggestions of a previous analysis of published data. Possible causes for diurnal variation in MTC include: variation in peripheral circulation; variation in fur piloerection; and differences in behavior of animals in metabolism chambers between night and day.

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DIURNAL VARIATION IN MINIMAL THERMAL CONDUCTANCE: A RE-ANALYSIS OF THEORY AND EXPERIMENTAL EVIDENCE IN THE WHITE-FOOTED MOUSE, Peromyscus leucopus

ABSTRACT

Minimal thermal conductance (MTC) has been used as a measure of the minimal rate heat loss from endotherms at low temperatures. An analysis of previously published data led to the suggestion of diurnal variation in MTC. However, the use of MTC has been debated on the grounds that it results from an incorrect and overly simplistic representation of the thermal exchange of small mammals. In this report, MTC is developed as a parameter in a linear, lumped-parameter model of the energy exchange of a small mammal at low ambient temperatures in a metabolism measurement chamber. This model shows that metabolism is more generally described as a function of the core temperature (T_c) minus the ambient temperature (T_a) ($\Delta T = T_c - T_a$) than as a function of T_a alone. It also seems more appropriate to define a critical temperature gradient (ΔT_{lc}) between core and ambient temperatures, where metabolism rises above basal levels than to define a lower critical ambient temperature. MTC may be defined as the rate of change of metabolic rate per ^{o}C change in ΔT at $\Delta T > \Delta T_{lc}$. Metabolic rate, evaporative water loss, and core temperature were determined for 10 Peromyscus leucopus during resting (day) and active (night) phases for the following temperatures: 0, 5, 10, 15, 20, 25, 27.5, 30, 32.5, and 35 ^{o}C. The steady state T_c increased with ambient temperature during resting phase, but not active phase, with resting phase body temperatures varying from 34.48 ^{o}C at T_a=0 ^{o}C to 37.3 ^{o}C at T_a=35 ^{o}C. Evaporative water loss was higher during active phase than resting phase.

Four different methods of estimating MTC were applied to these data. One method allows examination of variation in thermal conductance with T_a and showed that there was no systematic change in thermal conductance with T_a at low T_a's ($\leq$ 20 ^{o}C). Because thermal conductance seemed invariant with T_a at low ambient temperatures, a segmented regression procedure could be used to estimate MTC, ΔT_{lc}, and Basal Metabolic Rate (BMR) for each mouse for resting and active phases. There was significant diurnal variation in MTC. Resting phase wet MTC was 0.84 ($\pm$0.04) $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$. Active phase wet MTC was 1.05 ($\pm$0.08) $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$. Resting phase dry MTC was 0.88 ($\pm$0.06) $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$. Active phase dry MTC was 1.10 ($\pm$0.18) $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$. Two other methods of calculating MTC were examined. Calculation of MTC from regression of M on T_a underestimated resting phase MTC. This was because T_c decreased with T_a during the resting phase. This resulted in an overestimation of the amount of diurnal variation in MTC calculated in this manner. Calculation of MTC from $MTC = M/\Delta T$ resulted in the spurious appearance of a decrease in MTC with T_a. Calculation of MTC from segmented regression of M against ΔT appears to be the best method for measuring MTC as long as the necessary assumptions are met.

Diurnal variation in MTC was found to be 0.21 $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$. This is less than the 0.56 $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$ predicted from a regression based on previously published data. This difference is probably attributable to bias in the MTC data available in the literature. Factors biasing the available data apparently resulted in considerable overestimation of diurnal variation in MTC of P. leucopus.

INTRODUCTION

Minimal thermal conductance (MTC) is a measure of the minimal rate of heat loss from an endotherm to its environment at cold temperatures. MTC has been used in a variety of studies, including investigations of the energetics of burrowing by pocket gophers (Vleck 1979), the geographic distribution of armadillos (McNab 1980a), climatic adaptation in woodrats (Brown and Lee 1969), and community energetics of old-fields (Golley 1960). Other studies have scrutinized the use of MTC, and have considered such problems as proper measurement of MTC (McNab 1980b); pitfalls in use of MTC in physiological and ecological investigations (Tracy 1972); and the relationship between use of MTC and classical physical analyses of heat exchange (Kleiber 1961). Despite this diversity most studies that use the MTC concept can be placed in one of two categories: studies that discuss the methodology, meaning, or utility of the concept (e.g. Tracy 1972; Bakken and Gates 1975); and studies that use MTC as a tool in an ecological or physiological investigation (McNab 1980a; Brown and Lee 1969). In the latter category is Aschoff's (1981a) study that suggested the existence of diurnal variation in MTC. Diurnal variation in MTC might be expected given the existence of diurnal variation in many physiological parameters, including peripheral circulation (Aschoff and Pohl 1970).

Aschoff's (1981a) conclusion was based only on examination of data from the published literature. The goal of this work is to test directly the existence of diurnal variation in MTC using Peromyscus leucopus (the white-footed mouse), a small, nocturnal rodent (Falls 1968). However, many theoretical and methodological issues regarding MTC remain unsettled and merit careful attention. For example Bakken and Gates (1975) and Bakken (1976) claimed that the use of MTC depends on an incorrect and overly simplistic analysis of the energetics of endotherms. McNab (1980b) also claimed "widespread conceptual misunderstanding" of the meaning of MTC. There is a clear need for a careful analysis of the MTC concept that considers both the biophysical theory pertinent to use of MTC and methodological issues of MTC measurement.

The purposes of this report are to 1) examine the biophysical validity of the MTC concept (I will show that MTC may be defined as a parameter in a linear approximation of a mammal's heat loss at low ambient temperatures); 2) develop a method for estimating MTC; 3) compare this method with other methods for estimating MTC; 4) apply these methods to the estimation of MTC; and 5) determine whether or not there is diurnal variation in MTC of P. leucopus. The analysis of MTC begins with examination of a model of the energy exchanges between an animal and its environment.

Model: The energy relations of a mammal in a metabolism chamber

The model developed here is a "lumped-parameter" model (Bakken and Gates 1975; Kreith 1976). A number of special symbols and variable names will be used throughout this discussion; variable definitions are listed in Table 1.1.

The model used in this analysis treats small mammals as having a core of tissue at a uniform temperature T_c. Essentially all of the animal's metabolism occurs within the core. The core is surrounded by a layer of insulating flesh (including fat and the skin) and covered with fur (Figure 1.1). The simplest case is that of a core having a circular cross section, surrounded with concentric rings of insulating flesh and fur. This is the case that will be dealt with explicitly. Other biologically realistic cases may be analyzed by use of effective thicknesses and conduction coefficients (Kreith 1976; Bakken and Gates 1975). The fur is treated as a solid insulating layer having a smooth outer surface of emissivity ε_f. The area in contact with the substrate is A_{cond}. Radiative and convective heat loss take place from the remainder of the surface area (A_r). The temperature of the radiative surface is T_r.

This analysis requires that the chamber used for metabolic rate determinations meet several criteria: 1) the walls of the metabolism chamber have an emissivity of approximately 1.0 (Porter 1969); 2)

chamber dimensions are constant for all metabolic rate determinations used for a given set of comparisons; 3) air entering the chamber and the chamber walls are at a uniform temperature, T_a; 4) incident shortwave radiation is negligible. Also, the animal in the chamber is assumed to be at rest and postabsorptive. The condition that the air and chamber walls are at temperature T_a and that incident radiation is negligible allows the ambient temperature to be well defined. The operative environmental temperature (as defined by Bakken 1976) inside the chamber is equal to T_a.

A further condition is that convective heat loss should be primarily by free convection. Under forced convection conditions the rate of heat loss is higher than under free convection conditions (Kreith 1976, Gates 1980). Likewise, air flow through the chamber should be nonturbulent, since turbulence enhances heat loss (Kreith 1976). Thus, minimal thermal conductance must be investigated using chambers in which free convection predominates and airflow is laminar.

The energy exchanges between the mammal and its environment are given by (Porter and Gates 1969; Welch 1984):

$$\text{Energy In} = \text{Energy Out} \pm \text{Energy Stored} \qquad (1)$$

$$M + Q_{abs} + Q_{swrad} =$$

$$Q_{em} + Q_{conv} + Q_{cond} + Q_{bw} + Q_{ex} + Q_{sw} + W + S_H + P \qquad (2)$$

The rate of production of mature, fasted, nonreproductive mammals is generally an insignificant component of the energy balance

(Grodzinski 1975), so P is adequately approximated by zero.

$$P \approx 0 \tag{3}$$

Also, by assumption, the incident shortwave radiation in the metabolism chamber is negligible.

$$Q_{swrad} = 0 \tag{4}$$

All chamber walls and air in the chamber are at temperature T_a. From the Stefan-Bolzmann law (Porter and Gates 1969; Kreith 1976) the incident thermal radiation is

$$Q_{abs} = A_r \sigma \varepsilon_w \varepsilon_f T_a^4 \tag{5}$$

The emitted thermal radiation is

$$Q_{em} = A_r \sigma \varepsilon_f T_r^4 \tag{6}$$

Convective heat loss is assumed to occur from the same surface area as the radiative heat loss with the effective surface temperature being T_r. Convective heat loss is given by (Porter and Gates 1969; Kreith 1976):

$$Q_{conv} = A_r h_c (T_r - T_a) \tag{7}$$

Conductive heat loss can be written as a function of T_a, the animal's core temperature, and a conduction coefficient describing the rate of transfer from the core through the animal surface and to the substrate (Kreith 1976):

$$Q_{cond} = A_{cond} K_{cond} (T_c - T_a) \tag{8}$$

In practice, the experimental animal typically sits on a screen or perforated plexiglass plate. The conductivity coefficient K_{cond} is

thus a function of characteristics of the animal and its substrate. Thus, the MTC will be, to a certain extent, a function of both the animal and the plate upon which the animal sits. However, since conduction is typically a small portion of an endotherm's total heat loss (Gates 1980) variation of MTC with the thermal properties of the plate should be slight. The effect of the thermal properties of the plate can be minimized by use of a plate that is thin.

Incorporating eqs. (3) through (8) into eq. (2),

$$M + A_r \sigma \varepsilon_w \varepsilon_f T_a^4 = A_r \sigma \varepsilon_f T_r^4 + A_r h_c (T_r - T_a) + A_{cond} K_{cond} (T_c - T_a) + Q_{bw} + Q_{ex} + Q_{sw} + W + S_H \quad (9)$$

Metabolism chamber walls should have an emissivity of approximately 1 (ε_w=1) (Porter 1969). Incorporating this into eq. (9) and rearranging gives

$$M = A_r \sigma \varepsilon_f (T_r^4 - T_a^4) + A_r h_c (T_r - T_a) + A_{cond} K_{cond} (T_c - T_a) + Q_{bw} + Q_{ex} + Q_{sw} + W + S_H \quad (10)$$

Assume the animal is at rest and at a steady state so 1) M, Q_{ex}, and Q_{sw} are constant; 2) W=0; 3) the average body temperature is constant over time, so S_H=0. From these conditions and eq. (10),

$$M = A_r \sigma \varepsilon_f (T_r^4 - T_a^4) + A_r h_c (T_r - T_a) + A_{cond} K_{cond} (T_c - T_a) + Q_{bw} + Q_{ex} + Q_{sw} \quad (11)$$

The heat exchange due to bulk warming of inhaled air and water vapor, Q_{bw}, has been omitted from some analyses of small mammal heat exchange (cf. Porter and Gates 1969; Gates 1980). Also ignored in some analyses is the energy exchange due to bulk warming of inhaled water vapor. The heat loss due to bulk warming of inhaled air and water vapor is given by

$$Q_{bw} = [(T_a - T_{ex})c_a\rho_a + (T_a - T_{ex})c_w\rho_w]\dot{V} \qquad (12)$$

where T_{ex} is the temperature of expired gases, c_a is the specific heat of air, c_w is the specific heat of water vapor, ρ_a is the density of dry air, ρ_w is the density of water in the inspired air, and $\dot{V}$ is the respiratory exchange rate. Note that here we are not concerned with the latent heat of vaporization of water evaporated in the respiratory tract. Rather, equation (12) gives the heat loss due to warming of air and water vapor that is inhaled at one temperature and exhaled at another. Appendix 1 is an analysis of Q_{bw}. The data available that are pertinent to this subject are consistent with an approximately linear relationship between Q_{bw} and $(T_c - T_a)$ at low T_a's, if the ambient water vapor density is held constant. (Note that the available data are scanty and that this is a topic worth further investigation). Rewriting equation (12), then, we have

$$Q_{bw} = K_{bw}(T_c - T_a) \qquad (13)$$

Also, these terms comprise a small portion of the metabolic rate, and in some circumstances may be ignored.

T_r appears in the radiative and convective heat loss terms of eq. (11). For an animal at steady state, T_r may be expressed as a function of T_c and other organismal properties (Porter and Gates 1969):

$$T_r = T_c - \left\{ \frac{d_b(M - Q_{ex})}{K_b(A_{skin})} \right\} - \left\{ \frac{d_f(M - Q_{ex} - Q_{sw})}{K_f(A_{tot})} \right\} \qquad (14)$$

This equation is derived from assumptions that: 1) respiratory evaporative water loss occurs directly from the body core; 2) evaporative water loss from the skin occurs directly at the skin surface; 3) the insulating layer of flesh has a thickness of d_b and thermal conductivity of K_b; 4) the fur layer has a thickness of d_f and a thermal conductivity of K_f; and 5) the effective surface area of the animal and the surface area at the outer surface of the skin are approximately equal.

From eq. (14) we can derive an expression for T_r. This is substituted in eq. (11) to get:

$$M = A_r \sigma \varepsilon_f \left[\left\{ T_c - \frac{d_b(M - Q_{ex})}{K_b A_{skin}} - \frac{d_f(M - Q_{ex} - Q_{sw})}{K_f A_{tot}} \right\}^4 - T_a^4 \right]$$

$$+ A_r h_c \left[T_c - \frac{d_b(M - Q_{ex})}{K_b A_{skin}} - \frac{d_f(M - Q_{ex} - Q_{sw})}{K_f A_{tot}} \right] - T_a \qquad (15)$$

$$+ A_{cond} K_{cond} (T_c - T_a) \; K_{bw} (T_c - T_a) + Q_{ex} + Q_{sw}$$

Some algebraic rearrangement produces the following from eq. (15):

$$M = A_r\sigma\varepsilon_f(T_c^4 - T_a^4) + A_{conv}h_c(T_c-T_a) + A_{cond}K_{cond}(T_c-T_a) + K_{bw}(T_c-T_a) + Q_{ex} + Q_{sw} + F(M,Q_{ex},Q_{sw},T_c,A_r,h_c,d_b,K_b,d_f,K_f) \quad (16)$$

"$F(M,Q_{ex},Q_{sw},T_c,A_r,h_c,d_b,K_b,d_f,K_f)$" in eq. (16) results from expansion and rearrangement of the first two terms of eq. (15). The complete derivation of and expression for $F(M,Q_{ex},Q_{sw},T_c,A_r,h_c,d_b,K_b,d_f,K_f)$ is given in Appendix 2.

Using a linear approximation to the term $(T_c^4 - T_a^4)$, (Kreith 1976, Monteith 1973; Gates 1980) we have:

$$A_r\sigma\varepsilon_f(T_c^4-T_a^4) = A_r\sigma\varepsilon_f 4T_m^3(T_c - T_a) \quad (17)$$

where $T_a < T_m < T_c$

In an experiment using several T_a's, T_m will be between the average T_c and the average T_a (Buck 1978). The approximation can be very good for temperature differences of up to 20-40 ^oC (Bakken 1976, 1981; Kleiber 1961,1975; Kreith 1976). For example, assuming a T_c of 40 ^oC, and taking a linear approximation over a range of T_a's from 0 ^oC to 20 ^oC, the maximum error due to deviations from linearity will be no more than 5% of the radiative exchange term when T_m is chosen appropriately. Incorporating (17) into (16) yields the following, valid for a limited (but arbitrary) range of (T_c-T_a):

$$M = A_r\sigma\varepsilon_f T_m^3(T_c-T_a) + A_r h_c(T_c-T_a) + A_{cond}K_{cond}(T_c-T_a) + K_{bw}(T_c-T_a) + Q_{ex} + Q_{sw} + F(M,Q_{ex},Q_{sw},T_c,A_r d_b,K_b,d_f,K_f) \quad (18)$$

We have not yet made any assumptions about A_r, h_c, A_{cond}, K_{cond},

d_b, d_f, K_b, and K_f. These parameters may vary with T_a over some temperature ranges. However, it is typically assumed that at and below some value of T_a, called the lower critical temperature, small mammals minimize heat loss (Daniels 1984). In particular, suppose that A_r, A_{cond}, h_c, K_{cond}, K_b, and K_f are minimized (and therefore constant), and that d_b and d_f are maximized (and therefore constant) for $T_a \leq T_{lc}$, so that heat loss is minimized. Then

$$M = MTC(T_c - T_a) + Q_{ex} + Q_{sw} + F(M, Q_{ex}, Q_{sw}, T_c, A_r, d_b, K_b, d_f, K_f) \quad (19)$$

where $MTC = A_r \sigma \varepsilon_f T_m^3 + A_{conv} h_c + A_{cond} K_{cond} + K_{bw}$

equation valid for $T_a \leq T_{lc}$

Metabolic rate (M) is usually expressed as a function of T_a, not as a function of $(T_c - T_a)$. However it should be the magnitude of the thermal gradient, not T_a, that determines the rate of heat loss. The rate of heat loss in turn determines the metabolic rate necessary to maintain the thermal gradient. Thus, an equation such as (19) can be written as a function of T_a only if T_c assumes the same value whenever the animal is at a steady state. This is a very strict requirement that is unlikely to be satisfied. It seems more appropriate to assume the existence of a critical temperature gradient (ΔT_{lc}), since it is the temperature gradient between the animal's core and the environment that determines the rate of heat loss. For temperature gradients greater than ΔT_{lc} metabolism must rise beyond basal levels.

From eq. (19):

$$M = MTC(T_c - T_a) + Q_{ex} + Q_{sw} + F(M, Q_{ex}, Q_{sw}, T_c, A_r, h_c, d_b, K_b, d_f, K_f) \quad (20)$$

where $MTC = A_r \sigma \varepsilon_f T_m^3 + A_r h_c + A_{cond} K_{cond}$

equation valid for $\Delta T \geq \Delta T_{lc}$

$F(M, Q_{ex}, Q_{sw}, T_c, A_r, h_c, d_b, K_b, d_f, K_f)$ is a fairly complex function. However, several of the variables (d_b, K_b, d_f, K_f, A_r, and h_c) are assumed constant for a given animal for $\Delta T \geq \Delta T_{lc}$. Thus, M, Q_{ex}, Q_{sw}, and T_c are the only parameters of F that vary. An analysis of $F(M, Q_{ex}, Q_{sw}, T_c, A_r, h_c, d_b, K_b, d_f, K_f)$ for Peromyscus leucopus, Mus musculus (house mouse), Mesocricetus auratus (golden hamster), and Neotoma floridana (the eastern woodrat) is presented in Appendix 1. $F(M, Q_{ex}, Q_{sw}, T_c, A_r, h_c, d_b, K_b, d_f, K_f)$ was calculated for these species at T_a's of 0, 5, 10, 15, 20, and 25 ^{o}C. A regression of $F(M, Q_{ex}, Q_{sw}, T_c, A_r, h_c, d_b, K_b, d_f, K_f)$ vs. ΔT showed that the slope of this relationship is less than 1% of the standard error of the estimated MTC values for each species, and less than 1% of the measured diurnal variation in MTC for each species. Thus, the error involved in treating $F(M, Q_{ex}, Q_{sw}, T_c, A_r, h_c, d_b, K_b, d_f, K_f)$ as a constant seems negligible for these species. Further data should be collected on other species. However, the consistent result that $F(M, Q_{ex}, Q_{sw}, T_c, A_r, h_c, d_b, K_b, d_f, K_f)$ is adequately described as a constant suggests that we are justified in doing so in general. This

will be done for the remainder of the discussion, and $F(M,Q_{ex},Q_{sw},T_c,A_r,h_c,d_b,K_b,d_f,K_f)$ will be denoted simply by F. From eq. (20) we obtain:

$$M - Q_{ev} = MTC_d(T_c - T_a) + F \qquad \text{for } \Delta T \geq \Delta T_{lc} \qquad (21)$$

Thus, under the conditions for which eq. (21) was derived, the metabolic rate minus the heat loss due to evaporation may be expressed, to a good approximation, as a linear function of $(T_c - T_a)$ for $\Delta T \geq \Delta T_{lc}$. The metabolism of mammals is typically at constant (basal) levels for some range of $\Delta T \leq \Delta T_{lc}$ (the thermoneutral zone). We then have the following model of the metabolism of a mammal:

$$\begin{aligned} M - Q_{ev} &= MTC_d(T_c - T_a) + F \qquad && \text{for } \Delta T \geq \Delta T_{lc} \\ M - Q_{ev} &= BMR && \text{for } \Delta T_{lc} > \Delta T > \Delta T_{uc} \end{aligned} \qquad (22)$$

where ΔT_{uc} is the "upper critical temperature difference", the temperature difference below which the metabolism begins to increase (Gordon et al. 1977).

Dry Thermal Conductance

McNab (1980b) gave the following definition of thermal conductance: "Thermal conductance is a measure of the ease with which heat enters or leaves a body"; Hainsworth (1981) stated "... [minimal] thermal conductance is a measure of the rate at which heat is lost ... from an endotherm for every ^{o}C change in environmental temperature below the lower critical temperature (when body temperature remains

constant)." These quotes seem to convey accurately the spirit of many studies of MTC, and may be paraphrased and made more precise as follows: Minimal thermal conductance represents the slope of the linear relationship between metabolic rate and ΔT at $\Delta T \geq \Delta T_{lc}$. The slope factor MTC_d that relates the thermal gradient to $M-Q_{ev}$ in eq. (22) is referred to as "dry" thermal conductance (McNab 1980b; Hill 1983). If the conditions assumed in the derivation of eq. (22) are met, dry thermal conductance is the slope of the line relating $(M-Q_{ev})$ to ΔT for $\Delta T \geq \Delta T_{lc}$. MTC_d may be interpreted as a heat loss coefficient describing the minimal rate of heat loss through the combined routes of radiation, convection and conduction.

Wet Thermal Conductance

A discussion of "wet" thermal conductance requires further manipulation of eq. (21) and analysis of Q_{ev}. The treatment of heat loss due to evaporation is not a minor problem. The dynamics of evaporative water loss are poorly understood conceptually and difficult to measure empirically. Welch and Tracy (1977) and Welch (1980) demonstrate that even the qualitative nature of the relationship between T_a and respiratory water loss depends on the water vapor content of the inspired air. Furthermore, the relationship between evaporative water loss and T_a may not be linear. However, examination of the data presented by Welch and Tracy (1977)

and Welch (1980) suggests that in situations where the air entering the metabolism chamber is dry (dewpoint < -10 ^{o}C), we may as a first approximation write evaporative heat loss as a linear function of T_a.

$$Q_{ev} = m_1(T_c - T_a) + b_1 \tag{23}$$

The relationship between Q_{ev} and T_a ought to be nonlinear (Welch and Tracy 1977). However, eq. (23) should be useful as an empirical approximation as long as the deviations from linearity are small in comparison to the natural variation in the metabolic rate.

Incorporating eq. (23) into eq. (21) gives

$$M = (MTC_d + m_1)(T_c - T_a) + F + b_1 \tag{24}$$

This may be rewritten as

$$M = MTC_w(T_c - T_a) + F' \tag{25}$$

where $F' = F + b_1$

$MTC_w = MTC_d + m_1$

MTC_w is "wet" minimal thermal conductance. The development and interpretation of MTC_w are more tenuous than for "dry" MTC, since they depend on additional approximations beyond those used to develop MTC_d, and is valid under more limited conditions (specifically, the air entering the chamber should be dry).

Wet and dry MTC have been developed in this discussion in terms of the entire animal (e.g. in units of $W \cdot {}^{o}C^{-1}$). In many circumstances it will be more convenient to work with thermal conductance in mass-

specific terms (e.g. in units of $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$). The set of units in use at any given time will be indicated.

Comparison with other models for heat exchange relations

The following relationship has frequently been used to approximate the relationship between M and T_a below thermal neutrality (Burton, 1934):

$$M - Q_{ev} = C(T_c - T_a) \qquad (26)$$

However, even when this equation was first used, it was recognized as an approximation. This equation was originally derived from "Newton's Law of Cooling" which itself is an empirical approximation (Burton 1934), and C was a term interpreted as a measure of an animal's overall "conductance".

McNab (1980b) simplified an equation similar to (25) to produce

$$M = C'(T_c - T_a) \qquad (27)$$

This simplification carries the implicit assumption that the Q_{ev} may be expressed as a linear function of T_a extrapolating to 0 at $T_c = T_a$:

$$Q_{ev} = m_2(T_c - T_a) \qquad (28)$$

The slope factor C' in eq. (27) is referred to by McNab as "wet" minimal thermal conductance.

Another simplification of eq. (27) has been derived by making the further assumption that T_c is constant. The relationship then becomes

$$M = -CT_a + b_3 \quad (29)$$

where $b_3 = CT_c$

An equation similar to (29) may be derived from eq. (21), again by making the assumption that T_c is constant:

$$M - Q_{ev} = -CT_a + b_4 \quad (30)$$

where $b_4 = CT_c + F'$

The slope parameters of eqs. (21) and (25) clearly correspond to the definition of MTC. The slope parameters of eqs. (26) through (30) do not necessarily represent MTC. Consider eqs. (29) and (30) first. The slope parameter here measures the increase in energy required per degree drop in T_a, which is equal to the energy required per degree increase in $(T_c - T_a)$ only if T_c is constant. The assumption that T_c is constant requires that T_c be independent of T_a, which may not be the case (Gebczynski 1969; Golightly and Ohmart 1978; Hill 1983; McNab 1980b; Pauls 1979). This assumption also requires that T_c be regulated at the same temperature during all measurements of metabolic rate. The latter assumption ignores stochastic and diurnal variation in T_c.

The effect of correlation between T_c and Ta is particularly problematic. For example, suppose that T_c decreases with T_a, say:

$$T_c = m_5 T_a + 35. \quad (31)$$

Then from eq. (21):

$$M - Q_{ev} = MTC_d(35 + m_5 T_a - T_a) + F \quad (32)$$

$$M - Q_{ev} = -[(1 - m_5)MTC_d]T_a + (MTC_d 35 + F) \quad (33)$$

Comparison of eqs. (21) and (33) shows that in this case a positive correlation between T_c and T_a makes the slope between metabolism and T_a less than the slope between metabolism and $(T_c - T_a)$. Thus, regression of M as a function of T_a may underestimate MTC. Furthermore, if MTC is used in studies of thermal exchange properties of mammals the slope in eq. (30) is not an appropriate comparative tool because it depends on the animal's body temperature lability as well as its thermal exchange properties.

Comparison of eqs. (21) and (26) shows that they differ in the presence of the constant term F, which appears only in eq. (21). These equations differ because McNab's (1980b) development uses T_c in place of T_r in the radiative and convective heat loss terms of eq. (13), rather than using the more accurate relationship between T_c and T_r that was used to develop eq. (21). This results in different conclusions about extrapolation of the relationship between M and $(T_c - T_a)$. Eq. (21) shows that $M - Q_{ev}$ need not extrapolate to 0 at $T_a = T_c$. Equation (26) makes it appear that $M - Q_{ev}$ ought to extrapolate to 0 at $T_a = T_c$. This would be the case only if the effective radiative and convective temperatures of an animal were the same as the core temperature, which is generally not the case (Gates 1980).

The differences between the model defined by eq. (27), used by

McNab to define wet MTC, and the model developed in this paper are even greater, since eq. (27) carries with it the implicit assumption that Q_{ev} is a linear function of ΔT which extrapolates to 0 at $T_c=T_a$. This assumption is firmly contradicted by the available data (Welch and Tracy 1977; Welch 1980). The present model is similar to several other models of animal heat exchange relations, including the work of Porter and Gates (1969). Many of the basic assumptions used in the development of the model in this paper were first used by Porter and Gates (1969). The model developed here may be regarded in many ways as an application of the Porter and Gates model to the situation of a mammal in a metabolism chamber. Likewise, the present model can be regarded as a special case of the model of Bakken (1976) (with some differences in the approximations used in development of the model). However, several parameters (such as physiological offset temperature) defined by Bakken and Gates (1975) and Bakken (1976) are not needed here due to the assumptions of free convection and a uniform thermal environment in metabolism chambers.

Estimation of Minimal Thermal Conductance

The obvious way to measure MTC is to estimate the slope of the relationship between $(M-Q_{ev})$ and ΔT for ΔT's $\geq \Delta T_{lc}$. One problem in practice is that MTC, ΔT_{lc} , and BMR must be estimated simultaneously. Johnson (1969) discusses the statistical procedures

for this. I developed a Fortran V program to perform this analysis; the source code is presented in Appendix 3. This procedure will be referred to throughout the rest of the paper as the "segmented regression method".

If one assumes that T_c is constant and wishes to estimate MTC from the model described by eq. (26), then the appropriate method for doing so would be a segmented regression of M against T_a (Johnson 1969). The program presented in Appendix 3 also performs this analysis. Since the procedure of estimating MTC from the slope of the relationship between M and T_a was first used by Scholander et al. (1950) this method of estimating MTC will be referred to through the rest of the discussion as "Scholander's method".

McNab (1980b) worked from eq. (26) to recommend estimation of wet thermal conductance from the following expression:

$$MTC_w = \frac{M}{(T_c - T_a)} \tag{34}$$

The corresponding formula for dry thermal conductance is:

$$MTC_d = \frac{M - Q_{ev}}{(T_c - T_a)} \tag{35}$$

Use of formula (34) or (35) to estimate MTC will be referred to as "McNab's method."

An additional way to estimate MTC can be derived from the algebraic "two-point" method for calculating the slope of a line. If

metabolic rate is measured for two temperature gradient values (say ΔT_1 and ΔT_2), both greater than the critical temperature gradient, MTC should be approximated by:

$$MTC = \frac{(M_1 - M_2)}{(\Delta T_1 - \Delta T_2)} \qquad (36)$$

This formulation depends on a less stringent assumption about the animal than the a segmented regression method. For eq. (36) to be valid, the thermal conductance (slope of the relationship between M and ΔT) need only be constant over the range from ΔT_1 to ΔT_2. The use of the segmented regression method and Scholander's method requires that the thermal conductance be constant for all $\Delta T \geq \Delta T_{lc}$. One way to test this assumption, and the assumption that thermal conductance is minimized at ΔT_{lc}, is to use eq. (36) over successive temperature ranges (say, 0-5 C, 5-10 C, etc.) and thus determine if thermal conductance varies with temperature for $\Delta T \geq \Delta T_{lc}$. Estimation of MTC from eq. (36) will be referred to as the "two-point" method.

Many assumptions have been made in the development of the models discussed in this paper. A total of four different methods of estimating both "wet" and "dry" thermal conductance have been discussed, each depending upon slightly different assumptions. Table 1.2 is a summary of the design criteria for the metabolism measurement system used to obtain metabolic rate measurements. Table 1.3 is a

summary of assumptions about the test mammal that are common to all developments of methods for estimating minimal thermal conductance. Table 1.4 is a summary of the four different methods described here for estimating thermal conductance along with the assumptions unique to each method.

Thermal Conductance as a Parameter

The development of eqs. (21) and (25) demonstrates that both "dry" and "wet" thermal conductance are parameters in legitimate approximations of a mammal's heat loss under certain specified conditions, and thus MTC_d and MTC_w are well-defined parameters. They are not necessarily the result of a "gross oversimplification" (cf. Bakken and Gates 1975, p. 255), nor are they necessarily "incorrectly and imprecisely defined" (cf. Bakken 1976, p. 338). "Dry" MTC is the rate of change of metabolic rate (less evaporative heat loss) per degree change in (T_c-T_a) at $\Delta T \geq \Delta T_{lc}$. "Wet" MTC is the rate of change of total metabolic rate per degree change in (T_c-T_a) at $\Delta T \geq \Delta T_{lc}$. (The lower critical temperature gradient ΔT_{lc} need not be the same for "dry" and "wet" MTC).

The reason for use of MTC as a comparative tool is clear. A species with lower minimal thermal conductance may be thought of in some contexts as being better adapted or better acclimated to cold than a species with higher minimal thermal conductance. Bakken (1976) criticized the use of MTC on the basis that it does not provide

detailed information on different routes of heat loss. This, while technically correct, may be irrelevant. If an experiment is performed to answer the question: "Do two species differ in their overall insulation?" , the question can be answered (at least for the conditions prevailing in a metabolism chamber) without detailed information about specific routes of heat loss.

One critical matter is whether the assumptions made to develop eqs. (21) and (25) are met. The assumptions made regarding the metabolism chamber may be met by proper construction of the chamber. Many of the other assumptions may be met by proper selection of data (e.g. data are used only from times when the animal is at rest, core temperature is constant, and metabolic rate and evaporative water loss are at steady state). The assumption that thermal conductance is constant for $\Delta T \geq \Delta T_{lc}$ can be tested by approximating MTC from eq. (36) for various values of ΔT, and testing for a relationship between MTC thus estimated and T_a.

On a theoretical basis the use of a segmented regression of metabolic rate as a function of ΔT seems to be the best method for estimating minimal thermal conductance, since this method is not vulnerable to several conditions that could cause other methods to yield inaccurate results. [In cases where it is obvious that all ΔT's are greater than the critical thermal gradient, then simple linear regression of metabolism as a function of ΔT will produce results

that are identical with the results of the segmented regression procedure]. An important question is how severe the errors involved in other methods are in practice. In the remainder of this paper, I attempt to 1) investigate for P. leucopus the validity of the assumptions used in the various models of small mammal heat loss presented in this introduction; 2) determine whether violations of the assumptions encountered with P. leucopus result in substantive differences in the values of MTC estimated according to the four methods described; 3) determine if there is diurnal variation in minimal thermal conductance of P. leucopus.

METHODS AND MATERIALS

Collection and maintenance of animals

Peromyscus leucopus were trapped between July 10 and 20, 1984. The animals were trapped in a mature oak-hickory forest in eastern Monroe County, Indiana. Aluminum Sherman traps were used, and the traps were checked at least twice daily. All adult male P. leucopus captured were weighed, measured, and taken to a quarantine room at Indiana University. There was no trap mortality among P. leucopus. The animals were quarantined for two weeks at Indiana University Laboratory Animal Resources and then moved to animal rooms in the Biology Department of Indiana University. The P. leucopus were maintained at 22 $\pm$ 1.5 ^{o}C. The photoperiod was 15:9 (with lights on at 0600 EST). This approximates the normal summer photoperiod in Indiana. The mice were kept in 13 cm x 18 cm x 29 cm plastic cages with hardwood chip bedding, and were provided with Autoclavable Purina Lab Chow (5010) and water ad lib.

Design of Physiological Measurement System

Measurements of the metabolic rate of P. leucopus were made using the McClure Laboratory Physiological Measurement System, discussed in Smith and McClure (1985). The Physiological Measurement System is an open-flow respirometry system that includes a two channel Applied

Electrochemistry S-3A/11 Oxygen analyzer, a Beckman Model 864 Infrared Gas Analyzer, an E.G.&G. Model 911 Dewpoint Hygrometer, and a Union Carbide Linear Mass Flowmeter. A diagram showing the path of gas flows through the Physiological Measurement System is included in Appendix 4. Data are collected automatically by an Apple II Plus microcomputer which interfaces with the analysis equipment via an Interactive Structures Model AI-13 12 bit, 16 channel analog input system. The gas analyzers were calibrated using bottled gases of known composition and a Wosthoff Gas Mixing pump. The Linear Mass Flowmeter was calibrated with a Brooks Model 1055A Flow Rate Calibrator. The equations used for calculation of metabolic parameters and a schematic diagram of the metabolism system are included in Appendix 4.

The metabolism chamber used is described in chapter 4 of this dissertation. The metabolism chamber was submerged in a water bath, and the water temperature was regulated by a circulating Neslab water bath. Air entering the chamber first passed through a copper coil submerged in the water bath to insure that air entered the chamber at the same temperature as the walls of the chamber. Air was dried in a large column of Drierite before entering the chamber; the incurrent airstream dewpoint averaged -19.2 ^{o}C (equivalent to a water vapor density of approximately 2 gm/m^3). Air flow rates through the metabolism chamber were set between 0.40 and 0.44 $L \cdot min^{-1}$ (at

standard temperature and pressure).

Temperature telemetry

Temperature sensitive radio transmitters were used to determine the core temperature of mice during the course of metabolic rate measurements. Minimitter Model X transmitters were chosen due to their small size (1.7 grams, approximately 8% of the body mass of the mice used in this experiment). A small AM radio was used as a receiver. The minimitters were calibrated by immersing them in a water bath at temperatures ranging from 30 ^{o}C to 42 ^{o}C (in 1 ^{o}C increments) and counting the number of clicks transmitted per minute. The order of temperatures used in the calibrations was randomized. The temperature of the water bath was measured to the nearest 0.01 ^{o}C using a thermometer that was calibrated against an NBS certified thermometer. The relationship between the number of clicks per minute and the temperature of the transmitters is linear (Berry 1971), and a predictive relationship was calculated by linear regression. That the relationship between the click rate and temperature was in fact linear is indicated by a coefficient of determination (r^2) of greater than 0.99 for all minimitter calibration curves. The 95% confidence limits around the regression line were within 0.05 ^{o}C. (This is better than the transmitter manufacturer's stated accuracy of 0.1 ^{o}C). When all metabolic rate measurements for an animal had been finished, the

minimitter was removed and recalibrated to check for drift. There was no more than 0.1 ^{o}C difference between the "before" and "after" calibrations in the temperature predicted for a given click rate.

Peromyscus leucopus were anaesthetized using a combination of Avertin injected intraperitoneally and Flouthane administered as an inhalant. The minimitters were sterilized in ethanol. The minimitters were implanted in the peritoneal cavity and were held in place in the lower abdominal region by a single suture secured to the inside of the body wall. All animals recovered from surgery without infection or other apparent ill effects. A minimum of three days was allowed between implantation and the beginning of metabolic rate measurement for each animal, and all metabolic rate determinations were completed within one month of implantation. All metabolism measurements were made when the animals had been in captivity between one and three months.

Experimental Protocol

The metabolic rate of each of 10 adult male P. leucopus was determined during night and day at the following temperatures: 0, 5, 10, 15, 20, 25, 27.5, 30, 32.5, and 35 ^{o}C. Determinations of metabolic rate were made independently and in random order for each of the temperatures during both night and day. That is, a separate experiment (metabolic rate determination) was performed for each

temperature. Night time determinations of metabolic rate were done between 10:00 pm and 4:30 am. Daytime measurements were done between 8:00 am and 7:00 pm.

The protocol for an experiment was as follows: each animal was fasted for 4-6 hours prior to a metabolic rate determination. Each animal was weighed prior to being placed in the metabolism chamber. At the beginning of an experiment, incurrent air was sampled for at least 10 minutes. The excurrent airstream was then sampled continuously until the oxygen consumption, carbon dioxide production, evaporative water loss, and core temperature were stable for at least 10 minutes (with the animal at rest). This allowed ample time for lag in metabolism measurement systems response, as the measured time lag was approximately 2 1/2 minutes for a response of 95% of a step change in gas composition. Incurrent air was then sampled again in order to check for machine drift. The animal was then removed from the animal chamber and weighed. On several occasions an animal failed to provide stable resting values for over two hours. When this happened, the experiment was terminated, and the order of determination was re-randomized for all temperatures remaining to have metabolic rate successfully determined. Stable values were eventually obtained for all animals at all temperatures during both night and day.

Statistical procedures

Statistical tests were based primarily on the procedures recommended by Lindman (1974). Data analysis was carried out using SPSS version 9.0 and BMDP-83 installed on a CDC Cyber 170/855. Most statistical analyses were performed with both packages to check for accidental misspecification of statistical procedures in the programs. Since multiple measurements of metabolism rate were made on each mouse, the experiment was a repeated measures design. Diurnal variation in each of the parameters of the regression model was tested with a paired t-test. A repeated measures analysis of variance was used to determine whether or not there were significant differences among individuals in MTC. The existence of a relationship between T_a and the T_c at which all metabolic parameters stabilized was tested separately for the nighttime and daytime data using a repeated measures ANOVA with linear trend analysis (Lindman, 1974).

RESULTS

Metabolic Parameters

Metabolic parameters will be expressed on a "per kilogram" live mass basis. The relationship between phase, T_a, and metabolic rate is shown in Figure 1.2. Basal metabolic rate and lower critical temperature were calculated in two ways, from a segmented regression of metabolic rate as a function of (T_c-T_a), and from a segmented regression of metabolic rate as a function of T_a. These calculations can be done for two measures of metabolic rate, the total metabolic rate, and the metabolic rate minus evaporative heat loss ("dry" metabolic rate). Examination of the data revealed that the metabolic rate measured at 35 ^{o}C was consistently higher than the metabolic rate at 30 ^{o}C or 32.5 ^{o}C. Thus, 35 ^{o}C was determined to lie above the thermoneutral zone and metabolic rate data for 35 ^{o}C were excluded from the data set used to simultaneously estimate minimal thermal conductance, lower critical temperature, and BMR.

The estimated basal metabolic rate was 9.42 ($\pm$ 0.11) $W \cdot kg^{-1}$ for resting phase; 9.48 ($\pm$0.13) $W \cdot kg^{-1}$ for active phase (difference not statistically significant). The estimated "dry" basal metabolic rate ($M-Q_{ev}$) was 5.026 ($\pm$ 0.23) for resting phase; 6.112 ($\pm$ 0.25) for active phase ($p < 0.07$). The statistical analysis of data on the lower critical temperatures is summarized in Table 1.5.

Minimal thermal conductance was calculated from the data in four

ways, as discussed in the Introduction. These calculations were performed both for the measured metabolic rate (providing estimates of "wet" MTC) and $M-Q_{ev}$ (providing estimates of "dry" MTC). Two of the calculation methods (McNab's method and the two-point method) do not allow simultaneous estimation of the lower critical temperature. However, examination of graphs of M against T_a for each individual showed that the metabolic rate at 20 ^{o}C was consistently above that for T_a=25. Thus, for the two methods that do not provide simultaneous estimates of T_{lc}, I calculated average minimal thermal conductance as the average of the MTC values calculated for T_a's $\leq$ 20 ^{o}C.

The statistical analysis of MTC data is summarized in Table 1.6. All four estimation methods revealed statistically significant diurnal variation in MTC except McNab's method for calculation of dry minimal thermal conductance (Table 1.6). The calculated amount of diurnal variation in MTC was noticeably different depending on the calculation method used. In particular, diurnal variation in MTC as calculated from Scholander's method was higher than diurnal variation in MTC as calculated from the segmented regression method (Table 1.6). Table 1.7 shows the relationship between MTC and T_a for McNab's method and the two-point method. None of the relationships between MTC and T_a were statistically significant except the relationship between McNab's MTC_w and T_a, which showed a significant ($p < 0.05$) decrease with T_a.

Core Temperature Data

The relationship between phase, T_a, and the T_c at which steady state was reached is shown in Figure 1.3. A repeated measures ANOVA was used to analyze these data. Stable body core temperatures were significantly lower during resting phase (35.40 $\pm$ 0.12 ^{o}C) than active phase (36.44 $\pm$ 0.13 ^{o}C) ($p < 0.05$). A linear trend analysis (Lindman 1974) of the relationship between T_c and T_a was significant when data for all temperatures and both phases were considered ($p < 0.01$), and also for resting phase data alone ($p < 0.01$). A trend analysis for active phase alone was not statistically significant but was suggestive of a slight relationship ($0.05 < p < 0.10$)

Evaporative Heat Loss

The relationship between evaporative heat loss and T_a is shown for both active and resting phase in Figure 1.4. Average evaporative heat loss for all temperatures was higher during the active phase than during the resting phase (3.41 $\pm$ 0.16 $W \cdot kg^{-1}$ as compared to 3.59 $\pm$ 0.17 $W \cdot kg^{-1}$). This difference is statistically significant ($p < 0.05$). Linear regression was performed for each phase on Q_{ev} as a function of T_a and Q_{ev} as a function of $(T_c - T_a)$ for $T_a \leq 25$ ^{o}C. In all cases, the relationships were well modeled by a simple linear function for $T_a \leq 25$ (see Figure 1.4). The slopes of the

relationships between Q_{ev} and T_a during resting and active phases were not statistically significantly different (0.03087 for active, 0.04609 for resting; $p \geq 0.15$). Likewise, the slopes of the relationship between Q_{ev} and ΔT were not statistically significantly different between phases (-0.04039 for active, -0.02766 for resting; $p \geq 0.15$).

Variation Between Individuals

Since all methods of calculating MTC result in at least two estimates of MTC per individual, it is possible to test whether or not there is statistically significant variation between individuals by using a repeated measures analysis of variance (Lindman 1974). All methods of calculation of MTC showed statistically significant ($p < 0.05$) differences between individuals except calculation of MTC from the two-point method. Figure 1.6 shows the relationship between dry metabolic rate and ΔT for each individual P. leucopus, for both phases.

DISCUSSION

Core Temperature

The core temperature data reported in this paper represent the temperature at which the metabolic rate, evaporative water loss, and core temperature were simultaneously stable, that is, at steady state. There is clear diurnal variation in the core temperature, with an average day-night difference of 0.9 ^{o}C. The diurnal variation reported here is greater than the 0.6 reported for Peromyscus leucopus by Knuth and Barrett (1984), and also greater than the 0.7 ^{o}C predicted from the allometric equation presented in Aschoff (1981b). This may result from methodological differences. The equation of Aschoff (1981b) and the data of Knuth and Barrett (1984) were collected primarily by measuring the core temperature of an animal in its cage at various times of day, irrespective of activity level. This may obscure diurnal variation in the steady state (resting) core temperature. There is a clear relationship between T_c at steady state and the ambient temperature during the resting phase. The average T_c at 0 ^{o}C was 34.48 ($\pm$ 0.51) ^{o}C, the average at T_a=25 ^{o}C was 35.2 ($\pm$ 0.19) ^{o}C, and the average at 35 ^{o}C was 37.3 ($\pm$ 0.26) ^{o}C. These values fall within the "normal" range for Peromyscus (34-40 ^{o}C) (Hill 1983). Peromyscus are noted for body temperature lability, and Hill (1983)

has pointed out the associated energetic benefits. An interesting observation is the relative lack of T_c lability during the active phase, in spite of the animals being at steady state when the T_c values were recorded. P. leucopus are active at night. Perhaps there is some cost of this T_c lability in terms of ability to exercise (e.g. collect food, avoid predators) which makes it maladaptive to exhibit T_c lability at night when the mice are normally foraging, seeking mates, etc. During the resting phase P. leucopus are normally in their nest and are rarely called upon to exhibit a burst of metabolism, so any such "costs" would be minimal, while there would be noticeable benefits in terms of cost of thermoregulation.

Evaporative Water Loss

Evaporative heat loss amounted to approximately 11% of the total metabolic heat load at 0 ^{o}C, 30% of the total metabolic heat load at 30 ^{o}C, and 65% of the metabolic heat production at 35 ^{o}C. These data agree well with those reported by Welch (1980) and Conley (1983) for P. maniculatus. Conley (1983) calculated the fractional heat loss due to evaporation as approximately 9% at 0 ^{o}C, 14% at 25 ^{o}C, and 30% at 35 ^{o}C. Conley found lower relative evaporative heat loss at 35 ^{o}C than found in this experiment. This difference may be due to differences between species or methodological differences. The relative evaporative heat loss values found for 35 ^{o}C in this study

are in the upper range of values reported for small mammals (cf. Gates 1980). However, some animals were observed to have wet faces on removal from the metabolism chamber, indicating that they were actively attempting to facilitate evaporative heat loss.

Evaporative water loss rates were higher at night than during the day. Welch and Tracy (1977) developed a model that suggests that the rate of evaporative water loss from mammals should increase with both metabolic rate and the temperature of the internal nares. Both the core temperature and the metabolic rate were higher at night than during day. If one assumes that higher core temperatures at night are associated with higher internal nare temperatures, the higher evaporative water loss rates at night are consistent with the predictions of Welch and Tracy's (1977) model.

Evaporative water loss rates were linearly related to both the ambient temperature and ΔT for both active and resting phase. However, the slopes for these two relationships were not statistically significantly different ($p > 0.25$). Thus, while there is a significant linear trend between evaporative water loss and T_a, there is no apparent diurnal variation in the slope of the relationship.

Minimal Thermal Conductance

All four methods for determining MTC produced estimates that are in at least general agreement with other values presented in the

literature. The allometric equation given by Aschoff (1981a) predicts for a 22.5 g mammal (the average mass of the P. leucopus used in this study) a value of 1.06 $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$ for the resting phase and 1.62 $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$ for the active phase. The equation of Bradley and Deavers (1980), which is not separated by phase, produces an estimate of 1.2 $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$.

The assumption that metabolic rate measurements used for estimating MTC are made with the animal at steady state merits special note. The assumption that the core temperature is constant is necessary if heat storage is accurately to be assumed 0. However, few investigators measure core temperature simultaneously with metabolic parameters (McNab 1980b). Instead, many investigators simply record measurements when the gas exchange parameters have stabilized and either fail to measure core temperature at all, or measure rectal temperature of the test organism as soon as possible after the animal is removed from the test chamber (McNab 1980b). Figure 1.5 shows the time course of metabolic rate and body temperature in one particularly interesting experiment, where a stable metabolic rate was reached while the core temperature was dropping. After a few minutes, the core temperature stabilized and the metabolic rate increased to a new, higher steady value. Use of data from this period would have resulted in a 14% underestimation of the metabolic rate required to maintain a steady state. Transients similar to that shown in Figure 1.5 were

observed on many occasions. I also observed many instances where an abnormally high (but stable) metabolic rate was maintained while the body core temperature was rising.

Wet vs. Dry Thermal Conductance

In all four methods of calculating thermal conductance, the derivation of wet thermal conductance from the corresponding dry thermal conductance requires the assumption that evaporative heat loss be adequately described by a linear function of either T_a or (T_c-T_a). Examination of Figure 1.4 shows that in the present study, evaporative heat loss is reasonably well approximated by a linear function for T_a's below the thermoneutral zone. The deviations from linearity amount to a maximum of 0.6 $W \cdot Kg^{-1}$. This is considerably smaller than the average standard deviation of the metabolic rate at any temperature below 25 ^{o}C (2.46 $W \cdot kg^{-1}$). Thus, the deviations from linearity are small in comparison to the natural variation in metabolic rate, and we are justified in expressing Q_{ev} as a linear function of T_a below the thermoneutral zone, at least as a first approximation. However, the validity of this approximation (and thus the use of "wet" MTC) is a subject that needs further investigation.

For McNab's method of calculating wet MTC to be correct, Q_{ev} must have an approximately linear relationship with T_a that extrapolates to $Q_{ev}=0$ at $T_c=T_a$. It is clear from Fig. 1.4 that the relationship

between Q_{ev} and T_a does not even approximate this behavior. McNab's method calculates MTC_w from $M/\Delta T$. From eq. (23) we see that MTC_w is actually given by

$$MTC_w = \frac{M}{\Delta T} \quad \frac{-(Q_{ev}|_0 + F)}{\Delta T}$$

where $Q_{ev}|_0$ is the extrapolated value of Q_{ev} at $\Delta T=0$ of the linear approximation of the relationship between Q_{ev} and ΔT. Thus McNab's method missestimates MTC_w by the amount $(Q_{ev}|_0 + F)/(T_c - T_a)$. While F is quite small (about $-0.1\ W \cdot kg^{-1}$; Appendix 2), the extrapolated value of Q_{ev} at $T_a = T_c$ is approximately $5\ W \cdot kg^{-1}$. The error in use of McNab's method will decrease as ΔT increases, because $Q_{ev}|_0$ is a constant and F is approximately constant. Because $(Q_{ev}|_0 + F)$ is positive, McNab's method should overestimate MTC_w, and the degree of overestimation should decrease as ΔT increases. Examination of Table 1.7 shows a noticeable decrease in McNab's MTC_w with T_a. If this were the result of real variation in MTC with T_a, similar variation should be apparent in the two-point estimates of MTC_w, but this is not the case (Table 1.7). Thus, the decrease in MTC with T_a calculated by McNab's method seems to be an artifact of the calculation method, rather than changes in the thermal properties of the animal at low temperatures.

As mentioned above, the slope of the relationship between Q_{ev} and

T_a for $T_a \leq 25\ ^{o}C$ is similar for both resting and active phases (0.046 vs. 0.039). On this basis, one would expect all methods of estimating MTC (except possibly McNab's) to show approximately the same amount of diurnal variation for both wet and dry MTC. Examination of Table 1.6 shows that, in fact, all methods except McNab's show virtually the same amount of diurnal variation in wet MTC as dry MTC. This being the case, further comparison of different methods of calculating MTC will be done on the basis of dry MTC unless otherwise noted.

Comparison of different methods for estimating MTC

Two-point estimation of MTC

Estimation of MTC by the two-point method depends on only one fairly weak assumption beyond those assumptions common to all methods: that MTC is constant over the range $(\Delta T_1, \Delta T_2)$. Thus, while this method yields estimates of MTC with large confidence limits (due to the large effect of random variation in M on the estimate of the MTC), it is possible to use this estimation method to test whether MTC is constant for $\Delta T > \Delta T_{1c}$. This assumption is essential to Scholander's method and the segmented regression method. Violations of this assumption would result in the calculation of a single (and incorrect) slope parameter, when in actuality the slope parameter varies with ΔT. A violation of this assumption is difficult

to determine from a plot of M on either T_a or (T_c-T_a), because this would result only in a slight curvature in the relationship that might be impossible to distinguish due to random scatter in the data. In the case of the present data on Peromyscus leucopus, there appears to be no systematic variation of MTC with temperature over the range of temperatures used (Table 1.7).

McNab's Method

The problems associated with use of McNab's method for calculating MTC_w have already been discussed. McNab's method of calculating MTC_d will result in missestimation of MTC_d by the amount $F/\Delta T$. Values of F calculated in Appendix 2 show that F has a value of approximately 0.042 $W \cdot kg^{-1}$ for Peromyscus leucopus, which will cause some error in estimating dry MTC by McNab's method, but the absolute error should be relatively small, hence the lack of noticeable variation in McNab's MTC_d with ΔT (Table 1.7). However, there is no diurnal variation in MTC_d as calculated by McNab's method. There is no reason to expect F to have the same value for an individual during both night and day, and diurnal variation in F could obscure diurnal variation in MTC_d. Since the other three methods for calculating all show significant diurnal variation, it seems that McNab's method fails to discern diurnal variation in MTC that really exists.

Segmented Regression

Since use of the two-point method shows no noticeable variation in thermal conductance with T_a, it seems the assumption that thermal conductance is constant (minimized) at ΔT_{lc} is satisfied. Thus, assumptions required for validity of estimation of MTC from segmented regression are met.

Scholander's Method

Calculation of MTC by regression of M against T_a depends upon the assumption that the core temperature always stabilizes at the same value. This assumption is clearly violated with P. leucopus (Figure 1.3). The average stable core temperature varied, during resting phase, from 34.4 ^{o}C at Ta=0 ^{o}C to 35.1 ^{o}C at Ta=20 ^{o}C, or a total of 5% of that ambient temperature range. Furthermore, during active phase there was almost no variation of T_c with T_a at T_a's between 0 and 20 ^{o}C. The effect of this is that during the resting phase the range of (T_c-T_a) covered between T_a's of 0 to 20 ^{o}C is smaller than during the active phase. This erroneously decreases the value of minimal thermal conductance calculated for resting phase. This, in turn, inflates the apparent diurnal variation in minimal thermal conductance over that calculated from segmented regression of M against (T_c-T_a) (Table 1.5).

To summarize the comparison of different methods for estimating

minimal thermal conductance, we see that the assumptions required for estimation of MTC by the two-point method and the segmented regression method seem to be met. The segmented regression method should be used for routine calculations of MTC. The two point method is useful for testing a critical assumption needed for the segmented regression method, but it does not allow simultaneous estimation of MTC, T_{lc}, and BMR. Furthermore, the estimates resulting from the two-point method have a very high variance and do not provide maximum likelihood estimates of MTC (Hogg and Craig 1976).

Assumptions required for the other two methods of calculating MTC are clearly violated. T_c is clearly related to T_a during the resting phase. The effect of this violation is to be to inflate the apparent diurnal variation in MTC. Table 1.6 shows that the amount of diurnal variation in MTC calculated in this manner (both wet and dry) is about 20% greater than the amount of diurnal variation calculated from segmented regression against ΔT. Thus, the violation of a critical assumption results in distortion of the amount of diurnal variation in MTC. This method has traditionally been the most common method used for calculation of MTC. Use of this method should be discouraged, due to its sensitivity to variation in T_c with T_a.

Not only did regression of M against T_a distort the amount of diurnal variation present in P. leucopus, but use of this method could result in erroneous conclusions in comparisons between species. For

example, suppose the MTC of two species are being compared (using measurements obtained during resting phase), with these species of identical size and MTC. Suppose further that species "A" exhibits no variation of T_c with T_a, but that species "B" exhibits T_c lability with T_a such as that demonstrated in this paper for P. leucopus. Use of regression of M against T_a would result in the erroneous appearance of species "B" having a lower MTC than species "A".

Variation between Individuals in MTC

A repeated measures analysis of variance showed significant differences between individuals. This information is important to arguments that variation in MTC between populations or species reflects responses to natural selection on thermal exchange properties (McNab 1978a, 1978b, 1980a; Brown and Lee 1969). Phenotypic variation in a trait between individuals is a requisite for natural selection to affect that trait (Emlen 1984). Thus, demonstration of significant between-individual variation is an essential (and previously unverified) step in any demonstration that between-species differences in MTC reflect the effects of natural selection.

The significance of variation between individuals also affects procedures for comparing MTC among different species. When between-individual variation is significant, grouping of individual data points from several individuals to calculate a species average MTC is

invalid (Lindman 1974). More importantly, this procedure (used, for example, by McNab 1978a and 1978b) increases the apparent level of significance of differences between species, and could result in the false appearance of statistically significant differences between species (Box et al. 1978; Lindman 1974). Rather than grouping all points together for a given species, MTC should be calculated for each individual. These individual MTC values then form the basis of comparisons between species (Lindman, 1974).

Diurnal Variation in MTC

The remainder of the discussion will involve the values of thermal conductance calculated by segmented regression of M on ΔT. The amount of diurnal variation found in the present study is markedly less than the amount predicted from Aschoff's (1981a) equations. A few points should be made regarding the data used by Aschoff to generate these equations. Aschoff's data set did not contain any one species for which there were MTC values for both phases of the activity cycle. My own research in the literature also indicates that the current study is the first time diurnal variation in MTC has been measured directly for any mammalian species. Also, most data on MTC of small mammals has been collected during the day (Aschoff 1981a). Because many small mammals are nocturnal, most of the MTC data available for small mammals are for resting phase. Aschoff used MTC

data for 86 species. Of these 86 species active phase MTC data were available for only 27 species. Furthermore, the smallest mammal for which active phase MTC values were available was Eutamias merriami (approximately 90 grams body mass). Aschoff's data were also taxonomically biased, since species of mass under 100 grams in the data set were primarily cricetids, and a large portion of the active phase data were from sciurids. It seems that the tremendous amount of diurnal variation suggested by Aschoff's analysis is largely due to biases in the MTC data available in the literature.

Aschoff (1981a) suggested diurnal variation in peripheral vasoconstriction and fur piloerection as possible causes for diurnal variation in MTC. He further suggested that diurnal variation in MTC functions to facilitate heat loss during the active phase. However, it seems unlikely that a small mammal such as P. leucopus faces a need to do this, particularly at low ambient temperatures. In contrast, it may be that diurnal variation in MTC "functions" to reduce maintenance costs during the resting phase. P. leucopus may lower peripheral circulation during the resting phase as a result of decreased tissue metabolism. This could lower the rate of heat flow through the peripheral tissues, in turn lowering MTC. This would result in decreases in the cost of thermoregulation during the resting phase.

P. leucopus are known to employ several mechanisms for reducing resting phase maintenance costs, including huddling and diurnal

torpor. In the present study two other mechanisms that may function similarly have been found, variation in T_c with T_a during the resting phase, and lower MTC during the resting phase. The variation in T_c with T_a effectively reduces the temperature gradient between the animal and its environment. The lower MTC during resting phase reduces the rate at which heat flows across the temperature gradient.

CONCLUSIONS

There is clear diurnal variation in stable T_c of Peromyscus leucopus. Peromyscus leucopus shows a nearly linear relationship between stable T_c and T_a during the resting phase, but not during the active phase.

There is diurnal variation in the evaporative water loss rates of P. leucopus. During both phases, evaporative water loss is adequately described by a linear function of either T_a or ΔT, and the slopes for active and resting phases are approximately the same.

The development in this paper of a model of the relationship between (T_c-T_a) and metabolism at low ambient temperatures shows that it is possible to define minimal thermal conductance as a slope parameter that describes the change in M per degree change in ΔT at $\Delta T \geq \Delta T_{lc}$.

The "lower critical temperature" is more appropriately regarded as a critical temperature difference than an ambient temperature, because it is the thermal gradient, not the temperature per se, that should determine the lower limit of the thermoneutral zone. The theoretical development of wet MTC requires the use of approximations beyond those required for development of dry MTC. In particular, it requires the approximation of Q_{ev} as a linear function of ΔT for $\Delta T \geq \Delta T_{lc}$. While this seems valid as a first approximation in the present study, the relationship between evaporative water loss and ΔT merits further

study.

Three methods of computing MTC were compared; segmented regression of M against ΔT was found to be superior to the other two methods in common use in the literature because other methods depend on assumptions which may be violated, and were violated in the present case of P. leucopus.

There is diurnal variation in MTC of P. leucopus, but the diurnal variation is considerably less than that predicted by Aschoff's (1981a) equations. This seems largely due to bias in the data available in the literature regarding MTC of mammals. The present study marks the first time that MTC has been determined for both phases of the activity cycle for one species. Further work involving experimental determination of diurnal variation of MTC is essential for an accurate view of the amount of diurnal variation found in MTC of small mammals.

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Table 1.1. List of variable names and definitions.

Variable	Definition	Units
A_{cond}	Surface area of animal from which heat is lost by conduction	m^2
A_r	Surface area of animal from which infrared radiation is emitted and from which convection occurs	m^2
A_{skin}	Surface area of animal measured at skin surface	m^2
A_{tot}	Total surface area of animal (measured at outer surface of fur layer)	m^2
b_i	b_i (where i is an integer) is used as an intercept parameter (without any particular biological meaning) when such is needed in an intermediate step of the model development.	
BMR	basal metabolic rate	W
c_a	specific heat of air	$J \cdot gm \cdot K^{-1}$
c_w	specific heat of water vapor	$J \cdot gm.K^{-1}$
d_b	Thickness of insulative layer of flesh	m
d_f	Thickness of fur layer	m
h_c	Convection coefficient for animal's surface	$W \cdot m^{-2} \cdot K^{-1}$
K_b	Thermal transfer coefficient to insulative flesh	$W \cdot K^{-1} \cdot m^{-1}$
K_{bw}	Thermal transfer coefficient for bulk warming of inhaled air and water vapor	$W \cdot K^{-1}$
K_{cond}	Conduction coefficient from animal to substrate	$W \cdot K^{-1} \cdot m^2$
K_f	Thermal transfer coefficient for fur	$W \cdot m^{-1} \cdot K^{-1}$
F	Constant used in approximations in development	W

	of model of small mammal energy exchange	
M	Metabolic rate	W
m_i	m_i, (where i is an integer) is used as a slope parameter (without any particular biological meaning) when such is needed in an intermediate step of the model development.	
MTC_d	"Dry" minimal thermal conductance	$W \cdot K^{-1}$
MTC_w	"Wet" minimal thermal conductance	$W \cdot K^{-1}$
P	Production by animal (growth)	W
Q_{abs}	Energy absorbed from incident infrared radiation	W
Q_{bw}	Heat exchange due to bulk warming or cooling of inhaled air and water vapor	W
Q_{cond}	Heat exchange due to conduction	W
Q_{conv}	Heat loss due to convections	W
Q_{em}	Heat loss due to emitted thermal radiation	W
Q_{ev}	Total heat loss due to evaporation ($Q_{ev} = Q_{ex}+Q_{sw}$)	W
Q_{ex}	Heat loss due to evaporation in expired air (Respired Evaporative Heat loss)	W
Q_{swrad}	Energy absorbed from incident shortwave radiation	W
Q_{sw}	Heat loss due to evaporation from skin ("Sweating" Evaporative Heat Loss)	W
S_H	Heat storage by animal	W
T_a	Ambient temperature (measured as equivalent blackbody temperature as defined by Bakken 1976)	K
T_c	Temperature of body core of animal	K
T_{ex}	Temperature of exhaled air	K

T_m	Temperature used in linearization of thermal radiation heat exchange term	K
T_r	Temperature of radiative surface of animal	K
T_w	Temperature of wall of metabolism chamber	K
W	Work done by animal	W
$\dot{V}$	Respiratory Exchange Rate	$L \cdot s^{-1}$
ΔT	$T_c - T_a$	K
ΔT_{lc}	ΔT at which metabolic rate rises above basal level (progressing in the direction of ΔT increasing, with T_a decreasing)	K
ΔT_{uc}	ΔT at which metabolic rate rises above basal level (progressing in the direction of ΔT decreasing, with T_a increasing)	K
ε_f	Emissivity of fur	dimensionless
ε_w	Emissivity of wall of metabolism chamber	dimensionless
ρa	Density of dry air	$gm \cdot L^{-1}$
ρ_w	Density of water vapor in inspired air	$gm \cdot L^{-1}$
σ	Stefan-Boltzmann constant	$W \cdot m^{-2} \cdot K^{-4}$

Table 1.2. Assumptions regarding the design of the chambers used to hold animals for metabolism measurement.

-Air flow through the chamber is laminar.
-Airflow through the metabolism chamber is sufficiently slight that free convection predominates over forced convection.
-Emissivity of the inside walls of the metabolism chamber is approximately 1.0
-The physical dimesionsions of the metabolism chamber and the flow rate through the chamber are the same for all metabolic rate determinations used in a given set of comparisons.
-The air entering the chamber, the bulk fluid temperature of the air within the chamber, and the temperature of all internal surfaces, are all at a uniform temperature T_a.

Table 1.3. Assumptions about the test mammal common to all developments of thermal conductance discussed in this paper.

-A "lumped parameter" model may be used to describe the heat transfer within and from the animal. (In the present development, we are using a lumped parameter model that treats the animal as having a cross-section that may be reasonably approximated by a series of concentric layers around a central core. The particulars of the model, however, are less important than the critical assumption that a lumped parameter model is sufficiently accurate as to be useful.) The animal is represented as consisting of 1) a core of tissue at a uniform temperature Tc, in which essentially all of the animal's metabolism occurs; 2) a layer of insulating flesh consisting of fat, skin, and perhaps muscle tissue with vasoconstriction; 3) a layer of insulating fur with a smooth, uniform outer surface having an emissivity of essentially 1.0.
-Respiratory water loss occurs directly from the body core.
-Evaporative water loss from the skin occurs directly from the skin surface.
-The animal is postabsorptive and at rest.
-The animal's energy exchanges with the environment are at steady state. That is, the metabolic rate, evaporative water loss, and average body temperature are constant.

Table 1.4. Four different methods for estimating minimal thermal conductance and the assumptions required for each method (beyond those listed in Tables 2 and 3).

Method	Special Assumptions	References
1. "Scholander's method": regression of M against T_a	T_{lc} represents the temperature at which an animal has incorporated all physiological and behavioral mechanisms for minimizing heat loss. T_c is (during steady state conditions) regulated at a constant temperature.	Scholander *et al.* 1950; Gordon *et al.* 1975
2. "Segmented regression method": segmented regression of M against (T_c-T_a)	ΔT_{lc} is the temperature difference at which an animal has incorporated all the physiological and behavioral mechanisms available to it to minimize heat loss.	Johnson 1969; this paper
3. McNab's method:		
a: Dry MTC calculated from $M/(T_c-T_a)$	The relationship between M and ΔT extrapolates to 0 at $T_c=T_a$	McNab 1980b
b: Wet MTC calculated from $(M-Q_{ev})/(T_c-T_a)$	The relationship between $M-Q_{ev}$ and (T_c-T_a) extrapolates to 0 at $T_c=T_a$	
4. "Two-point method"; MTC calculated from $\frac{(M_1-M_2)}{[\Delta T_1-\Delta T_2]}$	Thermal conductance is constant between T_{a1} and T_{a2}. ΔT_1 and ΔT_2 are both greater than ΔT_{lc}	This paper

Table 1.5. Statistical analysis of lower critical temperature calculated by different methods. Note that in regressions of metabolism vs T_a, the temperature shown is lower critical temperature (T_{lc}), while in regressions of metabolism against ΔT, the temperature shown is a lower critical temperature difference, ΔT_{lc}. All values are shown as mean (±2 Standard errors).

Parameter	Mean (resting)	Mean (active)	T value	p (two-tailed paired t-test)
ΔT_{lc} calculated by segmented regression of (M-Qev) vs ΔT	6.02 (±1.08)	10.45 (±1.71)	4.05	.004
T_{lc} calculated by Scholanders method (seg. regression of $(M-Q_{ev})$ vs T_a	29.94 (±.599)	26.37 (±0.70)	3.77	.005
ΔT_{lc} calculated by segmented regression of M vs ΔT	7.53 (±1.36)	9.78 (±1.76)	1.99	.081
T_{lc} calculated by Scholanders method (seg. regression of M vs T_a	28.02 (±1.38)	26.60 (±1.35)	1.39	.201

Table 1.6. Statistical Analysis of Minimal thermal conductance calculated by different methods. Units are $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$; values are presented as mean (± 2 Standard Errors).

Calculation Method	Indep. Var.	Parameter	Mean (resting)	Mean (active)	T value	p (one-tailed, paired t-test)
Segmented Regression Method	ΔT	MTC_d	.877 (±.06)	1.098 (±.18)	2.40	.022
		MTC_w	.843 (±.04)	1.05 (±.08)	1.90	.047
Scholander's Method	T_a	MTC_d	.838 (±.06)	1.09 (±.18)	2.57	.016
		MTC_w	.809 (±.08)	1.04 (±.18)	2.16	.032
McNab's Method	ΔT	MTC_d	.877 (±.31)	.871 (±.26)	0.21	ns
		MTC_w	.991 (±.30)	1.00 (±.28)	0.35	ns
Two-point Method	ΔT	MTC_d	.892 (±.32)	.952 (±.34)	1.07	.082
		MTC_w	.861 (±.15)	.901 (±.18)	1.21	.045

Table 1.7. Relationship between T_a and wet and dry MIC as calculated by McNab's method and by the two-point method. Units are $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$; values are presented as mean (±2 standard errors).

Method	Phase	Ambient Temperature (T_a)				
		0.0	5.0	10.0	15.0	20.0
McNab's Method; MIC_w	rest.	.928(±.04)	.947(±.073)	.959(±.045)	1.06(±.056)	1.06(±.063)
	act.	1.05 (±.08)	.973(±.091)	.970(±.075)	1.02(±.074)	1.06(±.101)
McNab's Method; MIC_d	rest.	.868(±.05)	.863(±.073)	.845(±.048)	.931(±.037)	.878(±.065)
	act.	.988(±.08)	.870(±.081)	.859(±.057)	.824(±.069)	.816(±.038)
Two-Point Method; MIC_w	rest.	.774(±.10)	.862(±.127)	.549(±.143)	1.081(±.106)	
	act	1.490(±.09)	.843(±.110)	.931(±.105)	.829 (±.127)	
Two-Point Method; MIC_d	rest.	.863(±.09)	.872(±.120)	.497(±.108)	1.125(±.090)	
	act.	1.702(±.11)	.937(±.087)	1.094(±.119)	.751 (±.130)	

Figure 1.1. Diagram of the model used to represent the cross section of a mammal.

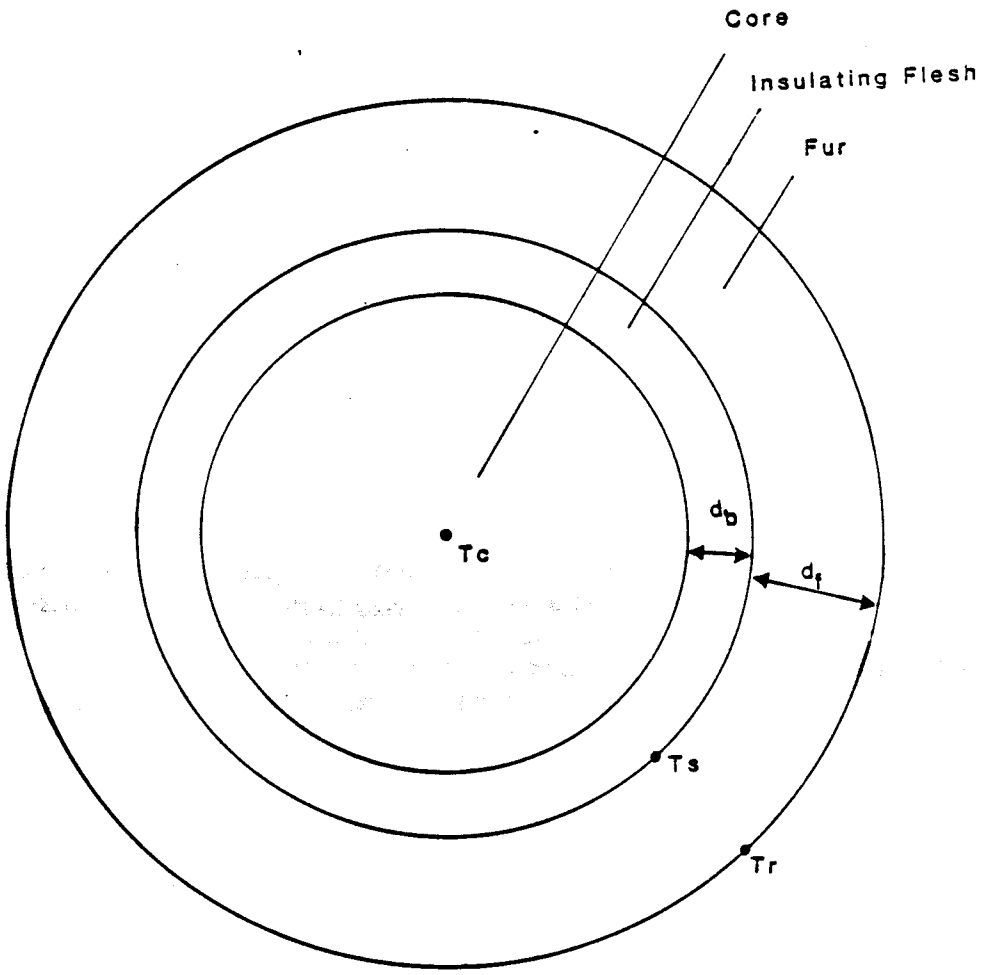

Core
Insulating Flesh
Fur
d_b
d_f
Tc
Ts
Tr

Figure 1.2. Relationship between metabolic rate ($M\text{-}Q_{ev}$) and ambient temperature for P. leucopus. Horizontal lines represent mean ($M\text{-}Q_{ev}$) for 10 adult male P. leucopus. Vertical bars indicate $\pm$ 2 SE. Vertical lines indicate ranges. Closed boxes indicate nighttime values. Open boxes indicate daytime values.

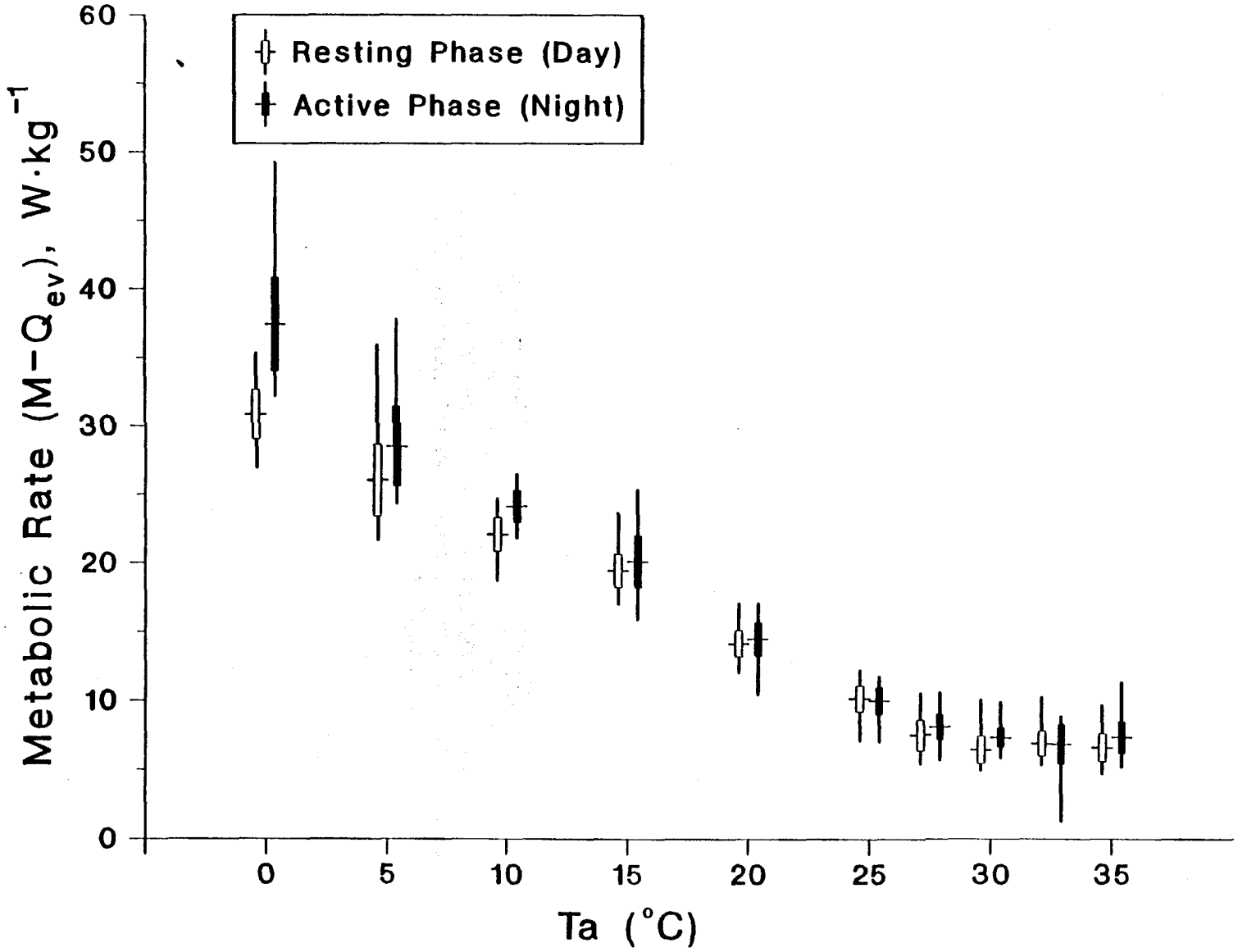

Resting Phase (Day)
Active Phase (Night)
Metabolic Rate (M−Qev), W·kg−1
60
50
40
30
20
10
0
0
5
10
15
20
25
30
35
Ta (°C)

Figure 1.3. Relationship between core temperature (T_c) and ambient temperature (T_a) for Peromyscus leucopus. Horizontal lines represent mean T_c for 10 adult male P. leucopus. Vertical bars indicate ± 2 SE. Vertical lines indicate ranges. Closed boxes indicate nighttime values. Open boxes indicate daytime values.

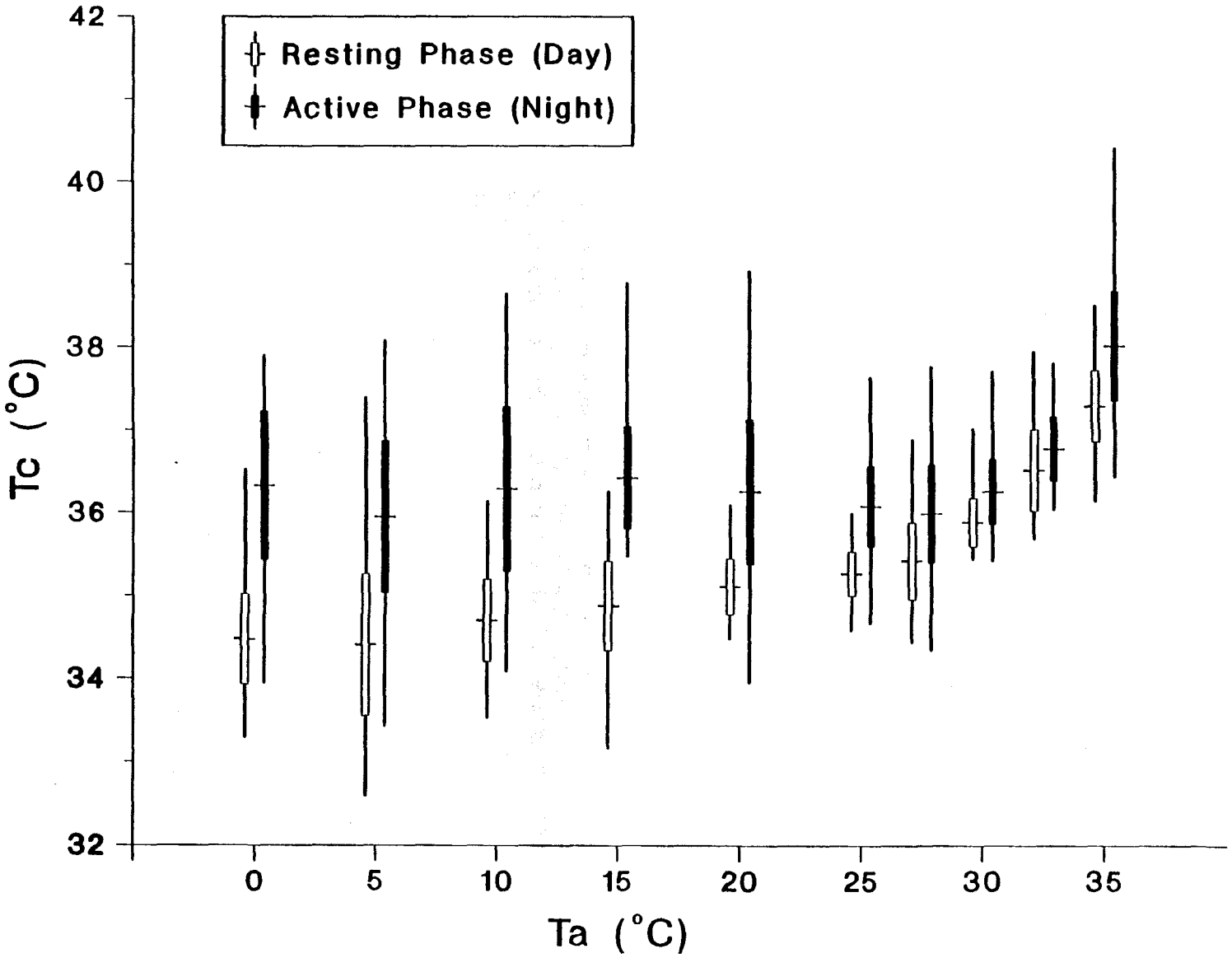

Resting Phase (Day)
Active Phase (Night)
42
40
38
36
34
32
Tc (°C)
0
5
10
15
20
25
30
35
Ta (°C)

Figure 1.4. Relationship between evaporative heat loss (Q_{ev}) and ambient temperature (T_a) for Peromyscus leucopus. Horizontal lines represent mean Q_{ev} for 10 adult male P. leucopus. Vertical bars indicate ± 2 SE. Vertical lines indicate ranges. Closed boxes indicate nighttime values. Open boxes indicate daytime values.

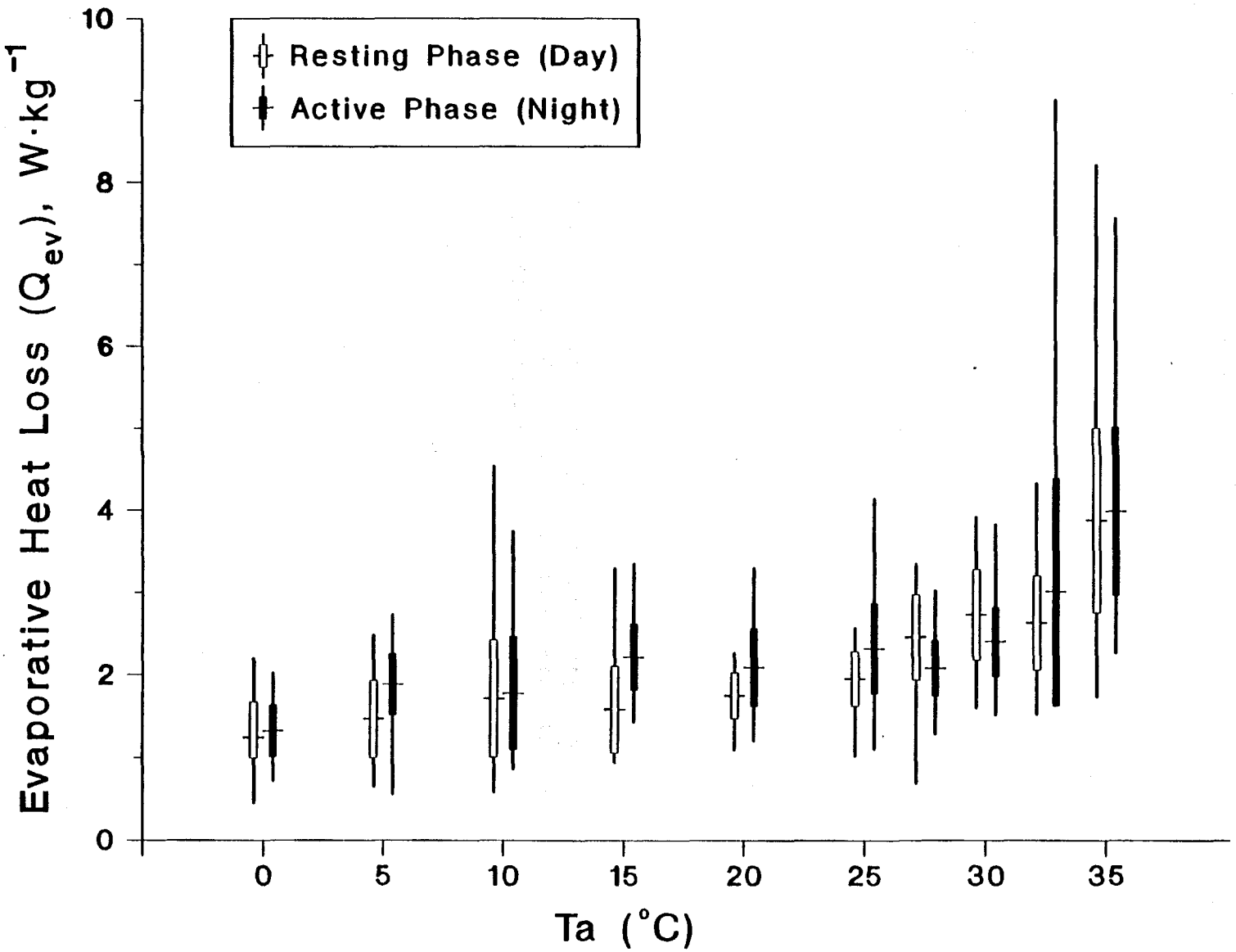

Resting Phase (Day)
Active Phase (Night)
Evaporative Heat Loss (Q_{ev}), $W \cdot kg^{-1}$
0
2
4
6
8
10
0
5
10
15
20
25
30
35
Ta (°C)

Figure 1.5. Time course of metabolic rate and core temperature for one experiment determing MR for an adult male Peromyscus leucopus at 20 °C, during the resting phase (daytime).

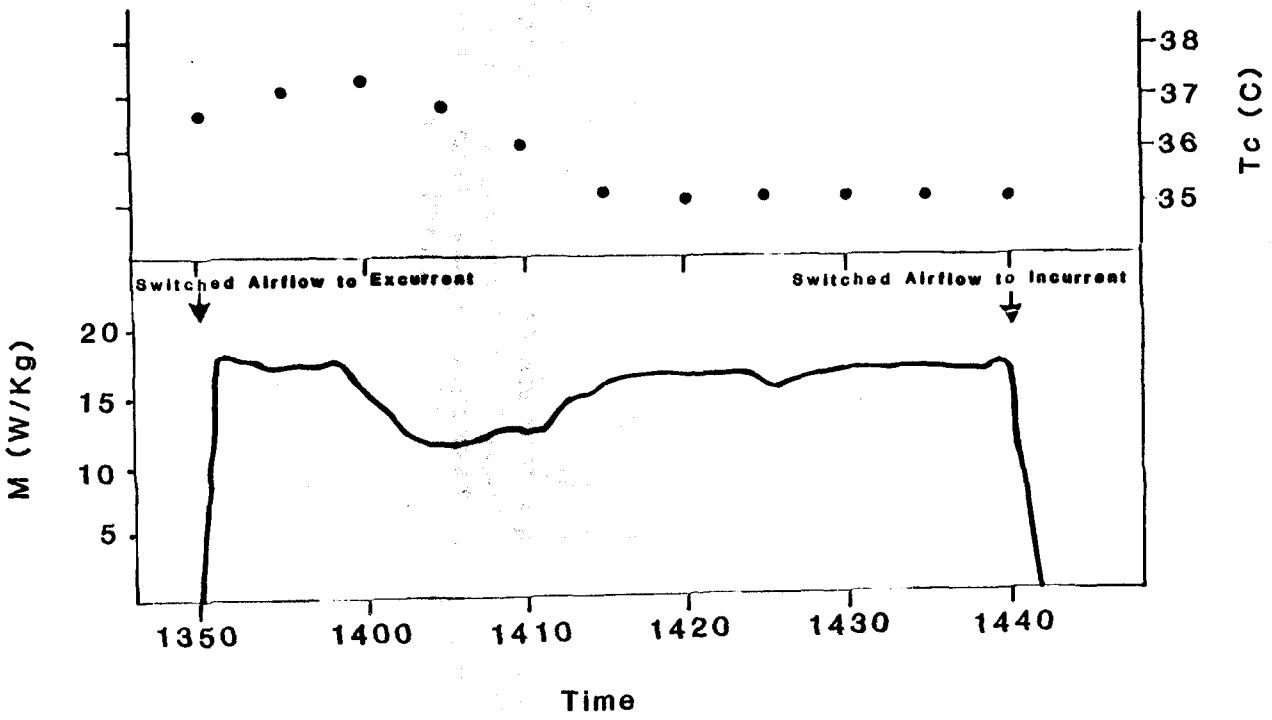
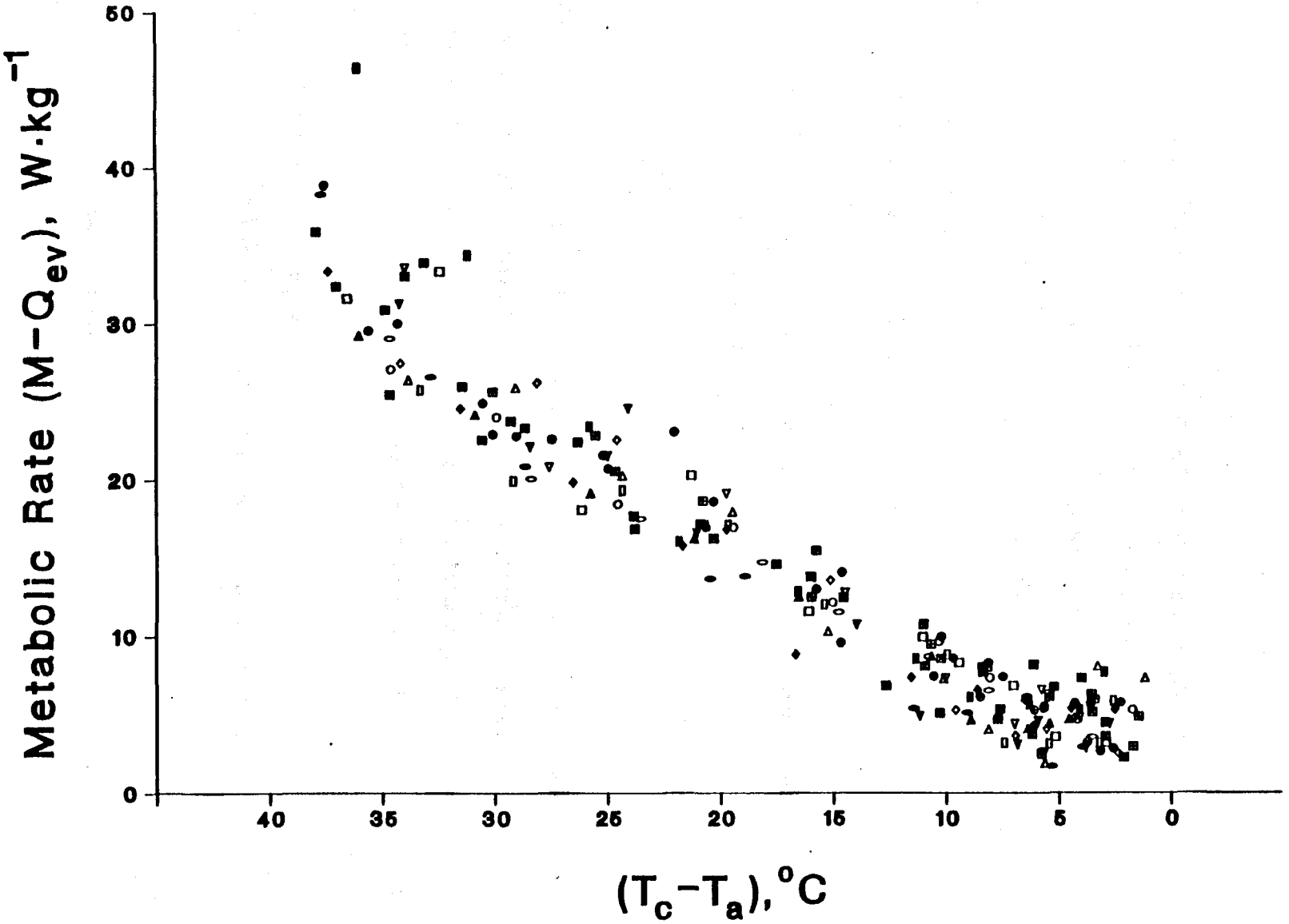

38
37
36
35
Tc (C)
Switched Airflow to Excurrent
Switched Airflow to Incurrent
20
15
10
5
M (W/Kg)
1350
1400
1410
1420
1430
1440
Time

Figure 1.6. Relationship between dry metabolic rate ($M\text{-}Q_{ev}$) and ΔT for individual P. leucopus, during resting and active phases. Different individuals are distinguished by different symbols. Resting and active phases are distinguished by shading of symbols. Open symbols represent resting phase measurements (made during daytime); shaded symbols represent active phase measurements (made during nighttime).


Metabolic Rate (M−Qev), W·kg−1
50
40
30
20
10
0
40
35
30
25
20
15
10
5
0
(Tc−Ta), °C

APPENDIX 1: ANALYSIS OF BULK RESPIRATORY HEAT LOSS

The purpose of this appendix is to analyze the bulk heat loss term (Q_{bw}) of equation (11) of the introduction:

$$M = A_r\sigma\varepsilon_f(T_r^4 - T_a^4) + A_r h_c(T_r - T_a) + A_{cond}K_{cond}(T_c - T_a) + Q_{ex} + Q_{sw} + Q_{bw} \quad (1a)$$

The heat loss due to bulk warming of inhaled air is given by

$$Q_{bw} = (T_a - T_{ex})[c_a\rho_a + c_w\rho_w]\dot{V} \quad (2a)$$

Welch and Tracy (1977) have shown that $\dot{V}$ may be related to V_{O2} through the following relationship:

$$\dot{V} = \frac{V_{O2}}{EF_{IO2}} \quad (3a)$$

Equation (3a) is modified from equation (3) of Welch and Tracy (1977) with the condition that $\dot{V}$ is expressed at standard temperature and pressure conditions). By converting units from eq. (14) of Kleiber (1961, p. 373) we can relate the metabolic rate (in Watts) to V_{O2} and R_E:

$$MR = (266. + 85.9R_E)V_{O2} \quad (4a)$$

Thus, it is possible to relate $\dot{V}$ and MR by combining eqs. (3a) and (4a).

$$\dot{V} = \frac{MR}{EF_{IO2}(266. + 85.9R_E)} \quad (5a)$$

So, from eqs. (2a) and (5a),

$$Q_{bw} = \frac{(T_a - T_{ex})[c_a\rho_a + c_w\rho_w]MR}{EF_{IO2}(266. + 85.9R_E)} \quad (6a).$$

The above expression can be simplified by making some approximations and substitutions. First note that the R_E of a fasted adult mammal is typically near 0.7. In a case where the R_E varies from a true value of 0.6 to a true value of 0.8, the error in substituting a value of 0.7 in eq. (5a) is only 2.54% of the correct value of Q_{bw}. Since R_E values will typically be very close to 0.7 for metabolism measurements of mature, fasted mammals it seems the error in using R_E=0.7 in eq. (5a) seems acceptable. Using this, and putting in place a value of 0.2094 for FIO2, we get from equation (6a)

$$Q_{bw} = \frac{(T_a - T_{ex})[c_a\rho_a + c_w\rho_w]MR}{68.29E} \quad (7a)$$

The heat capacity of air, c_a, is 1.00484 $J \cdot g^{-1} \cdot K^{-1}$ (Tracy et al. 1980). The density of dry air is 1.2929 $g \cdot liter^{-1}$ at STP. Substituting this into eq (7a) yields

$$Q_{bw} = \frac{(T_a - T_{ex})(1.00484 + c_w\rho_w)MR}{68.29E} \quad (8a)$$

In this treatment we are concerned with the warming of inhaled air and water vapor. So, the c_w term in equation (8a) is the water vapor density of the inhaled air. In the experiments in this dissertation, air entering the metabolism chamber was thoroughly dried (the dewpoint

of the incurrent air averaged -17.2 ^{o}C). The equivalent vapor pressure for a dewpoint of -17.2 ^{o}C is 4.84 x 10^{-3} g$\cdot L^{-1}$. Water vapor is mixed somewhat, however, in the animal chamber (Welch, 1980). The average excurrent dewpoint was 1.8 ^{o}C. The corresponding vapor pressure is 5.47 x 10^{-3} g$\cdot L^{-1}$. So, take a vapor pressure of 5.15 g$\cdot L^{-1}$ as an estimate of the actual water vapor density of the inhaled air. Substituting this into equation (8a), along with a value of 4.2141 J$\cdot g^{-1}\cdot K$ for c_w, gives

$$Q_{bw} = \frac{0.0194(T_a - T_{ex})MR}{E} \qquad (9a)$$

Welch (1984) showed that the temperature of the expired air can be written as a function of the temperature of the inspired air and vapor density of the inspired air. Under conditions where a series of experiments are performed using identical humidity conditions, T_{ex} may be written as a function of the temperature of the inspired air, T_a:

$$T_{ex} = m_1 T_a + b_1 \qquad (10a)$$

Welch's (1984) data do not deal with the question of whether T_{ex} may also be written as a linear function of ΔT. Under conditions where T_c may be assumed constant, then algebraic rearrangement of eq. (10a) yields an expression giving T_{ex} as a function of T_c and T_a. It seems plausible in other cases, where T_c might not be reliably assumed constant, that T_{ex} could also be written as a function of $T_c - T_a$. Thus,

$$T_{ex} = m_2 \Delta T + b_2 \qquad (11a)$$

From eqs. (9a) and (11a), after algebraic rearrangement,

$$Q_{bw} = \frac{0.0194(T_a - T_{ex})MR}{E} \qquad (12a)$$

Now, Welch and Tracy (1977) showed that the extraction coefficient, E, can be written as a linear function of the metabolic rate, that is,

$$E = b^* + m^*MR \qquad (13a)$$

Substituting this relationship into eq. (9a) yields a relationship giving Q_{bw} as a function of the product of MR and $(T_a - T_{ex})$. Using data from Welch (1984) and Welch and Tracy (1988) reveals that Q_{bw} is fairly well approximated as a linear function of either T_a or ΔT (deviations from linearity are less than 7% of the actual value). In addition, Qbw is a small part of the overall heat exchange (at least under conditions where the inhaled air is reasonably dry). While the data that relate to this topic are admittedly scanty, it seems that Q_{bw} can, at least for the purposes of this discussion, be approximated as a linear function of either Ta or ΔT.

APPENDIX 2: ANALYSIS OF $F(M,Q_{ex},Q_{sw},T_c,A_r,h_c,d_b,K_b,d_f,K_f)$

The purposes of this appendix are to: 1) fill in the algebraic steps between equations (13) and (14) of the introduction; 2) provide the analytic formula for $F(M,Q_{ex},Q_{sw},T_c,A_r,h_c,d_b,K_b,d_f,K_f)$; 3) discuss the behavior of $F(M,Q_{ex},Q_{sw},T_c,A_r,h_c,d_b,K_b,d_f,K_f)$ for the following species: Peromyscus leucopus, Mus musculus, Mesocricetus auratus, and Neotoma floridana.

Start with eq. (11) from the introduction:

$$M = A_r\sigma\varepsilon_f(T_r^4 - T_a^4) + A_r h_c(T_r - T_a) + A_{cond}K_{cond}(T_c - T_a) \quad (1a)$$
$$+Q_{ex} + Q_{sw} + Q_{bw}$$

The problem at this point is that equation (1b) involves T_r, and we would like to derive an equation that involves T_c as an independent variable. McNab (1980) simply wrote an equation analogous to (1b) using T_c as the independent variable. However, T_r is not equal to T_c in most mammals (Gates 1980). Thus, McNab's development involves an error, but probably more importantly, an error whose significance is unknown. As discussed in the Introduction of this dissertation, and in Porter and Gates (1969), T_r may be expressed as a function of T_c and the insulative properties of the animal:

$$T_c = T_r + \frac{d_b(M - Q_{ex})}{K_b\,(A_{skin})} + \frac{d_f(M - Q_{ex} - Q_{sw})}{K_f\,(A_{tot})} \quad (2b)$$

Rearrangement of eq. (2b) gives:

$$T_r = T_c - \frac{d_b}{K_b}\frac{(M - Q_{ex})}{(A_{skin})} - \frac{d_f}{K_f}\frac{(M - Q_{ex} - Q_{sw})}{(A_{tot})} \qquad (3b)$$

Equation (3b) is incorporated into eq. (2b) by substituting the right hand side of (3b) for the two T_r terms in equation (2b):

$$M = A_r \sigma \varepsilon_f \left[\left\{ T_c - \frac{d_b}{K_b}\frac{(M-Q_{ex})}{A_{skin}} - \frac{d_f}{K_f}\frac{(M-Q_{ex}-Q_{sw})}{A_{tot}} \right\}^4 - T_a^{\,4} \right] \qquad (4b)$$

$$+A_r h_c \left[\left\{ T_c - \frac{d_b}{K_b}\frac{(M - Q_{ex})}{A_{skin}} + \frac{d_f}{K_f}\frac{(M-Q_{ex}-Q_{sw})}{A_{tot}} \right\} - T_a \right]$$

$$+A_{cond} k_{cond} (T_c - T_a) + Q_{bw} + Q_{ex} + Q_{sw} + W + S_H$$

The term $\left\{ T_c - \frac{d_b}{K_b}\frac{(M - Q_{ex})}{A_{skin}} - \frac{d_f}{K_f}\frac{(M-Q_{ex}-Q_{sw})}{A_{tot}} \right\}^4$

is expanded, yielding:

$$
\begin{aligned}
M = A_r \sigma \varepsilon_f \Bigg[& T_c^4 + \frac{d_b^4 (M-Q_{ex})^4}{K_b^4 A_{skin}^4} + \frac{d_f^4 (M-Q_{ex}-Q_{sw})^4}{K_f^4 A_{tot}^4} \\
& - 4T_c^3 \frac{d_b (M-Q_{ex})}{K_b A_{skin}} - 4T_c^3 \frac{d_f (M-Q_{ex}-Q_{sw})}{K_f A_{tot}} \\
& - 4T_c \frac{d_b^3 (M-Q_{ex})^3}{K_b^3 A_{skin}^3} - 4T_c \frac{d_f^3 (M-Q_{ex}-Q_{sw})^3}{Kf3 A_{tot}^3} \\
& + 4 \frac{d_b^3 d_f (M-Q_{ex})^3 (M-Q_{ex}-Q_{sw})}{K_b^3 K_f A_{skin}^3 A_{tot}} \\
& + 4 \frac{d_b d_f^3 (M-Q_{ex}) (M-Q_{ex}-Q_{sw})^3}{K_b K_f^3 A_{skin} A_{tot}^3} \\
& + 6 \frac{d_b^2 d_f^2 (M-Q_{ex})^2 (M-Q_{ex}-Q_{sw})^2}{K_b^2 K_f^2 A_{skin}^2 A_{tot}^2} \\
& + 6T_c^2 \frac{d_b^2 (M-Q_{ex})^2}{K_b^2 A_{skin}^2} + 6T_c^2 \frac{d_f^2 (M-Q_{ex}-Q_{sw})^2}{K_f^2 A_{tot}^2} \\
& - 12T_c \frac{d_b^2 d_f (M-Q_{ex})^2 (M-Q_{ex}-Q_{sw})}{K_b^2 K_f A_{skin}^2 A_{tot}} \\
& - 12T_c \frac{d_b d_f^2 (M-Q_{ex}) (M-Q_{ex}-Q_{sw})^2}{K_b K_f^2 A_{skin} A_{tot}^2} \\
& + 12T_c^2 \frac{d_b d_f (M-Q_{ex}) (M-Q_{ex}-Q_{sw})}{K_b K_f A_{skin} A_{tot}} - T_a^4 \Bigg] \\
& + A_r h_c \left[\frac{T_c}{K_b} - \frac{d_b (M-Q_{ex})}{A_{skin}} - \frac{d_f (M-Q_{ex}-Q_{sw})}{K_f A_{tot}} - T_a \right] \qquad (5b) \\
& + A_{cond} h_{cond} (T_c - T_a) + Q_{bw} + Q_{ex} + Q_{sw}
\end{aligned}
$$

Algebraic rearrangement of this equation yields:

$$M = A_r \sigma \varepsilon_f (T_c^4 - T_a^4) + A_r h_c (T_c - T_a) + A_{cond} h_{cond} (T_c - T_a) + Q_{bw} + Q_{ex} + Q_{sw} + F(M, Q_{ex}, Q_{sw}, T_c, A_r, h_c, d_b, K_b, d_f, K_f) \quad (6b)$$

where $F(M, Q_{ex}, Q_{sw}, T_c, A_r, h_c, d_b, K_b, d_f, K_f)$ is given by:

$$F(M,Q_{ex},Q_{sw},T_c,A_r,h_c,d_b,K_b,d_f,K_f)=$$

$$A_r\sigma\varepsilon_f\left|\begin{array}{ll}
\dfrac{d_b^4}{K_b^4}\left(\dfrac{M-Q_{ex}}{A_{skin}}\right)^4 & +\dfrac{d_f^4}{K_f^4}\left(\dfrac{M-Q_{ex}-Q_{sw}}{A_{tot}}\right)^4 \\
-4T_c^3\dfrac{d_b}{K_b}\left(\dfrac{M-Q_{ex}}{A_{skin}}\right) & -4T_c^3\dfrac{d_f}{K_f}\left(\dfrac{M-Q_{ex}-Q_{sw}}{A_{tot}}\right) \\
-4T_c\dfrac{d_b^3}{K_b^3}\left(\dfrac{M-Q_{ex}}{A_{skin}}\right)^3 & -4T_c\dfrac{d_f^3}{Kf3}\left(\dfrac{M-Q_{ex}-Q_{sw}}{A_{tot}}\right) \\
+4\dfrac{d_b^3d_f}{K_b^3K_f}\left(\dfrac{M-Q_{ex}}{A_{skin}}\right)^3\left(\dfrac{M-Q_{ex}-Q_{sw}}{A_{tot}}\right) & \\
+4\dfrac{d_bd_f^3}{K_bK_f^3}\left(\dfrac{M-Q_{ex}}{A_{skin}}\right)\left(\dfrac{M-Q_{ex}-Q_{sw}}{A_{tot}}\right) & \\
+6\dfrac{d_b^2d_f^2}{K_b^2K_f^2}\left(\dfrac{M-Q_{ex}}{A_{skin}}\right)^2\left(\dfrac{M-Q_{ex}-Q_{sw}}{A_{tot}}\right)^2 & \\
+6T_c^2\dfrac{d_b^2}{K_b^2}\left(\dfrac{M-Q_{ex}}{A_{skin}}\right)^2 & +6T_c^2\dfrac{d_f^2}{K_f^2}\left(\dfrac{M-Q_{ex}-Q_{sw}}{A_{tot}}\right)^2 \\
-12T_c\dfrac{d_b^2d_f}{K_b^2K_f}\left(\dfrac{M-Q_{ex}}{A_{skin}}\right)^2\left(\dfrac{M-Q_{ex}-Q_{sw}}{A_{tot}}\right) & \\
-12T_c\dfrac{d_bd_f^2}{K_bK_f^2}\left(\dfrac{M-Q_{ex}}{A_{skin}}\right)\left(\dfrac{M-Q_{ex}-Q_{sw}}{A_{tot}}\right) & \\
+12T_c^2\dfrac{d_bd_f}{K_bK_f}\left(\dfrac{M-Q_{ex}}{A_{skin}}\right)\left(\dfrac{M-Q_{ex}-Q_{sw}}{A_{tot}}\right) &
\end{array}\right|$$

$$-A_rh_c\left[\dfrac{d_b(M-Q_{ex})}{A_{skin}}+\dfrac{d_f}{K_f}\left(\dfrac{M-Q_{ex}-Q_{sw}}{A_{tot}}\right)\right] \qquad (7b)$$

At this point it may seem that we are no further than at eq. (1b). However, as discussed in the introduction, the following parameters can be assumed constant for $\Delta T \geq \Delta T_{lc}$: A_r, d_b, K_b, d_f, K_f, and h_c. This means that the only parameters of $F(M,Q_{ex},Q_{sw},T_c,A_r,h_c,d_b,K_b,d_f,K_f)$ free to vary are M, Q_{ex}, Q_{sw} and T_c. Thus, it seemed reasonable to try to evaluate F and determine whether or not the whole function might be adequately described by a constant for $\Delta T \geq \Delta T_{lc}$.

$F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$ was evaluated for four species: the white-footed mouse (Peromyscus leucopus), the laboratory mouse (Mus musculus), the golden hamster (Mesocricetus auratus), and the eastern wood rat (Neotoma floridana).

Many of the parameters required to evaluate $F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$ had to be estimated. The values used for thermal conduction coefficients of fat (k_b) and fur (k_f) were 0.027 W/(m-K) and 0.4 W/(m-K), respectively (Hatfield and Pugh 1959; Hart 1965). The thickness of the fur layer was measured from frozen carcasses as described by Porter and McClure (1983), except that the fur was gently brushed so as to approximate the appearance of piloerected fur as much as possible. Since little of the ventral fur is exposed by a mammal curled up in a metabolism chamber (at cold temperatures) the fur thickness value used was the average thickness of

the fur on the back and sides of the animals.

The thickness of the fat and skin layers was measured from frozen carcasses. The carcasses were embedded in fiberglass resin, and the thickness of the combined fat and skin layers was measured from a mid-saggital cross section. The values used for the fat and skin layer was the average of eight measurements taken 45 degrees apart (i.e. evenly spaced around the outside of the body). The total surface area was calculated as recommended by Mitchell (1976).

The conductive surface area was measured from two carcasses frozen in the "curled up" position typical of small mammals in a metabolism chamber at low ambient temperatures. After the carcasses were frozen, printer's ink was spread on the underside of the animal. The carcass was then pressed against a piece of paper, so that an ink blot was left on the paper showing where the animal had touched the peper. The contact area was estimated by measuring the area of the inkblot with a compensating polar planimeter. The radiative and convective surface areas (which are by assumption equal) were calculated by subtracting the conductive surface area from the calculated total surface area.

The experiments discussed in Chapter 4 of this dissertation indicate that convective heat loss in the metabolism chambers used in this study is primarily via free convection. Thus, the convection coefficient used was calculated from the formula given by Yuge (1960) for a sphere in an enclosed space.

The heat loss due to bulk warming of inhaled air and water vapor was taken to be negligible ($Q_{bw} = 0$). The magnitude of Q_{bw} is discussed in Appendix 1.

For P. leucopus, M. auratus, and N. floridana, the MR and T_c values used were the average values for each of the following temperatures: 0, 5, 10, 15, 20, and 25 °C. Metabolic rates for a "hypothetical" Mus musculus were calculated for these temperatures from BMR, T_c, and MTC values predicted by the allometric equations of Peters (1983). Q_{ex} and Q_{sw} were estimated from measured total evaporative water loss rates by assuming that evaporative water loss from the skin represented 30% of the total evaporative water loss (Gates 1980; MacMillen 1983).

To determine whether treating $F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$ as a constant would cause errors in the estimation of MTC, F was evaluated at T_a's of 0, 5, 10, 15, 20, and 25 °C. These data were used to calculate the slope of the regression between $F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$ and ΔT.

Average values for F are shown in Table 1.2.1. The slopes of the regression of $F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$ as a function of ΔT are shown in Table 1.2.2, along with the species average values of MTC_d and the standard error of the estimate of the species average.

The absolute values of F are fairly small, generally about 5% of the basal metabolic rate. Furthermore, the slope of the relationship

between $F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$ is very small. There are a number of quantities that the slope of the regression could be compared to. The slope of $F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$ is more than three orders of magnitude smaller than the average values of MTC_d and more than two orders of magnitude smaller than the standard error of the average value of MTC_d. Thus, it seems a fair assessment that $F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$ can adequately be described by a constant. Doing this causes some error in the estimate of MTC_d, but the error is less than 1% of: 1) the standard error of the mean calculated MTC_d; 2) the difference between active and resting phase values of MTC_d. This means that the "true" slope of the relationship between MR and ΔT lies well within the 95% confidence limits on the estimates of MTC_d obtained in this dissertation. It also implies that the error could not possibly have a substantial impact on the calculated diurnal variation in MTC.

Thus, the error involved in treating $F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$ as a constant is negligible. Another analysis of the validity of treating $F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$ as a constant was performed: a factorial sensitivity analysis similar to those described by Box et al. (1978). The result of this analysis was the same as the result of the analysis reported here: a 20% variation in the parameters M, Q_{ex}, Q_{sw}, and T_c (with other variables having the same values as used in the preceeding analysis) resulted in

no more than a 3% variation in the value of $F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$. This indicates that at the values used for d_b, K_b, d_f, K_f, A_r, and h_c, $F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$ is insensitive to variations in the parameters that are free to vary at $\Delta T \geq \Delta T_{lc}$, and may adequately be regarded as constant for $\Delta T \geq \Delta T_{lc}$.

Table 1.2.1. Average values of $F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$. (Units are $W \cdot kg^{-1}$).

Species	Mean value of $F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$
P. leucopus	-0.042
M. musculus	-0.047
M. auratus	-0.159
N. floridana	-0.172

Table 1.2.2. Relationship between $F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$ and ΔT.

Species	Slope of $F(M,Q_{ex},Q_{sw},T_c,d_b,K_b,d_f,K_f,A_r,h_c)$ vs ΔT	Average MTC_d	Standard error of Average MTC_d
P. leucopus	0.00027	0.997	0.094
M. musculus	0.00021	1.053	*
M. auratus	0.00039	0.327	0.053
N. floridana	0.00051	0.214	0.061

* Impossible to calculate since data on metabolic rate were taken from allometric equations.

APPENDIX 3: SOURCE CODE FOR PROGRAM SEGREG

Appendix 3 is a listing of the source code for program SEGREG, a CDC Fortran V program designed to simultaneously estimate MTC, T_{lc}, and BMR. The program makes extensive use of IMSL subroutines. The statistical procedures are based on Johnson (1969).

```
      PROGRAM SEGREG(INPUT,OUTPUT,TAPE5,TAPE6=OUTPUT,TAPE7,TAPE8,
     :TAPE11,TAPE12,TAPE14,TAPE15,TAPE16)
      PROGRAM SEGREG(INPUT,OUTPUT,TAPE5,TAPE6=OUTPUT,TAPE7,TAPE8,
     :TAPE11,TAPE12,TAPE14,TAPE15,TAPE16)

C     ------------------------------------------------------------------
C     TAPE7  => TCDAT   THE DATA FILE WHICH CONTAINS THE OUTPUT DATA
C     TAPE8  => RSTAR   CONTAINS CONTENTS OF MATRICES RSTAR1 AND RSTAR2
C     TAPE11 => DATALIS A RELISTING OF THE DATA TO MAKE SURE IT WAS
C                       READ PROPERLY BY THE PROGRAM.
C     TAPE12 => MATRIX  A LISTING OF THE MATRICES METAB AND TEMP,
C                       WHICH IS CREATED TO ALLOW EASY CALCULATIONS
C                       FOR ALL FOUR DEPENDENT-INDEPENDENT VARIABLE
C                       COMBINATIONS.
C     TAPE12 => RES1OUT A RECORD OF THE CALCULATIONS MADE BY SUBROUTINE
C                       RESID1, TO ALLOW FOR EASY CHECKING OF THE
C                       SUBROUTINE.
C     TAPE15 => RES2OUT A RECORD OF THE CALCULATIONS MADE BY SUBROUTINE
C                       RESID2, TO ALOW FOR EASY VERIFICATION.
C     TAPE16 => MINOUT  A RECORD OF THE CALCULATIONS MADE BY SUBROUTINE
C                       MIN, TO ALLOW FOR EASY VERIFICATION.

C     ************************************************
C     * PROGRAM SEGREG DOES 2-PHASE SEGMENTED        *
C     * LINEAR REGRESSION WHERE THE FUNCTION IS ASSUMED*
C     * TO BE OF THE FORM:                           *
C     *    Y = B11 + B12*X      X < S                *
C     *      = B22              X > S                *
C     *                                               *
C     * WITH THE CONSTRAINTS:                        *
C     *    B11 + B12*S = B22                  (I)     *
C     *                                               *
C     * PROGRAM WRITTEN BY: CRAIG A. STEWART         *
C     *                     DEPARTMENT OF BIOLOGY     *
C     *                     JORDAN HALL               *
```

```
C     *                    INDIANA UNIVERSITY          *
C     *                    BLOOMINGTON, IN  47405      *
C     *                                                *
C     * FOR A TECHNICAL DISCUSSION OF THE STATISTICAL  *
C     * PROCEDURES INVOLVED, SEE:                      *
C     *                                                *
C     *       JOHNSON, K.P.  1969.  FITTING SEGMENTED  *
C     *       REGRESSION CURVES.  M.A. THESIS.         *
C     *       UNIV. MONTANA                            *
C     *                                                *
C     **************************************************
C
C
C     ----------------------------------------------------------------
C     DECLARATION OF INTEGER VARIABLES
      INTEGER BR,BREAK1,BREAK2,SAMPLEN,SPECIES,TOTIND,
     :COMB

C     ----------------------------------------------------------------
C     DECLARATION OF REAL VARIABLES
C

      REAL IHAT,INDEP,ISTAR1,ISTAR2,ITY1MIN,ITY2MIN,ITY4MIN,
     :LOCB11,LOCB12,LOCI,LOCR,LOC11,LOC12,LOC22,METAB,MR


C     ----------------------------------------------------------------
C     DIMENSION ARRAY VARIABLES

      DIMENSION SPECIES(1000),ID(1000),PHASE(1000),TA(1000),TB(1000),
     :MR(1000),DRYMR(1000),NO(1000),DELTAT(1000),
     :METAB(1000,4),TEMP(1000,4),
     :RSTAR1(50,20,4),ISTAR1(50,20,4),B11T1(50,20,4),
     :B12T1(50,20,4),B22T1(50,20,4),
     :RITY1MIN(100,4),ITY1MIN(100,4),BREAK1(100,4),
     :B111MIN(100,4),B121MIN(100,4),B221MIN(100,4),
     :RSTAR2(50,20,4),ISTAR2(50,20,4),B11T2(50,20,4),
     :B12T2(50,20,4),B22T2(50,20,4),
     :B112MIN(100,4),B122MIN(100,4),B222MIN(100,4),
     :RITY2MIN(100,4),ITY2MIN(100,4),BREAK2(100,4),
     :RITY4MIN(100,4),ITY4MIN(100,4),
     :B114MIN(100,4),B124MIN(100,4),
     :DEP(1000),INDEP(1000),
     :TYPE(100,4),B11(100,4),B12(100,4),
     :B22(100,4),
     :RMIN(100,4),IHAT(100,4),B11HAT(100,4),B12HAT(100,4),
```

```
     :B22HAT(100,4),
     :WHAT(100),WHO(100),WHEN(100)

C

C
C     ------------------------------------------------------------------
C     CALL SUBROUTINE SETUP, WHICH READS DATA FROM TAPE5 AND ORGANIZES
C     THE DATA IN TWO MATRICES: METAB AND TEMP

      CALL SETUP(SAMPLEN,TOTIND,SPECIES,NO,ID,PHASE,TA,TB,
     :MR,DRYMR,DELTAT,METAB,TEMP)

        DO 5900 I=1,200
        WRITE(6,5899) I, ID(I),PHASE(I)
5899     FORMAT (1X,'I= ',I3,' ID(I)= ',I3,1X,' PHASE(I) =',F3.0)
5900    CONTINUE
C     ------------------------------------------------------------------
C     THIS LOOP SETS THE STATISTICAL PROCEDURE TO GO THROUGH ALL 4
C     COMBINATIONS OF DEPENDENT AND INDEPENDENT VARIABLES
C
      DO 1000 COMB = 1,4

C       INITIALIZE I, N

        I=1
        N=NO(1)


C       ------------------------------------------------------------------
C       THIS LOOP SETS THE STATISTICAL PROCEDURE TO GO THROUGH THE
C       DATA FOR ON EACH INDIVIDUAL (WITH DEP-INDEP COMBINATION
C       DETERMINED BY THE OUTER LOOP - E.G., THE VALUE OF COMB)

        DO 900 INDNO=1,TOTIND


C       ------------------------------------------------------------
C       THIS LOOP SETS UP THE VECTORS DEP AND INDEP WITH VALUES

          DO 104 I6 = 1,N
            DEP(I6) = METAB(I+I6-1,COMB)
```

```
            INDEP(I6) = TEMP(I+I6-1,COMB)
104         CONTINUE


C           ------------------------------------------------------------
C           *****FIRST LOOK FOR JOINS OF TYPE 1*****
C

            DO 105 I14 =3,N-1

                CALL RESID1(INDNO,DEP,INDEP,I14,N,LOCR,LOCI,LOC11,
     :          LOC12,LOC22)
                    RSTAR1(INDNO,I14,COMB) = LOCR
                    ISTAR1(INDNO,I14,COMB) = LOCI
                    B11T1(INDNO,I14,COMB) = LOC11
                    B12T1(INDNO,I14,COMB) = LOC12
                    B22T1(INDNO,I14,COMB) = LOC22

                WRITE(8,110) INDNO,I14,COMB,RSTAR1(INDNO,I14,COMB)
110             FORMAT(1X,'RSTAR1(',I2,',',I2,',',I2,')= ',F14.5)

105         CONTINUE

C           SORT FOR MINIMUM VALUE OF RSTAR1(COMB,I14)

            CALL MIN(RSTAR1,INDNO,N,COMB,BR)
            RTY1MIN(INDNO,COMB)=RSTAR1(INDNO,BR,COMB)
            ITY1MIN(INDNO,COMB)=ISTAR1(INDNO,BR,COMB)
            B111MIN(INDNO,COMB)=B11T1(INDNO,BR,COMB)
            B121MIN(INDNO,COMB)=B12T1(INDNO,BR,COMB)
            B221MIN(INDNO,COMB)=B22T1(INDNO,BR,COMB)
            BREAK1(INDNO,COMB)=BR


C
C           ------------------------------------------------------------
C           *****NOW LOOK FOR JOINS OF TYPE 2*****
C

            DO 106 I15=3,N-1

            IF( RSTAR1(INDNO,I15,COMB).LT.99998) THEN
```

```
              RSTAR2(INDNO,I15,COMB) = 99999.
              ISTAR2(INDNO,I15,COMB) = -10
              B11T2(INDNO,I15,COMB)  = -10
              B12T2(INDNO,I15,COMB)  = -10
              B22T2(INDNO,I15,COMB)  = -10
            ELSE

               CALL RESID2(DEP,INDEP,I15,N,LOCR,LOCI,LOC11,LOC12,LOC22)
                 RSTAR2(INDNO,I15,COMB)=LOCR
                 ISTAR2(INDNO,I15,COMB) = LOCI
                 B11T2(INDNO,I15,COMB)=LOC11
                 B12T2(INDNO,I15,COMB)=LOC12
                 B22T2(INDNO,I15,COMB)=LOC22
            ENDIF

            WRITE(8,131) INDNO,I15,COMB,RSTAR2(INDNO,I15,COMB)
131         FORMAT(1X,'RSTAR2(',I2,',',I2,',',I2,')= ',F14.5)

106         CONTINUE

C           SORT FOR MINIMUM VALUE OF RSTAR2(COMB,*)

            CALL MIN(RSTAR2,INDNO,N,COMB,BR)

            RTY2MIN(INDNO,COMB)=RSTAR2(INDNO,BR,COMB)
            ITY2MIN(INDNO,COMB)=ISTAR2(INDNO,BR,COMB)
            B112MIN(INDNO,COMB)=B11T2(INDNO,BR,COMB)
            B122MIN(INDNO,COMB)=B12T2(INDNO,BR,COMB)
            B222MIN(INDNO,COMB)=B22T2(INDNO,BR,COMB)
            BREAK2(INDNO,COMB)=BR


C           *****NOW LOOK FOR JOINS OF TYPE 4*****

C           CALL RESID4(DEP,INDEP,N,LOCR,LOCB11,LOCB12)
            ITY4MIN(INDNO,COMB)  = 999.
            B114MIN(INDNO,COMB) = 99999.
            B124MIN(INDNO,COMB) = 999999.


C           ------------------------------------------------------------
C           *****DETERMINE JOIN TYPE*****
C

      WRITE(6,111) RTY1MIN(INDNO,COMB),RTY2MIN(INDNO,COMB),
```

```
     :RTY4MIN(INDNO,COMB), INDNO, COMB
111      FORMAT(1X,' RTY1MIN=',F10.3,' RTY2MIN=',F10.3,' RTY4MIN=',
     :F10.3,' INDNO =',I3,' COMB=',I3)

          IF(RTY1MIN(INDNO,COMB).LT.RTY2MIN(INDNO,COMB).AND.
     :     RTY1MIN(INDNO,COMB).LT.RTY4MIN(INDNO,COMB)) THEN

            TYPE(INDNO,COMB)=1
            RMIN(INDNO,COMB) = RTY1MIN(INDNO,COMB)
            IHAT(INDNO,COMB) = ITY1MIN(INDNO,COMB)
            B11HAT(INDNO,COMB) = B111MIN(INDNO,COMB)
            B12HAT(INDNO,COMB) = B121MIN(INDNO,COMB)
            B22HAT(INDNO,COMB) = B221MIN(INDNO,COMB)

          ELSE IF(RTY2MIN(INDNO,COMB).LT.RTY1MIN(INDNO,COMB).AND.
     :     RTY2MIN(INDNO,COMB).LT.RTY4MIN(INDNO,COMB)) THEN
            TYPE(INDNO,COMB)=2
            RMIN(INDNO,COMB) = RTY2MIN(INDNO,COMB)
            IHAT(INDNO,COMB) = ITY2MIN(INDNO,COMB)
            B11HAT(INDNO,COMB) = B112MIN(INDNO,COMB)
            B12HAT(INDNO,COMB) = B122MIN(INDNO,COMB)
            B22HAT(INDNO,COMB) = B222MIN(INDNO,COMB)


          ELSE IF(RTY4MIN(INDNO,COMB).LE.RTY1MIN(INDNO,COMB).AND.
     :     RTY4MIN(INDNO,COMB).LE.RTY2MIN(INDNO,COMB)) THEN
            TYPE(INDNO,COMB)=4
            RMIN(INDNO,COMB) = RTY4MIN(INDNO,COMB)
            IHAT(INDNO,COMB) = ITY4MIN(INDNO,COMB)
            B11HAT(INDNO,COMB) = B114MIN(INDNO,COMB)
            B12HAT(INDNO,COMB) = B124MIN(INDNO,COMB)
            B22HAT(INDNO,COMB) = -99.


          ELSE
             TYPE(INDNO,COMB)=99
          ENDIF


C         INCREMENT I AND N

            I=I+N
            N=NO(I)
```

```
900     CONTINUE
C       900 IS THE END OF THE LOOP FOR CALCULATIONS FOR ONE INDIVIDUAL
C       FOR ONE COMBINATION OF VARIABLES.  THE INNER LOOP IS PROCESSED
C       A TOTAL OF FOUR TIMES PER INDIVIDUAL.


1000  CONTINUE


C       *****REINITIALIZE I AND N*****

        I=1
        N=NO(I)

        DO 1200 IND = 1,TOTIND
          WHO(IND) = ID(I)
          WHAT(IND) = SPECIES(I)
          WHEN(IND) = PHASE(I)

             WRITE(6,1199) IND,N,WHAT(IND),WHO(IND),WHEN(IND)
1199        FORMAT(I3,1X,I3,1X,'WHAT:',F3.0,' WHO:',F3.0,' WHEN:',F3.0)

            I=I+N
            N=NO(I)

1200    CONTINUE



C       ---------------------------------------------------------------
C       WRITE OUT RESULTS

         WRITE(7,1490)
1490   FORMAT(1X,'TYPE',3X,'RMIN',5X,'B11HAT',5X,'B12HAT',5X,'B22HAT',
      :5X,'IHAT')


        DO 1400 IND = 1,TOTIND
          WRITE(7,1500) WHAT(IND),WHO(IND),WHEN(IND)
1500      FORMAT(1X,F4.0,2X,F4.0,2X,F4.0)

       WRITE(7,1520) TYPE(IND,1), RMIN(IND,1), B11HAT(IND,1),
      :B12HAT(IND,1), B22HAT(IND,1), IHAT(IND,1)

       WRITE(7,1520) TYPE(IND,2), RMIN(IND,2), B11HAT(IND,2),
```

```
     :B12HAT(IND,2), B22HAT(IND,2), IHAT(IND,2)

      WRITE(7,1520) TYPE(IND,3), RMIN(IND,3), B11HAT(IND,3),
     :B12HAT(IND,3), B22HAT(IND,3), IHAT(IND,3)

      WRITE(7,1520) TYPE(IND,4), RMIN(IND,4), B11HAT(IND,4),
     :B12HAT(IND,4), B22HAT(IND,4), IHAT(IND,4)

1520  FORMAT(F3.0,1X,F8.5,1X,F8.5,1X,F8.5,1X,F8.5,1X,F10.5,1X)

1400   CONTINUE


C      ********************************************************
C      END OF MAIN PROGRAM
C      ********************************************************

       END

      SUBROUTINE RESID1(IN,RDEP,RINDEP,SPLTD,ND,RR,RI,R11,R12,R22)

C     ------------------------------------------------------------
C     EXPLANATION OF PARAMETERS PASSED TO RESID1
C     RDEP      = VECTOR OF DEPENDENT VARIABLES
C     RINDEP    = VECTOR OF INDEPENDENT VARIABLES
C     SPLTD     = INDEX INDICATING UPPER BOUND OF PHASE 1
C     ND        = NUMBER OF DATA POINTS
C     ------------------------------------------------------------
C     EXPLANATION OF PARAMETERS CALCULATED BY RESID1
C     RR        = TOTAL RESIDUAL SUM OF SQUARES
C     RI        = ESTIMATE OF JOIN POINT
C     R11       = ESTIMATE OF B11 PARAMETER - THE INTERCEPT OF THE
C                 REGRESSION LINE FOR PHASE 1
C     R12       = ESTIMATE OF B12 PARAMETER - THE SLOPE OF THE
C                 REGRESSION LINE FOR PHASE 1
C     R22       = ESTIMATE OF B22 PARAMETER - THE INTERCEPT OF THE
C                 REGRESSION LINE FOR PHASE2


C     ------------------------------------------------------------
C     DECLARATION OF INTEGER VARIABLES

      INTEGER SPLTD,ND

C     ------------------------------------------------------------
```

```
C      DIMENSION ARRAY VARIABLES

       DIMENSION RDEP(1000),RINDEP(1000),XY(100,2),ALBAP(10),
      :DES(5),ANOVA(14),STAT(9),PR(100,7)

C      ------------------------------------------------------------------
C      INITIALIZATION OF CONSTANTS REQUIRED FOR IMSL SUBROUTINE RLONE.
C      AN EXPLANATION OF SUBROUTINE RLONE IS AVAILABLE IN THE
C      IMSL LIBRARY HANDBOOK

       IX=100
       IMOD = 0
       IPR = -1
       ALBAP(1) = 0.05
       ALBAP(2) = 0.05
       ALBAP(3) = 0.05
       IP=100
       NN=0

C      ------------------------------------------------------------------
C      SET UP THE ARRAY XY WHICH IS PASSED TO IMSL SUBROUTINE RLONE.
C      XY(*,1) CONTAINS VALUES OF THE INDEPENDENT VARIABLE
C      XY(*,2) CONTAINS CORRESPONDING VALUES OF THE DEPENDENT VARIABLE

       DO 3000 I20=1,SPLTD
         XY(I20,1) = RINDEP(I20)
         XY(I20,2) = RDEP(I20)
3000    CONTINUE

       DO 3200 I21=SPLTD+1,99
         XY(I21,1)=0.0
         XY(I21,2)=0.0
3200   CONTINUE


C      ------------------------------------------------------------------
C      WRITE OUT A RECORD OF CALCULATIONS DONE BY RESID1
C

       WRITE(14,3300)
3300   FORMAT(1X,'  ')

       WRITE(14,3305)
3305   FORMAT(1X,'-------------------------------------------------')

       WRITE(14,3310) IN
```

```
3310  FORMAT(1X,'RECORD OF CALCULATIONS IN RESID1 FOR INDIVIDUAL : ',I3)

      WRITE(14,3325)  SPLITD,ND
3325  FORMAT(1X,'SPLIT = ',I3,'  NUMBER OF SAMPLES = ',I3)

      DO 10 I22=1,10
      WRITE(14,3350) I22, XY(I22,1), XY(I22,2)
3350  FORMAT(1X,'INDEX= ',I2,'  INDEP = ',F7.2,'  DEP = ',F8.5)

10    CONTINUE


3500   CONTINUE


C
C     ------------------------------------------------------------------
C     CALCULATE RESIDUALS FOR PHASE 1
C

      CALL RLONE(XY,IX,SPLITD,IMOD,IPR,ALBAP,DES,ANOVA,STAT,PR,IP,NN,IER)

      IF(IER.EQ.129.OR.IER.EQ.130.OR.IER.EQ.131.OR.IER.EQ.36) THEN
        WRITE(6,4000) IER
4000    FORMAT(1X,'YOU BLEW IT IN RESID1. IMSL ERROR CODE  IER = ',I3)
      ENDIF

      RPHASE1 = ANOVA(5)
      R11 = STAT(5)
      R12 = STAT(1)



C
C     ------------------------------------------------------------------
C     CALCULATE RESIDUALS FOR PHASE 2
C
      SUMY = 0
      SUMYSQR = 0

      DO 4100 I22 = SPLITD+1,ND
          SUMY = SUMY + RDEP(I22)
          SUMYSQR = SUMYSQR + RDEP(I22)**2
4100       CONTINUE

      YBAR = SUMY/FLOAT((ND-SPLITD))
```

```
      RPHASE2 = SUMYSQR - (ND-SPLITD)*(YBAR**2)

      RR = RPHASE1 + RPHASE2
      R22 = YBAR

       RI = (R22-R11)/R12

C
C     ------------------------------------------------------------------
C     CHECK TO SEE IF THE LINES ACTUALLY INTERSECT IN THE GAP
C     IF NOT, SET RESIDUAL SS (RR) EQUAL TO 9999

      IF(YBAR.GE.R11+R12*RINDEP(SPLITD).
     :OR.YBAR.LE.R11+R12*RINDEP(SPLITD+1)) THEN
        RR=99999.
      ENDIF


C     ------------------------------------------------------------------
C     WRITE OUT A RECORD OF CALCULATIONS DONE BY RESID1
C


      WRITE(14,3360)
3360  FORMAT(1X,'  ')

      WRITE(14,3375) SPLITD,R11,R12,YBAR
3375  FORMAT(1X,'WITH SPLIT AT: ',I3,' B11*=',F8.5,'  B12* =',F8.5,
     :'  YBAR = ',F8.5)

       WRITE(14,3380) RPHASE1,RPHASE2,RR
3380   FORMAT(18X,'RPHASE1 = ',F8.5,' RPHASE2 = ',F8.5,'  RR = ',F15.5)

      WRITE(14,3390)
3390  FORMAT(1X,'  ')


      END



      SUBROUTINE RESID2(RDEP,RINDEP,SPLITD,ND,RR,RI,R11,R12,R21)
```

```
C     ------------------------------------------------------------------
C     EXPLANATION OF PARAMETETERS PASSED TO RESID2
C     RDEP      = VECTOR OF DEPENDENT VARIABLES
C     RINDEP    = VECTOR OF INDEPENDENT VARIABLES
C     SPLTD     = INDEX INDICATING UPPER BOUND OF PHASE 1
C     ND        = NUMBER OF DATA POINTS
C     ------------------------------------------------------------------
C     EXPLANATION OF PARAMETERS CALCULATED BY RESID2
C     RR        = TOTAL RESIDUAL SUM OF SQUARES
C     RI        = ESTIMATE OF JOIN POINT
C     R11       = ESTIMATE OF B11 PARAMETER - THE INTERCEPT OF THE
C                 REGRESSION LINE FOR PHASE 1
C     R12       = ESTIMATE OF B12 PARAMETER - THE SLOPE OF THE
C                 REGRESSION LINE FOR PHASE 1
C     R21       = ESTIMATE OF B21 PARAMETER - THE INTERCEPT OF THE
C                 REGRESSION LINE FOR PHASE 2


C     DECLARATION OF INTEGER VARIABLES
C
      INTEGER SPLTD,ND

C     DECLARATION OF REAL VARIABLES

      REAL C(20,20),CINV(20,20),CINVQT(20,20),CCINVQT(20,20),
     :Q(20,20),Z(20,20),B(20),LITTLEA,LITTLEB,QCINVQT(20,20)


       DIMENSION RDEP(1000),RINDEP(1000),XY(100,2),ALBAP(10),
     :DES(5),ANOVA(14),STAT(9),PR(100,7)

C     ------------------------------------------------------------------
C     INITIALIZATION OF CONSTANTS REQUIRED FOR IMSL SUBROUTINE RLONE.
C     AN EXPLANATION OF SUBROUTINE RLONE IS AVAILABLE IN THE
C     IMSL LIBRARY HANDBOOK

      IX=100
      IMOD = 0
      IPR = -1
      ALBAP(1) = 0.05
      ALBAP(2) = 0.05
      ALBAP(3) = 0.05
      IP=100
      NN=0
```

```
      DO 3000 I20=1,SPLITD
          XY(I20,1) = RINDEP(I20)
          XY(I20,2) = RDEP(I20)
3000  CONTINUE

      DO 3200 I21=SPLITD+1,99
           XY(I21,1)=0.0
           XY(I21,2)=0.0
3200  CONTINUE

C
C     ------------------------------------------------------------
C     CALCULATE UNCONSTRAINED RESIDUALS FOR PHASE 1
C

      CALL RLONE(XY,IX,SPLITD,IMOD,IPR,ALBAP,DES,ANOVA,STAT,PR,IP,NN,IER)

      IF(IER.EQ.129.OR.IER.EQ.130.OR.IER.EQ.131.OR.IER.EQ.36) THEN
        WRITE(15,4000) IER
4000    FORMAT('YOU BLEW IT! IER = ',I3)
         ENDIF

      RPHASE1 = ANOVA(5)
      R11 = STAT(5)
      R12 = STAT(1)


C
C     CALCULATE UNCONSTRAINED RESIDUALS FOR PHASE 2
C
      SUMY = 0
      SUMYSQR = 0

      DO 4100 I22 = SPLITD+1,ND
          SUMY = SUMY + RDEP(I22)
          SUMYSQR = SUMYSQR + RDEP(I22)**2
4100       CONTINUE

      YBAR = SUMY/(FLOAT(ND-SPLITD))


      RPHASE2 =  SUMYSQR - (ND-SPLITD)*(YBAR**2)

      R21 = YBAR
```

```
      WRITE(15,4170)
4170  FORMAT(1X,' UNCONSTRAINED PARAMETER VALUES ARE:')
       WRITE(15,4180) RPHASE1,RPHASE2,R11,R12,YBAR
4180  FORMAT(1X,' RPHASE1 = ',F8.5,'  RPHASE2 = ',F8.5,'R11 = ',F8.5,
     :  'R12 = ',F8.5,'  YBAR = ',F8.5)


C
C     ------------------------------------------------------------------

C     CALCULATE RESIDUAL SUM OF SQUARES FOR CONSTRAINED EQUATIONS

C     SET UP MATRIX Z

      DO 4200 I23 = 1,SPLITD
        Z(I23,1) = 1.
        Z(I23,2) = RINDEP(I23)
        Z(I23,3) = 0.
4200  CONTINUE

      DO 4300 I24 = SPLITD+1,ND
        Z(I24,1) = 0.
        Z(I24,2) = 0.
        Z(I24,3) = 1.
4300  CONTINUE

C     SET UP MATRIX Q
      Q(1,1) = 1
      Q(1,2) = RINDEP(SPLITD)
      Q(1,3) = -1

C     SET UP MATRIX B
      B(1) = R11
      B(2) = R12
      B(3) = R21


C     ------------------------------------------------------------------
C     CALCULATE C = Z-TRANSPOSE X Z

C     INITIALIZATION OF PARAMETERS REQUIRES FOR IMSL SUBROUTINE VMULFM

      L = ND
      M = 3
```

```
      N = 3
      IA = 20
      IB = 20
      IC = 20

      CALL VMULFM(Z,Z,L,M,N,IA,IB,C,IC,IER)


C     CALCULATE CINV

C     INITIALIZATION OF PARAMETERS REQUIRED FOR IMSL SUBROUTINE LINV2F

      N  = 3
      IA = 20
      IDGT = 0
      WKAREA = 100

      CALL LINV2F(C,N,IA,CINV,IDGT,WKAREA,IER)
           WRITE(15,99)
99        FORMAT(1X,' HERE ARE MATRICES CINV        AND Q')
          DO 20 I100=1,3
             WRITE(15,5) CINV(I100,1),CINV(I100,2),CINV(I100,3),
     :                   Q(I100,1),Q(I100,2),Q(I100,3)
5             FORMAT(1X,F8.5,F8.5,F8.5,10X,F8.5,F9.5,F8.5)
20        CONTINUE


C     CALCULATE Q X CINV X Q-TRANSPOSE

C     FIRST CALCULATE CINV X Q-TRANSPOSE

C     INITIALIZATION OF PARAMETERS REQUIRED FOR VMULFP

      L  = 3
      M  = 3
      N  = 1
      IA = 20
      IB = 20
      IC = 20

      CALL VMULFP(CINV,Q,L,M,N,IA,IB,CINVQT,IC,IER)

C     NOW CALCULATE Q X (CINV X Q-TRANSPOSE)


C     INITIALIZATION OF PARAMETERS REQUIRED FOR IMSL SUBROUTINE VMULFF
```

```
      L  = 1
      M  = 3
      N  = 1
      IA = 20
      IB = 20
      IC = 20

       CALL VMULFF(Q,CINVQT,L,M,N,IA,IB,QCINVQT,IC,IER)

C     ------------------------------------------------------------------
C      CALCULATE LITTLEB

       LITTLEB = QCINVQT(1,1)


C     ------------------------------------------------------------------
C      CALCULATE LITTLEA = Q X B*

       LITTLEA = 0

       DO 4400 I26 = 1,3
         LITTLEA = Q(1,I26) * B(I26)  + LITTLEA
4400   CONTINUE

       WRITE(15,4410) LITTLEA,LITTLEB
4410   FORMAT(1X,'  LITTLEA = ',F8.5,'  LITTLEB = ',F8.5)


C     ------------------------------------------------------------------
C      CALCULATE RR = CONSTRAINED SUM OF SQUARES

       RR = RPHASE1 + RPHASE2 + (LITTLEA**2)/LITTLEB


C      CALCULATE PARAMETERS FOR CONSTRAINED EQUATIONS


C     ------------------------------------------------------------------
C      CALCULATE CONSTRAINED VALUES FOR R11,R12, AND R21

       R11 =R11 +  (LITTLEA/LITTLEB)*CINVQT(1,1)
       R12 = R12 + (LITTLEA/LITTLEB)*CINVQT(2,1)
       R21 = R21 + (LITTLEA/LITTLEB)*CINVQT(3,1)
```

```
        WRITE(15,4500)
4500    FORMAT(1X,' CONSTRAINED ESTIMATES ARE:')
        WRITE(15,4600) RR,R11,R12,R21
4600   FORMAT(1X,' RR=',F8.5,' R11 =',F8.5,' R12 =',F8.5,' R21 =',F8.5)

        END

      SUBROUTINE RESID4(RDEP,RINDEP,ND,RR,R11,R12)


C     RDEP      = VECTOR OF DEPENDENT VARIABLES
C     RINDEP    = VECTOR OF INDEPENDENT VARIABLES
C     ND        = NUMBER OF DATA POINTS
C     RR        = TOTAL RESIDUAL SUM OF SQUARES
C     RI        = ESTIMATE OF JOIN POINT
C     R11       = ESTIMATE OF B11 PARAMETER
C     R12       = ESTIMATE OF B12 PARAMETER
C     R22       = ESTIMATE OF B22 PARAMETER


       DIMENSION RDEP(1000),RINDEP(1000),XY(100,2),ALBAP(10),
     :DES(5),ANOVA(14),STAT(9),PR(100,7)

        WRITE(6,191) ND
191     FORMAT(1X,'AT BEGINNING OF RESID4, ND= ',I4)

C     INITIALIZATION OF CONSTANTS REQUIRED FOR IMSL SUBROUTINE RLONE.
C     AN EXPLANATION OF SUBROUTINE RLONE IS AVAILABLE IN THE
C     IMSL LIBRARY HANDBOOK

       IX=100
      IMOD = 0
      IPR = -1
      ALBAP(1) = 0.05
      ALBAP(2) = 0.05
       ALBAP(3) = 0.05
      IP=100
      NN=0

      DO 3000 I20=1,ND
          XY(I20,1) = RINDEP(I20)
          XY(I20,2) = RDEP(I20)
3000   CONTINUE

      DO 3200 I21=ND+1,99
```

```
          XY(I21,1)=0.0
          XY(I21,2)=0.0
3200  CONTINUE

C
C     CALCULATE RESIDUALS
         WRITE(6,181)
181      FORMAT(1X,'IT GOT THROUGH THE SETUP IN RESID4')
C

      CALL RLONE(XY,IX,ND,IMOD,IPR,ALBAP,DES,ANOVA,STAT,PR,IP,NN,IER)

      IF(IER.EQ.129.OR.IER.EQ.130.OR.IER.EQ.131.OR.IER.EQ.36) THEN
        WRITE(6,4000) IER
4000    FORMAT('YOU BLEW IT! IER = ',I3)
        ENDIF

      RR = ANOVA(5)
      R11 = STAT(1)
      R12 = STAT(5)



      END

        SUBROUTINE MIN(RESID,INDNO,ND,I25,BR)

C     DECLARATION OF INTEGER VARIABLES
C

      INTEGER ND,BR
       DIMENSION RESID(50,20,4)


C       INITIALIZE BR AND CHECK

       BR=3


       DO 5000 I50=4,ND-1

       IF(RESID(INDNO,I50,I25).LT.RESID(INDNO,BR,I25)) THEN
            BR=I50
       ENDIF

5000   CONTINUE
```

```
C     ------------------------------------------------------------------
C     WRITE DATA TO TAPE11=MINOUT TO MAKE SRE SUBROUTINE MIN IS
C     WORKING PROPERLY

      WRITE(16,5100)
5100  FORMAT(1X,'  ')

      WRITE(16,5105)
5105  FORMAT(1X,'-------------------------------------------------')


      WRITE(16,5110) INDNO,I25
5110  FORMAT(1X,'RESULTS OF SUBROUTINE MIN FOR IND: ',I3,'  VARIABLE
     :COMBINATION:  ',I3)

       DO 5175 I49=3,ND-1
       WRITE(16,5150) I49, RESID(INDNO,I49,I25)
5150   FORMAT(1X,'WITH SPLIT AT : ',I3,'  RESID SS = ',F8.5)
5175   CONTINUE

          WRITE(16,5180)
5180      FORMAT(1X,'  ')


             WRITE (11,5200) BR
5200         FORMAT(1X,'AT END OF MIN, BREAK = ',I3)

              WRITE(16,5210)
              WRITE(16,5210)
5210          FORMAT(1X,'  ')

       END


       SUBROUTINE SETUP(NSAMPLE,NTOTIND,RSPEC,NNO,NID,RPHASE,
     :RTA,RTB,RMR,RDRYMR,RDELTAT,RMETAB,RTEMP)


C     ------------------------------------------------------------------
C     DIMENSION ARRAY VARIABLES

      DIMENSION RSPEC(1000),NID(1000),RPHASE(1000),RTA(1000),RTB(1000),
     :RMR(1000),RDRYMR(1000),NNO(1000),RDELTAT(1000),
     :RMETAB(1000,4),RTEMP(1000,4)
```

```
C
C
C
C     ------------------------------------------------------------------
C     READ TOTAL NUMBER OF DATA POINTS AND TOTAL NUMBER OF INDIVIDUALS
C
      READ (5,200) NSAMPLE,NTOTIND
200   FORMAT(I3,1X,I3)

C
C     ------------------------------------------------------------------
C     READ RSPEC CODE, NNO, NID NUMBER, RPHASE, TA, TB, RMR, AND RDRYMR
C
      DO 100 I1=1,NSAMPLE
      READ (5,201) RSPEC(I1),NNO(I1),NID(I1),RPHASE(I1),RTA(I1),RTB(I1),
     :  RMR(I1),RDRYMR(I1)
201   FORMAT(I1,1X,I2,1X,I3,1X,F2.0,F4.1,1X,F5.2,1X,F8.5,1X,F8.5)

100   CONTINUE
C

C
C     ------------------------------------------------------------------
C     WRITE DATA TO TAPE7=DATALIS TO MAKE SURE IT HAS BEEN
C     READ IN CORRECTLY.

C
      WRITE(6,141) NSAMPLE
141   FORMAT(1X,'THE TOTAL NUMBER OF DATA POINTS IS: ',I3)
      WRITE(6,142) NTOTIND
142   FORMAT(1X,'THE TOTAL NUMBER OF INDIVIDUALS IS: ',I3)

      DO 300 I2=1,NSAMPLE
      WRITE(6,301) RSPEC(I2),NNO(I2),NID(I2),RPHASE(I2),RTA(I2),
     :RTB(I2),RMR(I2),RDRYMR(I2)
301   FORMAT(1X,I1,1X,I2,1X,I3,1X,F2.0,1X,F4.1,1X,F5.2,1X,F8.5,1X,F8.5)
300   CONTINUE

C


C
C     ------------------------------------------------------------------
C     COMPUTE DELTA T
```

```
C

      DO 101 I2 = 1,NSAMPLE
          RDELTAT(I2) = RTA(I2) - RTB(I2)
101   CONTINUE

C
C     ------------------------------------------------------------------
C     THE DATA WILL NOW BE WRITTEN INTO TWO 4 X N MATRICES.  ONE
C     MATRIX IS CALLED RMETAB; IT CONTAINS THE VECTOR RDRYMR IN COLUMNS
C     ONE AND TWO, AND THE VECTOR RMR IN COLUMNS 3 AND 4.  THE OTHER
C     MATRIX IS CALLED RTEMP; IT CONTAINS THE VECTOR RDELTAT IN COLUMNS
C     1 AND 3, AND THE VECTOR TA IN COLUMNS 2 AND 4.  THESE MATRICES
C     ARE SET UP TO ALLOW EFFICIENT CALCULATION OF RDRYMR AND RMR AS A
C     FUNCTIONS OF TA ALONE OR RDELTAT ALONE.
C


C
C     FIRST SET UP THE MATRIX RMETAB, A 4 X N MATRIX OF DEPENDENT
C     VARIABLES
C

      DO 102 I3 = 1,NSAMPLE

          RMETAB(I3,1) = RDRYMR(I3)
          RMETAB(I3,2) = RDRYMR(I3)
          RMETAB(I3,3) = RMR(I3)
          RMETAB(I3,4) = RMR(I3)

102   CONTINUE


C     NOW SET UP THE MATRIX RTEMP, A 4 X N MATRIX OF INDEPENDENT
C     VARIABLES
C

      DO 103 I4 = 1,NSAMPLE

          RTEMP(I4,1) = RDELTAT(I4)
          RTEMP(I4,2) = RTA(I4)
          RTEMP(I4,3) = RDELTAT(I4)
          RTEMP(I4,4) = RTA(I4)

103   CONTINUE
```

```
C     ------------------------------------------------------------------
C      WRITE MATRIX RMETAB AND RTEMP OUT TO TAPE8=MATRIX TO MAKE SURE
C      IT HAS BEEN READ IN PROPERLY

      DO 111 COMB5=1,NSAMPLE

      WRITE(12,112) COMB5,RMETAB(COMB5,1),COMB5,RMETAB(COMB5,2),
     :COMB5,RMETAB(COMB5,3),COMB5,RMETAB(COMB5,4)
112   FORMAT(1X,'M(',I3,',1)=',F9.5,' M(',I3,'2)=',F9.5,
     :' M(',I3,',3)= ',F9.5,' M(',I3,',4)= ',F9.5)

111   CONTINUE


       DO 116 I37=1,NSAMPLE
      WRITE(12,115) I37,RTEMP(I37,1),I37,RTEMP(I37,2),
     :I37,RTEMP(I37,3),I37,RTEMP(I37,4)
115   FORMAT(1X,'TEMP(',I3,'1)=',F9.5,' TEMP(',I3,'2)=',F9.5,
     :' TEMP(',I3,',3)= ',F9.5,' TEMP(',I3,',4)= ',F9.5)

116   CONTINUE



C
       END
```

APPENDIX 4: EQUATIONS FOR METABOLISM VARIABLE CALCULATION

The purpose of this appendix is to present the equations used to calculate metabolism variables. Table 1.4.1 is a listing of variable names and their meanings. Table 1.4.2 is a listing of the equations used to calculate metabolism parameters. The formulae for V_{O2}, V, and R cannot be solved simultaneously. They can, however, be solved recursively, using successive approximations of the values of each of the variables to solve for new estimates of the variable values. This process continues until the estimates for all three variables stabilize (in the case of the present calculations, the variable values were assumed to stabilize when they changed by no more than 0.01% of the calculated value between recursions).

A schematic diagram of the gas analysis system used to collect data for this dissertation is shown in Figure 1.4.1. A listing of the instruments and their associated accuracies is shown in Table 1.4.3.

Table 1.4.1. Variable Names used in Appendix 4.

Variable Name	Definition	Units
V_E	Flow rate of airstream leaving metabolism chamber ("excurrent" airstream)	$cm^3 \cdot min^{-1}$
V_I	Flow rate of airstream entering metabolism chamber ("incurrent" airstream)	$cm^3 \cdot min^{-1}$
F_{IO2}	O2 fraction in incurrent airstream	(dimensionless)
F_{EO2}	O2 fraction in excurrent airstream	(dimensionless)
F_{ICO2}	CO_2 fraction in incurrent airstream	(dimensionless)
F_{ECO2}	CO_2 fraction in excurrent airstream	(dimensionless)
RE	Respiratory quotient	(dimensionless)
V_{O2}	O_2 consumption	$cm^3 \cdot min^{-1}$
V_{CO2}	CO_2 production	$cm^3 \cdot min^{-1}$
D_I	Dewpoint of incurrent airstream	^oC
D_E	Dewpoint of excurrent airstream	^oC
vp_i	Vapor pressure of incurrent airstream	mb
vp_e	Vapor pressure of excurrent airstream	mb
ρ_i	Water Vapor density in incurrent airstream	$gm \cdot m^{-3}$
ρ_e	Water Vapor density in excurrent airstream	$gm \cdot m^{-3}$
M_{H2O}	Evaporative water loss	$gm \cdot min^{-1}$

Q_{EV}	Evaporative Heat loss (energy equivalen of M_{H2O})	W
MR	Metabolic Rate	W

Table 1.4.2. Equations used to calculate metabolism variables and references.

Variable	Equation	Reference
V_{O2}	$= \dfrac{V_E(F_{IO2}-F_{EO2})}{(RE-1)F_{IO2}+1}$	Tucker 1968
V_{CO2}	$= \dfrac{V_E(F_{ECO2}-F_{ICO2})}{F_{ICO2}(1-(1/RE))+1}$	Tucker 1968
RE	$= V_{CO2}/V_{O2}$	by definition Gordon et al. 1975

vp_i =	`5.75285606*(10**10)`
	`*exp( -20.947031*(273.15/(D_I+273.15))`
	`-3.56654*ln(273.15/(D_I+273.15))`
	`-2.01889049/(273.15/(D_I+273.15))` if D_I <0
		Murray, 1967

	`7.95357242*(10**10)`
	`*exp( -18.1972839*(373.15/(D_I+273.15))`
	`+5.02808*ln(373.15/(D_I+273.15))`
	`-70242.1852*exp(-26.1205253/(373.15/D_I+273.15)`
	`+58.0691913*exp(-8.03945282*(373.15/(D_I+273.15)` if D_I >0	

vp_e =

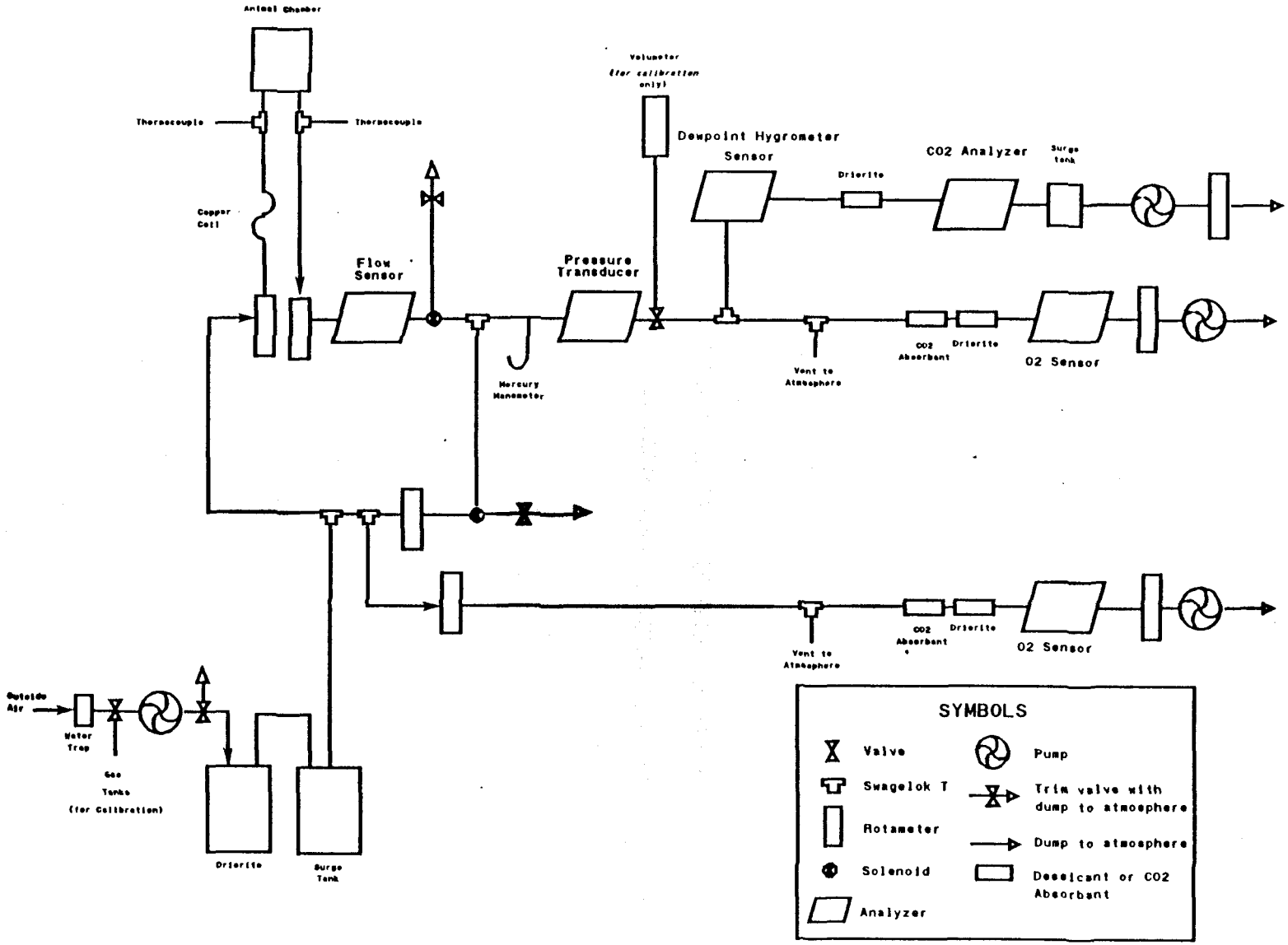
```
5.75285606*(10**10)                                    if D_E <0   Murray,
 *exp( -20.947031*(273.15/(D_E+273.15))                             1967
       -3.56654*ln(273.15/(D_E+273.15))
       -2.01889049/(273.15/(D_E+273.15))

7.95357242*(10**10)                                    if D_E > 0
 *exp( -18.1972839*(373.15/(D_E+273.15))
       +5.02808*ln(373.15/(D_E+273.15))
       -70242.1852*exp(-26.1205253/(373.15/D_E+273.15)
       +58.0691913*exp(-8.03945282*(373.15/(D_E+273.15)
```

ρ_I	=	vp_I*0.0018016/(.9998*8.31434*(T_a+273.15))	Tracy et al. 1980
ρ_E	=	vp_E*0.0018016/(.9998*8.31434*(T_a+273.15))	Tracy et al. 1980
V_I	=	$V_E + V_{O2} - V_{CO2}$	Bernstein et al. 1977
M_{H2O}	=	$\rho_E * V_E - \rho_I * V_I$	Tracy et al. 1980
Q_{EV}	=	M_{H2O}*40.455	Gates 1980
MR	=	V_{O2}*(0.266 + 0.0859*RE	Kleiber 1961

Table 1.4.3. Analysis instruments and manufacturer's stated accuracy

Instrument	Accuracy
Applied Electrochemistry Oxygen Analyzer	$\pm$.010 $\%O_2$
Beckman Model 864 Infrared Analyzer (CO2)	$\pm$ 1% of reading
Linde Flowmeter	$\pm$ 1.5% of reading
E G & G Dewpoint Hygrometer	$\pm$ 0.3 C

Figure 1.4.1. Schematic diagram of gas analysis system used to collect metabolic rate data (the McClure Lab Physiological Measurement System).


Animal Chamber
Thermocouple
Thermocouple
Copper Coil
Flow Sensor
Volumeter (for calibration only)
Dewpoint Hygrometer Sensor
Pressure Transducer
Drierite
CO2 Analyzer
Surge tank
Mercury Manometer
Vent to Atmosphere
CO2 Absorbant
Drierite
O2 Sensor
Vent to Atmosphere
CO2 Absorbant
Drierite
O2 Sensor
Outside Air
Water Trap
Gas Tanks (for Calibration)
Drierite
Surge Tank
SYMBOLS
Valve
Swagelok T
Rotameter
Solenoid
Analyzer
Pump
Trim valve with dump to atmosphere
Dump to atmosphere
Desiccant or CO2 Absorbant

DIURNAL VARIATION IN MINIMAL THERMAL CONDUCTANCE OF THE GOLDEN HAMSTER, *Mesocricetus auratus*

ABSTRACT

The existence of diurnal variation in MTC of P. leucopus was demonstrated in Chapter 1. The purpose of this report is to determine the amount of diurnal variation in MTC in Mesocricetus auratus, the golden hamster. M. auratus was chosen because it displays marked diurnal variation in several physiological parameters, making it a good candidate for displaying a high degree of diurnal variation in MTC.

Metabolic rate, evaporative water loss, and core temperature were determined for 10 M. auratus during resting and active phases for each of the following temperatures: 0, 5, 10, 15, 20, 22.5, 25, 27.5, 30, 32.5, and 35 C. The steady state T_c was significantly related to the ambient temperature when tested over all temperatures, but this was due to primarily to a rise in T_c with T_a at temperatures above 27.5 C. There was no relationship between T_c and T_a for T_a's $\leq$ 25 C. Evaporative water loss was significantly higher during active phase than resting phase. Within either phase, evaporative heat loss was adequately described as a linear function of ΔT. Diurnal variation in the slopes of these relationships was slight and not statistically significant.

In Chapter 1 I described procedures for determining when a segmented regression procedure is appropriate for estimating MTC. Use of the "two-point" method for estimating MTC showed that there was no systematic change in thermal conductance with T_a at low T_a's. Since thermal conductance seemed invariant with T_a at low ambient temperatures (T_a < 20), a segmented (two phase) regression procedure could be used to simultaneously estimate MTC, ΔT_{lc}, and BMR for each mouse for resting and active phases. There was significant diurnal variation in MTC. Resting phase wet MTC was 0.392 ($\pm$.01) $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$; active phase wet MTC was 0.0429 ($\pm$.03) $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$. Resting phase dry MTC was 0.399 ($\pm$.01); active phase dry MTC was 0.443 ($\pm$.03). A published allometric equation predicts diurnal variation in MTC of 0.208 $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$ for an animal of 140 gm mass (the average mass of the M. auratus used in this study). Diurnal variation in MTC was found to be considerably less (0.044 $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$).

It has been suggested that diurnal variation in MTC functions to facilitate heat loss during the active phase. There are several problems with this argument. It is questionable whether small mammals are faced with a "problem" of heat dissipation at low ambient temperatures. It seems more likely that diurnal variation in MTC results from a combination of physiological factors that allow reduction of maintenance costs during the resting phase due to the

lower resting phase MTC.

INTRODUCTION

In the first chapter of this dissertation, I examined the biophysical theory of Minimal Thermal Conductance; compared several different methods for estimating MTC; and determined the amount of diurnal variation in MTC of Peromyscus leucopus, the white-footed mouse. While there was statistically significant diurnal variation in MTC, the variation amounted to a much smaller percentage of the overall mean than predicted by Aschoff's (1981a) analysis. However, the MTC data available to Aschoff were highly biased in several ways. Whether the biases inflated the apparent amount of diurnal variation in MTC, or whether P. leucopus displays an unusually low degree of diurnal variation of MTC, remains an open question.

The purpose of this report is to determine experimentally the amount of diurnal variation in MTC of Mesocricetus auratus, the golden hamster. M. auratus is nocturnal and shows marked diurnal variation in a number of physiological parameters (Bridges and Goldman 1975; Stetson et al. 1977, 1978). Thus, M. auratus was thought to be a good candidate for displaying a high degree of diurnal variation in MTC if such exists among small mammals. In Chapter 1 of this dissertation, I showed that MTC could be defined in a manner that made it an unambiguous measure of an animal's maximal insulative properties at low ambient temperatures. Certain conditions for both the animal and

the metabolism measurement system must be satisfied for correct measurement of MTC for a given small mammal. In the rest of this paper I attempt to 1) show that the requirements outlined in Chapter 1 for correct measurement of MTC are met for M. auratus; 2) determine the amount of diurnal variation of MTC of M. auratus; and 3) compare this with the degree of diurnal variation predicted by Aschoff's (1981a) equations and with the amount of diurnal variation in MTC of P. leucopus.

METHODS AND MATERIALS

Maintenance of animals

Adult male Mesocricetus auratus (outbred strain Lak:LVG(SYR)) were purchased from Charles River Laboratories (Wilmington, Massachusetts). The M. auratus were maintained at 22 ± 1.5 ^{o}C on a 15:9 photoperiod (lights on at 0600 EST) throughout the experiment. The hamsters were kept in 16 cm x 20 cm x 26 cm plastic cages with hardwood chip bedding, and were provided with Autoclavable Purina Lab Chow (5010) and water ad lib.

Design of Physiological Measurement System

Measurements of the metabolic rate of M. auratus were made using the McClure Laboratory Physiological Measurement System, a computerized system discussed in Smith and McClure (1985), and described in Chapter 1 of this dissertation.

The metabolism chamber used is described in Chapter 4 of this dissertation. Air was dried in a large column of Drierite before entering the chamber. The incurrent airstream dewpoint averaged -19.2 ^{o}C (equivalent to a water vapor density of approximately 2 $g \cdot m^{-3}$). Air flow rates through the metabolism chamber were set to between 600 and 640 SCCM.

Temperature telemetry

Temperature sensitive radio transmitters were used to determine the core temperature of mice during the course of metabolic rate measurements. Minimitter Model M transmitters were used (mass 2.5 grams, less than 2% of the body mass of the M. auratus used in this experiment). A small AM radio was used as a receiver. The minimitters were calibrated as described in Chapter 1. The 95% confident limits around the transmitter calibration line were within 0.05 ^{o}C. This is more precise than the manufacturer's stated accuracy of 0.1 ^{o}C.

M. auratus were anaesthetized using a combination of Avertin injected interperitoneally and Flouthane administered as an inhalant. The minimitters were sterilized in ethanol. The minimitters were then implanted in the peritoneal cavity, and were held in place in the lower abdominal region by a single suture secured to the inside of the body wall. All animals recovered from surgery without infection or other apparent ill effects. A minimum of four days was allowed between implantation and the beginning of metabolic rate measurement for each animal.

Experimental Protocol

The metabolic rate of each M. auratus was determined during night and day at the following temperatures: 0, 5, 10, 15, 20, 22.5, 25, 27.5, 30, 32.5, and 35 ^{o}C. Determinations of metabolic rate were

made independently and in random order for each of the temperatures during both night and day. That is, a separate experiment (metabolic rate determination) was performed for each temperature. Nighttime determinations of metabolic rate were done between 10:00 pm and 4:30 am. Daytime measurements were done between 8:00 am and 7:00 pm. The protocol for an experiment was as follows: each animal was fasted for 4-6 hours prior to a metabolic rate determination. Each animal was weighed prior to being placed in the metabolism chamber. At the beginning of an experiment, incurrent air was sampled for at least 10 minutes. The excurrent airstream was then sampled continuously until the oxygen consumption, CO2 production, evaporative water loss, and core temperature were stable for at least 15 minutes (with the animal at rest). Incurrent air was then sampled again in order to check for machine drift. The animal was then removed from the animal chamber and weighed. On several occasions an animal failed to provide stable resting values for over four hours. When this happened, the experiment was terminated, and the order of determination was re-randomized for all temperatures remaining to have MR successfully determined. Metabolic rate measurements for each individual were determined for all temperatures during both night and day within one month of implantation of the body temperature transmitters.

Statistical and computational procedures

Minimal thermal conductance was calculated from a segmented regression of MR as a function of ΔT ($\Delta T = T_c - T_a$), using the program SEGREG described in Appendix 3, Chapter 1 of this dissertation. MTC was estimated separately for each individual for both resting and active phases.

Statistical tests were based primarily on the procedures recommended by Lindman (1974). Data analysis was carried out using SPSS version 9.0 and BMDP-83 installed on a CDC Cyber 170/855. Most statistical analyses were performed with both packages to check for accidental misspecification of statistical procedures in the programs. The statistical analyses were carried out as described for P. leucopus in Chapter 1.

RESULTS

Core Temperature

The relationship between phase, T_a, and the T_c at which steady state was reached is shown in Figure 2.1. A repeated measures ANOVA was used to analyze these data. Stable body core temperatures were significantly lower during resting phase (36.53 ^{o}C) than active phase (37.46 ^{o}C) ($p < 0.01$). A linear trend analysis of the relationship between T_c and T_a, considering all T_a's from 0 ^{o}C to 35 ^{o}C was statistically significant ($p < 0.05$). However, there was no evidence of a linear trend when data for $T_a \leq 25$ ^{o}C (roughly, all T_a's below the thermoneutral zone) were considered ($p > 0.25$).

Evaporative Water Loss

Metabolic and evaporative heat loss parameters will be expressed throughout on a "per kilogram" live mass basis. Average values will be presented as the mean ($\pm$ 2 standard errors of the estimate). The relationship between evaporative heat loss and T_a is shown for both active and resting phase in Figure 2.2 Average evaporative heat loss for all temperatures was higher during the active phase than during the resting phase (0.71 $W \cdot kg^{-1}$ as compared to 0.87 $W \cdot kg^{-1}$). This difference is statistically significant ($p < 0.05$). Linear regression

was performed for each phase on Q_{ev} as a function of T_a and Q_{ev} as a function of (T_c-T_a) for $T_a \leq 25\ ^{o}C$ (roughly, those ambient temperatures below the thermoneutral zone). In all cases, the linear regresseions were statistically significant ($P \leq 0.01$). The slope of the relationship between Q_{ev} and T_a was not statistically significantly different during resting phase than during active phase (0.0187 for active; 0.0127 for resting, $p \geq 0.15$). Likewise, the slopes of the relationship between Q_{ev} and ΔT were not statistically significantly different between phases (-0.0197 for active; -0.0124 for resting $p \geq 0.15$).

Metabolic Parameters

The relationship between phase, ΔT, and metabolic rate is shown in Figure 2.3. MTC, basal metabolic rate ΔT_{lc} were calculated for two measures of metabolic rate: the total metabolic rate, or the metabolic rate minus evaporative heat loss ("dry" metabolic rate). Examination of the data revealed that the MR measured at 35 ^{o}C was consistently higher than the MR at 30 ^{o}C or 32.5 ^{o}C. Thus, 35 ^{o}C was determined to lie above the thermoneutral zone and MR data for 35 ^{o}C were excluded from the data set used to simultaneously estimate MTC, ΔT_{lc}, and BMR.

The estimated basal metabolic rate was 4.63 ($\pm$0.50) $W \cdot kg^{-1}$ for resting phase; 5.14 ($\pm$ 0.26) $W \cdot kg^{-1}$ for active phase (difference not

statistically significant). The estimated "dry" basal metabolic rate ($M-Q_{ev}$) was 3.30 ($\pm$ 0.60) $W \cdot kg^{-1}$ for resting phase; 3.50 ($\pm$ 0.42) $W \cdot kg^{-1}$ for active phase (difference not statistically significant).

The estimated ΔT_{lc} for the relationship between MR and ΔT was 9.23 for resting phase, 10.86 for active phase ($p < 0.08$). The estimated ΔT_{lc} for the relationship between $M-Q_{ev}$ and ΔT was 9.00 for resting phase, 10.80 for active phase ($p < 0.07$).

Minimal thermal conductance was calculated from the data both for the measured MR (providing estimates of "wet" MTC) and on $MR-Q_{ev}$ (providing estimates of "dry" MTC). The average dry MTC in resting phase was 0.399 ($\pm$ 0.012); the average in active phase was 0.443 ($\pm$ 0.026). A paired t-test shows these to be statistically significantly different ($p < 0.05$). The average wet MTC was 0.392 ($\pm$ 0.014) in resting phase and 0.429 ($\pm$ 0.027) in active phase. This difference was statistically significant ($p < 0.05$).

As discussed in Chapter 1 of this dissertation, the assumption that thermal conductance is constant for $\Delta T > \Delta T_{lc}$ can be tested by calculating $MTC = (M_1-M_2)/(\Delta T_1-\Delta T_2)$ for different temperature ranges. MTC calculated in this way for several temperature ranges (0-5 ^{o}C, 5-10 ^{o}C, 10-15 ^{o}C, 15-20 ^{o}C, and 20-22.5 ^{o}C) are shown in Table 2.1. A linear regression between MTC calculated in this manner and T_a was not statistically significant ($p > 0.40$).

Significance of Variation Between Individuals

The statistical significance of variation in MTC between individuals was tested by a repeated measures analysis of variance (MTC by phase and individuals). Variation between individuals was statistically significant ($p < .05$).

DISCUSSION

Core Temperature

The core temperature data reported in this paper represent the temperature at which the metabolic rate, evaporative water loss, and core temperature were simultaneously stable, that is, at steady state. There is clear diurnal variation in the core temperature of M. auratus. The diurnal variation reported here (a day-night difference of 0.93 ^{o}C) is greater than the 0.6 ^{o}C predicted by the equation of Aschoff (1981b). This is similar to the results for P. leucopus discussed in Chapter 1, and again is most likely a function of methodology. The equation of Aschoff (1981b) was calculated from data collected mostly by measuring the core temperature of an animal in its cage at various times of day irrespective of its activity level. It seems that the use of core temperatures obtained during periods of exercise obscures diurnal variation in the steady state (resting) core temperature.

There is a statistically significant relationship between T_c at steady state and the ambient temperature when data from both phases are considered together. Examination of Figure 2.1 shows that this results primarily from the elevated T_c's found at an ambient temperature of 35 ^{o}C. There is no relationship apparent between T_c and T_a for T_a's $\leq$ 25 ^{o}C (roughly those T_a's that correspond to $\Delta T >$

T_{lc}). Thus, M. auratus does not exhibit the high degree of T_c lability exhibited during resting phase by P. leucopus (cf. Chapter 1). This may be related to the larger body mass, and correspondingly larger thermal inertia, of M. auratus. As discussed by Hill (1983) temperature lability has obvious energetic benefits for P. leucopus, but must also have some costs in terms of alertness, ability to support bursts of metabolism, etc. Peromyscus leucopus are capable of raising T_c very quickly due to their small body mass, thus mitigating any "cost" of temperature lability. M. auratus, in contrast, has much greater thermal inertia, and so would cool more slowly during periods of reduced metabolism. This would result in less "benefit" from reduced cost of metabolism. Also, M. auratus can not warm as quickly as P. leucopus (Lyman 1948; Hill 1975), due at least in part to its larger body mass. Thus, the potential benefits of T_c lability would be smaller for M. auratus than P. leucopus, and the potential costs greater. There are many ecological and physiological factors involved in interspecific differences in T_c lability. However, it seems that the potential net benefit of T_c variation with T_a is smaller for M. auratus than P. leucopus, and in fact such variation was not observed in M. auratus.

Evaporative Water Loss

Evaporative heat loss amounted to 5% of the total metabolic heat

load at 0 °C, 28% of the total metabolic heat load at 30 °C, and 35% of the metabolic heat production at 35 °C. These data agree well with those reported for the belding ground squirrel (Morhardt and Gates 1974) and several other small mammals (Welch 1980). The fraction of total metabolism made up by evaporation at 32.5 and 35 °C is lower for M. auratus than reported for P. leucopus in Chapter 1 of this dissertation. However, several P. leucopus were observed to have wet faces upon removal from the metabolism chamber during experiments at 35 °C. This occurred on only two occasions with M. auratus, and in both cases the degree of wetting of the face was slight. Thus, while 35 °C seems to lie outside the thermoneutral zone of M. auratus (Figure 1.3), this species seems less dependent upon evaporative heat loss at 35 °C than P. leucopus for body temperature regulation. Evaporative water loss rates were higher at night than during the day. This is similar to the situation in P. leucopus (cf. Chapter 1).

Welch and Tracy (1977) developed a model that suggests that the rate of evaporative water loss from mammals should increase with both metabolic rate and the temperature of the external nares. It seems reasonable to suppose that the temperature of the external nares varies with T_c. Both the core temperature and the metabolic rate were higher at night than during day, so the higher evaporative water loss rates at night are consistent with the predictions of Welch and Tracy's (1977) model.

Evaporative water loss rates were linearly related to both the ambient temperature and ΔT for both active and resting phase. However, the slopes for these two relationships were not statistically significantly different. Thus, while there is a significant linear trend between evaporative water loss and T_a, there is no apparent diurnal variation in the slope of the relationship.

Wet vs. Dry Thermal Conductance

The theoretical derivation of wet thermal conductance requires the assumption that evaporative heat loss be adequately described by a linear function of ΔT (See Chapter 1). Data available in the literature supports the use of this approximation when the air entering the metabolism chamber has been dried with a desiccant (Welch 1980; Welch and Tracy 1977). Examination of Figure 2.2 shows that in the present study evaporative heat loss is reasonably well approximated by a straight line for Ta's below the thermoneutral zone. The deviations from linearity are generally within the 95% confidence limits of the mean values at any given temperature. That is, the deviations from linearity are generally within the natural variation. So as a first approximation at least evaporative heat loss may be assumed to be a linear function of (T_c-T_a). This was also found to be the case in P. leucopus (Chapter 1). However, the validity of this approximation (and thus the use of "wet" MTC) needs further

investigation. A particular need is for sufficient data on evaporative water loss at low ambient temperatures to distinguish sampling variation from nonlinearities in the relationship between evaporative water loss and ΔT.

The slope of the relationship between Q_{ev} and T_a for $T_a \leq 25\ ^{o}C$ is similar for both resting and active phases. One would thus expect approximately the same amount of diurnal variation for both wet and dry MTC. Examination of Table 2.1 shows virtually the same amount of diurnal variation in wet MTC as dry MTC.

Minimal Thermal Conductance

There was significant variation in MTC between individual M. auratus, as was found in Chapter 1 for P. leucopus. The existence of significant variation between individuals makes it statistically inappropriate to calculate MTC by regressing metabolism against temperature when data have been pooled from measurements of several individuals (Lindman 1974). Rather, MTC must be calculated for each individual, and sample means calculated by averaging the individual MTC values. The biological importance of individual variation in MTC will be discussed further in Chapter 3.

The allometric equation presented by Aschoff (1981a) predicts for a 140 g mammal (the average mass of the M. auratus used in this study) a wet MTC value of 0.323 $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$ for the resting phase and

0.115 $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$ for the active phase. The equation of Bradley and Deavers (1981), which is not separated by phase, produces an estimate of 0.312 $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$).

The amount of diurnal variation in MTC found in the present study is markedly less than the amount predicted from Aschoff's (1981a) equations. The diurnal variation found for MTC of M. auratus was markedly lower than the nearly 50% of the 24-hour mean predicted from Aschoff's equations. It seems that the tremendous amount of diurnal variation in MTC of mammals suggested by Aschoff's analysis is largely due to biases in the MTC data available in the literature, as discussed in the first chapter of this dissertation. In contrast, the data on MTC of birds is much more evenly distributed across size ranges, so that MTC data for birds are available for both active and resting phase for a wide range of body mass. Aschoff (1981b) found significant diurnal variation in wet MTC of birds, but found that there was no diurnal variation in dry MTC of birds.

An interesting question is what causes diurnal variation in MTC and what, if any, function does this variation have. In birds it seems fairly clear that there is diurnal variation in wet MTC but that variation is due to diurnal variation in the relationship between evaporative heat loss and ambient temperature. There is no diurnal variation in dry MTC (Aschoff 1981a; Drent and Stonehouse 1971; Trost 1972). In contrast, there is diurnal variation in both wet and dry

MTC of P. leucopus and M. auratus. Examination of eq. (23) in Chapter 1 shows that wet MTC equals dry MTC plus the slope of the regression line relating Q_{ev} to ΔT. Since there is little diurnal variation in the slope of the regression line relating Q_{ev} to ΔT in P. leucopus and M. auratus, there should be about the same amount of diurnal variation in wet MTC as in dry MTC. This is indeed the cases in both species. Birds and mammals seem to differ, then, in the causes of diurnal variation in wet MTC. Birds have diurnal variation in MTC attributable to variation in the relationship between evaporative heat loss and ΔT. On the basis of the data presented in this dissertation for P. leucopus and M. auratus it seems that there is little (if any) diurnal variation in mammals in the relationship between evaporative heat loss and ΔT. Instead, in mammals there seems to be diurnal variation in dry minimal thermal conductance.

As stated by Aschoff (1981a) diurnal variation in dry MTC could result from "changing any of the links which build the chain of heat resistances from the body core to the environment." Diurnal variation in peripheral vasoconstriction and piloerection seem logical explanations for such variation in mammals. Greater peripheral vasoconstriction could lead to a decreased rate of heat transfer from the body core to the skin surface, with a consequent overall reduction in thermal conductance. Data on diurnal variation in skin temperature

for humans (Heise 1969; Schmidt 1972; Aschoff 1971) is indicative of diurnal variation in internal heat conduction to the skin surface, most likely due to differences in peripheral vasoconstriction (Aschoff 1981a). It is also possible that mammals achieve a greater degree of fur piloerection during the resting phase than during the active phase, which could contribute to diurnal variation in MTC. Another possible factor concerns the behavior of animals in the metabolism chamber. Every effort was made to obtain metabolic rate measurements at time when the test animal was at rest. However, slight movements on the part of the animal could conceivable go undetected. In general, it seemed to take longer for test animals in this study to achieve stable metabolic rates (while remaining still) during the active phase than during the resting phase (personal observation). This suggests that the test animals could be more prone to slight movements during active phase measurements than the resting phase measurements. Movement by the animal would disturb the boundary layer of air around it, causing an increase in the convective heat loss coefficient h_c (Kreith 1976). Thus, slight variation in behavior of the test animals in the metabolism chambers could contribute to diurnal variation in MTC.

The functional significance of diurnal variation in minimal thermal conductance has not yet been determined. Aschoff (1981a) suggests the "functional significance of this circadian rhythm is to

promote heat dissipation during the activity time when the basal metabolism is set at a higher level, and to conserve heat during the rest time when metabolism is low." There are several problems with this argument, however. MTC measures the minimal rate of change of metabolism per degree change in T_c-T_c at $\Delta T \geq \Delta T_{lc}$ (Chapter 1, this dissertation). If small mammals are faced with a problem of heat dissipation during the active phase, then they might exhibit diurnal variation in maximal ability to lose heat to the environment. MTC is often regarded as an indicator of an animal's overall thermal properties. However, it is not clear that differences in maximal and minimal heat loss rates should be related in any systematic way. For example, the use of "thermal windows" (Bakken 1981) and of panting and saliva spreading (Golightly and Ohmart 1978) are effective ways to facilitate heat loss. These mechanisms could change maximal heat loss rates independently of Minimal Thermal Conductance.

It is possible that the observed diurnal variation in MTC is simply an artifact of the animal's behavior in an artificial situation. If this is the case, then diurnal variation may have no function <u>per se</u>. While it seems unlikely that diurnal variation in MTC is purely artifactual, it is a possibility that should receive careful attention in further studies of MTC, and should temper speculation about the "function" of diurnal variation in MTC.

Aschoff (1981a) considered the functional significance of diurnal

variation from the standpoint of ascribing a function to the higher MTC during the active phase. A better perspective might be to simply consider differences between phases, rather than considering the MTC in one phase or another to be "high" or "low".

During the active phase, it is apparently beneficial to maintain high rates of metabolism because this better enables small mammals to perform important tasks such as foraging, finding mates, and escaping predators. During the resting phase animals are less likely to perform these activities and thus can decrease their existence cost by lowering tissue metabolism (at little loss of the benefits of active phase level metabolic rates such as preparedness for tasks requiring very high metabolic rates, which generally do not take place during resting phase). High rates of tissue metabolism may dictate greater peripheral circulation during active than resting phases. The lower resting phase tissue metabolism may be associated with lower peripheral circulation, which in turn could result in lower resting phase thermal conductance. The lower resting phase conductance in turn results in lower maintenance costs at low temperatures during resting phase than would be incurred otherwise. Thus, it is possible that the diurnal variation in MTC is part of a whole suite of diurnal physiological changes which allow small mammals to perform well activities such as foraging and mate-seeking during the active phase, while allowing metabolic economy during resting phase through

decreased maintenance costs.

CONCLUSIONS

There is clear diurnal variation in stable T_c of M. auratus, but unlike P. leucopus, there is little variation in T_c with T_a, and the only variation apparent at all is a slight increase in T_c at high ambient temperatures.

There is diurnal variation in the evaporative water loss rates of M. auratus. During both phases, evaporative water loss seems adequately described by a linear function of either T_c or ΔT, and the slopes for active and resting phases are approximately the same. While the use of a linear approximation to the relationship between ΔT and evaporative heat loss seems justified as a first approximation, the biophysical validity of the theoretical development of wet MTC depends upon the accuracy of this approximation. A significant need in the study of MTC, then, is data on evaporative heat loss at low ambient temperatures that allows nonlinearities in the relationship to be distinguished from sampling error.

There is diurnal variation in MTC of M. auratus, but like the situation for P.. leucopus, the diurnal variation is much slighter than that predicted by Aschoff's (1981a) equations. This seems largely due to bias in the data available in the literature regarding MTC of mammals.

Diurnal variation in wet MTC of birds seems due to diurnal variation in the relationship between evaporative water loss and T_a, with no diurnal variation in dry MTC. In contrast, the amount of diurnal variation in wet and dry MTC is very similar in M. auratus and P. leucopus. Diurnal variation in dry MTC could be caused by diurnal variation in peripheral vasoconstriction, piloerection, or by subtle diurnal variation in the behavior of mammals while in metabolism chambers in the laboratory.

Aschoff (1981a) argued that diurnal variation in MTC functions to facilitate heat loss during the active phase. It is not clear that variations in an animal's minimal rate of heat loss should "function" to facilitate heat loss, or whether such facilitation is often required. Furthermore, variation in mechanisms used by animals to increase maximal ability to lose heat when faced with heat stress may not be reflected in minimal thermal conductance. Diurnal variation in MTC may not have a physiological function per se. Diurnal variation in MTC may reflect differences in the behavior of test animals in metabolism chambers during different phases of the activity cycle. Diurnal variation in MTC may also reflect diurnal variation in other physiological parameters, such as peripheral vasoconstriction, which may function to meet higher tissue oxygen demands during the active phase. Thus, specific needs in the study of diurnal variation of MTC are to determine the factors causing diurnal variation in MTC, and to

determine the functional significance diurnal variation (if one exists) of diurnal variation in MTC.

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Table 2.1. Statistical analysis of BMR, ΔT_{lc}, and MTC of Mesocricetus auratus. Diurnal variation in BMR and MTC was tested by one-tailed paired t-tests; diurnal variation in ΔT_{lc} was tested by two-tailed t-tests. Units of MTC are $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$.

Parameter	Active	Resting	p
Dry BMR ($M-Q_{ev}$)	3.30(±0.60)	3.50(±0.42)	ns
BMR (M)	4.63(±0.50)	0.514(±0.26)	ns
MTC_d	0.399(±0.012)	0.443(±0.025)	0.05
MTC_w	0.392(±0.014)	0.429(±0.027)	0.05
ΔT_{lc} (for relationship between $M-Q_{ev}$ and ΔT)	9.23 (±1.52)	10.86 (±1.59)	0.08
ΔT_{lc} (for relationship between M and ΔT)	9.00 (±1.65)	10.80 (±1.73)	0.07

Table 2.2. Relationship between T_a and Wet and Dry MTC as calculated from $(Metabolism_1 - Metabolism_2)/[(T_{c1}^a - T_{a1}) - (T_{c2} - T_{a2})]$. (Units are $W \cdot {}^oC^{-1} \cdot Kg^{-1}$).

Variable	Phase	Ambient Temperature (T_a)			
		0.0	5.0	10.0	15.0
"Wet" MTC	rest.	0.351(±.281)	0.210(±.247)	0.512(±.292)	0.376(±.158)
	act.	0.456(±.348)	0.372(±.214)	0.468(±.220)	0.384(±.179)
"Dry" MTC	rest.	0.346(±.168)	0.280(±.251)	0.456(±.283)	0.396(±.182)
	act.	0.480(±.295)	0.414(±.207)	0.380(±.183)	0.510(±.286)

Figure 2.1. Relationship between core temperature (T_c) and ambient temperature (T_a) for Mesocricetus auratus. Horizontal lines represent mean T_c for 10 adult male M. auratus. Vertical bars indicate ± 2 SE. Vertical lines indicate ranges. Daytime values are indiacted by open boxes. Nighttime vales are indicated by solid boxes.

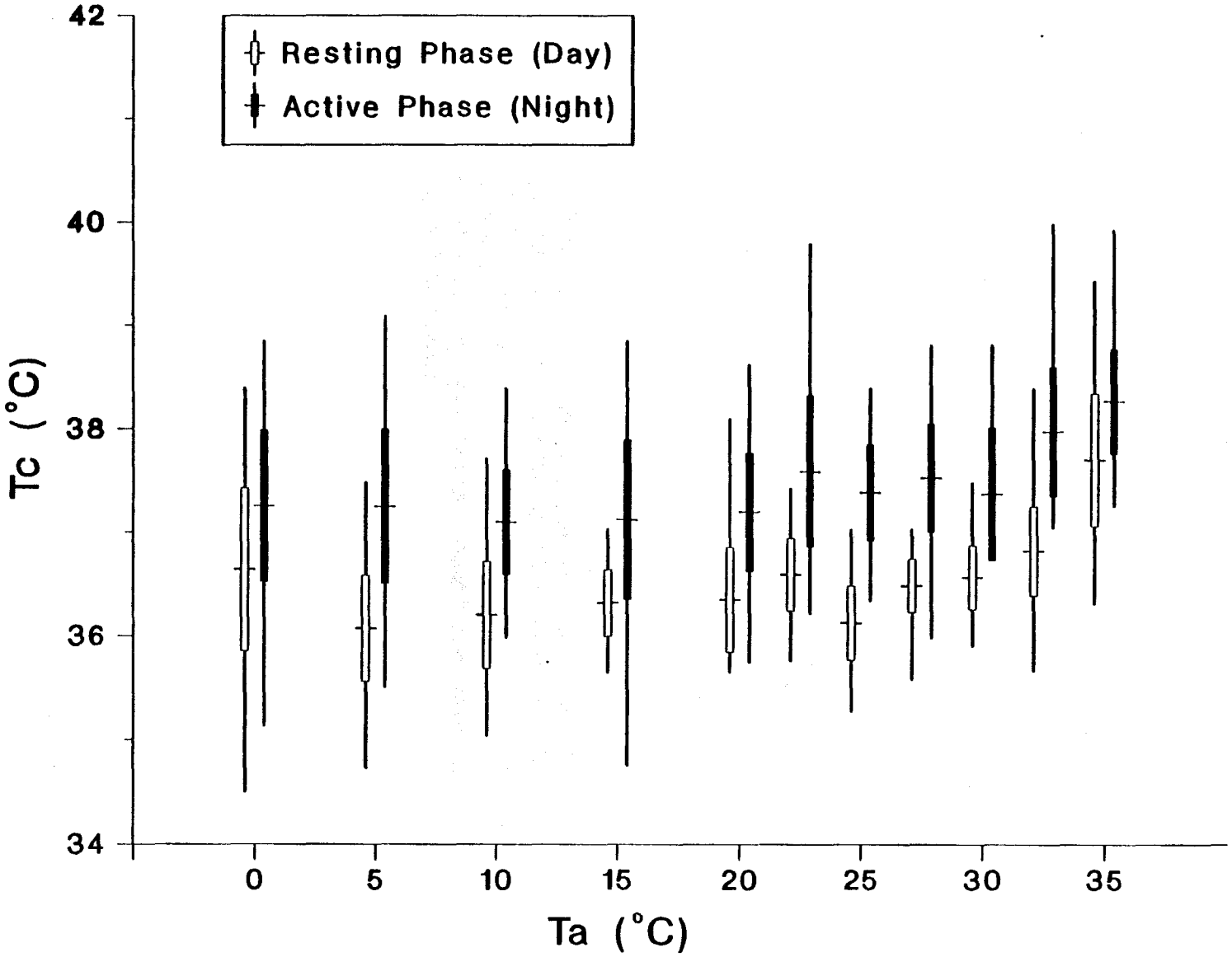

Resting Phase (Day)
Active Phase (Night)
42
40
38
36
34
Tc (°C)
0
5
10
15
20
25
30
35
Ta (°C)

Figure 2.2. Relationship between evaporative heat loss (Q_{ev}) and ambient temperature (T_a) for Mesocricetus auratus. Horizontal lines represent mean Q_{ev} for 10 adult male M. auratus. Vertical bars indicate ± 2 SE. Vertical lines indicate ranges. Daytime values are indiacted by open boxes. Nighttime vales are indicated by solid boxes.

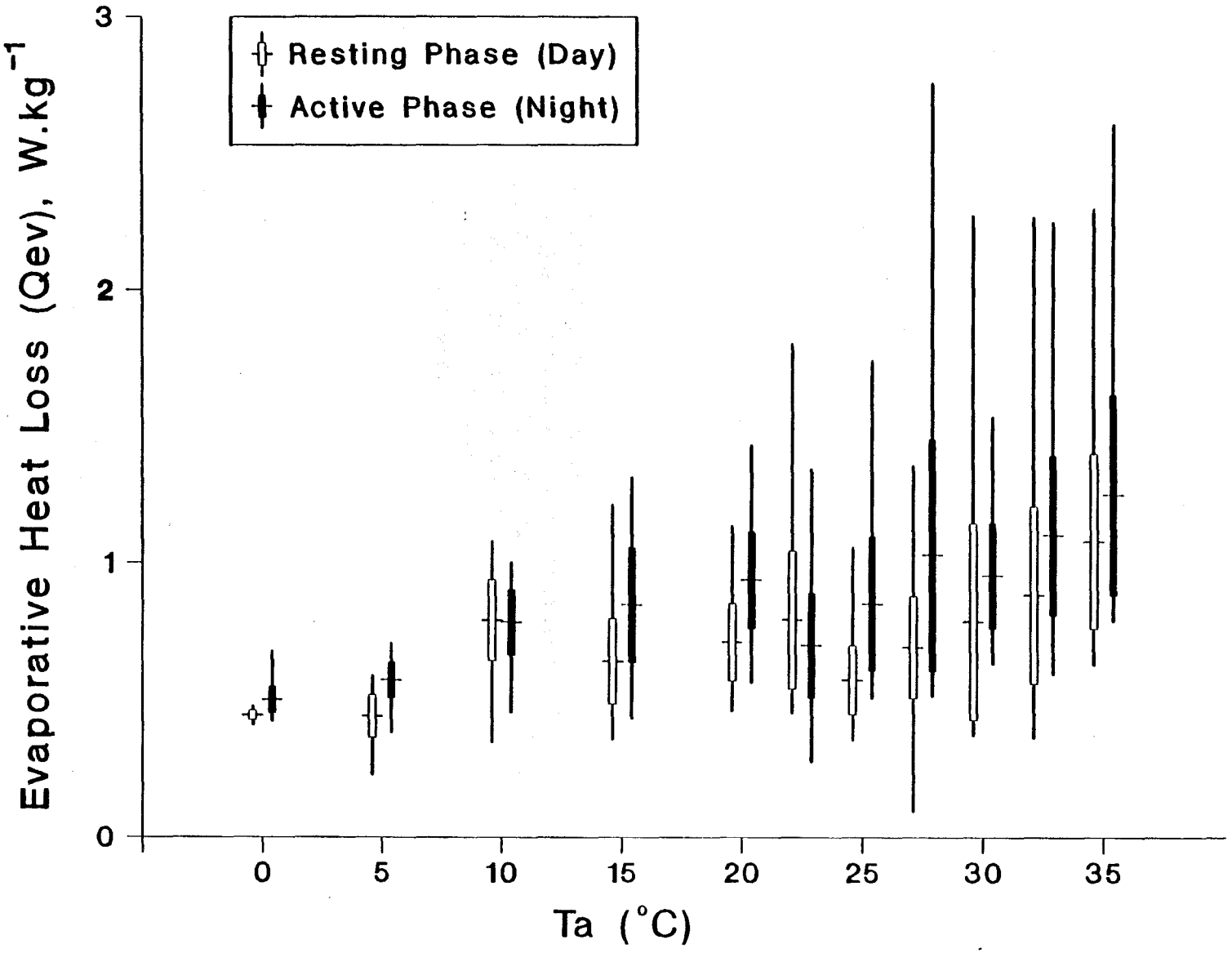
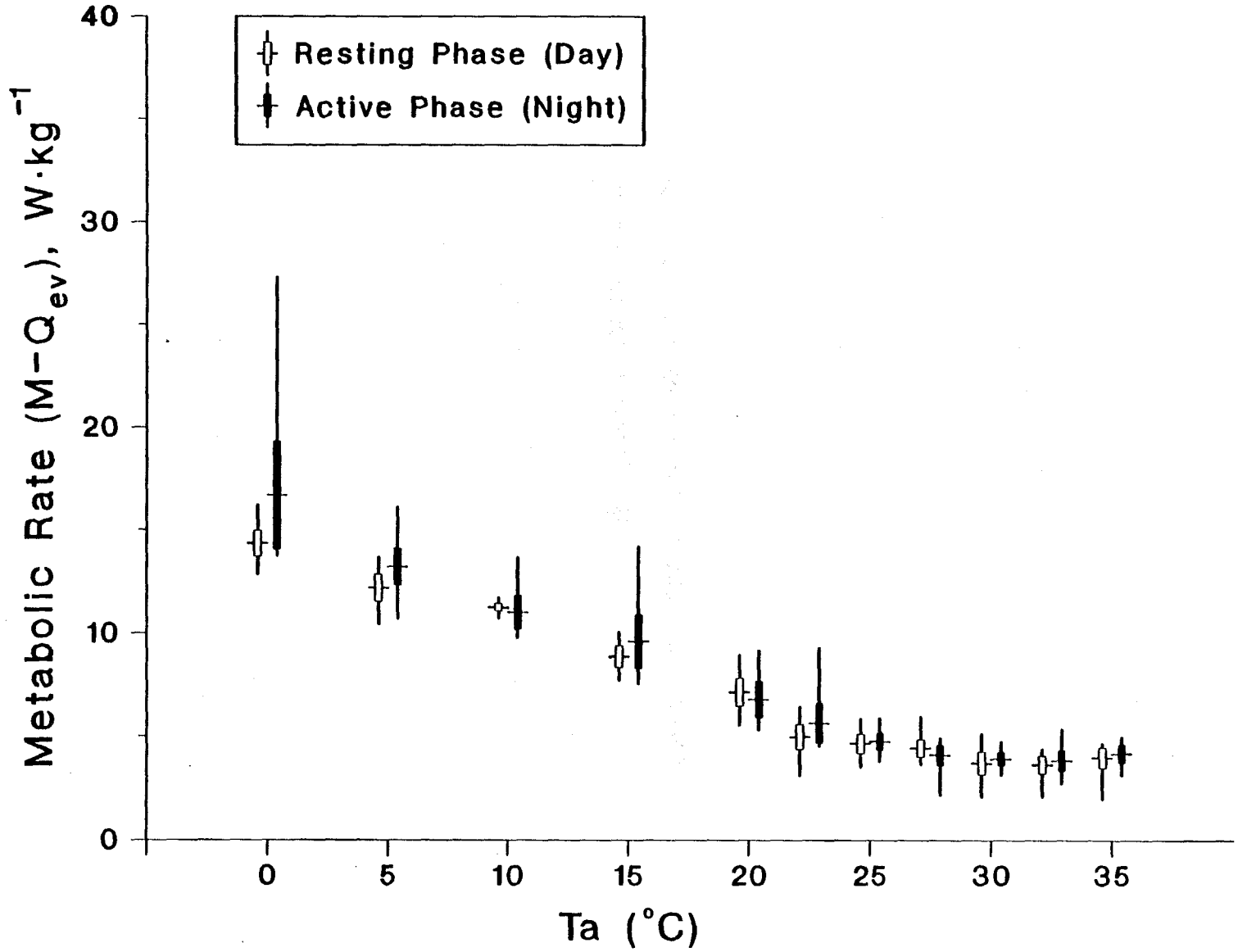

Resting Phase (Day)
Active Phase (Night)
Evaporative Heat Loss (Qev), W.kg^{-1}
3
2
1
0
0
5
10
15
20
25
30
35
Ta (°C)

Figure 2.3. Relationship between metabolic rate ($M\text{-}Q_{ev}$) and T_a for M. auratus. Horizontal lines represent mean ($M\text{-}Q_{ev}$) for 10 adult male M. auratus. Vertical bars indicate $\pm$ 2 SE. Vertical lines indicate ranges. Daytime values are indiacted by open boxes. Nighttime vales are indicated by solid boxes.


Resting Phase (Day)
Active Phase (Night)
Metabolic Rate (M−Qev), W·kg−1
40
30
20
10
0
0
5
10
15
20
25
30
35
Ta (°C)

DIURNAL VARIATION IN MINIMAL THERMAL CONDUCTANCE OF THE EASTERN WOODRAT, *Neotoma floridana*

ABSTRACT

The existence of diurnal variation in Minimal Thermal Conductance has been demonstrated for Peromyscus leucopus and Mesocricetus auratus. The purposes of this report are to 1) determine the amount of diurnal variation in MTC of Neotoma floridana, the eastern woodrat; 2) determine if diurnal variation in MTC of N. floridana is associated with diurnal variation in the relationship between subdermal temperature and T_a at low ambient temperatures; 3) using the data presented in this paper and Chapters 1 and 2 of this dissertation, calculate MTC as an allometric function of body mass for active and resting phases.

Metabolic rate, evaporative water loss, and core temperature were determined for 10 N. floridana during resting and active phases for each of the following temperatures: 0, 5, 10, 15, 20, 22.5, 25, 27.5, 30, 32.5, and 35 ^{o}C.

The steady state T_c was not related to the ambient temperature. Subdermal temperature was significantly related to T_a, and the slope of this relationship was greater during the resting phase than the active phase (although this difference was not statistically significant). Evaporative water loss was significantly higher during active phase than resting phase. Within either phase, evaporative heat loss was adequately described as a linear function of ΔT. Diurnal variation in the slopes of these relationships was slight and not statistically significant.

Use of the "two-point" method for estimating MTC showed that there was no systematic change in thermal conductance with T_a at low T_a's. Since thermal conductance seemed invariant with T_a at low ambient temperatures (T_a < 20 ^{o}C), a segmented (two phase) regression procedure could be used to simultaneously estimate MTC, ΔT_{lc}, and BMR for each rat for resting and active phases. There was significant diurnal variation in MTC. Resting phase dry MTC was 0.20 ($\pm$0.01) $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$; active phase dry MTC was 0.23 ($\pm$.03) $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$. Diurnal variation in MTC was found to be considerably less than suggested by an earlier allometric analysis of diurnal variation in MTC.

Possible causes for diurnal variation in MTC include diurnal variation in peripheral circulation, causing diurnal variation in internal heat transfer; diurnal variation in fur piloerection, causing diurnal variation heat transfer through the fur layer; differences between night and day in behavior of animals in the artificial environment of the metabolism chambers, resulting in an artifactual appearance of diurnal variation in MTC.

Diurnal variation in peripheral vasoconstriction should result in greater variation between subdermal temperature and ambient

temperature during the resting phase than during the active phase. While the data presented here show such a difference, the difference was not statistically significant. Nonetheless, the data suggest that diurnal variation in peripheral vasoconstriction may contribute to diurnal variation in MTC.

INTRODUCTION

The existence of diurnal variation in minimal thermal conductance (MTC) has been verified through direct experimentation in two small mammal species: Peromyscus leucopus, the white-footed mouse; and Mesocricetus auratus, the golden hamster (Chapters 1 and 2 of this dissertation). While in both species there was diurnal variation in MTC, the variation was considerably smaller than that predicted by Aschoff's (1981a) equations. As discussed in the first two chapters, the MTC data available in the literature are highly biased in several ways. These biases apparently inflated the amount of diurnal variation in MTC of small mammals as calculated by Aschoff (1981a).

The factors causing diurnal variation in MTC of mammals have not yet been firmly identified. In birds, diurnal variation in wet MTC seems due to diurnal variation in respiratory evaporative heat loss. There is little, if any, diurnal variation in dry MTC of birds (Aschoff 1981a; Drent and Stonehouse 1971, Trost 1972). In mammals, however, there is diurnal variation in dry MTC, and no difference in the amount of diurnal variation between wet and dry MTC. Aschoff (1981a) and I (Chapter 2, this dissertation) have suggested three possible causes for diurnal variation in MTC: diurnal variation in peripheral circulation, causing diurnal variation in internal heat transfer; diurnal variation in fur piloerection, causing diurnal

variation heat transfer through the fur layer; differences between night and day in behavior of animals in metabolism chambers (due to the artificial nature of environment), resulting in an artifactual appearance of diurnal variation in MTC. Diurnal variation in peripheral vasoconstriction should result in diurnal variation in the slope of the relationship between skin temperature and ambient temperature at low ambient temperatures. Thus, determination of skin (or subdermal) temperatures should help resolve the mechanistic basis for diurnal variation in MTC.

Neotoma floridana, the eastern woodrat, is a moderate sized nocturnal rodent (Whitaker and Mumford 1983; Genoways and Birney 1974). It was chosen for this study because of its large size (approximately 450 g). This large size offers the practical advantage that two separate radio transmitters (one to telemeter core temperature, one for subdermal temperature) may be implanted simultaneously. Also, the data presented in Chapters 1 and 2 of this dissertation on P. leucopus (mass approximately 24 gm), and M. auratus (mass approximately 140 gm) along with data on N. floridana (mass approximately 480 gm) allows examination of the relationship between body mass and ΔT_{lc}, and a re-examination of the relationship between mass, phase of the activity cycle, and MTC.

The main purposes of this report are to: 1) determine the amount of diurnal variation in MTC of Neotoma floridana; 2) determine if

diurnal variation in minimal thermal conductance of N. floridana is associated with diurnal variation in the relationship between subdermal temperature and ambient temperature at low ambient temperatures; 3) determine if there is a relationship between core temperature (T_c) and ambient temperature in MTC in N. floridana; 4) calculate MTC as an allometric function of body mass using the data presented in this dissertation for P. leucopus, M. auratus, and N. floridana, and 5) compare the resultant allometric equations with the equations of Aschoff (1981a).

METHODS AND MATERIALS

Maintenance of Animals

Adult male Neotoma floridana used in this study were part of a laboratory colony of this species maintained at Indiana University since 1974. The history of this colony is described in McClure and Randolph (1980). N. floridana were maintained at 22 ± 1.5 C on a 15:9 photoperiod (lights on at 0600 EST) throughout the experiment. The woodrats were kept in 20 cm x 22 cm x 46 cm plastic cages with hardwood chip bedding, and were provided with Autoclavable Purina Lab Chow (5010) and water ad lib.

Design of Physiological Measurement System

Measurements of the metabolic rate of N. floridana were made using the McClure Laboratory Physiological Measurement System, described by Smith and McClure (1985) and in Chapter 1 of this dissertation.

The metabolism chamber used is similar to that described in Chapter 4 of this dissertation, but of larger dimensions (20 cm diameter; 28 cm in height). Air was dried in a large column of Drierite before entering the chamber. The incurrent airstream dewpoint averaged -19.2 ^{o}C (equivalent to a water vapor density of approximately 2 gm$\cdot$m^{-3}). The air flow rate through the metabolism

chamber was set between 900 and 940 SCCM.

Temperature Telemetry

Temperature sensitive radio transmitters were used to determine the core and subdermal temperature of woodrats during the course of metabolic rate measurements. Minimitter Model M and Model T transmitters were used. An AM radio was used as a receiver for the Model M minimitters. A small CB radio was used as a receiver for the Model T transmitters. The minimitters were calibrated as described in Chapter 1. The 95% confidence limits around the minimitter calibration curves were within 0.05 ^{o}C. This is more precise than the manufacturer's stated accuracy of 0.1 ^{o}C. The model M minimitters are AM-band transmitters, while the model T transmitters are CB band transmitters. This allows implantation of one transmitter of each type in an individual rat. One minimitter is used for core temperature measurement, another for subdermal temperature measurement. The total mass of the minimitters implanted was less than 5% of the body mass of the animals in which they were implanted. Neotoma floridana were anaesthetized using a combination of Avertin injected interperitoneally and Flouthane administered as an inhalant. Minimitters were sterilized in ethanol. The bodies of both minimitters were implanted in the peritoneal cavity, and were held in place in the lower abdominal region by sutures secured to the

inside of the body wall. One of the transmitters had a long, thin, flexible probe that measured the temperature at the tip of the probe. This transmitter was implanted with the probe passing through the body wall and extending between the skin and the body wall to the mid-dorsal region of the rat's lower back. All animals recovered from surgery without infection or other apparent ill effects. A minimum of seven days was allowed between implantation and the beginning of metabolic rate measurement for each animal.

The subdermal temperatures recorded represent the temperature between the body wall and the skin at the middle of the rat's lower back. Ideally, the temperature at the surface of the skin would be measured (McClure and Porter 1983) rather than the subdermal temperature. Skin surface temperature could be determined from thermocouples glued to the skin surface with cyanoacrylate glue, similar to the procedures used by Conley (1983). However, the possibility of injury to the animal from repetition of such a procedure, plus the problems of disruption of the animal's behavior due to the thermocouple attachment, made the benefits of direct skin surface temperature measurement seem not worth the potential problems. Differences in peripheral vasoconstriction should be reflected in the subdermal temperature, although perhaps not to as pronounced a degree as would be apparent in direct measurement of skin surface temperature.

Experimental Protocol

The metabolic rate of each of ten adult male N. floridana was determined during night and day at the following temperatures: 0, 5, 10, 15, 20, 22.5, 25, 27.5, 30, 32.5, and 35 °C. (With one exception: for one rat, metabolism measurements were not collected for 22.5 °C.) Determinations of metabolic rate were made independently and in random order for each of the temperatures during both night and day. That is, a separate experiment (metabolic rate determination) was performed for each temperature. Night time determinations of metabolic rate were done between 22:00 and 04:30. Daytime measurements were done between 08:00 and 19:00.

The protocol for an experiment was as follows: each animal was fasted for 6-8 hours prior to a metabolic rate determination. Each animal was weighed prior to being placed in the metabolism chamber. At the beginning of an experiment, incurrent air was sampled for at least 10 minutes. The excurrent airstream was then sampled continuously until the oxygen consumption, CO2 production, evaporative water loss, core temperature, and subdermal temperature were stable. After stable values were attained, incurrent air was then sampled again in order to check for machine drift. The animal was then removed from the animal chamber and weighed. On several occasions an animal failed to provide stable resting values for over

six hours. When this happened, the experiment was terminated and the order of trials was re-randomized for all temperatures remaining to have MR successfully determined. Stable values were eventually obtained for all animals at all temperatures during both night and day. Measurements for each animal were completed within one month of implantation.

Statistical and Computational Procedures

Minimal thermal conductance was calculated from a segmented regression of MR with ΔT ($\Delta T = T_c - T_a$), using the program SEGREG described in Appendix 3, Chapter 1 of this dissertation. MTC was estimated separately for each individual for both resting and active phases.

Statistical tests were based primarily on the procedures recommended by Lindman (1974). Data analysis was carried out using SPSS version 9.0 and BMDP-83 installed on a CDC Cyber 170/855. Most statistical analyses were performed with both packages to check for accidental misspecification of statistical procedures in the programs. Statistical analyses were performed as described in Chapter 1. Nonlinear regressions were performed with SAS installed on a Vax 11/785.

RESULTS

Body Temperature

A repeated measures ANOVA was used to analyze the effects of phase and ambient temperature on core temperature. Stable body core temperatures were significantly lower during resting phase (36.8 $\pm$0.2C) than active phase (37.2 C $\pm$0.3) ($p < 0.01$). (Throughout the results section, values are presented as the mean ($\pm$2 standard errors of the mean)). A linear trend analysis of the relationship between T_c and T_a, considering all T_a's from 0 to 35 ^{o}C, showed that this relationship was not statistically significant ($p > 0.25$).

The subdermal temperature was higher during the night than during the day. During both phases, a trend analysis indicated a significant relationship between the subdermal temperature and the ambient temperature. The estimated slope of this relationship was greater during the day than at night, but the difference between these slope values was not statistically significant ($p > 0.25$).

Evaporative Water Loss

Metabolic and evaporative heat loss parameters will be expressed throughout on a "per kilogram" live mass basis. The relationship between evaporative heat loss and T_a is shown for both active and resting phase in Figure 3.1. Average evaporative heat loss for all

temperatures was higher during the active phase than during the resting phase (0.62 ± 0.04 $W \cdot kg^{-1}$ as compared to 0.67 ± 0.02 $W \cdot kg^{-1}$). This difference is statistically significant ($p < 0.05$). Linear regression was performed for each phase on Q_{ev} as a function of T_a and Q_{ev} as a function of $(T_c - T_a)$ for $T_a \leq 25$ C (roughly, those ambient temperatures below the thermoneutral zone). In all cases, the linear regressions were statistically significant ($p \leq 0.01$). The slope of the relationship between Q_{ev} and T_a during resting phase was not statistically significantly different from the relationship for the active phase. Likewise, the slopes of the relationship between Q_{ev} and ΔT were not statistically significantly different between phases.

Metabolic Parameters

The relationship between phase, ΔT, and metabolic rate is shown in Figure 3.2. MTC, basal metabolic rate, and ΔT_{lc} were calculated for two measures of metabolic rate: the total metabolic rate, or the metabolic rate minus evaporative heat loss ("dry" metabolic rate). Examination of the data revealed that the MR measured at 32.5 ^{o}C and 35 ^{o}C was consistently higher than the MR at 30 ^{o}C. Thus, 32.5 ^{o}C was determined to lie above the thermoneutral zone and MR data for 32.5 ^{o}C and 35 ^{o}C were excluded from the data set used to simultaneously estimate MTC, ΔT_{lc}, and BMR. The data and

statistical analyses for BMR, ΔT_{lc}, and MTC are summarized in Table 3.1.

As discussed in Chapter 1 of this dissertation, the assumption that thermal conductance is constant for $\Delta T > \Delta T_{lc}$ can be tested by calculating MTC = $(M_1-M_2)/(\Delta T_1-\Delta T_2)$ for different temperature ranges. MTC calculated in this way for several temperature ranges (0-5 ^{o}C, 5-10 ^{o}C, 10-15 ^{o}C, 15-20 ^{o}C, and 20-22.5 ^{o}C) are shown in Table 3.2. A linear regression between MTC calculated in this manner and T_a was not statistically significant ($p > .50$).

Significance of Variation Among Individuals

The statistical significance of variation in MTC between individuals was tested by a repeated measures analysis of variance (MTC by phase and individuals). Variation between individuals was statistically significant ($p < 0.05$).

DISCUSSION

Body Temperature

The core temperature data reported in this paper represent the temperature at which the metabolic rate, evaporative water loss, and core temperature were simultaneously stable, that is, at steady state. There is clear diurnal variation in the core temperature. The diurnal variation reported here is very close to that predicted by the equation of Aschoff (1981b).

The core temperature at steady state is independent of the ambient temperature in N. floridana. This is unlike the situation in P. leucopus and M. auratus. Neotoma floridana is considerably larger than either of these two species, and the lack of a relationship between T_c and T_a is probably related to the large size of N. floridana. The larger body size of N. floridana should "decouple" it from its thermal environment (Gates 1980). That is, even if N. floridana were physiologically capable of T_c lability, such lability would appear less pronounced than it is in P. leucopus and M. auratus simply due to the larger size of N. floridana.

The subdermal temperature was higher during the active phase than during the resting phase. Also, during both phases, the subdermal temperature was significantly related to the ambient temperature. There was some indication of a greater relationship between subdermal

temperature and ambient temperature during the day than during the night. However, this was not statistically significant. Thus, while there may be differences in peripheral circulation between phases, it is not possible to make a definitive conclusion from these data.

Evaporative Water Loss

The evaporative heat loss amounted to 3% of the total metabolic heat load at 0 ^{o}C, 22% of the total metabolic heat load at 30 ^{o}C, and 41% of the metabolic heat production at 35 ^{o}C. These data agree well with those reported for the belding ground squirrel (Morhardt and Gates 1974), the black tailed prairie dog (Welch 1980) and the cotton rat (Scheck 1982). The fraction of total metabolism made up by evaporation at 32.5 and 35 ^{o}C is higher for N. floridana than for M. auratus, and somewhat less than that reported for P. leucopus (Chapters 1 and 2 of this dissertation). The N. floridana without exception had wet faces on removal from the metabolism chamber after metabolic rate determinations at 35 ^{o}C, and frequently had wet faces on removal after metabolic rate determinations at 32.5 ^{o}C. This differs from the situation in P. leucopus and M. auratus, where wet faces were observed only after metabolic rate determinations at 35 ^{o}C. These observations, along with the total metabolic rate being consistently greater for N. floridana at 32.5 and 35 ^{o}C than at 27.5 ^{o}C and 30 ^{o}C, suggests that the upper critical temperature for N.

floridana is between 30 and 32.5 °C, while the upper critical temperature is between 32.5 and 35 °C for P. leucopus and M. auratus.

Peters (1983) suggested that the upper critical temperature may decrease as body size increases. However, as stated by Peters, the data available on this point are too limited for testing of this hypothesis. While the data presented here are consistent with a decrease in the upper critical temperature in larger animals, evaluation of this hypothesis awaits data on upper critical temperatures of more species, and more precise determination of upper critical temperature than was attempted here. As in P. leucopus and M. auratus, evaporative heat loss was higher during the active phase than during the resting phase. As discussed in Chapters 1 and 2, this is consistent with the predictions of the model of evaporative water loss developed by Welch and Tracy (1977).

Evaporative water loss rates were linearly related to ΔT for both active and resting phase. However, the slopes for these two relationships were not statistically significantly different. Thus, while there is a significant linear trend between evaporative water loss and T_a, there is no apparent diurnal variation in the slope of the relationship.

Lower Critical Temperature Difference

The lower critical temperature difference (ΔT_{lc}) was

significantly lower for active phase than for resting phase. This is consistent with the results presented in Chapters 1 and 2 for P. leucopus and M. auratus. While the diurnal variation in BMR has not proven to be statistically significant, the active phase BMR was consistently higher than the resting phase BMR in P. leucopus, M. auratus, and N. floridana. Given this and the existence of only slight diurnal variation in MTC, one would expect diurnal variation in ΔT_{lc}. Since the basal rate is higher during active phase, the animal should be capable of supporting a larger temperature gradient without an increase in metabolism above basal levels during active phase than during resting phase.

Peters (1983) suggested that the lower critical temperature decreases as animal mass increases. Given little, if any, relationship between T_c and body mass (Peters 1983), this would predict an increase in the critical temperature difference (ΔT_{lc}) with body mass. In Chapter 1 ΔT_{lc} of P. leucopus was found to be 6.02 ^{o}C for resting phase and 10.45 ^{o}C for the active phase. In Chapter 2, ΔT_{lc} of M. auratus was found to be 9.23 ^{o}C for resting phase and 10.86 ^{o}C for active phase. ΔT_{lc} was found to be 10.40 ^{o}C for resting phase and 12.42 ^{o}C for active phase in N. floridana. So, the data presented in this dissertation are consistent with the notion that ΔT_{lc} increases with body mass.

Wet vs. Dry Thermal Conductance

The theoretical derivation of wet thermal conductance requires the assumption that evaporative heat loss be adequately described by a linear function of ΔT (Chapter 1). Examination of Figure 3.1 shows that in the present study evaporative heat loss is reasonably well approximated by a linear function for $\Delta T > \Delta T_{lc}$. The deviations from linearity amount less than the average standard deviation of MR at any temperature below 25 ^{o}C. The deviations from linearity are less than the natural variation in metabolic rate. So as a first approximation, at least, evaporative heat loss may be assumed to be a linear function of ΔT.

The data presented in this Chapter for N. floridana, along with the data presented in Chapters 1 and 2 for P. leucopus and M. auratus supports the use of a linear approximation of the relationship between ambient temperature and evaporative heat loss when the air entering the metabolism chamber has been thoroughly dried with a desiccant. Data available in the literature also supports the use of this approximation. Examination of the data presented in Welch and Tracy (1977) and Welch (1980) suggests that this approximation is valid when the incurrent dewpoint is less than -10 ^{o}C.

Despite the consistent results that evaporative heat loss may adequately be described as a linear function of the ambient

temperature, the validity of this approximation (and thus the use of "wet" MTC) is a subject that needs further investigation. The biophysical validity of "wet" thermal conductance depends on the use of this approximation. When it is not possible to adequately describe evaporative heat loss as a linear function of T_a it becomes impossible to define a single value of "wet" MTC. This, plus consideration of the uses made of MTC in comparative studies, suggest that dry MTC may be a more generally useful parameter for comparative studies. In particular, comparative studies are often concerned with evolutionary or physiological responses to variation in the costs and benefits of reducing heat loss to the environment at low ambient temperatures (Brown and Lee 1969; McNab 1978, 1980; Hill 1983). Variation in dry MTC may well reflect evolutionary differences between species in the cost/benefit ratio of decreasing heat loss to the environment (McNab 1980). Wet MTC may also reflect these differences. However, evaporative heat loss is largely determined by morphological requirements for respiratory gas exchange (Welch and Tracy 1977) rather than by the advantages of energy conservation at low ambient temperatures. Thus, a comparison of the wet MTC of different groups of animals may be influenced by differences between groups in lung morphology and gas exchange capabilities rather than factors directly related to the minimal rate of heat loss at low T_a's. Comparisons based on dry MTC should reflect more directly

evolutionary or physiological responses to the evolutionary costs and benefits of reducing heat loss at low ambient temperatures.

Minimal Thermal Conductance

The allometric equation presented by Aschoff (1981a) predicts for a 470 g mammal (the average mass of the N. floridana used in this study) a wet MTC value of 0.224 $W \cdot {}^{o}C^{-1} \cdot Kg^{-1}$ for the resting phase and 0.286 $W \cdot {}^{o}C^{-1} \cdot Kg^{-1}$ for the active phase. The equation of Bradley and Deavers (1980), which is not separated by phase, produces an estimate of 0.227 $W \cdot {}^{o}C^{-1} \cdot Kg^{-1}$. The average wet MTC for N. floridana in this study was 0.214 $W \cdot {}^{o}C^{-1} \cdot Kg^{-1}$ for the resting phase, and 0.247 $W \cdot {}^{o}C^{-1} \cdot Kg^{-1}$ for the active phase. These values lie within the range of values found by Brown and Lee (1969) for several different species of woodrats (N. cinerea, N. albigula, N. lepida, and N. fuscipes). The amount of diurnal variation found in the present study is markedly less than the amount predicted from Aschoff's (1981a) equations. The diurnal variation found amounted to 0.03 $W \cdot {}^{o}C^{-1} \cdot Kg^{-1}$, as compared to a predicted variation of 0.06 $W \cdot {}^{o}C^{-1} \cdot Kg^{-1}$. As discussed in Chapters 1 and 2, the data set used by Aschoff to generate these equations was biased in several ways. There is clearly diurnal variation in thermal conductance of N. floridana, M. auratus, as in P. leucopus. However, in all three species, the diurnal variation found is much lower than the amount predicted from

Aschoff's (1981a) equations. It seems that the tremendous amount of diurnal variation in MTC of mammals suggested by Aschoff's analysis is largely due to biases in the MTC data available in the literature, and that there is less diurnal variation for animals of a broad range of sizes (20 to 500 g) than suggested by Aschoff's (1981a) analysis of the data available in the literature.

Three possible causes for diurnal variation were mentioned in Chapter 2 of this dissertation: diurnal variation in peripheral vasoconstriction; diurnal variation in piloerection; and subtle differences in how still the animals were when maintaining apparently stable metabolic rates. Diurnal variation in peripheral vasoconstriction should result in a greater slope in the relationship between subdermal temperature and T_a during resting phase than during active phase. The data collected in this study for N. floridana indicate that the subdermal temperature has a slightly stronger relationship with T_a during resting phase than during active phase (but this difference is not statistically significant). However, given the fact that the thermistor probes were implanted in direct contact with both the outer surface of the body core and the inner surface of the dermis, the existence of any difference between phases at all is notable. The existence of a difference in this relationship between phases is further evidence of diurnal variation of the thermal exchange properties of small mammals. In particular,

this seems to indicate that there is some diurnal variation in the thermal transfer within the body. However, diurnal variation in piloerection or animal behavior could contribute to the existence of diurnal variation in MTC.

Diurnal variation in internal conductance, due to differences in peripheral circulation, seems a more likely mechanism for generating diurnal variation in MTC than diurnal variation in piloerection. It seems that an animal exposed to an environmental temperature of 5 ^{o}C should do everything possible to minimize its heat loss. It is difficult to imagine a constraint that prevents a mammal during the active phase from erecting its fur as fully as during the resting phase. In contrast, there might well be a requirement for greater peripheral circulation during the active phase than during the resting phase, because of a greater demand for oxygen in peripheral tissues. Understanding the causes of diurnal variation in MTC will require further investigation. Further experiments will likely involving direct measurement of physiological parameters such as peripheral circulation as well as the degree of piloerection.

Relationship between Mass, Phase, and Minimal Thermal Conductance

It is possible, based on the data presented in Chapters 1, 2, and 3, to calculate a set of allometric relationships between MTC and

mass for each phase of the activity cycle, similar to the regression calculated by Aschoff (1981a). The results of the nonlinear regression are shown in Figure 3.4. The regressions presented in Aschoff (1981a) are also shown for comparison. The slopes of the relationships calculated using data only from this dissertation are similar to the slopes calculated by Aschoff (1981a). However, the intercepts are considerably closer together than in Aschoff's relationships. The relationships calculated by Aschoff (1981a) predict diurnal variation in MTC that amounts to 40% of the 24-hour mean. The regression lines calculated here predict diurnal variation amounting to approximately 14% of the 24-hour mean.

The current data, which were collected with particular care to allow valid comparisons between phases, result in the appearance of markedly less diurnal variation in MTC than the analysis of Aschoff (1981a) using data gleaned from the published literature. In further studies of diurnal variation in MTC of small mammals care should be taken to measure MTC for both phases of the activity cycle, with the amount of diurnal variation in MTC calculated by direct measurement, rather than by combination of data from one phase of the activity cycle with data already available in the literature. Measurement of MTC for one phase of the activity cycle, and subsequent determination of diurnal variation in MTC by comparison with data in the literature could lead to other factors (such as differences in methodology,

differences in the conditions under which the animals were held, or differences between populations of a given species) interfering with and biasing the comparison between different phases of the activity cycle.

In P. leucopus, M. auratus, and N. floridana there is statistically significant variation between individuals. The existence of variation between individuals has a profound effect on the way MTC should be viewed. MTC is fundamentally a property of an individual organism. Therefore, MTC should be determined for individual animals, and mean MTC values for different species should be calculated by averaging these individual values. Pooling of metabolic rate data from several individuals and subsequent calculation of MTC from a regression using the pooled data can lead to several problems, including: 1) calculation of incorrect values of MTC; 2) underestimation or overestimation of the confidence limits around the MTC; 3) incorrect conclusions in statistical tests of differences between individuals (Box et al. 1978).

Demonstration of individual variation in MTC is a critical part of any demonstration of adaptive variation in MTC. Two critical parts of such a demonstration remain unverified, however: 1) demonstration of heritability of MTC; 2) demonstration of a relationship between variation in MTC and variation in fitness in the wild. A variety of studies have considered variation in MTC between

species or populations to represent adaptive variation (e.g. Brown and Lee 1969). And, while it seems relatively easy to accept that variation in MTC ought to be heritable, there has yet to be published a convincing demonstration that MTC is related in to the fitness of mammals in the wild. Verification of a relationship between variation in MTC and variation in some measure of fitness is essential to use of MTC in studies of adaptation.

CONCLUSIONS

There is clear diurnal variation in stable T_c of N. floridana. There is no apparent variation between stable T_c and ambient temperature. This contrasts with the situation in P. leucopus and M. auratus, and is probably related to the larger thermal inertia of N. floridana caused by its considerably larger body mass.

There is diurnal variation in the evaporative water loss rates of N. floridana. During both phases, evaporative water loss seems adequately described by a linear function of either T_c or ΔT, and the slopes for active and resting phases are approximately the same. While the use of a linear approximation to the relationship between ΔT and evaporative heat loss seems justified as a first approximation, the validity of the theoretical development of wet MTC depends upon the validity of this approximation. Data on evaporative heat loss at low ambient temperatures that allows nonlinearities in the relationship to be distinguished from sampling error is needed to determine how valid the linear approximation is.

In general, dry MTC may be a better parameter for use in comparative studies than wet MTC for two reasons: 1) the use of the use of dry MTC is not affected by the accuracy of the approximation of evaporative heat loss as a linear function of ΔT; 2) dry MTC reflects the heat exchange properties of small mammals, while wet MTC

reflects these properties as well as gas exchange properties which on an evolutionary or ecological level may respond to requirements on respiratory gas exchange capabilities rather than the costs and benefits of minimizing heat loss at low temperatures. Dry MTC, then, represents a parameter that is a more precise indicator of the animal's thermal properties per se, rather than reflecting thermal properties as well as constraints on respiratory gas exchange capabilities. Also, conditions that would vitiate the use of wet MTC (significant nonlinearities in the relationship between Q_{ev} and ΔT) do not affect the validity of the use of dry MTC.

There is diurnal variation in MTC of N. floridana, but like the situation for P. leucopus and M. auratus, the diurnal variation is much slighter than that predicted by Aschoff's (1981) equations. This seems largely due to bias in the data available in the literature regarding MTC of mammals. Allometric equations relating MTC to body mass were calculated for active and resting phases using the data presented in this dissertation for P. leucopus, M. auratus, and N. floridana. The slopes of these relationships were similar to the slopes calculated by Aschoff (1981a), but the intercepts were considerably closer together than in Aschoff's equations. The equations presented here predict diurnal variation of approximately 14% of the 24-hour mean, while Aschoff's (1981a) equations predict diurnal variation of approximately 40% of the 24-hour mean. Further

studies of diurnal variation in MTC should directly determine MTC for both phases, rather than determine MTC for one phase and rely on comparisons with data available in the literature. Comparison with data on one phase of the activity cycle with data presented in the literature could result in biasing the comparison due to differences in methodology, differences in the conditions under which test animals are held or differences between populations of one species.

Diurnal variation in peripheral vasoconstriction should result in greater variation between subdermal temperature and ambient temperature during the resting phase than during the active phase. While the data presented here show such a difference, the difference was not statistically significant. Further studies of the mechanistic basis for diurnal variation in MTC should involve further study of peripheral vasoconstriction. Investigation of diurnal variation in fur piloerection and subtle behavioral differences between phases also merit study. Diurnal variation in peripheral vasoconstriction seems the most logical candidate for causing diurnal variation in MTC, but alternate causes should also be investigated carefully.

Minimal thermal conductance should be recognized as a property of individuals. Failure to treat MTC properly as an individual property can result in errors in both calculated values of MTC and the results of statistical comparisons of MTC of different groups of animals. A

profound need in use of MTC in studies of adaptive variation is a demonstration of a relationship between variation in MTC and variation in a mammal's fitness in the wild.

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Table 3.1. Statistical analysis of BMR, ΔT_{lc}, and MTC of Neotoma floridana. Diurnal variation in BMR and MTC was tested by one-tailed paired t-tests; diurnal variation in ΔT_{lc} was tested by two-tailed paired t-tests.

	Active Phase	Resting Phase	p
Dry BMR ($M\text{-}Q_{ev}$)	0.3192(±0.058)	0.3007(±0.051)	ns
BMR	0.3915(±0.037)	0.3219(±0.042)	ns
MTC_d	0.232(±0.029)	0.204(±.013)	0.05
MTC_w	0.227(±0.035)	0.198(±0.011)	0.05
ΔT_{lc} (for relationship between $M\text{-}Q_{ev}$ and ΔT)	13.21 (±0.91)	10.97 (±0.84)	0.05
ΔT_{lc} (for relationship between M and ΔT)	12.92 (±1.05)	10.40 (±0.97)	0.05

Table 3.2. Relationship of T_a with Wet and Dry MTC as calculated from $(Metabolism_1 - Metabolism_2)/[(T_{c1}^a - T_{a1}) - (T_{c2} - T_{a2})]$. (Units are $W \cdot {}^{o}C^{-1} \cdot Kg^{-1}$).

	Phase	Ambient Temperature (T_a)			
		0.0	5.0	10.0	15.0
"Wet" MTC	rest.	0.201(±0.281)	0.227(±0.247)	0.174(±0.292)	0.207(±0.158)
	act.	0.241(±0.348)	0.238(±0.214)	0.230(±0.220)	0.272(±0.179)
"Dry" MTC	rest.	0.195(±0.168)	0.236(±0.251)	0.204(±0.283)	0.245(±0.182)
	act.	0.260(±0.295)	0.275(±0.207)	0.259(±0.183)	0.281(±0.286)

Figure 3.1. Relationship between evaporative heat loss (Q_{ev}) and ambient temperature (T_a) for Neotoma floridana. Horizontal lines represent mean Q_{ev} for 10 adult male N. floridana. Vertical bars indicate ± 2 SE. Vertical lines indicate ranges. Open boxes represent resting phase (daytime). Closed boxes represent active phase (nighttime)

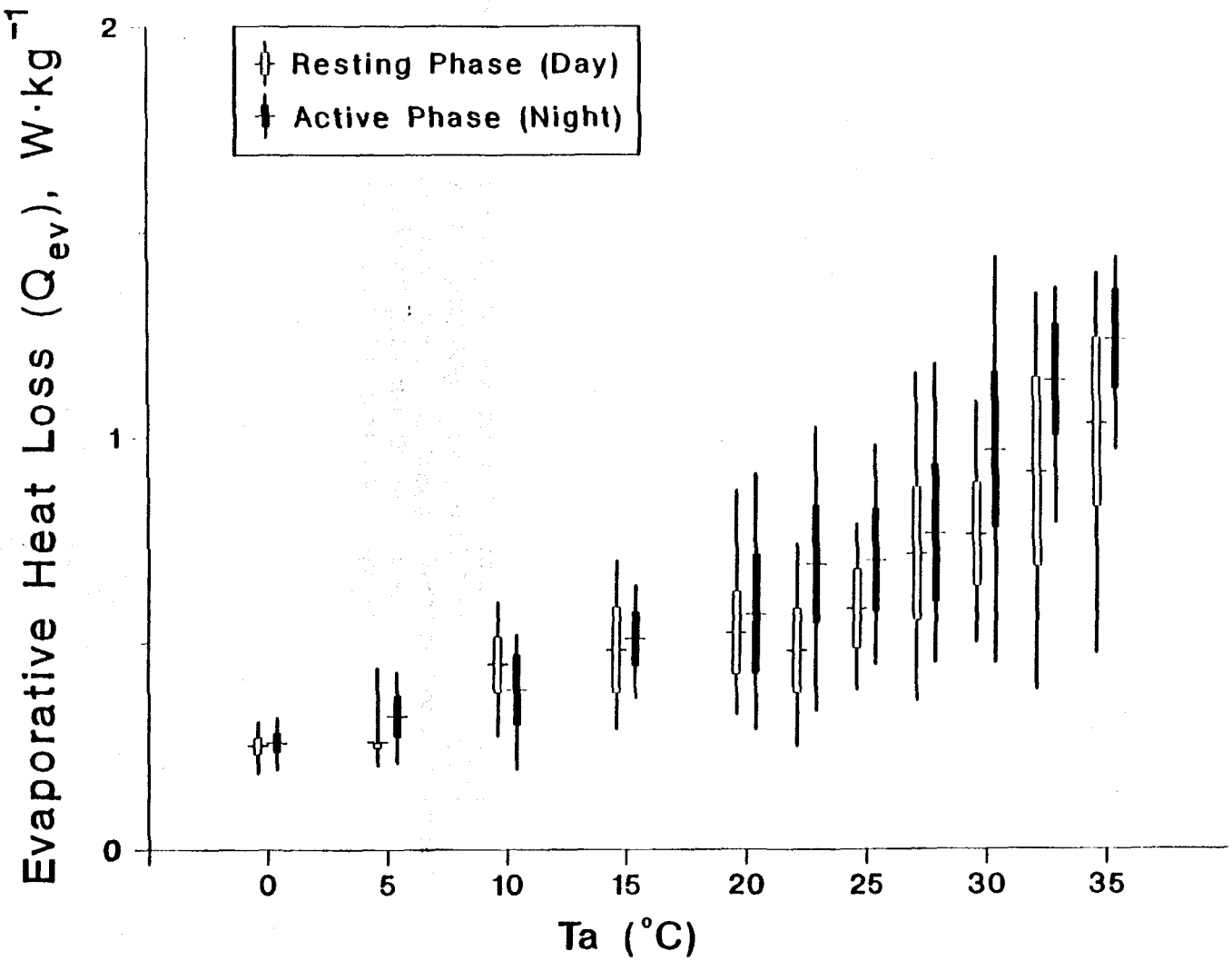

Resting Phase (Day)
Active Phase (Night)
Evaporative Heat Loss (Q_{ev}), $W \cdot kg^{-1}$
2
1
0
0
5
10
15
20
25
30
35
Ta (°C)

Figure 3.2. Relationship between metabolic rate ($M\text{-}Q_{ev}$) and ambient temperature for N. floridana. Horizontal lines represent mean ($M\text{-}Q_{ev}$) for 10 adult male N. floridana. Vertical bars indicate ± 2 SE. Vertical lines indicate ranges. Open boxes represent resting phase (daytime). Closed boxes represent active phase (nighttime)

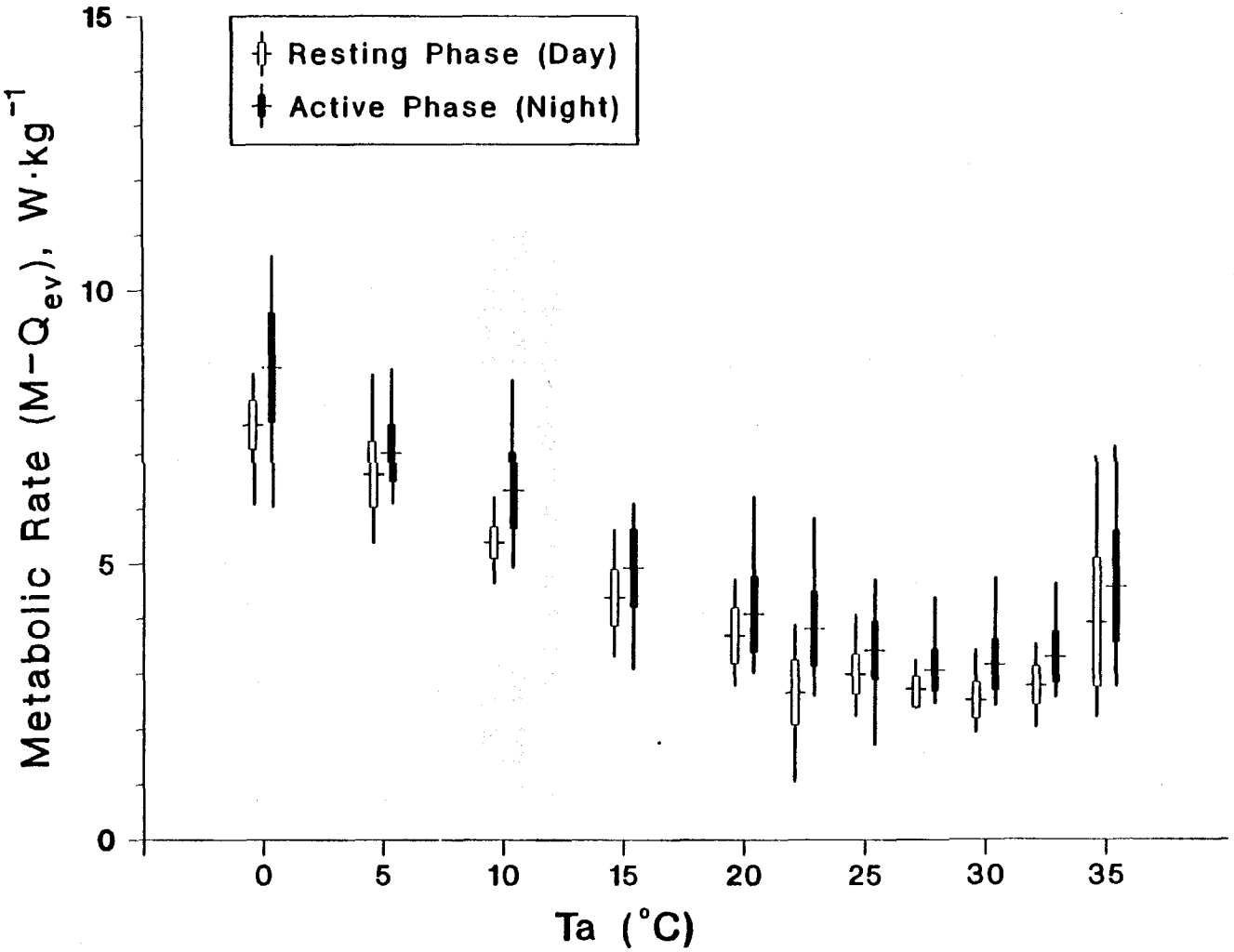
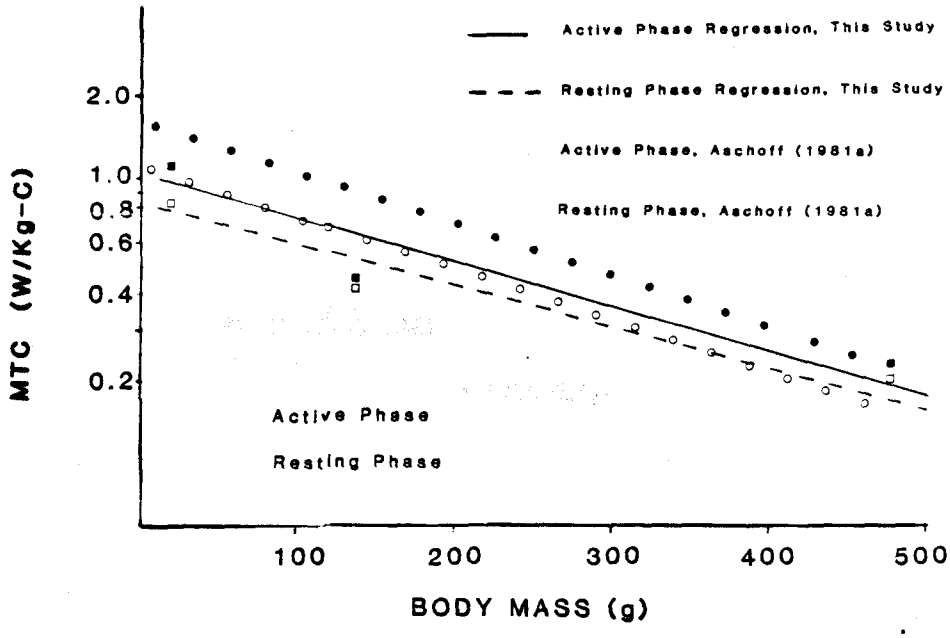

Resting Phase (Day)
Active Phase (Night)
Metabolic Rate (M−Qev), W·kg−1
15
10
5
0
0
5
10
15
20
25
30
35
Ta (°C)

Figure 3.3. Allometric relationships between body mass and MTC. Shown are relationships calculated from data in Chapters 1-3, as well as the relationships calculated by Aschoff (1981a).


Active Phase Regression, This Study
Resting Phase Regression, This Study
Active Phase, Aschoff (1981a)
Resting Phase, Aschoff (1981a)
MTC (W/Kg-C)
2.0
1.0
0.8
0.6
0.4
0.2
Active Phase
Resting Phase
100
200
300
400
500
BODY MASS (g)

CONVECTIVE HEAT LOSS AND AIR VELOCITY IN LABORATORY METABOLISM CHAMBERS

ABSTRACT

Many factors influence the measured metabolic rate of animals in laboratory metabolism chambers, including the emissivity of the chamber walls, humidity, and the convective regime inside the chamber. Convective heat loss is thought to be primarily by free (rather than forced) convection from the animal in the types of chambers typically used for metabolic rate determination. This has not been verified experimentally. The purpose of this study is to determine whether free or forced convection predominates in such metabolism chambers.

Thermal conductance was determined from cooling curves of Mus musculus carcasses in a metabolism chamber typical of those used for determining metabolic rate. Cooling curves were determined for four air flow rates: still air, 0.1 $L \cdot min^{-1}$ STP, 0.4 $L \cdot min^{-1}$ STP, and 0.9 $L \cdot min^{-1}$ STP. Thermal conductance was estimated from the cooling curves. There was no relationship between thermal conductance and the air flow rate, indicating that free convection predominates over forced convection over the range of air flows used in this study. Comparison of Grashof and Reynold's numbers also suggested that the free convection should predominate.

It has been argued that metabolic rates should be measured under forced convection conditions. However, a metabolism chamber in which free convection predominates is more appropriate for metabolic rate measurements used to determine minimal thermal conductance (MTC). No single set of experimental conditions will be appropriate for all experimental investigations. Forced convection conditions are required for investigation of the effect of wind penetrance on fur insulation. Free convection conditions are most appropriate for determination of MTC.

INTRODUCTION

Metabolic rate, oxygen consumption, and other metabolic parameters of small mammals are commonly determined from changes in the composition of a gas mixture passed through a chamber containing a test animal. This technique has been discussed by several authors, including Depocas and Hart (1957), Morrison and West (1975) and Randolph and Rau (1977). Several properties of the metabolism chamber itself are known to affect the measured metabolic rate including the emissivity of the chamber walls (Porter 1969); the ambient humidity inside the chamber (Welch 1980); and the convective regime inside the chamber (Neal 1976; Robinson et al. 1976; Hayes and Gessaman 1982).

When free convection predominates over forced convection the rate of convective heat loss depends primarily on the temperature difference between the animal and its environment (Bakken 1976a). When forced convection predominates, convective heat loss is greater than under free convection conditions, and convective heat loss depends on both the temperature difference and the airstream velocity. (Bakken and Gates 1975; Kreith 1976; Robinson et al. 1976).

Airstream velocity can be used as a rough guide to the relative importance of free and forced convection (Gates 1980). The relative

importance of free and forced convection can be estimated more accurately from the comparison of two dimensionless groups, the Reynold's number (Re) and the Grashof number (Gr) (Kreith 1976). The ratio of Gr/Re^2 is an indicator of the convective regime. This ratio measures the relative importance of heat loss from a warm object via buoyant air movement (due to air warming) to heat loss via air blown past the object. Forced convection is negligible in comparison to free convection when Gr/Re^2 is much greater than 1 (Kreith 1976; Avicros 1958).

Bakken (1976a) stated that free convection conditions prevail in metabolism chambers typically used in laboratory measurements of metabolic rate. However, there has been no experimental verification of this. The purposes of this study are to determine whether free or forced convection predominates in a metabolism chamber, using a chamber and flow rates similar to those typically used in laboratory measurement of metabolic rate, and compare the results of experimental determination of the predominant mode of convective heat loss with predictions based on comparison of Gr and Re. The importance of forced convection is determined experimentally from measurement of thermal conductance over a range of airflow velocities. If free convection predominates over a range of airflow velocities, then thermal conductance should be invariant with respect to air velocity. Significant forced convection results in an

increase in the convective heat loss coefficient with air velocity. This would increase the overall thermal conductance. Thus, the existence of significant forced convection should be reflected in an increase in thermal conductance with airstream velocity.

METHODS AND MATERIALS

The transition between free and forced convection occurs at an air velocity that depends in part on the size of the object losing heat (Kreith 1976). The smaller the animal, the lower the airstream velocity at which forced convection is important relative to free convection (Gates 1980). For this reason, a small mammal was chosen for this study: a black strain of the laboratory mouse (Mus musculus). (The average body mass of the mice used in this experiment was 30.3 gm; SE = 0.84 gm).

The chamber and flow rates used in this experiment are fairly typical of those used in studies of small mammal metabolism (cf. Hill 1975; Depocas and Hart 1957; Morrison and West 1975). The metabolism chamber used was made of acrylic pipe with an inside diameter of 11.5 cm and an inside height of 17 cm. A diagram of the chamber is shown in Figure 4.1. Air was delivered into the chamber with a copper tube. The test mouse was placed on an acrylic plate 1/4" thick with 1/4" diameter holes spaced on a 3/4" grid. This plate was held 4.5 cm above the bottom of the chamber. An identical grid was held 4.5 cm below the top of the chamber. The upper grid was built into the metabolism chamber so that during measurements of metabolic rate the gas leaving the chamber would be well mixed.

Thermal conductance was determined from carcass cooling curves

on a total of 40 Mus musculus. The mice were killed by CO2 inhalation. Cooling rates were determined immediately after killing the animal. A thermocouple was inserted through the rectum approximately 2.5 cm. into the abdominal cavity of the freshly killed mouse. The thermocouple was secured by taping it to the animal's tail. The animal was then placed in a metabolism chamber and positioned in the "curled-up" position typical of small mammals at rest in a cold environment. Fur was fluffed as much as possible by gently blowing air against the grain of the fur.

The metabolism chamber containing the mouse was placed in an ice-water bath. Air entering the chamber was dried in a Drierite column. The dried air then passed through a copper coil submerged in the ice-water bath, so that air entering the chamber was at the same temperature as the walls of the chamber (0 ^{o}C). The core temperature at the start of the experiments averaged 29.4 (SE = 1.2) ^{o}C. Cooling rate determinations were finished when the animal reached a core temperature of slightly under 10 ^{o}C. Cooling curves were determined for the following flow rates: still air; 0.1 L$\cdot$min^{-1} (STP); 0.4 L$\cdot$min^{-1}; and 0.9 L$\cdot$min^{-1}. Ten mice were used per flow rate (total of 40 mice). The flow rate used for each mouse was randomly assigned.

The cooling curves were analyzed with a version of Bakken's (1976b) program Newton II converted to run under Fortran V on a CDC Cyber 170/855 computer. Statistical analyses were done with BMDP

(University of California, Los Angeles, CA) run on a CDC Cyber 170/855.

RESULTS

The results of this experiment are summarized in Table 4.1. Neither an overall analysis of variance nor a trend analysis (Lindman, 1974) showed a significant effect of flow rate on thermal conductance (ANOVA, $F=2.7101$, $p=0.06$; Trend analysis, $F=2.889$, $p=0.09$). The overall mean thermal conductance was 1.094 $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$. The average equilibrium temperature calculated by Newton II was 0.182 ^{o}C (SE=0.082).

Average air velocities through the metabolism chamber were calculated by assuming laminar air flow with a constant flow profile through the chamber. Laminar airflow through the chamber was verified by passing smoke through the chamber ("smoke visualization"; Rae and Pope 1984). Reynold's and Grashof numbers were calculated using the velocities shown and treating the animals as a sphere with a radius of 0.02 m assuming a ΔT of 20 ^{o}C. The radius of a 30 gram mouse in a curled up posture is approximately 0.02 m. A ΔT of 20 ^{o}C falls in the middle of the range of body core temperatures encountered during the cooling rate determinations. The calculated Grashof number was several orders of magnitude greater than the square of the calculated Reynold's number for all flow rates.

DISCUSSION

Kreith (1976) shows that the relative magnitude of Reynold's and Grashof numbers can be used to determine whether free or forced convection predominates in a given situation. When Gr is much greater than Re^2, free convection predominates. The Grashof numbers shown in Table 4.1 are much greater than the respective Re^2 for all flow rates used in this study. This suggests that convective heat loss should be primarily via free convection. Gates (1980) also states that for small animals the airstream velocity may be used as a rough index of the relative importance of forced and free convection. Free convection should predominate when the airstream velocity is less than 0.1 $m \cdot s^{-1}$; the airstream velocities shown in Table 4.1 are all less than 0.002 $m \cdot s^{-1}$. The flow velocities shown in Table 4.1 were calculated from the average flow. The maximum flow rate of a laminar airstream flowing through a pipe is twice the average flow (Vogel 1981). However, the calculated airstream velocities are two orders of magnitude less than the velocity required for the Gr/Re^2 ratio to suggest significant forced convection.

The overall mean thermal conductance found for Mus musculus ($1.094\ W \cdot {}^{o}C^{-1} \cdot kg^{-1}$) is in good agreement with the value of 0.998 $W \cdot {}^{o}C^{-1} \cdot kg^{-1}$ estimated from the allometric equations presented by Peters (1983) (estimate based on a body mass of 30 g). The

calculated values of thermal conductance do not vary in any consistent manner with the air flow rate (Table 4.1).

Convective heat loss under the conditions of the measurements presented here is primarily via free convection, or else there would have been noticeable variation in the total thermal conductance with the air flow rate. This result does not contradict the results of other studies (e.g. Heller 1972; Neal 1976) that found variation in convection coefficients with air flow rates. At low flow velocities, free convection predominates, while at higher flow rates forced convection predominates and the convection coefficient varies with flow rate. The highest airstream velocity used in this study was approximately 0.0015 $m \cdot s^{-1}$. In contrast Heller (1972), in a study of convective heat loss from metal replicas of chipmunks, used air velocities as high as 0.23 $m \cdot s^{-1}$ Neal (1976), in a study of the effect of air velocity on metabolism of the eastern chipmunk (Tamias striatus), used flow rates as high as 4.17 $m \cdot s^{-1}$. Likewise Mitchell (1985) used flow rates ranging from 0.3 to 1 $m \cdot s^{-1}$ in a study of forced convective heat loss from domestic fowl. Thus, the airstream velocities used by Heller (1972), Neal (1976), and Mitchell (1985) were much higher than the air velocities used in this study. These airstream velocities are also higher than is typically used in metabolic rate determinations used for laboratory measurement of metabolic rate (cf. Morrison and West 1975).

Measurements of metabolic rate at low ambient temperature are often used in comparative studies. Such studies may involve estimation of minimal thermal conductance (MTC), a parameter frequently used in comparisons of thermal properties of small mammals (McNab 1980). Bakken (1976a) argues that metabolism measurements should be made under forced convection conditions, because under free convection conditions the fur insulation is " ... determined mainly by its thickness, and not its quality. Appreciable wind in the chamber allows the effect of penetration of wind into the pelage ... to be studied." However, there are significant concerns with use of forced convection conditions in metabolism chambers. Three problems are particularly significant when measurements of metabolic rate are used in estimation of MTC. These problems are listed below.

1) The physical requirements for constructing metabolism chambers having a repeatable forced convection regime are very stringent. In general, production of repeatable forced convection regimes requires the use of large metabolism chambers (Bakken 1976a). Large chambers have a strong buffering effect on variations in the composition of the gas in the metabolism chamber. This buffering may cause the metabolic rate to appear constant in spite of real fluctuations. The measured metabolic rate may also fail to reach stable minimal rates. This is because such rates

may not be maintained long enough for the composition of the excurrent gas mixture to stabilize at the appropriate values.

2) For small mammals, particularly rodents, stable minimal metabolic rates (at low ambient temperatures) are generally reached when the test animal is sitting in a curled up posture (personal observation). The natural situation most closely mimicked by this posture is that of an animal sitting in a burrow or sitting still in a protected area. Free convection is likely to predominate in such a circumstance (Gates 1980).

3) Measurements of thermal conductance are generally made for comparative purposes. Minimal thermal conductance is generally chosen as a standard for comparison. As McNab (1980) states "...it is of little interest to compare the minimal conductance of one species with an intermediate ... conductance of another." Forced convection results in greater heat loss than occurs in free convection. Thermal conductance measured in conditions of significant forced convection would be greater than that measured under free convection. Thus, minimal thermal conductance occurs under conditions of free convection.

Bakken (1976a) argued that forced convection should be

encouraged to enhance heat transfer between the walls of the chamber and the air, thus minimizing differences between air and wall temperatures. This may be a concern in closed wind tunnel systems. However, a metabolism chamber design such as that shown in Figure 4.1 (with a copper air cooling coil immersed the same water bath as the chamber itself) provides an airstream that enters the chamber at the same temperature as the walls of the chamber. The average equilibrium temperature estimated for the mice (by Newton II) in this experiment was 0.18 ^{o}C. This indicates that the effective blackbody temperature inside the metabolism chamber really is very close to 0 ^{o}C.

A further concern mentioned by Bakken (1976a) is the "elusive" nature of free convection. Stray air currents will alter convective heat loss and result in some scatter in measurements made under free convection conditions. However, careful construction of metabolism chambers should result in acceptable repeatability of measurements. The thermal conductance measures obtained in this study seem quite consistent. Furthermore, even while forced convection conditions may offer better repeatability than free convection conditions (Bakken 1976a), use of forced convection conditions creates problems in standardization for comparative purposes. Should a single, constant airstream velocity be used, or should the "standard" velocity be scaled to body size? Free convection conditions offer the advantage

of a well-defined standard condition. This important advantage seems to outweigh slight technical concerns regarding repeatability of measurements.

Many studies of minimal thermal conductance have used metabolism chambers in which free convection should predominate over forced convection (Bakken 1976a). The established use of free convective regimes, along with the points listed above, argues for use of metabolism chambers in which free convection predominates for studies of minimal thermal conductance.

CONCLUSION

This study investigated the convective heat loss from small mammals in a metabolism chamber typical of those commonly used for laboratory measurement of metabolic rate. The results of the cooling curve experiments indicated that, at the flow rates used, convective heat loss is primarily by free convection. This agreed with predictions based on the relative magnitude of Gr and Re. Investigators may not want to perform a large number of cooling curve experiments to determine the convective regime in a metabolism chamber. However, calculation of Gr and Re will allow estimation of the relative importance of free and forced convection.

Bakken (1976a) argued that fur "quality" was better determined under forced convection conditions than free convection conditions. However, fur quality, rather than being treated as a unidimensional parameter, should have several dimensions including insulative quality under free convection conditions, resistance to wind penetrance (Bakken 1976a), and resistance to wetting (Webb and King 1984). A clear need in the study of animal heat exchange is a basic understanding of the biologically important dimensions of fur properties.

The appropriate measurement conditions for investigating fur insulation cannot be determined by any hard and fast rule. Rather,

experimental conditions should reflect the nature of the questions being investigated. Studies of the effects of wind on the metabolism of animals (such as Morhardt and Gates 1974; Robinson et al. 1976; Hayes and Gessaman 1982) obviously require the use of forced convection conditions. Investigation of minimal thermal conductance is most appropriately performed with an environment where free convection predominates over forced convection.

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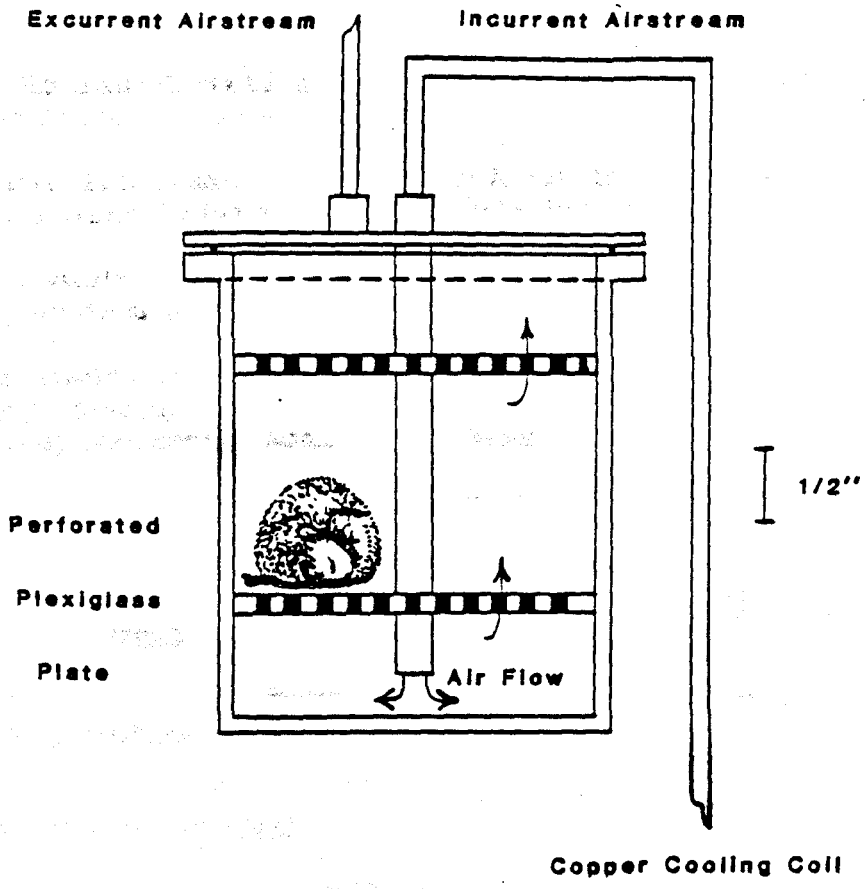
Table 4.1. Flow rates, air velocities, Reynold's numbers, Grashof numbers, and average values of thermal conductance, presented as mean (± 2 standard errors).

Flow rate ($L \cdot min^{-1}$ STP)	Air Velocity ($m \cdot s^{-1}$)	Re	Gr	Thermal Conductance ($W \cdot {}^{o}C^{-1} \cdot kg^{-1}$)
0	0	0	24640	1.060 (±0.049)
0.1	0.000160	0.2108	24640	1.051 (±0.078)
0.4	0.000641	0.8434	24640	1.168 (±0.054)
0.9	0.001442	1.8974	24640	1.096 (±0.057)

Figure 4.1. Diagram of the metabolism chamber used in cooling curve experiments. The entire chamber was submerged in an ice/water bath. Test subjects rested on the bottom plexiglass plate.


Excurrent Airstream
Incurrent Airstream
1/2"
Perforated
Plexiglass
Plate
Air Flow
Copper Cooling Coil

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Indiana University Doctoral Student Grant-In-Aid of Research ($400.), for the project, "Geographic variation in adaptation to winter in the White-footed mouse (Peromyscus leucopus)." 1984.

Indiana University Breckenridge Fellowship ($500), for the project "Diurnal variation in minimal thermal conductance of the White-footed mouse (Peromyscus leucopus)." 1984.

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