EFFECT OF WIND AND SOLAR RADIATION ON METABOLIC HEAT PRODUCTION IN A SMALL DESERT RODENT, *SPERMOPHILUS TERETICAUDUS*

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Summary

To understand better how complex interactions between environmental variables affect the energy balance of small diurnal animals, we studied the effects of the absence and presence of $950\,\mathrm{W\,m^{-2}}$ simulated solar radiation combined with wind speeds ranging from 0.25 to $1.00\,\mathrm{m\,s^{-1}}$ on the metabolic rate and body temperature of the round-tailed ground squirrel *Spermophilus tereticaudus*. As wind speed increased from 0.25 to $1.00\,\mathrm{m\,s^{-1}}$, metabolic heat production increased by 0.94 W in the absence of solar radiation and by 0.98 W in the presence of $950\,\mathrm{W\,m^{-2}}$ simulated solar radiation. Exposure to simulated solar radiation reduced metabolic heat production by 0.68 W at a wind speed of $0.25\,\mathrm{m\,s^{-1}}$, by 0.64 W at $0.50\,\mathrm{m\,s^{-1}}$ and by 0.64 W at $1.00\,\mathrm{m\,s^{-1}}$. Body temperature was significantly affected by environmental conditions, ranging from $32.5\,^{\circ}\mathrm{C}$ at a wind speed of $1.0\,\mathrm{m\,s^{-1}}$ and no irradiance to $35.6\,^{\circ}\mathrm{C}$ at a wind speed of $0.50\,\mathrm{m\,s^{-1}}$ with $950\,\mathrm{W\,m^{-2}}$ short-wave irradiance.

In addition, several unusual findings resulted from this study. The coat of *S. tereticaudus* is very sparse, and the observed heat transfer of $5.68\pm0.37\,\mathrm{W\,m^{-2}\,^{\circ}C^{-1}}$ (mean ± S.E.M., N=11) is much higher than expected from either allometric equations or comparative studies with other rodents of similar mass. Solar heat gain was remarkably low, equalling only 10 % of intercepted radiation and suggesting a remarkably high regional thermal resistance at the tissue level. Animals remained normally active and alert at body temperatures as low as $32.5\,^{\circ}\mathrm{C}$. These findings suggest a unique combination of adaptations that allow *S. tereticaudus* to exploit a harsh desert environment.

Key words: solar radiation, heat transfer, heterothermy, metabolic heat production, round-tailed ground squirrel, *Spermophilus tereticaudus*.

Introduction

Under natural conditions, the energy budget of a terrestrial homeotherm can be significantly affected by the interactions between environmental factors such as solar radiation, wind and air temperature. These factors interact in complex fashions (Campbell, 1998) to influence rates and levels of heat loss or gain by the animal and, consequently, the levels of metabolic heat production required to maintain thermal balance (Lustick, 1969; Walsberg, 1982; Walsberg and Wolf, 1995b,c; Walsberg et al., 1997; Wolf and Walsberg, 1996). Diurnal mammals occupying lower elevations in the Sonoran Desert, Arizona, USA, can incur tremendous heat loads as a result of interactions between these environmental factors. Air temperature at an elevation of 1.5 m above ground exceeds $20\,^{\circ}\mathrm{C}$ during daylight hours over most of the year and often approaches $50\,^{\circ}\mathrm{C}$ during the summer months. Solar radiation dominates the radiative environment, usually exceeding $900–1000\,\mathrm{W\,m^{-2}}$ on a plane perpendicular to the solar beam, and is 20 times greater than mammalian basal metabolic heat production expressed per unit of animal surface area (Kleiber, 1961). Total downward radiation levels (both long-wave and short-wave) during the summer months approach $1500\,\mathrm{W\,m^{-2}}$

(K. M. Wooden, unpublished data) and thus exceed basal metabolic heat production by 30-fold.

In the present study, we quantify the effects of ecologically relevant levels of simulated solar radiation and wind speed on metabolic heat production in the round-tailed ground squirrel (*Spermophilus tereticaudus*). This diurnal rodent inhabits the most barren habitats of the Sonoran Desert, such as plains dominated by creosote bushes. These habitats offer little or no cover from the intense solar radiation. While *S. tereticaudus* is fossorial and able to escape underground, it is the only small mammal in the lower Sonoran Desert to be found above ground and active at any time during daylight hours (Vorhies, 1945; Dengler, 1967; Drabek, 1973). In addition, *S. tereticaudus* is often found away from any vegetative shading for hours at a time at midday during the summer months (K. M. Wooden, personal observation).

Previous analyses of heat transfer through coat and skin preparations removed from the mid-dorsal region of *S. tereticaudus* show that the coat offers very little resistance to radiative and convective heat transfer (Walsberg, 1988). The low coat resistance of *S. tereticaudus* is presumably adaptive

in that it facilitates passive heat loss when body temperature exceeds environmental temperature. However, this poor insulation also results in more than 60 % of the solar heat load being transferred to the skin (Walsberg, 1988). Because of the absence of knowledge regarding factors affecting tissue thermal resistance in endotherms, it is not yet possible to equate the solar heat load at the skin to whole-animal rates of heat gain. In the following analysis, we quantify whole-animal rates of radiative heat gain and convective heat loss for *S. tereticaudus*. Solar heat gain is quantified as the decrease in metabolic heat production caused by the animal's exposure to simulated solar radiation. Similarly, changes in convective heat loss are quantified as the variation in metabolic heat production caused by exposure to changes in wind speed. The primary questions addressed by this study are as follows. (i) How does ecologically relevant variation in wind speed affect the heat balance of small diurnal mammals? (ii) How does solar radiation influence metabolic heat production in small diurnal desert mammals? (iii) How does the solar heat load to the skin in isolated coat samples correspond to the heat gain realized by intact animals?

Materials and methods

Animal collection and maintenance

Male *Spermophilus tereticaudus* Baird were trapped between June and July in the Sonoran Desert, approximately 25 km north of Gila Bend, Maricopa Co., Arizona, USA, at an altitude of approximately 225 m. Animals were maintained on a 14 h:10 h light:dark photoperiod at an air temperature (T_a) of 30 °C, fed Teklad rodent diet and supplied *ad libitum* with water. Mean body mass was 159.3±9.2 g (mean ± S.E.M., N=11).

Environmental simulation

Metabolic measurements were made both in the presence and absence of simulated solar radiation, with the animal placed in the closed-circuit wind tunnel described by Walsberg and Wolf (1995a). This wind tunnel had an effective volume of 54 l, calculated following Bartholomew et al. (1981). A variable-speed fan circulated air through the test section at speeds of 0.25–1.0 m s^{-1}, values typical of the Sonoran Desert (K. M. Wooden, unpublished data). Wind speed was measured using an Omega HHF92 thermoanemometer calibrated as described by Walsberg (1988). Horizontal and vertical louvers upstream from the test section were used to make wind speed more uniform within the chamber. Except within 1 cm of the chamber walls, wind speed varied by less than 5 % horizontally or vertically within the test section. Turbulence intensity was less than 3 % at all wind speeds used, as determined by measuring the signal output of a Thermonetics HWA-101 thermoanemometer using a true root-mean-square voltmeter (Beckman model 850) and computed using the method of Hinze (1959).

The chamber was maintained at a temperature low enough (15±1 °C) that the addition of solar heat gain would not drive the animals into the thermoneutral zone. Chamber temperature was held constant by placing the chamber in a temperature-controlled room and by circulating water from a constant-temperature reservoir through heat-exchange coils located in the chamber walls and in the airstream downwind of the test section. Air temperature was measured using a 26 gauge, type T thermocouple connected to a Campbell CR21x data logger.

Simulated solar radiation was produced by a Spectral Energy Series II solar simulator. This source filters light produced by a xenon arc lamp to simulate direct solar radiation at an air mass of 1.0. Irradiance in the test chamber was measured using a LiCor LI22sz pyranometer calibrated against an Oriel pyroelectric radiometer (model 7080). Simulated solar irradiance was maintained at 950 W m^{-2}, which is an ecologically realistic level of irradiance for the Sonoran Desert during both winter and summer (K. M. Wooden, unpublished data). When measured perpendicular to the solar beam, irradiance varied by less than 5 % with time or across the chamber floor. The long-wave radiant environment in the chamber was held nearly constant by painting the walls with flat black enamel and maintaining their temperature at 15±2 °C. Assuming an emissivity of 0.98 and calculating long-wave irradiance using the Stefan–Boltzmann relationship, we estimated that long-wave emission varied by less than 6 %.

Metabolic rate and evaporative water loss

Metabolic rate was determined from CO_2 production. Incurrent air was forced through the metabolic chamber at 20.2 l min^{-1} after being dried and having the carbon dioxide removed with a Puregas air dryer/CO_2 absorber system (model CDA1112). Airflow was measured using an Omega FL4002G-HRV rotameter calibrated to ±1 % of full scale with a 5 l soap-bubble flow meter. At these high flow rates, the entire respiratory apparatus equilibrated in 12 min (Lasiewski et al., 1966). A 150 ml min^{-1} subsample of gas was dried with anhydrous calcium sulfate and passed to a LiCor model 6252 CO_2 analyzer. Carbon dioxide concentrations in sample gas ranged from 270 to 680 p.p.m. The CO_2 analyzer resolved carbon dioxide concentrations to 1 p.p.m. or 0.1–0.4 % of measured values. The analyzer was calibrated daily with both CO_2-free air and a calibration gas known to contain 2840 p.p.m. CO_2.

All measurements were taken during the active phase of the animal's daily cycle after a minimum of 12 h without food. Data were collected at three wind speeds (0.25, 0.50 and 1.00 m s^{-1}) both in the presence and absence of simulated solar radiation. Animals were exposed to a given wind and radiation regime for 30–60 min. During measurements in the absence of solar radiation, animals were exposed to fluorescent lighting that allowed normal vision but was thermally insignificant (irradiance <3 W m^{-2}). All measurements of individual animals in the presence or absence of solar radiation at a given wind speed were taken on separate days. The order in which an animal was exposed to different wind speeds was randomized, and no animal was used on consecutive days.

Instrument signals were recorded on a Campbell CR21x datalogger and averaged at 1 min intervals. Values reported are the mean of the first 5 min following a minimum of 30 min under the experimental conditions and an entire 12 min equilibration period during which time there was no activity observed and the animal was resting quietly. Carbon dioxide production was calculated using equation 3 of Walsberg and Wolf (1995a) and corrected to STP (0 °C, 101 kPa).

This calculation and subsequent conversion to units of energy requires knowledge of the respiratory exchange ratio (RER). Because of the high flow rates required to reduce the equilibration time of such a large chamber, oxygen depletion was too small for accurate measurement and thus any subsequent calculation of RER. In addition, elevation of humidity in the wind tunnel, as measured using a Thunder Scientific PC2101 hygrometer, was too low (<1 mg H_2O l^{-1}) to allow accurate estimation of latent heat loss. Therefore, the RER and the fraction of metabolic power dissipated through evaporation were determined in separate measurements in which resting, post-absorptive animals were placed in a 1.3 l metabolic chamber at 15 °C in the absence of wind or solar radiation. Dry, CO_2-free air flowed into the chamber at 600–1100 ml min^{-1}. Carbon dioxide production and oxygen consumption were measured simultaneously for animals resting quietly in the dark. Carbon dioxide concentrations in the sample gas were measured from a 150 ml min^{-1} subsample of gas that was dried with anhydrous calcium sulfate and passed to a LiCor (model 6252) CO_2 analyzer. Values ranged from 670 to 1280 p.p.m. The CO_2 analyzer resolved carbon dioxide concentrations to 1 p.p.m. or 0.1–0.2 % of measured values. The analyzer was calibrated daily with both CO_2-free air and a calibration gas known to contain 2840 p.p.m. CO_2. Carbon dioxide production was calculated using equation 3 of Walsberg and Wolf (1995a).

The O_2 concentration of air entering and leaving the chamber was determined from a 50 ml min^{-1} subsample of efflux air from the chamber using an Applied Electrochemistry S3a oxygen analyzer. The standard method of calibrating this instrument calls for the adjustment of the instrument reading to a single point using the fractional composition of oxygen in dry air (F_{O_2}=0.2094) as a calibration gas. The accuracy of the response to changes in oxygen concentration was determined by altering the partial pressure of oxygen (P_{O_2}) in the sample cell. The cell's efflux of sample air was vented under 18 equally spaced depths of a 0.5 m column of distilled water. Under prevailing conditions (barometric pressure approximately 97 kPa), this was equivalent to a change in P_{O_2} equal to that which would be produced by changing F_{O_2} from 0.1993 to 0.2093. This equates to the maximum range normally experienced in metabolic measurements. This procedure revealed that the oxygen analyzer was highly linear in its response sensitivity (r^2=0.9998), but exhibited a response sensitivity 7 % greater than expected on the basis of changes in P_{O_2}. Values of oxygen concentration were corrected for this error, and the rate of oxygen consumption was calculated using equation 3 of Hill (1972).

Evaporative water loss was determined by measuring the humidity of effluent chamber air using a Thunder Scientific hygrometer (model PC-2101). This hygrometer was calibrated at low vapor pressures with air first humidified by bubbling through a water column at 23 °C and then passed at 50 ml min^{-1} through approximately 2 m of copper tubing with a 4 mm internal diameter. This tubing was held at nine temperatures between -35 °C and 11 °C by immersing it either in a water bath (for temperatures >0 °C) or in a slush composed of frozen CO_2 and calcium chloride brines (for temperatures <0 °C). The temperature of the saturated air was measured with an Omega HH23 thermocouple thermometer, and vapor density at these temperatures was obtained from List (1951). During determinations of animal heat production, the hygrometer signal output was measured using the Campbell CR21x data logger, which provided a resolution of 0.1 mg H_2O l^{-1} or 1–5 % of measured values. The latent heat of evaporation was calculated using a value of 2.42 kJ g^{-1} H_2O.

Body temperature

Body temperature (T_b) was measured using an Omega HH23 thermocouple thermometer with a 26 gauge, type T thermocouple. The thermocouple was inserted rectally to a depth of 3 cm within 30 s of removing the animal from either the wind tunnel or the metabolic chamber. The thermocouple was held in position for approximately 30 s prior to taking a measurement for the reading to stabilize.

Calculation of total surface area

Total surface area (A_s, cm^2) was determined after killing the animals by exposure to pure CO_2, as recommended by the American Veterinary Medical Association and approved by the Animal Care and Use Committee of Arizona State University. Each animal's skin was then removed and traced on a piece of paper, upon which reference distances were marked. The images were scanned, digitized and analyzed using NIH Image 1.6/ppc software to determine skin surface area.

Calculation of solar heat gain and projected surface area

As previously defined (Walsberg and Wolf, 1995b,c), solar heat gain to an animal is equivalent to the reduction in metabolic heat production resulting from exposure to simulated solar radiation. Solar heat gain is expressed in two ways, either as the change in mass-specific metabolic rate or as a fraction of the radiant heat flux intercepted by the animal. The latter expression facilitates comparisons among studies using different intensities of radiation, animals of differing size or shape, or comparisons between effects exhibited by live animals and the heat load measured at the skin beneath isolated coat preparations. For intact animals, fractional solar heat gain to the animal core (Q_A) is computed as:

$$Q_A = (M^- - M^+)/(A_P Q_I), \qquad (1)$$

where M^- is metabolic heat production in the absence of solar radiation (W), M^+ is metabolic heat production in the presence of simulated solar radiation that is intercepted by the animal

(W), A_P is the cross-sectional area of the beam of simulated solar radiation that is intercepted by the animal (m^2) and Q_I is simulated solar irradiance (W m^{-2}).

A_P was measured by orienting a video camera (Panasonic AG 456) vertically directly above each animal and recording the animal in its resting posture. The camera lens was 1.0 m above the floor of the holding container, which had reference distances marked on it. The digitized images were analyzed using NIH Image 1.6/ppc software to determine the projected surface area.

Calculations of heat-transfer coefficients

The combined non-evaporative heat-transfer coefficient (h; W m^{-2} °C^{-1}) is calculated by rearranging the equation outlined by Burton (1934):

$$h = (M - E)/(T_b - T_a),\qquad(2)$$

where M is the surface-area-specific metabolic heat production (W m^{-2}), E is the surface-area-specific evaporative heat transfer (W m^{-2}), T_b is core body temperature and T_a is air temperature (15 °C for experiments conducted in the absence of solar radiation). The combined non-evaporative heat-transfer coefficient (h) consists of the whole-body heat-transfer coefficient (h_b) and the environmental heat-transfer coefficient (h_e). The whole-body heat-transfer (h_b) coefficient subsumes the heat-transfer coefficient for the coat (h_{coat}) and that for the peripheral tissues (h_{tissue}) with heat flowing serially. The environmental heat-transfer coefficient (h_e) subsumes the convective heat-transfer coefficient (h_a) and the radiative heat-transfer coefficient (h_r) with heat flowing through these paths in parallel. To calculate the individual heat-transfer coefficients (h_{coat}, h_{tissue}) that appear in series:

$$h_b = 1/[(1/h_{coat}) + (1/h_{tissue})].\qquad(3)$$

This is rearranged to:

$$h_{coat} = 1/[(1/h_b) - (1/h_{tissue})].\qquad(4)$$

To calculate the environmental heat-transfer coefficient (h_e) that results from heat-transfer coefficients (h_a, h_r) occurring in parallel, the following equation of Campbell (1998) is used:

$$h_e = h_a + h_r.\qquad(5)$$

To establish whether free or forced convection prevailed in our experiments, we computed Reynolds (Re) and Grashof (Gr) numbers using the formulae of Campbell (1998). The characteristic dimension of our ground squirrels, the mean diameter of the spheroidal posture assumed for squirrels sitting at rest, parallel to airflow through the chamber, was taken as 0.07±0.006 m (mean ± S.E.M., N=11). Reynolds numbers ranged from 1200 at 0.25 m s^{-1} to 4800 at 1.00 m s^{-1}. The Gr/Re^2 ratio ranged from 0.01 to 0.3 at the wind speeds we used, indicating that forced convection predominated (Campbell, 1998).

To calculate the convective heat-transfer coefficient h_a, we assumed that convective heat loss from the coat surface approximated that from a sphere of similar size. Using the

equation for determining boundary layer resistance (r_a) derived by Webster and Weathers (1988):

$$r_a = [2.7d^{0.4}(\nu/u)^{0.6}]/D_H,\qquad(6)$$

and that for calculating the convective heat-transfer coefficient (W m^{-2} °C^{-1}) from resistance (s m^{-1}) (Monteith and Unsworth, 1989):

$$h_a = \rho C_p/r_a,\qquad(7)$$

we derived the following equation for calculating h_a:

$$h_a = \rho C_p D_H/2.7d^{0.4}(\nu/u)^{0.6}.\qquad(8)$$

Here, ρC_p is the volumetric heat capacity of air (taken as a constant 1200 J m^{-3} °C^{-1}), D_H is the thermal diffusivity of air at 15 °C (20.8 mm^2 s^{-1}), d is a characteristic dimension of the animal (0.07 m), u is the wind speed (m s^{-1}) and ν is the kinematic viscosity of air at 15 °C (14.6 mm^2 s^{-1}). The radiative heat-transfer coefficient (h_r) was calculated as:

$$h_r = \rho C_p/r_r,\qquad(9)$$

where r_r was obtained from Table A3 of Campbell (1977) for T_a=15 °C.

Statistical analyses

Statistical analyses were performed using SPSS base7.5 for Windows. Analyses were accomplished using a general-factorial one-way analysis of variance (ANOVA) followed by a *post-hoc* multiple-comparison test (Tukey type) for pairwise comparisons among groups or paired-samples *t*-test, as appropriate. All reported values are significant at $P<0.05$. Values are given as means ±1 S.E.M.

Results

Respiratory exchange ratio, latent heat loss and surface area measurements

The mean respiratory exchange ratio (RER) under post-absorptive conditions was 0.715±0.005 (N=11), suggesting near-total reliance upon lipids as a catabolic substrate (Kleiber, 1961). On the basis of this value, the thermal equivalent of carbon dioxide produced is estimated as 27.4 J ml^{-1} (Withers, 1992). Heat loss by evaporation, at an ambient temperature of 15 °C with no irradiance or wind, ranged from 3.0 to 8.0 % of total heat production with a mean of 5.1±0.50 % (N=11). The cross-sectional area of the beam of simulated solar radiation that was intercepted by the animal ranged from 57 to 87 cm^2, with a mean of 67±3.0 cm^2. Total animal surface area ranged from 202 to 275 cm^2, with a mean of 244±6.7 cm^2.

Metabolic heat production as a function of wind and irradiance

Increases in wind speed from 0.25 to 1.00 m s^{-1} elevated metabolic heat production both in the presence and absence of simulated solar radiation with no interaction effects (Fig. 1). In the absence of solar radiation, metabolic heat production increased from 2.90 to 3.84 W ($P<0.005$). In the presence of 950 W m^{-2} of simulated solar radiation, heat production
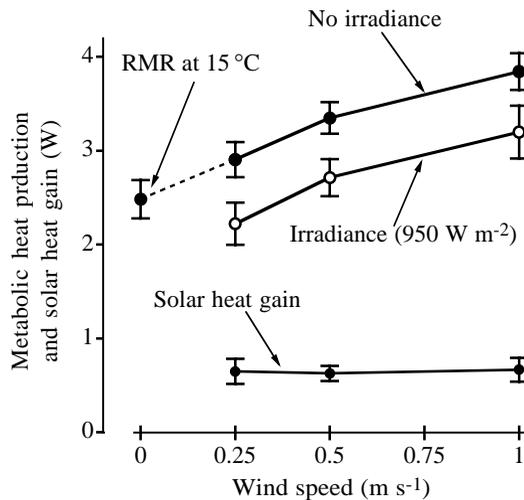
Fig. 1. Metabolic heat production and solar heat gain of round-tailed ground squirrels as a function of wind speed in the presence or absence of $950\,\mathrm{W\,m^{-2}}$ simulated solar radiation. Also shown is the value for resting metabolic rate (RMR) of post-absorptive squirrels held at an air temperature of $15\,^\circ\mathrm{C}$ in the absence of irradiance and forced convection during their active period. Values are means ± S.E.M. (N=11).

Fig. 2. Environmental (h_e), body (h_b) and combined (h) heat-transfer coefficients of round-tailed ground squirrels as a function of wind speed. Values of h and h_b are means ± S.E.M. (N=11).

increased from 2.22 to 3.20 W ($P<0.025$). Exposure to simulated solar radiation reduced metabolic heat production at all wind speeds with no interaction effects ($P<0.002$). In the presence of solar radiation, metabolic heat production decreased from 2.90 to 2.22 W ($P<0.00027$) at a wind speed of $0.25\,\mathrm{m\,s^{-1}}$. At a wind speed of $0.50\,\mathrm{m\,s^{-1}}$, metabolic heat production decreased from 3.35 to 2.71 W ($P<0.0095$). At a wind speed of $1.00\,\mathrm{m\,s^{-1}}$, metabolic heat production decreased from 3.84 to 3.20 W ($P<0.00037$).

Effects of wind on heat-transfer coefficients

The combined heat-transfer coefficient (h) increased from 6.16 to $8.72\,\mathrm{W\,m^{-2}\,^\circ C^{-1}}$ as wind speed increased from 0.25 to $1.00\,\mathrm{m\,s^{-1}}$ ($P<0.0005$) (Fig. 2). The environmental heat-transfer coefficient (h_e) increased from 14.65 to $26.70\,\mathrm{W\,m^{-2}\,^\circ C^{-1}}$ and there was no change in the whole-body heat-transfer coefficient (h_b) over the range of wind speeds used.

Body temperature as a function of wind and irradiance

Body temperature T_b varied as a function of irradiance, with no interaction effect from varying wind speed ($P<0.0005$) (Fig. 3). Mean T_b increased from 33.9 to $35.0\,^\circ\mathrm{C}$ ($P<0.0036$) at a wind speed of $0.25\,\mathrm{m\,s^{-1}}$. At a wind speed of $0.50\,\mathrm{m\,s^{-1}}$, mean T_b rose from 33.8 to $35.6\,^\circ\mathrm{C}$ ($P<0.00018$), and at a wind speed of $1.00\,\mathrm{m\,s^{-1}}$, mean T_b increased from 32.5 to $34.6\,^\circ\mathrm{C}$ ($P<0.00014$).

Discussion

Heat-transfer coefficients, and the effects of forced convection on metabolic heat production

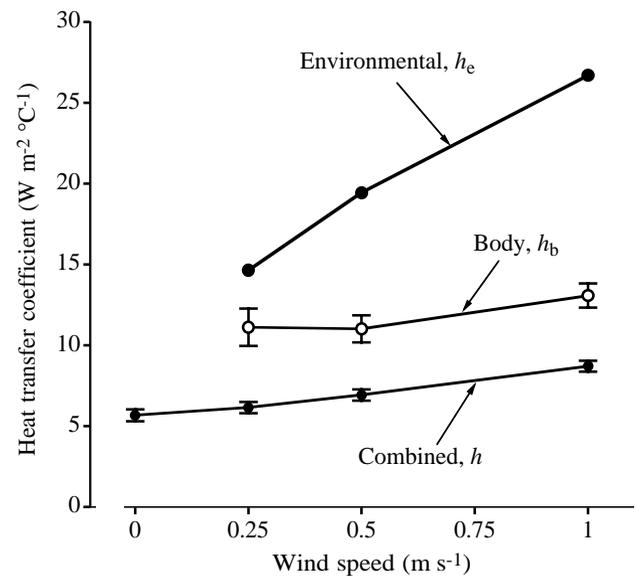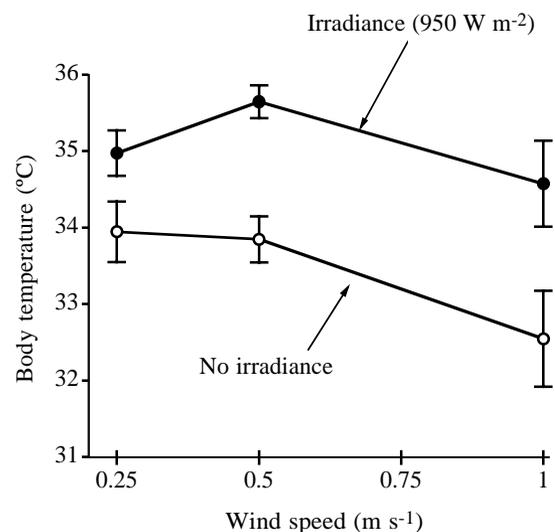On the basis of the classical concepts outlined by Burton

Fig. 3. Body temperature of round-tailed ground squirrels as a function of wind speed in the presence or absence of $950\,\mathrm{W\,m^{-2}}$ simulated solar radiation. Values are presented as means ± S.E.M. (N=11).

(1934), Newton's law of cooling has been used extensively by biologists to analyze heat-transfer processes involving convection combined with conduction and radiation in biological systems. The equation:

$$\mathrm{d}H/\mathrm{d}t = hA_\mathrm{s}(T_\mathrm{b} - T_\mathrm{a}), \qquad (10)$$

assumes that surface-area-specific heat exchange, $\mathrm{d}H\,\mathrm{d}t^{-1}A_\mathrm{s}^{-1}$ (where H is heat, t is time and A_s is total surface area; $\mathrm{W\,m^{-2}}$) between an organism and its environment can be conveniently expressed in terms of the temperature gradient ($T_\mathrm{b}-T_\mathrm{a}$; $^\circ\mathrm{C}$) multiplied by the combined heat-transfer coefficient (h;

W m^{-2} °C^{-1}) (Thomas, 1980). Models using resistance (r; s m^{-1}) for calculating heat transfer have proved to be useful because both serial and parallel resistances can often be identified between the core of an organism and the environment. In addition, these models utilize previously established analytical techniques from electronics to calculate heat transfer (Robinson et al., 1976). Resistance values, however, will not necessarily be normally distributed even if the data from which they are calculated are. Therefore, heat-transfer coefficients are preferred for statistical analyses (Campbell, 1998).

There are two primary difficulties in generating comparisons with published data in terms of heat transfer. The first is that few investigators report animal surface area, although there is no question that it is an important variable of heat transfer. A second common obstacle is that most investigators do not estimate the thermal equivalent of oxygen consumed on the basis of measured values of RER. Simply assuming an RER value can introduce as much as a 12 % error (Walsberg and Wolf, 1995a). There is, therefore, the potential of yielding as much as a 24 % total error when comparing two species. To avoid such potential errors, we express our data in two forms. For comparisons between our findings and those of other investigators, we present our results as wet thermal conductance reporting either whole-animal or mass-specific rates of oxygen consumption depending on the particular set of comparative data. We also present our data in the preferred heat-transfer coefficient units of W m^{-2} °C^{-1}, incorporating measured values of RER and total surface area, for both future comparative studies of heat transfer and for comparisons among the separate heat-transfer coefficients analyzed in this study.

An appropriate allometric relationship to use for comparisons is Aschoff's (1981) equation:

$$\log(C/m) = \log 1.539 - 0.517 \log m, \qquad (11)$$

for estimating wet thermal conductance based on reported values for 57 species of mammals studied in the active phase of their daily cycle and ranging in mass from 79.0 to 6600 g, where C represents minimal conductance (ml O$_2$ h^{-1} °C^{-1}) and m is body mass (g). In our study, the mean mass-specific wet thermal conductance for animals below their thermoneutral zone was 0.16±0.01 ml O$_2$ g^{-1} h^{-1} °C^{-1} (N=11), calculated from measurements of rates of oxygen consumption obtained during the study of RER. This is equivalent to a heat transfer of 5.68±0.37 W m^{-2} °C^{-1} and is 45 % higher than predicted by equation 11. Similarly, whole-animal wet thermal conductance (ml O$_2$ h^{-1} °C^{-1}) for round-tailed ground squirrels is the highest reported of 17 species of rodents ranging in mass from 100 to 200 g and measured during the active phase of their daily cycle (Table 1).

Increases in wind speed elevated metabolic heat production significantly in *S. tereticaudus* both in the absence and presence of simulated solar radiation. This apparently resulted from an increase in the combined heat-transfer coefficient (h) (Figs 1, 2). To understand how increases in wind speed affect heat transfer and, in turn, metabolic heat production, it is necessary to evaluate separately the effects on the various individual stages of heat transfer that account for the summed heat transfer between the animal and the environment. The combined heat-transfer coefficient (h), which accounts for the overall heat transfer between the animal and its environment, can be divided into two primary interfaces: (i) the whole-body heat-transfer coefficient (h_b), which accounts for transfer from

Table 1. *Whole-animal wet thermal conductance among rodents, in order of increasing conductance, for animals ranging in mass from 100 to 200 g and studied in their active phase of their daily cycle*

Species	Mass	Conductance, C (ml O$_2$ h^{-1} C^{-1})	Reference
Neotoma lepida	110	7.70	Lee (1963)
Citellus lateralis	200	8.60	Snapp and Heller (1981)
Neotoma lepida	139	8.76	Lee (1963)
Otomys irroratus	112	8.93	Richter et al. (1997)
Mesocricetus auratus	120	10.41	Lyman (1948)
Neotoma fuscipes	187	11.03	Carpenter (1966)
Neotoma albigula	194	11.25	Brown and Lee (1969)
Otomys slogetti	113	11.30	Richter et al. (1997)
Thomomys talpoides	106	13.25	Bradley et al. (1974)
Meriones tristrami	112	13.44	Haim and Izhaki (1993)
Cryptomys hottentotus	102	14.69	Haim and Fairall (1986)
Tachyoryctes splendens	171	16.42	McNab (1966)
Citellus tridecemlineatus	160	17.60	Pohl and Hart (1965)
Citellus mexicanus	201	21.31	Neumann and Cade (1965)
Geomys bursarius	197	23.84	Bradley and Yousef (1975)
Tamias striatus	200	25.00	Neal (1976)
Spermophilus tereticaudus	159	25.22	Present study

Correlation between mass and conductance for these data gives an r^2 of 0.153.

Table 2. *Solar heat gain for species of* Spermophilus *from different habitats*

Species	Habitat	Solar heat gain (% of intercepted flux)	Wind speed (m s^{-1})	Reference
S. lateralis	Coniferous forest	24–19	0.50–1.00	Walsberg and Wolf (1995b)
S. saturatus	Coniferous forest	20–21	0.50–1.00	Walsberg and Wolf (1995b)
S. variegatus	Sonoran desert (winter)	19–15	0.25–1.00	Walsberg et al. (1997)
S. variegatus	Sonoran desert (summer)	6–7	0.25–1.00	Walsberg and Wolf (1995c)
S. tereticaudus	Sonoran desert	10.5	0.25–1.00	This study

the core of the animal to its outer surface, and (ii) the environmental heat-transfer coefficient (h_e), which accounts for transfer from the animal's coat surface to the environment through the boundary layer.

The whole-body heat-transfer coefficient (h_b) for *S. tereticaudus* was not affected by wind speed, which is consistent with the findings of Walsberg (1988). The environmental heat-transfer coefficient (h_e), however, increased by 82 % as wind speed changed from 0.25 to 1.00 m s^{-1} and accounts for 41 % of the resistance to heat flow at a wind speed of 0.25 m s^{-1}, 35 % at 0.50 m s^{-1} and 32 % at 1.00 m s^{-1}. The radiative portion (h_r) of the environmental heat-transfer coefficient is assumed to be constant at all wind speeds (5.43 W m^{-2} °C^{-1} at 15 °C) (Campbell, 1977) and, therefore, the increase in h_e is due solely to a 130 % increase in the convective heat-transfer coefficient (h_a) from 9.29 to 21.34 W m^{-2} °C^{-1} over the range of wind speeds used.

Unexpectedly low solar heat gain

Using coat and skin preparations for *S. tereticaudus*, Walsberg (1988) found that energy equivalent to approximately 60 % of the solar radiation intercepted by the animal acts as a heat load on the skin (Fig. 4). Such a high solar heat load would seem to be maladaptive for a diurnal mammal that inhabits a very hot environment. During the Sonoran Desert summer, when midday air temperatures at the
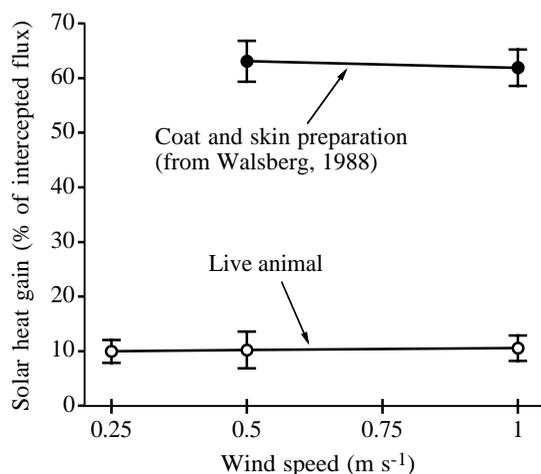

Fig. 4. Solar heat gain of round-tailed ground squirrels, expressed as a percentage of the radiant energy intercepted by the animal. Values are means ± S.E.M. (*N*=11). Values for the coat and skin preparations from Walsberg (1988) are also shown.

approximate squirrel height above the soil (3 cm) are often 46–63 °C (K. M. Wooden, unpublished data), absorbing over 600 W m^2 solar radiation would add a tremendous heat load on the animal that would have to be dissipated through evaporation. Commonly, the only source of exogenous water for this species is the leaves of creosote bush, which also contain high levels (20–30 % dry mass) of toxic phenols (Rhoades and Cates, 1976). Although many other species that inhabit these areas restrict the time and intensity of their daily activity, round-tailed ground squirrels appear to perform at the same level of activity throughout the day (K. M. Wooden, personal observation).

In sharp contrast to data collected using dried coat and skin preparations, solar heat gain in living *S. tereticaudus* equalled only approximately 10 % of intercepted solar radiation (Fig. 4). This is distinctly lower than that observed in other *Spermophilus* species that occupy higher altitudes and experience lower ambient temperatures (Table 2). How is this accomplished despite a very sparse coat and high heat-transfer coefficients? Reduction in heat gain suggests increased thermal resistance between the animal's core and the region heated by the solar radiation. In some species, this increase occurs within the coat and results from increased depth, increased density or altered hair optical characteristics. From the biophysical model of Walsberg et al. (1978) and using coat optical and structural properties determined for *S. tereticaudus* by Walsberg (1988), we calculate that coat depth would have to increase 10-fold to account for the low levels of solar heat gain we observed. Clearly, this is unrealistic. Alternatively, a 2.5-fold increase in the thermal resistance between the outer portion of the skin and the animal's core would achieve the same reduction in heat gain. This increase would, of course, only have to occur in areas exposed to solar heating and not over the entire body.

An alternative, but less likely, explanation for the low solar heat gain observed could be the wide range of body temperatures exhibited by round-tailed ground squirrels. If body temperature were changing during metabolic measurements, a heat-storage component would be introduced such that:

$$M - E - S = h(T_b - T_a), \qquad (12)$$

where S represents heat storage and is equal to the rate of increase or decrease in the heat content of the body. On the basis of data for continuous measurements of body temperature in *S. tereticaudus* over 8 h periods and at temperatures ranging from 10 to 40 °C, we have found that stable body temperatures are achieved within 20 min of exposure to the given air

temperature (K. M. Wooden, unpublished data). Body temperatures of the animals in the present study were taken after 35–65 min and had therefore probably stabilized. This strongly suggests that the low solar heat gain does not simply reflect changes in heat storage and therefore refocuses attention upon poorly understood variations in peripheral circulation as the potentially critical determinant of solar heat gain.

Combined effects of radiative and convective heat transfer on metabolic heat production

The effects of the varying levels of solar radiation, wind speed and air temperature on metabolic rate can be compared by calculating the standard operative temperature (T_{ES}) for each set of conditions (Bakken, 1976). T_{ES} equates the thermal stress produced in natural environments from the combination of radiative and convective heat transfer to the thermal stress produced by changes in air temperature (T_a) in a metabolic chamber under standardized convective conditions. In a black-body thermal environment, such as that produced by our metabolic chamber with high-emissivity walls when sunlight is absent, T_{ES} equals T_a under stipulated 'standard' convective conditions. We define the latter as $0.25\,\mathrm{m\,s^{-1}}$, the lowest wind speed used. T_{ES} is calculated by combining equations 19 and 20 from Bakken (1976):

$$T_{ES} = T_{bs} - [(M - E)/h_s].\qquad(13)$$

Variables are as defined previously, except that h_s is the combined heat-transfer coefficient under standard conditions and T_{bs} is the body temperature under these same conditions: at a wind speed (u) equal to $0.25\,\mathrm{m\,s^{-1}}$ in the absence of sunlight. Thus, T_{ES} represents the air temperature at a wind speed of $0.25\,\mathrm{m\,s^{-1}}$ that would produce the metabolic response equivalent to that elicited by the radiative and convective conditions actually prevailing.

In the absence of solar radiation, increasing wind speed from 0.25 to $1.00\,\mathrm{m\,s^{-1}}$ produced changes in metabolic heat production equivalent to decreasing T_a by $6.2\,°C$. In the presence of solar radiation ($950\,\mathrm{W\,m^{-2}}$), these same changes in wind speed equate to a reduction in T_a of $6.7\,°C$ (Fig. 5). The effect of solar radiation is represented by the difference in T_{ES} in the presence and absence of solar radiation at a given wind speed. At all wind speeds used, the presence of simulated solar radiation resulted in an approximately $4.6\,°C$ elevation of T_{ES} (Fig. 5). Overall, the combination of naturally occurring levels of irradiance and wind speed in the lower Sonoran Desert at a single air temperature can alter T_{ES} by $11\,°C$.

Heterothermy in round-tailed ground squirrels

Hudson (1964) noted that *S. tereticaudus* tend to be thermolabile, and described T_b for alert animals at rest as ranging between $35.5\,°C$ ($T_a=25\,°C$) and $41.6\,°C$ ($T_a=42\,°C$). We also observed significant shifts in T_b for alert animals at rest resulting from changes in irradiance level and wind speed (Fig. 3). Mean T_b ranged from $32.5\,°C$ at a wind speed of $1.00\,\mathrm{m\,s^{-1}}$ and no solar irradiance to $35.6\,°C$ at a wind speed of $0.50\,\mathrm{m\,s^{-1}}$ and $950\,\mathrm{W\,m^{-2}}$ short-wave irradiance. That body
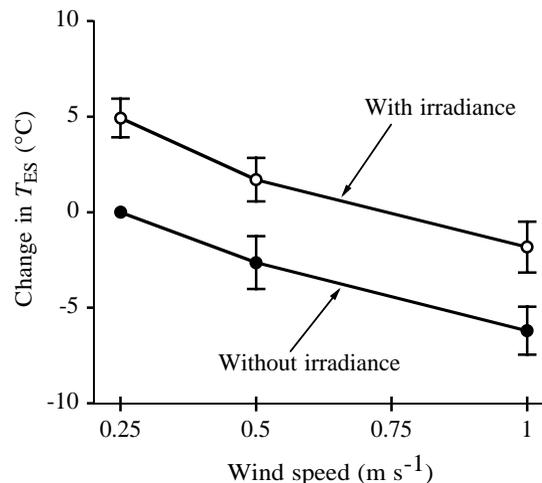

Fig. 5. Change in standard operative temperature (T_{ES}) as a function of wind speed in the presence and absence of $950\,\mathrm{W\,m^{-2}}$ simulated solar radiation. Standard conditions for the calculation of T_{ES} are a black-body radiative environment with a wind speed of $0.25\,\mathrm{m\,s^{-1}}$. Values are means ± S.E.M. ($N=11$).

temperatures are lower than the normally expected mammalian value of approximately $38\,°C$ and that they decreased significantly with decreasing T_{ES} is perhaps not surprising because of the high heat-transfer coefficient exhibited by these thinly furred rodents. More remarkable is that these animals remain normally active and alert at these low body temperatures, while most mammals would become pathologically hypothermic or enter torpor.

Ecological implications

A high heat-transfer coefficient combined with the unusual level of thermolability displayed by *S. tereticaudus* may provide an adaptive explanation for their ability to exploit such a harsh thermal environment as the lower Sonoran Desert during the summer months. Our study shows that *S. tereticaudus* has a substantially higher wet thermal conductance than that of rodents of similar mass and than expected from allometric equations, reflecting negligible insulation provided by a sparse coat. In addition, our data combined with those of Hudson (1964) show that *S. tereticaudus* is capable of maintaining apparently normal levels of alertness and activity over a range of body temperature as great as $9\,°C$. Combining the ability to function over a wide range of body temperatures with a high conductivity facilitates passive heat loss when body temperature exceeds environmental temperature and reduces the temperature gradient when environmental temperature exceeds body temperature. This reduces the need for evaporative heat loss and conserves body water under high ambient temperatures, and reduces metabolic costs and reliance upon energy resources that are either limited or toxic (e.g. creosote bush) in the lower Sonoran Desert when ambient temperatures are more moderate. In our study, the presence of solar radiation decreased metabolic rate by approximately

20 % and increased body temperature by 1–2 °C. This response undoubtedly provides substantial energetic savings.

A sparse coat provides for rapid heat transfer in *S. tereticaudus*. However, it also results in a high solar heat load at the skin (Walsberg, 1988). Although this appears maladaptive for hot environments with high levels of irradiance, our data shows that *S. tereticaudus* experienced substantially lower levels of solar heat gain than almost all other *Spermophilus* species studied under similar conditions. The exception is the rock squirrel, *S. variegatus*, in its summer coat (Table 2). Interestingly, *S. variegatus* is the only other squirrel species, for which solar heat gain has been measured, that occupies a hot desert. Solar heat gain in *S. variegatus* during the summer was only 6–7 % of intercepted solar radiation, which is less than half that in winter.

The remarkably low rate of solar heat gain apparently results from changes in thermal resistance at the tissue level. Given their potentially critical role, it is unfortunate that properties affecting localized heat transfer through peripheral tissues (such as variation in circulation) are so poorly understood.

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