

HEAT LOSS FROM DEER MICE (*PEROMYSCUS*): EVALUATION OF SEASONAL LIMITS TO THERMOREGULATION

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SUMMARY

This paper investigates the influence of seasonal adaptations to thermoregulatory heat loss for deer mice (*Peromyscus*) during summer and winter. A general, mechanistic model of heat transfer through fur was evaluated for the structural properties of the fur of deer mice. The model was validated against heat production determined from mice exposed to a range of radiative (wall) temperatures (t_r) at air temperatures (t_a) of 15, 27 and 34°C. Calculated heat loss from the appendages was subtracted from the measured heat production to yield heat loss from the furred torso. This calculated torso heat loss agreed closely with the predicted fur heat loss for all conditions, as shown by a regression slope near 1 (0.99). Simulations using models of fur and appendage heat loss reveal that the winter increase in thermogenic (heat production) capacity has a greater effect than changes in fur properties in expanding the limits to thermoregulation. Both wind and a clear night sky increase heat loss and can limit thermoregulation to air temperatures above those found in deer mice habitats during winter (–25°C). Thus, despite seasonal adaptations, these simulations indicate that thermoregulation is not possible under certain winter conditions, thereby restricting deer mice to within the protected environment of the leaf litter or snow tunnels.

INTRODUCTION

A general model of heat transfer based on the structural properties of fur provides a powerful tool for examining heat loss from mammals. Such a model can be used to study thermoregulation and its associated energetic costs under natural environmental or experimental conditions (McClure & Porter, 1983; Porter & McClure, 1984). In addition, the consequences of various morphological, behavioural and physiological adaptations to thermoregulatory heat loss can be theoretically explored. For many endotherms, such adaptations are found seasonally in the properties of fur and the capacity to produce heat (Chaffee & Roberts, 1971). These seasonal

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adaptations may be critical for small mammals, such as deer mice (*Peromyscus*), to be nocturnally active throughout the year under a wide range of environmental conditions (Hill, 1983; Wickler, 1980). Deer mice have been reported active in areas where air temperature drops to -25°C (Behney, 1936; Merritt, 1984) and where heat loss may be enhanced further by wind and thermal radiation to the clear night sky (Chappell, 1980*a,b*; Porter & Gates, 1969). A mechanistic model of heat loss from fur together with models of heat loss from appendages (Conley & Porter, 1985) permit assessment of the consequences of these seasonal adaptations to thermoregulatory heat loss under conditions found in the habitats of deer mice.

Several general models have been developed to represent heat loss based on the structure of fur (cf. Cena & Clark, 1979). However, these models have only been tested using artificial fur or pieces of natural pelts (Cena & Monteith, 1975*a,b*; Davis & Birkebak, 1974; Kowalski & Mitchell, 1979). Thus there is a need to evaluate these models for natural fur properties and to compare the model predictions against heat loss determined from a mammal. We chose to evaluate one model which predicts heat loss to within $\pm 7\%$ of that measured from artificial fur pelts (Kowalski & Mitchell, 1979).

The purpose of this paper is to assess thermoregulatory heat loss for the deer mouse for winter and summer environmental conditions. First, a general, mechanistic model of heat transfer through fur was evaluated for the structural properties of the deer mouse fur and tested against heat loss determined from the mouse under a range of conditions in the laboratory. Heat loss from the furred torso was determined from the difference between measured heat production from the mouse and heat loss calculated for the unfurred appendages (ears, feet and tail; Conley & Porter, 1985). Second, the seasonal fur and physiological properties of deer mice were used to determine the environmental limits to thermoregulation during winter and summer.

MATERIALS AND METHODS

Measurements

The deer mice were from a stock previously described (Porter & Busch, 1979). The 42 mice used in this experiment ranged in body mass from 11.3 to 20.2 g with a mean of 15.6 g. The experimental procedures and measurements described before (Conley & Porter, 1985) were used with the following modifications. A list of symbols appears in the Appendix.

Gas-analysis system

A two-channel flow system permitted measurement of respiratory gases and cutaneous evaporation by separate sampling of the two subsystems (Fig. 1). The mouse was restrained by a neck yoke and stood on a wire mesh platform within a 470 ml polyethylene-film chamber, which was transparent to infrared radiation. A 6 mm diameter dish was located below the platform to capture voided urine and faeces in paraffin oil. Cutaneous evaporation was collected through the top of the chamber, whereas respiratory gases were collected from a mask which protruded

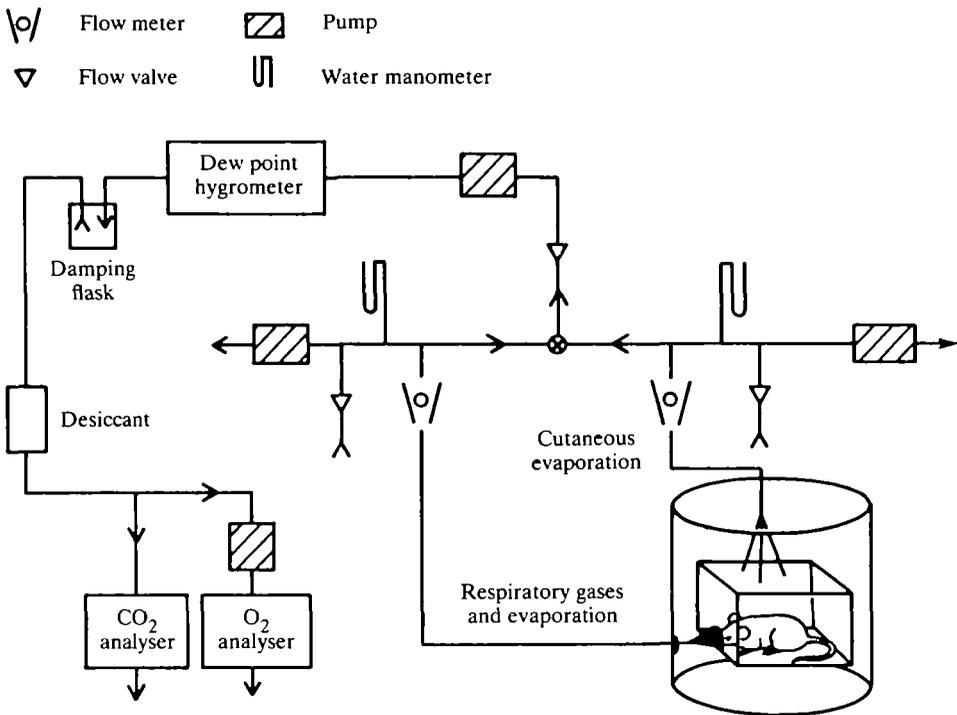


Fig. 1. Diagram of a two-channel gas analysis system and the apparatus for controlling wall temperature. A deer mouse was restrained within a polyethylene metabolism chamber with the head protruding through the polyethylene into a mask. Not shown are the restraining yoke and the thermocouples attached to the mouse.

through a slit in the chamber and covered the mouse's snout. Weekly calibration of both subsystems by dilution of ambient air with dry N_2 and CO_2 revealed a measurement accuracy better than $\pm 3\%$ for \dot{V}_{O_2} and \dot{V}_{CO_2} , respectively (Fedak, Rome & Seeherman, 1981).

Air flowed through each subsystem continuously through calibrated Brooks[®] rotameters (Emerson Electric Co., Hatfield, PA) at a rate that ranged between 480 and 575 $ml\ min^{-1}$ (STPD) at a pressure 0.4 kPa below atmospheric. Incurrent water vapour density (i.e. air humidity) was less than $5\ g\ m^{-3}$. Collection of respiratory gases by the cutaneous subsystem (i.e. gas cross-flow) averaged 1% as assessed by the O_2 and CO_2 concentrations recorded from the cutaneous subsystem.

Experimental procedures

Each mouse was anaesthetized with Halothane[®] and fitted subcutaneously with seven 36-gauge thermocouples at four locations under the torso fur, subcutaneously on the hindfoot and the tail, and superficially on the ear. A sheathed thermocouple was inserted 2–3 cm into the rectum and secured to the tail with tape for measurement of core temperature. The mouse recovered from anaesthesia, was fitted with a mask, placed in the apparatus, and covered with the polyethylene chamber. After

1–2 h of exposure to the experimental conditions, and once the mouse had achieved a constant core temperature and respiratory gas exchange, measurements were made for 15 min from the respiratory subsystem followed by a 10-min sampling period from the cutaneous subsystem.

Experiments were conducted at 15, 27 and 34°C with wall (t_w) equal to air (t_a) temperature, $t_w < t_a$, and at 15 and 27°C with $t_w > t_a$. Because the mice tended to struggle and become hyperthermic at 34°C, experiments were not run at this t_a with a higher t_w . A single temperature combination was run on a given day and the daily sequence of runs was randomly assigned.

Fur properties

Pelts from freshly killed mice were removed and sampled according to the methods of McClure & Porter (1983).

Calibration

Thermal radiation exchange was controlled by adjustment of the wall temperature of a cylinder 80 cm high, 38 cm diameter (top) and 45 cm diameter (bottom; Fig. 1). Perfusion of water through the cylinder regulated wall temperature, whereas the temperature of the surrounding air was controlled by a temperature regulating cabinet. The apparatus was calibrated using a heated copper cast of an 18 g mouse with no appendages. The details of this procedure have been previously described (Conley, 1983) and are summarized below.

Convection properties were characterized using a chrome-plated cast of a mouse (emissivity = 0.05; Gubareff, Janssen & Torborg, 1960) based on the procedures of Wathen, Mitchell & Porter (1971, 1974). Convective heat loss was not significantly different from that calculated for a cylinder of the same diameter (Conley & Porter, 1985). The surfaces surrounding the polyethylene chamber and the cast were later covered with matt-black paint and the emissivity of the paint (ϵ_{bp}) and the infrared transmittance of polyethylene (τ_p) were determined using the methods of Mount (1964). Our estimates of ϵ_{bp} and τ_p closely agreed with reported values (Table 1).

Table 1. *Thermal radiation properties of the experimental apparatus*

Property	Regression coefficient	Literature value	Reference
ϵ_{bp}	0.88 (0.86–0.90)	0.888	Wolfe, 1964
τ_p	0.82 (0.80–0.83)	0.9 [8–13 μm]	Wolfe, 1964
F_{ca-o}	0.40 (0.33–0.46)	0.32*	Siegel & Howell, 1972
F_{ca-p}	0.65 (0.57–0.73)	0.68*	Siegel & Howell, 1972

Symbols are: ϵ_{bp} , emissivity of black paint; τ_p , transmittance of polyethylene; F_{ca-o} , cast-to-oil configuration factor and F_{ca-p} , cast-to-polyethylene configuration factor.

Values are means and the 95% confidence intervals are in parentheses.

* Value calculated for a similarly positioned sphere.

Configuration factors

Thermal radiation exchange occurs between the mouse and the surrounding surfaces (Fig. 1). Configuration factors represent the fractional contribution that each surface makes to radiation exchange. Separate control of air and wall temperature permitted these configuration factors to be estimated for the mouse cast by multiple linear regression (Table 1; Conley, 1983).

Radiative temperature

The polyethylene film that surrounds the mouse reflects as well as transmits thermal radiation (Mount, 1964), which prevents a simple calculation of radiative temperature from the temperatures of the surrounding surfaces (Siegel & Howell, 1972). Instead, an effective radiative temperature must be calculated that takes into account the attenuation of radiation exchange by the polyethylene. This effective radiating temperature (T_r ; K) was calculated by weighting the difference between an approximate fur radiating temperature ($T_{r,f}$)

$$T_{r,f} = (T_{s,tor} + T_a) / 2 \quad (1)$$

and temperatures of the surrounding surfaces using configuration factors

$$T_r = \{T_{r,f}^4 - [F_{m-o}(T_{r,f}^4 - T_o^4) + F_{m-p}\tau_p(T_{r,f}^4 - T_p^4)]\}^{0.25}, \quad (2)$$

where the thermodynamic temperatures (K) are: $T_{s,tor}$ (mean torso skin), T_a (air), T_o (paraffin oil) and T_p (surface radiating through the polyethylene); and F_{m-o} and F_{m-p} are the mouse-cast-to-oil and the mouse-cast-to-polyethylene configuration factors, respectively.

*Calculations**Fur model*

The governing equations of the model of fur heat transfer are described below. For clarity of presentation, the nomenclature and equations appear in a slightly different form from the original presentation of the model (Kowalski & Mitchell, 1979).

Conduction and thermal radiation are assumed to be the only significant heat transfer mechanisms in fur at low wind velocities and without sunlight (Skuldt, Beckman, Mitchell & Porter, 1975). Thus effective conductive [$k_{eff} = (k'_x + k'_y) / 2$; $W m^{-1} C^{-1}$] and radiative (k_r) conductivities constitute the fur conductivity (k_f):

$$k_f = k_{eff} + k_r. \quad (3)$$

The conductivity along the x (k'_x) direction is represented by the surface area weighted mean of air (k_a) and hair (k_h) thermal conductivity:

$$k'_x = (A_h / A_f)k_h + (1 - A_h / A_f)k_a, \quad (4)$$

where A_h and A_f are the surface areas (m^2) occupied by the individual hairs and fur (hair plus air), respectively. In the y direction, conductivity is expressed as:

$$k'_y = [p_{eff}^{0.5}k_a(p_{eff}^{-0.5} - D_h)] + \{(D_h k_h k_a) / [(D_h k_a) + (p_{eff}^{-0.5} - D_h)k_h]\}, \quad (5)$$

where D_h is the hair diameter (m), p_{eff} is the effective hair density [$p_{\text{eff}} = p_h(L_h/z_f)$; hairs m^{-2}], L_h is hair length and z_f is fur depth.

An average absorption coefficient (β , m^{-1}) represents the thermal radiation properties of the fur:

$$\beta = (0.67/\pi)p_{\text{eff}}D_h, \quad (6)$$

which is used to determine the fur radiation conductivity:

$$k_r = 16\sigma[(T_{s,\text{tor}} + T_a)/2]^3/(3\beta), \quad (7)$$

where σ is the Stefan-Boltzmann constant ($5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$), and $T_{s,\text{tor}}$ and T_a are the torso skin and air thermodynamic temperatures (K), respectively.

Non-dimensional Biot numbers (Bi) characterize heat loss from fur as ratios of environmental conductances to fur conductance ($h_f = k_f/z_f$): for convection, $\text{Bi}_{\text{cv}} = h_{\text{cv}}/h_f$ and for radiation, $\text{Bi}_r = h_r/h_f$, where h_r is calculated as:

$$h_r = 4\epsilon\sigma[(T_{s,\text{tor}} + T_a)/2]^3. \quad (8)$$

The effective temperature gradient through the fur ($\Delta T = C_1 T_{s,\text{tor}}$) is a normalized function of $T_{s,\text{tor}}$, where

$$C_1 = [\text{Bi}_{\text{cv}}(1 - T_a/T_{s,\text{tor}}) + \text{Bi}_r(1 - T_r/T_{s,\text{tor}})] \times \\ [1 + \text{Bi}_{\text{cv}} + 2\text{Bi}_r(0.5 - \{0.333 - [E_4(\beta z_f)]\})]/(\beta z_f)]^{-1}. \quad (9)$$

T_a , $T_{s,\text{tor}}$ and T_r are in thermodynamic units (K) and E_4 is a fourth-order exponential integral (Gautschi & Cahill, 1964).

The non-linear temperature gradient through fur is compensated for by a factor δ (Kowalski & Mitchell, 1979):

$$\delta = 0.854 + \log \text{Bi}_{\text{cv}} 0.149. \quad (10)$$

Fur heat transfer (\dot{Q}_f ; W) is expressed as the product of the fur conductance ($h_f = k_f/z_f$), the effective temperature gradient (ΔT), fur surface area (A_f) and δ :

$$\dot{Q}_f = \delta h_f A_f \Delta T. \quad (11)$$

Appendage model

The modifications for this study in the calculation of appendage heat loss (\dot{Q}_{app}) from that previously described (Conley & Porter, 1985) include incorporation of radiation exchange between the fur and appendages. Calculation of radiation heat loss from each appendage used the general form below (expressed for ear radiative heat loss, $\dot{Q}_{r,e}$, as an example):

$$\dot{Q}_{r,e} = \epsilon_{\text{sk}} \sigma h_{r,e} F_{e-\text{en}} [F_{e-p} \tau_p (T_{s,e} - T_p) + F_{e-f} (T_{s,e} - T_{r,f}) + F_{e-o} (T_{s,e} - T_o)] A_e, \quad (12)$$

where ϵ_{sk} is skin emissivity (assumed to be unity); $h_{r,e}$ is the ear radiative conductance; $T_{s,e}$ is the ear skin temperature; $F_{e-\text{en}}$, F_{e-p} , F_{e-f} and F_{e-o} are the ear-to-environment, polyethylene, fur and oil configuration factors, respectively; and A_e is the ear surface area (m^2). For each appendage, the unique value for the configuration factor (Table 2) was inserted into equation 12 and radiative heat loss calculated. The configuration factors for appendage-environment exchange were approximated to

Table 2. Configuration factors for appendage radiation heat exchange

Exchange	Ears	Feet	Tail
Environment	$F_{e-en} = 0.80$	$F_{fe-en} = 0.90$	$F_{ta-en} = 1.00$
Fur	$F_{e-f} = 0.33$	$F_{fe-f} = 0.33$	$F_{ta-f} = 0.00$
Oil	$F_{e-o} = 0.00$	$F_{fe-o} = 0.35$	$F_{ta-o} = 0.33$
Polyethylene	$F_{e-p} = 0.67$	$F_{fe-p} = 0.32$	$F_{ta-p} = 0.67$

See Appendix for abbreviations.

those for similar geometries (Wathen *et al.* 1974). For ear and feet radiation exchange with fur, and feet and tail exchange with polyethylene, the configuration factors were approximated to 0.33. The remaining factors were calculated by subtracting the approximated factors for each appendage from unity, since the sum of all configuration factors must equal unity (Siegel & Howell, 1972). Convective heat loss from each appendage was calculated using the convection coefficient determined for a similarly shaped geometry (equation 16, below; Conley & Porter, 1985; Wathen *et al.* 1974). The sum of the respective thermal radiation and convective losses yielded the total heat loss from each appendage.

Metabolism

Metabolic heat production (\dot{Q}_M) was calculated from \dot{V}_{O_2} and \dot{V}_{CO_2} using the thermal equivalent of oxygen corrected for the respiratory quotient (Conley & Porter, 1985). Evaporative water loss was converted to heat loss using the latent heat of vaporization at body temperature. Net heat production (\dot{Q}_N) represents the difference between \dot{Q}_M and evaporative heat loss (\dot{Q}_E). The difference between appendage heat loss (\dot{Q}_{app}) and \dot{Q}_N yielded the heat loss from the furred torso ($\dot{Q}_{tor} = \dot{Q}_N - \dot{Q}_{app}$).

Thermal radiation

The change in radiative heat exchange from black-body conditions (i.e. $T_a = T_r$) was calculated by subtraction of the measured torso heat loss from that predicted for black-body conditions:

$$\Delta\dot{Q}_{r,tor} = (\dot{Q}_{tor} - \dot{Q}_{bb}), \quad (13)$$

where \dot{Q}_{tor} is the measured torso heat loss and \dot{Q}_{bb} is the fur heat loss predicted for black-body conditions. Similarly, the change in radiation heat exchange predicted by the fur model was calculated by substituting \dot{Q}_f for \dot{Q}_{tor} in equation 13.

Morphology

Fur properties were expressed for the calculations as means weighted by the relative surface area of the dorsal (0.55) and the ventral fur (0.45). The geometry of a prolate spheroid was used to calculate fur surface area (Selby, 1972). The radius at

the mouse mid-belly plus fur depth constituted the minor semi-axis of the spheroid. The equation for spheroid volume was rearranged to solve for the major semi-axis using body mass as the spheroid volume. The surface area of the spheroid represented the boundary area for fur heat exchange.

Statistics

Mean values were compared at a given air temperature for the effect of radiative temperature using a one-way analysis of variance. The 95 % confidence intervals that appear in the figures were calculated from the pooled standard error at each air temperature. These means were further distinguished using a multiple *t*-test. The linear least-squares method was used for estimation of regression parameters with the assumption that the errors were independent and normally distributed. The null hypothesis was rejected at the 0.05 level of probability.

Model simulations

An equivalent electrical circuit represents heat loss from the deer mice (Fig. 2). Just as current flows through a circuit based on voltages across electrical conductances, heat flows through this thermal circuit based on temperatures across thermal conductances (symbolized as resistors in Fig. 2). A separate circuit was used for ears, feet and tail as previously described (Conley & Porter, 1985), but only a single, composite circuit appears for the appendages in Fig. 2. The simplified thermal circuits shown for the appendages and the torso separate the processes of the physiological transfer of heat within the mouse from the physical processes that occur through the fur and to the environment. An internal conductance (h_{in} , $\text{W m}^{-2}\text{°C}^{-1}$) represents heat transfer by blood flow and tissue conduction to the skin surface. At and below an air temperature of 30°C, h_{in} remains constant for the torso and appendages of deer mice, which permits the use of the following mean values in the calculations: torso = 38.8, ear = 16.4, feet = 4.9, tail = 2.1 (Conley & Porter, 1985).

The physical processes of heat transfer from the skin surface or from the fur are represented by conductances for convection (h_{cv} : buoyancy and wind) and thermal radiation (h_r); detailed below are the modifications required for natural environmental conditions.

Convection

Deer mice occupy prairie and forest habitats within which wind velocity rarely exceeds 1.0 m s^{-1} below a height of 10 cm (Chappell, 1980a; Stromberg, 1979). Under this condition, the feet and tail are exposed to still air, whereas the torso and ears see a higher wind velocity. Convective heat loss was calculated for the range of calm (0.1 m s^{-1}) to windy conditions (1.0 m s^{-1}) from convective conductances (h_{cv}) evaluated from nondimensional numbers [Nusselt number (Nu) and Reynolds number (Re)], which relate shape to convective heat loss characteristics:

$$\text{Nu} = a \text{Re}^b \quad (14)$$

$$h_{cv} = \text{Nu } k_a / D, \quad (15)$$

where Nu and Re are unitless, a and b are unitless coefficients specific to a particular geometry, k_a is the air thermal conductivity ($W m^{-1} \text{ } ^\circ C^{-1}$), and D is the diameter of the torso or appendage (m). The coefficients for a sphere are appropriate for the torso: $a = 0.34$ and $b = 0.6$ (Mitchell, 1976). The standard cylinder coefficients adequately describe the appendage geometry: $a = 0.616$ and $b = 0.466$ (Wathen *et al.* 1971, 1974). Multiplication of Nu by 1.7 accounts for the effect of turbulent enhancement of wind in outdoor conditions that occur at the height of the mouse (2 cm). A wind velocity of 1 ms^{-1} enhanced by turbulence is equivalent to a measured wind of 1.7 ms^{-1} (Kowalski & Mitchell, 1976). Convective heat loss rate (\dot{Q}_{cv} , W) was calculated for the appendages as (using the ear as an example):

$$\dot{Q}_{cv,e} = h_{cv,e}(t_{s,e} - t_a)A_e, \quad (16)$$

where $h_{cv,e}$ is the ear convective conductance; $t_{s,e}$ and t_a are the ear skin and air temperatures ($^\circ C$), respectively. Torso h_{cv} appears in the model of fur heat transfer in Bi_{cv} (equation 9).

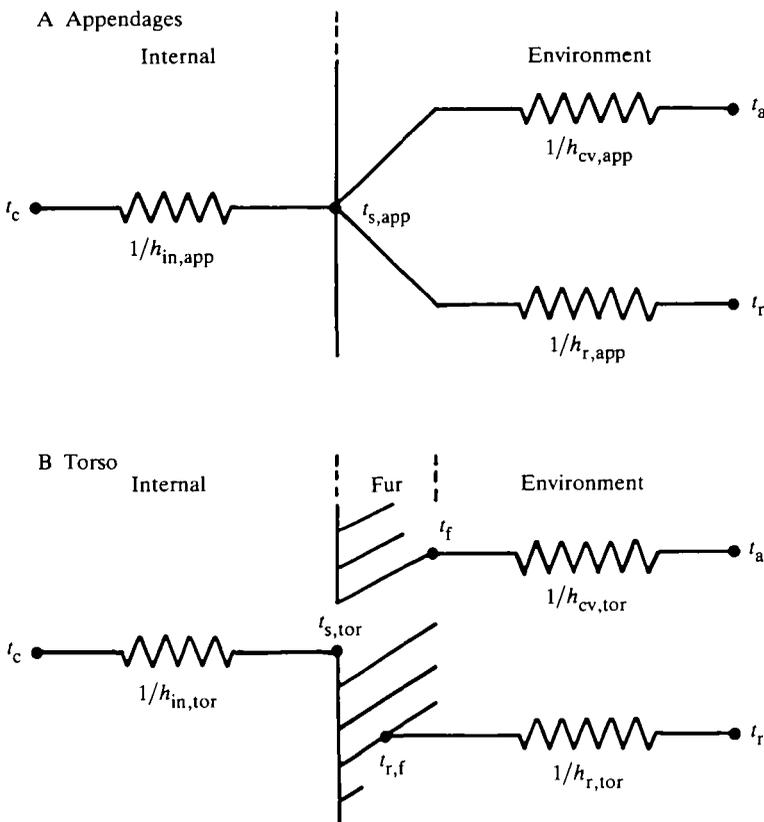


Fig. 2. Thermal circuit diagram for heat transfer from the core to the skin (internal) and from the skin to the surroundings (environment). (A) Composite circuit for the appendages; (B) circuit for the torso. Symbols are: t , temperature; h , conductance. Subscripts are: a, air; app, appendages; c, core; cv, convective; f, fur; in, internal; r, radiative; s, skin; tor, torso.

Thermal radiation

Exposure to sky thermal radiation exchange for deer mice ranges from a maximum under a clear night sky to a minimum under overcast conditions for which sky approximates air temperature (Gates, 1980). Thermal radiation exchange with the sky was assumed to occur over the upper half of the body and with the ground surface (at air temperature) over the lower half of the body. For clear sky conditions, radiative temperature was calculated as:

$$T_r = (0.5T_{sk}^4 + 0.5T_a^4)^{0.25}, \quad (17)$$

where T_r , T_{sk} and T_a are the thermodynamic radiative, sky and air temperatures (K), respectively. Swinback's equation permits calculation of T_{sk} for a clear night sky from air temperature (Swinback, 1963).

Thermal radiation heat loss of the appendages was partitioned among the sky, ground and fur using configuration factors as described above. Half the radiation exchange was assumed to occur for the ear and tail with the sky (F_{e-sk} and $F_{ta-sk} = 0.5$), for the feet and tail with the ground (F_{fe-g} and $F_{ta-g} = 0.5$), and for the ear and feet with fur (F_{e-f} and $F_{fe-f} = 0.5$). These configuration factors, along with h_r , permitted calculation of the rate of radiative heat loss for the appendages (equation 12).

Heat loss

Calculation of heat loss from each appendage and the torso requires skin temperature, which is unknown in the thermal circuits (Fig. 2). A unique value of skin temperature exists that yields the same heat transfer to the skin as lost from the skin for each appendage and the torso. An iterative numerical method was used to converge on the unique skin temperature value that resulted in a heat loss balance across the skin for each thermal circuit ($\dot{Q}_{in} = \dot{Q}_{en}$). Heat loss from the mouse was the sum of these individual heat losses calculated for the torso and each appendage. Calculations were made for an 18-g deer mouse with a body (core) temperature of 37°C and in a standing posture, which exposes the ears, feet and tail to heat exchange.

RESULTS

Fur properties

An initial sampling of two pelts at nine locations revealed significant variation in fur properties only between the dorsum and ventrum, which agrees with McClure & Porter (1983) for growing cotton rats. The remaining 10 pelts were sampled only at mid-dorsal and mid-ventral locations for which fur depth, hair length and hair density were statistically different (Table 3). These properties were expressed as means weighted by the relative surface area of dorsal (0.55) and ventral (0.45) fur for the heat loss calculations.

Metabolic measurements

Shown in Fig. 3 are the mean core (t_c) and torso ($t_{s, \text{tor}}$) temperatures (top) and the mass-specific values for net heat production (\dot{Q}_N/M_b), and torso heat loss (\dot{Q}_{tor}/M_b) for each air temperature (t_a) as a function of radiative temperature (t_r). Air

Table 3. *Fur properties of deer mice*

Property	Dorsal (s.e.)	Ventral (s.e.)
D_h	1.16×10^{-5} (4.5×10^{-7})	1.04×10^{-5} (2.98×10^{-7})
L_h	6.40×10^{-3} (2.19×10^{-4})	3.84×10^{-3} (9.47×10^{-4})
p_h	1.19×10^8 (4.62×10^6)	7.12×10^7 (4.4×10^6)
z_f	4.86×10^{-3} (7.4×10^{-5})	4.23×10^{-3} (1.4×10^{-4})

Values are means for $N = 12$ mice ($N = 7$ for z_f) and s.e. is the standard error.

Symbols and units are: D_h , diameter (m); L_h , length (m); p_h , hair density (hairs m^{-2}); z_f , fur depth (m).

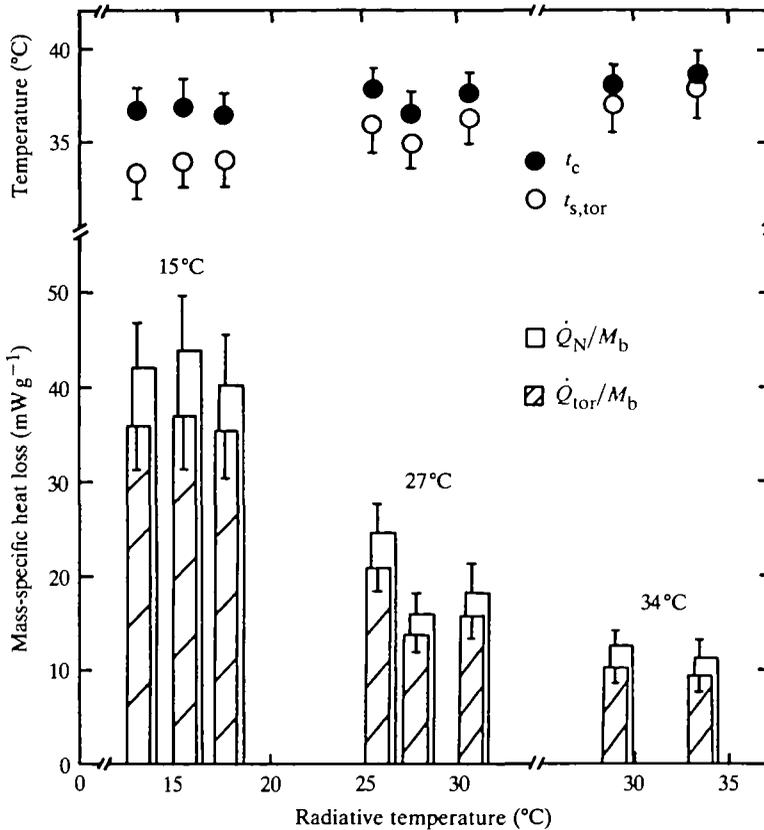


Fig. 3. Mass-specific heat losses and body temperatures vs radiative temperature. Air temperatures appear above the bars. Top: core (t_c) and mean torso skin temperature ($t_{s, \text{tor}}$). Bottom: mass-specific values for net heat production (\dot{Q}_N/M_b) and torso heat loss (\dot{Q}_{tor}/M_b). Values are means and the vertical lines are the 95% confidence intervals. $N = 6-10$.

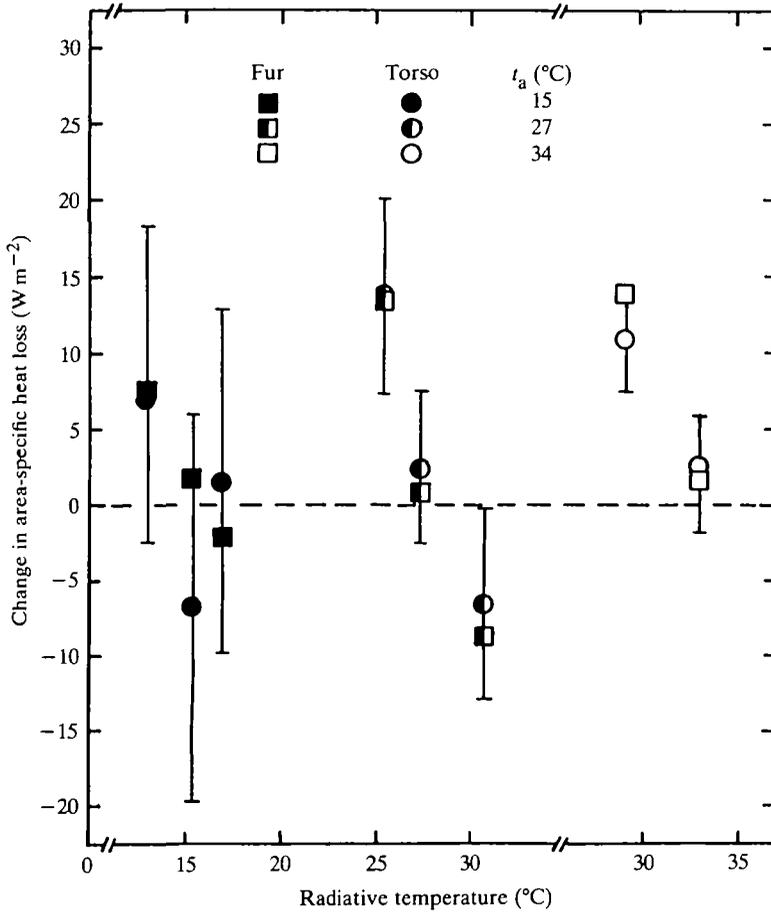


Fig. 4. Change from black-body conditions in area-specific radiative heat loss (\dot{Q}_r/A_f) determined for the furred torso (circles) and predicted for fur (squares) vs radiative temperature. Values are means and vertical lines are the 95% confidence intervals. $N = 6-10$.

temperature resulted in significant differences in both \dot{Q}_N/M_b and \dot{Q}_{tor}/M_b . Core temperature at 27 and 34°C was similar to that reported at the same air temperature for unrestrained deer mice (Chappell & Holsclaw, 1984; Conley & Porter, 1985; Wickler, 1980), which indicates the mice were thermoregulating normally under the experimental conditions.

Fur heat loss

A significant change in thermal radiation heat loss from black-body conditions was achieved for the torso at t_a values of 27 and 34°C (Fig. 4). The predicted and mean changes in radiative heat loss agreed favourably for the torso at all radiative temperatures, as shown by predicted values that fell within the 95% confidence intervals of the mean change. A close agreement was also found between the experimentally determined torso heat loss and that predicted for the fur under all

conditions (Fig. 5) as shown by a regression slope not significantly different from 1 (0.99; 95 % confidence interval: 0.93–1.05) and an intercept not different from zero (0.9; 95 % confidence interval: –4.8 to +6.6). This close agreement for both radiative and total heat loss validates our representation of fur properties for the calculation of heat loss from fur for deer mice.

Model simulations

Fur properties and thermogenic capacity

The seasonal changes in fur properties and thermogenic capacity reported by others appear in Table 4. The 19% greater density found by Huestis (1931) with

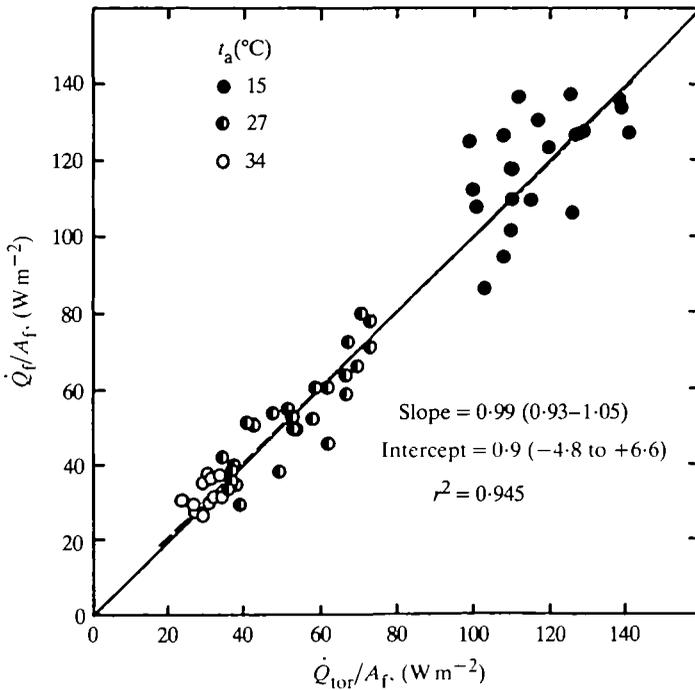


Fig. 5. Predicted fur (\dot{Q}_f/A_f) vs torso (\dot{Q}_{tor}/A_f) area-specific heat loss for all conditions. The regression equation determined for the two variables is dashed and the identity line is solid.

Table 4. *Metabolic, fur and thermal properties reported for summer- and winter-acclimatized deer mice*

Property	Summer	Winter	Change	Reference
C ($\text{ml O}_2 \text{g}^{-1} \text{ } ^\circ\text{C}^{-1}$)	0.286	0.231	–19 %	Wickler, 1980
$\dot{V}_{\text{O}_2\text{max}}$ ($\text{ml g}^{-1} \text{h}^{-1}$)	11.6	19.5	68 %	Wickler, 1980
p_h (hairs m^{-2})	1.9×10^8	2.27×10^8	19 %	Huestis, 1931
I ($^\circ\text{C cal}^{-1} \text{h}^{-1} \text{m}^{-2}$)	0.180	0.228	27 %	Hart, 1956
L_h (m)	6.59×10^{-3}	6.48×10^{-3}	–2 %	Sealander, 1951

Symbols are: C , thermal conductance; $\dot{V}_{\text{O}_2\text{max}}$, thermogenic capacity; p_h , hair density; I , insulation; L_h , hair length.

winter acclimatization was used to adjust the density values reported here for the simulations for winter conditions. A thicker fur depth in winter as compared with summer mice would not be expected to influence heat loss. As shown in Fig. 6, a nearly constant total fur conductance (K_f ; $W^\circ C^{-1}$) occurs between the fur depth measured on mice at $24^\circ C$ (open arrowhead) and that possible with full piloerection of the winter fur (filled arrowhead).

Heat loss vs air temperature

Under an overcast sky or in covering vegetation, the temperatures of the ground, air and sky are nearly equal (see Gates, 1980). The diagonal lines in Fig. 7 represent the calculated heat loss for these conditions in still air. The horizontal lines represent the thermogenic capacity reported for deer mice caught during winter and summer (Wickler, 1980). The intersection points of the horizontal and diagonal lines indicate the minimum air temperatures at which heat loss equals thermogenic capacity and a core temperature of $37^\circ C$ can be maintained. With a summer thermogenic capacity, thermoregulation is possible under calm, cloudy conditions to $0^\circ C$ and with a winter thermogenic capacity, thermoregulation is possible to $-23^\circ C$.

Environmental conditions

On the ground or snow surface under a clear night sky, the mouse may be exposed over half its body surface to a sky radiative temperature as low as $-70^\circ C$ (Swinback, 1963), which enhances heat loss and increases the minimum air temperature for thermoregulation by $5^\circ C$ for both summer and winter (Fig. 7). Wind also increases heat loss and elevates this minimum temperature for cloudy conditions to $12^\circ C$ ($\Delta 12^\circ C$) during summer and to $-12^\circ C$ ($\Delta 11^\circ C$) during winter. Thus, the range of wind velocity to which the mouse may be exposed has a somewhat greater influence on heat loss than does the range of sky temperatures.

Seasonal adaptations

The contribution of enhanced thermogenesis ($\Delta \dot{V}_{O_2 \max}$) was greater than the decrease in fur conductance (Δh_f) in extending the minimum air temperature for thermoregulation (Fig. 8). The increased $\dot{V}_{O_2 \max}$ between summer and winter extends this minimum temperature from $-3^\circ C$ to $-23^\circ C$. In contrast, the change in h_f , calculated using the relative increase in fur density reported (Table 4), extended this minimum temperature by only $5^\circ C$. This greater contribution of an increased thermogenic capacity in extending the minimum temperature for thermoregulation held for all environmental conditions.

DISCUSSION

Fur model validation

Evaluation of the structural parameters of the model of fur heat transfer may be complicated for many mammals by a non-uniform distribution of fur or the presence

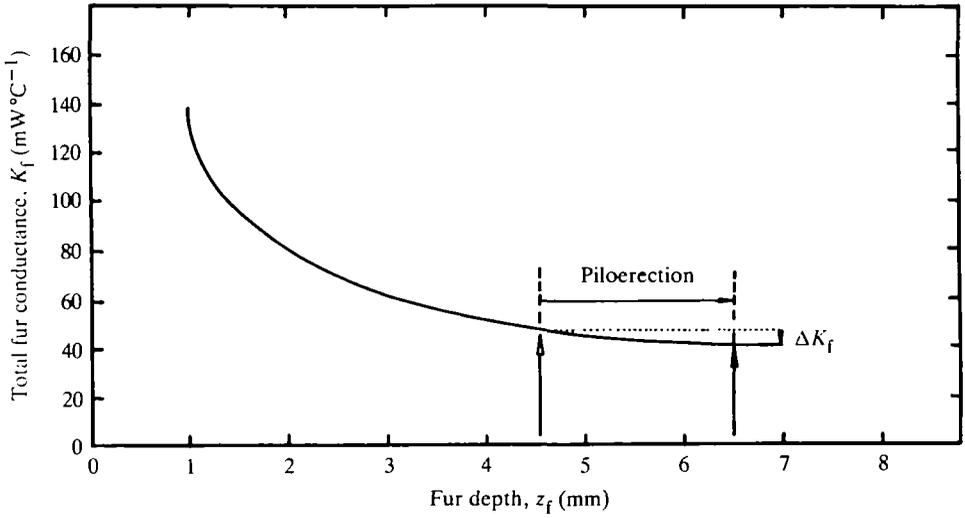


Fig. 6. Total fur conductance (K_f) vs fur depth (z_f). Open arrowhead indicates the measured fur depth at $24^\circ\text{C } t_a$ and closed arrowhead indicates fur depth for fully piloerected, winter fur.

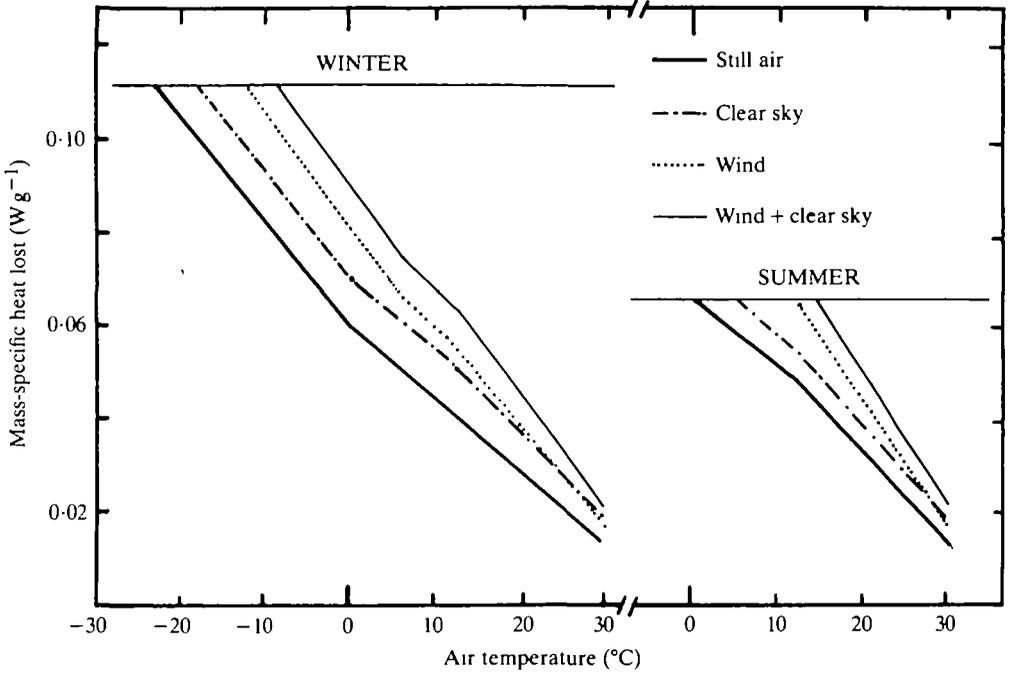


Fig. 7. Mass-specific heat loss (\dot{Q}_N/M_b) from deer mice vs air temperature (t_a) for winter and summer. Horizontal lines represent thermogenic capacity and diagonal lines are the calculated mass-specific heat loss for the designated environmental condition.

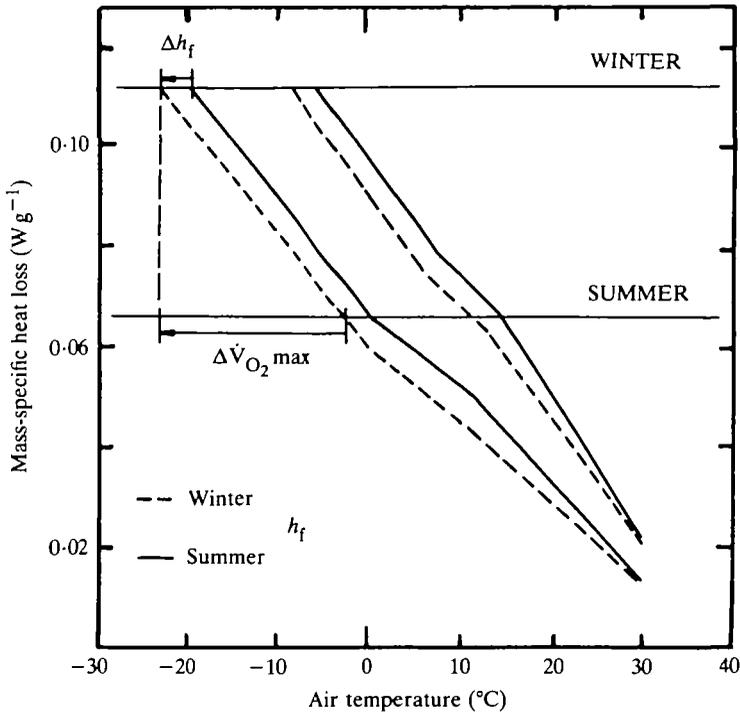


Fig. 8. Extension of the minimum air temperature for thermoregulation due to an increased thermogenic capacity ($\Delta \dot{V}_{O_2 \text{ max}}$) and decreased fur conductance (Δh_f).

of fur on the appendages (Bakken, 1981). However, characterization of the fur properties of deer mice is simplified by several factors. First, a clear distinction exists between the furred torso and the unfurred appendages. Second, the fur tends to cover the body contours, which permits using a simple geometry to represent the fur surface area. Third, significant variation in fur properties exists only between the dorsum and ventrum of the torso. Thus for the deer mouse representation of the fur structural properties is straightforward: the surface-area weighted mean of the dorsal and ventral values represents the fur structure, while a prolate spheroid geometry represents fur surface area.

To evaluate our representation of fur properties for use in the model of fur heat transfer, heat loss from the mouse was varied by the control of air (t_a) and radiative temperature (t_r). Control of the temperature of the wall surrounding the mouse (Fig. 1) permitted thermal radiation exchange to be varied independently from other avenues of heat loss. Thermocouples placed beneath the skin of the appendages and torso permitted calculation of heat loss from the appendages and prediction of fur heat loss under each condition. Subtraction of appendage heat loss from the measured net heat production (\dot{Q}_N) yielded heat loss from the furred torso (\dot{Q}_{tor}) for comparison with the predicted fur heat loss (\dot{Q}_f).

Heat loss from the torso significantly increased with decreases in air temperature (Fig. 3). In addition, control of wall temperature at each air temperature resulted in

significant changes in thermal radiation exchange from the torso at 27 and 34°C (Fig. 4). The predicted change in radiative heat loss from the fur fell within the 95% confidence intervals of the mean values determined for the torso at each radiative temperature. A similar close agreement was found for all thermal conditions, as shown by a slope not different from one (0.99) for the regression relating torso to fur heat loss (Fig. 5). Thus, good agreement was found between torso heat loss and the heat loss predicted using the structural properties of fur (Figs 4, 5) over a wide range of heat losses manipulated by both air and radiative temperature. This close agreement validates our representation of the fur properties of deer mice in this model and indirectly confirms the model of heat loss from the appendages (Conley & Porter, 1985). Together these models yield a physical representation of heat transfer which, in combination with models of the delivery of heat to the skin surface (Fig. 2), permit calculation of thermoregulatory heat loss in the habitats occupied by deer mice.

Model simulations

The similarity of summer acclimatized deer mice (*P. maniculatus* and *P. leucopus*) in fur properties (Stromberg, 1979) and thermogenic capacity (Hill, 1983) is also true for the seasonal changes in these properties. Both species show large increases in thermogenic capacity due to cold acclimation (40%, *P. maniculatus*; Heimer & Morrison, 1978) or winter acclimatization (70%, *P. leucopus*; Wickler, 1980). We chose the latter value for the model simulations because it represents natural seasonal acclimatization rather than laboratory cold acclimation. The increased thermogenic capacity that accompanied winter acclimatization greatly reduces the minimum temperature for thermoregulation under all environmental conditions (Fig. 7). Under calm, cloudy conditions, the increased thermogenic capacity extends this minimum temperature from 0°C for summer mice to -23°C for winter mice.

Winter acclimatization is also apparent for fur in both species based on either structural or thermal properties (Table 4). The increase reported for fur density (19%, *P. maniculatus*; Table 4) was similar to the relative increase found for fur insulation (27%; *P. maniculatus*) and thermal conductance (19%; *P. leucopus*). This similarity, along with the small influence of fur depth (Fig. 6), suggests that density differences underlie these seasonal insulation changes. An increase in the fur density of 19% results in an extension of the minimum temperature by 5°C, which was still far less than the 20°C found for an increased thermogenesis (Fig. 5). These results confirm reports by others that for small endotherms in general an increased thermogenic capacity rather than increased insulation plays the major role in permitting thermoregulation under winter conditions (Dawson & Carey, 1976; Hill, 1983; Wickler, 1980).

Environmental conditions also influence heat loss, elevating the minimum air temperature for thermoregulation by 15°C over the range of wind and thermal radiation conditions (Fig. 7). Under calm, cloudy conditions, the limit to thermoregulation is -23°C, which approximates the extreme air temperature expected in areas where the deer mice are known to be active throughout the winter (i.e. -25°C;

Merritt, 1984; Stromberg, 1979; Wickler, 1980). The additional heat loss to a clear sky or wind would increase this minimum temperature to as high as -8°C (Fig. 7), above the mean minimum temperature at night for the winter months (-10°C ; Stromberg, 1979; Wickler, 1980). Thermoregulation is possible under the extreme temperatures for calm, cloudy conditions, but the added heat loss to wind or the sky could limit thermoregulation to temperatures above that typically found during winter in the deer mouse habitats. Measurements reveal that air temperature remains above -5°C under leaf litter or within snow tunnels (subnivean environment) although air temperature above ground drops to -25°C (Merritt, 1984). The environment in subsurface runways would be similar to overcast, calm conditions since there is no exposure to either a clear night sky or wind. Not only would thermoregulation be possible throughout the winter at the air temperatures found in these subsurface environments, but the energetic cost of thermoregulation would also be greatly reduced compared to the exposed surface environment.

Heat loss could also be reduced by maintenance of a body temperature lower than 37°C . Hypothermia is frequently observed as daily torpor in deer mice and, in addition, a range of body temperatures from 32 to 39°C have been observed in alert deer mice (see Hill, 1983). However, thermogenic capacity decreases at lower body temperatures (Conley, Weibel, Taylor & Hoppeler, 1985). Thus, the extension of the air temperature limits due to a reduced heat loss may be counteracted by a reduced thermogenic capacity. The 37°C used here is close to the body temperature found for deer mice when exposed to air temperatures as low as -20°C (Wickler, 1980).

In conclusion, calculations reveal that the thermogenic and fur properties of deer mice, and the environmental conditions they encounter, significantly affect the air temperature limits for thermoregulation. The increase that occurs in thermogenic capacity between summer and winter plays the major role in extending these limits for thermoregulation in accordance with the seasonal changes in environmental conditions that occur in the habitats of deer mice. Despite these adaptations, conditions are possible within this microclimate under which maintenance of a high body temperature is not possible, thereby restricting deer mice to the protective environment within the leaf litter or the subnivean environment.

APPENDIX

<i>Symbols</i>	<i>Quantities</i>	<i>Units</i>
<i>A</i>	surface area	m^2
<i>Bi</i>	Biot number	unitless
<i>C</i>	thermal conductance	$\text{W m}^{-2}\text{C}^{-1}$
<i>C₁</i>	normalization function	unitless
<i>D</i>	diameter	m
<i>F</i>	configuration factor	unitless
<i>h</i>	conductance	$\text{W m}^{-2}\text{C}^{-1}$
<i>K</i>	total conductance	$\text{W}^{\circ}\text{C}^{-1}$.

k	conductivity	$\text{W m}^{-1} \text{ } ^\circ\text{C}^{-1}$
L	length	m
M	mass	g
Nu	Nusselt number	unitless
ρ	density	hairs m^{-2}
\dot{Q}	heat flow rate	W
Re	Reynolds number	unitless
t	temperature	$^\circ\text{C}$
T	thermodynamic temperature	K
\dot{V}	volume flow rate	ml min^{-1} (STPD)
z	depth	m
β	radiative absorption coefficient	m^{-1}
δ	correction factor	unitless
ε	emissivity	unitless
σ	Stefan-Boltzmann constant	$\text{W m}^{-2} \text{K}^{-4}$
τ	transmittance	unitless

Subscripts

a	air	en	environment	p	polyethylene
app	appendage	f	fur	r	radiative
bb	black body	fe	feet	s	surface (skin)
bp	black paint	g	ground	sk	sky
c	core	h	hair	ta	tail
ca	cast	in	internal	tor	torso
cv	convective	m	mouse	w	wall
E	evaporative	M	metabolic	x	x direction
e	ear	N	net	y	y direction
eff	effective	o	oil		

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REFERENCES

- BAKKEN, G. S. (1981). A two-dimensional operative temperature model for thermal energy management by animals. *J. therm. Biol.* **6**, 23–30.
- BEHNEY, W. H. (1936). Nocturnal explorations of the forest deer-mouse. *J. Mammal.* **17**, 225–230.
- CENA, K. & CLARK, J. A. (1979). Transfer of heat through animal coats and clothing. In *International Review of Physiology, Environmental Physiology III*, vol. 20 (ed. D. Robertshaw), pp. 1–42. Baltimore: University Park Press.

- CENA, K. & MONTEITH, J. L. (1975a). Transfer processes in animal coats. I. Radiative transfer. *Proc. R. Soc. B* **188**, 377–393.
- CENA, K. & MONTEITH, J. L. (1975b). Transfer processes in animal coats. II. Conduction and convection. *Proc. R. Soc. B* **188**, 395–411.
- CHAFFEE, R. & ROBERTS, J. (1971). Temperature acclimation in birds and mammals. *A. Rev. Physiol.* **33**, 155–202.
- CHAPPELL, M. A. (1980a). Insulation, radiation, and convection in small arctic mammals. *J. Mammal.* **61**, 268–277.
- CHAPPELL, M. A. (1980b). Thermal energetics and thermoregulatory costs of small arctic mammals. *J. Mammal.* **61**, 278–291.
- CHAPPELL, M. A. & HOLSCLAW, D. S. (1984). Effects of wind on thermoregulation and energy balance in deer mice (*Peromyscus maniculatus*). *J. comp. Physiol.* **154B**, 619–625.
- CONLEY, K. E. (1983). A heat transfer analysis of thermoregulatory heat loss in the deer mouse, *Peromyscus maniculatus*. Ph.D. thesis, Department of Zoology, The University of Wisconsin-Madison.
- CONLEY, K. E. & PORTER, W. P. (1985). Heat loss regulation: role of appendages and torso in the deer mouse and the white rabbit. *J. comp. Physiol.* **155B**, 423–431.
- CONLEY, K. E., WEIBEL, E. R., TAYLOR, C. R. & HOPPELER, H. (1985). Aerobic capacity estimated by exercise *vs* cold-exposure: endurance training effects in rats. *Respir. Physiol.* **62**, 273–280.
- DAVIS, L. B. & BIRKEBAK, R. C. (1974). On the transfer of energy in layers of fur. *Biophys. J.* **14**, 249–268.
- DAWSON, W. R. & CAREY, C. (1976). Seasonal acclimatization to temperature in cardueline finches. I. Insulative and metabolic adjustments. *J. comp. Physiol.* **112**, 317–333.
- FEDAK, M. A., ROME, L. & SEEHERMAN, H. J. (1981). One-step N₂-dilution technique for calibrating open-circuit V_{O₂} measuring systems. *J. appl. Physiol.* **51**, 772–776.
- GATES, D. M. (1980). *Biophysical Ecology*. New York: Springer-Verlag, 611 pp.
- GAUTSCHI, W. & CAHILL, W. F. (1964). Exponential integral and related functions. In *Handbook of Mathematical Functions* (ed. M. Abramowitz & I. A. Stegun), pp. 227–252. New York: Dover.
- GUBAREFF, G. G., JANSSEN, J. E. & TORBORG, R. H. (1960). *Thermal Radiation Properties Survey: a Review of the Literature*, 2nd edn. Minneapolis: Honeywell Research Center.
- HART, J. S. (1956). Seasonal changes in insulation of the fur. *Can. J. Zool.* **34**, 53–57.
- HEIMER, W. & MORRISON, P. (1978). Effects of chronic and intermittent cold exposure on metabolic capacity of *Peromyscus* and *Microtus*. *Int. J. Biometeorol.* **22**, 129–134.
- HILL, R. W. (1983). Thermal physiology and energetics of *Peromyscus*; ontogeny, body temperature, metabolism, insulation and microclimatology. *J. Mammal.* **64**, 19–37.
- HUESTIS, R. R. (1931). Seasonal pelage differences in *Peromyscus*. *J. Mammal.* **12**, 372–375.
- KOWALSKI, G. J. & MITCHELL, J. W. (1976). Heat transfer from spheres in the naturally turbulent, outdoor environment. *J. Heat Trans., Series C* **98**, 649–653.
- KOWALSKI, G. J. & MITCHELL, J. W. (1979). An analytical and experimental investigation of the heat transfer mechanisms within fibrous media. *Am. Soc. mech. engng Paper*, 79-WA/HT-40, 1–7.
- MCCLURE, P. A. & PORTER, W. P. (1983). Development of fur insulation in neonatal cotton rats (*Sigmodon hispidus*). *Physiol. Zool.* **56**, 18–32.
- MERRITT, J. F. (1984). Growth patterns and seasonal thermogenesis of *Peromyscus maniculatus* inhabiting the Appalachian and Rocky mountains of North America. *Ann. Carnegie Mus.* **53**, 527–548.
- MITCHELL, J. W. (1976). Heat transfer from spheres and other animal forms. *Biophys. J.* **16**, 561–569.
- MOUNT, L. E. (1964). Radiant and convective heat loss from the new-born pig. *J. Physiol., Lond.* **173**, 96–113.
- PORTER, W. P. & BUSCH, R. L. (1978). Fractional factorial analysis of growth and weaning success in *Peromyscus maniculatus*. *Science* **202**, 907–910.
- PORTER, W. P. & GATES, D. M. (1969). Thermodynamic equilibria of animals with environment. *Ecol. Monogr.* **39**, 245–270.

- PORTER, W. P. & MCCLURE, P. A. (1984). Climate effects on growth and reproduction potential in *Sigmodon hispidus* and *Peromyscus maniculatus*. In *Winter Ecology of Small Mammals* (ed. J. F. Merritt). *Spec. Publ., Carnegie Mus. nat. Hist.* **10**, 173–181.
- SEALANDER, J. A. (1951). Survival of *Peromyscus* in relation to environmental temperature and acclimation at high and low temperatures. *Am. Midl. Nat.* **46**, 257–311.
- SELBY, S. M. (1972). *Standard Mathematical Tables*, 20th edn. Cleveland, OH: The Chemical Rubber Co.
- SIEGEL, R. & HOWELL, J. R. (1972). *Thermal Radiation Heat Transfer*. New York: McGraw-Hill.
- SKULDT, D. J., BECKMAN, W. A., MITCHELL, J. W. & PORTER, W. P. (1975). Conduction and radiation in artificial fur. In *Perspectives in Biophysical Ecology, Ecological Studies*, vol. 12 (ed. D. M. Gates & R. B. Schmerl), pp. 549–558. New York: Springer-Verlag.
- STROMBERG, M. R. (1979). Experimental analysis of habitat performance and direct observation of deer mice (*Peromyscus*) in southern Wisconsin. Ph.D. thesis, Department of Zoology, The University of Wisconsin-Madison.
- SWINBACK, W. C. (1963). Longwave radiation from clear skies. *Q. Jl R. met. Soc.* **89**, 339–348.
- WATHEN, P., MITCHELL, J. W. & PORTER, W. P. (1971). Theoretical and experimental studies of energy exchange from jackrabbit ears and cylindrically shaped appendages. *Biophys. J.* **11**, 1030–1047.
- WATHEN, P. W., MITCHELL, J. M. & PORTER, W. P. (1974). Heat transfer from animal appendage shapes – cylinders, arcs and cones. *J. Heat Trans., Series C* **10**, 536–540.
- WICKLER, S. J. (1980). Maximal thermogenic capacity and body temperatures of white-footed mice (*Peromyscus*) in summer and winter. *Physiol. Zool.* **53**, 338–346.
- WOLFE, W. L. (1964). *Handbook of Military Technology*. Washington, DC: US Government Printing Office.