# Evaporative water loss: thermoregulatory requirements and measurements in the deer mouse and white rabbit

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**Summary.** Using a physical model of the capacity for non-evaporative heat loss and measurements of metabolic heat production, I evaluated the evaporative requirements for thermoregulation in the deer mouse, *Peromyscus maniculatus*, and the white rabbit, *Oryctolagus cuniculus*. The physical limit to non-evaporative heat loss was calculated from the heat transfer properties of the two animals and expressed as a maximum thermal conductance ($C_{max}$). Two physiologically-based thermal conductances were derived from evaporative water loss, respiratory gas exchange and core temperature measurements made between 8 and 34 °C on the deer mouse, and taken from published data for the white rabbit. The thermal conductance for non-evaporative heat loss ($C$) was calculated from net heat production, whereas $C_m$ represented the thermal conductance required to dissipate metabolic heat production. Evaporation is required when metabolic heat production exceeds the capacity for non-evaporative heat loss (as shown by $C_m > C_{max}$). However, evaporation increased in both animals although additional capacity to lose heat remained (i.e., $C < C_{max}$). Evaporation increased with $C$ above 30 °C for the mouse and at each 5 °C measurement interval from 15 to 30 °C for the rabbit. Thus, evaporation was greater than that required for thermoregulation for both animals as determined from a physical model of heat loss because both evaporation and $C$ increased together to regulate heat loss.

## Introduction

To thermoregulate under hot conditions or during exercise, endotherms must often supplement non-

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*Symbols:* see list on title page of preceeding paper

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evaporative heat loss with evaporation (Dawson 1982; Hales 1974). Delivery of heat by blood flow to the skin of peripheral, poorly insulated areas increases thermal conductance, thereby enhancing non-evaporative heat loss (Conley and Porter 1985; Thauer 1964). But a limit exists to these conductance changes for which evaporation provides an efficacious, alternative avenue for dissipating excess heat production (McLean 1974).

The relative reliance on evaporation is often related to the ability to lose heat non-evaporatively (McLean 1974). For example, with increasing body size, the relative ability for non-evaporative heat loss decreases due to a decreased ratio of surface area to heat production and increased evaporation is required for thermoregulation (Taylor 1977; Weathers 1981). Beyond this generalization, however, the factors governing the partitioning of heat loss between evaporative and non-evaporative avenues are not well characterized.

The purpose of this study was to evaluate the evaporation requirements for thermoregulation of two small mammals based on heat transfer properties and metabolic heat production. In the preceding paper of this series, the conductances to heat loss of the torso and appendages were characterized under laboratory conditions for the deer mouse, *Peromyscus maniculatus*, and from published data for the white rabbit, *Oryctolagus cuniculus* (Gonzalez et al. 1971). From these conductances, I calculated a maximum thermal conductance ($C_{max}$) for each animal, which represented the physical limit to non-evaporative heat loss. I assessed evaporation requirements by comparison of metabolic heat production to the physical heat loss limit.

## Material and methods

The animal characteristics, experimental procedures and results, the heat transfer calculations, and the nomenclature used

in this study appear in the preceeding paper (Conley and Porter 1985). The deer mouse results were based on measurements of evaporative water loss, respiratory gas exchange and skin and core temperatures made at air temperatures of 8, 21, 26, 30, and 34 °C. Similar measurements were made by Gonzalez et al. (1971) for the white rabbit and the results presented here were calculated from the mean values reported at 5 °C intervals from 5 to 35 °C. Detailed below are the methods specific to this study.

*Measurements.* The procedures and calculations for water loss measurements using dew-point hygrometry have been described in detail previously (Bernstein et al. 1977; Welch 1980). All reported values represent steady-state levels measured over a 15 to 30 min period that occurred during the 1–2 h experiment. A neck yoke restrained the mouse in a standing position to a wide-mess wire platform below which voided urine and feces were collected in mineral oil. This apparatus stood within a glass dessicator through which ambient air, dried using anhydrous $CaSO_4$ (W.A. Hammond Drierite Co, Xenia, OH), was drawn at flow rates from 480 to 576 $cm^3$ $min^{-1}$ (STPD). Excurrent air passed along stainless steel tubing through a calibrated rotameter (Brooks model R-2-15-D Emerson Electric Co, Hatfield, PA) to a dewpoint hygrometer (Model 440, EGG Co, Waltham, MA). Comparison of the known mass of water introduced into the system with that calculated from the hygrometric measurements revealed a measurement accuracy of $\pm 5\%$. An accuracy of better than $\pm 3\%$ for $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ was established by dilution of ambient air using known volumes of dry $CO_2$.

*Calculations.* Water vapor pressure was calculated from dew-point temperature using Teton's equation (Murray 1967) from which water vapor density was determined using the ideal gas equation. Evaporation rate was calculated as the difference between incurrent and excurrent water vapor density times the air flow rate (Welch 1980). Heat production rates were calculated from respiratory gas exchange of $O_2$ and $CO_2$ using the thermal equivalent of oxygen corrected for the respiratory quotient (Conley and Porter 1985, Eq. 1) and expressed in surface-area-specific units as either metabolic ($\dot{Q}_M A_{tot}^{-1}$; $Wm^{-2}$) or net heat production ($\dot{Q}_N A_{tot}^{-1}$). The latent heat of vaporization of water at core temperature was used to convert specific evaporation rates into heat loss rates ($\dot{Q}_E A_{tot}^{-1}$). The difference between metabolic and evaporative heat loss rates yielded the net or non-evaporative heat loss rate from the animal:

$$\dot{Q}_N = \dot{Q}_M - \dot{Q}_E. \qquad (1)$$

Two physiologically based thermal conductances were calculated from these heat production rates, and core ($T_c$, °C) and air temperature ($T_a$). The first represents the whole-animal thermal conductance for non-evaporative heat loss ($C$, $Wm^{-2}$ °$C^{-1}$) and was calculated from net heat production ($\dot{Q}_N$):

$$C = \dot{Q}_N (T_c - T_a)^{-1} A_{tot}^{-1}. \qquad (2)$$

The second represents the thermal conductance necessary to dissipate metabolic heat production ($C_m$), and was calculated by substitution of metabolic heat production ($\dot{Q}_M$) for $\dot{Q}_N$ in Eq. (2).

The physical limit to non-evaporative heat loss for the experimental conditions was calculated as the maximum thermal conductance ($C_{max}$). The previously determined external conductances ($h_{ex}$) were weighted by the appendage ($A_{app}$) and torso ($A_{tor}$) surface areas to yield $C_{max}$ (Conley and Porter 1985). For example, $C_{max}$ for the rabbit was calculated as

$$C_{max} = (h_{ex, tor} A_{tor} + h_{ex, e} A_e)/A_{tot} \qquad (3)$$

where $h_{ex, tor}$ and $h_{ex, e}$ are the torso and ear external conductances ($Wm^{-2}$ °$C^{-1}$), respectively; and $A_{tor}$ and $A_e$ are the torso and ear surface areas ($m^2$), respectively, of the rabbit. The same calculations were made for the mouse but included the separate conductances for the tail and feet.

A Student-Neuman-Kuels test was used for multiple comparison of means with statistical significance defined at the 0.05 level (Zar 1974).

## Results

The relation between surface-area-specific metabolic heat production ($\dot{Q}_M A_{tot}^{-1}$) and evaporative heat loss ($\dot{Q}_E A_{tot}^{-1}$) vs air temperature were different for the two animals (Fig. 1). For the mouse, $\dot{Q}_M A_{tot}^{-1}$ significantly decreased at each $T_a$ from 8 to 30 °C ($P < 0.001$ for all comparisons) but was not different between 30 and 34 °C ($P > 0.2$), which agrees with Chappell and Holsclaw (1984) for unrestrained deer mice under free convection conditions. In contrast, the rabbit $\dot{Q}_M A_{tot}^{-1}$ decreased to a plateau at 15 °C and increased above 30 °C. This range of $T_a$ of nearly constant $\dot{Q}_M A_{tot}^{-1}$ represents the thermoneutral zone and spans 15 °C for the rabbit but extended over a smaller range that included 30 and 34 °C for the mouse. Above 34 °C, the mice would not settle down in the restraining apparatus and rapidly became hyperthermic ($T_c > 40$ °C).

Surface-area-specific evaporative heat loss ($\dot{Q}_E A_{tot}^{-1}$) was similar for the two animals below 20 °C (Fig. 1). It was significantly less at 26 and 30 °C compared to 8 °C ($P < 0.01$ and $P < 0.05$, respectively) for the mouse, whereas it increased with $T_a$ for the rabbit. Above 30 °C, $\dot{Q}_E A_{tot}^{-1}$ increased for the mouse and was greater at 34 than at 26 or 30 °C ($P < 0.001$ and $P < 0.01$, respectively) but not greater than at 20 or 8 °C.

The three thermal conductances $C$, $C_m$, and $C_{max}$ *versus* air temperature appear in Fig. 2 for both animals. The brackets formed by the measured ($C$) and the maximum thermal conductance ($C_{max}$) represent the conductance range possible for adjustments of heat loss without evaporation. Such an adjustment is apparent in the larger mouse $C$ at 34 °C than at any other $T_a$ ($P < 0.001$), and the increased $C$ of the rabbit above 20 °C. The increase in $C_{max}$ apparent above 30 °C for the mouse resulted from enhanced free convection (i.e., bouyancy effects) that accompanied the vasomotor increase in appendage skin temperature and an increased torso conductance, presumably due to a pilomotor reduction in fur depth (Conley and Porter 1985). However, heat storage in the rabbit above 30 °C (Gonzalez et al. 1971) entered into the calculation of $h_{ex, tor}$ (Conley and Porter 1985) and
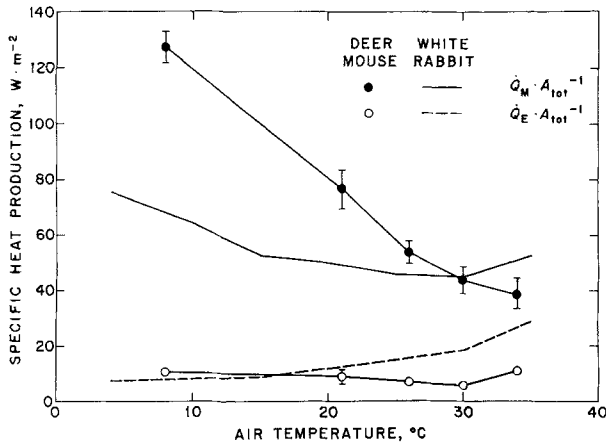
Fig. 1. Specific heat production ($\dot{Q}_M A_{tot}^{-1}$) and evaporative heat loss ($\dot{Q}_E A_{tot}^{-1}$) as a function of air temperature ($T_a$) for deer mouse and white rabbit. Values for deer mouse are means and vertical lines are the 95% confidence intervals
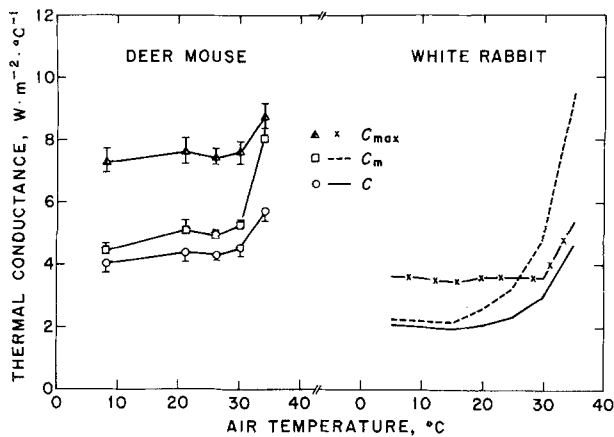


Fig. 2. Thermal conductances ($C_{max}$, $C_m$, and $C$) as a function of air temperature ($T_a$) for deer mouse and white rabbit. See text for definition of each conductance. Values are the same as in Fig. 1

ate the relationship between evaporation and the capacity to lose heat. This capacity was represented by $C_{max}$, below which non-evaporative heat loss was determined by $C$. Evaporation is required for thermoregulation when metabolic heat production exceeds this capacity for heat loss. Comparison of $C_{max}$ with the thermal conductance required to lose metabolic heat production ($C_m$) revealed the air temperature at which this evaporative supplement was required. As shown in Fig. 2, $C_m$ exceeded $C_{max}$ above 25 °C for the rabbit and above 34 °C for the mouse. Evaporation was elevated at these air temperatures for both animals (Fig. 1), but $C$ had not reached $C_{max}$ for either animal. Thus, a reserve in the capacity to lose heat non-evaporatively remained (i.e., $C < C_{max}$) for both animals. Therefore, evaporation was greater than that required based on the physical capacity to lose heat (i.e., $C_{max}$).

For both animals an increased $C$ accompanied the elevation in evaporation. In the rabbit, evaporation increased together with $C$ above 15 °C and at each subsequent 5 °C interval up to 35 °C. For the mouse, both evaporation and $C$ increased above 30 °C. Ingram et al. (1963) have shown that an increase in cutaneous evaporation accompanied the appendage vasodilation that underlaid thermal conductance changes in the ox. Similary, an increased blood flow through excised rabbit ears also increased cutaneous water loss (Hattingh 1975). It appears that the vasomotor changes that are responsible for increasing thermal conductance may also enhance cutaneous evaporation.

For the rabbit, respiratory evaporation also increased above 25 °C (Gonzalez et al. 1971). Respiratory evaporation in the rabbit is controlled by a combination of core and skin temperature (Stitt 1976), as has been shown for appendage vasodilation in other animals (Ingram et al. 1963; Lynch et al. 1980). This similar control may underly the simultaneous use of these two mechanisms in the regulation of heat loss.

A coupling of these mechanisms argues against a two step process in which thermal conductance first reaches its limit followed by an increase in evaporation (McLean 1974). Instead of simply compensating for a short-fall in the ability to lose heat non-evaporatively, evaporation acted in parallel with vasomotor-induced thermal conductance changes to balance heat loss to match heat production.

These results suggest that the contribution of evaporation to thermoregulation did not simply reflect the capacity to lose heat production non-evaporatively in these two animals. The measured

erroneously increased $C_{max}$ (Eq. 3). The conductance required to dissipate metabolic heat production ($C_m$) equals or exceeds the maximum thermal conductance at 34 °C for the mouse and above 25 °C for the rabbit. An enhancement of evaporation is required above these $T_a$ to dissipate the heat in excess of the non-evaporative heat loss capacity. However, both animals increased evaporation at $T_a$ at which $C$ was below its limit, $C_{max}$. An evaporation increase occurred above 30 °C for the mouse and above 15 °C for the rabbit. Thus, evaporation was greater than that required based on the capacity for non-evaporative heat loss represented by $C_{max}$.

## Discussion

Evaluation of the physical requirements for evaporation in thermoregulation permitted me to evalu-

contribution of evaporation was greater than that necessary based on heat loss requirements alone. In part, a coupling of evaporation with vasomotor changes may account for this larger contribution, but respiratory evaporation also increased for the rabbit at an air temperature lower than required. In addition, these and other results show an increase in evaporation below the thermoneutral zone of the mouse (due exclusively to cutaneous evaporation; Edwards and Haines 1978) and of the prairie dog (Welch 1980). Thus a physical model provides insight into the minimum evaporation requirements for thermoregulation, but factors such as the control of respiratory evaporation and a possible coupling of cutaneous evaporation with vasodilation may elevate evaporation above the minimum level.

# References

Bernstein MH, Hudson DM, Stearns JM, Hoyt RW (1977) Measurements of evaporative water loss in small animals by dew-point hygrometry. J Appl Physiol: Respirat Environ Exercise Physiol 43:382–385

Chappell MA, Holsclaw DS (1984) Effects of wind on thermoregulation and energy balance in deer mice (*Peromyscus maniculatus*). J Comp Physiol B 154:619–625

Conley KE, Porter WP (1985) Heat loss regulation: role of the appendages and torso in the deer mouse and the white rabbit. J Comp Physiol B 155:423–431

Dawson WR (1982) Evaporative losses of water by birds. Comp Biochem Physiol 71A:495–509

Edwards RM, Haines H (1978) Effects of ambient water vapor pressure and temperature on evaporative water loss in *Peromyscus maniculatus* and *Mus musculus*. J Comp Physiol 128:177–184

Gonzalez RR, Kluger MJ, Hardy JD (1971) Partitional calorimetry of the New Zealand white rabbit at temperatures 5–35 °C. J Appl Physiol 31:728–734

Hales JRS (1974) Physiological responses to heat. In: Robertshaw D (ed) Environmental physiology. Univ Park Press, Baltimore (Int Rev Science, Physiol Ser 1, vol 7, pp 107–162)

Hattingh J (1975) The influence of hormones and blood flow on transepidermal water loss. Comp Biochem Physiol 50A:439–442

Ingram DL, McLean JA, Whittow GC (1963) The effect of heating the hypothalamus and the skin on the rate of moisture vaporization from the skin of the ox (*Bos taurus*) J Physiol 169:394–403

Lynch WC, Adair ER, Adams BW (1980) Vasomotor thresholds in the squirrel monkey: effects of central and peripheral temperature. J Appl Physiol: Respir Environ Exercise Physiol 48:89–96

McLean JA (1974) Loss of heat by evaporation. In: Monteith JL, Mount LE (eds) Heat loss from animals and man. Butterworths, London, pp 20–31

Murray FW (1967) On the computation of saturation vapor pressure. J Appl Meteorol 6:203–204

Stitt JT (1976) The regulation of respiratory evaporative heat loss in the rabbit. J Physiol 258:157–171

Taylor CR (1977) Exercise and environmental heat loads: different mechanisms for solving different problems? In: Robertshaw D (ed) Environmental physiology II. Univ Park Press, Baltimore (Int Rev Physiol, vol 15, pp 119–146)

Thauer R (1964) Circulatory adjustments to climatic requirements. In: Circulation. Am Physiol Soc, Washington DC (Handbook of physiology, sect 2, vol III, pp 1921–1966)

Weathers WW (1981) Physiological thermoregulation in heat-stressed birds: consequences of body size. Physiol Zool 54:345–361

Welch WR (1980) Evaporative water loss from endotherms in thermally and hygrically complex environments: an empirical approach for interspecific comparisons. J Comp Physiol 139:135–143

Zar JH (1974) Biostatistical analysis. Prentice-Hall, Englewood Cliffs