Effects of wind on thermoregulation and energy balance in deer mice (*Peromyscus maniculatus*)

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Summary. The effects of various convective and temperature regimes on heat production, evaporative heat loss, and thermal resistance were studied in deer mice, *Peromyscus maniculatus*. Heat production (measured as oxygen consumption) increased with increasing wind speed (V) and decreasing ambient temperature (T_a), except at $T_a = 35\ °C$ which was thermoneutral for all V from 0.05 through 3.75 m/s. Evaporative water loss ($\dot{V}_{H_2O}$) increased with increasing T_a, but wind had little effect on $\dot{V}_{H_2O}$ except at high T_a. In the absence of forced convection, the animals' total resistance to heat transfer (r_t) was high and stable at T_a below thermoneutrality. However, at high V the r_t increased steadily with decreasing T_a. Although deer mice rarely experience high wind speeds in natural microhabitats, the convective regime is nevertheless important in determining rates of heat loss, and must be considered in studies of ecological energetics.

Introduction

Wind is a factor in the thermal balance of many terrestrial organisms, but it is particularly important for small endotherms. There have been numerous theoretical treatments of the effects of wind on energy exchange between organisms and their surroundings (e.g. Porter and Gates 1969; Monteith 1973; Davis and Birkebak 1975; Bakken 1976). In addition to the theoretical work, empirical studies of heat transfer in different convective environments have been performed on several birds (Gessaman 1972; Robinson et al. 1976; Hayes and Gessaman 1980; Bakken 1980; Goldstein 1983). In contrast, wind effects on mammals have received surprisingly little attention. Most of the existing studies have been based on heat exchange from pelt-covered metal models (Heller 1972; Chappell 1980; Chappell and Bartholomew 1981), or on simple geometrical forms covered with artificial fur (Kowalski and Mitchell 1980). Models can generate useful approximations, but they cannot duplicate many important responses of living mammals, such as vasomotor control and postural and pelage adjustments (McClure and Porter 1983).

The present study was designed to supplement the work on models with direct measurements on living small mammals. As part of an investigation of the thermoregulatory energy requirements of deer mice (*Peromyscus maniculatus*) in different natural environments, we determined rates of oxygen consumption and evaporative water loss in a variety of combinations of ambient temperature and wind speed. The gas exchange data allowed calculation of metabolic heat production, evaporative heat loss, and thermal resistance, which provide insights into the animals' ability to adjust rates of heat transfer.

Materials and methods

Animals. Deer mice (*Peromyscus maniculatus*) were housed in $30 \times 18 \times 12$ cm plastic cages in a 20–22 °C room kept on photoperiods approximately matched to the prevailing natural light-dark cycle. The animals were provided with laboratory mouse

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Symbols and Abbreviations: A animal surface area; HP_n net metabolic heat production; *EHL* evaporative heat loss; *MHP* metabolic heat production; r_t total resistance to heat transfer; r_{ext} external resistance component of r_t; *RQ* respiratory quotient; pc_p volumetric specific heat of air; T_a ambient temperature; t_b body temperature; t_e operative, or equivalent blackbody temperature of the environment; T_{sk} skin temperature; T_{es} standard operative temperature; V wind speed; $\dot{V}_{O_2}$ oxygen consumption; $\dot{V}_{CO_2}$ carbon dioxide production; $\dot{V}_{H_2O}$ evaporative water loss

chow and water *ad libitum*, supplemented occasionally with fresh fruit or vegetables. Mice (subspecies *sonoriensis*) were obtained from populations in eastern California. Some of the individuals used in the study were wild-caught; the rest were from laboratory lines periodically outbred to wild-caught stock. All animals were adults (mean body mass 21.3 g) that had been kept in the lab for at least six months prior to experiments.

Measurements. Most experiments were performed in an airtight closed-loop wind tunnel (internal volume approximately 3800 ml) constructed of aluminum and Plexiglas. Wind speed (V) in the tunnel could be continuously adjusted between 0.15 m/s and 4.5–5 m/s by means of a rheostat. During experiments, V was measured by a 'hot-bead' anemometer (Chappell and Bartholomew 1981) located upstream from, and calibrated for, the test section. Calibrations were performed with a life-sized pelt-covered model mouse in the center of the test section. A Thermonetics hot-wire anemometer was placed in the test section midway between the tunnel wall and the model mouse. Measurements of V in this location automatically compensated for any increase in air velocity in the test section due to blockage effects from the mouse. Ambient temperature (T_a) was obtained from several copper-constantan thermocouples attached to the interior wall and wired in parallel so as to average T_a. During runs, air temperatures did not differ from wall temperature by more than 1 °C. Within the test area (6 × 6.5 × 9 cm), air velocity was constant (plus or minus 15%) at all points in the cross-section except the extreme edges and corners (measured with the hotwire anemometer).

Measurements in the absence of forced convection were performed in a small aluminum chamber (internal volume approximately 800 ml) with a Plexiglas lid. At the flow rates used, air velocity in this apparatus averaged 0.05 m/s (measured with the hotwire anemometer with a model mouse in the chamber). The T_a was measured with several thermocouples attached to the chamber walls. In both wind tunnel and small chamber the mice sat on screen wire platforms over mineral oil, which covered any urine and feces voided during runs. The metabolism chambers were placed in an environmental chamber which could control temperature within 0.5 °C. We obtained data at six wind speeds between 0.05 and 3.75 m/s at temperatures of 0, 5, 10, 20, 30, and 35 °C; at −10 °C the mice were unable to maintain constant body temperature in windy conditions, so experiments at this temperature were performed only in the absence of forced convection. At least five (usually 8–10) mice were run at each combination of T_a and V. Animals were not starved prior to experiments and were kept in the apparatus for a maximum of 4 h at a time; each mouse required several runs to obtain complete data at all wind speed-temperature combinations. Runs were started at low or high T_a and low or high V on a random basis. The mice did not tolerate rectal thermocouples, so we were unable to obtain continuous body temperature (T_b) data during experiments. We spot-checked T_b at various wind-temperature regimes by quickly removing mice from the chambers and taking T_b readings with 36-gauge thermocouples inserted 1.5–2 cm into the rectum (T_b was read from a Bailey BAT-12 thermometer resolving 0.1 °C). Data from mice that became obviously hypothermic (as shown by uncontrollable shivering, lack of coordination, and/or T_b below 32 °C) were rejected. Hypothermia occurred only at low T_a (0–5 °C) and high V (2–3 m/s) in a few individuals; most mice were able to keep T_b above 34 °C throughout runs.

An open-circuit gas flow system was used for all experiments. Flowrates (800–1000 ml/min STP) of dry, CO_2-free air were maintained (plus or minus 1%) with Applied Materials mass flow controllers. Approximately 100 ml/min of the excurrent air from the chambers was diverted through a humidity

sensor (Weather Measure HT-100R), dried, passed through a CO_2 sensor (Applied Electrochemistry CD-3A), passed through CO_2 absorbent, dried again, and passed through an oxygen sensor (Applied Electrochemistry S-3A). The humidity meter was calibrated over salt solutions to within 0.5% R.H., and the CO_2 and oxygen analyzers were accurate to within 0.01% and 0.001%, respectively. During experiments, all gas sensors were periodically referenced against air diverted from immediately upstream of the metabolism apparatus. The concentration of O_2 in the chambers never fell below 20.4%, CO_2 concentrations never exceeded 0.5%, and chamber relative humidity never exceeded 50%. Response time of the system was 30–40 s. Data from thermocouples and gas analyzers were recorded every 20 s by a computer equipped with a precision analog-to-digital converter.

Data analysis. At each wind speed and temperature combination, oxygen consumption ($\dot{V}_{O_2}$), carbon dioxide production ($\dot{V}_{CO_2}$), and evaporative water loss ($\dot{V}_{H_2O}$) were averaged over periods of 10–15 min during which the animals were quiet and measurements were stable. The $\dot{V}_{O_2}$ was corrected for CO_2 removal according to the equations of Hill (1972). Metabolic heat production (MHP) and evaporative heat loss (EHL), both in watts (W), were calculated from $\dot{V}_{O_2}$ and $\dot{V}_{H_2O}$, using conversion factors of 20.1 Joules/ml O_2 and 2401 Joules/g H_2O. Net heat production (HP_n) was equal to MHP − EHL.

Rates of heat flow were analyzed using the conceptual framework of heat transfer resistances in order to facilitate comparison to other studies (Monteith 1973; Robinson et al. 1976; Chappell and Bartholomew 1981). The units for resistance are seconds/meter (s/m), which may be converted into the more familiar units of insulation (°C·m²/W) by dividing resistance by the volumetric specific heat of air (ρc_p; Joules/[m³· °C]). Values of ρc_p for the T_a used in this study were obtained from Tracy et al. (1980).

Surface areas were not difficult to estimate, since at almost all wind-temperature combinations the mice fluffed their fur and sat in the center of the test section, facing into the wind. In this posture their body form was approximately a sphere with diameter 3.2–3.5 cm. Surface area (A) was therefore 0.0035–0.0038 m². Diameter, and hence A, tended to decrease slightly at high V because of flattening of the fur. Total resistance (r_t) was calculated essentially as described in Robinson et al. (1976), but with a slightly modified equation:

$$r_t = [\rho c_p \cdot A(T_b - T_e)]/HP_n \tag{1}$$

In these experiments, T_e (the equivalent blackbody temperature of the environment) was approximately equal to the chamber wall temperature T_a. The $T_b - T_a$ gradient was computed using the following empirically-derived values for T_b: 41 °C at $T_a = 35$ °C; 39.5 °C at $T_a = 30$ °C; 37.5 °C at $T_a = 20$ °C; 36.5 °C at $T_a = 10$ °C, and 35 °C at T_a below 10 °C. Hill (1983) reported comparable data for several *Peromyscus* species including *P. maniculatus*. The largest uncertainty in T_b estimates (plus or minus about 2 °C) occurred at the lowest T_a where it had the smallest proportional effect on estimates of the $T_b - T_a$ gradient. The largest potential error from this source in calculations of r_t (Eq. 1) is about 8–10%.

Results

Oxygen consumption and carbon dioxide production

Oxygen consumption of the mice (ml/[g·min]) was strongly affected by both temperature and wind speed, with increasing wind speeds eliciting in-
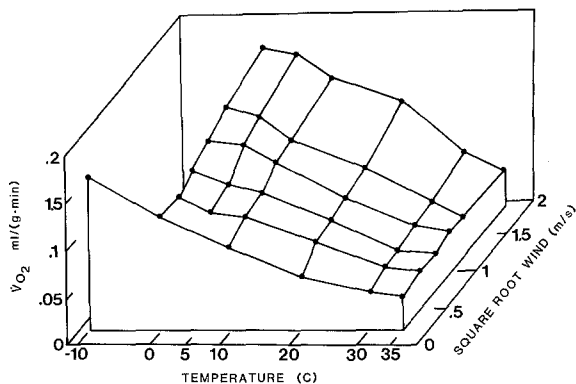
Fig. 1. Oxygen consumption ($\dot{V}_{O_2}$) of deer mice at different combinations of wind speed and ambient temperature. Dots are means of data points from at least five individuals

Fig. 2. Oxygen consumption as a function of wind speed at three ambient temperatures. Vertical lines are two standard errors

creased $\dot{V}_{O_2}$. At a given T_a, the $\dot{V}_{O_2}$ changed approximately as a linear function of the square root of wind speed (Fig. 1). The only exceptions to this general rule occurred at the highest T_a (30 and 35 °C), which were presumably within the thermal neutral zone. As can be seen in Fig. 2, wind had no effect on $\dot{V}_{O_2}$ at 35 °C and little effect at 30 °C until V exceeded about 1.5 m/s. The $\dot{V}_{O_2}$'s at 20 °C at all V were significantly higher than the corresponding 30 and 35 °C values. Hence, the thermoneutral zone for warm-acclimated *P. maniculatus sonoriensis* probably extends from about 25 °C (with no forced convection) through 30 °C (at low to moderate wind speeds) to at least 35 °C (in all convective regimes tested). If the thermoneutral data are excluded, $\dot{V}_{O_2}$ is accurately described by a two-way multiple regression:

$$\dot{V}_{O_2} = 0.116 - 0.003(T_a) + 0.0304(V^{0.5}) \qquad (2)$$
$$(r^2 = 0.85, P < 10^{-5})$$

A least-squares regression including only T_a is also significant, but has lower predictive value ($r^2 = 0.70$).

Maximum rates of oxygen consumption ($\dot{V}_{O_2}$ max) were elicited at -10 °C in the absence of forced convection and at 0 °C at wind speeds of 3–4 m/s. All animals quickly became hypothermic at -10 °C if V exceeded 0.5–1 m/s. The observed values of $\dot{V}_{O_2}$max (about 0.175 ml/[g·min] or 10.5 ml/[g·h]) were approximately the same as reported for warm-acclimated *Peromyscus leucopus* (Wickler 1980). There was no difference between the $\dot{V}_{O_2}$max values of wild-caught and lab-reared mice.

Rates of carbon dioxide production ($\dot{V}_{CO_2}$) closely paralleled the $\dot{V}_{O_2}$ data. The respiratory quotient (RQ) was usually about 1.0 at high T_a, falling to 0.7–0.8 in colder conditions. There was also some tendency for RQ to drop after the ani-
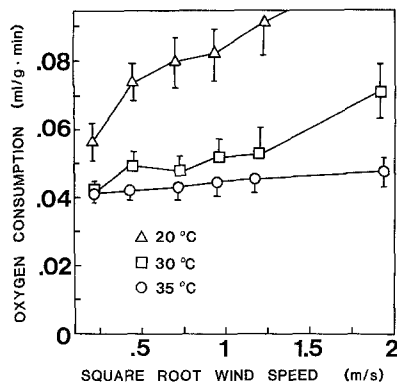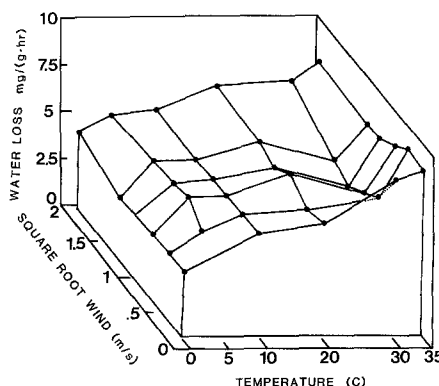

Fig. 3. Evaporative water loss from deer mice at different combinations of wind speed and ambient temperature. Dots are means of data points from at least five individuals

mals had been in the chamber for several hours; this probably indicated a shift to stored fats as the primary substrate for energy metabolism.

Water loss

We anticipated a considerable difference in rates of evaporative water loss over the various wind-temperature combinations, but the observed values were surprisingly constant (Fig. 3). Wind speed had little effect, although increased V was usually accompanied by a slight increase in $\dot{V}_{H_2O}$. As expected, there was an abrupt increase in $\dot{V}_{H_2O}$ between T_a's of 30 and 35 °C (the increase was more gradual at the lowest and highest wind speeds). Figure 4 shows the transition between the two T_a's in more detail. There was considerable individual variation in $\dot{V}_{H_2O}$, but the values for 30 °C averaged 20–30% lower than at 35 °C.

Rates of evaporation from deer mice are affected by water vapor density as well as temperature (Edwards and Haines 1978; Welch 1980).
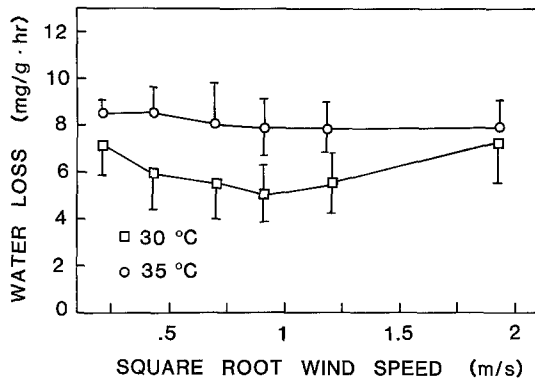
Fig. 4. Evaporative water loss as a function of wind speed at two ambient temperatures. Vertical lines are two standard errors
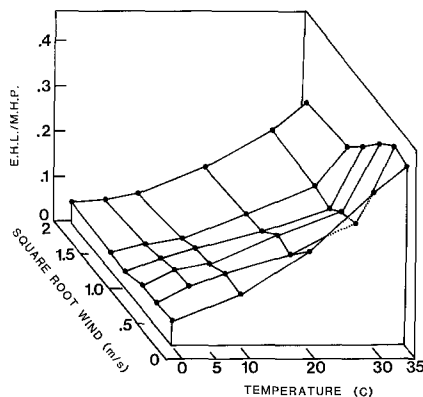

Fig. 6. Reynolds (Re) and Nusselt (Nu) numbers calculated from data on wind speed, metabolic heat production, and evaporative heat loss

Fig. 5. The ratio of evaporative heat loss to metabolic heat production ($E.H.L./M.H.P$) at different combinations of wind speed and temperature. Dots are means of data points from at least five individuals

During the present study, vapor density in the metabolism chambers was 1.5–6 g H_2O/m^3 at all T_a, well below saturation levels. The observed rates of evaporation were similar to those reported by Welch (1980) at comparable temperatures and vapor densities.

The ratio of evaporative heat loss to metabolic heat production (EHL/MHP, Fig. 5) rose smoothly from about 0.05 at low temperatures and high wind speeds to 0.15–0.2 at $T_a = 30$ °C, increasing more abruptly to 0.25–0.4 at $T_a = 35$ °C. Wind speed had little effect except at high T_a; at 30 and 35 °C, the EHL/MHP ratio decreased considerably with increasing V.

Nusselt and Reynolds numbers

The convective characteristics of animals of different sizes and shapes can be conveniently compared by converting heat loss data into Reynolds (Re) and Nusselt (Nu) numbers. The Re is an expression
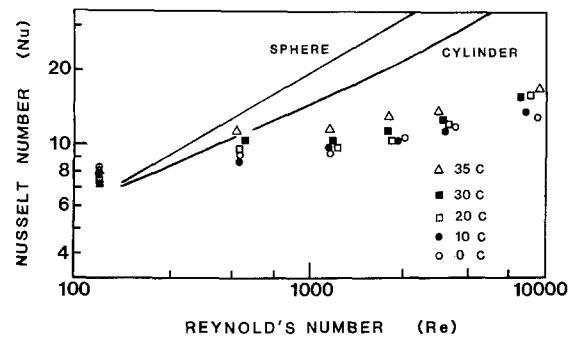
of the relationship between body size and wind speed, and Nu is a nondimensional heat transfer coefficient. Using data on net heat production, we calculated Nu for deer mice at all combinations of T_a and V. The body diameter (fur tip to fur tip; 3.2–3.5 cm) was used as the characteristic dimension to compute Re. When plotted against Re (Fig. 6), the calculated Nu data were close to the values expected for ideal spheres and cylinders at low Re, but less than the sphere and cylinder values at high Re (the regression equation was: log Nu = $0.500 + 0.172$[log Re]; $r^2 = 0.81$; $N = 30$). Results from studies of model animals and fur-covered cylinders are comparable, except than in most cases regressions of Nu on Re were approximately parallel to the lines for ideal spheres and cylinders (Mitchell 1976; Chappell 1980; Kowalski and Mitchell 1980).

Resistance to heat transfer

As expected, the total resistance to heat transfer, r_t, was strongly affected by wind speed. At all T_a, r_t decreased approximately as an inverse function of $V^{0.5}$ (Figs. 7, 8). Previous analyses of the effects of forced convection on pelage indicated that wind should have no effect on heat transfer until a critical windspeed is exceeded (Davis and Birkebak 1975; Kowalski and Mitchell 1980). However, we could not discern any nonzero critical windspeed – significant changes in r_t occurred even between V as low as 0.05 and 0.2 m/s (Fig. 8).

In the absence of forced convection, r_t increased rapidly as T_a fell from 35 to 20 °C, remaining high at lower T_a. This trend is consistent with the observed lower critical temperature of about 25 °C in unstirred air.
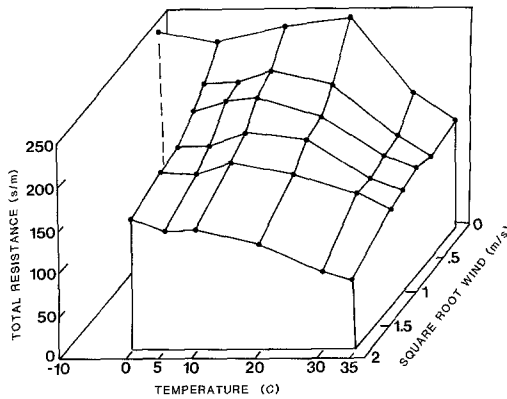
Fig. 7. Total thermal resistance of deer mice at different combinations of wind speed and ambient temperature. Dots are means of data points from at least five individuals
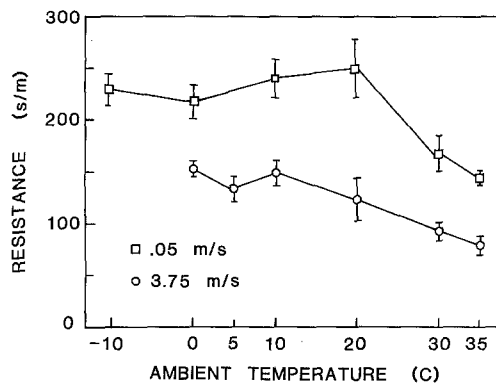

Fig. 8. Total thermal resistance as a function of ambient temperature for two different wind speeds. Vertical lines are two standard errors

In contrast, at high V the r_t continued to increase at T_a considerably cooler than the lower critical temperature (33–35 °C at $V=3.75$ m/s; Fig. 2), although resistance showed signs of leveling at 10 °C and below. Since the external component of resistance (r_{ext}) is fairly constant at a given wind speed (except for minor temperature effects), the observed changes in r_t must be related to actions by the animal, probably peripheral vasoconstriction or vasodilation and/or pelage adjustments. At low V, deer mice could change r_t by a factor of 1.7 (from 145 s/m at 35 °C to 245 s/m at 20 °C). At high wind speeds ($V=3.75$ m/s), r_t changed by a factor of 1.9 (from 85 to 152 s/m) between T_a's of 35 and 0 °C.

Discussion

The conventional model of endothermic temperature regulation (e.g., Bartholomew 1977) assumes that within the zone of thermoneutrality, endo-

therms maintain stable body temperatures by adjusting thermal resistance to match rates of heat loss to the (relatively constant) rate of metabolic heat production. When the 'operative' or 'environmental' temperature (the combined thermal effects of ambient temperature, radiant load, and convective regime) falls below thermoneutrality, resistance to heat transfer is maximized and at lower temperatures the animal must increase metabolic heat production to match the increased rate of heat loss. In contrast, water loss is expected to be low at air temperatures below thermoneutrality, becoming progressively larger as T_a rises to the upper end of the thermoneutral zone. This change is partially due to the increased potential for evaporation at higher T_a. Also, as the $T_b - T_a$ gradient decreases and sensible heat transfer becomes difficult, animals must increase evaporative heat loss to dissipate metabolic heat production.

Based on this general model of endotherm temperature regulation, and on new approaches explicitly incorporating different convective regimes (e.g., Kowalski and Mitchell 1980; McClure and Porter 1983), a number of predictions can be made about the effects of wind on thermoregulation in deer mice:

(1) Wind increases the rate of heat loss by disrupting the pelage and the boundary layer surrounding the animal. Assuming the animal maintains a relatively constant T_b, at temperatures below thermoneutrality the rate of heat production should increase with increasing wind speed, as well as with decreasing ambient temperature.

(2) High wind speeds should shift the animal's thermoneutral temperature range upwards, so (again assuming that T_b is constant) in high winds the animal should maximize its thermal resistance and begin increasing metabolic heat production at higher T_a's than in the absence of forced convection.

(3) At high T_a, increased convective heat transfer should reduce the requirement for evaporative heat loss (unless T_a exceeds the maximum tolerable T_b).

Heat production and evaporative heat loss

In some respects the deer mice matched these predictions closely. Metabolic heat production (measured as oxygen consumption) was strongly correlated with both air temperature and wind speed, except at T_a's within the thermoneutral zone (roughly 30 °C and above). At any T_a below about 25 °C, the change from unstirred air to a wind of 3.75 m/s was equivalent to reducing T_a by 10 °C

at constant low V. Bakken (1976, 1980) suggests use of an artificial 'standard operative temperature' index (T_{es}), which incorporates wind-induced resistance changes to normalize thermal conditions to standard convective environments (e.g., metabolism chambers). If blackbody radiant conditions and a standard convective regime of $V=0.05$ m/s are assumed, the T_{es} for deer mice can be expressed as:

$$T_{es} = T_a - (2.67 \cdot V^{0.5}) \qquad (3)$$

Also as predicted by the general model, at high T_a increases in wind speed were associated with decreased evaporative water loss, although there was considerable variability in $\dot{V}_{H_2O}$. The trend was most apparent at 30 °C (Fig. 4), and can also be seen in the EHL/MHP ratios (Fig. 5). A rise in $\dot{V}_{H_2O}$ at high V at 30 °C probably resulted from increased $\dot{V}_{O_2}$ and the associated increase in ventilation. A similar interaction between MHP requirements, ventilation, and $\dot{V}_{H_2O}$ may be responsible for the relatively high rates of water loss observed at T_a below thermoneutrality.

Heat transfer and thermal resistance

Analysis of heat transfer and thermal resistance was complicated by the uneven distribution of air velocity over the animals. Because the mice were perched on a platform rather than suspended in the air stream (e.g., Heller 1972; Robinson et al. 1976; Chappell 1980), air velocity on the dorsal and lateral surfaces was probably higher than on the belly and legs. Values of V used in calculations of Nusselt and Reynold's numbers were therefore accurate over no more than 60–70% of the animals' pelage surface. That error, along with postural changes and, more importantly, the physiological adjustments of piloerection and peripheral vasoconstriction, probably account for the low values of Nu observed at high V. Regardless of interpretive difficulties, the conditions in these experiments are probably representative of those faced by wild mice, which spend most of their time on the ground.

In the absence of forced convection, the thermal resistance of the mice conformed to expectations. Resistance was low at $T_a = 35$ °C, increasing rapidly to a maximum at $T_a = 20$ °C – slightly below thermoneutrality according to the oxygen consumption data. The maximum values of r_t for deer mice in unstirred air were about 62% of those reported for a similar-sized bird, the white-crowned sparrow (Robinson et al. 1976), and slightly greater than in the larger (90 g) but more sparsely-

furred antelope ground squirrel (Chappell and Bartholomew 1981). At temperatures below 20 °C, resistance dropped slightly, but the decrease was not statistically significant. The drop in resistance may be associated with increased perfusion of the extremities to keep them from becoming too cold. A similar response was reported for white-crowned sparrows by Robinson et al. (1976).

At high wind speeds the thermal resistances of deer mice did not respond as expected to changes in air temperature. The lower limit of thermoneutrality is about 35 °C at $V=3.75$ m/s (Fig. 1), so if mice conform to the standard model the r_t at this wind speed should be high and constant at all T_a below 35 °C. Instead, r_t was relatively low at 30–35 °C and increased gradually as T_a decreased (Figs. 7, 8). These findings are puzzling, since mice should be able to reduce the energy cost of thermoregulation by maximizing resistance at all T_a below thermoneutrality.

Changes in the vasomotor components of body resistance which affect skin temperature (T_{sk}) are the most plausible explanation for this observation. Mathematical formulations and empirical data on heat loss through fur suggest that vasoconstriction and other responses affecting T_{sk} are important in determining rates of heat transfer (Kowalski and Mitchell 1980; McClure and Porter 1983). Peripheral vasoconstriction responses could occur in any convective environment, but their magnitude may be dependent on wind speed. Strong winds disrupt the insulation of the pelage, so at a given T_a below thermoneutrality, skin temperatures may be considerably colder at high wind speeds than in unstirred air. If vasoconstriction is a function of T_{sk}, lower T_{sk} would elicit correspondingly larger vasoconstriction responses, which would become progressively stronger as T_a (and hence T_{sk}) decreased. Furthermore, at high V the proportional contribution of tissue resistance to r_t is larger than in unstirred air, due to the decline in pelage insulation. This combination of factors at high wind speeds could produce the observed gradual increase in r_t as temperature falls below thermoneutrality.

Energetic and ecological considerations

In cold conditions, the cost of thermoregulatory heat production in deer mice is highly dependent on the convective regime. Strong winds (3–4 m/s) can double MHP requirements at T_a's of 5–15 °C. Wild deer mice are unlikely to experience wind speeds this high, since they spend most of their time in cover or in the layer of relatively still air

near the ground. Nevertheless, even moderate winds of 1–2 m/s can substantially increase thermoregulatory costs. Convection becomes especially important at T_a's below 5 °C, since at these T_a's the oxygen consumption requirements for MHP alone may approach $\dot{V}_{O_2}$ max, leaving the mouse little aerobic scope for locomotion or other activities. Even in summer, nighttime temperatures in *P. maniculatus sonoriensis* habitat often fall to 0 °C or below (unpublished data).

Heat loss rates from wild mice probably differ slightly from rates measured in otherwise comparable convective regimes in laboratory environments. Free-ranging animals will be much more active than mice sitting quietly in a wind tunnel. McClure and Porter (1983) emphasize that postural adjustments can have significant effects on heat transfer through mammal pelages, and movement also affects pelage properties (e.g., Wunder 1970). However, for most studies of ecological energetics, Eq. (2) or (3) will provide adequate estimates of thermoregulatory cost for deer mice in blackbody radiant conditions. For non-blackbody environments, the operative temperature T_e can be calculated or measured directly with pelt-covered model animals (Bakken 1976; Chappell and Bartholomew 1981), and substituted for T_a in equations (2) or (3).

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